ODONTOGRAPHY;

OR, A

TREATISE

COMPARATIVE ANATOMY OF THE TEETH;

THEIR PHYSIOLOGICAL RELATIONS, MODE OF DEVELOPMENT,

AND

MICROSCOPIC STRUCTURE,

IN THE

VERTEBRATE ANIMALS.

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ODONTOGRAPHY;

OR, A

TREATISE

ON THE

COMPARATIVE ANATOMY OF THE TEETH.

TO

THOMAS BELL, F.R.S.

PROFESSOR OF ZOOLOGY IN KING'S COLLEGE, LONDON, &c.

My dear Bell,

Independently of the pleasure with which I embrace this opportunity of expressing the feelings of Friendship and Esteem which I have long entertained towards you, there is no one to whom the present Work could with more propriety be dedicated than the acute Observer who was the first to point out Pathological Phenomena in the Human Teeth, consistent only with a higher organization and mode of development than it has been usual to attribute to them, but which it is the chief object of the following pages to demonstrate as common to the teeth of all vertebrate animals.

I am,

Your's, very sincerely,

Richard Owen.

London, June 18, 1845.

PREFACE.

The present Work includes the substance of the Lectures on the Comparative Anatomy and Physiology of the Teeth, which formed part of the Hunterian Courses delivered at the Royal College of Surgeons in the years 1837, 1838, and 1839. In the first of these courses the teeth were considered in their relation to the Osseous System, and the intimate structure of their component tissues was more especially treated of: in the second, they were regarded as parts of the Digestive System, and, besides their structure, their various configurations and proportions, in subserviency to the habits and food of the different species, were described: in the third, the development of the Teeth was considered in connection with that of the epidermal appendages of the Tegumentary System, in consequence of a close analogy in the form, structure, temporary duration, and reproduction of the formative matrix.

The views of the structure and development of the Teeth, and the consequent deductions as to their place in the system of tissues, their physiological relations, and their value as zoological characters, advanced in those Lectures and in contemporary publications,* are more fully and connectedly treated of in the following pages.

Like the other subjects of the Hunterian Lectures, and in accord-

* 'Report of the British Association,' vol. VII, 1838, p. 135. 'Comptes Rendus de l'Académie des Sciences,' 4to. 1839, p. 784.

ance with the principle of arrangement of the Physiological department of the Hunterian Museum, the Dental System is here traced from its more simple to its more complex conditions. But this progress is partially subordinated to the limits of zoological arrangement. For, although the tooth of a *Myliobates* or a *Labyrinthodon* be, in structure, more complex than many Mammalian teeth, yet this complexity is associated with other characters, such as mode of attachment, frequent shedding and renewal, &c., which indicate an essentially inferior grade, and connect them, respectively, in closer natural relationship with the more simple teeth of other species of Fishes and Reptiles. A distinct Part, or division of the Work is, therefore, appropriated to the Dental System of each of the three great Classes of Vertebrated Animals which possess teeth.

In the Mammalian series the course of progressive complication of the teeth is closely followed, irrespective of the general grade of organization of the species, and the Human dentition falls, accordingly, into the middle of the series. Guided by the evidence of the teeth I have sometimes deviated from the accepted Zoological systems, as will be seen in the last Chapter, devoted to the complex dentition of the great Family of Hoofed herbivorous quadrupeds, and especially in the value there assigned to the Ruminant modification of the Ungulate type.

In each Class, the chief characters of the teeth of the extinct species are described in connection with those of the allied existing forms. For so vast is now the extent, and so rapid the progress of Palæontology, and so important are the links in the chain of Being thus recovered, that no treatise on the Comparative Anatomy of the enduring parts of animals can fulfil its expected purpose, if it be restricted to the description of such parts in existing species alone.

With regard to the Teeth, some of the most interesting and extraordinary modifications were peculiar to species that have long since passed away from the stage of animated existence; and, indeed, no comprehensive view could be obtained of the dental tissues without a knowledge of those intermediate conditions which

they present in fossil teeth. I need only refer to the *Acrodus*,* the *Sphærodus*,† the *Saurocephalus*,‡ the *Dendrodus*,§ the *Labyrinthodon*,‖ the *Iguanodon*,¶ and the *Megatherium*,** in illustration of the value of Fossil remains, and of the microscope, as an instrument in the determination of their nature and affinities.

This important application of the microscope has, however, its limits, and from the difficulty of testing the described results by repetition of the observations, and from other causes, it is liable to be abused.

A knowledge of the structure of the entire fossil tooth should be obtained by longitudinal and transverse sections; at least by a transverse section through the entire thickness of the crown. With this knowledge a fragment of the tooth of the same species may afterwards be determined: and also in many cases those of other species of the same genus, or natural family: without it, great mistakes may be committed. If, for example, a microscopic observer had begun his examination of an Iguanodon's tooth by a slice of a fragment from the outer half of the crown, and had afterwards examined another fragment of the tooth of the same species taken from the inner half, he would, most probably have referred such fragments to two very distinct species of animals. The requisite knowledge of the characteristic combination of one lateral moiety of dentine, and another of vaso-dentine in the same tooth, pre-supposes the examination of a section of an entire specimen. In like manner, to pronounce on the generic and specific distinctions of fossil Proboscidians from the characters of portions chipped off the exterior of their tusks, is an abuse of the microscope, and betrays an ignorance of the mode and limits of its application.††

One consequence of an attempt, like the present, to determine

* Pl. 14. † Pl. 32. ‡ Pl. 55.

§ Pl. 62 B. The teeth of this extinct Fish afford a beautiful example of the unexpected application of microscopic characters of dental tissue in the determination of an important geological problem.—See Appendix to Mr. Murchison's 'Geology of Russia,' p. 635.

‖ Pl. 64 A. ¶ Pl. 71. ** Pl. 84.

†† Thus, out of portions of tusks of young and old individuals of the *Mastodon giganteus*, the genera *Missourium*, *Tetracaulodon*, and their different species, have been attempted to be established.—See Geological Proceedings, June 29, 1842.

the true nature and mode of development of a class of organs by tracing the modifications of such through the entire range of the series of animals to which it is peculiar, is, that, from the length of time required to complete and arrange the extended series of observations, partial glimpses and illustrations of the main conclusions sought to be established are published by authors who are excited to pursue some limited branch of the subject, and have leisure for following it out. The right of priority of original observation thus affected, is, however, a matter only of personal interest, and of small moment in comparison with the benefit which science derives not only from the collateral and independent evidence thus adduced, but also from the stimulus to further research emanating from the discussion of such right. Where the concurrent investigations are liberally pursued in the spirit of truth, they ought to produce no other feeling than that of friendly emulation. It is with unalloyed pleasure that I have seen the investigations commenced in the first Part of the present Work, extended by the beautiful illustrations of the microscopic structure of the Teeth of Fishes in the later Numbers of the 'Poissons Fossiles,' of M. Agassiz, in which most of my descriptions are verified,* and my indications of the labyrinthic structure of the teeth of certain Fishes have received direct illustration by the figures of the microscopic structure of those of the *Lepidosteus*. In like manner the Memoirs of M.M. Erdl, Bibra, and Duvernoy,† have confirmed and extended my

* With regard to the *Psammodus* and allied extinct Fishes, in which the medullary canals are affirmed by M. Agassiz to open directly upon the grinding surface of the tooth, it would be as reasonable to suppose that the long vascular and sensitive pulp should be exposed upon the working surface of the perpetually growing incisor of a Rodent. But apart from any physiological objection to the opinion of the learned Ichthyologist of Neuchatel, I have made new sections of the teeth of different species of Psammodonts, and have demonstrated their perfect agreement with my descriptions, and with Plate 20, in the first Part of this Work, to the satisfaction of Sir Philip Egerton, Mr. Stokes, Mr. Broderip, and other scientific friends. All these specimens show that, as the grinding surface is worn down, the vascular contents of the medullary canals have become calcified within a short distance from that surface, and thus, in the existing Fish, were the cavities of the canals defended from the effects of friction.

† I regret that the pages in Part III, descriptive of the Teeth of the Insectivora were printed off before I received the last memoir of M. Duvernoy containing his observations and beautiful figures of the microscopic structure of the teeth of the Shrews.

earlier observations on the microscopic structure of the teeth of Mammals.

The published Parts of the great Work by Prof. De Blainville, entitled 'Ostéographie, ou Description Iconographique Comparée du Squelette et du Système Dentaire des cinq Classes d'Animaux Vertébrès,' contain accurate and beautiful figures of the external forms of the teeth of various genera of Mammalia. These Fasciculi, the immortal 'Ossemens Fossiles' of Baron Cuvier, and the express Treatises on the Comparative Anatomy of the Teeth of Mammalia by M. Fr. Cuvier, and Dr. Rousseau, the able assistant in the Museum of Comparative Anatomy in the Garden of Plants, have supplied the third Part of the present Treatise with figures of some of the instructive and valuable specimens of the dental organs in that rich Collection; but my descriptions have been taken, in every instance, from the specimens themselves, or from the teeth of the same species, which, when not present in the Collections of this country, I have examined in the Parisian Museum, or in the Anatomical and Zoological Collections at Leyden and Frankfort. My best acknowledgments are due to Prof. Temminck, Dr. Rüppell, and M. Laurillard, for the facilities which they kindly afforded me in studying those valuable Foreign Collections, which impart essential aid to all who would treat systematically of the dental or osteological characters of the Vertebrate Animals.

The present Work would, however, have been very incomplete, if I had not been privately aided by the liberal contributions of teeth of rare fossil and recent animals, which were not available for the purpose of microscopic examinations when present in public collections.

The Earl of Enniskillen and Sir Philip Egerton have supplied me with the requisite specimens of *Cochliodus*, *Saurichthys*, the *Chimæroids*, and other fossil Fishes. To Charles Darwin, Esq., I owed the opportunity, at an early period of my investigations of dental structures, of examining microscopically the fossil teeth of the *Megatherium*, *Mylodon*, *Scelidotherium*, and *Toxodon*. Through Sir Woodbine Parish and M. Falconett, I have been able to examine the teeth of the *Glyptodon*. Prof. Pflieninger, of Stuttgard, most

kindly transmitted to me the portions of the tooth of the great *Mastodonsaurus*, or *Labyrinthodon*, from which the sections described and figured in the present Work are taken. Dr. Lloyd of Leamington, liberally consented to sacrifice his specimens of the extremely rare teeth of the English Labyrinthodonts, for the requisite comparison of their structure with that of the teeth of the more gigantic species of the Wirtemberg Keuper Sandstones. To Alex. Robertson, Esq., of Elgin, and R. I. Murchison, Esq., P.G.S., I owe the opportunities of examining the teeth of the *Dendrodus*. Mr. George Bennett of Sydney, and Dr. Hobson of Melbourne, have transmitted to me the jaws and teeth of the rare *Cestracion* of the Australian seas. Dr. Mantell has supplied me with the teeth of the *Iguanodon* and *Gyrodus*. Dr. Buckland, Dr. Agassiz, Capt. Jones, R.N., Charles Stokes, Esq., Fred. Dixon, Esq., of Worthing, J. C. Bowerbank, Esq., and other friends and colleagues in the Geological Society, have most liberally contributed subjects described in the present Work. Messrs. Stokes, Bowerbank, and Lister, have also kindly granted me the use of their valuable miscroscopes whenever I wished so to test or verify observations made with my own.

My grateful acknowledgements are more especially due to the PRESIDENT and COUNCIL of the ROYAL COLLEGE OF SURGEONS: for to them I owe the appointments which have made the pursuits most congenial to my tastes a duty, and at the same time have supplied the best means and opportunities of fulfilling it. In whatever degree, therefore, I may have contributed in this or previous Works to the advancement of Comparative Anatomy, or may have aided in its application to collateral sciences, I can only regard myself as instrumental, in such measure, in carrying out the great objects which the College of Surgeons had in view in accepting the important trust of the Hunterian Museum, and which the College has ever since most strenuously promoted.

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ERRATA.

Page	31	line	7	from top, for	*Goniadus* read *Goniodus*.
	103		8	from bottom, ..	*Pharyngnies* read *Pharyngions*.
	134		4	from top, ..	*figure b* read figure 6.
	136		15	.. ..	(*f*) read (fig. 5, *f*)
	147		18	.. ..	4) read 3)
	188		8	.. ..	*fig.* 1) read fig. 5.
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	244		8	from bottom, ..	*laminaries* read *laniaries*
	311		3	from bottom of note, for	*palates* read *palate*
	396			Note (1)	Pl. 91 read Pl. 90.
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	408		2	from top, ..	Pl. 168 read Pl. 108.
	419		12	from bottom, ..	*m.* $\frac{4—4}{4—4}$: = 42. read *m.* $\frac{3—3}{3—3}$: = 44.
	443		11	from top, ..	*fig.* 1 & 2 read fig. 2.
	458		9	& 7 from bottom, for	*osseo-dentine* read *osteo-dentine*.
	460			Note (1)	dele Pl. 122 *a*, fig. 1.
	—			Note (3) for	Pl. 124 *a*, fig. 4. read Pl. 122 *a*, fig. 4, *a*.
	465			Note (1) ..	fig. 1 & 2 read fig. 1 *e*.
	466			Note (2) ..	p. lxvi read p. lviii.

INTRODUCTION.

TEETH are firm substances attached to the parietes of the beginning of the alimentary canal, adapted for seizing, lacerating, dividing and triturating the food, and are the chief agents in the mechanical part of the digestive function.

As secondary uses, arising out of the relations of co-existence with other organs and endowments, or from a special development of the teeth themselves, may be cited their subserviency to speech(1), as ornaments, as characterizing age and sex(2), as inflictors of wounds either in combat(3) or defence(4), as aids to locomotion(5), means of anchorage(6), implements of transport and for working of building materials(7).

The dental system thus presents many and peculiar attractions to the anatomist and naturalist, for independently of the variety, beauty and even occasional singularity of the form and structure of the teeth themselves, they are so intimately related to the food and habits of the animal as to become important if not essential aids to the classification of existing species.

And, while the value of dental characters is enhanced by the facility with which, from the position of the teeth, they may be ascertained in living or recent animals, the durability of the teeth renders them not less available to the Palæontologist in the determi-

(1) Man. (2) Orang, Narwhal. (3) Dog. (4) Elephant, Musk-deer. (5) Morse. (6) Dinothere. (7) Beaver.

nation of the nature and affinities of extinct species, of whose organisation the teeth are not unfrequently the sole remains.

Teeth consist of a cellular and tubular basis of animal matter containing earthy particles, a fluid, and a vascular pulp.

In general the earth is present in such quantity as to render the tooth harder than bone, in which case the animal basis is gelatinous, as in other hard parts where a great proportion of earth is combined with animal matter. In a very few instances among the vertebrate animals, the hardening material exists in a much smaller proportion, and the animal basis is albuminous; the teeth here agree in both chemical and physical qualities with horn.

True teeth consist of two or more tissues, characterized by the proportions of their earthy and animal constituents, and by the size, form and direction of the cavities in the animal basis which contain the earth, the fluid or the vascular pulp.

The tissue, which forms the chief part or body of the tooth, has, hitherto, received no distinct and specific name in our language; a particular modification of it, which characterizes the tusks of the elephant, is called 'ivory.' Some Anatomists have extended the application of this term to the analogous substance in all teeth; others have treated of it under the name of the 'bone of the tooth'(1) or 'tooth-bone'; by the German Anatomists it is termed 'knochensubstanz', 'zahnbein' and 'zahnsubstanz'; and some of the latest and most close-thinking writers on dental anatomy have preferred the literal translation of one or other of these terms to the use of the word 'ivory', which unavoidably recalls the idea of the peculiar modification of the

(1) Hunter, Natural History of the Human Teeth. Bell's Ed. 1835, 8vo. p. 15, 16.

'tooth-substance' in the elephant's tusk, to which it is restricted in common language and in the best zoological works.(1) I propose to call the substance which forms the main part of all teeth 'dentine.'(2)

The second tissue, which is the most exterior in situation, is the 'cement'(3).

The third tissue, which, when present, is situated between the dentine and cement is the 'enamel'(4).

'Dentine' consists of an organized animal basis disposed in the form of extremely minute tubes and cells, and of earthy particles: these particles have a two-fold arrangement, being either blended with the animal matter of the interspaces and parietes of the tubes and cells, or contained in a minutely and irregularly granular state in their cavities.

The density of the dentine arises principally from the proportion of earth in the first of these states of combination; the tubes and cells contain, besides the granular earth, a colourless fluid, probably transuded 'plasma' or 'liquor sanguinis,' and thus relate not only

(1) The accurate Illiger distinguishes the 'substantia ossea' of a tooth from 'ebur,' and separately defines both these modifications of the tooth substance. *Prodromus Systematis Mammalium*, 8vo. 1811, p. 20.

(2) *Dentinum.*—Besides the advantage of a substantive name for an unquestionably distinct tissue under all its modifications in the animal kingdom, the term 'dentine' may be inflected adjectively, and the properties of this tissue be described without the necessity of periphrasis; thus we may speak of the 'dentinal' pulp, 'dentinal' tubes or cells, as distinct from the corresponding properties of the other constituents of a tooth. The term 'dental' will retain its ordinary sense, as relating to the entire tooth or system of teeth.

(3) *Cæmentum, Cortex osseus*, Tenon. *Crusta petrosa*, Blake.

(4) *Encaustum, Adamas, Substantia vitrea.*

to the mechanical conditions of the tooth, but to the nutrition of the dentine.

Dentine, thus organized, is 'unvascular': the teeth of most mammals and reptiles, and of a few fishes present this modification of their main constituent. But the dentine in the teeth of most fishes, of a few mammals, and of still fewer reptiles, is traversed by canals containing blood vessels or a vascular pulp; the tooth-substance, thus modified, I term 'vascular dentine.' Both the 'vascular' and 'unvascular dentine' may be present in the same tooth, as in those of the sloth, the walrus, and the cachalot: the transition from the vascular dentine to true bone is gradual and close.

'Cement' always closely corresponds in texture with the osseous tissue of the same animal, and wherever it occurs of sufficient thickness, as upon the teeth of the horse, sloth or ruminants, it is also traversed, like bone, by vascular canals. In reptiles and mammals, in which the animal basis of the bones of the skeleton is excavated by minute radiated cells, forming with their contents the 'corpuscles of Purkinjé', these are likewise present, of similar size and form, in the 'cement', and are its chief characteristic as a constituent of the tooth. The hardening material of the cement is partly segregated and combined with the parietes of the radiated cells and canals, and is partly contained in aggregated grains in the cells, which are thus rendered opake.

The relative density of the dentine and cement varies according to the proportion of the earthy material, and chiefly of that part which is combined with the animal matter in the walls of the cavities, as compared with the size and number of the cavities themselves. In the complex grinders of the elephant, the masqued boar and the

capibara, the cement, which forms nearly half the mass of the tooth, wears down sooner than the dentine.

The ' enamel' is the hardest constituent of a tooth, and consequently the hardest of animal tissues; but it consists, like the other dental substances, of earthy matter arranged by organic forces in an animal matrix. Here, however, the earth is mainly contained in the canals of the animal membrane, and, in mammals and reptiles, completely fills those canals, which are comparatively wide, whilst their parietes are of extreme tenuity. The hardening salts of the enamel are not only present in far greater proportion than in the other dental tissues, but, in some animals, are peculiarly distinguished by the presence of fluat of lime.

The absolute and relative size, form, disposition, direction and intercommunication of the cellular and tubular cavities characterizing the several tissues of the teeth will be the subjects of the special descriptions of these organs in the different classes and species of animals; but a brief notice of the leading steps to the present knowledge of the structure peculiar to each tissue may be appropriately given in this place(1).

In a retrospect of the history of the science of the organization of animal bodies, anatomy may always be perceived to have made a marked advance in connection with the progress of some collateral science. With regard to the hard parts of our frame in particular, our knowledge of the elementary constitution of the earthy salts has been due to the refinement of chemical

(1) The review here given of the discovery of the tubular structure of the dentine is essentially the same as that prefixed to my own observations on the subject communicated to the British Association in August, 1838.—See Trans. of the Brit. Assoc. 1838, p. 135.

analysis: the late improvements in mechanical optics have led to a resumption of the microscopical observations originally commenced by Malpighi and Leeuwenhoek; and the consequent acquisition of more exact knowledge of the mode in which the particles of the phosphate of lime and other salts are arranged in the animal basis or matrix of bone and tooth.

As regards the teeth, the principle of chief import to the physiologist arises out of the fact, which has been established by microscopic investigations, that the earthy particles of dentine are not confusedly blended with the animal basis, and the substance arranged in superimposed layers; but that these particles are built up, with the animal basis as a cement, in the form of tubes or hollow columns, in the predetermined arrangement of which there may be discerned the same relation to the acquisition of strength and power of resistance in the due direction, as in the disposition of the columns and beams of a work of human architecture.

The disposition of the calcareous particles of bone in the parietes of the Haversian canals, Purkinjian cells and of the fine tubes which radiate from these cavities, was ascertained before the analogous conditions of the intimate structure of dentine were discovered.

Until a recent period the analogy of dentine to bone was supposed to be confined to their chemical constitution, and the nature of the hardening material; while the arrangement, as well as the mode of deposition of the firm tissue, were considered to be wholly different from that of bone, and the dentine to agree in its general nature and mode of growth with hair and other extravascular horny parts, with which most teeth closely correspond in their vital properties.

The structure of a tooth, in fact, was regarded as simply

laminated, and the ivory was described as being formed layer within layer, deposited by, and moulded upon the formative superficies of the vascular pulp. The illustrations and supposed proofs of this structure and mode of growth were derived from the apparently detached condition of the newly-formed particles of dentine on the pulp's surface when exposed by the removal of the calcified part of the tooth; from the appearances observed in the teeth of animals fed alternately with madder and ordinary food, which undoubtedly illustrate the true progress of dental development; from the illusory traces of laminated structure observed in vertical sections of teeth when viewed by the naked eye, or with a low magnifying power; and lastly, and chiefly, from the successive hollow cones into which a tooth is commonly resolved in the process of decomposition.

With regard, however, to the appearances presented by the teeth of animals under the influence of madder, and to the separation of the dentine into superimposed lamellæ during decomposition, the same conclusions as to intimate structure and mode of development might be drawn respecting true bone, which also commonly resolves itself into concentric lamellæ during decomposition, and presents the same appearance of alternate white and red layers in animals fed alternately with madder and ordinary food during the progress of its growth.

The lines running parallel to each other and to the contour of the crown presented by the cut surfaces of vertical sections of teeth, especially of the elephant's tusk, or of the tooth of the cachalot, are due to a totally different structure from that to which they have been ascribed. The lamellated arrangement, thus seemingly demonstrated, is, moreover, far from being a constant appearance; on the contrary, the superficies of vertically cut or fractured surfaces of the human

and most other teeth, offer a very different character, and one which has led to many approximations and allusions to the true structure of dentine, in the works of anatomists who have recorded their own original observations.

Whoever attentively observes a polished section or a fractured surface of a human tooth may learn, even with the naked eye, that the silky and iridescent lustre reflected from it in certain directions is due to the presence of a fine fibrous structure.

Malpighi, in whose works may be detected the germs of many important anatomical truths that have subsequently been matured and established, says that the teeth consist of two parts, of which the internal bony layers (dentine) seem to be composed of fibrous, and as it were, tendinous capillaments reticularly interwoven. (1)

Retzius cites many recent authors, as Sœmmering, Schreger(2) and Weber,(3) who mention the silky glistening lustre of the dentine ; and Frederick Cuvier in the preliminary discourse of his admirable work the ' Dents des Mammifères,' observes : " Les dents de l'homme, de singes, de carnassiers ont un ivoire d'apparence soyeuse, qui semble formé de fibres," p. xxvii. These intelligible hints of the true structure of the dentine, which the foregoing observers received from a superficial but unprejudiced inspection, failed, however, to incite them to a closer interrogation of Nature.

One of her more persevering investigators had, nevertheless, long before obtained a true and definite answer to his more direct inquiries. Leeuwenhoek, having applied his microscopical observations

(1) " Duplici excitantur parte, quarum interior ossea lamella fibrosis et quasi tendinosi capillamentis in naturam implicetis constat."—Anatome Plantarum, Lugd. Batav. 1687, p. 37.

(2) Isenflamm und Rosenmüllers Beiträgen zur Zergliederungskunst, band i, p. 3, (1800).

(3) See his Edition of " Hildebrand's Handbuch der Anatomie," band i, p. 206.

to the structure of the teeth, discovered that the apparent fibres were really tubes, and he communicated a brief but succinct account of his discovery to the Royal Society of London,(1) which was published, together with a figure of the tubes, in the 140th Number of their Transactions. This figure of the dentinal tubes, with additional observations, again appears in the Latin edition of Leeuwenhoek's works, published at Leyden in 1730. The dental substance (dentine) of the human teeth, and of those taken from young hogs is described as being " formed of tubuli spreading from the cavity in the centre to the circumference." He computed that he saw a hundred and twenty of the tubuli within the forty-fifth part of an inch.(2)

Leeuwenhoek also shows that he was aware of the peculiar substance, distinct from the ivory and enamel, and now termed the cement or *crusta petrosa*, which enters into the composition of the teeth of the horse and ox(3) ; a component part of the tooth which Hunter speaks of as a second kind of bone ; and which was first accurately and specifically described by Tenon and Blake.

But these microscopical discoveries may be said to have appeared before their time: the contemporaries of Leeuwenhoek were not prepared to appreciate them ; besides, they could neither repeat nor confirm them, for his means of observation were peculiarly his own: and hence it has happened that, with the exception of the learned Portal,(4) they have either escaped notice, or have been

(1) Microscopical Observations on the Structure of Teeth and other Bones.—Philos. Trans. 1678, p. 1002.

(2) See Hoole's Translation of the select works of Leeuwenhoek, 4to. 1798, p. 114.

(3) Parvi molares, quos bos, dum ad huc admodum juvenis sive vitulus, habuerat, undiquaque *alio osse* circumducti erant " *Continuatio Epistolarum*, 4to. Lugd. Bat. 1689, p. 7.

(4) Histoire de l'Anatomie et de la Chirurgie, Paris, 1770, Tom. iii, p. 460, in which

designedly rejected by all anatomists until the time of the confirmation of their exactness and truth by Purkinjé in 1835.

The results of the laborious investigations of this most original and indefatigable observer were published, as is the custom in many German Universities, in two inaugural thesises, the one by Fraenkel entitled "De penitiori dentium humanorum structura observationes;" the other by Raschskow, entitled "Meletemata circa dentium evolutionem;" both of which were defended in the University of Breslau in the month of October, 1835.

Purkinjé states that the dentine (zahnsubstanz, *substantia dentis*) consists, not of superimposed layers, but of fibres arranged in a homogeneous intermediate tissue, parallel with one another, and perpendicular to the surface of the tooth, running in a somewhat wavy course from the internal to the external surface; and he believed these fibres to be really tubular, because on bringing ink into contact with them, it was drawn in as if by capillary attraction.(1)

Upon the publication of this discovery it was immediately put to the test by Professor Müller, by whom the tubular structure of the ivory was not only confirmed, but the nature and one of the offices

Leeuwenhoek's Letter to the Royal Society is noticed as follows: "Les dents sont composées de très petits tuyaux transparents et étroits, dont six ou sept cents égalent à peine un poil de la barbe." The merit of directing the attention of anatomists to Leeuwenhoek's discovery of the structure of dentine is due to Retzius.

(1) Cruorine extravasated during intense inflammation of the pulp, or by an over-distension of the vessels produced mechanically as in hanging or drowning, would in like manner be carried, with the plasma, into the dentinal tubes, and occasion red spots in the tooth-substance; the bile-stained serum, in the case of jaundice, would equally affect the capillary tissue of the tooth with its peculiar tinge; but it does not follow that the tubes which imbibe such coloured fluids must necessarily be capillary blood-vessels, and these phenomena, therefore, afford no proof of the vascularity of human dentine.

of the tubes were determined. He observed that the white colour of a tooth was confined to these tubes, which were imbedded in a semi-transparent substance, and he found that the whiteness and opacity of the tubes were removed by acids. On breaking a thin lamella of a tooth transversely with regard to its fibres, and examining the edge of the fracture, Müller perceived tubes projecting here and there from the surfaces; they were white and opaque, stiff, straight, and apparently not flexible: this appearance is well represented in the old figure by Leeuwenhoek. If the lamellæ had been previously acted upon by acid, the projecting tubes were flexible and transparent, and often very long. Hence, Professor Müller inferred that the tubes have distinct walls, consisting of an animal tissue; and that, besides containing earthy matter in their interior, their tissue is, in the natural state, impregnated with calcareous salts.

Thus, the discovery by microscopical examinations that the dentine of the teeth in man and various animals was traversed by minute tubes disposed in a radiated arrangement in lines proceeding every where perpendicularly from the surface of the cavity containing the pulp, may be regarded as established, and to be due principally to the learned and ingenious Purkinjé, who, however, was all the while unconscious that he had been anticipated, as to the main fact, a long time before, by Leeuwenhoek.

But the tubular structure of ivory is not the only important fact in dental anatomy, made known in the Breslau Thesises of 1835. Purkinjé also discovered that the distinct layer of substance, previously known to surround the fang of the simple teeth of man and many mammalia, contained corpuscles like those

which characterize the structure of true bone: and he observed in one instance that this bone-like substance was continued upon the enamel of the crown of a human incisor.

This fact I have confirmed(1) as regards the human teeth and the simple teeth of many mammals and reptiles. The layer of coronal cement varies in thickness; its tenuity is extreme in the teeth of man and the quadrumana.

Purkinjé also found that the third substance, *crusta petrosa* or cement of compound teeth, as those of the horse and ox, was in like manner characterized by the presence of numerous bone-corpuscules or cells; and thus proved that the difference between the so called simple and compound teeth depended, not on the presence of a third and additional substance in the latter, but on its greater abundance and different disposition in the tooth.

At the time that these observations were being made at Breslau and Berlin, it appears that similar investigations had been set on foot at Stockholm. Professor Retzius of the University in that city informs us that he had been led by the iridescence of the fractured surface of the substance of a tooth to conceive that that appearance was due, as in the crystalline lens, to a fine fibrous structure, and that he communicated his opinions as to the regular arrangement of these fibres to some of his colleagues in 1834; and that the University having obtained, in the summer of 1835, a powerful microscope, by Plessl of Vienna, he commenced a series of more exact researches on the intimate structure of the teeth in man and the lower animals. He operated on thin sections of teeth both before, and after, the removal of the earthy matter by means of acid, and atten-

(1) Trans. Brit. Assoc. 1838, vol. vii. p. 136.

tively examined the fractured and polished surfaces of the ivory part: he determined the exact arrangement, course, and size of the tubuli in the teeth of different animals, and detected the finer ramifications given off by the tubuli during their divergence,(1) and the anastomoses of their finest terminal branches with the cells in the intertubular, or as it is sometimes termed, interfibrous tissue.

Retzius also claims to have discovered the radiated or purkinjian corpuscles(2) in the dentine; and to have thus succeeded in displaying a far greater identity between tooth-bone and proper bone than had been before anticipated.

He exhibited the preparations and drawings illustrative of these interesting observations to Berzelius, Urede, and Professor Wahlberg at the latter end of 1835; being then unacquainted with the discoveries of Purkinjé; and communicated his researches to the Royal Academy of Sciences at Stockholm on the 13th of January, 1836. They were published in the same year in those Transactions and in the following year as a distinct treatise(3).

At the early part of that year, 1837, I received from Mr. Darwin

(1) Leeuwenhoek appears to have suspected the existence of such branches; he says," upon examining the tubuli round about this small cavity (the pulp-cavity) I perceived that they all arose from thence and spread themselves all round towards the circumference. I endeavoured to examine still farther, beyond the part where this cavity ended, in order to discover whether from these first-formed tubuli others might not arise or branch forth; but this part of nature's work was inscrutable to me." Hoole's Leeuwenhoek, 4to. p. 113.

(2) I have not yet been able to detect the radiated cells or corpuscles in the dentine of the horse's tooth, in which they are described by Retzius; but they are very numerous and conspicuous at the peripheral portion of the dentine of the dugong's grinder, pl. 94.

(3) Mikroskopiska Undersökningar öfver Jädernes särdeles Tandbenets struktur: Stockholm, 1837.

many fragments of the teeth of the extinct *Megatherium*, *Megalonyx*, *Mylodon* and *Toxodon* collected during his travels in South America. Some of these fragments were in a state of incipient decomposition: and my attention was forcibly arrested by the fact that these fragments, instead of being resolved, like the fossil tusks of the mammoth and mastodon, into parallel superimposed conical lamellæ, separated into fine fibres, arranged at right angles to the plane of the layers which, according to the lamellar theory of dental structure, ought to have presented themselves to view. I exhibited the most characteristic of these specimens at my lectures on the teeth, at the Royal College of Surgeons, in May, 1837, and stated that "the appearances which they presented were inexplicable on the lamellar hypothesis: but that I should investigate the subject further, and endeavour to elucidate the apparent anomaly before the following session." At the conclusion of that course, I had sections of these fragments prepared for the microscope; and stimulated by the amount of clearly defined and beautiful structure which they exhibited,(1) I proceeded to examine similar sections of the human teeth and of those of many of the lower animals. The excitement of the research became heightened as the sphere of observation expanded, and I had collected extensive materials for a Treatise expressly on the Structure of Teeth, when the fourth number of Müller's Archiv fur Physiologie, for the year 1837, containing an Analysis of Purkinjé's and Fraenkel's Treatise, came into my hands, in December, 1837, and awoke me from the dream of discovery in which I had been indulging. I received, shortly after, the fifth number of the same volume of Müller's Archiv, containing Dr. Creplin's German Translation of the Treatise of Retzius,

(1) See Plates 79 and 84.

upon the perusal of which I abandoned my intention of publishing those general observations on the structure of the teeth which I had before deemed to be new, but now found to have been mainly anticipated by Purkinjé and Retzius.

I was not, however, discouraged by this disappointment, but, feeling convinced that no work on the Comparative Anatomy of the Teeth would henceforth be regarded as complete without an account of the leading modifications of the dentinal tissue in the different classes of animals, I proceeded to the microscopical investigation of that tissue in many animals in which it had not been previously so examined. The number of characteristic differences which presented themselves, and which are described in the body of the present work, led to the perception of the value of the microscopic structure of the teeth as a test of the affinities of extinct animals, and to the institution of researches into the laws of development of the dental tissues, which, as then accepted and taught, were irreconcileable with the general demonstration of the intimate structure of those tissues which was yielded by the teeth of fishes, reptiles and mammals.(1)

The prelude to this generalization may be summarily recapitulated as follows: the discovery of Leeuwenhoek that the dentine was made up of very minute tubes, which proceeded from the inner to the outer surface of the tooth, was confirmed by Purkinjé, so far as regarded their existence; but Purkinjé added an exact and particular account of the direction of these tubes in the human dentine, and showed that, in addition to them the dentine contained an interme-

(1) The chief results of these researches have been successively communicated to the British Association at the Newcastle Meeting, August, 1838, (Transactions of the Association, vol. vii, p. 135;) in the Proceedings of the Geological Society for 1838 and 1839, and in the Comptes Rendus de l'Académie des Sciences, December 12, 1839.

diate or inter-tubular tissue ; this he describes as homogeneous and without structure, and as entering into the composition of the dentine in a greater proportion than the tubes themselves.

The more extensive, varied and minute observations of Professor Retzius led to the discovery of the cells of the intertubular tissue, of the ramuli sent off from the main calcigerous tubes into that tissue, and of the anastomoses of the ramuli with each other, with the intertubular cells, and with the cells at the periphery of the dentine. According to the researches of Dr. Schwann the animal basis of the intertubular tissue possesses a fibrous structure.

Besides the primary and secondary branches of the calcigerous tubes Retzius first clearly described their curvatures and undulations, which may be defined as follows : as a general rule the dentinal tubes are directed, as affirmed by Leeuwenhoek and Purkinjé, from the inner to the outer surface of the tooth, and vertically to those surfaces ; but in their course the tubes describe two, three, or more curvatures, appreciable by a low magnifying power: these I have termed the ' primary curvatures.'(1) With a higher power, the tubes are seen to be bent throughout the whole of their flexuous course into minute and equal oblique undulations or gyrations, two hundred of which were counted by Retzius in one tenth part of an inch's length of a human calcigerous tube ; these I have termed the ' secondary curvatures' or gyrations.(2) Both the primary and secondary curvatures of one tube are usually parallel with those of the contiguous calcigerous tubes, and from the radiated course of these tubes they occasion the appearance of lines running parallel with the external

(1) Trans. Brit. Assoc. vol. vii, p. 148. See Plates 24, fig. 1 ; 64 A, fig. 2 ; 74, fig. 1 ; 94.

(2) Ibid, p. 141. See Plates 16, fig. 3 ; 24, fig. 2 ; 64 A, fig. 3.

contour of the tooth; for, when the surface of a longitudinal section of a tooth is viewed with the naked eye, the light is differently reflected from the different parts of the oblique secondary curves of the tube on which it falls; but the curves being parallel to each other and to the superficial contour of the section, they appear like the cut edges of a series of parallel and super-imposed lamellæ. In many teeth, moreover, and especially in the tusks of the elephant, the secondary branches of the dentinal tubes dilate into intertubular cells along lines, which in like manner are parallel to the coronal contour of the tooth; hence another cause of the appearance of concentric lamellæ and of the actual decomposition of such teeth into super-imposed lamelliform cones.

Such appearances and modes of decomposition are peculiar to the dense or unvascular dentine; but are by no means common to that modification of the tissue. They are never witnessed in any of the varieties of vascular dentine.(1) The prolongation or persistence of cylindrical canals of the pulp-cavity in the dentinal tissue, which is the essential character of vascular dentine, manifests itself under a variety of forms. In mammals and reptiles these canals, which I have termed 'medullary'(2) from their close analogy with the so called canals of bone, are straight and more or less parallel with each other; they bifurcate, though rarely; and when they anastomose, as in the megatherium, it is by a loop at, or near, the periphery of the vascular dentine. In the teeth of fishes, in which the distinction between the dentinal

(1) This substance was first characterised as a component of tooth, 'distinct from ivory, enamel, cement, and true bone, and as easily recognisable,' in my paper communicated to the British Association, in 1838; loc. cit. p. 137.

(2) Ibid.

and osseous tissues is gradually effaced, the medullary canals of the vascular dentine, though in some instances straight and parallel and sparingly divided or united, yet are generally more or less bent, frequently and successively branched, and the subdivisions blended together in so many parts of the tooth as to form a rich reticulation. The calcigerous tubes sent off into the interspaces of the net-work partake of the irregular character of the canals from which they spring, and fill the meshes with a moss-like plexus.(1)

Closely analogous to this modification of the vascular dentine, but differing in the presence of the radiated cells, is the tissue into which the residue of the pulp is converted in the teeth of certain reptiles, as the Iguanodon, Hylæosaurus and Ichthyosaurus, and of those of a few mammalia, as the Cachalot(2). This tissue approaches, in the combined presence of medullary canals and calcigerous cells, as closely to that of the skeleton of the species in which it occurs, as the reticulate modification of the vascular dentine in the teeth of fishes does to the osseous tissue of their skeleton. It has been uniformly described by the authors who have observed it, as Cuvier(3) and Conybeare,(4) as the result of ossification of the pulp.

If the first described modification of vascular dentine, which forms the chief part of the teeth of the Sloths and Megatherium, be regarded as a fourth dental tissue, this second modification of vascular dentine, from its closer resemblance to bone might be reckoned as a fifth; in proportion, however, as it resembles bone, so likewise it approaches to the structure of cement.

(1) See Plates 6, 7, 53, 54, 55.

(2) Plate 89, fig. 2, c.

(3) Leçons d'Anat. Comp. 1e. ed. tom. iii, p. 113; Ossem. Fossiles, 2e. ed. tom. v. 2e. partie, p. 274.

(4) "The teeth in these genera (the Lacertæ) become completely solid, its interior cavity being filled up by the ossification of the pulpy substance."—Trans. Geol. Soc. vol. vi. p. 106.

The organized structure and microscopic character of the cement were first determined by Purkinjé and Faenkel; and the acquisition of these facts led to the detection of the tissue, as has been already observed, in the simple teeth of man and carnivorous animals. The cement is most conspicuous where it invests the fang of the tooth, and increases in thickness as it approaches the apex of the fang. The animal constituent of this part of the cement had been recognized by Berzelius, as a distinct investment of the dentine, long before the tissue of which it formed the basis was clearly recognized in simple teeth. Berzelius describes the cemental membrane as being less consistent than the animal basis of the dentine, but resisting longer the solvent action of boiling water, and retaining some fine particles of the earthy phosphates when all such earth had been extracted from the dentinal tissue. Cuvier, likewise, states that the cement is dissolved with more difficulty in acid than the other dental tissues. Retzius, however, states that the earth is sooner extracted by acid from the cement than from the dentine of the teeth of the horse.

In recent mammalian cement the radiated cells, like the dentinal tubes, owe their whiteness and opacity to the earth which they contain. According to Retzius, "numerous tubes radiate from the cells, which, being dilated at their point of commencement, give the cell the appearance of an irregular star. These tubes form numerous combinations with each other, partly direct and partly by means of fine branches, of $\frac{1}{10,000}$th to $\frac{1}{50,000}$ of an inch in diameter.

"The cells often vary in size, and some put on the appearance of a canal or tube; this is especially seen in recently formed cement. The average size of the Purkinjian cells in human cement is $\frac{1}{1,600}$th of an inch. In sections made transversely to the axis of the tooth it is clearly seen that these cells are arranged in parallel or

concentric striæ, of which some are more clearly and others more faintly visible, as if the cement were deposited in fine and coherent layers. The layer of cement is found in the deciduous teeth, but is relatively thinner and the Purkinjian cells are more irregular.

"In growing teeth with fangs not fully formed, the cement is so thin that the Purkinjian cells are not visible: it looks like a fine membrane, and has been described as the periosteum of the fangs, but it increases in thickness with the age of the tooth, and is the seat and origin of what are called *exostoses* of the fang which are wholly composed of it." These growths are subject to the formation of abscess, and all the other morbid actions of true bone.

It is the presence of this osseous substance which renders intelligible many well-known experiments of which human teeth have been the subjects; such as their transplantation and adhesion into the combs of cocks, and the establishment of a vascular connection between the tooth and the comb; the appearances which the Hunterian specimens of these experiments present, and of the reality of which Professor Müller satisfied himself during his visit to London, are no longer perplexing, now that we know that the surface of the tooth, in contact with, and adhering to the vascular comb, is composed of a well organised tissue, closely resembling bone.

This correspondence of the cement, which, when it exists in sufficient quantity, becomes almost identity, with true bone, is illustrated by the varieties of microscopic structure which the cement presents in different classes of animals, and which always correspond with the modifications of the osseous tissue of the skeleton in those animals; thus the cement in the osseous fishes, in which the bone is not characterized by the radiated calcigerous cells, likewise ceases to present that character; and, in reptiles and mammals in which

the radiated cells are present in the bone of the skeleton and in the dental cement there is a close conformity as to their size and shape in both tissues.

The most remarkable modification of mammalian cement is presented by the thick layer of that substance which invests the molars of the extinct megatherium ;(1) besides abounding in calcigerous cells it is here traversed by straight, parallel and occasionally bifurcated medullary canals, arranged with regular intervals, and directed from the exterior of the tooth somewhat obliquely to the surface of the unvascular dentine, close to which they anastomose by loops, corresponding with, and opposite to those formed by the medullary canals of the vascular dentine of the same tooth(2).

Under every modification the cement is the most highly organized and most vascular of the dental tissues, and its chief use is to form the bond of vital union between the denser and commonly unvascular constituents of the tooth and the bone in which the tooth is implanted. In a few reptiles (now extinct) and in the herbivorous mammalia the cement not only invests the exterior of the teeth, but penetrates their substance in vertical folds, varying in number, form, extent, thickness and degree of complexity, and contributing to maintain that inequality of the grinding surface of the tooth which is essential to its function as an instrument for the comminution of vegetable substances.

The higher an animal is placed in the scale of organization, the more distinct and characteristic are not only the various organs of the body, but the different tissues which enter into their composition.

(1) Plate 84, *b*. (2) Pl. 84, *a*.

This law is well exemplified in the teeth, although in the comparison of these organs we are necessarily limited to the range of a single primary group of animals. We have seen, for example, that the dentine is scarcely distinguishable from the tissue of the skeleton in the majority of fishes: but that its peculiarly dense, unvascular and resisting structure, which is the exceptional condition in fishes, is its prevalent character in the teeth of the higher vertebrates.

So likewise with the enamel; this substance, which under all its conditions bears a close analogy with the dentine, is hardly distinguishable from that tissue in the teeth of many fishes(1). The fine calcigerous tubes are present in both substances, and undergo similar subdivisions; the directions only of the trunks and branches being reversed, agreeably with the contrary course of their respective developments. The proportion of animal matter is also greater in the enamel of the teeth of fishes than of the higher vertebrata; and the proportion of the calcareous salts incorporated with the animal constituent of the walls of the tubes is greater as compared with the sub-crystalline part deposited in the tubular cavities. In reptiles, the proportion of the hardening salts and consequently the density of the enamel are increased, but the course, size, and ramification of the calcigerous tubes still bear considerable analogy to those of the dentine; and the prismatic form of the calcigerous tubes,(2) their minute striations, and the superficial transverse wavy linear ridges, which constitute the characteristic features of the enamel in the mammalian class, are not present in that tissue in the cold-blooded vertebrates.

The enamel is the least constant of the dental tissues: it is more

(1) *Sargus*, Pl. 43, fig. 2; *Phyllodus*, Pl. 44, fig. 2; *Scarus*, Pl. 50, Pl. 52.

(2) I apply this term to the so-called prismatic fibres of human and other mammalian enamel for reasons which will appear in the sequel.

frequently absent than present in the teeth of the class of fishes; it is wanting in the entire order Ophidia among existing reptiles; and it forms no part of the teeth of the Edentata and many Cetacea among mammals.

The enamel may be distinguished, independently of its microscopic and structural characters, by its glistening, subtransparent substance, which is white or bluish-white by reflected light, but of a gray-brown colour when viewed, under the microscope, by transmitted light.

The microscopical characters of the enamel have hitherto been taken from the modification of that tissue in the class Mammalia, where it presents its most distinctive and consequently highest condition.

This condition of the enamel, however, like the corresponding one of the mammalian dentine, in the same degree as it distinguishes them from the true osseous tissue, and perfects them for their mechanical applications, removes them from the influence of the conservative and reparative powers of the living organism. The mammalian enamel, therefore, once formed and exposed, is least able to resist vitally the influence of the external decomposing forces; but this inferiority is amply compensated by its superior mechanical endowments. Nevertheless, it undergoes more change, after becoming exposed by the eruption of the tooth, than does either the dentine or cement, especially in regard to its original membranous constituent; and no true idea of its organic structure can be obtained except by an examination soon after its formation.

The enamel of the molar tooth of a calf, which has just begun to appear above the gum, and which can readily be detached from the dentine, especially near the commencement of the fangs, is resolvable

into apparently fine prismatic fibres; if these fibres be separately treated with dilute muriatic acid and the residue examined, with a moderate magnifying power, in distilled water, or, better, in dilute alcohol, portions of more or less perfect membranous sheaths or tubes will be discerned, which inclosed the earthy matter of the minute prism, and served as the mould in which it was deposited.

Professor Retzius, who obtained a small portion of organic or animal substance from the enamel-fibres of an incompletely-formed tooth of a horse, conjectured that it was a deposition of that fluid which originally surrounds the loose enamel-fibres, and that, "in proportion as these fibres are pressed tighter together, and additional fibres are wedged between them, the organic deposition is forced away."

It is certain that the small proportion of animal matter which can be obtained from the enamel of a tooth, that has been completely formed and in use, does not yield any indication of its primitive organic form; this may, however, be ascertained, if the enamel be examined under the conditions above described. The tubular structure of the membranous constituent of recently formed enamel has been observed by Dr. Schwann(1) in the teeth of the hog: and he has shown that the fine membrane of the enamel-prism is not a mere deposition from the fluid in which the new-formed prisms are bathed, but an organized part specially formed and arranged in the enamel pulp in order to ensure the right disposition and direction of the calcareous salts of the enamel.

Retzius accurately describes the enamel-fibres of the horse as presenting the form of angular needles, about $\frac{1}{5,000}$th of an inch in diameter, which are traversed by minute and close-set transverse

(1) Loc. cit. p. 118.

striæ, over the whole, or a part of the fibre; and he conjectures that if the enamel-fibre be a mass of the calcareous salts, surrounded by an organic capsule, that the striæ may then belong to the capsule and not to the enamel-fibre. The later researches of Dr. Schwann add to the probability of this conjecture, and the absence of the minute striæ in the enamel of fossil mammalian teeth, at least in the examples which I have submitted to microscopic investigation, may depend upon the destruction of the original organic constituent of the enamel.

The enamel-fibres are directed at nearly right angles to the surface of the dentine, and their central or inner extremities rest in slight but regular depressions on the periphery of the coronal dentine. Thus in the human tooth, the fibres which constitute the masticating surface are perpendicular or nearly so to that surface, while those at the lower part of the crown are transverse, and consequently have a position best adapted for resisting the pressure of the contiguous teeth, and for meeting the direction in which external forces are most likely to impinge upon the exposed crown of the tooth. The strength of the enamel fibres is further increased by the graceful wavy curves in which they are disposed; these curves are in some places parallel, in others opposed; their concavities are commonly turned towards each other where the shorter fibres, which do not reach the exterior of the enamel, abut by their gradually attenuated peripheral extremities upon the longer fibres. Other shorter enamel-fibres extend from the outer surface of the enamel towards the dentine and are wedged into the interspaces of the longer fibres. In the teeth of fishes, the calcigerous tubes or fibres of the enamel, which ramify and subdivide like those of the dentine, have their trunks turned in the opposite direction, or towards the periphery of the tooth; so likewise even in the human teeth the analo-

gous condition may be discerned in the slightly augmented diameter of the enamel-fibres at their peripheral, as compared with their central extremities. When the extremities of the human enamel-fibres are examined with a magnifying power of 300 linear dimensions, by reflected light, they are seen to be co-adapted, like the cells of a honey-comb, and like these to be, for the most part, hexagonal.

The external surface of the enamel is marked by fine transverse lines or ridges, of which Retzius counted twenty-four in the vertical extent of one tenth of an English inch of the crown of a human incisor; these lines are parallel and wavy, and, like the analogous markings on the surface of shells, indicate the successive formation of the belts of enamel-fibres that encircle the crown of the tooth. These lines may be traced around the whole crown, but are very faint upon its inner or posterior surface.

Retzius cites Leeuwenhoek as the discoverer of these superficial transverse lines of the enamel: but the older observer supposed them to be indicative of the intervals between the successive movements in the cutting of the tooth through the gum.

The enamel by virtue of its physical qualities of density and durability forms the chief mechanical defence of the tooth, and is consequently limited, in most simple teeth, to the exterior surface of the exposed portion of the dentine, forming the ' crown ' of the tooth.

It sometimes forms only a partial investment of the crown, as in the molar teeth of the iguanodon, the canine teeth of the hog and hippopotamus, and the incisors of the Rodentia. In these the enamel is placed only on the front of the tooth, but is continued along a great part of the inserted base, which is never contracted into one, or divided into more fangs; so that the character of the crown of the tooth is maintained throughout

its extent as regards both its shape and structure. The partial application of the enamel in these 'dentes scalprarii' operates in maintaining a sharp edge upon the exposed and worn end of the tooth, precisely as the hard steel keeps up the outer cutting edge of the chisel by being welded against an inner plate of softer iron.

In the herbivorous mammalia, with the exception of the Edentata, vertical folds or processes of the enamel are continued into the substance of the tooth, varying in number, form, extent and direction, and producing, by their superior density and resistance the ridged inequalities of the grinding surface on which its efficacy, in the trituration of vegetable substances, depends.

In the development of a tooth, composed of the above-mentioned differently organised tissues, a matrix of equal complexity was first recognised to be concerned by John Hunter; the several parts of this matrix, here termed respectively the 'dentinal pulp,' the 'enamel pulp,' and the 'capsule' or 'cœmental pulp,' being first distinctly indicated in the 'Natural History of the Human Teeth.'

In this otherwise instructive and original treatise the reader will, however, seek in vain for any definite or detailed account of the part which each formative organ plays in the development of its corresponding tissue, or of the development of the matrix itself.

The latter subject has been chiefly elucidated by the observations of Arnold(1), Purkinjé and Raschkow(2), Valentin(3), and Goodsir(4):

(1) Salzburg Mediz. Chirurg. Zeitung. 1831, erster band, p. 226.

(2) Meletemata circa Mammalium Dentium Evolutionem, 4to. 1835.

(3) Handbuch der Entwickelungsgeschichte des Menschen, 8vo. 1835, p. 482.

(4) On the Origin and Development of the Pulps and Sacs of the Human Teeth. Edinburgh Medical and Surgical Journal, vol. li, p. 1.

the modifications in the development of the dental matrix in different animals and their analogies with those described by the foregoing authors in the Human Subject and other mammalia are detailed in the body of the present work.

The dentinal pulp is always the first developed part of the matrix, and makes its appearance in the form of a papilla, budding out from the free surface of a fold or groove of the mucous membrane of the mouth, and generally of that which covers the inner side of the jaws or their rudiments. In certain fishes, as the shark, the tooth is completed without the development of the matrix proceeding beyond this 'papillary' stage.

The first papilla may be distinctly recognized in the maxillary mucous groove of a human embryo, one inch in length; the others quickly follow. By the growth of the contiguous mucous membrane, the papilla appears to sink into a follicle, and, by the development of three or four lamellar processes from opposite sides of the mouth of the follicle, and their mutual cohesion, the papilla is inclosed by a capsule; this 'capsular' stage of development is completed in the human fœtus at the fifteenth week(1). The capsule is the part of the matrix destined for the development of the cement. In many fishes and in serpents, the teeth are completed without the development of the matrix proceeding beyond this stage.

In those teeth which are defended by enamel, a pulp destined for its production is developed from the inner surface of the capsule opposite that to which the dentinal pulp is attached. In the human subject the enamel-pulp makes its appearance as a soft gelatinous substance adhering to the opercular plates closing the capsule, and

(1) Goodsir, loc. cit. p. 11.

the adjoining inner surface of the capsule, at the sixteenth week; the surface of adherence of the 'enamel-pulp' is progressively extended until it is separated by a mere linear interspace from the base of the 'dentinal pulp.' "Whatever eminences or cavities the one has, the other has the same, but reversed; so that they are moulded exactly to each other."(1)

With regard to the development of the dentine, Hunter describes it as an 'ossification,' but without indicating the relation that the pulp bears to the process. "As the ossification advances it gradually surrounds the pulp till the whole is covered by bone, excepting the under surface; and while the ossification advances, that part of the pulp which is covered by bone is always more vascular than the part which is not yet covered. The adhesion of the pulp to the new-formed tooth or bone is very slight, for it can always be separated from it without any apparent violence, nor are there any vessels going from the one to the other; the place, however, where it is most strongly attached is round the edge of the bony part, which is the last part formed." "Both in the body and in the fang of a growing tooth, the extreme edge of the ossification is so thin, transparent and flexible, that it would appear rather to be horny than bony, very much like the mouth or edge of the shell of a snail when it is growing; and, indeed, it would seem to grow much in the same manner, and the ossified part of a tooth would seem to have much the same connexion with the pulp as a snail has with its shell."(2) Hunter does not explain the nature of this connexion or the mode of formation of shell; but he has been generally regarded by Physiologists as having been the author of the theory that the pulp stood to

(1) Hunter, loc. cit. p. 42. (2) Ibid, p. 39, 40.

the tooth-bone in the relation of a gland to its secretion; that the formative virtue of the pulp resided in its surface; that the dentine was deposited upon and by the formative or secretive surface of the pulp in successive layers; and that the pulp, exhausted as it were, by its secretive activity, diminished in size as the formation of the tooth proceeded; except in certain species, in which the pulp was persistent, and maintained an equable secretion of the dentine throughout the life-time of the animal(1).

This idea of the pulp's function, modified only by the phraseology required to express the later-acquired knowledge of the form and condition of the newly-developed dentine in contact with the pulp, has predominated in the minds of most subsequent writers on the development of teeth.

The successive steps to the establishment of the doctrine that the cells of the ivory, under which form Dr. Schwann has described the nascent dentine to make its first appearance, are actually part of the pulp itself, pre-existing in that body before their calcification and confluence, and continuing in organic connexion therewith after their conversion into the tubular dentine, are few, well-marked, and easily traced. The first advance was made by Purkinjé and Raschkow in submitting to careful microscopical observation the structure of the dentinal pulp prior to the formation of the dentine, and in similarly tracing the changes which it undergoes during that process.

(1) Cuvier, by whom this opinion of the formation of dentine is most clearly set forth, premises the following acknowledgment: "Quant à la manière dont les dents en général naissent et croissent, nos observations nous paroissent confirmer la théorie de *Hunter*, plutôt que toutes les autres, dans ce qui concerne la partie de la dent qu'on nomme substance osseuse."—Ossem. Foss. 4to. 1812, p. 59.

These authors describe the parenchyme of the dentinal pulp as being composed of minute uniform spherical granules, without any of the characteristic filaments of cellular tissue, and, in this respect, differing from the enamel-pulp. The free surface of the granular tissue is covered by a peculiarly dense, structureless pellucid membrane, which they term the 'preformative membrane' because the formation of the dentine commences therein. Blood-vessels soon penetrate the granular pulp, form several anastomoses in their course, through its substance, and terminate in a rich and delicate net-work of capillaries on that part of the surface of the pulp where the dentine has begun to be formed; the rest of the pulp's surface is covered by the preformative membrane and does not display any capillary reticulation. True nervous filaments cannot be distinguished in the pulp until after its vascularity has been established. The granules of the pulp immediately beneath the preformative membrane have a more elongated form than the rest, and are placed either vertically, or at an acute angle with the membrane.

The formation of the dentine is preceded by the development of numerous minute elevations on the surface of the pulp, at and near its apex; these are conjectured to be subsequently transformed into the undulating ridges in which the enamel-fibres are firmly inserted. The preformative membrane becomes of a stony hardness, except at the margin of the recently formed dentine, where it is soft and easily rent. The dentine begins to be formed at the apex of the pulp immediately beneath the preformative membrane.

Of the exactness of the preceding observations by Purkinjé and Raschkow I have had repeated evidence. The more obscure parts of their description of the development of the dentine are quoted and commented on by Dr. Schwann, whose observations on this

subject are as follows: after observing that the blood-vessels of true bone are confined to the medullary canals, and that the presence or absence of blood-vessels in a tissue occasions no essential difference in its mode of growth; he proceeds to classify teeth with bones in an order of tissues, characterized by the parietes of their primordial cells becoming confluent either with each other, or with the intercellular substance(1).

Dr. Schwann identifies the pulp-granules of Purkinjé with his nucleated cells, and asks, "In what relation does the dentine stand to the cells?" He then proceeds to say, "I must confess, at the outset, that I am unable to answer this question with certainty, and that my observations are not mature. Purkinjé and Raschkow describe the formation of the dentine as follows:—"Primordio substantia dentalis e fibris multifariam curvatis convexis lateribus sese contingentibus ibique inter se concrescentibus composita apparet.—In ipso apice istæ fibræ æqualiter quamcunque regionem versus se diffundunt, attamen parietes laterales versus directio longitudinalis prævalet, dum fibræ sinuosis flexibus æqualique modo se invicem contingentes ibique ubi concavæ apparent lacunas inter se relinquentes, ab apice coronali radicem versus ubicunque procedunt. Nonnisi extremi earum fines tunc molles sunt cæteræ autem partes brevissimo tempore indurescunt ..Postquam....fibrarum dentalium stratum depositum est, idem processus continuo ab externa regione internam versus progreditur, germinis dentalis parenchymate materiam suppeditante.....Convexæ fibrarum dentalium flexuræ, quæ juxta latitudinis dimensionem crescunt, dum ab externa regione internam versus procedunt, sibi

(1) Microskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen. 8vo. 1839, p. 117.

invicem appositæ continuos canaliculos effingunt, qui ad substantiæ dentalis peripheriam exorsi multis parvis anfractibus ad pulpam dentalem cavumque ipsius tendunt, ibique aperti finiuntur, novis ibi, quamdiu substantiæ dentalis formatio durat, fibris dentalibus aggregandis inservientes."—Raschkow, l. c. p. 6.

" I must confess," Dr. Schwann proceeds to say, " that there is much obscurity in this description. If I rightly understand it, the dentine consists of fibres, formed layer-wise out of material afforded by the pulp, which become confluent with each other but leave interspaces which are the dentinal tubes. But these tubes cannot be mere interspaces between fibres, since Müller has proved them to possess distinct parietes... If a young tooth be removed from its capsule and steeped for one day in not too much diluted muriatic acid, the animal basis of the dentine, which, at the first removal of the earth, was of cartilaginous hardness, becomes quite soft, so that one can only detach small pieces from it by the forceps. If this pultaceous mass be examined, it will be seen to consist of fibres, which can be separated from one another. These fibres are too thick to be merely the walls of the canals ; they constitute the whole substance. Neither can they be a mere artificial product, since the acid penetrating the canals first dissolves the immediately contiguous substance, and then the intertubular substance remains as a fibre; besides, they are too regular and smooth. It appears, moreover, that the dentine is composed of these reciprocally united fibres, since they are identical with the fibres which, according to Purkinjé and Raschkow, form by their confluence the dentinal cartilage; and this confluence of the fibres is not so complete but that they can be again artificially separated. The fibres in the human teeth run in the same direction as the canals. I could not discern the canals in their interspaces. The peripheral

layer of the dentine, immediately beneath the enamel, which was more decomposed by the acid, could only be resolved into finer fibres of a different nature, crossing each other in the most various directions, and which I presume to be the remains of the dentinal tubes.

" The dentine thus consists of interblended fibres between which run canals with proper parietes. Both the fibres and tubes in human teeth are nearly perpendicular to the pulp-cavity. What relation, then, do the fibres and the tubes bear to cells? I might incline to the old notion that the dentine is the ossified pulp. According to Purkinjé and Raschkow the pulp consists at first of granules nearly similar in size and form without vessels and nerves; then vessels and lastly nerves penetrate it. At the superficies of the pulp the granules are more regularly arranged and more elongated, and are directed outwards either vertically or at a slightly acute angle. *These longitudinally drawn out globules are plainly cylindrical cells.* In recent teeth they very distinctly contain the characteristic nucleus and its nucleolar corpuscles and closely resemble the prisms of the enamel-membrane (Tab. iii, fig. 4). The interior substance of the pulp consists of round nucleated cells, between which run the vessels and nerves. If the pulp be drawn out of the cavity of a young tooth, and the dentine be observed either recent or after the earth has been removed by acid, there remains on its inner surface, at least where it is yet thin and soft, a layer of the cylindrical cells that constitute the pulp: these are about as thick as the solid fibres of the dentine, and have the same course, and *as they cohere more firmly with the dental substance than with the pulp and remain attached to the former, so I presume that here a transition takes place*, and that the cylindrical cells of the pulp

(1) " Ich möchte mich zu der älteren Ansicht hinneigen, das die Zahnsubstanz die verknocherte Pulpa ist," loc. cit. p. 124. Compare the Literary Gazette, September 21st, 1839, p. 598, and Medical Gazette, January 3d, 1840, p p. 540, 541.

are only the earlier stage of the dentinal fibres, since these cells are filled with organized substance become solid and osseous. Sometimes these cylindricules are not found on the dentine, but then we see in their place a number of cell-nuclei; these are very pale and ultimately united with the dentine so that they may be easily overlooked. When once attentively observed, they are not easily mistaken, and are separated by extremely minute intervals. Against the opinion that the dentine is the ossified part of the pulp, the facility with which the one is separated from the other has been objected, and I allow the force of that objection. But it is at least weakened by the fact that a part of the pulp remains attached to the dentine, and that in half-ossified ribs, the cartilage can be easily detached from the ossified portion, and that in teeth the separation must be so much the easier as the difference is greater between the dentine and the pulp.

There are at least sufficient grounds for going more closely into the detail of this view. The pulp agrees with all the other tissues of the fœtus, and more especially with cartilage, inasmuch as it consists of cells; it differs in consistence from mammalian cartilage, inasmuch as whilst the quantity of cytoblasts (nucleated cells), on which the hardness of mammalian cartilage depends, is very small, the cylindrical cells, at least on the surface of the pulp, are closely aggregated together. In this respect the pulp more nearly resembles certain cartilages in the lower animals, in which the cytoblasts are present in smaller quantity and the consistence of the cartilage depends upon the thickening of the walls of the cells. Whether, in the presumed transition of the cells of the pulp into the dentinal fibres, the obliteration of the cavity is effected by the thickening of the walls of the cells, I know not, since

I have not observed this transition. If it really so happens, then the cavities of the cells so completely disappear, as to leave no trace of the cartilage-corpuscles. From the observations of Retzius it might be supposed that some of the cells retained their cavity and even were converted into radiated cells, since Retzius observed true bone corpuscles in the dentine. If, then, the superficial layer of the pulp, consisting of cylindrical cells, is converted by ossification into the dentine, then the subjacent layer of the pulp's parenchyme, consisting of round cells, must first be converted into cylinders, the vessels of this layer become obliterated, and this layer then become ossified, &c.

" What then are the dentinal tubes? Retzius compares them with the calcigerous tubes that radiate from the bone-corpuscles, and I was at first of the same opinion, and accordingly I regarded them as prolongations of the cells, the bodies of which lay in the pulp. If the pulp be drawn out of the pulp-cavity of a hog's tooth and the margin of the pulp be examined, it is seen that each of the superficial cylindrical cells is prolonged, opposite the dentine, into a short fine fibre and that these fibres correspond in diameter with the dentinal tubes projecting from the surface of the pulp. I once believed that they projected into the dentinal tubes, and that the intertubular tissue was merely the intercellular substance between these elongations of the cells. But I have given up these ideas since I observed nothing of the kind in human teeth, and since this explanation brings with it a difficulty in regard to the teeth of the pike. In these teeth, according to Retzius, there is a direct transition from dentine to bone. If one of the large teeth of the lower jaw be sawed off, the earth dissolved by muriatic acid, and fine longitudinal sections removed, the dentine is seen to form a hollow cone which is filled by bone.

The dentine is transparent and consists of fibres which proceed from the point to the base of the cone. The bone is traversed by canals, which resemble the medullary canals of ordinary bone, except in being less regular. The dentinal tubes are connected with these medullary canals of the proper osseous substance, and it is plain that the tubes are continued funnel-wise from the medullary canals. The canals ramify in the dentine and as they proceed transversely across the thickness of the tooth-cone, so they decussate the dentinal fibres. Accordingly here the dentinal tubes correspond with the medullary canals of bone not with the calcigerous tubes which radiate from the bone-corpuscles.

" A more certain knowledge of the whole structural relations of dentine seems to be only possible when its development is studied in very differently constructed teeth."(1)

The main facts, then, which may be considered as established by the researches of Purkinjé and Schwann, relative to the formation of dentine and the changes which the dentinal pulp undergoes during that process are the following: the proper tissue of the pulp consists of minute nucleated cells, with capillary vessels and nerves, invested by a dense structureless membrane(2) which disappears during the formation of the dentine. The superficial pulp-cells assume an elongated form; they correspond in diameter and direction with the tubes of the contiguous cap of dentine. These or similar cells are observed, in a state of transition into dentine, in the interspace between the pulp and the previously formed cap of dentine; they adhere to the latter when it is displaced from the pulp.

(1) Schwann, loc. cit. p. 128.

(2) The capsule of the entire dental matrix will be understood to be quite a distinct part from the 'preformative membrane' of the pulp.

The chief points that remain to be determined are the relation of the dentinal pulp to the transitional cells between it and the dentine; the nature of the transition, and the relation of the cells to the dentinal tubes and the intertubular tissue. From the expression used by Purkinjé and Raschkow in the passage already quoted;—"After a stratum of dental fibres has been deposited between the parenchyme of the pulp and the preformative membrane the same process is continued from the external to the internal region, the pulp supplying the material;"—it may be inferred that they considered the formation of the dentine to be a process of deposition from the formative surface of the pulp, like a secretion from a gland. If such were not the idea of these authors of the relation of the formative pulp to the dentine they nowhere clearly express the contrary opinion, and the formation of the dentine by its deposition in successive strata from the pulp continued to be taught in the best works on physiology subsequently published.(1)

(1) Müller's Physiology, by Baly, part i, 2nd ed. p. 429.

Mr. Bell who appears to have clearly recognized, long before the publication of the Thesis of Raschkow, the 'preformative' or external membrane of the pulp, supposed that it was persistent, and that it was the true formative organ of the dentine. (See Anatomy, Physiology and Diseases of the Teeth, 8vo. 1829). In his valuable edition of Hunter's Natural History of the Human Teeth, in reference to Hunter's statement that the teeth are formed from the pulp, Mr. Bell observes: "The statement that the bone of a tooth is produced from the pulp is erroneous. This substance constitutes only the mould upon which the ossification is formed, between which and the pulp is placed a membrane of extreme tenuity, which I have termed the proper membrane of the pulp. It is slightly attached to the surface of the pulp, which it completely covers, and it is from the outer surface of this membrane that the bone is secreted. As the pulp recedes on the deposit of the successive laminæ of bone, the ossific membrane continues to cover it, and ultimately forms the well-known membrane lining the internal cavity of the perfect tooth." —Bell's 'Hunter on the Teeth,' 8vo. 1835, p. 38.

Dr. Schwann was the first to express his leaning to the ancient doctrine that ' the dentine is the ossified pulp.' But the nature of the subjects selected by him for his observations left him in a state of doubt and indecision on this point: and the author by whom Dr. Schwann's observations were communicated to the British Association in August, 1839, although he adopted the doctrine of the formation of ivory by the ossific transition of cells, rejected the idea that the dental substance was the ossified pulp, and declared ' the cells of the ivory to be altogether a distinct formation.'(1)

In fact, the subjects chosen by both Dr. Schwann and his contradictor, for the examination of the development of the dentine, were inadequate to the exhibition of the relations of that substance to the formative pulp during any part of the process of its formation. The shape of the teeth of the mammalia selected by them for examination will not yield a view of the cap of new-formed ivory and the subjacent pulp, in undisturbed connection, by transmitted light with the requisite magnifying power; and, if placed under the microscope as an opake object, the light is reflected from the cap of ivory, and displays only the characters of its surface and not its relations to the surface of the pulp in contact with it. To examine this surface microscopically in either a human tooth or that of any of our domestic quadrupeds the cap of dentine must be removed, and the exposed surface of the pulp and the corresponding surface of the dentine be examined as opake objects by reflected light. Or, if the layer of the dentine be thin enough to allow the transmission of sufficient light, it must be removed from the subjacent pulp before it can be so examined.

(1) Report of the Papers read at the Medical Section of the British Association at Birmingham, Literary Gazette, Sept. 21, 1839, p. 598.

It is, therefore, obvious that any inference as to the structure of the pulp's surface, or the nature of its previous connection with the transitional cells and the superincumbent layer of dentine, which may be founded on appearances observed under the circumstances above mentioned, is liable to the objection that the natural relations of the parts observed have been destroyed. If the dentine be the ossified pulp, as Dr. Schwann was disposed to believe, then the calcified part of the growing tooth has been violently displaced from the uncalcified part, and the part of the pulp which thus presents itself for examination is a lacerated and not a natural surface.

But to the observer who regarded the dentine as a secretion from the pulp's surface, every modification which he might detect on that surface after the displacement of the dentine, would appear natural, and be perhaps described as such with the view to the elucidation of the secreting process. Thus the cells which might be observed in progress of ossific transition into dentine would appear as independent parts, and the products of a secreting property; their detached condition being, all the while, a necessary result of the artificial displacement of the new-formed cap of ivory, and the consequent laceration of the pulp's substance.

In the terms of the 'excretion theory' the exposed surface of the pulp over which the cells lie scattered is a 'formative surfaces; the nucleated cells are naturally 'detached,' and the ivory or dentine resulting from their calcification and metamorphosis, is, in respect to the pulp, 'altogether a distinct formation, and by no means an ossification of the pulp.'

Such is the interpretation which an advocate of the excretion-theory has given to the true phenomena of dental development first observed and described by Purkinjé, Raschkow and Schwann.

Observations on the pulp, in its various stages of conversion into dentine, whilst in undisturbed connection with the calcified portion, in the thin, transparent, lamelliform teeth of a fetal Shark (*Carcharias*), first yielded me unequivocal demonstration of the organic continuity of the cap of dentine with the supporting vascular pulp; they also indicated some stages of the progress of the conversion of the pulp into dentine, and produced that clear idea of the nature and relations of dental development, which is expressed in the 'Theory of dentification by centripetal calcification of the pulp's substance,' submitted to the French Academy in December, 1839.(1)

The following are the progressive steps of the calcifying processes, according to my microscopic researches on the formation of the different substances which compose the more complex teeth of Reptiles and Mammals, pursued in various species of both classes, but chiefly in the higher organized domestic animals.

Three formative organs are developed, as already described, for the three principal or normal dental tissues. The dentinal pulp (Pl. 122 *a*, figs. 5, 6, 7 & 8, *d*), or pulp proper, for the dentine; the 'capsule' (ib. *c*) for the cement, and the 'enamel-pulp' (ib. *e*) for the enamel. The essential fundamental structure of each formative organ is cellular; but the cells differ in each organ, and derive their specific characters from the properties and metamorphoses of their nucleus, upon which the specific microscopical characters of the resulting calcified substances depend.

(1) The general results only of this communication were given in the 'Comptes Rendus,' 1839, p. 784. The Commission appointed by the French Academy to report on a subsequent Memoir on the same subject advert to some of the phenomena previously communicated by me. "Quant aux préparations qui montrent l'aréolité de la pulpe, non seulement nous les avons reproduites avec succès, mais de plus nous avons constaté, à l'état frais, la granulation des aréoles signalée par M. Richard Owen," loc. cit. 1842, p. 1063.

In the cells of the dentinal pulp the nucleus fills the parent cell with a progeny of nucleoli before the work of calcification begins: in the enamel-pulp the nucleus of the cell disappears, like the cytoblast of the embryo plant in the formation of most vegetable tissues: in the cells of the capsule, the nucleus neither perishes nor propagates, but retains its individuality, and gives origin to the most characteristic feature of the cement, viz:—the radiated cell.

The primordial material of each constituent of the tooth-matrix is derived from the blood, and special arrangements of the blood-vessels pre-exist to the development and growth of the constituent substances. A pencil of capillaries is directed to a particular spot in the primitive dentiparous groove, and terminates there by a looped net-work, from which spot a group of nucleated cells begins to arise in the form of a papilla. The cells of the papilla are, however, colourless, and the plexus of capillaries is confined to its base. In the Mammalia (embryo Calf of three inches in length) membranous septa are formed, into which the vessels extend, which cross the groove and inclose the papilla in a follicle. From the free margin of this follicle the processes are developed, which indicate the configuration of the future crown of the tooth, and, in the molars of the calf, subsequently develope the re-entering folds on which the complex structure of the crown of the molar tooth depends.

The primary dentinal papilla and its capsule rapidly increase by successive additions of nucleated cells, apparently derived from material supplied by the capillary plexus at the base; the capillaries now begin to penetrate the substance of the pulp itself, where they present a sub-parallel or slightly diverging penicillate arrangement, but preserve their looped and reticulate termination near the apex

of the pulp. Fine branches of nerves accompany the capillaries and terminate also in loops.

The primary cells of the papilliform pulp, the "grana æqualia globosa" of Purkinje, are described by him as pre-existing to the appearance of vessels and nerves in the pulp; they are undoubtedly unaccompanied by the blood-vessels at their first aggregation to form the papilla; but they bear the same relation to the capillary net-work at the base of the papilla, which the subsequently formed cells do to the capillaries that extend into the substance of the papilla or pulp, when it is more developed. The primary cells and the capillary vessels and nerves are imbedded in, and supported by a homogeneous, minutely sub-granular, mucilaginous substance, the 'blastema.' The cells (Pl. 1, fig. 1, *a*) which are smallest at the base of the pulp, and have large, simple, subgranular nuclei (ib. *a'*), soon fall into linear series directed towards the periphery of the pulp: where the cells are in close proximity with that periphery, they become more closely aggregated, increase in size, and present the following changes in their interior. A pellucid point appears in the centre of the nucleus which increases in size and becomes more opake around that central point, rendering the compressorium requisite for its demonstration. A division of the nucleus in the course of its long axis is next observed (ib. *b*). In the larger and more elongated cells, still nearer the periphery of the pulp, a subdivision of the nuclei has taken place, and the subdivisions become elongated with their long axes vertical or nearly so to the plane of the pulp, and to the field of calcification (ib. *c*). The subdivided and elongated nuclei become attached by their extremities to the corresponding nuclei of the cells in advance; and the attached extremities become confluent (ib. *d*). Whilst these changes

are proceeding, the calcareous salts of the surrounding plasma begin to be accumulated in the interior of the cells, and to be aggregated in a semi-transparent state around the central granular part of the elongated nuclei, which now present the character of secondary cells, and the salts occupy, in a still clearer and more compact state, the interspaces of such cells (ib *e*) : the elongated granular matter of the terminally confluent secondary cells establishes the area of the tubes, by resisting, as it would seem, the encroachment of the calcareous salts ; the nuclear tracts (ib. *f*.) receiving a smaller proportion of the salts, in the condition of minute disgregated particles, which are usually arranged in a linear series of nodules, and contribute to cause the white colour of the moniliform area, of the tube when viewed by reflected light, and its opacity when viewed by transmitted light. Thus the primitive existence of the granular nuclei, their multiplication in the primary or parent cell, their elongated form, their serial arrangement end to end, and terminal confluence, are indicated in the calcified pulp by the areæ of the dentinal tubes (fig. 2, *c*) ; the interspaces of the metamorphosed nuclei being occupied by calcareous salts in a clearer and more compact state, with evidence, however, of a distinctness of the nucleolar membrane or secondary cell (fig. 2, *b*) from the cavity of the common containing cell, which sustains the interpretation of the proper parietes of the dentinal tube. The indications of the primitive boundary or proper parietes of the parent-cell (fig. 2, *a*) are in like manner more or less distinctly retained, through a modification of the arrangement of the calcareous salts in the boundaries and in the interspaces of the cells. The salts are sometimes blended with the blastema in these interspaces in a disgregated condition which renders them almost as opake as the areæ of the tubes. When a layer of the calcified cells is carefully detached, the exposed

uncalcified surface of the pulp (fig. 3, *b*) presents the appearance of a net-work, the meshes being formed by the exposed cells, and the intervening very thin layer of blastema. Each mesh, however, which gives a transparent or bright contour to the cell, when viewed by transmitted light, instead of presenting a single stellate nucleus, shows by well directed light under a higher power, several points, each of which is the centre of one of the meshes of a finer network: these points are the ends of the granular elongated nuclei,(1) which have been torn from the cavities of the dentinal tubes in the displaced cap of dentine. A piece of the thin transparent margin of the cap of a growing tooth, which may be cut off with a pair of fine scissors, easily affords the means of demonstrating the corresponding structure in that calcified part of the pulp. A slight change of focus is required to bring the ends of the tubuli in view, from that in which the clear outline of the dentinal cell is best seen.

In proportion as the progress of calcification approximates the cells, and as these have undergone the changes in their nucleolar contents, preparatory to the proper arrangement of the hardening salts within, the proportion of the basal substance in the interspaces of the cells to the enlarged cells themselves decreases, and the cells become more readily detached and seemingly independent, when torn out in the displacement of the cap of dentine. Although they are less adherent laterally to the basal substance of the pulp, they are more coherent with the cells of the same linear series: the tubes of the calcified cell accepting or effecting an union with the peripheral ends of the elongated granular nuclei or nucleolar cavities

(1) The term 'granulation des aréoles,' used by the French Academicians in referring to my observations in support of the theory of centripetal calcification of the pulp, expresses the appearance produced by the nuclei, which are converted into the dentinal tubes, as seen in the area of their parent dentinal cell.

of the contiguous cell in the next central layer; the angles at which the elongated nuclei or successive portions of the dentinal tubuli thus unite constitute the secondary gyrations or curves of those cells. The primary curves depend upon the arrangement of the primary linear series of the parent-cells.

The original contour of these cells is most discernible after calcification in the teeth of the Mammalian class, and here with different degrees of distinctness in different species. They are the true dentinal cells, and must not be confounded with the so called 'intertubular or interfibrous cells', the first notice of which is due to Retzius.(1) The diameter of the dentinal or calcified

(1) The able Translator of "Müller's Physiology," Part I, 2nd. Edit., p. 431, gives the fact that the substance between the tubuli of the ivory is composed of distinct cells, some of which contain smaller cells, on the authority of a "Report of the Meeting of the British Association," Athenæum, No. 620, 1839. Retzius ("Mikroskopiska undersökningar öfver Tändernes, särdeles Tandbenets, struktur," 8vo. 1837, passim) describes the intertubular cells in the dentine of several of the animal's teeth which he examined. In the molar of the Hog, for example, he says: "short branches proceed from the sides of the main tubes throughout their whole extent, some of which terminate in dilated ends, like cells;" and a little further on: "only a few opake cellules" (kalk celler) "were visible in the interspaces of the tubes," (pp. 33 & 34.) In the molar of a Rhinoceros, Retzius saw many of the lateral branches of the dentinal tubes terminating in large cells:—"These cells," he says, "were thinly arranged in the intertubular spaces," (af hvilka många tydligen syntes sluta sig i stora kalk celler; dessa lägo glest kring spridda i stamrörens mellanrum) p. 32. M. Serres in his Report on certain Microscopic preparations, submitted by Mr. Nasmyth to the French Academy, in proof of his discovery of the intertubular cells, says of four sections from the teeth of the Megalichthys, Lamna, Cachalot, and Elk:—"Sur ces préparations et sous un grossissement de deux à quatre cents diamètres on distingue entre les fibres dont l'ivoire se compose, des aréoles nombreuses à parois distinctes." He verifies this as the "fait capital du travail de M. Nasmyth," and gives it the character of novelty by contrasting it with an alleged opinion of Retzius, whom M. Serres affirms to have regarded the intertubular tissue (*tissue interfibreux*) as amorphous! ('Compte Rendu de Séance de l'Académie des Sciences,' 5 Décembre, 1842, p. 1055.) On what authority M. Serres cites me (loc. cit. pp. 1056 & 1057) as contending for the priority of the discovery of the intertubular, or interfibrous cells, I know not: he does not

primary cells of the pulp is usually one fourth or one half larger, than that of the blood-disc of the species manifesting them. These cells are figured, in the present Work, in the molar of the Mylodon (Pl. 79), in the incisive tusk of the Dugong (Pl. 95), in the premolar (Pl. 113) and the canine (Pl. 113 *a*) of the Pteropus, in the incisor of the Chimpanzee (Pl. 119 *a*), and of the Human Subject (Pl. 123), and in the molar of a Rhinoceros Pl. 139. In the calcification of the dentinal pulp the thin transparent membrane which covers the free surface, or that in contact with the enamel-pulp, is the first to receive or become impregnated with the hardening salts; and hence has been called the 'preformative membrane.' But at this early stage the calcifying membrane yields to the pressure of the ends of the prismatic cells of the enamel pulp, which are, likewise, beginning to take from the surrounding plasma the hardening salts and impact them in their interior. Thus are formed the pits upon the outer surface of the coronal dentine of enamel-covered teeth, by which the enamel gains a firmer mechanical connection with the dentine. As the process of calcification of the multi-nucleated cells of the dentinal pulp extends in its centripetal course, the pulp, in most teeth, progres-

refer to any publication of mine from which he derived the idea. I describe the intertubular cells in many of the subjects of my "Memoir" in the 'Transactions of the British Association,' 1838. In *Ptychodus*, for example: "The interspaces of the canals are also occupied by the same minute anastomosing reticulate tube-work. Numerous minute calcigerous cells are also present in the interspaces," p. 140. But instead of putting forth this as a discovery, and misrepresenting Retzius as describing those interspaces to be amorphous, I premise by citing Retzius's discovery "of the cells in the clear interspaces of the tubes," p. 136. The true dentinal cells, a figure of which in the tooth of the Mylodon was published in the 2nd Part of this Work, Pl. 79, in 1840, are very different from the intertubular cells on which M. Serres reports. In most animals they include many tubes and intertubular spaces, and it is much more exact to say that those cells include a tubular structure, than that the intertubular space is cellular.

sively decreases in size, fewer nuclei are developed in the cells, and these do not acquire so large a size. The diminution in both respects proceeds, however, unequally, in the cells of the same stratum. Here and there the linear tract formed by the nuclear matter in a part of a smaller calcifying cell, containing fewer nuclei, may be observed to unite with the converging extremities of two residuary tracts (areæ of dentinal tubes) of a calcified cell in advance (Pl. I. fig. 1, *g*). It is thus that the bifurcation of the tubes is produced, and a repetition of this confluence, which becomes more frequent as the calcifying process approximates the centre and base of the pulp, gives rise to the dichotomous divisions of the main tubes. In some of the cells at and near the central and basal part of the pulp, the nucleus has undergone no division, but has become merely elongated and sometimes angular or radiated. In others it has disappeared; such cells occur not unfrequently close to the field of calcification, when the process has made much advance in its centripetal course. The altered mode of action or change in the nuclei of the smaller central cells of the pulp is the first and essential step in the modification of the dentinal tissue which produces the substances which I have termed osteo-dentine and vaso-dentine. In the former many of the cells retain their nucleus undivided, and the hardening salts are impacted around it in the interior of the cell, but enter only partially into the granular substance of the nucleus, in the minutely disgregated form, which produces the opacity and whiteness of the resulting corpuscle. In the formation of vaso-dentine many of the cells lose their nucleus which seems to have become dissolved. In both the latter modifications of dental tissue the blood vessels remain, and establish the wide tubular tracts in the calcified substance to which the name of 'vascular canals' is given. In true, hard, or unvascular

dentine no trace of the blood vessels remains; all has been converted into a much more minute calcified tubular tissue by the assimilative or intus-susceptive properties of cells, and by the modification of their nucleolar contents.(1)

(1) That the dentine is the ossified pulp is, as Dr. Schwann observes, an old opinion; but an opinion is not a theory. Almost every true theory has been indicated, with various degrees of approximation, before its final establishment; but he has ever been held, in exact philosophy, to be the discoverer of a theory, by whom it has been first clearly enunciated and satisfactorily proved. Thus established, on the basis of careful and sound induction, it is sooner or later received to the exclusion of the, till then, prevalent and generally accepted erroneous doctrine, at which period the truth of the antecedent hints and indications of the true theory begins to be perceived, and it is not uncommon to find their value exaggerated in quotations by the emphasis of type Thus the remark of Blake:—"As the bone of the tooth increases in thickness, the pulp is proportionally diminished: and seems as it were converted into bone," (Essay, 8vo. 1801, p. 7) is quoted in the article "Zoology," 'Encyclop. Metropolit.,' vol. VII, p. 232, with "*converted into bone*" in italics. So also Mr. Conybeare's observation that the interior cavity of the teeth of the Ichthyosaurus was obliterated "by the ossification of the pulpy nucleus"; and that "the ossified pulp has become a spongy mass of reticulated bony fibres," (Geological Transactions, Second Series, vol. I, 1824, p. 107) might be cited in italics, as the older hypothesis of Rau (De ortu et regeneratione dentium) has been, in depreciation of the value or necessity of researches establishing the true relation of dentification to ossification. But the actual value and bearing of such casual expressions would have been more fairly and truly set forth, if, when the theory of the formation of dentine by successively excreted layers, as promulgated by Hunter and Cuvier, universally prevailed in the systems of Physiology, that theory had been formally combatted on the strength of such facts and observations in the development of dentine, which it could be shown that Raw, Blake, Conybeare, and others, had advanced in support of their expressions of the seeming, or actual conversion of the pulp into bone.

Such expressions are, however devoid of scientific value, in regard to the question of development on which they are quoted to bear, precisely because they are unsupported by the observations requisite to prove what they affirm, and they have, therefore, been deservedly neglected by the best authorities in Physiology, who have treated *ex professo* on the development of teeth, prior to 1839.

In the edition of the English translation of "Müller's Physiology" of 1837, many facts are cited from Blake's excellent Treatise, but not his idea of the seeming conversion of the pulp into bone. The Translator, indeed, adds to the text the microscopic observations of

But the vascularity of the dentinal pulp, and, especially, the rich network of looped capillaries that adorns the formative peripheral layer at the period of its functional activity, have attracted

Purkinje on the texture of dentine, which show that, if the pulp was converted at all, it must be into a very different tissue from bone, and consequently by a different process from ossification.

The nature of the process not having been discovered at that period, the formation of dentine is described to be "by the secretion of layers of dental substance," and the shell of osseous substance so formed, is said to have "no organic connection with the matrix; it is formed by the deposition of the mineral components of the tooth mixed with some animal matter, and may be lifted off its matrix," (pp. 391 & 392).

So also Prof. de Blainville, in the fasciculus of his great work "Ostéographie d'Animaux Vertèbres," submitted by him to the French Academy, on the same day on which I communicated to that learned body, my "Theory of the development of dentine by centripetal calcification of the pulp," (December 16, 1839. See the 'Compte Rendu' of the Séance of that day), says: "Pour bien comprendre la forme générale d'un phanéros," (by this name the Professor designates the class of organs called 'teeth') il faut savoir que c'est une partie morte et produite, exhalée à la surface d'un bulbe producteur ou phanère, en continuité organique avec le corps animal; et implantée plus ou moins profondément dans le derme et même dans les tissus sous-jacents; et que, par conséquent, la forme du bulbe producteur détermine rigoureusement celle du produit on du phanéros. Or, par la production seule des couches de celui-ci appliquées successivement, en dedans les unes des autres, sur le bulbe producteur seul vivant, seul lié par le système vasculaire et par le système nerveux au reste de l'organisme, ce bulbe diminue de volume en même temps que de puissance productrice; en sorte qu'il arrive un moment où les cônes composants, ayant cessé de s'accroître en diamètre avec le bulbe lui-même, commencent à diminuer avec lui."—*Fascicule Premier, Primates*, p. 15.

These formal expressions of well weighed ideas of the nature and formation of teeth, set forth by the celebrated Professors of Berlin and Paris, afford the true indications of the state and the needs of that branch of physiology at the close of the year 1839. By only one writer had the casual expression by Dr. Schwann, in his general Treatise on the Correspondance between Animals and Plants in their structure and development, of his leaning towards the old and exploded opinion, that the dental substance is the ossified pulp, been cited prior to that date, in reference to the question of dental development. It occurs in the full Report of the communications by Mr. Nasmyth to the 'British Association' at Birmingham, in August, 1839, in the 'Literary Gazette' of September 21st, 1839; and, as these 'Communications' betray a full knowledge of all that Schwann had published relative to the development of

general notice, and have been described by Hunter and subsequent authors on Dental Development. By most this phenomenon has been regarded as evidence of the secreting function of the surface of the pulp, and the dentine as an out-pouring from that vascular

teeth, the conclusion to which Mr. Nasmyth had then arrived as to the 'formation of ivory by ossification of the pulp,' may afford some indication of the value of Schwann's facts, and the cogency of his observations in establishing that theory. It is true that Mr. Nasmyth has formally denied, in his subsequent Communication to the French Academy, (Comptes Rendus, Octobre, 1842, p. 680), that he had any knowledge of Schwann's Treatise when he read his Memoirs to the Meeting at Birmingham. Any one who may care to see to what extent deliberate plagiarism from an original Author may be impudently attempted to be foisted on the scientific public, as a record and evidence of original research, may compare the 'Report' cited, with the observations, which occupy the whole of page 125 and part of the preceding and succeeding pages of Schwann's "Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen, 8vo. 1839." The unacknowledged abstract fills more than a column of the 598th page of the Literary Gazette (Sept. 21). From the passage beginning with "According to Purkinje," and ending with "and of the dental bone," the report of Mr. Nasmyth's Memoir, excepting that where Schwann asserts "Mr. Nasmyth observes," and that where Schwann believes "Mr. Nasmyth presumed," is a coarsely literal translation of the German Author.

Some of the borrowed paragraphs might have excited a doubt, if rightly understood by Mr. N., of the truth of the idea at that time maintained by him, of the formation of dentine "by the calcification of detached cells on the formative surface of the pulp," or "of the deposition of the ivory by thin ossific layers on the surface of the pulp." As, for example:—

Schwann, l. c. p. 125.

"Diese in die Länge gezogenen kugelchen sind nun offenbar cylindrische Zellen."

"Da sie auf der anderer Seite doch mit der Zahnsubstanz fester zusammenhängen als mit der Pulpa, und an der ersteren hängen bleiben *so vermuthe ich*, das hier ein Uebergang statt findet."

Literary Gazette, l. c. p. 598.

"These longitudinally drawn out globules, *Mr. Nasmyth observed*, are plainly cylindrical cells"—*Also Medical Gazette*, Jan. 3rd, 1840, p. 540.

"As they cohere more firmly with the dental substance than with the pulp, and remain attached to the former, *Mr. Nasmyth presumed* that here a transition takes place."—*Literary Gazette*, l. c. p. 598, and *Medical Gazette*. l. c. p. 541.

surface, which was supposed to shrink or withdraw from the matter excreted. For, it has been asked, 'If the unvascular dentine be the effect of conversion of the vascular pulp, by what process is

Then again, when Schwann admits the validity of an objection to the theory of the ossification of the pulp, which I have proved to have no real weight, Mr Nasmyth likewise, admits its force in the words of his Author:—

Schwann, l. c. p. 126.

"Gegen die ansicht, dass die Zahnsubstanz der verknöcherte Theil der Pulpa ist, hat man die leichte Trennbarkeit beider von einander eingeworfen, und ich erkenne das Gewicht dieses Einwurfs wohl an."

Literary Gazette, l. c. p. 598.

"Against the theory that the dental substance is the ossified portion of the pulp, the facility with which the one is separated from the other has been adduced; and he (Mr. N.) allowed the force of that objection."

But the influence of the old doctrine of the discontinuity of the pulp with the calcified layers of the ivory, was then dominant in the mind of the plagiarist of Schwann: he says in the original part of the Report:—"Schwann regards the dental substance as the ossified pulp, whilst Mr. N.'s observations lead him to conclude that the cells of the ivory are altogether a distinct formation."—*Literary Gazette*, p. 598. Mr. N, in fact, exaggerated at Birmingham every statement of Schwann which led towards the doctrine of ossification of the pulp in order that he might refute him. Thus, according to the 'Literary Gazette,' he makes Schwann "regard the dental pulp as a simple cartilage;" he drags the dubious expression of his inclination towards the ancient doctrine of the tooth being the ossified pulp, from a remote part of Schwann's treatise, converts it into a positive affirmation, and places it in juxta-position with the statement of Schwann's ideas of the relation between the dental pulp and cartilage, in order to formally contradict the conclusions of the original German observer, who, Mr. Nasmyth says: "starts with a ready-made hypothesis, and founds his opinion rather on the observations of others, and on the inferences he draws from them, than on his own actual research."—*Literary Gazette*, loc. cit. p. 598.

Thus, whatever influence the observations of Dr. Schwann might have had in drawing Physiologists back towards the old doctrine expressed by Raw and Blake, must have been greatly deteriorated by those who might place any confidence in the labours of Mr. Nasmyth, on which his communication to the British Association, in August 1839 was based. The right interpretation of Schwann's observations, required, in fact, a new series of researches, and that interpretation only became obvious to Mr. Nasmyth, after the publication of my "New Theory of Dental Development," in the 'Compte Rendu' of December, 1839.

all trace of the vascular ramifications obliterated, since none can be detected in such dentine?' The same question is equally applicable to the nerves of the pulp. In the explanation of this

New Reports of the 'Communication to the British Association,' in August, 1839, were then inserted in the Medical Gazette and Lancet for 1840, with various modifications, to make the Birmingham Memoir of August, 1839, accord with the 'New Theory' of December, 1839. These interpolations may be judged of by the following paragraphs touching the ossification of the pulp :—

"Schwann regards the dental substance as the ossified pulp, whilst Mr. N.'s observations lead him to conclude that the cells of the ivory are altogether a distinct formation." —*Literary Gazette*, September, 1840, p. 598.

"He concluded, therefore, *that the ivory is neither more nor less than the ossified pulp, and that it can in nowise be considered as an unorganized body.*" —*Lancet*, June, 1840.

"L'ivoire n'est donc pour moi qu'une portion de la pulpe ossifiée."

Comptes Rendus de l'Académie des Sciences, Octobre 2. 1842, *p.* 680 :—

and by many others which I pointed out in an exposure of Mr. Nasmyth's attempt to appropriate to himself my discovery of the true 'Theory of Dental Development.'

When the inconsistencies between the reports of Mr. Nasmyth's Papers read before the British Association at Birmingham, in August 1839, as published in the Literary Gazette and Athenæum of September, 1839, and the Reports of the same Papers communicated by Mr. N. to the Lancet and Medical Gazette of June, 1840, were demonstrated : Mr. Nasmyth replied :— "My answer to this is, that I did *not* furnish the Report to the Literary Gazette, and that the notice of my Papers which I sent to the Athenæum, was so abbreviated and cut to pieces that I cannot be responsible for it."—Medical Gazette, June 26th, 1840, p. 545. If this assertion is to be credited, the Report in the Literary Gazette must be regarded, however marvellous the fact, as the work of a *bonâ fide* Reporter taking down the communication of an English *soi-disant* discoverer, and publishing it in the form of a literal translation of a German Work : or, that the Reporter mistook a quotation by Mr. Nasmyth from Dr. Schwann's work for the terms in which Mr. N. was narrating his own observations.

But Mr. Nasmyth, in his Communication to the "Académie des Sciences," Oct. 3, 1842, in reference to Schwann's work, from which a literal translation of the observations on the Teeth is given in the Literary Gazette of Sept. 1831, as a Report of part of Mr. N's Paper read in the preceding month at Birmingham, states :—"Son ouvrage ayant été publié à l'époque

process attention must first be paid to the almost straight and sub-parallel course of the vessels in the pulp's substance, and to the remarkable regularity of form and size of the meshes of the

où j'adressai mes premières communications au Congrès de Birmingham, *je n'avais pu en avoir connaissance.*"—Comptes Rendus, Octobre, 1842, p. 680.

In the 'Addendum to the Report of the Transactions of the Sections in 1839,' published in the 'Report of the Eleventh Meeting of the British Association,' 1842; the Council of the Association adduce the following testimony of the Editors of the Literary Gazette and Athenæum :—

"Notices of Mr. Nasmyth's papers appeared in the Athenæum and Literary Gazette of the period: those journals usually obtain such notices either from authors themselves or from reporters of their own: in the present case the Council have been informed by the respective Editors, that the report in the Athenæum of the two papers read to the Medical Section was supplied, and the proofs corrected, by Mr. Nasmyth himself, and the notice of the geological paper by the reporter of the Athenæum; and that the report in the Literary Gazette was drawn up by the reporter of that journal, from a rough manuscript furnished to him by Mr. Nasmyth."

Upon these 'Reports,' furnished and corrected by Mr. Nasmyth, the following opinion has been published :—

"Reference having been made to us by a Council of the British Association for our opinion whether the report of Mr. Nasmyth's paper, as published in the Literary Gazette and Athenæum, or in either of those two periodicals, or the report of that paper sent by Mr. Nasmyth to Mr. Phillips for publication in the Report of the Ninth Meeting of the Association, held at Birmingham, is more correct with regard to the points under discussion between Professor Owen and Mr. Nasmyth, we have carefully examined these several documents, and it appears to us that the main point under discussion between these two gentlemen is, whether the account of the process of dentition, contained in Mr. Nasmyth's paper, did or did not comprise the theory that the ivory of the teeth is formed by the ossification of the pulp. We find, with reference to this question, that in the accounts of Mr. Nasmyth's paper, given in the Literary Gazette and Athenæum, his opinions on that subject are involved in considerable ambiguity; for, while some passages in them would imply that he considered the proper substance of the teeth as being formed by the addition of ossific matter in the original structure of the pulp, commencing and proceeding on its surface, these reports contain, at the same time, other passages, in which the theory of the ossification of the pulp is distinctly and

terminal reticulation on the surface of the pulp. At the part where calcification has commenced, I have commonly found the extremities of the capillaries in a state of congestion and crowded

expressly disclaimed by Mr. Nasmyth; whereas in the abstract of his paper, drawn up by himself, with a view to publication in the Report of the Association, this theory is very explicitly and unequivocally maintained. Whether this theory was distinctly advanced in the original paper read to the Medical Section at Birmingham, it is not in our power to determine, because that paper is not before us, and because we have no other evidence of the nature of its contents than the printed documents already referred to.

(Signed) JAMES MACARTNEY,

One of the Vice-Presidents of the Medical Section at the Birmingham Meeting.

P. M. ROGET,

One of the Vice-Presidents of the Medical Section at the Birmingham Meeting.

G. O. REES,

One of the Secretaries of the Medical Section at the Meeting at Birmingham.

November 16th, 1840.

It will be found by comparing the Reports in the Literary Gazette and Athenæum with Schwann's Treatise above cited, that the passages which imply that the proper substance of the teeth is formed by addition of ossific matter in the original structure of the pulp, are verbal translations, taken, without acknowledgement, from that Treatise, which is only referred to with a view of contradicting a conclusion to which Schwann inclines, without proving either satisfactorily to himself or to others.

Whatever testimony Mr. Nasmyth may procure as to his private views on dental development in 1839, it is incredible that he should have discovered, in the proper sense of the word, that "the ivory is neither more nor less than the ossified pulp," and yet omit to state this discovery in the Reports which, the Editors of the Athenæum and Literary Gazette affirm that he himself furnished, and, in one Journal, corrected the proofs.

Mr. Nasmyth made another attempt to establish his date of priority ; the nature of which will be understood by the following extract from the "Adendum," p. 11, 'Report of British Association,' 1842 :—

with blood-discs, which were pressed together into polyhedrons, and apparently stagnated and left out of the current of circulation.

These aggregated blood-discs exhibited, in various and often

"The Council have since thought proper to request the Committee, to whom they have added the President (*a*) and Vice Presidents (*b*) of the Geological Section of the Association at Birmingham, to inquire into the authority supposed to be given to Mr. Nasmyth's abstract by a printed document, in the shape of a printer's revise, purporting to be the report, by the Editorial Secretary, Dr. Lloyd, of another paper of Mr. Nasmyth's read to the Geological Section, at the same meeting of the Association, which revise, he alleges, contains the following passage, viz., '*the ivory is neither more nor less than the ossified pulp,*' and on which he founds an argument that an affirmation to that effect had been distinctly made by himself in that paper.

"The present Committee, to whom this question has been specially referred, have procured, through the kindness of Colonel Sabine, one of the General Secretaries, a certified copy (*c*) of the original manuscript report referred to by Mr. Nasmyth, and which it appears was drawn up immediately after the paper had been received, by Dr. Lloyd, one of the Secretaries of the Geological Section. It is as follows:"

"(It is the subjoined document marked B.)"

"On comparing this manuscript copy with the printed revise, as quoted by Mr. Nasmyth at p. 3 of his printed letter to the Council, it appears that several alterations have been made in the original in its progress to that stage of revision in which Mr. Nasmyth now produces it; and in particular, that the expression quoted by him in italics, as especially corroborating the fidelity of his abstract, *is not contained in it.*"

This needs no comment: it is here cited along with Mr. Nasmyth's assertion to the French Institute, that Schwann's Treatise was unknown to him when he read his Memoir at Birmingham, and with the statements which he hazarded in print, that he did not furnish the Report to the Literary Gazette, and that the Report in the Athenæum had been so mutilated that he could not be responsible for it, in order to show the value of that person's subsequent assertions on other points relating to the present work.(*d*)

(*a*) Dr. Buckland. (*b*) Leonard Horner, Esq., Charles Lyell, Esq.

(*c*) "A copy, certified by Dr. Lloyd, of the rough copy preserved by himself of the original manuscript."

(*d*) For the refutation of these assertions see Medical Gazette, July, 1840.

in striking degrees, those changes of the contained matter to which I have elsewhere suggested that their own multiplication might be due. In the present situation and condition it is obvious that such changes must be preparatory, either to their disappearance and removal, or to some important share which they are destined to take in the development of the dental tissue. The stagnant corpuscles nearest the vascular and unchanged pulp presented the irregularity of contour, which has given rise to the term 'mulberry,' or 'granulated' applied to such altered blood-discs, when seen in other circumstances. These corpuscles in other respects, as colour, size, and general form, retained their usual character. The blood-discs nearer the cap of dentine exhibited more plainly the contained granules, to the commencing development of which the irregular contour above-mentioned is due: this appearance was associated with an increase of size, a change from the circular to the elliptical form, and a gradual loss of the characteristic colour, which was longest retained by the central granular matter. The tunics of the capillary vessel containing the above aggregated and altered blood-discs become gradually attenuated, and disappear, as if dissolved, before reaching the field of conversion. I once inclined to the belief that these modified blood-discs afforded fresh cell-material to supply the space left by the retreat of the circulating currents.

The open mouths of the central last-formed ends of the calcified dentinal tubes are always ready to receive the plasma transuded from the capillaries remaining in the uncalcified part of the pulp or in those tracts of it which constitute the vascular canals.

The enamel pulp differs from the dentinal pulp at its first formation by the more fluid state of its blastema and by the fewer and more minute cells which it contains. (Pl. 1, fig. 4, *h*.) The

source of this fluid blastema (ib. *g*) appears to be the free inner vascular surface of the capsule. As it approaches the dentinal pulp the blastema acquires more consistence by an increased number of its granules, and it contains more numerous and larger cells; many of these show a nuclear spot (ib. *h'*): others a nucleus and nucleolus: the spherical nucleolar cells in the part of the blastema further from the capsule are so numerous as to form an aggregate mass, with a small quantity of the condensed blastema in the minute interspaces left between the cells, which are pressed together into hexagonal or polygonal forms, (ib. fig. 2, *i*). In this state they constitute a great part of the enamel pulp, which is of considerable extent in the complex molar teeth of the Ruminants. The appearance produced by these aggregated cells, in a section of the tooth matrix of a Calf's molar, (Pl. 122 *a*, fig. 9, *e*) is compared by Raschkow to the actinenchyma of certain vegetable tissues, and the connecting condensed blastema to threads of cellular tissue. The field of the final metamorphosis of the cells into the moulds for the reception of the solidifying salts is confined to close contiguity with the surface of the dentinal pulp (ib. *e'*, *e'*).

Here the cells increase in length, lose all trace of their nucleus, and become converted into long and slender cylinders usually pointed at both ends, and pressed by mutual contact into a prismatic form (Pl. I. fig. 4, *k*, *l*). These cylinders have the property of imbibing the calcareous salts of the enamel from the plasmatic fluid, and of compacting them in a clear and almost crystalline state in their interior: the disappearance of the nucleus being evidently the condition of the absence of any permanent cavity, cell, canal, or other modification of the mineral matter, at least in the enamel fibres of the Calf. In the Human subject it is probable that the cavity of the cylinder may be subdivided by a multiplication of

delicate nucleoli into compartments; or that the remains of such multiplied nucleoli may cause a modification of the walls of the cylinder, and so produce the characteristic transverse striæ of the enamel-fibre. This appearance is not present in the enamel of the Frog's tooth, nor in that of the teeth of the Hog, or Calf, in which animals my observations of the development of this tissue have been chiefly made. As the development proceeds, the cells in immediate contiguity with the calcified prisms undergo the same changes as their predecessors, and become united to them by their peripheral pointed extremities, whilst the fluid plasmatic contents of the cells are exchanged for the dense salts of which the enamel is chiefly composed. The selective surface formed by the organic membrane of the cell would seem to be destroyed by the very pressure resulting from its own action, and exerted by the contents of the closely-packed contiguous prisms, when the cavities of the cells are completely filled. The membrane ceases at least to be distinguishable under the microscope, from the solid contents of the cell, except at that surface of the enamel next the capsule, and which is still in progress of growth, (as in Pl. 123, fig. 2.)

What is remarkable, here, is that not the whole of the actinenchymatous part of the enamel-pulp is converted into the long and slender prismatic cellular basis of the enamel; at least, in the valleys of the complex crown of the molar of the Ruminant and Pachyderm, (Calf and Colt), this part of the enamel-pulp originally occupies more space than the subsequent layer of enamel does: and the superfluous peripheral part seems to be absorbed, and its place to be occupied by a growth or thickening of the vascular capsule. No capillaries pass from the capsule into the actinenchymatous pulp of the enamel: nor have I been able to trace a blood vessel into that part of the capsule which was actually the

seat of the calcifying processes.(1) Here, as in the dentinal and enamel pulps, the calcareous salts are selected and arranged by the assimilative, selective, or intus-susceptive, properties of the cell-walls and by the repulsive power of their nuclei.(2)

The blastema or fundamental tissue of the capsule is, at first, semitransparent and of a pearly or opaline colour; but is soon richly ornamented by the plexiform distribution of the blood-vessels, (Pl. II). As the period of its calcification approaches, which is later than that of the dentinal pulp, it becomes denser, and exhibits numerous nucleated cells. The blastema itself (Pl. I. fig. 5, *n*) presents more evidently a fine cellular or granular structure in which the calcareous salts are impacted in a comparatively clear state constituting the framework (*n'*) of the cemental tissue. The characteristic features of this tissue are due to the action of the proper nucleated cells (ib. *m*) upon the salts of the plasma diffused through the blastema in which those cells are imbedded. The cells being characterised by a single large granular nucleus (ib. *p*) which almost fills the clear area of the cell itself. If, when the formation of the cement has begun in the incisor or molar of a Colt, one of the detached specks of that substance, with the surrounding and adhering part of the inner surface of the capsule in which it is imbedded, be examined, these nucleated cells are seen, closely aggregated around the calcified part, in concentric rows; the cells of which are further apart as the rows recede from the field of calcification. Those next the cement (ib. *o*) rest in cup-shaped cavities in the periphery of the calcified part just as the first calcified cells of the thick cement which covers the

(1) This has led me to doubt whether the altered blood-discs of the capillaries of the dentinal pulp are converted into the cells of the pulp which occupy the place of the capillaries in the calcifying field.

(2) It might be supposed that the cell-membrane and the surface of the nucleus were in different electrical states.

crown of a complex molar are lodged in cavities on the exterior of the enamel. These exterior cavities of the cement are formed by centrifugal extension of the calcifying process in the blastema in which the cells are imbedded. The calcareous salts penetrate in a clearer and more compact state the cavity of the cell, but their progress is arrested apparently by the nucleus which maintains an irregular area, partly occupied by the salts in a subgranular opake condition, but chiefly concerned in the reception and transit of the plasmatic fluid which enters and escapes by the minute tubes which are subsequently developed from the nucleolar cavity as calcification proceeds. The radiated cells or cavities (p^1) thus formed, are the most common characteristic of the cement, but not the constant one. The layer of the capsule which surrounds the crown of the Human teeth and of the simple teeth of Quadrumana and Carnivora, consists simply of the granular blastema, without nucleated cells, and the radiated corpuscles are, consequently, not developed in the cement which results from its calcification. In the thicker parts of the inflected folds of the capsule of the complex teeth of the Herbivora traces of the vascularity of that part of the matrix are persistent, the blastema calcifying around certain of the capillaries and forming the medullary canals. The varieties of these canals are traversed by minute tubules continued from or communicating with the radiated cells. These tubules, and the more parallel ones which traverse the thickness of the cement in many Mammalia, are the remains of linear series of the minute granules of the blastema.

In the deep sockets of the teeth of persistent growth the matrix is maintained by the constant additions of new blastema and cell-material to the bases of the dentinal, enamel and cemental pulps. I have demonstrated the partial growth of the enamel pulp

along the side of the capsule corresponding to the convexity of the scalpriform incisor of the under jaw of the Porcupine in the preparation, now in the Physiological Series of the Hunterian Collection, No. 375 A.

Chemical analyses(1) of the composite substances, built up by the organising processes in the fundamental tissues of the matrix, above described, have yielded the following results.

INCISORS OF ADULT MAN.

	Dentine.	Enamel.	Cement.	
				II.
Organic substance . .	28.70	3.59	29.42	29.12
Inorganic substance . .	71.30	96.41	70.58	70.88
	100.00	100.00	100.00	100.00

MOLARS OF ADULT MAN.

	Dentine.	Enamel.
Phosphate of lime with a trace of fluate of lime . .	66.72	89.82
Carbonate of lime	3.36	4.37
Phosphate of magnesia	1.08	1.34
Salts	0.83	0.88
Chondrine (2)	27.61	3.39
Fat	0.40	0.20
	100.00	100.00

BERZELIUS' ANALYSIS GIVES:

Phosphate of lime, with a trace of fluate of lime . .	64.0	88.5
Carbonate of lime	5.3	8.0
Phosphate of magnesia	1.0	1.5
Soda and muriate of soda	1.4	—
Cartilage and other animal matter . . .	28.0	2.0
	100.0	100.0

(1) These results are cited chiefly from Bibra's "Chemische Untersuchungen über die Knochen und Zähne," 8vo. 1844.

(2) "Knorpelsubstanz."

CANINE OF A LION.

	Dentine.	Enamel.
Phosphate of lime with a trace of fluate of lime	60.03	83.33
Carbonate of lime	3.00	2.94
Phosphate of magnesia	4.21	3.70
Salts	0.77	0.64
Chondrine	31.57	9.39
Fat	0.42	A trace.
	100.00	100.00

TEETH OF A DOLPHIN. (*Delphinus Delphis.*)

	Dentine.	Cement.
Phosphate of lime with a trace of fluate of lime	66.37	69.42
Carbonate of lime	1.84	1.79
Phosphate of magnesia	1.36	1.47
Salts	0.99	0.93
Chondrine	28.62	25.73
Fat	0.82	0.66
	100.00	100.00

TUSK OF ELEPHANT.

	Ivory.
Phosphate of Lime with a trace of fluate of lime	38.48
Carbonate of lime	5.63
Phosphate of Magnesia	12.01
Salts	0.70
Chondrine	42.94
Fat	0.24
	100.00

TUSK OF WILD-BOAR.

	Dentine.
Phosphate of lime with a trace of fluate of lime	60.00
Carbonate of lime	2.51
Phosphate of magnesia	6.43
Salts	0.43
Chondrine	30.50
Fat	0.13
	100.00

INCISORS OF OX.

	Dentine.	Enamel.	Cement.
Phosphate of lime with a trace of fluate of lime .	59.57	81.86	58.73
Carbonate of lime	7.00	9.33	7.22
Phosphate of magnesia . . .	0.99	1.20	0.99
Salts	0.91	0.93	0.82
Chondrine . . .	30.71	6.66	31.31
Fat	0.82	0.02	0.93
	100.00	100.00	100.00

CROCODILE.

	Dentine.	Cement.
Phosphate of lime, with a trace of fluate of lime .	53.69	53.39
Carbonate of lime	6.30	6.29
Phosphate of magnesia	10.22	9.99
Salts	1.34	1.42
Chondrine	27.66	28.15
Fat	0.79	0.76
	100.00	100.00

PIKE (*Esox Lucius*).

	Large teeth of lower jaw.
Phosphate of lime with a trace of fluate of lime . .	63.98
Carbonate of lime	2.54
Phosphate of magnesia	0.73
Salts	0.97
Chondrine	30.60
Fat	1.18
	100.00

The proportion of mineral or inorganic substance would seem to vary, within certain limits, in different individuals of the same species: thus in the molar teeth of one man Bibra found 79.00 of inorganic matter, and in another 71.99; whilst Berzelius found 72.0. The proportion of inorganic matter in hard dentine will depend in some degree upon the number of dentinal tubes, from the areæ of which the salts are in part excluded: thus in the modified dentine (ivory) of the Elephant's tusks, in which the tubuli are

more numerous, close-set, and extensively undulated, in a given space, than in ordinary dentine, the organic bears a greater proportion to the inorganic matter, than in the dentine of the teeth of most other Mammals. The cement of the composite molar teeth of the Ruminants and of the Elephant contains a little more organic matter than the dentine does; but in the cetaceous Dolphin it contains a rather less proportion, and is consequently harder.

The nerves of the teeth (1) are derived from the trigeminal, or fifth pair, of which the second division supplies those of the upper jaw, the third division those of the lower jaw. In the Human Subject the three dental branches of the infra-orbital nerve intercommunicate by their primary branches, from which, and from a rich plexus formed by secondary branches upon the membrane lining the antrum, two sets of nerves are sent off to the alveolar processes of the upper jaw; one set (*rami dentales*) supplies the teeth, the other (*rami gingivales*) the osseous tissue and the gums; the latter agree in number with the intervals of the teeth, as the proper dental nerves do with the teeth themselves. These two sets are not, however, so distinct but that some intercommunications are established between the fine branches sent off in their progress to the parts they are specially destined to supply. The *rami dentales* take the more direct course through the middle part of the osseous tissue to the teeth; penetrate the orifices of the fangs, and form a rich plexus with rhomboidal meshes upon the coronal surface of the pulp; the peripheral elementary filaments returning into the plexus by loops.

In the lower jaw the dental nerve, besides supplying the proper nerves to the teeth, also forms a rich plexus, in which it is joined

(1) Swan, Demonstration of the Nerves of the Human Body, fol. 1830, pl. xii. Schumacher, Ueber die Nerven der Kiefer und des Zahnfleisches, 4to. 1839.

by some branches from the division of the nerve that afterwards escapes by the foramen mentale, and from this plexus the cancellous tissue of the bone and the vascular gums are supplied.

In the Dog and other Carnivora the nerve of the laniary tooth is conspicuous from its size; that which supplies the still more developed analogous tooth or tusk of the Boar, is still larger having relation also to the continual reproduction of the matrix at the base of the tusk.(1)

In the lower jaw of the Porcupine the nerve of the great incisor is given off from the dental nerve near the middle of its course through the osseous canal, and returns at an acute angle to penetrate the cavity at the base of the scalpriform tooth, and supply its persistent pulp.(2) This recurrent course indicates the progressive change in the relative position of the pulp to the origin of its nerve. Besides the branches for the molar teeth, many smaller filaments penetrate the spongy texture of the bone, and form a rich plexus from which the gum derives its filaments.

The maxillary plexus is most developed, in the Horse, above and between the alveoli of the three premolar teeth; it is less complex where it supplies the molar teeth, their alveoli and the gums. In the lower jaw of the Horse a very rich plexus begins to be formed in the cancellous substance of the bone by branches of the dental nerve, soon after its entry into the canal.

The intercommunications between the dental and gingival nerves, and those supplied to the osseous tissue from the supra-maxillary and infra-maxillary plexuses explain the sympathies manifested in neuralgy and rheumatic pains between the teeth and the osseous cavities in which they are implanted.

I have been represented as having arrived at the conclusion

(1) Pl. 140, fig. 2. (2) Pl. 104, fig. 1, 1*.

"that the structure of the teeth, as manifested by means of the microscope, forms a new, distinct, and specific guide for classifying the different members of the animal kingdom, and determining their respective types:"(1) the absurdity of which will be obvious to the youngest student of Zoology, who knows that true teeth are developed only in one of the primary divisions of the animal kingdom. What I have stated is, that the teeth, by their microscopic structure, as well as their more obvious characters, form important, if not essential aids to the classification of existing, and the determination of extinct species of Vertebrated animals: but in this comparatively restricted sphere the teeth have different degrees of value, as zoological characters, in different classes; the lowest degree being in the Class of Fishes, and the highest in that of Mammals. Numerous rows of teeth, for example, gradually succeeding and displacing each other, characterise the higher organized or Plagiostomous Fishes, and particular modifications of the form and

(1) "The labours of Purkinje, Muller, and Retzius on the structure of the teeth have now been recorded, and the views entertained by these physiologists have been most ably investigated and confirmed by Mr. Owen, who has submitted to microscopical examination the teeth of several other animals, both recent and fossil. From an excellent Report of these Researches read at the last Meeting of the British Association, I have great satisfaction in finding that he has arrived at the same conclusion which I had previously embodied in the first announcement of this work, viz., that the structure of the teeth, as manifested by means of the microscope, forms a new, distinct, and specific guide for classifying the different members of the animal kingdom, and determining their respective types. From the enduring nature of these organs, the characteristic modifications which they present, will form, as Mr. Owen has admirably pointed out, a most valuable accession to geological science."—Mr. Nasmyth, 'Researches on the Teeth,' 8vo. 1839, p. 123. Where this Author obtained the idea, "which he had previously embodied" to the best of his comprehension, is of little moment. The paragraph is cited to show that when Mr. Nasmyth penned and printed his eulogy on my "Report" of 1838, he seemed not to feel it as "a strange and unlooked for opposition" as he has represented it since the exposure, in 1840, of the nature of his 'Papers' read at Birmingham.

size of these teeth distinguish the primary subdivisions of the same Order. A few other groups of Fishes are well defined by dental characters, as the Pycnodonts, Gymnodonts, Goniodonts, and Chætodonts. But in most of the natural Orders, and in many of the subordinate groups of the Piscine class, the dental system is subject to very great diversity in regard to the form, number, and position of the teeth; and in some natural families there is also a want of constancy in the structure of the teeth. There are extremely few genera of Fishes that can be characterized by a definite numerical dental formula, like most of the Mammalian genera. Indeed, in the first introduction of true teeth into the animal series, regarded in the ascending order, they manifest, like the mouths of the *Polypi*, the stomachs of the *Polygastria*, and the generative organs of the *Tæniæ*, the principle of vegetative or irrelative repetition; and, in many Fishes, are too numerous to be counted. The limits within which the teeth are applicable as means of classification in Fishes will be readily, and I trust, accurately appreciated, by the descriptions in the first part of this Work. Traced from species to species they are of great importance in the determination of the fossils of this class.

With regard to microscopic structure, the second and third of the modifications defined in Chapter I, Section 8, are peculiar to and characteristic of the Piscine Class; the first modification is, with the exception of one Mammalian genus, *Orycteropus*, peculiar to Fishes; unvascular or fine-tubed dentine forms the crown of the teeth in a few Fishes, but is more common in those of the higher Classes.

In the Class *Reptilia* the teeth serve to characterize smaller and more definite groups than in *Pisces*, as, for example, the venomous and non-venomous Ophidians; and the acrodont, pleurodont, and thecodont Saurians. Certain Genera, and even Species may likewise be known

by peculiar forms of teeth; but a definite dental formula can rarely be assigned as a generic character of a Reptile. There is no decided modification of dental structure peculiar to any of the class of Reptiles; the poison-fang is rather a modification of form. The labyrinthic structure reaches its maximum of complexity in the great extinct Sauroid Batrachians of the Keuper Sandstones, but "it also exists at the base of the tooth in a few Fishes," (Part II, p. 201), and specific instances of it in that class (*Lepidosteus*, and a few other *Sauroids*) have, since Part II. was published, received illustrations in the works of Prof. Agassiz(1) and Dr. Wyman.(2) The only constant and general character of the teeth of the cold-blooded classes of Vertebrata is derivable from the brief period of their existence in the individual, so that the few teeth which develope roots have these always simple and undivided, usually hollow, and with the germ of a successor in or near them.

With the exception of the composite dental masses of the Chimæroids, and the anomalous rostral teeth in *Pristis*, no existing species of Fish or Reptile could be said to have permanent teeth; and no extinct species of either class has yet been found with teeth having divided roots implanted in sockets, or manifesting evidence of perpetual growth by a persistent pulp, excepting the singular extinct Saurians of South Africa, with two long canine tusks in the upper jaw, which must have grown and been maintained throughout life, of due size and strength, like the tusks of the Boar and Walrus.(3) With the exception of these two anomalous teeth, the jaws of the Dicynodonts were edentulous.

In the Mammalian Class the value of the dental organs, as

(1) Poissons Fossiles, Notice sur les Sauroides, Janvier, 1843.

(2) Trans. Boston Society of Natural History, August, 1843.

(3) Memoir on the *Dicynodon*, Geological Transactions, 2nd series, vol. vii.

characters of classification, is much greater than in Reptiles or Fishes, as will be seen in Part III. Yet there is a difference in this respect in the different Orders, and the Dental System of the *Cetacea* and *Bruta* has a much greater range of variation, and a less constant relation to the other characters on which the families and genera are founded, than in the Ungulate and higher Unguiculate Species. But, with respect to these also, the value of the teeth as zoological characters has been overrated.(1)

It is true, indeed, that the most manifestly natural Mammalian genera are those, the species of which are provided with absolutely similar molar teeth : and, that those genera, which include species with molars of different forms, do not present the same character of unity. But it does not follow that, by combining species of Mammals with similar molars, a group will be formed perfectly analogous to those which may be considered as the most natural or perfect. Neither the molar teeth, nor any other solitary character will serve to establish a natural classification.

The molar teeth will least mislead in this respect where their modification is most extreme, as when they are adapted to divide the flesh of animals, in which case they must of necessity be associated with the faculties and instruments for seizing and destroying prey. But molar teeth may be similarly modified, and equally well adapted for crushing vegetable substances, which substances may be sought for by one species on the dry land, by a second in

(1) M. F. Cuvier says "Cette recherche me fit reconnaître que tous les genres manifestement naturels, et admis comme tels par tous les naturalistes, étaient formés d'espèces pourvues de machelières absolument semblables; que ceux qui comprenaient des espèces dont les mâchelières différait, n'offraient point ce caractère d'unité qui était le partage des premières ; et, enfin, qu'en réunissant les espèces à mâchelières semblables on reformait des groupes parfaitement analogues à ceux que l'on pouvait considérer comme les plus parfaits." Dents de Mammifères, 8vo. 1825, p. ix.

marshes, and by a third in the sea, or on the banks of rivers. The grinding surface of the molar tooth, for example, may for this purpose be elevated into a pair of transverse ridges, and we find such molars in the Kangaroo, the Tapir, and the Manatee, as also in the extinct *Diprotodon*, *Nototherium*, and *Dinotherium*. The small anterior molars of the *Mastodon giganteus* likewise present this form. It would be difficult to select from the Mammalian Class the constituents of a more heterogeneous group than would be constituted by the character which M. F. Cuvier has assigned as the true guide to the formation of the most natural and uniform genera in Mammalogy.

Even in regard to teeth adapted to carnivorous habits, were these characters to form the sole guides in classification, species of placental Mammalia would be associated with those of the ovoviviparous sub-class; and M. F. Cuvier, in illustrating his generalization, observes: "Les sarigues, les péramèles, et les dasyures se sont réunis aux Insectivores, &c., &c., et je crois avoir été conduit à ces modifications par des motifs légitimes."(1)

The class of tissues in which teeth should rank, has frequently been a subject of controversy in Systems of Histology; the fact being overlooked that they have not the same unity of composition as bones or epidermal appendages. One constituent of teeth, viz., the cement, unquestionably ought to rank with the osseous tissue; and the dentine, or ivory, which was described for the last time in this country, in July, 1838, as being "like the hair, arranged in concentric layers," (2) bears, on the contrary, a close

(1) Loc. cit. p. xi.

(2) Medico-chirurgical Review, p. 43. In France the dentine continued to be described, as late as the end of 1839, as "composé de cones lamelleux extrêmement minces, s'emboîtant les unes les autres, &c." De Blainville, 'Ostéographie' Fascicule premier, Primates, p. 14, 1839.

structural resemblance to bone and is almost identical in chemical composition: its modifications, which I have called 'vaso-dentine' and 'osteo-dentine,'(1) forming intermediate gradations between the hard dentine and true bone. True enamel is a tissue *per se;* but in the teeth of Fishes there are several intermediate stages of gradation which link enamel to dentine, as the dentine itself, in most Fishes, passes gradually into bone.

Heusinger admits that the relation of the teeth to the corneous tissue (Horngewebes) is not clearly elucidated in Human Anatomy, but he affirms that it is most conclusively established in that of the lower classes of animals. (2) No doubt in tracing the modifications of the dental system through the Animal Kingdom, we find true horny productions substituted for teeth in certain Vertebrate Species, as the Ornithorhynchus, Whale, Tortoise, &c.

(1) These tissues are respectively defined, as follows, in the 'Report of the British Association, 1838.' "With respect to the component structures of a tooth, Professor Owen commenced by observing, that in addition to those usually described and admitted, there were other substances entering into composition of teeth, and presenting microscopic characters equally distinct both from ivory, enamel, and cement, and from true bone, and as easily recognisable. One of these substances was characterized by being traversed throughout by numerous coarse canals, filled with a highly vascular medulla or pulp, sometimes anastomosing reticularly,—sometimes diverging, and frequently branching,—sometimes disposed nearly parallel with one another, and presenting more or fewer dichotomous divisions. The canals in many cases are surrounded by concentric lamellæ, and thus resemble very closely the Haversian canals of true bone; but the calcigerous tubes which everywhere radiate from them are relatively much larger. The highly-organized tooth-substance just described differs from true osseous substance, and from the cæmentum in the absence of the Purkingian corpuscles or cells. This structure is exemplified in the teeth of many fishes and some Edentate Mammalia. Another component substance of tooth more closely resembles true bone and cement, inasmuch as the Purkingian cells are abundantly scattered through it; it differs, however, in the greater number and close parallel arrangement of the medullary canals. This structure is exhibited in the teeth of the *Megatherium*, *Mylodon*, and other extinct Edentata," p. 137.

(2) System der Histologie, 4to. 1823, p. 160.

So likewise the office of teeth is performed, in the Articulate Classes, by parts (modified as to form) of the crustaceous and chitinous integuments. But I know of no transitional or intermediate structures, such as Heusinger alludes to, between teeth and nails, horns or hair. The lamellar disposition traceable in the texture of the hardest dentine, is much more closely similar to that of bone, especially to the concentric plates surrounding the Haversian Canals, than to the texture of nails. The structure of the tooth of the Orycteropus, is essentially like that of all true teeth: the apparent resemblance which it presents to the horn of the Rhinoceros, or to Baleen, arises from its being compounded of many minute parallel and elongated denticles.

And the close resemblance in intimate structure and chemical composition between true teeth and bones being established, it may be observed that the osseous tissue is not confined to the endo-skeleton: it is developed largely to form the exo-skeleton in many Fishes, in the Loricate Reptiles, and even in the Mammalian Class, as, for example, in the Armadillos (*Dasypus*), where, to strengthen the integument, bone is substituted for horn, which forms the scaled armour of the allied Pangolins (*Manis.*) Now the relation of the tooth of the Armadillo to that of the Ornithorhynchus is precisely analogous to that which subsists between the osseous plates of the Armadillo and the corneous scales of the Pangolin; but this relation no more establishes identity of tissue or system of tissues in the one case than in the other.

The general form of the dental matrix and its relation with its calcified product, bear a close analogy with those of the formative organ of hairs, bristles, and other productions of the epidermal system. In these the papilla, or pulp, is developed from the external skin; in the teeth from the mucous membrane, or internal skin.

Teeth further agree with the extravascular appendages of the skin in being shed and reproduced sometimes once, sometimes frequently, during the life-time of an individual: the latter may be termed 'interrupted' reproduction. In some cases again, as with certain epidermal appendages, the reproduction of the tooth is uninterrupted, and goes on during the life-time of the individual; new matter being added to the base as the old is worn away from the apex, or working surface of the tooth. A tooth, when fully formed, is subject to decay, but has no inherent power of reparation. A tooth of limited growth can only increase in size after its formation is completed by abnormal growth of its most highly organised constituent, the cement. Thus, then, it appears that, the analogy of the dental organs to those of the corneous system holds only in their mode of development(1), in their shedding and reproduction, and in their exposure to external influences and to the contact of extraneous bodies: but the antlers of Deer are similarly exposed, and are likewise shed and reproduced annually, and also contemporaneously with the fall of the hair; but antlers are not, therefore, classed with the corneous tissues, any more than is the bony core of the horns of the cavicorn Ruminants.

(1) The cells and fibres of the horny tissues are formed in and not excreted from the surface of their formative pulps.

ODONTOGRAPHY.

PART I.

DENTAL SYSTEM OF FISHES.

CHAPTER I.

GENERAL OBSERVATIONS ON THE TEETH OF FISHES.

If the ichthyologist have reason to complain of the monotony which unavoidably pervades his descriptions of the external characters of the objects of his study,(1) the anatomist in treating of the dental system of fishes, finds, on the contrary, his difficulty in obtaining the command of language sufficiently varied to pourtray the singular diversity and beauty, and the interesting physiological relations which are manifested in that part of their organization. The teeth of fishes, in fact, in whatever relation they are considered, whether in regard to number, form, substance, structure, situation, or mode of attachment, offer more various and striking modifications than do those of any other class of animals.

2. *Number.*—If we commence with the lowest species, as the glutinous hag and other myxinoid fishes, we find that, the armature of the tongue excepted, the dental system is represented by a single tooth developed on the median line of the palate. In the carp, a single median tooth above the pharynx is opposed to two dentigerous plates below. In the *Ceratodus* and *Ctenodus*, the jaws are armed with four teeth, two above and two below. In the chimæra, two lower maxillary teeth are opposed to four above. From these species may be traced every gradation in the progressive multiplication of the teeth up to the pike, silurus, and other fishes in which the mouth is crowded with innumerable teeth.

3. *Form.*—The great variety of forms of the teeth of fishes

(1) Cuvier, Eloges, iii, p. 313.

has attracted the attention of most comparative anatomists, and yet such is the rapidity with which new species, either of the present or a past creation, are added to the catalogues of the ichthyologist, that this part of the subject is far from being exhausted. All the known differences which the teeth of fishes present in this respect may, however, be referred to modifications, either of the cone, the plate, the prism or the cylinder.

The conical teeth may be slender, sharp-pointed, and so minute, so numerous, and closely aggregated as to resemble the plush or pile of velvet; these will be termed villiform teeth, they are the *dents en velours* of Cuvier, and are sometimes so short as to be more easily felt than seen: when the teeth are equally fine and numerous but longer, they will be called ciliiform teeth : when long and slender, but a little stronger, they are the *dents en brosse* (brush-teeth) of Cuvier. Conical teeth as close-set and sharp-pointed as the villiform teeth, but of larger size, are the *dents en rape*, or *en cardes* of the French anatomist. These modifications of the whole or a part of the dental series are common to a great number of fishes. The perch has all its teeth *en velours;* the pike presents the rasp-like teeth on the posterior part of the vomer ; the armature of the palate bone of the silurus (Pl. 1, fig. 1,) as well as that of other bones of the mouth of the same fish, presents all the gradations between the *dents en velours*, and the *dents en cardes.*

The conical teeth may be so long and slender as to resemble bristles, as in the chætodonts (Pl. 1, fig. 2.) These setiform teeth are sometimes bifurcate at their free extremity, as in the genus *Citharina ;* or they may terminate in three diverging points, as in the anterior maxillary teeth of the genus *Platax* (Pl. 1, fig. 2*), and here the cone merges into the long and slender cylinder. Or the elongated cone may be compressed into a slender trenchant plate ; and this may be pointed, recurved, or even barbed like a fish hook, as in the *Trichiurus* (Pl. 1, fig. 8,) and some other scomberoid fishes ; or it may be bent upon itself like a tenter-hook, as in the *Pimelipterus* and *Gonyodontes.* In other species as in the bonito, (Pl. 1, fig. 3,) the conical teeth present a progressive thickening of the base, and this modification being combined in certain predatory fishes with an increase of size and a slightly recurved direction, they resemble the

laniary or canine teeth of the carnivorous quadrupeds. Of this kind are the larger teeth of the pike and *Rhizodus* (Pl. 35), and the anterior teeth of the *Dentex*, (Pl. 41). A moderately long, stout and more or less straight cone is a form exemplified in the anterior teeth of the wolf-fish, (Pl. 60 & 61,) and the transition by progressive blunting, flattening and expansion of the apex is very gradual from this form of the cone to the thick and short cylinder, such as is seen in the posterior teeth of the wolf-fish, and similar grinding or crushing teeth of many other existing genera. The working surface of these short cylindrical teeth may be rounded as in the sheep's-head-fish (*Sargus*, Pl. 42, fig. 1,) or flattened as in the pharyngeal teeth of the wrasse, (*Labrus*, Pl. 45, fig. 4). Sometimes the hemispheric teeth are so minute and numerous as to give a granulated surface to the part of the jaw to which they are attached (Pl. 45, fig. 1).

A progressive increase of the transverse over the vertical diameter may be traced in the molar teeth of different fishes, and sometimes in those of the same individual, until the cylindrical form is lost in that of the depressed plate. Of this change we have a good example in the posterior teeth of the gilt-head (*Chrysophrys*), when arrived at maturity, and likewise in the fossil genus *Placodus*, (Pl. 30). The dental plate, instead of offering the cylindrical form, may be elliptical, oblong, square, triangular, semilunar, sigmoid, and with the grinding surface variously sculptured. The broadest and thinnest depressed laminæ are seen in the component denticles of the molar tubercle of the diodon, and in the teeth of the *Phyllodus*.

The incisors of the sargus, (Pl. 1, fig. 13,) flounder, and some other fishes present the compressed laminated form, at least, in the protruded coronal portion. Numerous wedge-shaped dental plates are set vertically in the pharyngeal bones of the *Scarus* or parrot-fish. A thin lamella, slightly concave like a finger-nail, is the singular form of the tooth of an extinct genus of cartilaginous fishes, which I have, on that account, named *Petalodus*, (Pl. 22, figs. 2, 3, 4.) Sometimes the flattened incisive crown is notched in the middle of the cutting edge, as in the incisors of the species of bream (*Sargus unimaculatus*) figured in Pl. 1, fig. 9. Sometimes there is a double notch rendering the crown of the incisor trilobate, as in the genus

Aplodactylus, (fig. 10); in the lower maxillary teeth of the *Boops*, the crown is divided into five lobes by a double notch on each side of the middle and largest lobe, (fig. 11).

In the great barracuda-pike (*Sphyræna*), the crown of both the large and small lamelliform teeth is produced into a sharp point, and closely resembles a lancet, (Pl. 1, fig. 4, & Pl. 53). A similarly shaped piercing and cutting tooth may be accompanied by one or more accessory compressed cusps at its base, as in the teeth of certain sharks, (Pl. 3 & 4,) or the margins of the crown may be variously notched, serrate, e. g., as in the priodon, (Pl. 1, fig. 12,) and in the teeth of the great sharks of the genus *Carcharias*, or crenate as in the genus, hence called *Crenidens*, (fig. 7,) and in the teeth of the *Acanthuri*, (Pl. 44,) of which the species called *Ctenodon* is remarkable for the deeply crenated, expanded and spatulate crowns of its teeth, (Pl. 1, fig. 6). Prismatic teeth of three sides are present in the jaws of the *Myletes*, where each angle of the coronal surface is produced into a point. The small teeth with which the jaws of the *Scarus* are paved are four sided prisms; the strong flat teeth which form the tesselated pavement of the jaws of the Eagle-rays (*Myliobates*), present beautifully regular hexagonal or pentagonal forms (Pl. 25).

4. *Situation.*—Before proceeding to consider the situation of the teeth of fishes, a few words may be premised respecting the bones which enter into the formation of the mouth in the ordinary osseous species. In these, the upper margin of the mouth is bounded generally by the intermaxillary bones alone, which extend backwards from the middle line to the angles of the mouth; in this case, the superior maxillary bones(1) run parallel with and above the horizontal portion of the intermaxillaries;(2) but when, as in the lophius and salmon-tribe, the intermaxillary bones do not extend to the angles of the mouth, the osseous boundary is completed above by the superior maxillaries.(3) The lower border of the mouth is formed by the premandibular bones,(4) this name being given to the anterior of the two pieces of which each ramus of the lower jaw consists in fishes. The roof of the mouth is formed anteriorly by three bones which extend backwards from the interspace of the intermaxillary bones; the two lateral ones are the pa-

(1) Pl. 41, *b*. (2) Pl. 41, *a*. (3) Pl. 60, fig. 1, *b*. (4) Pl. 41, *c*.

latines, (*b b* Pl. 61), the median one is the vomer, (*c* Pl. 61). Two flattened bones on each side, called the pterygoid and transverse bones, complete the bony arch or buttress which extends from the intermaxillaries to the pedicle supporting the lower jaw. Posteriorly, the roof of the mouth is completed by the sphenoid and sub-occipital bones.

The floor of the mouth is supported by the median longitudinal chain of lingual bones, to the sides of which are attached the inferior extremities of the branchial arches; these form the sides of the posterior part of the mouth, which gradually contracts to the pharynx; this orifice is strengthened by bones above and below, varying in number from one to six, and called the pharyngeal bones.

In the roach, dace, barbel and most other cyprinoid fishes, the teeth are limited to the pharyngeal bones; in the carp, the upper pharyngeal dental plate is wedged into a cavity of the occipital bone. In the ordinary sharks and rays, on the other hand, the teeth are confined to the maxillary cartilages bounding the anterior aperture of the mouth. The wrasse, (*Labrus*), and parrot fish, (*Scarus*), are instances in which the intermaxillary and premandibular, as well as the pharyngeal bones are provided with teeth, both the anterior and posterior apertures of the mouth being thus surrounded by instruments for dividing or comminuting the food. In other fishes, we find the teeth situated not only on the bones which bound the anterior and posterior orifices of the mouth, but in the intermediate positions, as on the palatines, the vomer, the lingual bones, or the branchial arches; sometimes, also, but more rarely, on the transverse, or pterygoid, the sphenoid,(1) and the superior maxillary bones, of which latter situation the fishes of the Halecoid(2) tribe and the extinct *Lepidotus*, afford examples in the present class. Among the anomalous positions of teeth may be cited, in addition to the occipital alveolus of the carp, the accessory rostral cartilages, which in the *Pristis* are elongated, and so ossified as to be adapted to retain in sockets the strong sharp lateral teeth, constituting its formidable saw. In the lampreys, and in one of the osseous fishes (*Helostomus*) most of the teeth are attached to the lips. Lastly, I may observe, that it is peculiar to the class of fishes among vertebral animals, to

(1) Pl. 48, fig. 2. (*Sudis*).

(2 In this family M. Agassiz includes the Salmonoid and Clupeoid fishes of Cuvier.

present examples of teeth developed in the median line of the mouth, as in the palate of the myxines, or crossing the symphysis of the lower jaw, as in the scymnus and myliobates.

5. *Attachment.*—The teeth of fishes present greater diversity in their mode, as well as place of attachment, than is observable in those of any other class of animals. In a few instances, they are implanted in sockets, to which they are attached only by the surrounding soft parts, as e. g., the rostral teeth of the saw-fish.(1) Some have their hollow base supported, like the claws of the feline tribe, upon bony prominences, which rise from the base of the socket; the incisors of the file-fish afford this curious example of a double gomphosis, the jaw and the tooth reciprocally receiving and being received by each other.(2)

The teeth of the *Sphyræna*, *Acanthurus*, *Dictyodus*, &c., are examples of the ordinary implantation in sockets, with the addition of a slight anchylosis of the base of the fully-formed tooth with the parietes of the alveolar cavity. But by far the most common mode of attachment of the fully-formed teeth in the present class, is by a continuous ossification between the dental pulp and the jaw; the transition being gradual from the structure of the tooth to that of the bone: the tooth, prior to the completion of the anchylosis, is connected by ligamentous substance, either to a plain surface, an eminence, or a shallow depression in the jaw-bone.

Sometimes not the end, but one side of the base of the tooth is attached by anchylosis to the alveolar border of the jaw; it might be supposed that, in this case, the crown of the teeth in both jaws would project forwards instead of being opposed to one another, and such, in fact, must have been their position were it not that, in some instances, as in the *Pimelipterus*, the teeth have the crown bent down at nearly a right angle with the base. In the scarus, and likewise in the marginal teeth of the diodon, where the teeth are straight, and attached horizontally to the margin of the jaws, their sides instead of their crowns are actually opposed to one another.

In the cod-fish, wolf-fish, and some other species, in proportion as the ossification of the tooth advances towards its base and along the connecting ligamentous substance, the subjacent portion of the jaw-bone receives a stimulus, and developes a process corres-

(1) Pl. 8, fig. 3. (2) Pl. 40, figs. 3 and 5, *a*.

ponding in size and form with the solidified base of the tooth. In this case, the inequalities of the opposed surfaces of the tooth and maxillary dental process fit into each other, and for some time they are firmly attached together by a thin layer of ligamentous substance; but in general, anchylosis takes place to a greater or less extent before the tooth is shed. The small anterior maxillary teeth of the angler (*Lophius*) are thus attached to the jaw, but the large posterior ones remain always moveably connected by highly elastic, glistening ligaments which pass from the inner side of the base of the tooth to the jaw-bone. These ligaments do not permit the tooth to be bent outwards beyond the vertical position, when the hollow base of the tooth rests upon a circular ridge growing from the alveolar margin of the jaw; but the ligaments yield to pressure upon the tooth in the contrary direction, and its point may thus be directed towards the back of the mouth; the instant, however, that the pressure is remitted, the tooth flies back, as by the action of a spring, into its usual erect position; the deglutition of the prey of this voracious fish is thus facilitated, and its escape prevented. The broad and generally bifurcate osseous base of the teeth of sharks is attached by ligaments to the ossified or semi-ossified crust of the cartilaginous jaws. The teeth of the Salarias and of certain Mugiloids are simply attached to the gum. The small and closely-crowded teeth of the rays are also connected by ligaments to the subjacent maxillary membrane. The broad tesselated teeth of the eagle-rays have their attached surface longitudinally grooved, to afford them better holdfast; and the sides of the contiguous teeth are articulated together by true serrated, or finely-undulating sutures; which mode of fixation of the dental apparatus is unique in the animal kingdom.

If the engineer would study the model of a dome of unusual strength, and so supported as to relieve from its pressure the floor of a vaulted chamber beneath, let him make a vertical section of one of the crushing pharyngeal teeth of the wrasse.(1) The base of this tooth is slightly contracted, and is implanted in a shallow, circular cavity, the rounded margin of which is adapted to a circular groove in the contracted part of the base; the margin of the tooth, which immediately transmits the pressure to the bone, is strengthened by an

(1) Pl. 46.

SALAR JUNG LIA

inwardly projecting convex ridge. The masonry of this internal buttress and of the dome itself, is composed of hollow columns, every one of which is placed so as best to resist or transmit in the due direction the superincumbent pressure. The advantages gained by this beautiful example of animal mechanics will be explained when the dental system of the labroid fishes is described.

In another case, in which long and powerful piercing and lacerating teeth were evidently destined, from the strength of the jaws, to master the death-struggles of a resisting prey, we find the broad base of the tooth divided into a number of long and slender cylindrical processes, which are implanted, like piles, in the coarse osseous substance of the jaw; they diverge as they descend, and their extremities bend and subdivide like the roots of a tree, and are ultimately lost in the bony tissue. This mode of implantation of the teeth, which I have detected in a large extinct sauroid fish (*Rhizodus*),(1) is, perhaps, the most complicated which has yet been observed in the animal kingdom.

6. *Substance.*—The teeth of fishes, in respect to their substance, present various degrees of density and complexity. In most of the chætodonts they are flexible and elastic, of a yellowish, shining, and subtransparent tissue. The labial teeth of the helostome are also of this kind, as are also the anterior maxillary teeth of the gonyodonts, and of the percoid species, hence called *Trichodon*. In the cyclostomes, the teeth consist of an albuminous tissue, of a somewhat denser nature. The upper pharyngeal molar of the carp, consists of a peculiar brown and semi-transparent tissue, harder than the true horny teeth of the lamprey.

The greater number of fishes have their teeth composed of an osseous substance, somewhat denser than the jaws to which they are affixed. In some instances, as in the teeth of the flying-fish (*Exocœtus*), and sucking-fish (*Remora*), the substance of the tooth is uniform, and not covered by a layer of a denser texture. In others, as the shark, sphyræna, &c., the tooth is coated with a dense, shining, enamel-like substance; but this is not true enamel, nor the product of a distinct organ; it differs from the body of the tooth only in the greater proportion of the earthy particles, their more minute diffusion

(1) Pl. 36.

through the gelatinous basis, and the more parallel arrangement of the calcigerous tubes; but it is developed in and by the same matrix, and, resulting from the calcification of its external layer, is the first part of the tooth which is formed. In the *Sargus* and *Balistes*, the dentine, or proper osseous substance of the tooth, is harder than that of the fishes last cited, and is covered with a thick layer of a denser substance, developed by a distinct organ, and differing from the enamel of the higher animals only in the more complicated and organized mode of deposition of the earthy particles. The ossification of the capsule of the matrix gives the enamel of the teeth of the file-fish, and some others, a thin coating of a third substance analogous to the " cæmentum, or crusta petrosa," of the mammalian teeth. And in the pharyngeal teeth of the parrot-fish, a fourth substance is added to the structure of the tooth by the coarser ossification of the pulp, after its peripheral portion has been converted into the dense ivory. The teeth, thus consisting of dentine, enamel, cement, and coarse bone, are the most complicated as regards their substance that have yet been discovered.

7. *Chemical composition.*—With respect to the chemical composition of the teeth of fishes, little remains to be added to what has been stated on this subject in the preliminary general observations. The animal base of the horny teeth of the cyclostomes is albuminous, as in true horn; that of the calcified teeth is gelatinous, and the proportion of gelatin to the usual hardening salts, diminishes as their density increases. According to the analysis of Lassaigne,(1) the teeth of the shark yield

Phosphate of lime . .	52, 6
Carbonate of lime . .	13, 9
Animal matter . .	33, 5
	100, 0

The inferior pharyngeal teeth of the carp contain

Phosphate of lime . .	49
Carbonate of lime . .	16
Animal matter . . .	35
	100,0

(1) Berzelius, Traité de Chimie, par Esslinger 1828, tom. vii, p. 480.

In the brown upper pharyngeal tooth of the carp, Stromeyer(1) detected a small proportion of magnesia.

8. *Structure.*—The tubular structure common to the dentine of all classes of animals, though not first discovered in the teeth of fishes, has been most frequently recognised, because most conspicuous, in them: and, as in several fishes, the coarser features of this structure are obvious to the naked eye, it was admitted as applicable to a greater or less proportion of that class by some comparative anatomists, before the researches of Purkinje and Retzius had established its existence in the teeth of the higher vertebrate animals. Leeuwenhoek, indeed, in his account of the minutely tubular structure of the teeth of man and of the ox,(2) attributes the same structure to the tooth of the haddock, in which he states that the dental tubes are smaller than in the ox. Mr. André(3) detected the ramified canals which pervade the substance of the tooth of the Acanthurus. Cuvier(4) first described the coarser tubes composing the teeth of the rays and of the wolf-fish; and Von Born(5) ascribes to the teeth of a greater number and variety of fishes the same structure, which was regarded by both these anatomists as analogous to the tubular structure of the teeth of the ornithorhynchus and orycteropus, and also compared with that of whalebone and of the horn of the rhinoceros. Such comparisons, however, are wanting in accuracy when applied in that loose and general manner.

In the following pages there will be shown to be, at least, four principal modifications of the tubular structure in the teeth of fishes. Premising that the essential character of this structure is a *cavitas pulpi*, or medullary canal, from which the calcigerous tubes radiate, the first modification which may be noticed is where the tooth is traversed by a number of equidistant and parallel medullary canals, each canal and its system of medullary tubes representing a cylindrical or prismatic denticle, and being separated from the contiguous denticles by a thin coat of bone or cement. This modification is exemplified in the rostral teeth of

(1) Gilbert's Annalen, Bd vii, 1811.

(2) Philos. Trans., 1678, p. 1003.

(3) Ib. vol. 74, Description of the teeth of Chætodon (Acanthurus) nigricans.

(4) Leçons d'Anat. Comparée, tome iii, p. 113 (1805).

(5) Heusinger's Zeitschrift, Bd. i, 1827.

the saw-fish, *(Pristis)*, the tesselated teeth of the eagle-rays, (*Myliobates*, *Zygobates*, &c.), and the maxillary plates of the chimæroids. The dense dental case of the jaws of the parrot-fishes, (*Scarus*), may likewise be regarded as an extreme instance of this modification, and we shall find the same structure re-appearing in some of the inferior genera of the mammiferous class. In the parrot-fishes, the denticles are quite distinct from one another, but in the saw-fish, chimæra, and eagle-rays, the contiguous medullary canals occasionally anastomose together. In the chimæroid fishes these anastomoses are more numerous, and the boundaries of the component denticles less distinct, so that they form a transition between the preceding, and what may be regarded as the second variety of the tubular structure.

In this modification, the substance of the tooth is traversed by medullary canals, somewhat less regularly equidistant and less parallel than in the first; having the boundaries of their respective systems of radiated calcigerous tubes indicated by the minute calcigerous cells, with which the terminal branches of those tubes communicate; these boundaries being more or less obscured by the terminal branches of the calcigerous tubes extending across into the interspaces of the corresponding branches of an adjoining system of tubes, and anastomosing with them immediately, or through intervening dilatations or cells. The medullary canals here dichotomize more frequently than in the first modification; their anastomoses are more numerous, and the whole tooth, which is generally of large size, is consequently more individualized and compacted. The teeth of the Port-Jackson shark (*Cestracion Phillippi*,) afford a good example of this modification, which also prevails in those of the extinct genera *Ptychodus*, *Psammodus*, *Helodus*, *Ctenoptychius*, &c. In the teeth of the extinct *Acrodus*, the medullary canals, which likewise traverse in great numbers the body of the tooth, assume a more or less wavy course; and this disposition, combined with their numerous anastomoses, leads to the third modification, which at the same time is the most common and characteristic of the dental structure, in the class of fishes.

In teeth manifesting this variety of the tubular structure, the dentine is permeated by a network of medullary canals, of which the

interspaces are occupied by the calcigerous tubes and cells. The medullary canals are directly continued from those of the common bone with which the base of the tooth is anchylosed, or into which it has been converted. As the medullary canals proceed through the tooth, they maintain a course more or less parallel, and more or less straight, or wavy; but they ramify abundantly, and gradually diminish in calibre as they approach the surface of the tooth. The illustrations of this modification of the dental structure in the present work, are taken from the teeth of the extinct *Lamna*, *Dictyodus*, and *Saurocephalus*, and from those of the recent *Sphyræna* and *Acanthurus*. In the latter genus the dendritic arrangement of the medullary tubes recognized by Mr. André, has subsequently been figured by V. Born. V. Born and Retzius have described a similar structure in the teeth of the wolf-fish (*Anarrhichas*), of which Mr. Nasmyth has given a figure in his useful translation of some of the recent treatises on dental anatomy.

The reticulate medullary tubes pervade the structure of the teeth of the percoid, sciænoid, cottoid, and gobioid families of fishes; and of those of the *Capros*, *Naseus*, and other genera of the *Theuties* of Cuvier, besides the teeth of the *Acanthuri* already cited. A similar reticulate structure is common to the teeth of the *Chætodontes* and the *Pleuronectes*: in the cycloid fishes, we find it almost universal in the scomberoid, lucioid, salmonoid, and clupeoid families: it is exchanged for a higher type of structure in the maxillary teeth of the lophioid fishes, and in the pharyngeal teeth of the cyprinoids, but it again reappears in the teeth of the blennioid, gadoid, and murænoid families; and the same coarse bone-like structure pervades the dental plates of the supposed amphibious *Lepidosiren*.

The higher type of structure just alluded to is that which characterises the teeth of most reptiles and mammalia. Here the dentine consists of a single medullary or pulp canal, and a single system of calcigerous tubes radiating from the central or sub-central canal, at right angles to the periphery of the tooth. The teeth of the extinct sauroid fishes and pycnodonts, the maxillary teeth of the existing file-fishes (*Balistes*), and angler (*Lophius*), the incisors, canines, and molars of the breams or sparoid fishes, the pharyngeal pavement-teeth of the wrasse-tribe (*Labridæ*), the maxillary and

pharyngeal denticles of the scari, and the lamelliform denticles of the crop-fishes, *diodon* and *tetrodon*, likewise the maxillary teeth of some of the genera of sharks and rays, afford examples of this structure.

I have spoken of it as belonging to a higher type because it is characteristic of the teeth of the vertebrate animals which are higher in the scale than fishes; but if the grade of organization of a tooth be rated according to the proportion of vascular substance and vital power which it possesses, then those teeth which most resemble bone should be regarded as the most highly organized, and such are the teeth most common in the class of fishes.

As the inorganic calcareous particles are deposited principally in the parietes of the calcigerous tubes and their terminal ramuli and cells, it follows that the density of the tooth will increase, and its vital properties diminish as the calcigerous preponderate over the medullary tubes, and in proportion as the calcigerous tubes in a given space are more numerous and minute. But the change from one modification of dental structure to another, from bone to the densest ivory, is so gradual, that the physiologist, entertaining a belief in the inorganic nature of the teeth, would be at a loss where to draw the line, or to determine where the vital forces ceased their manifestation, and at which step in the series of tubular structures the tooth became an inert body. The uniform result of my researches, on the structure of the teeth in all grades of vertebrate animals, and in their natural and diseased states, has been a conviction of the untruthfulness of the terms inert, dead, and unorganized as applied to the substance of any tooth whatever. Extra-vascular undoubtedly is all that portion which consists of the calcigerous tubes; the capillary circulation is confined to the pulp or medullary canals; but since every secretive process and the development of the primordial cells of every tissue are due to changes produced in the liquor sanguinis transuded from and beyond the sphere of the ultimate capillaries, the absence of these vessels in the dense dental substance is as little conclusive against its vital and organized nature, as it would be to prove the inert condition of the germinal membrane of the ovum before the thirtieth hour of incubation.

In no teeth is the dentine rendered so dense as in those of certain

fishes, especially the *Scarus* and *Diodon*, which have been cited as examples of the fourth modification of the dental structure. These teeth strike fire with steel, yet they present an organized structure of minute complexity, and the calcigerous tubes are nowhere so numerous, so minute, so beautifully ramified and interlaced together.

It has already been observed that the prismatic maxillary denticles of the *Scarus*, being compacted together side by side and with their single medullary canals parallel to each other, produce a compound dental plate analogous to those which were first cited in illustration of the present subject. In the *Diodon*, each denticle, which is composed as in the *Scarus* of a single system of minute calcigerous tubes, assumes the form of a thin plate: the pulp cavity instead of being contracted into a tube, as in the elongated teeth, is here spread over the under surface of the dental lamella; the calcigerous tubes proceed in a direction more or less vertical to the upper surface (in the teeth of the lower jaw); and the compound dental mass results from the superposition and successive development of similar plates, separated only by a layer of thin bone or cæmentum. In the pharyngeal teeth of the *Scarus*, the denticles are also more or less lamelliform, but their position is vertical, and they are joined side to side by means of the intervening cement or the ossified capsule: compound dental masses similarly constructed are present in the capybara, elephant, and others of the mammalia, generally cited as affording examples of the most complex teeth.

9. *Development.*—The teeth of fishes are formed according to the general laws of dental development already discussed;(1) but the process, in many instances, does not extend beyond the earlier and simpler stages observable in the higher classes of animals. In all fishes, as in other vertebrate animals, the first step is the production of a simple papilla from the free surface of either the soft external integument, as in the young *Pristis*,(2) or of the mucous membrane of the mouth, as

(1) Introduction, p. vi.

(2) A very close analogy exists between the dermal bony tubercles and spines of the cartilaginous fishes and their teeth. The thick enamelled scales of the ganoid fishes of Agassiz exhibit an organization similar to that of the teeth: the system of minute parallel tubes, with their branches and anastomoses, in the thick scales of the extinct *lepidotus*, is as complicated as in

in the rest of the class. In these primitive papillæ there can be very early distinguished a cavity containing fluid, and a dense membrane, *(membrana propria pulpi)* surrounding the cavity, and itself covered by the thin external buccal mucous membrane, which gradually becomes more and more attenuated as the papilla increases in size. In some fishes, as the sharks and rays, the dental papillæ do not sink into the substance of the vascular membrane from which they grow, but become buried in depressions of an opposite fold of the same membrane; these depressions enlarging with the growth of the papillæ, and forming the cavities or capsules in which the development of the tooth is completed. They differ from the capsules of the matrix of the mammiferous tooth in having no organic connexion with the pulp, and no attachment to its base: the teeth when fully formed are gradually withdrawn from the above described extraneous capsules, to take their place and assume the erect position on the alveolar border of the jaws.

Here, therefore, is represented on a large and, as it were, persistent scale, the first and transitory papillary stage of the development of the mammalian teeth; and the simple crescentic cartilaginous maxillary plate, with the mucous groove behind it containing the germinal papillæ of the teeth, offers in the shark a magnified representation of the earliest condition of the jaws and teeth in the human embryo.

In many fishes, as the lophius and pike, the dental papillæ become buried in the membrane from which they arise, and the surface to which their basis is attached becomes the bottom of a closed sac. But this sac is never lodged in the substance of the jaw, the development of the tooth being completed in the tissue of the thick and soft gum or mucous membrane from which the papillæ were originally developed: hence teeth in various stages of growth are frequently brought away with that membrane when it is reflected from the jaw-bone. The ultimate fixation of the teeth, so formed, is effected by the development of ligamentous fibres in the submucous tissue between the jaw and the base of the tooth; which fibres become the medium

many teeth, and equally militates against the theory of formation by transudation of layers being applied, at least, to the ganoid scales.

of connexion between those parts, either as elastic ligaments, or by continuous ossification.

Here we have the second step in the development of the mammalian tooth represented, viz: the imbedding of the pulp in a follicle of the mucous membrane; but the eruptive stage of the tooth takes place without any previous inclosure of the follicle and pulp in the substance of the jaw.

In the *Balistes*, *Sparoids*, *Sphyræna*, *Scarus*, and many other fishes, the formation of the teeth presents all the usual stages which have been observed to succeed each other in the dentition of the highest organized animals: the papilla sinks into a follicle, becomes surrounded with a capsule, and is then included in a closed alveolus of the growing jaw, where the development of the tooth takes place, and is followed by the usual eruptive stages.

The development of the dental pulp in fishes, prior to the deposition of the calcareous particles in it, corresponds in the main with the process described by Purkinje and Raschkow in the mammalia. The pulp-substance, or contents of the *membrana propria* remain, in fishes, for a longer period in a fluid or semi-fluid state, and the granules or nucleated cells which are first developed, float loosely or in small aggregated groups in the sanguineo-serous fluid: they first attach themselves to the inner surface of the *membrana propria*, if these be not originally developed from that surface, and the whole of the contents of the growing pulp becomes soon after condensed by the numerous additional granules which are rapidly developed in it after it has become permeated by the capillary vessels and nerves. The arrangement of these particles into linear series, or fibres, is first observable at the superficies of the pulp to which the fibres are vertical: and, at this period, ossification has commenced in the dense and smooth *membrana propria* of the pulp: it is thence continued centripetally in the course of the above-mentioned lines, towards the base of the pulp, either regularly progressive, as in the incisors of the *Sargus* and *Balistes*, or radiating, as in *Sphyræna* and (if we may judge by *à posteriori* observation of the structure of the fully developed teeth) in most other fishes, from the various centres formed by the persistent capillaries of the pulp, around which the cells or granules become

condensed into concentric layers, which then become, as they are successively impregnated with the calcareous salts, the walls of the medullary canals.(1)

In the shark, and all those fishes in which the teeth are completely formed without going beyond the papillary stage of development, there is no distinct enamel-pulp; the dense exterior layer of the tooth is formed by the calcification of the 'membrana propria' of the pulp, which, therefore, precedes the formation of the ordinary dentine. But in the file-fish *(Balistes)*, the sargus, the gilt-head *(Chrysophrys)*, and some other fishes, a conspicuous enamel-pulp is developed from the inner surface of the capsule which surrounds the bone-pulp: this enamel organ terminates, as in the human subject, before the capsule is reflected upon the base of the pulp. It has a firmer tissue, more closely resembling that of the ordinary pulp, than in the mammalia: and, when examined under the microscope, presents numerous and close-set fine fibres near that surface which is next the bone-pulp, and to which these fibres are generally placed at right angles. The base of the enamel organ, which is attached to the capsule, presents a granular and fibrous tissue blended together. I have not been able to trace any capillaries from the capsule into the substance of the

(1) In those fishes, and they include the greatest part of the class, in which the teeth are attached by anchylosis to the jaws, the mode in which the calcareous particles are deposited in the gelatinous frame-work or pulp is modified as the calcification approaches more or less gradually towards the base of the tooth, until at length the pattern or texture of the calcified pulp cannot be distinguished from that of the bone with which it thus becomes continuous. It is not without interest to observe how Cuvier, who had clearly detected this actual ossification of the base of the pulp in the teeth of many fishes and reptiles, should have conceived it to be a process so distinct from that peculiar to the supposed inorganic tooth, that he felt himself called upon to correct the error he had fallen into in stating, in his "Leçons d'Anatomie Comparée," this ossified base of the anchylosed tooth to be its root. Describing the teeth of lizards, in his "Ossemens Fossiles," tom. V, 2e partie, p. 274, Cuvier says:—"Cette base ne se divise point en racines; mais quand la dent a pris son accroissement, il arrive le même phénomène que dans les poissons. Le noyau gélatineux s'ossifie; il s'unit intimement d'une part, à l'os de la mâchoire, en contractant, de l'autre, une adhérence intime avec la dent qu'il a exsudée.—J'avais déjà exposé l'histoire de cette dentition dans mes Leçons d'Anatomie Comparée, III. iii. 113, etc.; mais j'y ai aussi commis l'erreur d'appeler *racine* cette partie celluleuse et osseuse qui s'unit à l'os maxillaire." The application of the microscope to the investigation of the structure of the teeth has brought to light many instances in which the *crown* of the tooth ought, for the same reasons, to have as little title to be considered a part of the tooth as the root.

enamel-pulp. In the incisors of the sargus, the development of the enamel and dentine begins simultaneously upon the contiguous surfaces, and when we observe how close and compact is the package of the matrix of the tooth in the alveolar cavity of the jaw, it is hardly possible to conceive how either of these substances could be the product of transudation from their respective pulps. It is, however, easier to separate the primary layers of the enamel and dentine from their respective pulps than from each other; yet if the denuded surfaces of the uncalcified portions of the pulps be examined by reflected light under a compound lens of a half-inch focus, they are seen to be ragged and punctate, and evidently different from the original surfaces prior to the commencement of the deposition of the calcareous salts in them. The formation of the enamel resembles more closely that of the dentine in the fishes cited than it does in the mammalia, and the enamel contains a greater proportion of persistent animal matter.

The course of calcification of the two pulps takes opposite directions, and in the balistes, the process finishes by the ossification of the outer layer of the capsule itself, by which both the enamelled crown and the base of the tooth are coated with a thin layer of bone. I have not been able to discern any radiated cells in this analogue of the "crusta petrosa," or cement of the mammalian teeth. It soon wears off from the crown of the extruded tooth.

In all fishes, the teeth are shed and renewed, and this not once only, as in most mammalia, but frequently and during the whole life time of the animal.(1) Fishes, indeed, can hardly be said to have permanent teeth. The rostral teeth of the pristis constitute, perhaps, the sole exception; and these may be regarded rather as modified dermal spines.

In all cases where the first teeth are developed in alveolar cavities, the succeeding ones follow them in the vertical direction, and owe the origin of their matrix to the continuation, from the mucous capsule of their predecessors, of a cæcal process, in which the papillary rudiment of the dental pulp is developed according to the laws explained in the

(1) In a few cases it is observed, that as the fish gets old, some of the deciduous teeth are not replaced; in old *Salmonidæ*, the vomer thus becomes edentulous, or nearly so.

General Introduction. But in the great majority of fishes, the germs of the new teeth are developed, like those of the old, from the free mucous membrane of the mouth throughout the whole period of succession, a condition which is peculiar to the present class. The angler, the pike, and many of our common fishes, illustrate this mode of dental reproduction: it is very conspicuous in the cartilaginous fishes, in which the entire phalanx of their numerous teeth is ever moving slowly forward in rotatory progress over the alveolar border of both upper and lower jaws, the teeth being successively cast off as they reach the outer margin, and new teeth rising in equal proportion from the mucous membrane behind the rear rank of the phalanx.

This endless succession of new and sometimes, as in *Balistes*, and *Sargus*, of highly complicated matrices,—this constant development of a new apparatus for the production of each new tooth, even where its final development is unaccompanied by an eruptive stage, and where the destruction of any part of the formative apparatus is not a necessary consequence of the completion of the tooth, could hardly seem other than a waste of the formative energies to the reflecting physiologist entertaining the doctrine of dental development by transudation, and by whom the dental pulp must have been regarded in the capacity of a gland. The destruction or waste of other glands by no means follows the natural exercise of their functions: the disappearance of the pulp *pari-passu* with the growth of the tooth, is only an inevitable consequence when that growth is effected by deposition of the calcareous particles in the substance, instead of by transudation from the surface of the formative pulp, and when fresh material is not progressively added to the base of the pulp. In the cyclostomous fishes, where the albuminous, horn-like teeth seem really to be transuded from the pulp, these are persistent; and the new teeth are formed immediately beneath the old, and from the same surface of the reproductive pulp.

CHAPTER II.

TEETH OF CYCLOSTOMES.

MYXINES.

10. In the class of fishes, as in that of reptiles and mammalia, there are species which are wholly destitute of teeth. These edentulous fishes are most common in the cartilaginous division of the class. The sand-prides (*Ammocetes*), the sturgeons (*Acipenser*), the paddle-fishes (*Planirostra* and *Aodon*), are examples. The whole order of *Lophobranchii* of Cuvier, which includes the pipe-fishes (*Syngnathus*), and the *Hippocampus*, is edentulous.

The lowest organized fishes with worm-like bodies and parasitic habits, as the myxinoids and lampreys, are also destitute of true calcified teeth, but have them replaced by horny substances of a conical, sharp-pointed, and often slightly recurved form, resembling the teeth of the entozoa, the habits of which these suctorious fishes simulate. The hag-fish (*Myxine glutinosa*), and other cognate species now grouped together by Müller under the genus *Bdellostoma*, have a single tooth on the median line of the palate, and a double serrated horny plate on each side of the upper surface of the tongue. The palatal tooth(1) is moderately long, conical, and recurved, with a tumid margin around its base, which is hollow, and supported upon a conical pulp, firmly attached to a fibro-cartilaginous plate,(2) situated beneath the anterior commissure of the palatal cartilage. The basal-plate of this tooth is further attached by ligaments, the anterior of which passes to the hinder part of the rostral cartilage, and the posterior one to a cavity at the commissure of the marginal palatal cartilage.

The lingual dental plates(3) are four in number, two on each side, of a curved form, hollow at the base, and implanted, like the palatal tooth, on a reproductive pulp of a corresponding form.(4) This pulp, and the margin of the base of the dental plates are attached to the perichondrium of the lingual cartilage. The dentations of these lingual plates are conical, sub-compressed, sharp-pointed, with the

(1) Pl. 2, fig. 1, *b*. (2) *ib*. *a*. (3) *ib*. fig. 2, *b*. (4) *ib*. fig. 3, *d*.

points reflected backwards. They are usually described as distinct teeth, and, viewed as such, form two concentric curved lines interrupted at the middle of the tongue. In the *Myxine glutinosa* the number of lingual teeth is $\frac{8-8}{8-9}$, *i. e.*, there are eight teeth in both the right and left anterior rows, while there are eight in the left posterior row, and nine in the right posterior row. In the *Bdellostoma heptatrema*, there are $\frac{8-8}{7-8}$ lingual teeth; in *Bdell. heterotrema*, the number is $\frac{12-12}{11-12}$; in the *Bdell. hexatrema*, the lateral rows of lingual teeth are symmetrical, being $\frac{11-11}{11-11}$; in *Bdell. cirratum*, there are $\frac{12-12}{11-11}$ teeth; in *Bdell. dombeyi*, the number is $\frac{11-11}{7-7}$. These formulæ appear to be constant in the species; this is, at least, the case in the glutinous hag. The middle teeth are always the longest, the rest gradually diminish towards the lateral extremities of the rows.(1)

I have already alluded to the parasitic habits of these low organized fishes. When they first attach themselves to their prey, the single median recurved palatal tooth is thrust into its flesh, and serves as a holdfast, while the work of destruction is carried on by the laterally opposed lingual saws, aided by the suctorious action of the mouth. The usual situation in which the myxine is found, is the interior of a cod or other large fish, into whose carcase it has thus penetrated, and on whose soft parts it has preyed.

LAMPREYS.

11. In the lampreys *(Petromyzon)*,(2) there are labial and inferior maxillary, as well as palatal and lingual teeth; all these are likewise horny substances, of a simple, conical, sharp-pointed, form, and of a somewhat less dense texture than in the myxinoids. They are hollow, and supported on conical, reproductive pulps. The pulps of the labial teeth are firmly attached by their base to the fibrous tissue of the lining membrane of the lip.

The labial teeth of the outer or marginal circle are the smallest; from these, the teeth increase in size as they approach the centre of the cavity of the mouth. The converging series in the mesial plane are arranged in a straight line; those of the sides in curved lines, with the concavity towards the lower margin of the mouth. In the

(1) See Müller, über den Myxinoiden, p. 20. (2) Pl. 2, figs. 4 and 5.

Petromyzon marinus, the innermost teeth of four of the lateral series on each side are bicuspid, or consist each of two cones, which are confluent at the base. There are twenty converging rows of labial teeth in this species, and from four to eight teeth in each row.

The single tooth supported by the palatal cartilage(1) and analogous to that in the myxinoids, consists here of two horny cones, placed in the transverse direction, and joined, in the *Petr. marinus*, in the median line. In the lampern (*Petr. fluviatilis*) the cones are more remote. The matrix of this tooth is hollow at the base, and is supported on a conical process of the palatal cartilage, which Cuvier describes as the upper jaw. The broad bicuspid palatal tooth is opposed by the dentated semilunar horny plate, with which the cartilage, representing the lower jaw,(2) is sheathed. This plate consists of eight conical teeth, laterally united together; its reproductive matrix is fixed upon a prominent semilunar ridge at the anterior part of the mandibular cartilage.

The lingual teeth consist of three dentated horny plates, the dentations being much smaller than in the palatal or mandibular plates, or than in the lingual plates of the myxinoids. But their analogy with the latter can be readily traced, the third or posterior lingual plate of the lampreys evidently corresponding with the two posterior lingual plates of the myxinoids conjoined.

Each of the anterior lingual plates is slightly concave, with the mesial extremity abruptly bent towards the upper surface of the mouth; its anterior margin is divided into eleven sharp-pointed, recurved, minute, dental processes. The posterior and inferior dental plate may be said to consist of two similar but smaller semilunar pieces, with the mesial margins approximated and conjoined; the number of dentations on each of the lateral moieties of this lingual armature, is seven.

The mode of development and reproduction of all these teeth is the same both in the myxinoids and lampreys. The matrix is persistent, as in most other horny productions, and the new conical tooth is developed immediately within and beneath the base of the old one; the same secreting surface which formed the one, produces

(1) Pl. 2, fig. 5, *a*. (2) *ib. b*.

the other. A vertical section of any of the teeth of the lamprey displays one or two cones of reserve, between the tooth in use, and the surface of the matrix;(1) and the outermost is in general readily displaced; often, indeed, difficult to preserve *in situ* in the preparation.

Thin transverse sections of the teeth of the lamprey, viewed by a magnifying power of a quarter of an inch focus,(2) exhibit their structure as composed of closely-aggregated parallel tubes, placed perpendicular to the secreting surface, and having a diameter of $\frac{1}{4000\text{th}}$ of an inch.

In chemical composition, the teeth of the Cyclostomes resemble horn.

CHAPTER III.

TEETH OF PLAGIOSTOMES.

SHARKS, OR SQUALOIDS.

12. All the genera of true or fixed-gilled plagiostomes, save *Pristis*, are characterised by numerous teeth, which are restricted in their situation to the upper and lower jaws. Here, they are arranged in a greater or smaller number of rows, which succeed each other from behind forwards, and are attached only to the mucous and fibrous membranes covering the maxillary cartilages.

Before entering upon the consideration of the teeth, a few words seem necessary respecting the analogies of these dentigerous cartilages or jaws. In the common skate, they are in the form of simple arches, each arch consisting of a pair of cartilages joined together by a ligamentous symphysis at one extremity, and suspended by the opposite end through the medium of a common cartilaginous pedicle from the sides of the cranium. This pedicle is obviously the homologue of that to which the lower jaw is suspended in the higher oviparous vertebrates, and which includes more or fewer

(1) Pl. 2, fig. 6.

(2) The instrument employed in these observations, and referred to throughout the present work, is the compound achromatic microscope of Ross.

elements of the temporal bone. In its simplicity, in the plagiostomes, it participates with the character of the rest of their cartilaginous cranium, in which the several distinct bony elements found in the reptiles and osseous fishes cease to be recognisable. Of the several bones concerned in the formation of the jaws, we have to seek, in the simple cartilaginous arches of the skate, the pterygoid, palatine, maxillary, intermaxillary, mandibular, and premandibular bones; and to these may be likewise added the labial cartilages, which are so largely developed in the cyclostomous fishes. Are all these elements combined in the dentigerous cartilages of the skate? or if not all, which? These questions have been differently answered by different comparative anatomists. The essential character of the pterygoid and palatine bones manifests itself, in the oviparous classes, in the formation of buttresses extending between the vomer and the articular pedicle of the jaw. In the *Carcharias glaucus*, or blue-shark, and in the *Lamna*, or porbeagle, a distinct flattened process of cartilage extends from each side of the vomerine region of the skull, and abuts against the proximal extremity of the pedicle, and the contiguous part of the cranium. These processes, I regard as analogous to the palato-pterygoidean buttresses. In the common torpedo, there is a distinct cartilage in the corresponding situation, and in the Brazilian torpedo,(1) Dr. Henlé has discovered a second broader cartilage, anterior and internal to the pterygoidean pedicle, and which he considers to be the analogue of the true palatine bone; this cartilage has not been found separately developed in any other plagiostome.

With respect to the labial cartilages these are wanting, according to Müller, in the following subgenera of the ray tribe, *Raia*, *Trygon*, *Rhinobates*, *Cephaloptera*, and *Myliobates;* they are also absent in the *Carcharias*, *Cestracion*, and *Pristis* among the sharks. They are present in the Tope (*Galeus*), which has one on each side of the upper lip; in *Scymnus* there are corresponding cartilages, which are elongated and extend below the angle of the mouth; in *Scyllium* and *Mustelus*, there is one on each side of both upper and lower lips;

(1) *Torpedo braziliensis*, the type of the sub-genus *Narcine* of Müller and Henlé.

in *Centrina*, and *Squatina*, there are two on each side of the upper, and one on each side of the lower lip; these are figured at *a b* and *c*, Pl. 10, fig. 2, in the monk-fish. In the *Narcine* or Brazilian torpedo, distinct labial cartilages are associated with the dentigerous maxillary arches, and also with the palatine and pterygoidean cartilages; Professor Müller has, therefore, rejected the interpretation of Cuvier, according to which, the anterior or superior dentigerous arch of the plagiostomes is the homologue of the palatine bones, and the posterior one, the homologue of the post-mandibular element of the lower jaw, the intermaxillary, maxillary, and premandibular bones being represented by the edentulous labial cartilages. This interpretation, besides being invalidated by the anatomy of the *Narcine*, also involves the anomaly of the teeth being developed on the articular, or post-mandibular element of the lower jaw, where they are never situated in any other vertebrate animal. A more extended comparison than Cuvier had the means of instituting, and especially a study of the structure of the cranium of the *Cestracion*, in which the labial cartilages have disappeared, and the development of the dentigerous arches have advanced nearer to the osseous type than in other plagiostomes, clearly prove that the dentigerous cartilaginous arches of the sharks and rays represent, the one, the combined maxillaries and intermaxillaries, the other, the confluent articular and dentary elements of the lower jaw.

The teeth are not immediately connected with these cartilaginous arches; no cartilaginous fish has teeth implanted in maxillary alveolar cavities, or confluent with the substance of the jaw even when the external crust is ossified, but they are always attached as already stated, to the fibrous and mucous membranes which cover the maxillary cartilages;(1) hence, it occurs in certain genera, as *Myliobates* and *Scymnus*, that a single tooth in the median plane may lie directly across the symphysis, and be supported by the two rami of the jaw. The plagiostomes, like many other natural families of fishes, pre-

(1) Any organic fossil which exhibits a tooth implanted by two fangs in a double socket must be mammiferous, since the only fishes' teeth which approach such a tooth in form are those with a bifurcate base, belonging to certain sharks, while the socketed teeth of reptiles have only a single fang.

sent such modifications of their common and characteristic type of structure as fits them for very different habits of life and the acquisition of different kinds of food. The active, and predatory sharks are here associated with the sluggish omnivorous rays, and the dental system presents every grade of modification from the laniary to the molary type; the *Lamna* with its teeth exclusively adapted for holding, piercing, and lacerating, and the *Myliobates* with its maxillary mosaic pavement of flattened molars forming the two extremes of the series.

13. The sharks, or *Squaloid* plagiostomes, with few exceptions, have teeth of a conical, sharp-pointed, more or less compressed form; sometimes with trenchant or serrate edges and accessary basal denticles; they are arranged along the margin and posterior surface of the jaws in close-set vertical rows, of from three to thirteen teeth in each row, according to the species. The teeth of the contiguous rows in certain genera, as *Selache*, and *Lamna*, are parallel with each other, but in *Galeus*, and *Carcharias*, they are placed alternately, so that the base of one tooth advances laterally into the interspace of two teeth of the contiguous row, and reciprocally; but the laterally contiguous teeth are never articulated with each other as in certain rays. In the *Scymnus*, the median row of teeth crosses the symphysis of the jaw, and their base overlaps the adjoining margins of the contiguous teeth; the lateral teeth have an imbricated arrangement.

In general the anterior or external tooth only of each row is erect, the rest being recumbent; the contrast, in this respect, is most marked in the lower maxillary lancet-shaped teeth of the *Scymnus*, (Pl. 4, fig. 3). In *Lamna*, however, the second and third teeth are commonly seen in positions intermediate between those of the erect anterior and the recumbent posterior teeth, (Pl. 5, fig. 1,) and in the rays where the teeth are much more numerous in each row than in the sharks, they exhibit every gradation between the recumbent, reflected, erect, and porrect positions. It is scarcely necessary to repeat, that although the teeth of the sharks possess greater individual mobility than those of the rays, the recumbent ones cannot, as has been supposed, be voluntarily erected; these teeth are still in progress of development, and several of them are covered by a re-

flection of the mucous membrane of the mouth, which would be lacerated by such a movement; it is by a gradual change of position in the fibrous membrane to which their base is attached, that the altered direction of the consolidated teeth is effected.

The teeth present the smallest relative size among the sharks, in the sub-genus *Rhinodon* of Dr. Smith, where they may be compared with the teeth *en brosse*, of certain osseous fishes; here they are of a simple conical, slightly recurved form; there are twelve or thirteen teeth in each vertical row, and about two hundred and fifty of such rows in each jaw.

In the sub-genus *Selache*, to which the great basking shark, (*Squalus maximus*, Home), belongs, the teeth, though small, are relatively larger than in *Rhinodon*. They are conical, recurved, and with a somewhat obtuse apex. In a specimen about thirty-six feet in length, the teeth, which are alike in both jaws, measure not quite half an inch in length, and between two and three lines across their rounded base. The sharks with teeth of larger size and more formidable aspect present many modifications of shape, by which, with other characters, the genera and sub-genera of squaloids are distinguishable. The principal varieties of form are illustrated in plates 3 and 4. Varieties of form, however, it should be remembered, are not only indicative of generic distinctions, but sometimes of a difference of age of the same individual. In the common spotted dog-fish, for example, the one or two lateral denticles at the base of the principal cusp described as characteristic of the teeth of the genus *Scyllium*, frequently disappear in the old fishes. In the young of the blue-shark (*Carcharias glaucus*) the teeth have smooth trenchant edges, but in the old ones, the margins are dentated. In many genera, again, the teeth of the upper differ in form from those of the lower jaw; this is most remarkably the case in the genus *Scymnus:* they also frequently differ in shape as well as in size in different parts of the same jaw. But while a knowledge of these facts should impress the observer with due caution in giving an opinion on the specific or generic relations of an extinct shark from the examination of a single tooth, the peculiarities of form characteristic of different genera of existing squaloids are sufficiently constant and well marked to render dental

characters of great value in the determination of both recent and extinct forms.

The teeth of the genus *Lamna* present an elongated triangular sub-compressed form, with the anterior or outer surface less convex than the posterior, especially in the median teeth and in those of the lower jaw. The margins are trenchant and converge to a sharp point, equally or symmetrically in the median teeth, but unequally in the lateral ones in which the point is inclined backwards. In some species, as in the porbeagle shark (*Lamna Cornubica*), and in that great extinct species of which the teeth occur in the London clay and other members of the eocene formation in this country, and on which Agassiz has founded his sub-genus *Otodus*,(1) the teeth are complicated by a small accessory cusp on each side of the base of the principal cone. In other species, as in the *Lamna oxyrhina* of Cuv. and Val., (Pl. 3, fig. 1,) the accessory cusps are wanting, at least in large and full grown specimens: in both subgenera of *Lamna*, the third vertical row of teeth counting backwards in the upper jaw is much smaller than the contiguous rows(2) ; the rest gradually diminish in size as they are situated nearer the angles of the mouth. In the sub-genus *Odontaspis*, the teeth are narrower than in *Lamna*, the middle cusp is longer, straighter, and more acute, and is provided with two similar sharp pointed cusps on each side of its base. In the upper jaw, the fourth, fifth, sixth, and seventh vertical rows of teeth are smaller than the contiguous ones ; in both jaws, the first tooth is small and the posterior teeth progressively diminish as they approach the angles of the mouth.(3) The size and strength of the teeth thus modified for piercing and lacerating render the *Odontaspis* the most formidable among the shark tribe ; and the habits of the typical species, (*Odontaspis ferox*) as indicated by its trivial name, correspond with

(1) Pl. 5, fig. 5.

(2) M. Agassiz in his description of the dentition of this genus, mentions as one peculiarity of it that, " la troisième et quelquefois la quatrième et la cinquième dent de la *mâchoire inférieure* est sensiblement plus petite que les autres, tandis qu'à la *mâchoire supérieure* les dents, à l'exception de la première qui est plus petite que les suivantes, vont en diminuant uniformément de grandeur jusqu'à la partie postérieure de la gueule." In a skull of the *Lamna Cornubica* now before me, I find, as in the *Lamna oxyrhina*, (Pl. 3, fig. 1,) that the sudden diminution of size in the third tooth is characteristic of the upper and not of the lower jaw.

(3) Pl. 3, fig. 2.

the destructive character of its maxillary armour. The characteristic dentition of the shark tribe may be studied with advantage in the spotted and spiny dog-fishes common on our coasts; the former, which is the type of the genus *Scyllium*, exhibits teeth of a triangular form with a large middle cusp, complicated, at least, in the young animal, with one or two small cusps on each side of its base; the base is always more or less furrowed longitudinally. In *Crossorhinus*, a sub-genus of *Scyllium*, the teeth are characterized by having the osseous base divided into three lobes. In *Ginglimostoma*, the teeth have a simple rhomboidal base supporting one large median cone, and from two to four obtuse denticles on each side: the teeth of this genus of dog-fish are remarkable for their somewhat unusual number, there being frequently ten in each vertical row.

In the spiny or piked dog-fish (*Spinax*, Cuv.), the teeth (Pl. 3, fig. 3,) are alike in both upper and lower jaws; they are thin triangular plates with the apex inclined backwards, so that the anterior edges are opposed to each other; the enamel does not terminate below in a horizontal line, but is continued along the middle of the bony base. In an allied species, the teeth of the upper jaw are smaller and of a different form from those of the lower jaw, being tricuspid, as in the spotted dog-fish; some ichthyologists restrict the subgeneric name *Spinax* to the spiny dog-fishes which are characterized by this modification of the teeth.

In the genus *Notidanus*, the teeth are not only of different forms in the upper and lower jaws, but also vary considerably, in this respect, at the anterior and posterior regions of the same jaw, (Pl. 3.) In the upper jaw, the anterior teeth are large, compressed, triangular plates, with the pointed apex arched backwards, and the margins slightly dentated, except in the two anterior ones. The posterior teeth are in the form of simple obtuse furrowed tubercles. In the lower jaw, the large anterior teeth have the apex less produced; the anterior margin is finely serrate, and the posterior divided into three or more denticles. The posterior minute teeth resemble those in the upper jaw. Of the larger teeth there are rarely more than four in each vertical row.

In the subgenus *Carcharias*, the teeth present the form of

triangular plates with a broad base, sharp apex, and trenchant or finely dentated edges. The anterior surface is nearly flat, the posterior slightly convex: the teeth of the lower jaw are rather narrower, and thicker, and somewhat smaller than those of the upper jaw. The dentition figured(1) is that of the great and formidable "white shark" of navigators,—the type of the subgenus *Carcharodon* of Müller. In the United Service Museum there are preserved the jaws of a *Carcharodon*, of which the upper one measures four feet and the lower one three feet eight inches, following the curvature. The length of the largest tooth is two inches, the breadth of its base one inch nine lines: the total length of the shark was thirty-seven feet.

Fossil teeth precisely corresponding in form with those of the *Carcharodon* occur abundantly in the tertiary formations of both the old and new continents; some of these teeth exhibit the extraordinary dimensions of six inches in length, and five inches across the base. If, therefore, the proportions of these extinct *Carcharodons* corresponded with those of the existing species, they must have equalled the great mammiferous whales in size; and, combining with the organization of the shark its bold and insatiable character, they must have constituted the most terrific and irresistible of the predaceous monsters of the ancient deep.

In the blue-shark, (*Carcharias glaucus*, Cuv.), the teeth of the lower jaw are longer and narrower than in the white-shark, and approach nearer to the form characteristic of the genus *Lamna;* they may be distinguished, however, by their broader base, the angles of which are less produced downwards, and by their finely dentated edges.

In the subgenus *Physodon*, which is nearly allied to *Carcharias*, the teeth of one or two median rows are disproportionately small.

The teeth of the hammer-headed sharks (*Zygæna*), are triangular flattened plates, with finely dentated margins, as in *Carcharias*, but the points are bent backwards, and the posterior margin is concave.(2)

In the genus *Galeus*, to which the grey-shark or tope of our coast belongs, the teeth are relatively thicker than in the *Zygæna*, and the posterior margin is notched, with the basal part produced backward, and divided into three or more denticles: the anterior margin is

(1) Pl. 4, fig. 1. (2) Pl. 4, fig. 2.

finely serrated.(1) This description applies to the lateral rows of teeth in which the points are inclined backwards and outwards; the teeth of the mesial row in both jaws are of a symmetrical figure. The teeth are alike in the upper and lower jaws.

There is the same correspondence, as regards the upper and lower jaws in the singularly formed teeth, which characterize the *Squalus spinosus* of Schneider,—the type of the genus *Goniadus* of Agassiz (Pl. 4, fig. 4). In these teeth, the point is so far inclined backwards, that the anterior margin forms a nearly horizontal trenchant edge, applied to the corresponding margin of the opposite tooth: two denticles project horizontally forwards from the base of the anterior margin, and one or two similar denticles from the opposite side of the tooth.

In the genus *Scymnus*, (Pl. 4, fig. 3,) the teeth of the lower differ so much from those of the upper jaw, that nothing save actual inspection of the jaws *in situ* could lead to the belief that they belonged to the same animal. The teeth of the upper jaw are small, conical, subcompressed, with slightly recurved points; those of the median or anterior rows present a nearly subulate form; the posterior ones are somewhat broader: their osseous base is bifurcate, as in *Lamna*. The teeth of the lower jaw are about eight times larger than those above; they are straight, flattened, symmetrical, lancet-shaped plates, with finely dentated margins. The base of the tooth is bifurcate, the divisions being parallel, and divided by a fissure which becomes slightly dilated near the enamelled crown. The middle tooth of the series rests upon the symphyseal line, and has one basal fork attached to each ramus of the lower jaw; its parallel lateral edges overlap those of the contiguous teeth; the posterior edge of each lateral tooth overlaps in a similar manner the anterior one of the tooth behind: this imbricated disposition is quite peculiar to the *Scymnus*, among sharks. There are four recumbent teeth in each vertical row, the apices of which are turned down in a direction diametrically opposite to that of the erect exterior tooth. The shedding of the outer teeth appears to be simultaneous, and the change of position of the succeeding series must be very rapid, as well as extensive.

(1) Pl. 28, fig. 9.

In the genus *Mustelus*, to which our "smooth dog-fish" belongs, the teeth deviate from the form typical of the sharks and approach those of the rays, being obtuse and rounded, with fine transverse ridges, without a piercing cusp or cutting edge, but adapted for bruising and crushing: they are numerous, small, nearly equal, arranged like a pavement in the quincuncial order.

The maxillary teeth of the saw-fish *(Pristis)* resemble those of the smooth dog-fish, but as the more formidable part of the dental system of this genus offers some peculiar characters, it will be subsequently described.

In the *Cestracion* both prehensile and crushing teeth are associated together in the same jaws, but as we here meet with a modification of the microscopic texture of the teeth different from that of the teeth in the true sharks, a separate section will be devoted to their description, and to that of the teeth of numerous cognate fossil species of plagiostomes.

In all the genera of sharks, the body of the tooth is principally occupied with the two kinds of canals which I have termed "medullary" and "calcigerous."(1) The latter are, however, essentially minute branches or continuations of the former, and although, in the newly formed tooth distinguishable by the nature of their contents, yet this difference is gradually obliterated by the progressive deposition of calcareous matter by concentric layers in the medullary canals.

In plate 6, a view of the structure of the tooth of an extinct species of shark (*Lamna elegans*, Ag.) is given as seen in a thin longitudinal section under a compound lens of one inch focus. With this power the medullary canals alone are visible, the minute calcigerous tubes giving rise to the cloudy appearance in their interspaces. The medullary canals are continued from the short and small pulp-cavity at the base of the tooth. The principal branches run parallel with the axis of the tooth, but quickly give off ramuli, which are directed transversely, and again ramify at right angles or nearly so, and anastomose, so as to form a beautiful reticulate arrangement of tubes, very similar to a network of capillary vessels, throughout the whole substance of the

(1) Report of the British Association, 1838, vol. vii, p. 135.

tooth: they ultimately terminate in flattened sinuses, which anastomose and form the boundary line between the central osseous and the dense exterior enamel-like substance of the tooth. The whole of the superficial part of the tooth is occupied by minute calcigerous tubes,(1) which proceed in a wavy course, generally at right angles to the external surface; they ramify at very acute angles, and their terminal branches anastomose, and most of them end in a series of calcigerous cells, situated beneath the outer stratum of enamel. In this stratum, however, there are evident traces of a series of much finer tubes, continued from the preceding layer of cells. The medullary canals in the body of the tooth are surrounded by concentric layers, traversed by the calcigerous tubes which are everywhere given off at right angles from the larger canals; and have a more irregular wavy course than the superficial calcigerous tubes. They form, by their numerous anastomoses an inextricable reticulation,(2) and their terminal ramuli dilate into or communicate with calcigerous cells.

The medullary canals of the teeth are occupied in the recent dog-fish by a sanguineous medulla, closely resembling that which fills the medullary cells of the coarse bone of which the base of the tooth is composed, and with which cells the anastomosing reticulate canals of the crown of the tooth are directly continuous. In the old exterior teeth a great proportion of the medullary canals are consolidated by concentric layers of earthy deposit.

In the fully formed flat teeth of the fœtal *Carcharodon*, which were sufficiently transparent to render their texture perfectly discernible by transmitted light, this was seen to be essentially the same as in the *Lamna;* but the disposition of the medullary canals was more regular: the median branches were continued as in *Lamna* to the apex of the tooth parallel with the axis, the lateral ones gradually inclined to the sides of the tooth, their direction being more transverse as they approached the base; and here inclining downwards to the bilobed osseous root. The branches of the medullary canals are

(1) A highly magnified view of the calcigerous tubes continued from the peripheral medullary tube *b* is given in Pl. 7.

(2) See the view of these tubes between the medullary canals *a* and *b*, Pl. 7.

given off nearly at right angles, but are relatively smaller and shorter than in *Lamna*. The calcigerous tubes in the body of the tooth form a fine but inextricable moss-like reticulation; those at the periphery are straighter, and run parallel to one another, and vertical to the outer surface. A stratum of fine calcigerous cells receives the terminations of these peripheral tubes, and intervenes between them and the dense enamel-like exterior covering of the tooth.

In the great fossil teeth of the *Carcharias megalodon*, the calcigerous tubes, at the superficies of this tooth, are disposed in groups which, with an insufficient magnifying power, appear like single coarse tubes; but with a higher power are seen to be composed of congeries of parallel tubes, apparently twisted together. The interspaces are nearly equal to the diameter of these fasciculi: they are occupied by more scattered tubes, and by short oblique or transverse anastomosing branches. At one part of a section of this tooth, which was sufficiently transparent to be examined with the highest powers, the peripheral coarse sinus or canal, which always runs parallel with the superficies, gave off an infinite number of minute tubes, which formed a plexus, (or plexiform stratum), and from the outer part of this plexus, the tubes above described, passed, at right angles, to the surface. In the longitudinal section of this tooth, the twisted appearance above described of the peripheral calcigerous tubes was seen to be due to the number of side branches given off at an acute angle, and obliquely to the main tube. At the apex of the tooth, the marginal calcigerous tubes radiate, as in the *Lamna*, and suddenly diverge to proceed transversely to the sides. In the body of the tooth, the main canals are surrounded by concentric lamellæ, traversed by radiating and anastomosing calcigerous tubes, which form a fine net-work in the interspaces of the medullary canals.

In the flat lancet-shaped teeth of the lower jaw of the *Scymnus*, the texture of the tooth presents a closer correspondence with that in the higher organized animals, in consequence of the principal or medullary tubes being relatively smaller, more aggregated, straighter, and more parallel in their course, than in the sub-genera of sharks just described. These tubes advance in two fasciculi from the osseous bifid base; the median tubes slightly converge and proceed straight

to the apex of the tooth, the lateral ones also run parallel to each other, and to the axis of the tooth, at the beginning of their course, and then bend gently outwards to the margins of the tooth. The secondary curvatures of the medullary tubes are pretty regular, and of an angularly undulating character; the whole of the clear outer enamel-like covering consists of parallel and extremely minute calcigerous tubes with intermixed cells. The calcigerous tubes, in the body of the tooth, are given off at an acute angle from the medullary tubes through their whole course.

It has been already observed that the formation of the teeth of the sharks, as of many other fishes, exemplifies, on a large scale, the earliest or papillary stage of dental development in the higher classes of animals. It is not succeeded here by either a follicular or an eruptive stage; the formative papillæ are never inclosed, and consequently never break forth. The pulp, when consolidated by the deposition of the calcareous salts in the pre-existing cells and tubes, is gradually withdrawn from the protective sheath which the thecal fold of mucous membrane afforded it during the early stages of its formation. I have studied the development of the teeth of the squaloids, in the genera *Galeus*, *Carcharias*, and *Scymnus*. In the uterine fœtus, one foot long, of the great white shark, (*Carcharodon*) the jaws seem at first sight to be edentulous; a fissure presents itself on the inner side of the margin of each jaw running parallel with it, between the thin smooth membrane covering the convex edge of the cartilage, and the free margin of a fold of mucous membrane which lies parallel to, and upon the inner side of the jaw. When this fold is drawn away from the jaw, the minute teeth are exposed, arranged in the usual vertical rows; their points are all directed backwards and towards the base of the jaw, and are seen to slip out of fossæ, or sheaths in the membranous fold, as this is gradually reflected backwards to its line of attachment near the base of the jaw. Here the anterior lamina of the fold, which, from its office may be termed "thecal," is continuous with the mucous membrane at the base of the rows of teeth; the posterior layer is reflected backwards to the frænal line of attachment of the tongue. Close to the anterior line of reflection there is a row of simple conical papillæ, in

the succeeding row, the papillæ are larger, the cone broader and flatter, and its apex is covered with a small cap of dense and glistening dental substance which is readily removed; though not without displacement of part of the pulp, the granules of which, adherent to the cavity of the displaced dental cap, are always readily recognizable under the microscope. The third series of papillæ, counting from below in the lower jaw, have acquired the size and shape of the future tooth, with the crenate edges well marked; half the tooth is completed, and its removal from the fleshy base of the pulp cannot be effected without evident laceration of the pulp; when this is done under the microscope, the torn processes of the pulp continued into the medullary canals of the new formed tooth are plainly visible. The fourth tooth is completely formed, as also the fifth and sixth, in the ascending series; these progressively diminish in size. The last or highest, which is first exposed on reflecting the thecal fold, and the first which was completed in the order of development, consists of a simple cone, similar in form and size to the apical third of the ordinary sized teeth below it; yet its growth is quite completed, and its base firmly attached to the maxillary membrane.

In a fœtus of a *Carcharias*, three inches long, which had not lost its external branchiæ, the membranous groove between the jaw and thecal fold was much shallower, and only two rows of papillæ were present on the maxillary membrane. The minute anterior teeth in the more advanced fœtus are doubtless developed from these primitive papillæ, which must be succeeded by others of progressively larger size till the normal form and dimensions of the adult teeth are attained.(1)

The unossified pulps, examined with a high power, consist of semi-opaque polyhedral granules or cells suspended in a clear *matrix*, and the whole is inclosed in a tough transparent membrane which forms the outer surface of the pulp. Beneath this membrane at the crenate margins, the granules or cells are arranged in lines precisely correspond-

(1) The fœtal shark is peculiarly favourable for such comparisons, as it presents numerous pulps and teeth in every stage of formation, easily detached and without violence from their exposed situation, and of a flattened form well adapted for microscopical observation.

ing with those of the subsequent calcigerous tubes. The formation of the tooth commences by the deposition of earthy particles in the tough external membrane of the pulp. I have been unable to recognize the distinct arrangement of the hardening salts in this layer. It is transparent, extremely dense, and forms the enamel-like polished coating of the tooth; in sections of fully formed teeth, the finest terminal branches of the parallel peripheral calcigerous tubes are lost in the above clear enamel-like substance. When the enamel-like outer layer of the apex of the tooth is completed, it is so easily detached from the subjacent pulp that it might be readily supposed that there was no organic connection between them. If, however, the so exposed pulp be now examined with the microscope, and compared with an uncalcified pulp, it is seen to be no longer covered with the smooth dense membrane observable in the latter; but the apical edges, from which the enamel-like cap has been detached, appear villous or flocular. It is obvious that the first shell of the tooth has been neither transuded from the superficies of the external membrane of the pulp nor has been deposited between that membrane and the granular part of the pulp, but is due to a conversion of the external membrane into a dense enamel-like bone. The formation of the body of the tooth by deposition of earthy particles in pre-existing and pre-arranged cavities is still more satisfactorily demonstrable. In proportion as the formation of the tooth has advanced, the difficulty of separating the calcified from the uncalcified portion of the pulp is increased, and at the same time it becomes easier to detect the continuation of the processes of the pulp into those medullary canals which form so many separate centres of radiation of the plexiform calcigerous tubes.

The application of the principle of dental development by conversion and not by transudation, as illustrated in the dentition of the shark, to the formation of the mammiferous tooth, is by no means forced, but natural and obvious. In the ivory part of a simple mammiferous tooth there is a single medullary canal, the *cavitas pulpi*, and a single system of radiated calcigerous tubes; but the plan and principle of formation is the same as in the shark.

In proportion to the quantity of earthy matter deposited in the

pulp, and in the ratio of the number, minuteness and aggregated disposition of the cavities containing that earthy matter, is the facility of detaching the ossified from the unossified part of the tooth increased. But this facility of separation is quite inadequate to prove an absence of organic connection between the separated parts, and a formation of the calcified layer by transudation from a free secreting surface. The calcigerous tubes of the mammiferous tooth have distinct parietes in both the calcified and uncalcified portions of the pulp; these parietes are rendered brittle by the deposition therein of earthy particles in the calcified part of the pulp, and separate readily from the uncalcified continuation of the tubes in the remaining pulp; while the minuteness of the ruptured tubes renders the irregularity of the denuded surface of the pulp invisible to the naked eye; but the appearance thus presented of a naturally free transuding surface is deceptive.(1)

(1) Since these facts and the general conclusions as to the nature of dentification deduced rom them were mentioned in my Lectures at the College of Surgeons (May 1839), and subsequently communicated with more detail to the French Academy, I have perused the work by Dr. Schwann, entitled "Untersuchungen ueber Einstimmung der Struktur und Wachsthum der Pflanze und Thiere," 8vo., 1839: or, "Observations on the Correspondence between Plants and Animals in their Structure and Growth." Not anticipating, from the title of this work, that it contained observations bearing immediately on dental anatomy, I have to regret that some months elapsed after its publication before I ordered it from my bookseller. Dr. Schwann describes the results of microscopic observations, which he instituted on the development of the dentine in mammalian teeth, and arrives at the conclusion that the process-like ossification, is one of intus-susception. Thus the theory of dentification, which I applied analogically from observation of the process in the shark, to the same process in the higher vertebrate animals, is established *ex visu* by one of the most accurate and experienced micrographers of the present day. A full analysis of his observations will be given in the general introduction to the present work. Cuvier, after stating that the teeth of fishes grow like those of quadrupeds, by layers, adds in the first edition of the Leçons d'Anatomie Comparée, iii, p. 112, "Mais les dents qui ne tiennent qu'à la gencive seulement, comme celles des Squales, croissent à la manière des épiphyses des os, c'est-à-dire que toute leur substance est d'abord tendre et poreuse, et qu'elle se durcit uniformément, et finit par devenir entièrement dure comme de l'ivoire." I have never seen an instance of such uniform hardening—if by this is meant a uniform deposition of the earthy particles through the whole substance of the pulp—in the tooth of any shark or other animal; and, were such actually the case, it would not be like the ossification of an epiphysis. It seems that Cuvier himself had withdrawn his confidence in the observation and conclusion above quoted, as the passage is suppressed in the second edition of the Leçons, by M. Duvernoy, in 1835. It is true, however, that the teeth, not only of sharks, but of the higher animals, are developed like bones; the hardening salts in both cases are deposited in preformed cavities organized in a pre-existing mould or

As a consequence of a formation of a tooth by *conversion of*, instead of *transudation from* a pre-existing pulp, the successive formation of these pulps necessarily follows, where a succession of teeth is required; these reproductive pulps are developed in the shark in the vascular mucous membrane at the angle of reflection of the thecal fold upon the groove at the basal line of the jaws. They gradually advance from this situation towards the margin of the jaw, the centripetal ossification extends as they advance, and consolidation is completed by the time they are ready to change their recumbent for the erect position, and take the place of the tooth previously shed.

This change of place and direction is well known to be not the effect of muscular contraction, but of partial absorption and deposition operating upon the membrane to which the teeth are attached. This membrane is gradually brought to the exterior of the jaw, and is then removed together with the attached tooth, supposing the latter not to have been already violently displaced. But the following question now offers itself:—Does this movement of growth take place simultaneously in the membrane and the jaw to which it is attached, or is it a slow and gradual sliding motion of the dentigerous membrane upon the jaw?

To determine this question would require an experiment similar to those by which Duhamel and Hunter traced the change of place in the particles of growing bone; a foreign body e. g. should be inserted into the base of the jaw of the shark, and a tooth in the corresponding place should be so marked, as at a subsequent period it might be recognized, and its position compared with the perforated part of the jaw. Such an experiment would not be very practicable in the carnivorous inhabitants of the deep we are now considering, but accident has satisfactorily supplied its place. The jaws of a large *Galeus* passed into the private collection of an English anatomist, in which the barbed spine of a sting-ray (*Trygon*) had been driven, during a predatory attack of the shark, into the lower jaw through

matrix of animal matter; but they differ as to the direction of the deposition, which in bone is from the centre to the circumference, in tooth from the circumference to the centre; the progress of calcification in the one is centrifugal, in the other centripetal.—See *Comptes Rendus de l'Académie des Sciences*, 1839, *p.* 784.

the posterior row of teeth, and had been broken off and fixed in that position.(1) Now, had the growth of the jaw proceeded *pari passu* with the movement of the teeth, the foreign body would in time have been brought with the posterior row of teeth, to the outer margin of the jaw, and have been discharged. If the shark had been captured during this change, the teeth developed behind the wounded row, might be expected to have been of the natural size and form; the appearances, however, presented by this interesting preparation are as follows: a double row of imperfectly formed teeth is continued from the perforated part of the jaw to the margin supporting the erect teeth.(2) Hence it is obvious, that besides the original injury to the formative pulps in existence at the time of the wound, the presence of the foreign body had continued to affect the normal development of the subsequently formed pulps. Thus it is proved that the teeth and their supporting membrane advance forwards without a corresponding movement of the particles of the cartilaginous jaw to which they are attached.

14. *Pristis*.—The maxillary teeth of the saw-fish, which is an active and predatory shark, are notwithstanding extremely small, simple, obtuse,(3) and wholly inadequate to destroy and secure the prey requisite for its subsistence; but this seemingly imperfect armature of the mouth is compensated for by the development from the anterior part of the head of a very singular and formidable weapon, provided with strong lateral teeth, and which, from its resemblance to a saw, has given rise to the vernacular name of "saw-fish," applied to the present species of shark.

In most of the plagiostomes but especially in the group of squaloids, a conical projection or cutwater is continued from the fore part of the head, and its frame work is composed of peculiar and superadded cartilages, articulated to the anterior extremities of the frontal, nasal and vomerine bones. These rostral cartilages (in the common saw-fish (*Pristis antiquorum*), from which the following description is taken) are blended into a horizontally flattened plate which is produced to a length equalling one third that of the entire fish; this process is more completely ossified than any other part of the skeleton,

(1) Pl. 28, fig. 9, *b*. (2) *ib*. fig. 9, *a*.

(3) In *Pristis cirratus* the apex of the small maxillary teeth is produced into a sharp point.

and a series of deep alveoli is excavated in each of its lateral margins.

The teeth which are lodged in these sockets are elongated, compressed in the same plane as that of the body of the saw, and the margins converge to a sharp point, which is situated a little behind the axis of the tooth; the anterior border of the tooth is convex, but grows sharper towards the point; the posterior margin is concave or grooved, and the groove glides upon a corresponding ridge which projects into the back part of the socket. The rostral tooth is solid, as shewn in the longitudinal section of the one figured in Pl. 8, fig. 3; its base, (fig. 5,) is slightly concave and porous, like the section of a cane, but the pores are finer and more numerous. The walls of the socket are formed by ossification of the rostral cartilage to the adequate extent, (*b.* fig. 3); but as undue weight, under any circumstances, and especially at the fore end of the fish would be a cumbrous impediment to its motions, the intervening spaces (*d.* fig. 3) between the sockets are hollow and filled with a gelatinous medulla. A large vascular canal (*c.* fig. 3) traversed by branches of the facial artery, and of the second division of the fifth pair of nerves, and inclosed in a cellular and gelatinous tissue, runs parallel with the axis of the saw along the back part of the alveoli, and supplies the materials for the increase of the teeth, which are not shed and renewed like the maxillary teeth, but grow with the growth of the body by constant addition of fresh pulp-material progressively ossified at their base.(1)

The structure of the rostral teeth of *Pristis* has the nearest resemblance to that of the maxillary dental plates of *Myliobates;* they are traversed throughout by medullary canals which run parallel to each other and to the axis of the tooth; but they exhibit more frequent anastomoses and dichotomous sub-divisions than in *Myliobates.* The diameter of the medullary canals is $\frac{1}{100}$th inch, and their interspaces $\frac{1}{70}$th of an inch near the base of the tooth; they are surrounded by concentric laminæ which increase in number as the

(1) In the *Pristis cuspidatus* the rostral teeth are broad, and lancet-shaped; in the *Pristis microdon* they are very short; in the *Pristis cirratus* the rostral teeth vary in length, there being from three to five smaller ones interposed between the longer teeth, which are sharp-pointed and slightly recurved. The base of these teeth expands, and is excavated more deeply than in the common saw-fish; it is not socketed but anchylosed to the margin of the rostrum. The rostral teeth in this species extend along the sides of the head beyond the angles of the mouth.

canals approach the apex of the tooth. The calcigerous tubes are characterized by their frequent branching and inosculation; the branches go off generally at right angles to the trunk, which they nearly equal in size; these quickly anastomose and again send off smaller branches which similarly anastomose with others of corresponding size, until the terminal tubes are, for the most part, lost in a series of minute calcigerous cells which form the boundaries of the system of calcigerous tubes developed from each medullary canal. Some of the terminal tubes of contiguous systems anastomose across this boundary. Each of the systems of calcigerous tubes represents a separate denticle, of a prismatic figure, exhibiting in transverse section generally a more or less regular hexahedron. Towards the point where two contiguous medullary canals inosculate the terminal calcigerous tubes of each system begin to exhibit more frequent anastomoses, and the boundary line is thus gradually obliterated: the letters *a*, *b*, and *c*, pl. 9, fig. 2, exhibit two systems of calcigerous tubes blending together near the point where the two contiguous medullary canals were about to inosculate.

The reticulate arrangement of the calcigerous tubes is more, and the radiated one less, conspicuous in the rostral teeth of *Pristis* than in the teeth of any other species which I have yet examined. The diameter of the calcigerous tubes at their origin is $\frac{1}{6000}$th of an inch, their terminal branches may be traced to the minuteness of $\frac{1}{20.000}$th of an inch.

In the embryo of a *Pristis* six inches long, to which the umbilical chord was still attached, I found a series of depressions in the skin along the margins of the rostral prolongation corresponding in number and relative position with the future teeth; and at the bottom of each of these dermal follicles, there was a papilla which formed the apex of a pulp, whose base had already begun to penetrate the cartilaginous plate of the rostrum. The pulp had the usual dense and unyielding external 'membrana propria,' and its apex was covered by a continuation of the tegumentary follicle of extreme thinness, but there was no true capsule or enamel organ. The calcareous particles had not begun to be deposited in the tissue of the pulp.

The teeth of the young specimen, of which the head and saw are figured in Pl. 8, fig. 1, were fully calcified, and except that the num-

ber of medullary canals were fewer, and the proportion of the calcigerous tubes greater, they were in every respect miniature resemblances of the teeth of the full grown fish, such as are figured of the natural size at Pl. 8, figs. 3 and 4.

15. *Squatina.*—In the monk-fish, (*Squatina Angelus*), which makes the transition from the sharks to the rays, the teeth are arranged along the jaws in well defined vertical rows; including six teeth in the anterior and gradually decreasing to three teeth in the posterior rows. The margins of the teeth are smooth; a small tubercle projects from the middle of the outer side of the base; these characters serve to distinguish them from the lower teeth of the *Carcharias*, which in other respects they pretty closely resemble. It may be further observed, that there is not that difference in the position of the first and second teeth in each row which is so conspicuous in most sharks; but here, as in the ray tribe, the change of direction of the apex is very gradual and regular from the innermost to the outermost tooth: this character, and the anterior position of the jaws are illustrated in Pl. 10, fig. 2.

RAIIDÆ.

16. The teeth of the rays are, in general, more numerous than those of the sharks; they have less mobility, are more closely impacted, and in some cases are laterally united together by fine sutures, so as to form a kind of mosaic pavement on both the upper and lower jaws. The *Myliobates* or eagle-rays, which present the last mentioned condition,—unique in the vertebrate subkingdom, have large and massive teeth; but in the rest of the present family of cartilaginous fishes, they are remarkable for their small size, as compared with those of the sharks. The teeth in some species of rays, are adapted for crushing, but in others they have the middle or one of the angles of the crown produced into a sharp point. In all genera of the ray tribe, whatever the diversity of size and shape of the teeth, they are placed in several rows and succeed each other uninterruptedly from behind.

In the common skate, (*Raia Batis*), the teeth are smaller, much more numerous and the vertical series are more closely approximated than in the *Squatina*, which is the most ray-like of the sharks; their gene-

ral form is that of a broad base or plate from which a short spine is produced; this is most conspicuous in the central rows of teeth where the spine is developed from the inner angle, but it gradually diminishes as the teeth approach the sides of the jaws. The vertical series of teeth describe nearly a complete circle at the middle part of the jaws, and include about twenty teeth each.

The teeth of the *Torpedo* are somewhat stronger, their base is more extended transversely, and the pointed cusp is more produced than in the common rays.

In the thornback (*Raia clavata*), the teeth present the form of small transversely oval, obtuse masses; and the vertical series are so closely arranged, that being alternate, they are less conspicuous than the oblique rows which result from this approximation. Mr. Yarrell describes the following sexual character in the teeth of the Thornback ray. "While both sexes are young, the teeth in both are alike broad and flat; but as the male acquires age and sexual power, the teeth that are nearest the centre begin to alter in form, and become pointed by an elongation of the internal angle; all the points being directed backwards or towards the throat."(1)

The quincuncial arrangement of the teeth prevails in the different species of *Trygon*, or fire-flare, in which the teeth are of very small size. Their crowns consist of a triangular plate, with the internal angle or point most produced; this plate is supported on a hollow pivot.

In the genus *Rhina* each tooth is supported on a short fang or pivot, which tapers as it recedes from the crown; there is a groove along the posterior part of this pivot, and a perforation on each side; the crown is lozenge-shaped, convex above, and sculptured with a series of transverse and slightly undulating and punctate ridges; presenting a pattern which somewhat resembles that of the grinding surface of the comparatively gigantic tooth of the extinct *Ptychodus*.(2) The modification of the dentigerous surface of the jaws, and the beautiful quincuncial arrangement of these teeth are exhibited in Pl. 23, figs. 1, and 2. The middle part of the upper jaw forms a bold prominent

(1) British Fishes, ii, p. 416.

(2) Compare the magnified view of a denticle of *Rhina* in Pl. 23, fig. 3, with the tooth of *Ptychodus latissimus*, Pl. 17, figs. 1 and 2.

convexity separated by a depression on each side from a lateral and less produced rising. The contour of the dentigerous surface of the lower jaw presents depressions corresponding to the eminences above, and *vice versâ*.

The structure of the tooth of the *Rhina* exhibits a modification of the tubular structure, very different from that which characterises the tooth of the extinct *Ptychodus*. A representation of this structure, as displayed in a longitudinal vertical section of the tooth, is given in Pl. 24, which corresponds with that of the teeth of the rays above described.

The pivot-like base of one of the component teeth of the pavement of the jaws of the *Rhina* consists of a bony texture, denser than that of the ordinary bone of fishes ; it is traversed by undulating, diversely directed, medullary canals, with concentrically laminated walls ; numerous wavy calcigerous tubes radiate from the medullary canals, subdivide in their interspaces, anastomose together, and intercommunicate with numerous minute calcigerous cells. The structure of this part of the tooth, we shall find to be similar to that which pervades the entire tooth in another family of plagiostomous fishes. The crown or body of the tooth in the *Rhina* exhibits, however, a denser structure, and one that approaches nearer to the ordinary structure of the dentine in the higher vertebrate classes. Some of the medullary tubes of the base of the tooth open into the remains of the *cavitas pulpi*, now closed up below by the ossification of the base of the tooth. This cavity presents a conical form, with an oval transverse section. A uniform system of calcigerous tubes radiates in every direction, from the pulp-cavity towards the periphery of the tooth, and vertical to that surface ; those which are continued from its lower part, bend down towards the root of the tooth ; the lateral ones are continued directly outwards to the sides, and the superior tubes proceed vertically to the upper surface ; the intermediate tubes present every gradation of oblique curvature.(1) All the tubes have a minutely undulating course ;(2) they dichotomize as they proceed towards the surface, and give off minute branches, generally at an angle of 45° in every part of their course. These branches anastomose together, and with rhomboidal calcigerous cells in the

(1) Pl. 24, fig. 1. (2) *ib.* fig. 2.

interspaces of the main tubes. These tubes, at their origin, present a diameter of $\frac{1}{3000}$ of an inch, with interspaces equal to those of their diameters. The smallest branches into which they are resolved, and which are lost in the clear enamel-like external stratum of the tooth, have a definable diameter of $\frac{1}{87.087}$ of an inch. This external layer is thickest at the upper surface of the tooth, and the boundary between it and the tubular substance of the tooth, is here defined by a stratum of calcigerous cells. Some of the fine peripheral branches of the calcigerous tubes unite and form loops, the convexity of which is turned towards the cells, and from which the finer branches proceed to communicate with the superficial calcigerous cells.

17. *Myliobates*.—The modification of the plagiostomous type of teeth, for the purpose of crushing the alimentary substances, is most complete in this genus. A view of this armature of the mouth, as seen from behind in the *Myliobates Aquila* is given Pl. 25, fig. 1. Both jaws are covered with a pavement of broad teeth, with a flat grinding surface, vertical and finely undulated sides, by which contiguous teeth are joined together as by a suture, (Pl. 27, *c*) and a base divided into a number of small parallel longitudinal ridges.

The entire phalanx of dental plates of the upper jaw describes the segment of a circle. In the *Myliobates marginata* (subg. *Rhinoptera* of Kuhl), the teeth are hexagonal, the middle row being the broadest, and the lateral ones diminishing as they recede; the outermost are mostly pentagonal. I have seen an example of the jaws of this subgenus of *Myliobates*, in which one of the rows next the median was subdivided into two unequal series, as represented in fig. 2, pl. 25. In *Myl. Jussieui* (*Zygobates*, Agass.), the three middle rows of teeth are much broader than the two marginal rows. In *Myliobates* proper, the median row itself forms the principal part of the dental covering of the jaws, which is bordered by three narrow rows of teeth, having the same antero-posterior extent as the median plates. Finally, in *Myliobates Narinari* (*Aetobatis*, Müller), the small marginal teeth have entirely disappeared, and the jaws support a single row of broad dental plates. In the upper jaw, these plates are arched, with the convexity turned forwards; in the lower jaw, they pass straight across, with the extremities only a little bent backwards. The jaws

which support and work these dense and heavy teeth, are proportionally strong; and in *Aëtobatis*, they nearly approach to the density of true bone. In this subgenus, the upper jaw is shorter and more curved than the lower one, the anterior extremity of which projects beyond the upper jaw, and can be used, like a spade, in digging out shell-fish, &c., from the sandy bottoms frequented by these rays.(1)

Microscopic examination of the texture of the teeth of Myliobates has yielded the following results. A longitudinal and vertical section of a single dental plate, viewed by a compound lens of an inch focus (Pl. 26), exhibits at its base (*a*) a coarse network of large irregular canals, filled with a vascular medullary pulp. From this network smaller medullary canals proceed, towards the flat grinding surface, in a straight and slightly diverging course, subdividing dichotomously with interspaces equal to their own diameter at the base, but much wider at the working surface of the tooth. In a transverse section of the tooth, under the same power, the area of the medullary canals is seen to present generally an irregular elliptical form, from which radiating calcigerous tubes are faintly perceptible. Each canal and its series of tubes is surrounded by a line of generally a hexagonal form, and which constitutes the boundary between contiguous canals and tubes, the whole tooth being thus composed of an aggregate of slender, elongated, commonly six-sided prismatic teeth, placed vertically to the grinding surface. A section through the roots of the tooth (*b*, pl. 26), shows that these parts are occupied by a network of irregular canals, which anastomose by arched branches with the network of the contiguous root, and these with the network of coarser tubes which occupy the basis of the tooth for an extent exceeding the length of the root itself.

With a higher power, $\frac{1}{8}$th inch focus, the calcigerous tubes are seen to radiate in all directions from the medullary canals, and are sent off throughout the whole course of the canal. These tubes are short, wavy, richly arborescent, and form numerous anastomoses with each other. The transverse sections of the tooth show that the area of each medullary canal has been filled up or diminished by the depo-

(1) Pl. 16, fig. 1.

sition of a series of concentric lamellæ in proportion to its term of use.

The ramification of the calcigerous tubes in this tooth, presents the same general character as those of the *Acrodus*, but they are shorter; and each medullary canal, with the radiating series of tubes, is seen in the transverse section to be separated from the contiguous one, by the regular boundary lines above-mentioned, which lines distinguish the teeth of the *Myliobates* from those of the *Acrodus*, *Psammodus*, *Cestracion*, or any of the shark-tribe. The rostral teeth of the saw-fish, and those of the *Orycteropus*, among mammalia, present the nearest resemblance in their intimate structure to the teeth of the *Myliobates*. Plate 27 gives a correct general idea of the structure of the present tooth as displayed by a transverse horizontal section near the root.

The teeth of the *Myliobates*, like those of the rest of the plagiostomes, are successively formed at the posterior part of the tesselated series in proportion as they are worn away in front. A series of minute and closely aggregated papilliform matrices rise from the mucous membrane behind the teeth, and are covered by a fold of the same membrane which is reflected forward so as to conceal the pulps and the last formed teeth. The papilliform pulps are ossified by the deposition of the calcareous salts in the peripheral cells and radiating tubes, but the medullary or central canal of each pulp continues to retain its organizer and vascular contents till the whole of the compound tooth is completed; the calcified wall of the medullary canal is then thickened, and the area diminished by the successive formation of concentric laminæ of osseous matter. In *Zygobates*, the subgenus in which I have studied the development of the teeth of this family of rays, the middle tooth of each transverse series is first developed; the formative papillæ of the two broad lateral teeth begin to rise first at the mesial and anterior parts of the tooth, and from these points succeed each other to the posterior and outer sides: that facet which is adapted to the posterior-lateral facet of the median tooth is first completed, and at this period the broad lateral tooth presents a trigonal instead of a hexagonal contour, the whole length or vertical diameter of the mesial side of the tooth is completed before the formation of the outer

side of the tooth is begun. These facts are strikingly opposed to the theory of the formation of a tooth by the transudation of layers from the superficies of a pre-existing glandular pulp.

As the teeth of the *Myliobates* are gradually carried forwards into action by the direction of growth of their basis of support, the areæ of the medullary canals become progressively diminished, as in bone, by osseous deposition in concentric layers, and are thus finally consolidated in the anterior teeth.

CESTRACIONTS.

18. The dental characters of this family of cartilaginous fishes, are chiefly manifested in a form of tooth, better adapted for crushing or comminuting alimentary substances which offer only passive resistance, than for piercing, cutting and lacerating a living prey; and this less formidable character of the maxillary armour is compensated, in general, by the development of two formidable spines upon the back of the fish. In most of the species, the teeth also vary in form and size in the same individual to a greater degree than in the sharks; and in all the cestracionts, their substance is traversed by medullary canals whose systems of calcigerous tubes are not separated by well defined boundaries, as in the *Myliobates*.

Of the numerous singular forms of this tribe of cartilaginous fishes that once peopled the seas of the northern hemisphere, and which have left their less perishable remains in the secondary strata of the present dry land, all have now disappeared, and the sole existing representative is the genus *Cestracion*, of which the most common species is met with in the Australian Seas: a second species has been indicated which frequents the southern coasts of China. The ancient fossils above alluded to would have been scarcely intelligible unless the key to their nature had been afforded by the teeth and spines of the existing *Cestracion*.

In the Port Jackson shark, (*Cestracion Phillippii*), the jaws form a greater proportion of the skull than in any other existing cartilaginous and plagiostomous fish;(1) they are also more elongated and directed more horizontally forwards, thus approaching nearer to the

(1) Pl. 10, fig. 1.

usual position of the jaws in the osseous fishes. In consequence also of the greater extent of ossification in these parts, the indications of the separation of the upper jaw into maxillary and premaxillary, and of the lower jaw into mandibular and premandibular pieces begin to be visible. The upper jaw, besides being suspended to the tympanic or articular pedicle, is articulated by a distinct convex process with a corresponding concavity on each side of the vomerine portion of the cranium. A similar connection of the upper maxillary bone, in the *Scarus*, illustrates the analogy here advanced between the upper dentigerous arch in the *Cestracion* and other *Plagiostomes* and the ordinary maxillary and intermaxillary bones. This arch is also attached by ligamentous matter, as in other sharks, to the frontal and nasal parts of the cranium, with which it is in contact. The maxillary portion of the upper jaw sends outwards a strong process which is connected with a corresponding external process of the lower jaw, and a very strong ligament attaches the inner side of the posterior extremity of the superior maxillary bone to the inner side of the broad transverse condyloid extremity of the lower jaw. The interspace of the upper maxillary bones is occupied by a thin triangular plate of cartilage representing the matrix in which, in osseous fishes, the palatine bones are developed, and two lateral posterior processes of this cartilage which abut against the tympanic pedicle, represent the transverse and pterygoid bones.

The labial cartilages, regarded by Cuvier in the *Squatina* and some other *Plagiostomes* as the rudimental and toothless representatives of the maxillary, intermaxillary, and premandibular bones, and which in the *Cestracion* might have been expected, in harmony with the general tendency of its cranial structure, to have been present with a corresponding advance towards their hypothetical maxillary character, have, on the contrary, totally disappeared.

The lower jaw, consisting of the articular and premandibular elements still confluent, is suspended partly to the slender tympanic pedicle, but principally to the expanded posterior extremity of the superior maxillary bone. It closely resembles the upper jaw in form, but is of greater depth, and the symphysis, which is never obliterated, is of greater breadth, and is terminated more squarely.

The teeth are arranged, as in the Plagiostomes generally, in

several antero-posterior rows, along the margin and inner surface of both jaws; but the rows are more oblique than in the sharks, although less so than in certain rays, as *Rhina;* and the teeth present greater diversity both of form and size, than in any other existing plagiostome. The teeth of the upper jaw are delineated in fig. 2, Pl. 11.

The teeth at the anterior part of the jaws are the smallest; they present a transverse, sub-compressed, conical figure, with the apex produced into a sharp point; these points are worn away from the used teeth at the anterior and outer parts of the jaw, but are strongly marked in those which still lie below the margin. There are six subvertical rows of these small cuspidate teeth on each side of the jaw, together with a median row close to the symphyseal line; and from twelve to fourteen teeth in a row. Behind the cuspidate teeth, the five consecutive rows of teeth progressively increase in all their dimensions, but principally in their antero-posterior extent; the sharp-point is converted into a longitudinal ridge, traversing a convex crushing surface; and the ridge itself disappears in the largest teeth. As the teeth increase in size, they diminish in number, in each row; the series of the largest teeth includes from six to seven in the upper, and from seven to eight in the lower jaw. Behind this row, the teeth, although preserving their form as crushing instruments, progressively diminish in size; while at the same time, the number composing each row decreases. From the oblique and apparently spiral disposition of the rows of teeth, their symmetrical arrangement on the opposite sides of the jaw, and their graduated diversity of form, they constitute the most elegant tesselated covering of the jaws which is to be met with in the whole class of fishes.

The modifications of the form of the teeth above described, by which the anterior ones are adapted for seizing and retaining, and the posterior for cracking and crushing alimentary substances, we shall find to be frequently repeated with various modifications and under different conditions in the osseous fishes. They indicate, in the present species, a diet of a lower organized character than in the true sharks, and a corresponding difference of habit and

disposition is associated therewith. The testaceous and crustaceous invertebrate animals constitute, most, probably, the principal food of the *Cestracion*.

The teeth are attached to the maxillary surface by a slightly contracted and truncated basis: the part which may be termed the crown of the tooth is covered with a layer of dense white substance, analogous to enamel, the surface of which is impressed by numerous minute pits. Below the crown, the surface of the tooth is still more irregular, and the basis is composed of coarse fibres with intervening fissures and foramina. The small anterior teeth, which resemble those of certain sharks, may be distinguished by their rugous base, which is also broad and flat.

When the dense outer layer is removed from the crown of the newly formed teeth, the orifices of the medullary canals or tubes perforating the whole body of the tooth are brought into view. The texture of this tooth, in fact, like that of the *Myliobates*, is precisely such as would suggest the idea of the tubular texture assigned by Cuvier to the compound teeth of fishes. These tubes or canals, which are visible to the naked eye, are more or less occupied in the recent fish by a vascular and organized medulla or pulp. They are continued directly from the irregular and reticularly disposed cells and canals of the semi-ossified cartilaginous crust of the jaw. In the large crushing teeth, the greater number of the medullary canals proceed in a pretty regular and slightly wavy course towards the grinding surface, while the outer ones incline towards the lateral surfaces; but they soon begin to divide, and the divisions continue to ramify dichotomously; the branches anastomose together, especially near the surface, and form loops of which the convexity is always directed but flattened, towards the unattached surface of the tooth. The medullary canals are, in general, slightly dilated before they dichotomize, and the branches maintain throughout nearly the same size as the trunk.

Plate 12 shows the general appearance of the medullary canals in a vertical section, including part of the lateral surface of the tooth, as seen by transmitted light through a compound lens of half an inch focus. The dark colour of the wide medullary canals is due to the

opacity occasioned by the earthy matter deposited in them from their peripheral extremities to within a short distance of the base of the tooth. The fine calcigerous tubes, from the same cause, appear as dark lines in the interspaces of the medullary canals, and as they pass into the enamel-like superficial layer.

In Plate 13 is exhibited a portion of two of the terminal medullary loops, with the calcigerous tubes continued from them as seen under a magnifying power of 600 diameters. The interspaces of the medullary canals are traversed throughout the substance of the tooth by calcigerous tubes, which have a general direction vertical to the medullary canal from which they proceed.

The calcigerous tubes present, at their origin, a diameter, generally, of $\frac{1}{4000}$th of an inch. They are more ramified, and have a more undulatory course than the medullary canals, especially those which occupy the interspaces of these canals, where they form a moss-like network, in the meshes of which are minute cells, with which the finest branches of the calcigerous tubes are in communication. The calcigerous tubes of the grinding surface of the tooth have a general direction, vertical to that surface, and the enamel-like coating is formed principally by the finest terminal branches of these tubes, imbedded in a transparent and apparently structureless matrix. Under a power of $\frac{1}{10}$th inch focus, longitudinal series of irregular and partially confluent rhomboidal cells are discernible in many parts of this external layer.

The jaws of the *Cestracion*, like those of the other sharks, exhibit the teeth in various stages of formation. At the innermost extremity of some of the rows, may be seen a small, flat, punctate, milk-white, calcareous plate, of a friable texture, resulting from the recent deposition of the earthy particles in the microscopic cells and tubes of the superficies of the formative matrix; the only part which as yet is developed from the common mucous and ligamentous basis of the teeth. The rest of the matrix is progressively added until the tooth acquires its full size; the deposition of the calcareous salts proceeding from the crown to the base simultaneously along the whole breadth of the tooth.

The process of dentification is here most clearly seen to be one

of conversion, not of excretion. As the teeth advance into use, the organized pulp of each medullary canal becomes consolidated by the formation of concentric osseous layers at its circumference, and by an irregular calcareous deposition in its centre. The new teeth are carried forward and outward by the same rotatory movement of the membranes supporting them, as in the ordinary Squaloids.

19. *Acrodus.*—Among the extinct Plagiostomes recognizable by teeth or spines, the genus *Acrodus*, according to M. Agassiz, presents the closest affinity with the existing *Cestracion*. The teeth of the *Acrodus*, (Pl. 14, fig. 1,) are of an oblong form with a convex or slightly conical crown, supported on a coarse osseous base, in the form of a parallelogram, obliquely truncated at its inner side. The crown swells out beyond the base, and is expanded in the middle, and contracted, generally unequally, towards the extremities; it is traversed by fine ridges, which diverge from one which runs along the middle of the long diameter of the tooth. Portions of the jaw of the *Acrodus* have been discovered which show that these teeth were arranged, as in *Cestracion* in oblique rows, with, at least, seven teeth in a row. Those at the anterior part of the jaws were short, with the middle of the crown raised into an obtuse cone; the posterior teeth were more elongated and depressed.

Professor Agassiz has remarked that ancient writers on Natural History have mistaken the teeth of the *Acrodus* for fossil insects or worms: by the quarry men of this country they are commonly called petrified leeches: by some naturalists, they have been regarded as auditory ossicles or otolithes of fishes; but, independently of more obvious evidence, a single inspection of a transparent slice of one of these fossils in an adequate magnifying power, would suffice to demonstrate their real nature, (Pl. 14 and 15).

The teeth of the *Acrodus nobilis* are composed of two substances, viz: a thin external almost colourless layer, which represents the enamel, and an amber-coloured coarser dentine composing the body of the tooth, and continuous with and passing into its coarse cellular bony basis and support. Microscopic sections of this tooth afford the most beautiful appearances, and, perhaps, the most instructive illustration of the relation of dentine to bone. The body

of the tooth consists of groups of short, branched and frequently irregularly wavy medullary canals imbedded in a clear matrix. These canals are surrounded by concentric layers, and closely resemble the Haversian canals in true bone. The calcigerous tubes, which radiate from the medullary canals, have a graceful undulatory course, and are much branched; but towards the periphery of the tooth, the ramified tubes are all directed, as in ordinary dentine, at right angles to the superficies, and thus constitute a regular layer of hollow columns disposed so as to offer the greatest resistance to external pressure. This layer is equal in thickness to about one-fifteenth part of the vertical diameter of the thickest part of the tooth.

The finest or terminal branches of this peripheral layer of tubes, I have traced in various places into what, at first sight, appears to be the enamel. Under a magnifying power of 400 diameters, however, this outermost layer is seen to be composed of extremely minute tubes, $\frac{1}{10000}$th of a line in diameter (Pl. 16, fig. 2,); they are branched like the coarser tubes of the body of the tooth; irregularly wavy in their course, having a general tendency to an arrangement at right angles to the superficies, but inextricably interwoven, and connected anastomotically together, so as to require a strong light to penetrate even the thinnest section, and render their structure and arrangement visible. The continuation of these finer superficial tubes with the coarser tubes of the body of the tooth, is best observed by slightly changing the focus of the glass with which they are viewed, which brings the transitional tubes at different depths in the section into view. In some parts of the section, a medullary or Haversian canal is displayed longitudinally; and the parallel lines of the surrounding concentric strata on each side are exhibited. The canal maintains a general uniform diameter, but slightly dilates where it divides or sends off a cross branch to communicate with the adjoining canals. These canals commence from the large cells of the bony base, and pass into the substance of the tooth towards its periphery; they communicate by transverse canals, but all ultimately terminate in bundles of the wavy ramified calcigerous tubes of the body of the

tooth. The unobliterated area of the medullary canals was occupied by a vascular pulp in the living animal, and the silicious matter with which they are filled in the fossil, has received a dark stain, probably from the colouring matter of the vascular pulp; but the finer tubes, from the want of this difference of colour, are in many parts obscurely visible, if at all. They are discernible in some situations crossing the concentric lamellæ at right angles to the central canal. The chief difference between the appearance presented by the Haversian canals of the tooth of *Acrodus*, and those in bone, is in the absence of the radiated cells or corpuscles. At the base of the tooth, there are cells interspersed with the medullary canals, irregular in size and form, very minute, and appearing like simple granules without radiating lines. The character of the main or coarser canals and calcigerous tubes of the ivory of the tooth of *Acrodus*, reposes on their undulating course, their rapid diminution and branching, and the moderately acute angles at which the branches are given off, except at the circumference of the tooth, where they run nearly parallel to each other. The line of demarcation between the coarser and finer ivory, is formed by a series of small cells having the form and arrangement represented in Pl. 16, fig. 3, in which many of the finer branches of the coarse ivory terminate, and from which the minute tubes of the enamel-like ivory commence. The superficies of the tooth is slightly punctated; the depressions, however, do not correspond with the mouths of tubes, but with the interspaces of whole groups of the coarser tubes.

20. *Hybodus*.—The remains of the extinct genus of Plagiostomes to which M. Agassiz has given the name of *Hybodus* occur in the secondary formations from the upper red sandstone to the chalk inclusive. They consist of teeth and large osseous spines, which have been discovered so associated together as to leave little doubt that the recent animal was armed with a pair of spines, one to each dorsal fin, as in the Cestracion, and that the jaws were beset with closely packed vertical rows of teeth, containing from six to seven in each row, (Pl. 11, fig. 1). The teeth are in the form of transversely elongated depressed cones, and consist of two pretty equal parts, viz: a

coarse, osseous, wrinkled base, and an enamelled crown. The crown is separated from the base by a slight constriction, above which it swells out and then quickly diminishes to an apical ridge, which traverses its long diameter, and presents a series of pointed cusps; of these, the middle one is the largest and highest; the rest quickly diminish in size as they recede from it. The sides of the crown are traversed by well marked but fine ridges, which converge from below towards the middle cusp, but are variously disposed in the different species of *Hybodus*.

The cusps of the exterior teeth are erect, those of the internal or posterior ones are recumbent, but the transition from one position to the other is gradual and progressive as in *Squatina* and the anterior teeth of *Cestracion*. The development of these teeth corresponds with that in the *Cestracion*, where the whole breadth of the pulp is progressively ossified from above downwards, instead of from the external surface of the whole crown inwards; hence, the last formed teeth are not hollow, as in the true sharks.

The teeth of some species of *Acrodus*, as the *Acrodus minimus* of Agassiz, resemble so closely those of a *Hybodus* in external form, as to be liable to be mistaken for those of that genus. The microscopic structure of the teeth, in these closely allied genera, is very similar in its general plan. In *Hybodus*, however, the calcigerous tubes in the body of the tooth have a less wavy disposition than in *Acrodus*.

21. *Ptychodus*.—The fossil teeth, on which M. Agassiz has established the genus *Ptychodus*, have not as yet been discovered undisturbed in their natural position in the jaws, so as to demonstrate the affinity of the extinct fish to the recent Plagiostomes, with the same certainty as in the case of the *Hybodus* and *Acrodus;* nevertheless, their number, their external form, and the absence of any other parts of the skeleton in the localities where they are most abundant, alike bespeak that they belonged to a cartilaginous fish, which M. Agassiz conjectures to have been nearly allied to the *Cestracion*. The microscopic texture of these interesting fossils, which I described at the meeting of the British Association in 1838, afforded the demonstration finally required of their true nature. The entire tooth (Pl. 17,

figs. 1 and 2) presents a quadrangular form, and consists of a root and a crown; a wide but shallow groove forms the line of demarcation between these parts. The root, which presents a coarse, porous, osseous texture, is flat below, and gradually enlarges towards the crown. The crown suddenly expands above and beyond the root, especially beyond its anterior part. The anterior and two lateral surfaces of the crown are convex, the posterior surface (fig. 1) is concave, apparently for the reception of the convexity of the succeeding tooth. The broad upper surface of the crown is more or less convex, and sculptured with minute tubercles and wrinkles at the circumference, and with large angular transverse ridges in the centre. These ridges are separated by wide grooves, and generally have their extremities bent towards the anterior part of the tooth; the surface of the crown is smooth and polished like enamel. In fig. 2, the sculptured grinding surface of a tooth of the *Ptychodus latissimus* is represented of the natural size.

The texture of the tooth of the *Ptychodus*, examined in a longitudinal vertical section at half an inch focus, as in Pl. 18, presents a congeries of medullary and calcigerous tubes, having the same general arrangement as in the *Cestracion*. The medullary tubes are, however, relatively smaller; they proceed from the coarse canals of the osseous base in a nearly straight and parallel direction towards the surface of the crown, diverging from each other, and branching dichotomously, so as to maintain a direction vertical to the surface towards which they proceed. Their interspaces are pretty regular, and about five or six times the diameter of the canals themselves. They are surrounded by concentric lamellæ (fig. 2, Pl. 19), and send off through the whole of their course numerous minute calcigerous tubes; these are transverse to the medullary canals near the base of the crown, and come off at an acute angle as they approach nearer the summit, close to the surface of which the medullary canals resolve themselves into fasciculi of calcigerous tubes (fig. 1, Pl. 19); in a few places, two contiguous medullary canals anastomose, and form a loop, with the convexity directed towards the surface of the tooth; one of these loops is shown in fig. 1, Pl. 19. The calcigerous tubes are more

wavy than the medullary canals; they quickly ramify, and sub-divide to extreme minuteness in the interspaces, and finally terminate by anastomosing with each other, either immediately or by the interposition of calcigerous cells.

The intimate structure of the tooth of the *Ptychodus* differs from that of the tooth of the *Cestracion*, in the medullary tubes being narrower, the interspaces wider, and the terminal anastomosing loops fewer. The calcigerous tubes, also, are relatively larger, more wavy, and more branched. It differs from the structure of the tooth of the *Acrodus* in the straighter course, and fewer divisions of the medullary canals, and in the absence of the straight parallel superficial series of calcigerous tubes.

22. *Psammodus*.—Under this name, M. Agassiz had formerly associated all those teeth of fishes "which combine a structure like that which characterizes the teeth of the *Cestracion*,"—that is to say, a crown formed of small vertical tubes,—"with a surface of the crown more or less smooth, and presenting only that sanded or punctate character which results from the structure of the crown."

Here, however, I must observe that neither in the teeth of *Psammodus* nor in those of *Cestracion* have the punctate impressions of the enamelled surface any relation with the medullary canals or the large visible vertical tubes to which the learned Ichthyologist just quoted refers. These tubes always terminate at a short distance from the surface of the tooth, either by anastomosis or by subdivision into other tubes of such extreme minuteness that the combined diameters of five hundred of them would barely equal the breadth of a single superficial punctation. These impressions on the teeth of the *Psammodi*, like the transverse ridges of those of the *Ptychodi*, are consequences of the conformation of the original matrix, and can be regarded only as adaptations conformable with the habits and food of the extinct species; and as they are not due to a certain tubular structure, so neither can they be viewed as evidence of such structure when it has not otherwise been proved to exist.

The term *Psammodus* is now restricted by M. Agassiz to the extinct fishes, the teeth of which combine a broad, flat, punctate,

grinding surface, with a great breadth of crown. It is of one of those teeth of the typical *Psammodi* which I have submitted to microscopic examination. A transverse section of the tooth of this genus presents the appearance, under a moderate magnifying power, as if it were composed of close-set coarse tubes, the areæ of which were thus exposed. Such a section, viewed with a power of 400 diameters, shows that these tubes are surrounded by concentric lamellæ, like the Haversian canals; and that these lamellæ, and the clear interspace, which is generally equal to the thickness of the lamellæ, are permeated by minute irregularly disposed tubes, which anastomose in the clear interspace, and open into extremely minute cells, scattered through that part. A longitudinal section of the same tooth shows, in many places, the whole course of the canals; they run nearly perpendicularly to the convex superficies of the tooth, and, consequently, incline outwards at the sides of the section. They lie nearly parallel with each other, with interspaces equal to from six to eight times the diameter of their area, and branch dichotomously once or twice in their course. Each canal is surrounded by concentric layers of a dark colour, encroaching upon one-third of the interspace, which thus presents two semi-opake streaks and one intermediate clear line; the whole of these interspaces is perforated by the irregular wavy, branched, anastomosing calcigerous tubes. The terminations of the medullary canals near the periphery of the tooth are slightly dilated, and give off in every direction calcigerous tubes corresponding to those in the interspaces of the canals. The calcigerous tubes, at this part of the tooth, run obliquely along the side of the medullary canal, from which they are continued, for a short distance before they pass off through the concentric layers into the clear interspace; to this structure is due the appearance, which the medullary canal presents, of being composed towards its termination of a fasciculus of spirally twisted tubes. I have not observed this structure in any part of the medullary canals of the tooth of the *Ptychodus*, which further differs from that of *Psammodus* in the more frequent bifurcation of the medullary canals, and in the smaller extent of their opake concentrically-laminated walls. The structure of the tooth of *Psammodus*, like that of

Ptychodus, differs from that of *Acrodus* in the greater number and more parallel course of the medullary canals, their fewer branches, and in the absence of an external layer of fine parallel tubes.

The Psammodontoid teeth which are elongated, more or less contracted and truncated at the two extremities, and of which the surface of the crown is reticulated, are now regarded by M. Agassiz as indicating a distinct subgenus, to which he gives the name of *Strophodus*, (Pl. 17, fig. 4). Other fossil teeth, which resemble in general structure those of *Psammodus*, but which have the centre of the crown elevated into an obtuse transverse cone, and traversed by a ridge, from which oblique furrows diverge, but with a more or less transverse direction, towards the circumference and there ramify, have been referred by the same authority to a genus called *Orodus*. These fossils occur in the older secondary rocks.

Similar fossil teeth, having the crown in the form of an elevated obtuse cone, but perfectly smooth on the surface, form the type of the genus *Helodus*. Agas.

In a fourth form, the crown is compressed and elevated, and sometimes terminates in a sharp edge like the tooth of a *Carcharias;* its base is always surrounded by a series of concentric folds. This is the type of the genus *Chomatodus*. Agas.

A fifth form of Psammodontoid teeth, in which the crown is raised, subcompressed and subdivided by deep transverse ridges into dentations, varying as to number and degree of sharpness or obtuseness, has given rise to the establishment of the genus *Ctenoptychius*, Agas.

23. *Petalodus*.—In the teeth of many of the subgenera of *Psammodus*, the crown is produced into a median or submedian ridge; if the body of the tooth be supposed to be still more compressed, so that the ridge should terminate the contour of the crown like a trenchant edge, there will then be produced the lamelliform figure which characterizes the teeth of the subgenus in question.

In the specimen of the tooth of *Petalodus Hastingsii* now before me, which I owe to the kindness of Sir Philip Egerton, the trenchant margin is slightly convex and finely serrated, the crown of the tooth is invested with a thin layer of dense enamel, with a smooth and shining surface, the

punctation of which is too minute for the naked eye; the enamel is disposed in a series of concentric lines around the base of the crown; these lines extend lower down on the posterior than on the anterior part of the tooth; and the enamel terminates on both sides in a line which is convex towards the base of the tooth, contrariwise to the terminal contour of the enamel in the compressed teeth of the sharks. The osseous basis of the tooth terminates in an expanded obtuse convex margin. This lamelliform tooth is bent slightly upon itself so that a vertical section exhibits a slight sigmoid flexure (see Pl. 22, figs. 3, 4, and 5.)

In a second species of *Petalodus (Pet. serratus)*, the trenchant margin of the tooth is more strongly serrated, and in a third species, *Pet. dentatus*, it is notched or dentated.(1)

The body of the tooth of the *Petalodus* is everywhere traversed by medullary canals, which are fewer, relatively larger, and more irregularly and reticulately disposed than in the teeth of *Chomatodus*, or of any other genus of Cestraciont. The interspaces of the medullary canals do not quite equal the diameter of the canals themselves: they are traversed by calcigerous tubes, as numerous and minute as in the *Psammodus*, but similar in their wavy disposition to those of the *Acrodus*. The short terminal branches of the medullary canals, which distribute the calcigerous tubes to the enamel-like outer layer, are slightly bent downwards, or towards the base of the tooth.

24. A very interesting modification of the teeth which resemble in structure those of *Psammodus*, is presented in the extinct genus *Cochliodus* of Agassiz. Here the jaws are paved with teeth arranged in a few oblique contorted series, as in the *Cestracion*, but a single tooth occupies the space covered by an entire row in the existing Australian genus. In the specimen figured, in the collection of Capt. Jones, R.N., there are three of these large contorted dental plates in each ramus of the jaw, (Pl. 22, fig. 1.)

The microscopic structure of these large teeth closely resembles that of the true *Psammodus;* the medullary canals have the same

(1) Both these species are founded on specimens in the beautiful collection of the fossils of the mountain limestone, in the possession of Capt. Jones, R.N. M.P.

straight, sub-parallel course, and sparing dichotomous sub-divisions, but they are relatively wider, and are separated by interspaces of less breadth.

The calcigerous tubes are also wider at their origin; they come off not quite at right angles to the medullary canal, but are slightly inclined to the grinding surface of the tooth; they quickly ramify, sending off their branches at nearly right angles, and are less flexuous in their course than in the *Petalodus*; they dilate into angular cells at many parts of the mid-space between the medullary canals.

In the genus *Ceratodus* the dental system is represented by a single large plate on each side of both upper and lower jaws, (Pl. 22, fig. 2.) The detrition to which these plates were subject was repaired by a continued development of the posterior part of the dental plate in the manner which will be explained in the account of the teeth of the *Chimæra*.

The large and singularly sculptured dental plates, to which M. Agassiz has given the name of *Ctenodus*, are likewise conjectured not to have exceeded four in number in the mouth of the extinct species indicated by these remains. The texture of the tooth, like that of others of the *Psammodus* kind, presents a coarse osseous structure at the base, supporting a dense osseous or enamel-like layer; the surface of the crown is minutely punctate. The crown is traversed by twelve nearly parallel ridges, each of which is notched or divided into a series of obtuse cones, which gradually increase in size towards the outer border of the tooth.

Such are the principal modifications of form and structure presented by the teeth of those extinct fishes, of which the *Cestracion* of the Australian seas is the nearest living analogue.

Were this genus to become extinct, all that would remain of it in a few years would be its teeth and dorsal spines, the only hard and durable parts of its frame. Fortunately we still possess the evidence of the general form and organization with which they are associated. But had even the teeth alone of the *Cestracion* remained, a microscopic investigation of their intimate structure must have led to an insight into the close affinities subsisting between the extinct animal and higher cartilaginous fishes. For it is peculiar to

the Plagiostomous order, among fishes, to include so many genera which exhibit in the dental substance the rich organization of vascular and calcigerous tubes that has already been described, and the modifications of which become the more important and interesting, when, as in the case of the extinct *Psammodus*, *Acrodus*, and *Hybodus*, they are almost the sole features of the organization of those most ancient vertebrate animals which remain for the contemplation of the anatomist and physiologist.

CHIMÆROIDS.

25. I next proceed to consider a well marked modification of the same highly organized dental structure in the genus *Chimæra*, which, like the *Cestracion*, is an extreme but still more anomalous modification of the chondropterygious type, having the branchiæ unattached externally: this genus is also the representative of several extinct forms of fishes.

The jaws of the Chimæroid fishes are armed, says Cuvier, in the characters assigned to this family in the Règne Animal,(1) with hard and indivisible plates instead of teeth, four above and two below, and in the 2nd edition of the Leçons d'Anatomie Comparée,(2) these dental plates are described as being salient, trenchant and striated. They have not, as yet, been more particularly described, but the coarse medullary tubes which enter into their composition, and to which Cuvier alludes when he compares the structure of these teeth with those of the Orycteropus in his Histoire Naturelle des Poissons,(3) are illustrated in Pl. 40, fig. 20, of the great work on Fossil Fishes by M. Agassiz.

The teeth of the *Callorhynchus* or *Chimæra Australis*, are represented as they appear on looking into the widely opened mouth in Plate 28, fig. 1. The upper jaw presents two anterior dental plates, of a small size and semi-elliptic form, and two posterior

(1) Tom. ii, p. 382.

(2) Tom. iv, p. 362.

(3) Tom. i, p. 496. Cuvier's words are, "Leur tissu intérieur est percé de tubes fins, comme un jonc ou comme les dents de l'oryctérope." The tubes here mentioned are the medullary or vascular canals, and are merely the centres from which the true calcigerous tubes radiate.—*See Report of British Association*, 1838, p. 145.

triangular plates, six times larger than the preceding. The anterior angles of these plates are rounded, and conceal the posterior half of the anterior plates: the inferior broad surface of the anterior teeth is sinuous, and joins the lateral surface at a sharp edge; the grinding surface of the posterior plates is convex in every direction, and there is a raised portion in the middle of each, of the figure represented in the plate (Pl. 28, fig. 1). The upper surface of each of these teeth is concave from side to side, so that it encases or sheaths the alveolar border of the upper jaw, in a manner analogous to the broad teeth of the *Cestracion*.(1) Both the anterior and posterior dental plates in the upper jaw, meet at the median line of the mouth. The two dental plates of the lower jaw are of a subtriangular form, with the posterior and external sides gently curved; the broad grinding surface is convex on the inner and concave on the outer side; a trenchant margin divides this from the lateral surfaces of the dental plate. When a longitudinal vertical section is made of these teeth (as in fig. 3, pl. 28), their coarse tubular texture is evident to the naked eye. There is a large pulp-cavity at the posterior parts of both the upper and lower dental plates, and, when the pulp is removed, the exposed surface of the base of the tooth presents a reticulate character from the large areæ of the medullary tubes into which the processes of the pulp are continued. These tubes radiate towards the grinding surface of the tooth and dichotomize as they proceed. As these tubes advance towards the surface, their cavity becomes gradually obliterated by calcareous salts, deposited in concentric layers and perforated every where by the minute calcigerous tubes which radiate from the medullary canal; thus the substance of the tooth increases in density as it approaches the triturating surface.

A diminished view of the appearance of a longitudinal section of the dental plate of a *Chimæra*, as seen under a magnifying power of 400 diameters, is given at Pl. 29, fig. 1, and of a transverse section at fig. 2. But before proceeding to describe this structure, a few words are requisite touching the modifications of form presented by the dental plates of *Chimæra monstrosa*, (Pl. 28, figs. 4 and 8), and of some allied ex-

(1) The genus *Cochliodus* appears to have been an extinct transitional form between *Cestracion* and *Callorhynchus*.

tinct species which present the same intimate structure of the dental substance.

In the *Chimæra monstrosa*, the dental plates differ considerably in their general form and disposition from those of the *Chimæra* or *Callorhynchus australis;* they are extended in the vertical more than in the horizontal direction, sheath the exterior of the jaws, and serve as instruments for cutting and dividing rather than for triturating and crushing. The anterior teeth of the upper jaw, more especially, present characters of which we find no trace in the teeth of the last described recent species ; the dental substance being so arranged as to resemble a series of oblique superimposed lamellæ. The fossil dental plates of the extinct species of *Chimæra*, discovered and described by Dr. Buckland, resemble the northern rather than the southern Chimæra of the present day ; some of these teeth, as those of *Chimæra Colei*, and *Chim. Owenii*, resemble in size, though they differ in form from the dental plates of *Chimæra monstrosa*, but the dental plate of the lower jaw of the *Chimæra Townsendii*, which is upwards of six inches in length, indicates a species which, *ceteris paribus*, must have surpassed eight feet in length.

In the marine eocene formation called the London clay, at Sheppey, the dental plates and portions of the jaws of an extinct *Chimæra*, three or four times the size of the existing species, are occasionally found ; the laminæ of the anterior tooth of the upper jaw are bent obliquely, so that the outer margin of the plate presents a series of lines, which are horizontal on its anterior part, and bent obliquely upwards at the side. The posterior dental plate has its outer wall composed of a series of vertical columnar portions, the lower ends of which, as they are worn by attrition, cause the trenchant margin of the jaw to be notched and irregular. The inner surface of the same plate is convex, smooth and punctate ; it encloses, as it were, a portion of the jaw itself.

In the extinct Chimæroid subgenera *Edaphodon* and *Passalodon*, discovered and so called by Dr. Buckland, the teeth are long, broad, and thick, with surfaces adapted for crushing and bruising, like the dental plates of *Callorhynchus;* but, instead of encasing the alveolar borders of the jaws, they are themselves inclosed in the sub-

stance of the jaw, which presents the coarse cellular structure of the bone of osseous fishes. The teeth are not, however, loosely implanted in these alveolar cavities, but wherever they are in contact with the bone, they are anchylosed thereto. Their structure is, nevertheless, strikingly different from that of the jaw itself, and corresponds with the modification of the tubular structure presented by the teeth of the *Chimæra*. In the *Edaphodon* there are three of these large teeth on each side of both jaws: their position is nearly horizontal and their grinding surface is pitted with small impressions.(1)

In the tooth of the Chimæra, the complex structure arising, as it were, out of an aggregation of long slender and simple cylindrical teeth is most conspicuous. Each of the parallel medullary or vascular canals, which from their large size are easily distinguishable by the naked eye, is the centre of radiation to very numerous and closely compacted calcigerous tubes, having a diameter of $\frac{1}{19000}$th of an inch at their origin, but ramifying and diminishing in size as they recede, and ultimately terminating in a minute irregular cellular ossification which occupies the interspaces of the different systems of radiated tubes, and cements them together in a continuous mass in the recent dental plate. The course of the calcigerous tubes is at right angles to the medullary canal, and they have a wavy disposition; their primary branches are sent off at an acute angle, and the fine ramuli from these branches dilate or terminate in minute cells considerably smaller than the radiated cells of mammiferous bone.

In the fossil teeth of the large extinct *Chimæræ*, the coarser cellular structure, which cements together the systems of calcigerous tubes, is generally more or less decomposed, while the denser parietes of the medullary canals formed by the calcigerous tubes remain; the coarse tubular structure of the tooth thus displayed, is accurately figured by M. Agassiz in the *Chimæra Townsendii*. But the medullary canals and their radiated systems of calcigerous tubes are not only cemented together by the ossified capsules, but are still more effectually connected together by the frequent anastomoses of the parallel medullary canals themselves. The portion of the tooth figured (Pl. 29, fig. 2) exhibits some of these anastomoses. In those parts of the section in

(1) Proceedings of the Geological Society, 1838, p. 687.

which the parietes of the medullary canal have been divided parallel to its course, the calcigerous tubes are cut through transversely, and their areæ, from the calcareous nature of their contents, are seen like fine dots.

SPATULARIÆ.

26. *Polyodon.*—Of the other free-gilled Plagiostomous fishes the *Sturionidæ* or family of Sturgeons and the *Planirostra* are edentulous. The *Polyodon*, which belongs to the same natural family as the *Planirostra*, viz: the *Spatulariæ* of Müller, has small recurved teeth on the maxillary and anterior branchial cartilages, at least, at the earlier periods of life. The specimens of *Polyodon*, (e. g. in the Parisian Museum), which exceed three feet in length are, like the *Planirostra*, edentulous; but in a *Polyodon* of the same species about one foot long, there are two rows of small and slightly recurved teeth in the upper, and a single row of similar teeth in the lower jaw: similar teeth occur likewise on the two anterior branchial arches, where these join the tongue; and again on their expanded extremities which are attached to the palatal region of the mouth: (1) here, therefore, there are both maxillary and branchial teeth. Thus the *Spatulariæ* not only exhibit a tendency to the structure of the ordinary osseous fishes in the condition of their branchial apparatus, but likewise in that of their dental system; the *Polyodon* being the only plagiostomous fish which has both maxillary and branchial teeth.

CHAPTER IV.

TEETH OF THE GANOID FISHES.

LEPIDOIDS.

27. The consideration of the teeth of this family of Ganoid fishes is not without interest, although as compared with the Plagiostomes, few modifications require to be noticed. All the representatives of the family have disappeared from the present theatre of vital phenomena; yet although the period when they existed is the

(1) Müller, Vergleichende Anatomie der Myxinoiden, p. 150.

earliest of those in which palæontologists have recognized the traces of animal life, the same peculiarities are manifested in the structure and disposition of their dental organs, as in those of many of the existing osseous fishes. The teeth are always present on the palatine bones, and are arranged in several rows on the alveolar margins of the intermaxillary and premandibular bones; those of the outer row are the largest, and are sometimes in the form of obtuse cones; the posterior ones are small, simple and close-set, like the bristles of a brush.

In the genus *Amblypterus* all the teeth are of the latter kind, and their minute slender character is the more remarkable on account of the disproportionate magnitude of jaws. In the genera *Palæoniscus* and *Semionotus*, the maxillary teeth also resemble a fine brush; indicating, Dr. Buckland observes, " the habit of these fishes to have been to feed on decayed sea-weed, and soft animal substances at the bottom of the water."

In the large enamel-scaled fishes of the Lias formation belonging to the genera *Dapedius* and *Tetragonolepis*, the teeth are stronger and better developed, especially the exterior ones. In the *Tetragonolepis*, the summit of the crown is simply pointed, but in the *Dapedius* it is notched or bifurcate; and this modification is not due to usage or compression, for the teeth of all the rows and in both jaws exhibit the same character, which is also well marked in the successional teeth that have not come into place. In *Dapedius Orbis*, the teeth of both jaws are strongly dilated and compressed from before backwards, at their summits, and resemble a chisel with a notched cutting edge.(1)

In the extinct genus *Lepidotus*, the mouth was small and the jaws short and rounded. The intermaxillary bones form only the anterior part of the upper margin of the mouth, the maxillaries completing the posterior part of that border. The margins of both these bones, according to M. Agassiz, are beset with small teeth; the outer row presenting the form of circular obtuse cones; and within these are many rows of smaller sessile hemispherical teeth, more or

(1) M. Agassiz assigns pterygoid, as well as palatine and intermaxillary teeth to the genus *Dapedius*, t ii, p. 187.

less constricted at their base, and supported on a short pedicle, which is anchylosed to the osseous substance of the jaws. (Pl. 30, fig. 1). The detached hemispherical teeth of the Lepidoid fishes are so like those of some of the genera of the Pycnodont family, as to be scarcely distinguishable.

The only difference which M. Agassiz recognizes between the teeth of *Lepidotus* and those of *Sphærodus* is, that in the former they have a slight constriction at the base of the enamel. But having ascertained this character not to be constant, I submitted the teeth of the *Lepidotus Mantellii* to microscopic examination, and have compared their intimate texture with that of the similarly shaped teeth of *Sphærodus Bucklandi*. The dense substance of the tooth of the *Lepidotus* (Pl. 31) is composed of fasciculate tubes continued directly from the cells of the osseous base, radiating, with a direction vertical to the surface of the tooth, and giving off branches, at an acute angle, from their very commencement; thus far the general character of the texture of the tooth is the same as that of *Sphærodus*, afterwards to be described; but the fine branches into which the fasciculate tubes resolve themselves in *Lepidotus*, diverge at a much more open angle from the main trunk, are spread out more widely, are more curved, and present the appearance of the stems of corn beaten down with heavy rain. These fine terminal branches are inextricably interwoven, and present the appearance of numerous anastomoses, but do not form so dense a plexus of calcigerous tubes and cells as in the teeth of *Sphærodus* in which the corresponding tubes and cells intercept the light.

PYCNODONTS.(1)

28. In this family of fishes, of which all the representatives are extinct, the teeth present a greater diversity of character, and a higher degree of development than in the preceding; the prevalent form approaches to that of the *Lepidotus;* the teeth being generally adapted for crushing, and having a smooth convex or flattened crown. In some genera they attain a very large size; when smaller they are arranged in several rows. They have been observed in the intermaxillary, premandibular, palatine and vomerine bones.

(1) πυκνος, thick, οδους, a tooth; thick-toothed fishes.

In the genus *Pycnodus* the teeth are more or less elongated, with the crown slightly expanded, and convex and smooth above. The disposition of these teeth on the vomerine bone is seen in figs. 1 and 2, Pl. 34. A central row of transversely oval grinders is bounded on each side by a double alternate row of smaller circular teeth. Similarly shaped teeth were arranged in three or four rows on the jaws; but the exact number and disposition of the maxillary teeth have not yet been ascertained.

The modifications of external form which characterize the teeth of the different species of this genus, which have yet been discovered, are exhibited in the great work on Fossil Fishes by M. Agassiz, tab. 72, *d*, vol. ii.

Sphærodus.—This genus is founded on detached teeth, which are the sole remains of the species composing it that have as yet been brought to light. These teeth are of a hemispherical form, with a smooth upper surface, (Pl. 33, figs. 1 and 2), and most probably were distributed over the same bones as in the *Pycnodus*. The basis of the tooth is a bone of the coarse cellular structure usual in osseous Fishes. (Pl. 32). The body of the tooth consists of coarse tubes, which arise insensibly from the basis, where they have a diameter of $\frac{1}{1000}$ th of an inch, and proceed directly and perpendicularly to the surface of the tooth. The characteristics of these tubes are, first, that they are so closely arranged together that only one-fourth of their own diameter intervenes between them at their origins. Secondly, they present the appearance of being composed of a closely-twisted bundle of smaller tubes,—an appearance produced by the oblique direction and acute angle at which the calcigerous tubes are continued from them into the clear intervening substance. Besides these smaller tubes, the main trunks begin immediately to give off short and somewhat coarse branches at very acute angles; these branches increase in number, and the trunks proportionally diminish, until they have traversed two-thirds of the vertical diameter of the tooth; they then resolve themselves into fasciculi of extremely minute twigs, which interlace together, and in many places dilate into, or communicate with, numerous minute calcigerous cells, and form so dense a layer as to intercept the light, excepting

towards the circumference of the tooth, and consequently at the two extremities of the section, where only the structure above described is visible. Several small twigs pass beyond this plexus into the clear enamel-like outer layer of the tooth, in some parts of which traces were perceptible of a plexus of still more minute tubes, or *striæ*, which gradually diminished until they escaped the highest magnifying power employed in this examination. (Pl. 33). The enamel-like layer is clearly a continuation of, and part of the same substance as the rest of the tooth; its dense and clear texture indicates the extreme subdivision and abundance of the earthy salts: this stratum is of considerable thickness in the *Sphærodus crassus* of Agassiz.

In the genus *Gyrodus* the surface of the teeth is furrowed sometimes irregularly, sometimes regularly and deeply as in *Gyr. rugulosus*. (Pl. 34, figs. 6 and 7). The teeth are present in the intermaxillary, premandibular, palatine and vomerine bones.

In the *Gyrodus umbilicatus* each premandibular bone supports four rows of teeth (Pl. 34, figs. 4 and 5); those of the external and third rows are of a transversely oval form, and are larger than those of the second and internal rows, which have a circular contour. The intermaxillary and premandibular teeth are fewer in number, and present an obtuse conical form in the *Gyr. circularis*. The vomer in this species is covered with five longitudinal rows of teeth; those of the middle one being the largest as in the *Pycnodus*.

In the tooth of a *Gyrodus cretaceus*, I find that the tendency to the structure of the dense ivory of the teeth of the higher *Vertebrata*, which is obvious in the teeth of *Sphærodus* and *Lepidotus*, is carried on to a close correspondence. The base of the tooth is excavated by a large and simple pulp-cavity, presenting a quadrate figure in a vertical section of the tooth; this cavity is immediately continuous with the large cells and reticulate canals of the bony base. The body of the tooth consists of close-set minute calcigerous tubes, having a diameter of $\frac{1}{1000}$th of a line at their origin, radiating in a direct line, but with a minute and regularly undulating course, and a gradually diminishing diameter to the superficies: the lateral tubes pass horizontally, and those continued from the summit of the pulp-cavity vertically, to the

grinding surface. They give off very regular, but extremely minute branches, which are lost in the clear and dense enamel-like superficial layer of the tooth.

In the genus *Microdon*, the teeth, though presenting all the general characters of the Pycnodontal structure, are reduced to their smallest dimensions. They present a flattened angular form, and are arranged in many rows on the intermaxillary, premandibular and vomerine bones. The whole substance of the tooth is composed of calcigerous tubes, which are straighter, more parallel, and relatively finer than in *Gyrodus*, whence there results a texture of still greater density, and one that approaches very closely to that of the molar teeth of the Gilt-head (*Chrysophrys*). The arrangement of the component tubes of the tooth of *Microdon* is shown in Pl. 43, fig. 1.

The pavement of thick, round, convex or flattened teeth of the genera of Pycnodonts, above described, was adapted, like the corresponding teeth of existing fishes, to break and crush small testaceous and crustaceous animals. These teeth, under the name of Bufonites, occur most abundantly in the oolite formation.

The teeth of the extinct fishes of the genus *Placodus* present reverse proportions to those of the *Microdon*, and here attain their maximum of development in the Pycnodont family. Plate 30, fig. 2 exhibits the alveoli of the prehensile intermaxillary teeth, and the molar teeth of the same bone *in situ* of the *Placodus Andriani*, Ag. The prehensile anterior teeth were arranged in two transverse rows of six in each row. The anterior were the largest, and presented a singularly elongated cylindrical form, with a conical slightly recurved obtuse crown (fig. 3). In *Placodus gigas*, the crown of the incisor is more expanded and more abruptly bent. These teeth, like the divergent anterior teeth of the Wolf-fish, must have served to grapple with large *Testacea* or *Crustacea*, the crushing and comminution of which were then completed by the posterior dental plates. These are arranged in four rows, of which the two external ones include each four smaller subcircular teeth ; the two internal rows consist each of three large tetragonal dental plates with the angles rounded off, and the upper surface flattened and smooth.

In the lower jaw it would seem that three similar dental plates in

each premandibular bone were opposed to the molar teeth above. The side view of these teeth (Pl. 30, fig. 4) shows their elevation above the jaw. In the vomer, a median row of transversely oblong teeth is bounded by smaller subcircular teeth, as in the other Pycnodonts.

SAUROIDS.

29. This family of voracious fishes is represented in the existing creation by extremely few species, which are severally the types of the genera *Lepidosteus*, *Amia*, and *Polypterus;* and these genera are distributed at remote distances in the great rivers of the American and African continents. The general character of the teeth in this family is to have larger ones of a conical form intermixed with more numerous teeth of smaller size.

The Sauroid fishes have teeth on the intermaxillary, premandibular, palatine and vomerine bones. These teeth are conical and sharp-pointed: some are large, and are separated by interspaces occupied by similarly shaped but much smaller and more numerous teeth. The larger teeth are grooved longitudinally at the base, and have a large conical pulp-cavity within. Their fluted base sinks into an alveolar cavity of the jaw, but is intimately blended with its bony walls, in a manner which will be more particularly described in the teeth of the *Rhizodus*.

In the jaws of the *Polypterus* of the Nile, there are two rows of equal, fine, sharp, approximated teeth; those of the anterior row are the largest; the posterior ones are like the teeth of a rasp.

In the Stony-gar (*Lepidosteus*) of the North American rivers, the elongated jaws are also armed with similar laniary and rasp-like teeth: the outer row consists of numerous conical sharp-pointed teeth, which are separated by regular intervals containing the sockets of old teeth which have been shed, and the germs of new ones. External to these larger teeth there is a less interrupted row of smaller conical teeth.(1) The inner border of the dentigerous margin of the jaw is beset with a series of small rasp-like teeth; and similar teeth are present on the vomer and the palatine bones. The larger conical teeth are developed in alveolar cavities, but their basis becomes

(1) Pl. 35, fig. 1.

anchylosed to the jaw-bone when their growth is completed; and, as in most other fishes, the succession of new teeth seems to be uninterrupted.

The extinct genera of this family were much more formidably armed, and the great conical laniary teeth of some of the individuals compete in size and strength with those of the largest Ichthyosaurs and Crocodiles. Plate 35, fig. 2, is a reduced figure of the dislocated and fractured premandibular bones of an extinct sauroid species of the genus *Rhizodus*, a genus nearly allied to the *Holoptychus* of Agassiz, but differing in the greater number, and more robust and obtuse shape of the smaller conical teeth. In each premandibular bone there are three elongated conical teeth, with several smaller and more obtuse conical teeth in the interspaces.

The larger teeth have an ovate transverse section, with a trenchant posterior margin, and terminate above in a sharp point; they are thus alike fitted for piercing and cutting. Their base is irregularly fluted in the longitudinal direction, and sinks deep into the substance of the jaw, with which it is firmly anchylosed. The peculiarly efficient mode in which these large destructive teeth are implanted in the jaws, indicates the violence and force with which they were wielded in the predatory contests of the living fish. Fig. 1, Pl. 36, shows the external form of one of the larger teeth of the *Rhizodus*. A longitudinal and vertical section has been removed from the grooved base, showing its solidity, and the coarse longitudinal fibrous structure which it presents to the naked eye. Fig. 2 exhibits the complicated organization which a section of a portion of the basis of the tooth presents under a magnifying power of $\frac{1}{4}$ inch focus.

The exserted body of the tooth is hollow, as in other Sauroids, but the pulp-cavity is relatively smaller; the parietes of this cavity consist of a dense ivory, composed of minute calcigerous tubes. The diameter of these tubes at their origin is $\frac{1}{1000}$th of a line. They proceed in slight curvatures from the central canal at right angles to the periphery of the tooth, with interspaces equal to four of their diameters; throughout their course they are minutely undulated, and occasionally divide dichotomously; they give off ramuscules at very acute angles, which are lost in the clear interspaces. The thin external enamel-

like coating of the tooth receives numerous similar parallel ramuscules from the stratum of calcigerous cells which forms the boundary between this external layer and the ivory of the tooth. The pulp-cavity, which has a compressed ovate section, is gradually contracted and finally obliterated in the basis of the tooth, where it divides into numerous minute canals which subdivide and anastomose as they penetrate deeper into the jaw, and finally terminate in minute tortuous canals, which become continuous with those of the coarse osseous substance in which they are imbedded. All the preceding branches of the pulp-cavity are the centres of radiation of as many systems of calcigerous tubes, similar in size to those of the body of the tooth. The primary curvatures of these tubes are shorter, and the interspaces somewhat wider; the calcigerous cells in which the fine branches of these calcigerous tubes terminate, are also coarser. The interspaces of the divisions of the base of the tooth are occupied with the coarse cellular bone of which the jaw is composed.

The teeth of the *Rhizodus* thus include two very different types of structure, which pass insensibly into one another; the exserted body of the tooth is like the dense ivory of the ordinary mammiferous or saurian tooth, the inserted basis presents the compound structure of the teeth of the *Myliobates* and *Orycteropus*. Each division of the tooth's basis, however, presents in the *Rhizodus* greater strength and density than the corresponding parts of the tooth of the *Myliobates*, in consequence of the greater minuteness, increased number, and more aggregated and parallel disposition of the calcigerous tubes, and the smaller diameter of the medullary cavity in the former species. The advantage which was obtained for the teeth of the extinct carnivorous Sauroid by the root-like implantation above described, in resisting displacement and fracture, is too obvious to need further illustration. Finally, as the teeth of no species of reptile or fish are similarly subdivided and implanted in the jaws, the teeth of the *Rhizodus*, notwithstanding the organization of the crown, may be readily and certainly distinguished from them.

The large conical laniary teeth of the extinct genera *Holoptychus* and *Megalichthys* present a similar structure to that of the tooth above described. The whole body of the tooth is composed in

Megalichthys of minute close-set calcigerous tubes, having a diameter of $\frac{1}{1100}$th of a line, with interspaces of twice that diameter. The calcigerous tubes have a minutely undulated course, and pass in nearly a straight line from the internal to the external surface of the tooth; the pulp-cavity extends about half-way through the body of the tooth, and has a narrow elliptic transverse section; it becomes gradually smaller at the base of the tooth, and there branches out into several ramifications, which are continued into the cylindrical processes of the dental substance, and these are imbedded, like so many piles, in the coarse osseous texture of the jaw.

GYMNODONTS.(1)

30. To the theory of dental development by intus-susception or the deposition of calcareous tubes in the pulp's substance, as opposed to that of apposition or the transudation of layers of calcareous matter from the pulp's surface, may be objected the structure and mode of formation of the compound teeth of the gymnodont fishes, as described by Cuvier(2) and Von Born.(3) In the *Diodon*, more especially, the lamellated structure of the tooth, and its reproduction by successive transudation of layers from a persistent pulp, were supposed to be clearly demonstrated in the broad rounded triturating tubercle which is situated behind the alveolar border of the jaws. The exposed surface of this tooth presents, in fact, a series of transverse and parallel striæ (Pl. 38, fig. 1), which, in a vertical section (*ib.* fig. 2) are seen to be the margins of thin, superimposed, horizontal, and slightly flexuous plates, which have been partially abraded by trituration in an oblique plane. The superior layers are the most worn, and are evidently, as Cuvier observed, the oldest; in proportion as they descend, in the lower jaw, they increase in breadth; and finally, instead of being soldered together, they become detached, thinner, and of a more friable texture, the lowest and incompletely developed plates lying loosely in the cavity of the jaw beneath the superincumbent dental mass (*ib.* fig. 2, *a*). If a vertical section of the tubercle be made on one side of the median

(1) γυμνος *naked*, οδους a *tooth*, fishes with teeth exposed.

(2) Leçons d'Anatomie Comparée, 1st and 2nd editions.

(3) Heusinger's Zeitschrift, 1827.

plane, the laminæ are seen to be developed in two distinct lateral moieties, which become anchylosed together by means of a thin median vertical osseous partition at their median margins; their lateral margins are similarly anchylosed to the outer walls of the dentigerous cavity. It is quite clear, as Cuvier observes, that the laminæ are developed successively: and that, in proportion as the anterior ones are worn away, the posterior ones appear in readiness to replace them, so that the due number of ridges, on the triturating surface, is always maintained.

Nevertheless, these facts will be shown to be quite insufficient to establish the theory of dental development by transudation of layers. Any example of a continual reproduction of teeth in vertical succession, would be as available in that point of view; the peculiar application of the tooth of the *Diodon* to illustrate the theory of transudation, is due merely to the form of the denticles which compose that compound tooth.

Cuvier, in his examination of the dentition of the gymnodonts, had employed the microscope so far as to detect the fine reticulate impressions on one of the surfaces of the dental laminæ of the *Diodon*, which he rightly attributes to the impressions of vessels; a low power, as that of the ordinary pocket-lens, is sufficient to demonstrate these markings. To examine the structure of the lamelliform denticles, it is necessary to make extremely thin sections in a direction vertical to their plane. A portion of such a section, seen by transmitted light with a focus of half an inch, presents the appearance delineated in Plate 39, fig. 2. Each plate here exhibits, instead of an amorphous or sub-crystalline mass of excreted calcareous matter, a series of extremely minute calcigerous tubes, occupying its whole extent and having a general direction vertical to its plane. The tubes are obviously wider at the lower side of the plate, and gradually disappear in the clear and dense substance at the opposite surface. When the thinnest and most transparent parts of the same section are examined with a compound lens of $\frac{1}{8}$ inch focus, the horizontal partitions, which occupy the interspaces of the lamelliform teeth, are seen to consist of a coarse cellular osseous texture, without any radiated (Purkinjian) corpuscles, but similar to the texture of the rest of the

endo-skeleton of the *Diodon*. The main tubes of the dental plate are continued immediately from the cells of the osseous septum; they proceed for a short distance vertically, or with a slight curvature, in the substance of the dental plate, and then quickly divide and subdivide, the branches generally coming off at an angle of 45°, being slightly bent, crossing each other in an inextricable manner, and terminating ultimately in the clear matrix of the upper surface of the dental plate.

Each dental lamella presents, at every part, the same organized structure which is above described and delineated; there is no part which offers the crystalline characters of true or mammalian enamel. The mucous membrane of the mouth and periosteum of the jaws, are reflected into the cavities at the base of the compound tooth (Pl. 38, fig. 2, *a*); the periosteum lines the parietes of the cavity, and the mucous membrane forms a thick cushion, extended across its floor. From this surface, a lamelliform pulp is developed, in which the calcifying process takes place in a direction from above downwards: at first, the earthy salts are deposited in the state of such minute subdivision and in such a direction and abundance as to produce the dense and minutely tubular structure of the dental plate; when this has acquired its due thickness, the rest of the pulp becomes ossified, *i.e.* the calcareous salts are deposited in less abundance, and in the parietes and interspaces of coarse cells, instead of those of minute tubes. The margins of the ossified pulps, by this process, become confluent with the parietes of the general dental cavity, and the mutual adhesion of the flattened surfaces of the impacted lamelliform teeth is promoted by the pressure to which their exposed surfaces is subject. By the time that ossification has begun in one pulp, a second has been developed beneath it, and it is the portion of the pulp solidified by the fine tubular calcification which gives rise in the macerated and dried jaws to the loose and thin lamellæ in the dental cavity. These lamellæ become fixed by means of the coarser calcification or ossification which subsequently takes place in the remains of the pulp, and their margins are thus anchylosed to the surrounding bone, in a manner analogous to the fixation of the base of the ordinary shaped teeth in other fishes.

The structure and formation of the compound tooth of the *Diodon*, illustrate the nature and causes of the apparently lamellar structure of the teeth of certain mammalia, especially of the conical tusks, the growth of which is uninterrupted. The polished surface of a vertical longitudinal section of one of these teeth exhibits concentric lines which run parallel with the outer contour of the section; these teeth, moreover, are commonly resolved by decomposition into a series of superimposed laminæ, or sheathed cones, and this fact has been regarded as indubitable proof of their original formation by successively transuded layers of dental substance. Nevertheless, microscopic sections of such teeth have uniformly displayed a structure of tubes running in a direction diametrically opposite to the plane of the lamellæ. These lamellæ are, in fact, due, not to successive transudations from the free surface of the formative pulp, but to alternations of states of comparative activity and repose in the organizing processes by which the stratum of the pulp, in immediate connection with the last formed or basal surface of the tooth, is prepared to receive the hardening salts, combined with alterations in the nature itself of the organizing process. These alternate changes are indicated by the layers of abundant calcigerous cells which are scattered through the intertubular tissue of the tooth in planes corresponding with the apparent stratification of the dental substance, and with which cells angular inflections of the calcigerous tubes frequently correspond. A separation of corresponding layers of parallel aggregated segments of calcigerous tubes, in the tusks which manifest the preceding structure, is the usual result of their decomposition.

In the compound dental plate of the *Diodon*, similarly parallel and aggregated series of short calcigerous tubes are separated by thin layers of a cellular bone; and by decomposition, such a tooth would, in like manner, exhibit the lamellated structure; but the lamellæ in this case, as in the tusk of the elephant, or the conical molar of the cachalot, equally present an organized structure of aggregated calcigerous tubes, directed more or less at right angles to the plane of the lamella, and indicating that higher mode of development by calcification of the pulp, which it is the chief object of the present researches to exemplify.

The exposed margins of the upper and lower jaws of the *Diodon*, which appear to be covered with a thick irregular layer of the same dense white dental substance as that of the posterior triturating masses above described, owe their apparently simple character to a still more complicated structure. They consist of a series of narrow flattened denticles lying horizontally, and at right angles to the anterior surface of the jaw; so that those of the exterior row of one jaw have their sides opposed to the corresponding row in the opposite jaw when the mouth is closed. These denticles are developed in a cavity, between the outer and inner walls of the jaws, the floor of which is formed by a thin cribriform osseous plate, separating the cavity containing the teeth (Pl. 38, fig. 2, *b*) from the wide vascular canal *(c)* which occupies the substance of the jaw. At the bottom of the dental cavity, the denticles are seen in different stages of formation, unattached, but closely packed, and with their lateral margins overlapping each other. They are of an oval form, with the under surface, or that next the floor of the cavity, slightly concave and smooth: the opposite surface convex, and honeycombed: the denticles gradually diminish in size from the middle to the outer ends of the dentated margin. As their formation reaches its completion, the denticles become anchylosed to each other and to the osseous parietes of their cavity by ossification of the capsules of the calcified pulps. The thin layer of bony matter or cement enclosing the denticles is soon worn away when they reach the margins of the jaws, the irregularity of which is caused by the alternately overlapping arrangement of the exposed denticles.

The order of development and succession is the same in the marginal as in the posterior teeth, they ascend in the lower and descend in the upper jaw, but are pushed on in the horizontal instead of the vertical direction. The chief difference is, that whereas in the posterior dental tubercle there are only two broad lamelliform teeth in the same plane, in the marginal series there are upwards of forty narrower denticles.

Cuvier observes that the *Tetrodons* differ from the *Diodons* inasmuch as they have no posterior triturating disk, but only the marginal plates; and have the jaws divided, each into two portions by a den-

tated suture. In the upper jaw of many species of Tetrodon, there is a rudimental posterior dental series, consisting of three or four plates which project downwards and backwards from the base of the intermaxillary bones, and intercept a space in which the apex of the lower jaw is received when the mouth is closed. In Plate 39, fig. 1, is given a figure of the beak-like jaws of the *Tetrodon lineatus*, showing the median suture, the lines of stratification of the marginal dental plates, and, at (*a*), the posterior lamelliform teeth above described. The marginal lamelliform teeth are from ten to twelve in number in each half of the mandible; the innermost are the broadest, and they become narrower as they pass outwards. The intervening portions, or bases of their respective pulps remain longer in the unossified state than in the Diodon. The microscopic structure of the teeth of the Tetrodon closely agrees with that of the dental tubercle of the Diodon.

SCLERODERMS.

31. The teeth in the file-fishes *(Balistes)* are limited to the intermaxillary, premandibular and pharyngeal bones.

In the *Balistes forcipatus*, Pl. 40, the teeth of the upper jaw are fourteen in number, and are arranged in two rows, seven in each intermaxillary bone, four in the front row and three behind. In the lower jaw there are eight teeth corresponding with the front row above. The anterior or external teeth of the upper resemble those of the lower jaw; they are strong, conical, subtrihedral, hollow at the base, which is obliquely truncated, and rounded and obtuse at the apex. The mesial pair is slightly curved, and is the largest; the rest decrease in size to the outermost. The external facet of each tooth is covered with a smooth, dense, enamel-like substance, which, towards the apices of the teeth, presents a yellow colour, and calls to mind the peculiar colour of the enamel in some of the *Rodentia*. These outer maxillary teeth are arranged in close contact with one another (Pl. 40, figs. 1 and 7). The form of the alveolus in which the base is fixed, is peculiar in the dental system, resembling rather the surface of attachment for the claw in the ungueal phalanges of the feline quadrupeds. A conical process of the bone rises from the middle of the alveolar depression, and is adapted to the cavity in the base of the

tooth (Pl. 40, figs. 3 and 5). The circumference of the base of the fully formed tooth is attached by a slight anchylosis to the margin of the alveolus, but the confluence of the tooth with the bone is much less complete than in many other fishes.

There would seem to be a constant and pretty quick succession of these teeth, for in all the jaws of different species which I have examined, there were the crowns of a second or new series of teeth, generally pretty far advanced in their development. The successors of the external teeth of the right intermaxillary bone, exposed by removing the outer wall of their alveoli, are represented *in situ* in fig. 5 of Plate 40: (*a*) points to the osseous tubercle on which the tooth about to be displaced was fixed; the absorbent process has commenced at its apex: at (*b*) the corresponding bony tubercle has been thus entirely removed, and the obtuse apex of the new tooth has protruded in the socket of that which it has displaced. The cavities containing these teeth communicate with the exterior of the jaw by foramina, situated as in most other fishes, on the outer side of the base of the teeth in place (Pl. 40, figs. 1 and 3).

The teeth of the posterior row, which are peculiar to the upper jaw, are six in number, three in each intermaxillary bone: they present the form of elliptical plates, compressed laterally, rounded at the base, and slightly pointed at the apex. The anterior tooth is the largest, measuring in *Balistes forcipatus* six lines in length, and three in breadth, but scarcely half a line in thickness; the two other teeth progressively diminish in size (Pl. 40, fig. 4). These posterior teeth lie in close juxtaposition with the outer row, and like the posterior small upper incisors of the hare and rabbit, receive part of the appulse of the inferior teeth. They are affixed by a very oblique and slightly excavated base to a shallow alveolus, having a convex rising of bone in its middle (Pl. 40, fig. 6). They are also deciduous, and the presence of well developed reserve-teeth in cavities of the jaw, immediately internal to those of the exterior row, would indicate that the succession of the teeth of the inner row is likewise unlimited. The foramina leading to the cavities of the successional teeth are seen immediately above the bases of the teeth in place. The germs of the successors of the inner row of teeth ex-

posed in their alveoli in the left intermaxillary bone, are figured in Plate 40, fig. 6.

The number of the teeth is not constant in the genus *Balistes*, but in no species examined by me were the posterior teeth of the upper jaw absent. In an Australian species, I found six teeth in the outer row and four in the inner row of teeth in the upper jaw. The apices of the mesial pair of the posterior row projected between those of the first and second teeth of the outer row.

In all the file-fishes, the pharyngeal teeth are small, conical, laterally compressed, curved and sharp-pointed; regularly arranged in two rows upon the opposed margins of each of the two upper and lower pharyngeal bones. A view of the upper and lower left pharyngeal bones, *in situ*, is given in figure 2, Plate 40. The direction of the curvature and the relative size of the anterior and posterior teeth are reversed in the two bones, which thus form an admirable carding machine for "teazing" the bruised and coarsely divided sea-weeds or other marine nutrient substances which the fish has obtained by means of its large maxillary teeth.

Microscopical sections of these dense teeth in the *Balistes forcipatus* present a structure so closely corresponding with that described by Professor Retzius in the *Balistes Vetula*, that a better idea of it cannot be conveyed than in the words of that excellent observer. He says,(1) "That the dentine (zahnknoche) of both the Balistes and Sparus resembles most in internal structure that of the teeth of mammalia and reptiles, being white and hard, like ivory, and displaying under the microscope beautiful, regular, minute and parallel tubes. These, in *Balistes vetula*, are $\frac{1}{1000}$ of a Paris line(2) in diameter, and are beautifully parallel, save in their last formed parts at the coronal end of the pulp-cavity. Their undulations are long and slight. Their interspaces are equal to their own diameter. The larger branches lie close to the trunks, while the smaller ones generally bend away in a

(1) Müller's Archiv. 1837, p. 523.

(2) The French inch of twelve lines is so nearly one-fifteenth more than the English inch, that the conversion of the fraction of a French line into the fraction of an English inch by multiplying the denominator of the former by 11¼, is sufficiently accurate for all practical physiological purposes; thus the calcigerous tube measuring $\frac{1}{1000}$th of a Paris line, will be $\frac{1}{1125}$th of an English inch.

direction transverse to that of the main tubes, and towards the root. The main tubes terminate near the superficies of the tooth in bold parallel curvatures. The greater part of the tooth of this fish is surrounded by a thick and dense enamel, into many parts of which the tubes of the dentine appear to be continued; it is full of fissures directed outwards. A kind of cement seems to surround the base of the tooth."

In his comparison of the structure of the enamel in the teeth of different animals, Professor Retzius again refers to that of the *Balistes*, and mentions the remarkable number and regularity of the fissures in it, which, as he correctly states, somewhat resemble the tubes of the dentine. "The cæmentum is characterized by its large, and extremely irregular cells, which are in many parts confluent, or communicate immediately, with each other. The minute plexiform tubes have an extremely irregular course. This coating of cement is very thin, and seems to terminate below the margin of the enamel."(1)

The similarity between the enamel and dentine of the file-fish, as of the parrot-fish (see Pl. 50), is not less close in regard to the organization of their respective pulps, and their mode of calcification, than in their microscopic structure when completely formed. The cæmentum is the result of the ossification of the capsule which includes the pulps of the dentine and enamel; and consequently it corresponds in its coarse cellular structure with the rest of the osseous system.

GONIODONTS.(2)

32. The teeth of all the species of this family are long, slender, filiform, or setaceous, and are bent like awls or tenterhooks, whence is derived the name of the family. In some of the genera, the teeth of the short and broad intermaxillaries are disposed in lines radiating from behind towards the anterior margin, and are thus somewhat analogous to the vertical rows in which the teeth of the sharks are arranged. They further resemble the squaloid teeth in being attached, not to the bone, but to the membrane investing the maxillæ, and are consequently moveable, both forwards and backwards.

(1) Loc. cit. p. 541. (2) Γωνια, an angle, οδους, a tooth; Pl. 48, figs. 1, 2 and 3.

In the genus *Acanthicus*,(1) the maxillary teeth are bisinflected; the first, or anterior tooth of each of the radiating rows, is the shortest, and is curved outwards, the rest, to the number of seven or eight, being bent backwards: there are from twenty-five to thirty of these rows on each side of both upper and lower jaws.

The setaceous teeth of the *Rhinelepis*(2) have a similar arrangement in antero-posterior radiated rows, and a similar moveable connection with the maxillary membranes; but the foremost tooth in each row has its inflected summit split, and thus presents the singular form of a bicuspid hook; the posterior succeeding teeth, in each row, have a simple hooked apex.

The foremost tooth of each radiated series in the *Hypostoma*(3) is much shorter than the second, and is bent outwards: the second, third and fourth teeth, counting backwards, are twice curved, with the apex bent inwards; the succeeding teeth grow shorter, present a simple curve, and thus gradually disappear.

In the *Loricaria* the bisinflected setaceous teeth are arranged in a simple series along the alveolar border of the intermaxillary and premandibular bones: the summit of each tooth is curved inwards and backwards.

From the constancy observed in the different sizes, shapes and directions of the teeth composing the vertical or radiated rows in the above genera, it is to be inferred that they do not succeed each other, and are not on the constant move from behind forwards, as in the Plagiostomous fishes, with which in other respects the teeth of the Goniodonts offer some striking analogies.

SILUROIDS.

33. The dental armature of this extensive and singular family of fresh-water fishes is never of a predatory or formidable character, the teeth being always small and simple, or of a minutely villiform kind. Some species are almost edentulous, but there are others which exhibit peculiar conditions of the teeth not elsewhere observable in the vertebrate division of animals.

In the genus *Cetopsis* a single series of simple conical teeth

(1) Pl. 48, fig. 3. (2) Ib. fig. 2. (3) Ib. fig. 1.

projects from the premandibular and vomerine bones, and one or more rows of similar teeth from the intermaxillaries. The corresponding teeth in the *Doras* are either minutely villiform, or are replaced by equally minute uncalcified papillæ, which permanently represent the very earliest stage of dental development.

The slightly calcified papillæ on the intermaxillary and premandibular bones of the *Hypophthalmus* are so minute as to require the aid of a pocket lens for their detection: but the branchial arches support more conspicuous organs, which are clearly referable to the dental system:(1) these are slender, elongated, pointed, whitish, rigid, and fragile lamellæ, attached in a close-set row to the concave side of the arch, and with their points projecting towards the gullet. Those of the first pair of branchial arches are most developed, equalling the gills in length; the rest gradually diminish as they approach the pharynx.

In the *Pimelodus* villiform teeth are arranged in several rows upon the intermaxillaries and premandibulars, and a few graniform teeth upon the vomer (*Pimel. Spixii*). In the *Pimelodus ctenodus*, the first row of jaw-teeth is composed of larger, rounded conical denticles, with an obtuse apex. Other species of *Pimelodus* have teeth on the palatine bones, but not on the vomer: and the species called by Cuvier *Pimelodus genidens* offers the singular peculiarity of a patch of moveable calcified denticles upon the inside of each cheek, or lateral membrane closing the mouth.

In the genus *Platystoma*, the intermaxillary, premandibular and vomerine bones are beset with broad bands of strong villiform and setiform teeth gradually increasing in length as they are placed deeper in the mouth:(2) the pharyngeal arches are covered with similar, but finer denticles.

In the *Plotosi*, the vomerine teeth are obtuse and rounded.

The premandibular teeth of the *Synodontes* present compressed crowns terminated at one end by a recurved apex, and attached by the opposite end or base to a flexible peduncle.(3)

(1) Agassiz. Spix, Pisces Brazilienses, p. 15.

(2) Pl. 1, fig. 1, exhibits the under surface of the right intermaxillary bone of a Siluroid fish of the subgenus *Platystoma*.

(3) " La machoire inférieure porte un paquet de dents très applaties latéralement, terminées

The largest and most fully developed teeth of the Siluroids, as those of the *Platystoma*, present under the microscope a modification of the reticulo-medullary type of structure, which nearly resembles that of the salmon and the pike: the meshes of the anastomosing medullary canals being open, pretty regular, and either subcircular or polygonal. The thin outer crust of the tooth is traversed by minute calcigerous tubes, having the usual direction vertical to the surface.

CHAPTER V.

TEETH OF THE CTENOID FISHES.

PERCOIDS.

34. ALTHOUGH the fishes of the present tribe are of predatory and voracious habits, like the common perch—their type, yet their teeth are never developed to any considerable size, but in all the species are small, numerous, and closely aggregated, resembling the plush or pile of velvet. In the perch, *(Perca fluviatilis)*, there is a broad band of these teeth 'en velours,' on each of the intermaxillaries and premandibulars, a narrow band on each palatine, and across the fore part of the vomer; a small patch of similar teeth is also present on the anterior extremity of each external pterygoid, or transverse bone, which is a rare locality for teeth. There is a series of small plates armed with similar villiform teeth along the concave surface of each of the branchial arches; and the exposed surfaces of the upper and lower pharyngeal bones are entirely covered with them. The points of these minute denticles are all turned towards the gullet; and thus, although none of the teeth are sufficiently developed to kill by piercing or laceration, they all combine to hold, to crush and to aid in the deglutition of a living prey.

In the genus *Labrax*, besides the localities above mentioned, the tongue is covered with villous teeth.

In the *Etelis*, there is a row of moderately long, recurved, conical

en crochet, et suspendues chacune par un pedicule flexible, dentition dont il n'y a point d'autre example connu."—*Cuvier, Règne Anim.* ii, p. 294.

teeth on the intermaxillary and premandibular bones, besides the villous teeth in the ordinary situations.

In the *Lucio-perca*, a row of longer pointed teeth are intermixed with the villous teeth of both the maxillary and palatine bones; they are most developed in the lower jaw and the palatine. There are no lingual teeth.

The Enoplose of New Holland, (*Chætodon armatus*, Shaw), instead of the hair-like teeth of the genus to which it was originally referred, has a narrow band of villous teeth on each intermaxillary, premandibular and palatine bone, and a small transverse band upon the vomer; the tongue is also similarly armed at its base; the rest of the organization of this fish is in like manner conformable to the percoid type.

Villous teeth constitute the only armour of the mouth, according to Cuvier, in the Percoid genera, *Apogon*, *Cheilodipterus*, *Pomatomus*, *Anabassis*, *Aspro*, *Grammistes*, *Acernia*, *Polyprion*, *Pentaceros*, *Centropristis*, *Grystes*, *Rypticus*, *Chironemus*, *Centrarchus*, *Pomotis*, *Priacanthus*, *Dules*, *Therapon*, *Datnia*, *Pelates*, *Helotes* and *Polynemus*.

In the *Uranoscopus*, the mouth is cleft in the vertical direction behind and nearly parallel with the anterior facet of its cubical head. The teeth of the upper jaw (intermaxillaries) are villiform and arranged in three rows, the middle ones of the posterior row being the largest. In the lower jaw there are six large conical teeth on each side, set wide apart in a single row, with some villiform teeth in the middle. The vomer has a small band of villiform teeth on each of its anterior angles; the palatines are armed with somewhat larger teeth; the tongue and branchial arches are edentulous; the pharyngeal bones have rasp-like teeth.

The Mullet and Surmullet (*Mullus barbatus and Surmuletus*) are but feebly provided with teeth; the intermaxillaries and palatine bones are edentulous; there is a narrow band of villiform teeth on the lower jaw; and a large oval plate covered with a pavement of small obtuse teeth on the vomer. The *Upeneus vittatus*, or *Mullus vittatus* of Forskäel, has villous teeth like the Percoids, on the intermaxillary, premandibular, palatine and vomerine bones; in the *Upeneus flavolineatus*, the teeth are wanting on the palatines.

In the *Serrani*, or Sea-perches, the dentition begins to assume a more carnivorous character, and long, sharp-pointed, conical teeth are intermixed with the teeth 'en brosse,' which are arranged in bands more or less broad on the intermaxillary and premandibular bones. In the *Serranus Scriba*, the two or three laniary teeth near the middle line are most developed. The palatines and pharyngeal bones are armed simply with villous teeth; these are arranged in the form of a chevron on the vomer; the tongue is edentulous.

The *Plectropromes*, *Mesoprions* and *Cirrhites* have the same type of dentition as that of the Sea-perches. The larger conical teeth are also superadded to the villiform teeth of the jaws in some species of the genus *Sillago*.

In the genus *Trichodon*, the villiform teeth are more elongated than usual, slightly recurved; and those of the exterior rows have more a horny than a bony consistence, whence the name of the species (*Trachinus trichodon*) which Cuvier has made the type of a genus.

In the genus *Myripristis*, there are very fine villiform teeth on the palatines, vomer, and jaw-bones; but in front of the latter, there are five or six of larger size, but of an obtuse conical shape. The tongue is smooth, but the branchial arches and pharyngeal bones are armed with villiform teeth.

The beautiful *Holocentra* and the large-eyed *Beryx* have simply villiform teeth on the same localities as the *Myripristis*. The weevers (*Trachinus*), have also the pterygoid bones similarly armed. In the *Percis*, a row of larger unciform teeth are placed in front of the villiform teeth of the jaws; the palatine and lingual bones are edentulous.

In the *Percophis*, there are five long, recurved, sharp-pointed teeth in each intermaxillary; and a greater number of similar teeth in the lower jaw, besides the teeth 'en velours.' The palatine, as well as the vomer, are armed with villiform teeth.

COTTOIDS.

35. In the Cottoid or mailed-cheeked fishes, (*Joues cuirassées* of Cuvier), the only teeth which maintain a constant character are those of the pharyngeal bones, which are always villiform. In the common

Gurnards (*Triglæ Lyra* and *Gurnardus*), and the Bullhead, (*Cottus Gobio*) the maxillary, vomerine and branchial teeth are of the same kind; the tongue and palatine bones are edentulous. In the *Cottus scorpius*, or Father-lasher, the teeth are a little more strongly developed. In the *Cottus grunniens* these larger teeth are continued from the vomer upon the palatine arches; while those of the jaws are villiform. In the Stickle-backs (*Gasterosteus*), similar teeth are arranged in a narrow band along the intermaxillary and premandibular bones; but the palatines, vomer, and tongue are edentulous. In the Flying Gurnard, (*Dactylopterus*), the teeth are likewise limited to the jaws, but they are obtuse and form a little pavement of four or five rows, which grow narrower towards the angles of the mouth: the pharyngeal bones preserve their typical character; and in the mailed Gurnards, (*Peristedion*), they are the only bones of the buccal cavity which support teeth.

SPAROIDS.

36. In the Bream-tribe of Fishes, the teeth are restricted to the intermaxillary, premandibular and pharyngeal bones, but are remarkable for their variety of form, and frequently for their large size.

Dentex.—Few fishes are armed with a more formidable apparatus, or one better adapted for the seizure and destruction of a living prey, than are those which belong to the genus of Sea-bream(1) called *Dentex* by Cuvier. This name was, in fact, applied to a Mediterranean species of bream by the Latins, on account of its large pointed teeth, which project from the fore-part of the mouth.

With the exception of a pavement of minute rounded teeth, which defends the inner side of the alveolar wall of the jaws, all the teeth of the *Dentices* are conical, sharp-pointed, and slightly recurved, corresponding in shape with the laniaries or canine teeth in the mammalia. They are limited to the intermaxillary and premandibular bones, and form a single row on each side of each jaw. In some species, as the *Dentex multidens*, the laniary teeth are large and of nearly equal size all round the mouth; but in most species, as in the one figured, (*Dentex argyrozona*, Pl. 41), four of these teeth in the upper, and four in the lower jaw are produced, at the anterior part of the mouth,

(1) The River-Bream (*Cyprinus Brama*, L.) belongs to a different family, characterized by toothless jaws; see *Cyprinoids*.

into very long and strong tusks, and considerably exceed the other teeth in size. They are supported on strong tumid processes of the jaws, with which their bases are firmly anchylosed. In the jaws represented at fig. 1, one of the large teeth has been shed, and the cavity is laid open to expose its successor, of which the crown is partly formed. Similar new teeth, preparing to take the place of the smaller lateral laniaries, are exposed in their cavities. These reserve teeth are situated above and a little to the outside of the base of the tooth, which they are destined to displace; and, in the more advanced examples, a perforation leading to the cavity may be seen on the outer side of the old tooth. Absorption of the anchylosed base of the tooth commences at this part, and gradually extends inwards.

In fig. 2, an inside view of the jaws of the left side is given, to show the pavement of minute rounded denticles along the inner side of the bases of the laniary teeth. The jaws are of great strength in relation to the force with which the teeth are destined to be exerted.

In the *Dentex hexodon* only six of the teeth in each jaw present the laniary figure and size, the rest being small and closely aggregated in a comb-like form. The tongue and palate are quite smooth, the bones of these parts, as well as the vomer, being edentulous. The pharyngeal bones, from the small size of their numerous teeth, resemble fine combs.

The *Dentices* devour small fishes, cephalopods and crustacea; their intestinal canal is short, the pyloric cæca few, and the stomach simple and membranous. They frequent rocky places.

37. The gilt-heads (*Chrysophrys*) are distinguished by a dentition on the same general teleological principle as in the *Cestracion* and *Anarrhicas*, the anterior teeth being adapted for seizing, and the posterior ones for crushing the alimentary substances. These teeth are limited in their position to the intermaxillary and premandibular bones. The elongated conical anterior teeth are never fewer than four, or more than six in each jaw. The posterior obtuse rounded grinding teeth, are arranged in three or more rows.

In the species of Gilt-head, (*Chrysophrys Australis*), of which the jaws are figured in Plate 42, fig. 3, the principal or long anterior conical teeth are four in each jaw; those of the lower are more widely

separated than those of the upper jaw, and in the interspace of the two middle ones of the lower jaw, there are two small conical teeth. In the upper jaw, the first tooth of the external row of molar teeth, presents a conical crown ; the rest are rounder and more obtuse, but present a small mammilloid apex ; after the eighth, there are three or four much smaller teeth. The molar teeth of the second row are less than the outer ones ; some much smaller granulated teeth, less regular in their arrangement and size, are developed at the inner side of the base of the second series. The principal molars of the lower jaw are also in two rows, internal to which are some smaller and less regular teeth, which are fewer in number than those of the upper jaw.

There is a constant and pretty quick succession of teeth in the jaws of the gilt-heads. In the specimen figured, the outer plate, of the intermaxillary and maxillary bones has been removed to show the successors of the outer row of teeth, in various stages of formation, but with the crown of the tooth nearly completed in most of them. These germs are each lodged in a cavity close to the base of the tooth which is to be replaced ; their course is directed towards the outside of that base, and the cavity, which is occasioned by the absorption consequent on the pressure, is enlarged from without inwards, contrary-wise to the progress of the excavation which is produced in the succession of the teeth of the Reptilia.

The matrix of the teeth of the *Chrysophrys*, as in most other fishes, becomes ossified when the crown of the tooth is fully completed ; and the tooth is thus fixed by anchylosis to the margins of the jaws.

In the present and many other exotic species of *Chrysophrys*, the new teeth always resemble in shape and size those which they succeed ; but in our common gilt-head (*Chrysophrys aurata*), some of the posterior and internal molars, which in the young fish are hemispherical, are succeeded in the mature fish by one or sometimes two larger grinders of an oval form.

In this species there are six holders, or produced anterior teeth, in each jaw ; they are relatively stronger, longer, and more curved than in the *Chrysophrys Australis*. The obtuse grinding teeth are

arranged, in the young specimens, in four rows, and all present the hemispherical form. When the individuals have attained seven or eight inches in length, the third row presents three teeth of conspicuously larger size. In a Gilt-head of eleven inches in length, the molar teeth of the upper jaw are in five rows, and the fourth row presents three teeth larger than the rest, of a sub-elliptic form, with the long diameter transverse; the large elliptic molars of the adult, of which the long diameter is in the axis of the body, is now formed, but is still concealed in the substance of the jaw. When it has come into place, the mature dentition may be said to be complete. The base of the fully formed teeth in use is anchylosed, but in a slighter degree than usual, to a thin osseous lamella, which forms the floor of a shallow depression or alveolus in which the base is lodged. The flat lamella is perforated by numerous foramina, and the sides of the alveolar depression are grooved with numerous radiating lines.

The texture of both the pointed and obtuse teeth is extremely dense; it consists of a body of hard white dentine, and a coat of organized enamel, analogous to that of the incisors of the file-fish. The crowns of the rounded molars of the gilt-head hardly suffer the saw to make an impression upon them. Their calcigerous tubes are very numerous and extremely minute, and cross each other towards the periphery of the tooth at acute angles, as in the molars of Lepidotus. The microscopic structure of the anterior pointed teeth resembles that of the incisors of the *Sargus*, which will be described in the next section.

38. *Sargus*.—Fishes which present so close a correspondence in their general conformation and zoological characters as to be included by Linnæus in the same genus, and by Cuvier in the same natural family, may, nevertheless, differ widely in their habits and be nourished by the most opposite kinds of food, and these peculiarities will be associated with modifications of the digestive system, and especially of the teeth. Of this we have a striking example in the Bream-tribe. In the Dentex (the *Sparus dentex* of Linnæus), the dentition was of a predatory and destructive character, all the teeth being formed to seize, and pierce, and lacerate. In the *Chrysophrys*

(*Sparus aurata*, &c. Linn.), the laniary type was limited to the anterior teeth, while those which corresponded with the lateral teeth of the Dentex had exchanged their piercing for a crushing form, and the small miliary denticles which are scattered over the inner side of the alveolar border in the *Dentex argyrozona*, had risen, as it were, from their rudimental condition, begun to assume a functional character, and to be counted as a second and third row of molar teeth.

In the sub-genus, of which the dentition is now to be described, the transition from the carnivorous to the herbivorous type is effected by simply modifying the form of the large anterior teeth, and converting them from piercing to cutting instruments.

Their crowns, instead of tapering to a point, are widened laterally, compressed from before backwards, and truncated at the extremity; they are flat or slightly convex on the outer surface, and concave on the opposite side, and in the larger species of *Sargus* closely resemble, in size and shape, the incisors of the human subject. This resemblance has caught the attention of most ichthyologists who have had occasion to describe any of the species of the present genus. Salviani characterises his *Sargo* or *Sargone*, among other marks, by the "*dentibus latis, humanis similibus;*" Klein and Cuvier extend the same comparison to the "Sargues" in general; and had Scheuchzer founded his supposed discovery of the *Homo diluvii testis* on a fossil incisor of the present genus, instead of the skeleton of a gigantic salamander, the mistake would have been more venial, and might not so soon have been rectified.

"Tout-à-fait semblables aux incisives de l'homme,"(1) is, however, a somewhat exaggerated expression of this relation, even in the *Sargus Rondeletii*. The fang of the fully formed, but unattached tooth, (such as those of which the crowns are figured(2) protruding through the apertures exterior to the base of the incisors in place), grows wider to its free extremity instead of contracting; while, in the incisors in use, this fang is anchylosed to the alveolar margin of the jaw, as in fishes generally. The antero-posterior diameter of the fang is also greater in proportion to its lateral diameter than in the human incisor.

(1) Cuv. and Val. Hist. Nat. des Poissons, vi, p. 16. (2) Pl. 42, fig. 2.

The number of these incisors is sometimes eight in the upper and six in the lower jaw, as in the *Sargus Rondeletii* and *Sar. Salviani;* sometimes it is eight in both jaws, as in the *Sargus annularis*, *Sargus Vetula*, and in the well known Sheep's-head fish of the coasts of New York (*Sargus Ovis*). In another species (*Sargus rufescens*, O.) there are six incisors in the upper and eight in the lower jaw. In the *Sargus unimaculatus*,(1) in which the incisors present the same number, their cutting margin is notched, as in the teeth of the *Glyphisodons*.

The incisors are arranged in close and compact order; in some species they are placed nearly vertically; in others, more obliquely in the jaws; but they always form an instrument well adapted for cropping the sea-weed and other marine plants, which constitute the food of the fishes of the present genus.

In the common Mediterranean species (*Sargus Rondeletii*), the whole of the broad alveolar margin of the intermaxillary bones is paved with rounded molars, similar to each other in form, but becoming larger as they are placed further back in the mouth: they are arranged in three rows; those of the innermost row are the largest, those of the middle row the smallest.

The premandibular pieces of the lower jaw are similarly paved with two rows of hemispherical molars, those of the inner row being the largest. In the *Sargus unimaculatus* there are two rows of molars in each jaw. In the *Sargus Noct*, (Ehrenb.), the molars form four rows in the upper and three in the lower jaw. In the Sheep's-head fish, and in the *Sargus rufescens*, in which the molars are similar in number to those of the *Sargus Rondeletii*, the external row present a somewhat more conical form than the others. In the *Puntazzo* bream they are reduced to a single row in each jaw, and are of very small size.

There is a free and constant succession of teeth in the phytiphagous *Sargues*, as in the rest of the Sparoid tribe. At whatever age the fish may be, foramina will be seen on the outer side of the bases of the incisors, and external grinders, and on the inner side of the internal grinders; and the foramina lead to cavities which contain the crowns of new teeth in different stages of development. The old teeth and the alveolar surfaces to which they are anchylosed are dis-

(1) Pl. 1, fig. 9.

placed by the absorbent process, and their successors become in their turn anchylosed to the bony plate which, in the progress of growth, has at length reached the level of the alveolar margin.

A vertical longitudinal section of the incisor of the *Sargus*,(1) sufficiently thin to be examined microscopically by transmitted light, shows that it consists of a central body of compact dentine, composed, as in the human tooth, of fine, parallel, close-set calcigerous tubes; and that the crown is covered by a thick layer of a distinct substance analogous to enamel.

The structure of the external substance is, however, very unlike that of the true enamel of the human or mammiferous tooth: other broadly-marked distinctions are at once seen in the continuation of the pulp-cavity to the apex of the crown, and in the expanded fang or base of the tooth.

The calcigerous tubes of the ivory, in the body of the tooth, make a bend when they leave the pulp-cavity, with the convexity turned towards the apex; they are then slightly curved in the opposite direction, and again bend outwards, with the convexity as in the first curve, thus describing a beautiful sigmoid undulation. At the base of the tooth the direction of the calcigerous tubes is more transverse, and the number of undulations is greater. Near the apex the middle bend is gradually lost, and the tubes as they proceed outwards describe a simple curve, with the convexity next the apex of the tooth. The secondary curvatures of the calcigerous tubes are beautifully and minutely undulatory (*a*, fig. 2). The main tubes at their commencement near the base of the conical cavity of the pulp are more irregularly flexuous, for a short distance than in the body of the tooth. They send off minute branches throughout their whole course, at very acute angles, except near their extremities, where the branches bend outwards and are consequently more readily discerned. The peripheral extremities of the calcigerous tubes seem to terminate somewhat abruptly in a clear and apparently structureless space or stratum, which intervenes between the tubuli of the ivory and those of the enamel. External to this is an opake stratum, apparently composed of the ex-

(1) Pl. 43, fig. 2.

tremely numerous and minute extremities of the enamel-tubuli. These, commencing as it seems from the external surface, divide and subdivide as they pass inwards towards the dentine, not maintaining a parallel course, but crossing each other, in an irregularly and variously bent direction (*b*, fig. 2).

The pulp-cavity becomes consolidated in the old incisors by a coarse cellular ossification of the remains of the pulp (*c*, fig. 2).

39. There are certain species of Sparoid fishes, which, like the Gilt-heads, have four or six strong, conical, laniary teeth at the anterior extremity of each jaw, with hemispherical molars behind ; but these teeth never exceed two rows, and the small graniform teeth, when present, are limited to the space posterior to the laniaries. This dentition, which characterizes the genus *Pagrus* of Cuvier, is represented at fig. 15, Plate 1. The pharyngeal teeth likewise differ in form from those of the *Chrysophrys*, being small and sharp pointed. In the Braise (*Pagrus vulgaris*), these teeth are arranged in strong pectinated rows. They are fewer in number, and of a conical form in the *Pagrus Orphus*. In one species, the anterior conical teeth of the upper jaw are directed forwards and project from the mouth, the two external ones being longer than the rest ; from this structure Cuvier has designated the species *Pagrus laniarius*.

In another group of Sparoid fishes (*Pagellus*, Cuv.) which have rounded molars, like the *Chrysophrides* and *Pagri*, the anterior teeth are restricted in their development, and form one or more pectinated or villous rows at the front of the mouth (1).

The pharyngeal teeth are unciform and stronger than in the *Pagri*.

There is one species of *Pagellus* which offers an anatomical peculiarity so closely connected with the dental apparatus as to merit a brief notice. The superior maxillary bones are expanded, and their texture is as dense as that of the hard enamel of fishes' teeth : but they are edentulous as in most other fishes. The habits of the species, hence called *Pagellus lithognathus*, are not sufficiently known to afford a knowledge of the use of these petrous maxillaries : they characterize

(1) The intestinal canal is generally longer in the *Pagelli*, which are compelled, from the inferior armature of the mouth, to feed on organized matter of a lower grade than do the more formidably toothed *Pagri* and *Dentices*.

the adult period, when the fish, for example, has acquired a length of three feet: in a specimen measuring a foot long, the enlargement of the maxillaries has scarcely begun to take place.

An extinct genus of Sparoid fishes, called *Sparnodus* by M. Agassiz, has conical teeth on the outer margin of both jaws, but with an apex so obtuse that they present nearly the form of the molars of *Chrysophrys*: the dentition differs from that of the Gilt-heads, inasmuch as the molars form only a single row.

In the genus *Lethrinus* the intermaxillary and premandibular bones are furnished with villiform, laniary, and molar teeth; but the latter are always restricted to a single row, and are sometimes of a large size. The laniary form and development is confined to the four or six anterior teeth, behind which are placed the minute villiform teeth; the single row of large molars distinguish the Lethrines from the other Sparoid genera.

In the *Lethrinus latidens*, a species discovered by the French voyagers, MM. Quoy and Gaimard, on the coasts of New Guinea, there are six strong laniary teeth in the upper, and four in the lower jaw; the first molar of the upper jaw is small and round: the second is twice as broad in the transverse as in the antero-posterior direction; the three following teeth are of still larger size, and are remarkable for their great breadth: the last molar is the smallest. This dentition is interesting on account of its analogy with that of the singular extinct genus *Placodus*.

Cantharus.—The Sea-breams belonging to this genus have their teeth of small size, and closely aggregated on the alveolar borders of the jaws, like the teeth of a rasp; the anterior ones being a little longer and more curved than the rest.

The Sparoids of the genus *Box* (Cuv.) have a single row of closely-packed flattened teeth in each jaw; the anterior ones have simple crowns, while those at the sides are notched in the middle of the cutting margin.

The *Scathari* have a single row of flattened, pointed, but not notched teeth, in each jaw.

The *Oblatæ* have a single row of flattened and notched teeth,

like the *Boges*, but they have also a band of villous denticles behind the flattened teeth.

A fish of the Red-sea, the *Sparus crenidens* of Forskäl, has two rows of compressed teeth in each jaw ; the external ones being larger than those of the second row. These teeth are compressed, broad, and their cutting edge is subdivided into five denticles, which give it a festooned contour. Behind their crenate teeth, there are some small granular denticles. The pharyngeal teeth in this genus form a fine rasp. A figure of this singular dentition, after Cuvier, is given in Pl. 1, fig. 7. It concludes the series of modifications of the dental system which have hitherto been discovered in the fishes of the Bream tribe.

SCIÆNOIDS.

40. In all this family of fishes, as in the Sparoids, the vomer and palatine bones are edentulous. In the Maigres or true *Sciænæ*, there is a single row of wide-set, moderately large, conical, pointed and slightly recurved teeth, with several smaller ones in the interspaces, in both jaws.

In the *Corvinæ*, the larger conical teeth are restricted to the upper jaw ; the villiform teeth are present in both jaws ; on the pharyngeal bones the teeth present the form of obtuse cones in the centre of the dental group, and are villiform at the circumference. The maxillary teeth of the *Leiostomes* are so minute, as to have escaped the notice of some naturalists, and the name of the genus(1) was conceived under this misapprehension ; extremely fine villiform teeth are, however, present, and form a narrow band on each intermaxillary and premandibular bone ; the teeth on the posterior part of the pharyngeal bones are obtuse and form a fine pavement.

In the genera *Eques*, *Larimus*, *Lepipterus*, *Dascyllus* and *Heliasis*, the maxillary teeth are minute and villiform. But in the *Boridiæ*, each jaw is armed with three or four rows of thick, short, blunt teeth, of which the six or eight anterior ones are conical and larger than the rest.(2)

(1) λειος, smooth ; στομα, mouth. (2) Pl. 1, fig. 14.

In the *Conodon* there is a single row of conical teeth in each jaw; the six anterior ones are longer than the rest. Behind the conical teeth there is a band of villiform teeth.

In the *Otolithes* there are two teeth in the upper jaw much larger than the rest.

The *Ancylodons* are also characterized by the extreme length of certain of their maxillary teeth. In the *Ancylodon jaculidens* these teeth are slightly dilated in the middle, and sharp pointed, so as to present a certain resemblance to an arrow, whence the specific name of the fish. There are two rows of these teeth in each intermaxillary bone, and in the anterior part of the interspace of these rows there project two teeth much longer and more curved than the rest. The premandibulars are each armed with a single row of arrow-shaped laniaries, of which the three anterior ones and the fifth are the longest. Besides these laniaries the jaws support a narrow band of fine villiform teeth. The tongue is smooth and edentulous. The pharyngeal teeth are villiform, but the middle ones above are stronger than the rest. The *Ancylodon brevipinnis* has a single row of laniary teeth in each intermaxillary bone of which the two median or anterior ones are the longest; in the lower jaw the median teeth are short, and those at the sides are most developed.

In the *Amphyprions*, *Pomacentrums*, and *Glyphisodons*, there is a single row of small conical or trenchant teeth on each jaw. Those of the lower jaw in the *Glyphisodon* are slightly notched on the cutting edge.

In all these genera the teeth, when fully developed, become anchylosed to the substance of the jaws, but are subject to displacement by the absorbent process, excited by the pressure of their successors. In the Maigre (*Sciæna Aquila*) the microscopic texture of the teeth corresponds with the third modification, as exemplified in the teeth of the genus *Sphyræna* (Pl. 53).

TÆNIOIDS.

41. In the *Trachypterus Falx*, a species of the first genus of the present family in the Cuvierian system, the mouth is transverse, with a vertical aspect and nearly parabolic form. There are six or eight

conical teeth on a transverse row at the anterior margin of both the upper and lower jaw. Three or four similar teeth are arranged longitudinally along the anterior end of the vomer. The palatines are roughened by small callous papillæ, but otherwise are edentulous. In the *Trachypterus Bogmarus* there are six pretty large and sharp-pointed teeth in the upper jaw, directed backwards towards the gullet; the lower jaw is armed with eight similar teeth.

In the Vaegmaer or Deal-fish, (*Gymnetrus arcticus*) the intermaxillaries and premandibulars are armed with small conical pointed teeth. In the *Gymnetrus gladius* the maxillary teeth are so extremely minute as hardly to be felt, and to be visible only with the aid of a lens.

In the Band-fish, (*Cepola rubescens*) there is a row of slender pointed, slightly curved teeth on the outer margin of each jaw; those of the lower jaw projecting considerably. The vomer, palatine bones and tongue are edentulous.

In the *Lophotes* the palatines and vomer, as well as the intermaxillaries and premandibulars, support teeth which are small and rasp-like.

The teeth of the Tænioids or Ribband-shaped fishes resemble those of the Sciænoids in their microscopic texture, fixation, and mode of reproduction.

GOBIOIDS.

42. The Gobies (*Gobius* Lacépède) are distributed by Cuvier into four subgenera according to modifications of their dental system. The original generic term *Gobius*, is restricted by Cuvier to those species which have only small villous or carding teeth on both jaws, the anterior row being sometimes more developed than the rest. Of this sub-genus our common Rock-fish (*Gobius niger*) is the type.

The Gobies which have a single row of pointed teeth on each jaw, and the lower series placed horizontally, with two teeth developed in the form of canines behind them, form the family *Apocryptidæ*. In one species of this group, (*Amblyopus Hermannianus*, Cuvier), the mouth is cleft vertically, and the teeth are long, sharp-pointed, recurved, and interlock when the mouth is closed; there are eight or ten of

these teeth in each jaw, and they are always exposed to view, the lips not being sufficiently developed to cover them.

In the sub-genus *Sicydium* the intermaxillary bones are beset with more than a hundred teeth, as fine and flexible as hairs ; these teeth in the *Sycidium Plumieri* are of a golden colour; in the *Sicydium lagocephalum*, they are extremely delicate. In the lower jaw, behind a series of similar, but shorter flexible denticles, there is a row of well-developed conical sharp-pointed and slightly recurved teeth.

In the *Boleophthalmus* the teeth of the upper jaw resume their functional character as piercers and lacerators; and in one species, hence called *dentatus*, the six anterior ones are larger than the rest, project from the mouth and descend in front of the lower jaw.

In the Dragonets (*Callionymus*) the jaws are feebly armed with minute and villiform teeth; in the *Callionymus Lyra* the anterior teeth of the lower jaw are somewhat larger than the rest. In the *Comephorus* or *Callionymus Baikalensis*, the maxillary teeth are so minute, as to give a scabrous character to the dentigerous surface; but the denticles are hard, and when viewed with a lens, present a recurved sharp-pointed form.

43. There is a small family of fishes, in which the pharyngeal bones are so modified as to be subservient to the respiratory as well as the digestive functions ; the surface of these bones is increased by being produced into laminæ variously convoluted, and intercepting labyrinthiform spaces, in which a certain quantity of water can be kept in store. Thus provided, many of these fishes voluntarily quit their proper element, and all of them can maintain life for a considerable time out of water. These Gobioid fishes form a separate family, called 'Pharyngnies Labyrinthiforms,' in the system of Cuvier.

The Climbing Perch (*Anabas scandens*), has the third pair of superior pharyngeal bones armed with close-set conical teeth, which are opposed to similar teeth on the inferior pharyngeals; the posterior part of the vomer, which lies between the dentigerous upper pharyngeals, supports a group of villiform teeth ; and there is a transverse row of similar teeth on the anterior part of the same bone ; this distribution of vomerine teeth is peculiar to the *Anabas*. The palatines are eden-

tulous; there is a band of villiform teeth on each intermaxillary and premandibular bone.

The *Helostomes*(1) are remarkable for the small size and shape of their mouth, which resembles the head of a nail driven into the muzzle, whence their generic name; their teeth are not less extraordinary, being attached solely to the inside of the lips, and moving with them; they may be regarded, in fact, as a row of slightly calcified labial ciliiform papillæ. The palatines and vomer are edentulous; the posterior and inferior pharyngeals support small conical teeth. In the genera *Colisa*, *Macropodus* and *Trichopus*, the teeth are attached to the jaws, but are very small or villiform; the anterior maxillary teeth in the Gourami (*Osphromenus*), are a little longer than the rest. The *Spirobranchus* is the only genus among those with labryrinthiform pharyngeals which has palatal teeth. These are short, coarse and villiform; there are similar teeth on the vomer, intermaxillary and premandibular bones; the side teeth in the latter locality are longer than the rest.

44. The fishes of the family called *Theuties*, by Cuvier, have a small mouth, with a single row of teeth on the intermaxillary and premandibular bones; the palate and vomer are edentulous.

The jaw-teeth of the *Axinurus* are extremely slender; those of the *Naseus* are simply conical and sharp-pointed.

In the genera *Prionurus*, *Priodon*, *Amphacanthus* and *Acanthurus*, the teeth are commonly notched or serrate at the margins. Mr. André has given an accurate magnified view of the external form of the teeth of the *Acanthurus nigricans*, (*Chætodon nigricans* of Linnæus), in the *Philosophical Transactions*, and had recognized the arborescent medullary canals in the body of the tooth, "through which," he says, "the blood-vessels ramify, which are destined for its growth and nourishment." He very justly observes, that a fish having teeth of a crystalline hardness, and arranged in a single row, cannot be naturally associated with the Chætodonts, which are characterized by numerous rows of flexible teeth, of a totally different form.

The medullary canals in the maxillary teeth of the *Acanthurus nigricans* are directly continued from a conical pulp-cavity at the

(1) ηλος, a nail; στομα, a mouth.

base of the tooth, and are occupied, not by blood-vessels only, but by processes of the organized medulla or pulp, including the nutrient vessels, nerves, and connecting tissue. The diameter of the medullary canals at their origin is $\frac{1}{1200}$th of an inch, and their interspaces equal from four to six of these diameters; their general course is parallel to each other and to the axis of the tooth; but they begin to send off side-branches soon after their origin, and continue to ramify abundantly throughout their course. The ramifications anastomose and form arches, of which the convexity is directed towards the margin of the tooth. Both the main canals and their branches gradually diminish in size as they approach the margins. The calcigerous tubes, which are every where continued from the medullary canals, are of extreme tenuity; the marginal ones, which have a direct course perpendicular to the surface of the tooth, do not exceed $\frac{1}{25000}$th of an inch in diameter. A diminished view of four of the teeth of the *Acanthurus nigricans*, as seen with a magnifying power of sixty linear dimensions, is given in Pl. 44, fig. 1. The imbricated disposition of the teeth is here shewn.

CHÆTODONTS.(1)

45. The name of this family of fishes is significative of the peculiar form of the maxillary teeth, which resemble the hairs of a fine brush, and are of a soft subtransparent flexible texture, in the majority of the genera composing it. The pulp-cavity is continued to near the apex of these slender elongated denticles.(2) The true Chætodonts thus characterized, have no teeth on the palatine, vomerine or lingual bones.

In the genus *Chætodon* proper, the setiform teeth are longer than in the genera *Heniochus* or *Phelmon*, in the latter of which they resemble rather the pile of velvet. In the genus *Zanclus* the setiform maxillary teeth are directed forwards.

In the *Holacanthus*, the setiform teeth are finely pointed; but in *Platax*,(3) the outer row have their extremities compressed, slightly expanded and terminated by three pointed lobes.

(1) χαιτη, a bristle; ὀδους, a tooth. Pl. 1, fig. 2 (2) Pl. 44, fig. 3, *a* and *b*. (3) Pl. 1, fig. 2, *a*.

In the *Toxotes* and *Pempherides*, the jaws support only minute villiform teeth; but there are similar teeth on the palatines.

In the *Bramæ*, the maxillary teeth are somewhat coarser, or 'en cardes' and some of the outer and anterior ones are developed into small canines. The palatine teeth form a narrow band 'en cardes,' on each side of the roof of the mouth.

In the genus *Pimelipterus*(1) there is a band of villiform teeth on each jaw; and external to these there is a row of moderately developed trenchant teeth, which present the singular modification of having the part analogous to the fang, bent at right angles to the crown. This fang is horizontal, and is anchylosed by one side to the margin of the jaw. In the *Pimelipterus Boscii* it is of equal length with the vertical crown; in *Pimel. incisor* it is somewhat longer; and in the *Pimel. fuscus* the root is three times the length of the crown. This portion of the tooth is generally oval, compressed, and sharp-edged. There are between twenty and thirty of these teeth in each jaw. They are subject to uninterrupted shedding and replacement, and their successors pierce the jaws in front of those which are displaced. In all the *Pimelipteri* there are rough granular discs on the palatines, pterygoids and vomer.

In the *Dipterodons* the external row of teeth are more developed than in the *Pimelipteri*, and are straight; the crown is broad and terminates in a trenchant chisel-shaped edge. There are six of these incisors in the upper jaw, and ten in the lower jaw of the Cape *Dipterodon;* the middle ones are the longest. The posterior villiform teeth are more developed than in the *Pimelipteri*. The *vomer* and *palatines* are edentulous. The inferior pharyngeals are covered with a pavement of round obtuse teeth; those above are similar but smaller.

PLEURONECTOIDS.

46. Among the Pleuronectoids or Flat-fish, the soles (*Solea*) manifest their affinity to the preceding family in their fine ciliiform teeth; these, in their unequal distribution, partake of the main characteristic of the *Pleuronectidæ*, which are the least symmetrical of vertebrate animals, and are limited, in the intermaxillary and premandibular

(1) Pl. 1, fig. 5.

bones, to that side which corresponds with the under or white surface of the fish ; the pharyngeal bones are beset with similar teeth.

In the Plaice (*Platessa*), there is a regular curvilinear series of about twenty teeth, which are miniature resemblances of the incisors of the Sargus, in the left intermaxillary bone, and only three smaller and ill-shaped teeth near the median extremity of the right intermaxillary. A like disproportion in the number of the teeth prevails in the premandibular bones ; there being about thirty incisors, similar to those above in the left, and but two or three incisors in the right premandibular bone. The dentigerous intermaxillaries and premandibulars are stouter, more curved and longer than those of the opposite side.

The food of these ground-fish being below them, and the side of the head being applied to the bottom, instead of having the mouth opening symmetrically upon the under surface of the head as in the Rays, the premandibulars and intermaxillaries corresponding with the under or white side of the fish are elongated and curved, and the teeth, if not restricted to them, as in the sole, are more numerous and more regularly disposed, than on the corresponding bones of the opposite side.

The pharyngeal bones of the Plaice are paved with flattened molar teeth, larger than the incisors, and generally presenting a cubical form.

The pectinated processes from the concave side of the branchial arches are sharp-pointed, but do not support teeth.

The Turbot (*Rhombus*) has numerous small unciform teeth in the jaws, a small group of similar teeth on the palate, and others on the branchial arches and pharyngeal bones.

In the Holibut (*Hippoglossus*), the giant of the flounder-tribe, the arrangement of the teeth is less unsymmetrical than in the flounder or sole, there being nearly as many teeth on the left intermaxillaries and premandibulars as on the right. Both these and the pharyngeal teeth are conical, sharp-pointed, and recurved, and the same form is presented by the minute teeth which are placed upon the branchial arches ; the whole dental system thus presents a predatory character.

The intermaxillary teeth are arranged in two or three irregular

rows, the largest being external. The teeth are hollow to near the apex. They are first attached by ligaments to prominences of the thick alveolar margin, which ligaments become converted by the ossific process into bony cylinders, corresponding in size with the base of the tooth to which they are finally anchylosed. The teeth, when shed, separate from these cylindrical bases, which are removed by a subsequent process. The branchial teeth are arranged in small groups on the summits of the short obtuse apophyses which project at regular distances from the concave margin of the branchial arches. The pharyngeal teeth resemble in form and arrangement those of the jaws, but are smaller in size.

CHAPTER V.

TEETH OF CYCLOID FISHES.

LABROIDS.

47. The fishes included in the family *Labroides* of Cuvier, are chiefly distinguished by the great size and strength of their pharyngeal bones, of which there are two above and one below, all armed with teeth which vary as to their forms in different groups or genera of the family. Besides the pharyngeal teeth, which are adapted to give the final comminution to the food, the fishes of the genus *Labrus* of Linnæus, or the "Wrasses," have teeth which are commonly well developed and of a conical form on the intermaxillary and premandibular bones, but none on the superior maxillaries, palatines, or vomer.

In the sub-genus *Clepticus*, the pharyngeal teeth form, collectively, small plates with a serrated margin. In the *Clep. genizara* the superior pharyngeals support five rows of these saw-like plates, which work upon a similar dental armature of the inferior pharyngeal bone.

In the species of *Chromis* (Cuv.), and its subgenera *Cychla*,

Plesiops, and *Malacanthus*, the pharyngeal teeth are small, conical, and arranged like the teeth of a comb. In *Chromis* proper and *Malacanthus*, the anterior teeth of the intermaxillary and premandibular bones are conical and of larger size; behind these teeth, which form a single row, are others of smaller size which resemble those on the pharyngeal bones. In the *Cychla* there is a broad band of villous teeth in each jaw.

In the genus *Labrus* (Cuvier), and most of its sub-genera, the intermaxillary and premandibular teeth are arranged in one or two rows, the outer ones presenting a conical form, slightly recurved, with a few at the anterior and sometimes at the posterior part of the dental series much longer than the rest. In the genus *Anampses*, however, there are only two flat and somewhat recurved teeth in each jaw, which project from the mouth; while in the *Cossyphus* there are several minute granular teeth behind the normal conical teeth of the jaws (figs. 1 and 2, Pl. 45); and in *Ctenilabrus* a band of villous teeth occurs behind the long anterior conical maxillary teeth. In all these fishes the pharyngeal bones are paved with hemispherical molars more or less flattened at the crown. In the genus *Lachnolaimus* these teeth are confined to the posterior part of the pharyngeals, the rest of the bones, as the name of the genus implies,(1) being covered with a soft villous and vascular membrane.

In the more typical Labroids (*Labrus*, *Cossyphus*, and *Julis*), the whole of the unattached surface of the pharyngeals is covered with the molar teeth.(2) They vary in size and shape in different parts of the pharyngeal bones; some are angular instead of round, and the smaller ones at the external angles sometimes present a conical form. Each tooth is attached by the circumference of a slightly contracted base to the margin of a shallow alveolus; this margin is traversed by fine vertical grooves, which are morticed into corresponding grooves in the osseous margin of the base of the tooth. The floor of the alveolus is a thin plate, perforated by numerous foramina, and does not become anchylosed to the base of the tooth; nor, indeed, does it sustain any of the superincumbent pressure. The pharyngeal tooth, when first in place, has its base excavated by a wide but shallow

(1) λαχνη *lanugo*, λαιμος, *guttur*. (2) Pl. 45, figs. 3 and 4.

pulp-cavity. This is gradually diminished by a formation of dentine from the margins of the base, which encroaches towards the centre, until it finally forms a partition between the pulp-cavity and the alveolus.

In most of the specimens of the pharyngeal bones of the Wrasse-tribe, some of the alveoli are empty, and the round extremity of a new tooth is generally seen protruding for a greater or less extent through the cribriform base. When a vertical section of one of these paved pharyngeals is made, as in Plate 46, figure 1, a regularly formed cavity is exposed beneath the base of each of the bisected teeth, containing a successional tooth (*b*), more or less advanced in growth. Smaller cavities for lodging processes of the formative pulp are seen extending from the base of those containing the most advanced teeth, and forming the rudiments of future alveoli.

When the structure of one of these pharyngeal molars is microscopically examined, in a thin vertical section, numerous densely aggregated and extremely fine calcigerous tubes are observed to radiate in all directions from the pulp-cavity, and in a direction vertical to the plane of the surface from which they are continued. Those which descend, soon terminate in cells that communicate with the canals in the thin plate of bone to which the tooth is affixed. Those which pass out laterally towards the side of the tooth, follow the curve of the side as it rises from the base, and form a band with the convexity next the base. Those which pass to the upper surface and upper part of the lateral surface, have a pretty direct course: but all the tubes, when viewed with a high power, are found to be minutely and beautifully undulated.

When they reach the clear enamel-like covering of the tooth, the calcigerous tubes lose their undulatory disposition, and instead of continuing parallel, they cross each other in graceful curves in all directions.

In the small scale on which such a section as has been described is figured (Pl. 46), only the general course of the calcigerous tubes can be indicated; but it is impossible to view the disposition of these minute hollow columns, in connection with the mode in which the whole tooth is fixed in its alveolus, without being forcibly struck

with the beautiful illustration of the best mechanical principles by which enormous pressure can be sustained and transferred to particular points.

To crush the hard shells of marine testacea and comminute them for deglutition requires strong teeth and the requisite power to work them; and of a dentition adequate to such purposes we have frequent examples in the class of fishes. The jaws of the wolf-fish, figured in plate 60, are peculiarly well provided with instruments for this operation. But in the wrasse, the waste of the molar teeth consequent on the rude attrition to which they are subject, is repaired by the development of new teeth directly beneath those in use, whilst in the wolf-fish the new teeth are formed by the side of the old. Here, then, a new difficulty was to be obviated; had the crushing tooth rested by the whole of its basis upon the alveolus, as in the wolf-fish (see the section of the jaw of that species figured in Pl. 60, fig. 2), the supporting plate, gradually undermined by the growth of the new tooth, would have given way, and been forced upon the subjacent delicate and highly vascular matrix with the half-formed tooth: this, therefore, must have either sustained the irritation and injury of the undue pressure, or the important functions of the pharyngeal grinders must have been temporarily suspended, until the undermined tooth had been shed, and its successor sufficiently solidified and adequately fixed.

To obviate this evil, the centre of the pulp of the pharyngeal molar remains uncalcified long after the tooth has taken its place, and the circumference only of the base of the tooth rests upon the raised margin of the alveolus. The part of the tooth which sustains and transmits the pressure is strengthened by the development of a strong convex ridge projecting from its inner surface into the pulp-cavity; and the calcigerous tubes of this ridge, while simply following the ordinary course of development, acquire a direction the best adapted for diffusing the pressure equally to every point, by radiating from the plane of resistance. The pressure received by the border of the alveolus is transferred to the walls which divide the vaulted cavities containing the germs of the new teeth. The roof of these cavities, which forms at the same time the floor of the alveolus above,

being thus independent of the superincumbent weight, freely yields to the absorbent process consequent on the growth of the new tooth; and before the latter becomes subjected to any pressure from above, its formation has been sufficiently perfected to enable it to sustain that pressure without injury.

The lateral walls of the cavities containing the reserve teeth, to which the pressure is transferred from the margins of the sockets of those in use, consist of a much denser osseous tissue than the other parts of the pharyngeal bone.

The Wrasses feed on testaceous Mollusks, Crustaceans, *Echini*, &c., which they seize with their long anterior conical teeth, and crack and bruise by means of their powerfully armed pharyngeals. Some of the sub-genera of Labroids, *Epibulus* and *Clepticus*, have the intermaxillary bones provided with very long ascending processes, and an arrangement of muscles, which producing a rotatory motion of the maxillaries and a sudden descent of the intermaxillaries, accompanied at the same time with a protraction of the lower jaw, produces a tubular elongation of the whole mouth, and adds to their power of catching the smaller marine animals.

48. *Scarus*.(1)—There is a genus of fishes adapted to browse on the lithophytes which clothe, with a richly tinted verdure, the bottom of the sea, as the ruminant quadrupeds crop the herbage of the dry land.

The irritable bodies of the gelatinous polypes which constitute the food of these fishes retract, however, when touched, into the star-shaped cavities of their stony support, and the *Scari* consequently require a dental apparatus strong enough to break away and reduce to a pulp these calcareous recesses. Their jaws are, therefore, prominent, short, and stout, and the exposed portions of the intermaxillaries and premandibulars are shaped like the beak of a parrot, whence the name of "parrot-fish," usually given to these brightly-tinted species of the Labroid family. But the mandibles instead of being sheathed with horn, are encased by an extremely dense and singularly complicated dental covering.

Each intermaxillary bone presents a triangular form, with the superior and posterior angles produced, and separated by an oblique

(1) Pl. 49, 50, 51.

excavation or concavity, in the middle of which there is a small oval articular depression, to which a corresponding convex trochlea of the maxillary bone is adapted. Powerful muscles are inserted into the two produced angles of the intermaxillary bone, by means of which it is worked upon the hinge-like joint above described. The premandibular piece of the lower jaw differs from the intermaxillary bone above in the absence of the posterior median process, but in other respects it closely resembles that bone in form.

When the intermaxillary and premandibular bones are viewed from their outer side, they appear to be edentulous, and to have their osseous texture converted, at the anterior and outer part, into an enamel-like substance, with a surface chequered by small lozenge-shaped smooth or tuberculate plates arranged in a quincuncial order, (Pl. 49, fig. 1). When viewed from the inside, (Pl. 49, fig. 3), the irregular trenchant margin of these bones is seen to be composed of short and thick sub-conical four-sided columns, placed almost vertically to the outer surface of the jaw, along a great part of which surface similar columns are arranged, which form by their exposed bases the tesselated surface above mentioned. These small columns are the teeth ; the exposed base is the crown, and the opposite contracted end, which is slightly excavated, corresponds with the fang(1). If a vertical section of the jaw be made, as in fig. 3, these teeth or denticles will be exposed in various stages of formation in a cavity (*b*) below the dental series in the premandibulars, and in the reverse situation in the intermaxillaries. The formative quadrilateral pulps are contained in this cavity, with their bases attached to the vascular membrane lining its posterior wall, and with their free extremities projecting horizontally forwards towards the anterior or outer wall. Alveolar or capsular processes of vascular membrane are continued backwards from the outer wall and inclose the pulps, like the capsule of the matrix of ordinary teeth. At the uppermost part of the dentigerous cavity in the upper jaw, the broad anterior extremity of the columnar tooth is seen to be formed by calcification of the summit of the pulp : a little lower down, the whole length of the tooth is completed, but the base is excavated by a conical

(1) Cuvier, Leçons d'Anatomie Comparée, Nouv. Ed. Paris, 1836, tom. iv, p. 226.

cavity containing the remains of the pulp, and the tooth is loose, or is suspended only by its pulp and capsule: still lower down, the capsule is observed in different stages of ossification; and the tooth becomes thereby anchylosed, first by its anterior, and afterwards by its posterior extremity, to the opposite walls of the formative cavity. The pulp-cavity becomes diminished in size by the progressive calcification of its organized contents, and at length the tooth, by the complete ossification of its external capsule, becomes adherent laterally to the contiguous teeth, as well as to the walls of the dental cavity by its extremities: thus the dense, exposed anterior portions of the premaxillary and premandibular bones are converted into an aggregated and anchylosed mass of teeth.

When the microscopic structure of one of the maxillary denticles is examined in a longitudinal section, the conical pulp-cavity may be traced to near the coronal end of the tooth. The calcigerous tubes, which at their origin do not exceed $\frac{1}{17000}$ of an inch in diameter, are very closely aggregated, being separated by intervals equal to only one and a half of their own diameters; those at the base of the pulp-cavity descend, and on one side of the denticle, incline inwards, tending to close that cavity; the greater number of the calcigerous tubes proceed directly outwards, at right angles to the sides of the denticle: near the coronal surface they begin to bend towards that end, and to pass more obliquely from the pulp-cavity, until they assume, in the centre of the crown, a direction parallel to the axis of the tooth. Besides the primary curvatures, which are most marked at the two extremes of the denticle, all the calcigerous tubes present the most regular and graceful undulations throughout their entire course: these undulations require a compound lens of $\frac{1}{8}$th inch focus to be distinctly seen, and, with the fine lateral branches of the tubes, form no mean test of the powers of the microscope employed. The pulp-cavity becomes finally occupied by a coarse cellular bone, and a thin coating of the same kind of tissue invests the exterior of the denticle. The general disposition of the calcigerous tubes, and the form of the detached denticle and its pulp-cavity are figured in Pl. 50.

The thick external enamel-like layer of each denticle, which

is indicated by its lighter colour in the plate, consists likewise of minute fibres or tubes, which are thickest and straightest at the periphery of the tooth, but bend and cross each other as they approach the central tubes, appearing to interlace and anastomose at the boundary line.

The outer wall of the common alveolar cavity in which the denticles are developed, is much weaker than the dense and compact inner wall; it becomes thinner as it approaches the margin of the jaws, and disappears at different distances in different species of *Scari*, before it reaches that margin. Where it exists at the base of the jaws, it is sometimes, as in *Scarus muricatus*, (Pl. 49, fig. 1), perforated by numerous small foramina, through which foramina, in the recent fish, processes of the external periosteum are continued to the analogous membrane, lining the dentigerous cavity, and forming the capsule of each denticle. These processes are analogous to the gubernacula of the second series of teeth in the mammalia, and, like them, serve to conduct the new teeth to the exterior of the jaw. The growing denticles become elongated by the addition of successively calcified portions of their pulp to their basal or posterior extremities; the opposite end exerts a proportional pressure against the circumference of the foramen, and, causing its absorption, begins to protrude. The tuberculate crown of the denticle is exposed about the time when its sides have become anchylosed to those of the previously protruded row. Thus from the close apposition of the protruding denticles, the whole of the outer parietes of their common alveolar cavity, subjected to the stimulus of their pressure, is finally removed, and is replaced by the pavement of mutually anchylosed teeth.

In certain species of parrot-fish one or more of the denticles, at the posterior part of the intermaxillary bones, are longer than the rest, and their coronal extremity is produced into a sharp and sometimes recurved point; these teeth extend beyond the pavement formed by the other denticles and constitute a weapon of offence, as in the *Scarus aurofrenatus*, *Sc. vetula*, *Sc. quadrispinosus* and the species figured in Pl. 49, fig 2.

In some other species, as the *Scarus flavescens* of Bloch and

Scarus spinidens, Quoy and Gaimard, the anterior denticles are imbricated or arranged like tiles in several rows, and the lateral ones in the upper jaw are always separated and pointed. There is, also, an internal row of very small intermaxillary teeth. Cuvier has grouped together the parrot-fishes with this type of dentition under the sub-generic term *Callyodon*, which was applied by Gronovius to all the *Scari*.

The parrot-fishes, like the wrasses, have no teeth on the superior maxillary, palatine or lingual bones, but are provided with strongly developed pharyngeal bones peculiarly well furnished with an apparatus of teeth for comminuting the coarse fragments of blended gelatinous and calcareous matters, which the protruded jaws are organised to break off.(1)

Certain parrot-fishes in which the tooth-paved mandibles are more slender and spoon-shaped than in the true *Scari*, and hence probably subsisting on a different diet than the madrepores on which such species browse, have the pharyngeal bones provided, as in the *Labri*, with numerous obtuse rounded denticles, but more closely packed together; these parrot-fishes constitute the sub-genus *Odax* of Cuvier.

The typical *Scari* have both upper and lower pharyngeal bones paved with strong thick lamelliform teeth, set vertically and transversely in the opposed surfaces of those bones. It is the posterior

(1) The general assertion by Cuvier, that the Scari, like the terrestrial ruminants feed exclusively on vegetables, "comme les ruminans terrestres, le Scare ne se nourrissait que de végétaux," (*Cuvier, Histoire Naturelle des Poissons*, tom. xiv, p. 100)—must be received with a certain restriction, although coming from an anatomist who so well understood, and who was the first to describe intelligibly, the plan and principle of the powerful and complicated dental armature of the parrot-fishes. It is true that Aristotle, in the passage quoted by Cuvier; asserts that "the Melanurus and the Scarus subsist on sea-weed;" but then the Greek Naturalist also pushes the analogies of the *Scarus* to the terrestial ruminants so far as to quote, and sanction, the belief that this fish actually ruminated. Some of the species with weaker and sharper-edged mandibles may crop the sea-weeds as well as other substances, but both Commerson and Dussumier testify to the coral-feeding habits of the parrot-fishes of the Isle of France and the Séchelles, etc. Mr. Darwin, who dissected several Scari soon after they were caught, found their intestines laden with nearly pure chalk, and observed that such, likewise, was the nature of their excrements; whence he classes these fishes among the geological agents to which is assigned the task of converting the skeletons of the Lithophytes into chalk.

pair of the upper pharyngeals which are thus armed; the lower pharyngeal bone is single.(1)

The superior dentigerous pharyngeals present the form of an elongated, vertical, inequilateral triangular plate; the upper and posterior margin is sharp and concave; the upper and anterior margin forms a thickened articular surface, convex from side to side, and playing in a corresponding groove or concavity upon the base of the skull; the inferior boundary of the triangle is the longest, and also the broadest; it is convex in the antero-posterior direction and flat from side to side. It is on this surface that the teeth are implanted, and in most species they form two rows; the outer one consisting of very small teeth, the inner one of large teeth. These present the form of compressed conical plates or wedges, with the basis excavated and the opposite margin moderately sharp, and slightly convex to near the inner angle which is produced into a point: these plates are set nearly transversely across the lower surface of the pharyngeal bone, and are in close apposition, one behind the other: their internal angles are produced beyond the margin of the bone, and interlock with those of the adjoining bone when the pharyngeals are in their natural position; the smaller denticles of the outer row are set in the external interspaces of those of the inner row, (Pl. 51, fig. 2).

The single inferior pharyngeal bone consists principally of an oblong, dentigerous plate, of the form represented in Plate 51, fig. 3; its breadth somewhat exceeds that of the conjoined dentigerous surfaces of the pharyngeals above, and it is excavated to correspond with their convexity. This dentigerous plate is principally supported by a strong, slightly curved, transverse osseous bar, the extremities of which expand into thick obtuse processes for the implantation of the triturating muscles. A longitudinal crest is continued downwards and forwards from the middle line of the inferior pharyngeal plate, anterior to the transverse bar, to which the protractor muscles are attached.

A longitudinal row of small oval teeth alternating with the large lamelliform teeth, like those of the superior pharyngeals, bounds

(1) Cheselden has given a figure of this bone at the end of the first chapter of his "Osteography."

the dentigerous plate on each side; the intermediate space is occupied exclusively by the larger lamelliform or wedge-shaped teeth, set vertically in the bone, and arranged transversely in alternate and pretty close-set series.

The pharyngeal denticles are developed in wide and deep cavities in the substance of the posterior part of the *lower*, and of the anterior part of the *upper* pharyngeal bones. Each denticle is inclosed in its proper capsule which contains an enamel-forming pulp and a dentinal pulp, in close cohesion with each other, and with the thin external capsule. The teeth exhibit progressive stages of formation as they approach the posterior part of the upper and the anterior part of the lower pharyngeal bones: as their formation advances to completion they become soldered together by ossification of their respective capsules, and soon afterwards are anchylosed by ossification of the base of the dentinal pulp to the pharyngeal bone itself. The line of demarcation between the dentified and ossified portions of the pulp is well defined, so that when the pharyngeal bone and teeth are sawn through vertically the fully formed teeth appear as hollow cones, set upon wedges of bone, as shown in Pl. 51, fig. 1.

The dentine of the pharyngeal teeth of the Scarus consists of calcigerous tubes and a clear intermediate substance. The calcigerous tubes average a diameter of $\frac{1}{20.000}$th of an inch, and are separated by interspaces equal to twice their own diameter. The course of these tubes is shown in Pl. 52, fig. 2, *b*, in which they are exposed by a vertical section through the middle of one of the inferior denticles. They all, on leaving the pulp-cavity, form a curve with the convexity turned towards the base of the tooth, and then bend slightly in the opposite direction; the sigmoid curve being most marked in the calcigerous tubes at the base of the denticles, whilst those towards the apex become longer and straighter. Besides the primary curvatures exemplified in the figure, each calcigerous tube is minutely undulated; it dichotomizes three or four times near its termination, sends off many fine lateral branches into the clear uniting substance (Pl. 52, fig. 3), and finally terminates in a series of minute cells and inosculating loops at the line of junction with the enamel.

This substance (Pl. 52, *c.*) is as thick as the dentine and consists of a similar combination of minute tubes and a clear connecting substance. The tubes may be described as commencing from the peripheral surface of the tooth, to which they stand at right angles, and, having proceeded parallel to each other half way towards the dentine, they then begin to divide and subdivide, the branches crossing each other obliquely, and finally terminating in the cellular boundary between the enamel and dentine.

The teeth, which present this complex structure, are successively developed at one extremity of the bone, in proportion as they are worn away at the other; not, however, as Cuvier describes, from behind forwards, in both upper and lower pharyngeal bones,(1) but in opposite directions in the opposite bones, the course of succession being from before backwards in the upper, and from behind forwards in the lower pharyngeal bones. In the progress of the attrition to which they are subjected, the thin coat of cement resulting from the ossification of the capsule is first removed from the apex of the tooth, then the enamel (*c*) constituting that apex, next the dentine (*b*), and finally the coarse cellular central bone (*a*), supporting the hollow-wedge-shaped tooth, and thus is produced a triturating surface of four different substances of different degrees of density. The enamel, being the densest element, appears in the form of elliptical transverse ridges, inclosing the dentine and central bone, and external to the enamel is the cement which binds together the different denticles.

The Comparative Anatomist, conversant with the modifications of the dental system in the mammiferous class, cannot but be struck with the close analogy between the adherent pharyngeal denticles of the Scarus and the complicated grinders of the elephant, both in form, structure, and in the reproduction of the component denticles in horizontal succession. But in the fish, the complexity of the triturating surface is greater than in the mammal, since, from the mode in which the wedge-shaped denticles of the Scarus are implanted upon, and anchylosed to, the processes of the supporting bone, this likewise enters into the formation of the masticatory surface when the tooth is worn down to a certain point.

(1) Histoire Naturelle des Poissons, tom. xiv, p. 116.

MUGILOIDS.

49. The teeth in this family of fishes are so minute as to be often imperceptible to the naked eye. In the Mediterranean mullet, (*Mugil cephalus*), they form a simple row along the margin of the upper and lower jaws, and are attached to the gum, so as to be moveable like the teeth of the Gonyodonts.(1) The inferior pharyngeals are covered with flexible ciliiform teeth; those of the superior pharyngeals are so delicate, that the bones seem to be clothed by a soft and finely papillose velvet. The final comminution of the food is effected, in the present family, in the stomach itself, which presents a structure similar to that of the gizzard of birds.

In the genus *Cestræus* the lower jaw is always edentulous; but there is a row of small and slender teeth along the margin of the intermaxillary bones; the palatines and vomer are without teeth, as in the true *Mugiles*: the intermaxillary teeth are extremely fine in the *Cestræus plicatilis*; they are stronger, and disposed in several rows in the *Cestræus oxyrhynchus*. In the *Dajaus* there are villiform teeth on both jaws, and also on the palatines and vomer; it is interesting to observe, that, with this modification which indicates a diet of an animal character, the stomach is much less muscular than in the true mullets. In the *Nestes*, the jaws, vomer, and pharyngeals are armed with teeth 'en cardes,' but the palatines are edentulous. In the *Tetragonurus* the maxillary teeth are more developed than in the previous genera; there are twenty-four teeth which are simple, conical, and slightly recurved in each intermaxillary bone; there are fifty on each side of the lower jaw, arranged in a single row; these are stronger, more compressed and more pointed than the upper ones. Both series of teeth are but feebly attached to the bone, but those of the lower jaw offer most resistance. There are longitudinal rows of finer teeth on the vomer and palatine bones. The tongue is not armed with teeth; the pharyngeal bones support each an oval patch of teeth 'en cardes.'

ATHERINES.

50. The sand-smelts or fishes of the family of Atherines have very

(1) Page 85.

small but acute teeth; these are sometimes present on the jaws only, as in *Atherina Brasiliensis* and other species of the new world; sometimes also they are developed, but of extremely minute size, upon the palatine bones, as in the *Atherina Hepsetus;* and lastly they may be found on the jaws, palatines and vomer, as in the *Atherina Boieri*, and other broad and flat-headed species of the present family. The pharyngeal bones in the common Atherine or sand-smelt, *(Atherina Presbyter)*, are furnished with numerous small and close-set conical teeth.

SCOMBEROIDS.(1)

51. In this family of cycloid fishes the dental system presents many modifications, of which the Sword-fishes *(Xiphias)*, and the Scabbard-fishes *(Lepidopus)* offer, perhaps, the extremes.

The Sword-fish might be reckoned among the edentulous fishes, were it not that the pharyngeal bones are covered with a villosity of extremely fine and minute denticles; but all the ordinary bones of the mouth, of the tongue, and even of the branchial arches, are without teeth. In the Opah or King-fish, *(Lampris guttatus)*, the ordinary bones of the mouth are likewise edentulous; the pharyngeals have not been examined in this species.

In the *Stromateus* there is a single row of denticles on each jaw, but these are so delicate and short that they cannot be recognised without the aid of a lens. The palatine, vomer, and hyoid bones are edentulous, as in the Sword-fish.

The dentition of the *Rhombus* is similar to that of the *Stromateus*, but the maxillary teeth are a little more developed.

The margins of the jaws are roughened by numerous close-set, short, villiform teeth in the *Tetrapturus;* the palatine and pharyngeal bones bear similar denticles in this genus.

In the *Histiophorus* the broad, dentigerous margins of the jaws are covered with minute dental granulations only, some of which are developed, in the lower jaw, into small pointed teeth.

The dental system is not more formidable in the genus *Trachurus*. In the mailed mackerels, (*Caranx*), the tongue is beset with villiform

(1) Pl. 53, 54, and 55.

teeth, and the exterior maxillary teeth are pointed. In the Carangue, (*Caranx carangus*), there is a row of conical teeth exterior to the band of villiform denticles in the upper jaw; there is also a similar, but more close-set row in the lower jaw, the two anterior of which are produced, like canine teeth, beyond the rest.

In the pilot-fish, (*Naucrates Ductor*), the maxillary teeth are villiform, and are arranged in a narrow band on each jaw, there is a broader, but shorter band of similar teeth in the palatines, and along the middle of the tongue. The dentition of the genera, *Kurtus*, *Seriola*, *Gallichthys*, *Blepharis*, *Olistes*, *Vomer*, *Brachinotis* and *Elacates* is similar to that of the *Naucrates*; but the pharyngeal teeth in the latter genus, are more strongly developed. The pharyngeals are paved with small obtuse teeth in the genus *Hynnis*. In the *Apolectus*, *Centrolophus*, and *Astrodermus*, the minute maxillary teeth are rather ciliiform than villiform, and are disposed in a single row.

In the *Chorinemus* two rows of small conical teeth rise above the villous band of denticles in the intermaxillary and premandibular bones. The pterygoid, as well as the palatine, vomerine, and lingual bones, support oval patches of villiform teeth in this genus.

The jaws of the common mackerel, the type of the Scomberoid family, are feebly armed with a single row of small pointed and slightly recurved teeth; the anterior part of each palatine bone is similarly provided, and there are three or four small teeth on each anterior angle of the vomer. The tongue is smooth, but the pharyngeal bones are beset with teeth so long, delicate and flexible, as to resemble hairs.

The maxillary teeth of the tunny, (*Thynnus vulgaris*), are relatively smaller than those of the mackerel, and resemble the points of small pins, slightly bent inwards and backwards; there are about forty of these denticles on each side of the jaw, those of the lower jaw being somewhat the largest. The *Scomber pelamys* of Linnæus or the striped-bellied bonito, (*Thynnus Pelamys*, Cuv.), has teeth like those of the tunny; but the true, or striped-backed bonito (*Pelamys Sarda*, Cuv.(1) has the maxillary teeth more strongly developed; they are conical, slightly compressed, sharp-pointed, and arched towards

(1) Plate 1, fig. 3.

the interior of the mouth; the third on each side is a little longer than the rest. There is a row of very small conical teeth, on the outer margin of each palatine bone; but the vomer is edentulous.

In the king-fishes, (*Cybium*), and the temnodonts, the maxillary teeth are relatively larger than in the bonitos, and are lancet-shaped, with very sharp points and edges. There are twenty-five of these teeth on each intermaxillary bone, and twenty on each premandibular bone. In the *Cybium Commersonii* the jaw-teeth present the form of an isosceles triangle, with trenchant margins. A crescentic plate on the anterior part of the vomer, a band on each palatine and nearly the whole of the oral surface of the pterygoid bones are roughened with close-set microscopic villiform teeth. The dentition of the Scomberoids of the genus *Thyrsites* is distinguished from that of the king-fishes chiefly by the increased length of a few of the anterior intermaxillary teeth, and by the development of the palatal teeth into small pointed laniaries. In the genera *Gempylus*, *Lepidopus*, and *Trichiurus* or hair-tail, the elongated anterior intermaxillary teeth present a small retroverted point or barb at the posterior margin near the apex.

In the scabbard-fish there is a row of twenty to twenty-two compressed sharp-pointed teeth on each intermaxillary bone, and just behind the anterior part of each row are two or three teeth four times as large and long as the others, slightly bent inwards; six of these, Mr. Yarrell observes, is the correct number, but two or three are generally observed to be broken. The under jaw has also one entire row of teeth, with two longer ones. The vomer is edentulous, but the long external edge of each palatine bone has one row of very minute teeth; the pharyngeal bones and branchial arches are also furnished with teeth that are exceedingly minute.(1)

In the genus *Lactarius* the jaws and palatine bones are beset with villiform teeth; besides which there are at the fore part of each of the intermaxillaries two or four long, curved and sharp-pointed teeth, and in the premandibulars a row of fine, acute, recurved and closely packed teeth. There is a small chevron-shaped group of

(1) British Fishes, i, p. 179

fine and pointed teeth on the vomer, and the two margins of the tongue support minute granular teeth.

The jaws of the *Nomei* are provided with a single row of small, recurved, conical teeth, without the addition of laniary or villiform teeth.

In the dolphin, (*Coryphæna Hippurus*), the intermaxillary and premandibular bones support each an exterior row of small recurved conical teeth, within which there is a broad band of teeth 'en cardes;' these latter reach further back in the lower than in the upper jaw. There is a rhomboidal patch of similar denticles on the vomer, and a longitudinal band on each palatine bone. The tongue supports a broad plate of villiform teeth, which are likewise present on the origins of the branchial arches. The pharyngeal denticles are more strongly developed.

A narrow band of incurved teeth 'en cardes,' but not very thickly set, extends along each intermaxillary and premandibular bone in the dory (*Zeus faber*), which has also a small group of similar teeth on each side of the anterior part of the vomer, but none on the palatines or tongue. The branchial arches are furnished with tubercles, and these, together with the small pharyngeal bones, are beset with the same kind of teeth as those on the vomer and jaws. The boar-fish (*Capros Aper*), the type of an allied genus, has a dentition similar to that of the dory; the maxillary and vomerine denticles are somewhat finer and are placed deeper within the jaws, and those of the pharyngeal bones and branchial arches are villiform. The jaws of the *Equula ensifera* are provided with a narrow band of flexible setiform teeth; in some other species, as the *Equula dentex*, two of the anterior teeth in both jaws are more developed than the rest, and are pointed and incurved.

In the genus *Alepisaurus*, the mouth is as well armed as in the hair-tail, or scabbard-fish, and the teeth present a similar inequality of size, and the compressed, pointed, lancet-shaped figure, so common in the Scomberoid family of fishes. The margin of each long intermaxillary bone is serrated by a row of small compressed teeth, the anterior being rather larger than the hinder ones, and the first tooth projecting forwards. The anterior part of the palatine bones is

armed with a group of three very large, slightly recurved, lancet-shaped teeth, placed in a triangle, of which the apex is directed forwards; then on each side there is a single lancet-shaped tooth, about half the size of the preceding, and behind these, there is a row of seven smaller and close-set teeth. The lower jaw has a pair of long sub-conical teeth in front, one on each side, with a smaller one between them; and below these, on the outer side of the symphysis, there is a single conical tooth projecting forwards. Behind the first pair of teeth, there extends along each ramus of the jaw a row of five much smaller teeth, followed by three rather larger, which become gradually more compressed; then there are two lancet-shaped teeth, considerably larger, which lock into the interval in the upper jaw, and after a short diastema follows a row of eleven short but broad and compressed teeth. All these teeth, when fully formed, are firmly anchylosed by their bases to depressions in the jaw bones.

In all the Scomberoid fishes the succession of teeth is uninterrupted; the pulps of the new teeth are developed in most of the species in the soft gum or integument covering the dentigerous margins of the bones, and the calcification of the pulp is completed as it lies recumbent and buried loosely in the substance of the gum. The point of the new tooth, which, in this state, is directed backwards, is then exposed by a gradual rotatory movement of the tooth from the horizontal to the vertical position; the jaw bone grows around its base, and, ossification proceeding along the ligamentous attachment of the tooth, finally fixes it to the jaw by continuous anchylosis.

In a large exotic *Trichiurus*, I find six large barbed fangs at the anterior part of the upper jaw, three recumbent and loose, and three erect and fixed. These are situated alternately, so that in one specimen two of the fixed teeth may be implanted in the right, and one opposite the interspace of the preceding, in the left palatine bone; while in another specimen the situation of the fixed teeth is reversed, as is also that of the recumbent and loose successional teeth.(1)

(1) The discovery of the larger teeth, lying loosely in the gum, near the base of the fixed teeth they are destined to supplant, is apt to occasion surprise in those, who may not be acquainted with their mode of development. Thus, the excellent Ichthyologist from whose description

In the *Paralepis*, the intermaxillary teeth are so small that they are indistinguishable without the aid of a lens; thus magnified, they are seen to be very numerous and close-set, like the teeth of a saw. The premandibular and palatine teeth, on the contrary, are large, but slender, recurved and sharp-pointed, set wide apart, with smaller teeth in the interspaces. There are no teeth on the vomer or tongue.

52. *Sphyræna.*—The most formidable dentition exhibited in the extensive Scomberoid family of the system of Agassiz is that which characterizes the *Sphyræna*, and some extinct fishes allied to this predatory genus. In the great barracuda of the southern shores of the United States, (*Sphyræna Barracuda*, Cuv.) the lower jaw contains a single row of large, compressed, conical, sharp-pointed, and sharp-edged teeth, resembling the blades of lancets, but stronger at the base.(1) The two anterior of these teeth are twice as long as the rest, but the posterior and serial teeth gradually increase in size towards the back part of the jaw; there are about twenty-four of these piercing and cutting teeth in each premandibular bone. They are opposed to a double row of similar teeth in the upper jaw, and fit into the interspace of these two rows, when the mouth is closed. The outermost row is situated on the intermaxillary, the innermost on the palatine bones; there are no teeth on the vomer or superior maxillary bones. The two anterior teeth in each intermaxillary bone equal the opposite pair in the lower jaw in size; the posterior teeth are serial, numerous and of small size; the second of the two anterior large intermaxillary teeth is placed on the inner side of the commencement of the row of small teeth, and is a little inclined backwards. The retaining power of all the large anterior teeth is increased by a slight posterior projection, similar to the barb of a fish hook,

of the "Alepisaurus" most of the foregoing details of its dental organs are derived, observes, with respect to the successors of the larger palatine teeth, "Whether they were originally, like the others, fixed, and are merely loose from injury or fracture, or are properly moveable and free, I can scarcely venture to decide. At first sight and from the way in which they lie amongst the loose gelatinous integuments of the palate, with no appearance of a regular attachment by the base, their condition seems the effect of accident."—*Transactions of the Zoological Society*, vol. i, p. 396.

(1) Pl. 1, fig. 4, and Pl. 53, fig. 1.

but smaller. The palatine bones contain each nine or ten lancet shaped teeth, somewhat larger than the posterior ones of the lower jaw. All these teeth afford good examples of the mode of attachment by implantation in sockets, which has been denied to exist in fishes.(1)

The loss or injury to which these destructive weapons are liable in the conflicts which the sphyræna wages with its living and struggling prey, is repaired by an uninterrupted succession of new pulps and teeth. The existence of these is indicated by the foramina,(2) which are situated immediately posterior to, or on the inner margin of the sockets of the teeth in place; these foramina lead to alveoli of reserve, in which the crowns of the new teeth in different stages of development are loosely imbedded. It is in this position of the germs of the teeth that the Sphyrænoid fishes, both recent and fossil, mainly differ as to their dental characters from the rest of the Scomberoid family, and proportionally approach the Sauroid type. The base or fang of the fully-developed tooth of the Sphyræna is anchylosed to the parietes of the socket in which it is inserted. The pressure of the crown of the new tooth excites absorption of the inner side of the base of the old, which thus finally loses the requisite strength of attachment, and its loss is followed by the absorption of the old socket, as in the higher animals.

It is interesting to observe that the alternate teeth are, in general, contemporaneously shed; so that the maxillary series is always preserved in an effective state. The relative position of the new teeth to their predecessors, and their influence upon them, resemble, in the Sphyræna, some of the phenomena which will be described in the dentition of the Crocodilian reptiles. To the crocodiles the present voracious fish also approximates in the alveolar lodgment of the teeth, but it manifests its ichthyic character in the anchylosis of the fully developed teeth to their sockets, and still more strikingly in the intimate structure of the teeth.

Few microscopic objects are more beautiful than a longitudinal and transparent section of the tooth of the Sphyræna, which accurately

(1) *Cuvier, Histoire Naturelle des Poissons*, tom. i, p. 492.

(2) Pl. 53, fig. 1, *a*, *a*.

typifies that of the teeth in all the Scomberoid fishes. It consists of a thin external coating of fine enamel-like dentine, and a body of coarse dentine. The most successfully injected vascular membrane could not surpass in the number and delicacy of its ramified capillaries the arrangement of the medullary canals, which pervade the whole body of the tooth in this fish. The smallest marginal or peripheral divisions of the medullary canals anastomose in curved loops whose convexity is turned towards the superficies of the tooth; the branches, which, by their terminal division, constitute those loops, successively anastomose, as they widen and slightly converge towards the central part of the tooth.(1) Here the main medullary tubes run nearly parallel to each other, with interspaces equalling from four to six times their own diameter. In their progress towards the base of the tooth, they give off numerous branches which subdivide and anastomose in the interspaces of the main canals. These canals, in the fully formed anchylosed teeth, communicate directly with the medullary canals of the jaw-bones, which run at right angles with those of the teeth.(2) The reticulate medullary canals every where send off the much more minute calcigerous tubes, which quickly subdivide into tufts or pencils; these soon begin to bend and interlace together and fill the meshes of the medullary reticulations by their inextricable anastomoses. The peripheral loops of the medullary canals, in like manner, give off pencils of fine calcigerous tubes; but these maintain, as do the tubes of ordinary dentine, a more regular and parallel course; they penetrate, and constitute with the clear uniting substance, the external hard and white coating of the tooth; the first two-thirds of their course is at right angles to the plane of the surface towards which they are directed; their finer ramifications then begin to bend from side to side, and terminate in reticular inosculations of extreme minuteness, which are finally lost in the clear dense substance of the outer layer.

Sphyrænodus.—The same general distribution of the medullary

(1) A diminished view of the structure, as seen in a longitudinal section of the apex of the tooth, is given at fig. 2, pl. 53.

(2) The solid tissue of the maxillary bones presents a close-set parallel arrangement of undulating calcigerous tubes, and nearly resembles the texture of the dentine in the higher mammiferous teeth. There are no Purkingian corpuscles or radiated cells in this bone.

and calcigerous tubes pervades the whole substance of the tooth in many, and probably in all, of the Scomberoid Fishes, and not only in those of the existing epoch, but the same beautiful and complicated structure may be discovered with equal distinctness in the fossil teeth of species and genera which are now extinct. At Plate 54 is given a view of the reticulate disposition of the medullary tubes, as seen by a low power, in a transparent longitudinal section of the fossil tooth of a large Scomberoid Fish, from the eocene formation called the London clay, at the Isle of Sheppey. The tooth, which I formerly described under the name of *Dictyodus*,(1) in reference to the arrangement of the medullary tubes, belongs to the extinct genus of fishes called by M. Agassiz, *Sphyrænodus*, from its affinity to the existing genus, *Sphyræna*, the largest species of which it must have equalled in size.

The natural form of this tooth, which is from the lower jaw, is conical and subcompressed, but relatively thicker than any tooth of the Sphyræna: its base is broad, but implanted as in that genus, in a deep socket, to the bottom of which it is anchylosed. The main body of the tooth consists of a coarse dentine, incased by a thin layer of fine and hard enamel-like dentine. The coarse dentine is pervaded by an assemblage of medullary canals, directly continued from the large irregular medullary sinuses and cells at the anchylosed base, and thence proceeding in a general parallel course towards the apex, sparingly dichotomizing, and gradually diminishing as they proceed: they are separated by interspaces, which are generally equal to three or four of their own diameters, and send off, throughout their course, short transverse branches, which anastomose and intercept in the interspaces of the longitudinal tubes, quadrangular, sub-elliptical, pentagonal, or hexagonal spaces, generally elongated in the axis of the tooth, but becoming shorter as they approach the periphery, especially at the apex, where the structure of the tooth resembles an irregular lace-work. In this fossil I have been able to detect the fine calcigerous tubes only in the hard peripheral layer of dentine, into which they pass directly from the nearest medullary canals, dividing and subdividing at acute angles, but with a general direction vertical to the

(1) Trans. Brit. Association, 1838, p. 142.

surface of the tooth. The relative thickness of this layer of fine-tubed dentine is shown in the figure; the diameter of the calcigerous tubes at the middle of the layer does not exceed $\frac{1}{15,000}$th of an inch. The traces of the corresponding tubes in the clear interspaces of the ramifications of the medullary canals were almost obliterated in the fossil examined by me, but the analogy of the recent Scomberoid teeth, and of some allied fossils, especially that about to be described, hardly permits a doubt as to their existence.

Saurocephalus. — There are few instances in which the value of the characters derived from the microscopic structure of teeth has been more strikingly displayed than in regard to the *Saurocephalus* and *Saurodon*, under which names two interesting fossils of distinct species, of the same or very nearly allied genera, have been described as extinct members of the Saurian Order of Reptiles, by Dr. Richard Harlan(1) and Dr. Isaac Hays.(2)

These fossils consisted of portions of jaws with teeth of a simple conical subcompressed form, arranged in a single row, fixed in distinct and deep alveoli, each with a broad and simple fang, generally excavated by the pressure of a new tooth developed near its base. Prof. Agassiz was led from the external characters of the jaws and teeth in question to believe that they might belong to the Scomberoid family in the class of Fishes, and an inspection of Plate 55, which gives a view of a small portion of a transparent longitudinal section of one of the teeth of the *Saurocephalus*, will demonstrate the accuracy of the judgment of that acute Palæontologist.

I am indebted to Dr. Richard Harlan for the opportunity of making the requisite sections of the tooth of the genus in question. The plan of structure closely corresponds with that already described in *Sphyræna* and *Sphyrænodus*. The larger medullary tubes (*a a*, Pl. 55), maintain a nearly parallel longitudinal course, throughout the body of the tooth, exhibiting here and there a dichotomous subdivision, and gradually decreasing in diameter as they approach the summit of the tooth. The lateral or transverse branches are, upon

(1) Journal of the Academy of Natural Sciences of Philadelphia, vol. 3, p. 331.

(2) Transactions of the American Philosophical Society, vol. 3, part 2, p. 471. In the Saurian system of Herm. v. Meyer these genera are placed between *Phytosaurus* and *Teleosaurus*, see his Palæologica, 8vo. 1832, p.p. 114, 222.

the whole, relatively larger than in the *Sphyrænodus*, and are more flexuous in their course; and the spaces intercepted by their anastomoses are less angular. These spaces (*b*) exhibit every where plexiform groups of flexuous calcigerous tubes proceeding from the medullary canals. The clear and dense investment of the tooth presents the same structure as the peripheral dentine in other Scomberoid fishes, being traversed by sub-parallel and acutely-branched calcigerous tubes, passing from the nearest medullary tubes, at right angles to the surface of the tooth, and diminishing to extreme tenuity in the clear outer portion of the investing layer, *c*. No Saurian tooth recent or extinct has presented the type of structure here described: the distribution of branched and reticularly anastomosing medullary or pulp-canals through the whole body of the tooth is a peculiarly Ichthyic condition of the dental structure; and the modifications of this condition presented by the tooth of the *Saurocephalus*, are most closely allied to those which characterize the teeth of the Scomberoid Fishes.

In Plate 55 an entire tooth of the *Saurocephalus lanciformis* and a portion of jaw, containing two others imbedded in their sockets, are represented of the natural size, by the side of the magnified section. The small foramen opposite the fang of each tooth is described by Dr. Hay, as being for the transmission of nerves and blood-vessels to the teeth. I have little doubt, from the analogy of the Sphyræna, that these foramina lead to the cavities containing the germs of the successional teeth. They are placed as in the Sphyræna, on the inner side of the alveolar process.

LUCIOIDS.

53. The fishes of the family typified by the voracious Pike, and hence termed 'Lucioids,' have a more complicated dentition than those of the preceding family; but the teeth are characterized by a similar reticulo-medullary tubular structure, distinguished chiefly by the more regular size and form of the meshes or interspaces of the anastomostic net-work.

The *Scomberesox* is a genus which connects the Scomberoid with the Lucioid family of fishes. The jaws of a species of this genus from

Van Diemen's Land, now before me, which exceed six inches in length, have the whole of their convex alveolar border beset with a band of minute sharp conical rasp-like teeth; along the inner border of each band there is a row of moderately long, slender, straight and very acute teeth, with intervals of from four to six times their own diameter. Their dentition resembles very closely that of the true Sauroid Fishes.

The Garpike, (*Belone vulgaris*), has a row of large sharp conical and recurved teeth, together with many small ones upon each of its long intermaxillary and premandibular bones; but the palatines and hyoid are edentulous. There is a small patch of villiform teeth on the vomer. The pharyngeals are paved with small tuberculate teeth. The *Mormyri* have a simple row of small compressed and notched teeth on each jaw: and villiform teeth on the tongue and vomer.

The *Esox Lucius* or common Pike has an immense number of teeth, all of which are conical, slender and sharp-pointed. They are placed on the intermaxillary, premandibular, palatine, vomerine, lingual, branchial and pharyngeal bones. The largest and most formidable of these teeth are those situated in the lower jaw, and at the anterior part of the palatines and vomer. The intermaxillary teeth are small and slightly recurved, placed in a single or double alternate row: the teeth at the anterior part of the lower jaw correspond in size and arrangement with the intermaxillary ones; but the posterior teeth are much longer and stouter, especially the first; they form a single row, and are separated by wide intervals in which are situated the successional teeth in different stages of development in a recumbent position, directed inwards, and concealed by the gum.

The teeth of the palatines and vomer are arranged in numerous close-set rows, the largest being placed at the anterior part of these bones, and along the mesial edges of the palatines; those on the vomer are so numerous, small, and close set, as to resemble the teeth of a rasp. The mesial chain of hyoid bones supports four longitudinally oblong patches of smaller rasp-like teeth. Similar teeth are arranged along the inner surfaces of all the branchial arches; and the four superior and two inferior pharyngeal bones are beset with somewhat larger teeth of a similar conical, sharp pointed, recurved form.

It is somewhat unusual in the present class, to find such an immense number of teeth, so variously disposed over the parietes of the mouth, yet presenting so uniform a shape; but all are here adapted to pierce, seize, and retain a living prey, and are thus in perfect conformity with the predaceous habits of the species. The fully developed and functional teeth are attached by a confluence of their bases with the surface of the jaw-bones, and not, as in *Sphyræna*, with the parietes of an alveolar cavity. The germs of the successional teeth, also, instead of being developed in alveolar cavities, complete their growth in the original seat of their formation, viz. the vascular membrane or gum, which covers the dentigerous margins of the jaws.

That the formation of a tooth is an act of conversion of the substance, and not of cells upon a formative surface of the pulp, is clearly illustrated in the Pike. The cone-shaped cap which the half-developed tooth forms upon the remaining matrix can only be removed by overcoming a certain resistance, and this resistance is seen to be due to the processes of the pulp which extend into the medullary canals of the tooth; the broken ends of these processes give an irregular surface to the exposed pulp, and their continuation into the tooth may be seen by sawing the latter across. This connection between the substance of the tooth and of the pulp is still better demonstrated in a finely injected specimen: the mechanical relation between the tooth and the pulp is then seen to be of precisely the same kind as those between an ordinary osseous nucleus and the cartilaginous matrix in which it is developed: it is in the course or direction of development that the chief difference exists; in the tooth it is centripetal, in the bony epiphysis centrifugal; but the mode of development is the same. In both cases a soft and vascular model and framework of the future hard part is prepared: in it the cells are formed and the tubes are excavated according to the plan destined for the future arrangement of the calcareous particles; which arrangement is not one of indiscriminate diffusion, but accords with the best known mechanical principles, and is in prospective harmony with the peculiar resistance which the calcified part is destined to overcome. A vertical section of the matrix of a Pike's tooth and the

supporting process of gum is represented at Plate 44, fig. 5; *a* is the superficial calcified layer of the pulp *c*, the base of which is sunk into a fossa, or open capsule of the gum *b*; *d* is the nerve entering the base of the pulp. In figure *b*, Pl. 44, the course of the branches of the fifth pair of nerves, through the permandibular bone of the pike, to supply the pulps of the teeth, is shown; the size of the dental nerve bears relation to the vascular and organized texture of the tooth, and to the rapidity of its growth.

Retzius' accurate description of the microscopic structure of the tooth of the Pike (*Esox Lucius*, *L.*) is as follows. "It consists of an internal part or nucleus with coarse tubes, and an outer thinner part, with fine and parallel tubes, which form the covering of the nucleus. The coarse main-tubes, which occupy the internal and imperfectly developed parts of the ivory, present at their widest part a diameter of about $\frac{1}{900}$th of an inch. Their course is almost parallel with each other and with the axis of the tooth, and they unite by numerous larger or smaller anastomoses. Near the basis of the anchylosed teeth, the larger oblique anastomoses are so near together that their interspaces are scarce equal to the diameter of the larger tubes. In recent teeth these tubes contain a blood-red substance, which might be regarded as a complex pulp. Beautifully minute and very short tubules of from $\frac{1}{6000}$ to $\frac{1}{12,000}$th of an inch in diameter, proceed mostly in a transverse direction from the larger tubes; and subdivide, as they proceed, into groups of finer tubes, which form innumerable reticular anastomoses with each other, and thus fill up the interspaces of the larger canals. The boundary between the central and peripheral substances is well defined, and is formed by anastomoses of the exterior longitudinal bent coarse tubes; beyond which no coarse tube extends, but only a series of fine and parallel tubes; these tubes manifest the same direction as those in the thin and hollow shell of the incompletely formed teeth of the higher organized animals: i. e. the fine tubes that are nearest the apex of the tooth, are almost parallel with the axis of the tooth, while those which are nearest the root, proceed transversely to the axis. They soon divide into pencils of finer branches, which mutually and reticularly anastomose, and give off at their peripheral extremities close-set parallel tubes, from $\frac{1}{13,000}$ to

$\frac{1}{23,000}$th of an inch in diameter, in which I could perceive neither branches, anastomoses nor cells. The exterior ivory-like substance viewed in a section of a Pike's tooth by a low magnifying power resembles a layer of enamel. It is extremely thin where it commences near the base of the tooth, and is thicker at the apex where the fine branches of the tubes exhibit the most beautiful dendritic arrangement. The central substance of the tooth is grey in recent teeth, and yellowish in dried specimens; the peripheral substance is of the purest white, and is much harder and more compact than the central substance. So hard, indeed, is it in dried teeth, that I supposed it might be covered with an extremely thin layer of enamel, but I could not by means of the microscope discover any such layer."

CLUPEOIDS.

54. The Clupeoid family of Fishes, of which the Herring is the type, is interesting in relation to the dental anatomy of the class on account of the examples which it offers of very general and extensive distribution of teeth over the bones which surround the oral cavity, and of he unusual share which the superior maxillary bones, from their relative position and development, take in supporting the teeth of the upper jaw. The different genera, however, of the Clupeoid as of other natural groups of fishes, present very diversified conditions of the dental system; the almost edentulous *Clupanodon*, and he rapacious *Erythrinus* or the gigantic *Sudis*, offering the extremes of these modifications.

In the *Clupanodon* an almost imperceptible coating of the finest villiform teeth, upon the pharyngeal bones, forms the sole trace of a dental system.

The Herring (*Clupea Harengus*) has very minute sharp-pointed teeth on the jaws and tongue.

The *Pritigaster* presents similar teeth on the large intermaxillaries, on a small part of the superior maxillaries, and upon the hyoid, palatine, vomerine and pterygoid bones.

The little Anchovy, the type of the genus *Engraulis*, is a good example of that higher development and allocation of the superior maxillary bone, which is so rare in the class of fishes; they here

form the greater part of the superior margin of the mouth, and together with the small intermaxillaries, and the slender premandibulars, are armed with small, but very sharp-pointed teeth: the vomer and the long palatines support similar, but smaller teeth, arranged in a single series: the pterygoid, hyoid, branchial and pharyngeal teeth are villiform.

The *Sudis gigas*, the largest not only of the Clupeoid family but of all fresh-water fishes, is not less remarkable for the number of the teeth, than for the number of bones over which they are distributed, the dental system is represented in figs. 4. 5 & 6, Pl. 48. Not only do the intermaxillary (*a*) the superior maxillary bones (*b*), the premandibulars (*f*), the palatine (*c*), the vomerine (*e*), the lingual (fig. 6), the branchial and pharyngeal bones support teeth, as in many Clupeoid and Salmonoid fishes, but the internal pterygoid bones (*d d*) and the basisphenoid (*f*) have their under surfaces beset with innumerable denticles.

The maxillary teeth are implanted in a continuous alveolar groove of the bones which circumscribe the aperture of the mouth, and are attached to the groove by a ligamentous union. These teeth are conical, much compressed, with an obtuse apex, near to which the pulp-cavity extends. The other dentigerous bones are beset with numerous, close-set, minute, short, cylindrical teeth, with convex, graniform summits. The surface of the tongue is formed by the hard granulated dentigerous surface of the median ossicles of the *os hyoides*, which are broad and flat; the anterior of these ossicles is much elongated; in a *Sudis gigas*, seven feet in length, it measures six inches in length and two inches in breadth.(1)

In the genus *Erythrinus*, the intermaxillary, maxillary and premandibular bones are formidably armed with conical sharp-pointed teeth, alternately large and small; the palatine, pterygoid, hyoid, and pharyngeal bones are beset with minute villiform teeth. The rapacity of these clupeoid fishes corresponds with the power of their maxillary weapons. In the stomach of a specimen of the *Erythrinus macrodon*, brought from Brasil in spirits, and dissected by M. Agassiz, he found another species of the same genus, more than a third part of the length of the fish by which it had been swallowed.2)

(1) It is used as a rasp for culinary purposes by the Indians of the Brazs.

(2) Spix, Pisces Brasilienses, p. 41.

In the genus *Osteoglossum*, the dental system of which is shown in the large middle figure of Plate 48, the intermaxillary bones (*a*) form only a small portion of the median and superior margin of the mouth; the remainder is completed by the superior maxillaries (*b b*), which, with the premandibular bones in the lower jaw, are armed with a single series of equal, small, conical and sharp-pointed teeth: near the lax symphysis of the lower jaw, there is a second series of similarly shaped retroverted teeth. The vomer and anterior part of the palatine bones are beset with small acute teeth; the posterior part of the palatines and the entire lower surface of the pterygoids are covered with villiform denticles, but there is a row of longer sharp-pointed teeth at the inner border of each pterygoid bone. The broad, long, and flat lingual bone, (*e*), is covered with minute close-set pointed teeth, converting the upper surface of the tongue, into a hard boney rasp, whence the name of the genus. The branchial arches and the inferior pharyngeals support villiform teeth.

The genus *Glossodus* affords additional examples of those fishes in which the body of the os hyoides is provided with tubercular teeth which are opposed to similar instruments for crushing the alimentary substances, attached to the body of the sphenoid and to the pterygoid bones. The maxillary, vomerine, palatine, branchial and pharyngeal bones, both superior and inferior, are beset with minute villiform teeth.

In the three preceding genera of South American tropical fresh-water fishes the broad, long and flat dentigerous plate, into which one of the median hyoid ossicles is developed, forms a striking characteristic of their dental system, and I shall here describe similar dentigerous plates, found fossil, in the eocene formation, called the 'London Clay,' at the Isle of Sheppey.(1)

As these remains have hitherto been met with detached and unconnected with the other bones of the skull, and exhibit little more than the dentigerous covering, it cannot be unequivocally determined whether they are the dentigerous armature of a broad lower pharyn-

(1) Specimens of these are preserved in the well known collection of Sheppey. Fossils of J. S. Bowerbank, Esq., F.G.S., whose liberality in permitting their description on this, as on many other occasions, I have gratefully to acknowledge.

geal bone, like that of the Scarus, or of the maxillæ, as in the Diodon, or whether they belong to the hyoid system, or other median bone of the cavity of the mouth; as, however, it is the structure of the teeth and not of the cranium that it is proposed to describe in this place, the ambiguity which may attach itself to the precise homology of the supporting bone is of less consequence.

55. *Pisodus.*(1)—The form of the teeth scattered over the surface of the large flat oval dentigerous bone, figured in Pl. 47, fig. 3, suggested the name of the extinct genus of fishes, which the present remarkable fossil unequivocally indicates. It measures four inches and a quarter in length, two inches and a quarter in breadth, and seven lines in depth at the thickest part, which is at the middle of the plate. The teeth are distributed irregularly over the whole of the upper surface, and in pretty close contact, except where they have been displaced by attrition, as from the large flat and polished surface at the anterior part of the bone, or where they have been broken or shed, at the interspaces of the unworn teeth. These all present the same form and nearly the same size: they have a hemispherical smooth and polished crown, and are inserted each by a large short hollow conical fang or base into a socket of corresponding form and dimensions. The crowns of some of the teeth project two lines beyond the surface of the bone, others are just protruding above that surface; indicating that they are shed and renewed in vertical succession: the middle of the edentulous anterior surface is worn smooth and flat, but its circumference is pitted with the remains of the sockets. On the under surface of the dental plate there is a regular elliptical space occupying four-fifths of that surface, and defined by a raised margin; this indicates the place of attachment of the plate to another bone of the skull, most probably, as in the *Glossodus* and *Sudis* to a median bone of the hyoid system.

The teeth of the Pisodus are adapted for crushing shells, crustacea, or vegetable substances; their texture is extremely dense, and corresponds with that of the teeth of the Microdon.

56. *Phyllodus.*(2)—The dentigerous plates, which have suggested to Professor Agassiz this name for the extinct species of

(1) πίσον, a pea, ὀδους, a tooth.

(2) φύλλον, a leaf, ὀδους, a tooth.

fish to which they have belonged, present a contour somewhat like that of a simple leaf: the posterior part being contracted, as if for the attachment of a stalk, the opposite end being rounded and thinned off. The largest specimen of this fossil, which I have yet seen, is figured in Plate 47, fig. 1 and 2. It consists of an anchylosed mass of superimposed more or less flattened, lamelliform teeth, of which those forming the middle longitudinal row are the largest, and present a transversely elongated oblong figure: these are surrounded by smaller oblong dental lamellæ, irregularly placed, and diminishing in size to the circumference of the mass, where they exchange the oblong for a circular form. All the dental lamellæ are convex on the upper surface (fig. 1) and concave on the under surface (fig. 2.) On a superficial inspection the middle lamellæ might be supposed to be as thick as the mass of which they form part, but this is evidently not the case with the marginal lamellæ; these are seen to be superimposed in nearly vertical tiers, like the lamellæ of the maxillary dental mass in the Diodon. The number of lamelliform teeth in each pile, increases from the anterior to the posterior part of the mass, where, in the specimen figured, nine or ten denticles might be counted in a single tier. To ascertain whether the large middle teeth were also lamelliform, and similarly superimposed, I had made, by the kind permission of Mr. Bowerbank, a vertical section through a dental mass of the same species of *Phyllodus* as the one figured, and found that the same lamellar condition and arrangement pervaded all the teeth. Between the upper and the lower of the two longest median denticles, there were interposed six plates similar to the two superficial ones of which the upper surface is shown in figure 1, and the lower surface at fig. 2. A magnified view of a thin transparent slice taken from the surface of the vertical section, including a portion of four of the superimposed plates of two contiguous piles, is given at Plate 44, figure 2. It displays a structure analogous in essential points to that of the pharyngeal teeth of the Scarus. If, for example, the cone, of which a section is figured at Plate 52, were flattened down and rolled out, it would form a lamelliform tooth composed of a layer of enamel and a layer of dentine of equal thickness, supported on a thinner layer of coarse cellular bone. Such is the microscopic texture of a single

lamelliform tooth of the Phyllodus but these teeth being piled one upon the other, the entire mass presents a succession of strata of the three substances.

The osseous substance (*a*, fig. 2, Pl. 44), is characterized by the large, reticularly anastomosing medullary canals, without radiated cells in their interspaces, which are peculiar to the structure of the bones and ossified basis of the teeth in fishes. The dentine (*b*) consists of numerous, close-set calcigerous tubes and the clear uniting substance; the tubes are characterized by their straight, and parallel course; at the middle part of the plate, they are directed vertically to its plane, and at the margins which are bent down, they incline so as to maintain the same relative position to that part of the surface of the plate; their diameter does not exceed $\frac{1}{15,000}$th of an inch; their subdivision into pencils of smaller tubes takes place nearer to the enamel than usual. I could plainly discern the anastomoses of these divisions of the calcigerous tubes in some parts of the section. The enamel *c*, which, as in the denticles of the Scarus and many other fishes, closely approximates in structure to the dentine, exhibits, however, much less parallelism in the course of its component tubes in the Phyllodus; but these are as numerous and distinct, though somewhat more minute than those of the true dentine.

It would seem that in the matrices or pulps of both the enamel and dentine, the progress of calcification followed the same law, viz: from the circumference to the centre, or from the surface to the attached base of the pulp. In specimens of the Scarus preserved in spirit, and in other fishes, I find that neither surface of the formative pulps is free, for, while that which may be termed the base of the enamel-pulp is adherent to the capsule, and while the base of the dentinal pulp turned in the contrary direction, coheres with the mucous surface from which it was originally developed, the opposite surfaces of both pulps firmly adhere to one another. It is at this surface, however, in each case that the process of calcification commences. The linear groups of cells being here irregular in their position, form, by their confluence, tubes as irregularly disposed; but as the deposition of the hardening salts proceeds, the tubes

become more regular and parallel. This parallelism has taken place in the Phyllodus, much sooner in the dentine than in the enamel, as is the case in the Scarus, and hence the difference of the disposition of the fine calcigerous tubes, which mainly distinguishes the texture of the dentine and enamel in fishes.

The fossils here described very clearly exhibit the effects of attrition and waste at one extremity, and of renovation at the opposite end of the dental mass; but they likewise show the same antagonist influences operating at the upper and the lower surfaces of the mass; the work of destruction and of reproduction has proceeded in both the longitudinal and vertical directions. As the lamelliform teeth at the top of each pile were worn away, the loss was supplied by new lamellæ added to the bottom of the pile, according to the mode of reproduction described in the dental system of the Diodon. But as the attrition was greatest at the anterior extremity of the dental plate, and the power of reproducing the lamellæ in the vertical direction limited, the loss of entire piles of teeth was supplied by the addition of new piles to the posterior extremity of the dentigerous plate, according to the mode of reproduction described in the pharyngeal teeth of the Scarus. In the Diodon we see illustrated the law of succession of the permanent to the deciduous teeth in the Mammalia, viz: in the vertical direction, but the process is much more frequently repeated. In the Scarus, the course of succession of the true molars in the Mammalia, viz: in the horizontal course was followed. In the Phyllodus, both kinds of displacement and succession are exemplified; and the peculiarities of the Diodon and Scarus were combined, with the same frequent and uninterrupted repetition of the renovating processes, in a single dentigerous bone of that extinct species.

SALMONOIDS.

57. Many fishes of the Salmon tribe, like those of the Clupeoid family, have the superior margin of the mouth formed in a greater or less degree by the superior maxillary as well as by the intermaxillary bones, both of which, excepting in the edentulous species, as the *Salmo edentulus*,(1) Bloch, are armed with teeth.

(1) The type of the genus Anodus of Spix.

In the *Prochilodus*, however, both these and the bones of the lower jaw are feeble and are imbedded in the thick fleshy lips, to which, and not to the bones themselves, the minute, flexible, incurved, bristle-like teeth, characteristic of the genus, are attached: they are arranged in a single close-set row.

The superior maxillary bones are edentulous, and are placed backwards, transversely to the angle of the mouth in the subgenera *Schizodus*, *Serrasalmo*, *Myletes*, and *Xiphostoma;* but in the true *Salmones* and other cognate genera, they support a part, and often nearly the whole of the teeth of the upper jaw.

In the Salmonidæ of the River Nile, which belong to the genus *Citharina* of Cuvier, the maxillary teeth are nearly as fine and as close-set as in the Chætodonts, but their free extremity is forked. The pharyngeal bones are beset with velutine teeth.

In the *Schizodus*, the intermaxillary and premandibular teeth are broad, and of the incisive type of form, with a crenate superior margin. In the *Serrasalmo*, (Pl. 48, fig. 8,) the corresponding teeth preserve the compressed form, but have a sharp apex, a broad base, and trenchant and finely serrate edges; these lancetted teeth are arranged in a single series both above and below.

The *Myletes* is remarkable for the prismatic three-sided figure of its teeth, the working surfaces of which are cuspidated by the production of the angles into sharp points, (Pl. 48, fig. 10). There is a single series of these teeth in each premandibular, and a double row in each large intermaxillary bone; behind the two median teeth of the lower jaw there are two simple conical pointed teeth; similar but much smaller pointed teeth are scattered over the pharyngeal bones.

In the genus *Raphiodon*(1) the teeth, as the generic name implies, are long, slender, and extremely sharp-pointed; they are implanted in the short intermaxillary, the superior maxillary and the premandibular bones; shorter teeth of a similar shape, alternate with the longer ones; the pair next the symphysis of the lower jaw, exceed all the rest in size.

The elongated jaws of the species of *Xiphostoma* are provided with a single row of small, sharp-pointed, slightly-reflexed teeth; those on the alveolar border of the short superior maxillaries

(1) ῥαφίς, acus, ὀδούς, dens.

which cross obliquely the angle of the mouth, are directed forwards. In the genus *Saurus*, the mouth presents the anomalous condition among fishes of edentulous intermaxillaries, with a formidable array of teeth in the upper jaw, supported exclusively by the superior maxillary bones; these meet at the middle line, and the small intermaxillaries, which are recognizable by their characteristic ascending process, are placed above and parallel to the median extremities of the maxillary bones; the teeth are slender, conical, and very acute; they are arranged in three or four rows, and form conical groups, with the longest tooth in each placed innermost; these teeth have their apices slightly expanded. Similar spear-shaped teeth are arranged on the premandibular bones below; and likewise crowd the palate, the tongue, the branchial arches, and the upper and lower pharyngeals.

The disposition and usual form of the teeth in the typical genus *Salmo* are represented in a diminished view of them in the common salmon, as seen in looking into the cavity of the open mouth, (Pl. 48, fig. 9). The teeth all present the same simple form, short, stout, pointed, and incurved; from four to five are implanted in each intermaxillary bone, the remainder of the single row which arms the upper margin of the mouth, being supported by the superior maxillary bones. In the young salmon there are two or three teeth on each side of the anterior part of the vomer; but, as growth proceeds, they are reduced in number, and finally disappear in aged fish; each palatine bone supports a single row of teeth, nearly parallel with, but smaller than, those of the maxillary rows; there is a single row, on each premandibular bone; and a double row united by a crescent-shaped series on the anterior part of the tongue. The pharyngeal bones are armed with similar teeth.

The principal difference observable in the allocation of the teeth in the species of *Salmo* obtains in the vomer; upon which, in the salmon-trout and common trout(1) for example, the teeth are extended backwards in a row, and deeply indent the surface of the tongue between the two lateral rows of lingual teeth.

The teeth are anchylosed by their bases to the several dentigerous

(1) Mr. Yarrell has given a figure of the dentition of the common trout in vol. ii, p. 3, of the British Fishes.

bones, and are separated by intervals usually greater than their own breadth; in their mode of development, shedding, reproduction and microscopic structure, they so closely resemble, in both the Clupeoid and Salmonoid families, those of the Pike,(1) as not to require further description in this place. The mutual affinity of the herring and salmon-tribe, is not only manifested in that part of their anatomy which is described in the present work, viz: the very general distribution of the teeth, and especially their location in the superior maxillary bones, but is also illustrated in other parts of their organization, and is regarded by M. Agassiz as of so intimate a nature, that he has combined the Clupeoids and Salmonoids of Cuvier into one natural family under the name of "*Halecoids.*"(2)

CYPRINOIDS.

58. The family of Cycloid fishes, whose dental system we next proceed to consider, is as remarkable for the paucity of teeth and the edentulous character of the bones of the mouth, as are the Halecoids, for their general and formidable armature. It is only, in fact, in one small section of the Cyprinoids that any teeth at all are present on what may be considered the true bones of the mouth; these being restricted in the rest of the carp-family to the bones of the pharynx.

The exceptional genera with maxillary as well as pharyngeal teeth are *Anableps*, Artedi, *Pœcilia*, Schn., *Lebias*, Cuv., *Fundulus*, Lacep., *Molinesia*, Less., and *Cyprinodon*, Lacep.; all of which are grouped together by M. Agassiz under the name of Cyprinodonts.

In the *Anableps*, or "four-eyes," the intermaxillary and premandibular bones are furnished with delicate setiform teeth, like those of the Salmonoid genus *Citharina;* the pharyngeal teeth are

(1) Cuvier cites the salmon and the pike together as examples of fishes that have teeth on all the situations of the mouth where teeth can be placed. "Il y a des poissons qui ont des dents dans tous les endroits de la bouche ou il peut y en avoir; tels sont le saumon, le brochet."—*Leçons d'Anatomie Comparée*, Ed. 1835, tom. iv, p. 337. But besides the pharyngeal, branchial, hyoid, vomerine, palatine, premandibular, intermaxillary and maxillary teeth, (the last are wanting in the Pike), there are examples of fishes, as the great Sudis and Glossodus that have in addition to all these teeth, both pterygoid and sphenoid teeth.

(2) It is not to be understood that the Pisodus or Phyllodus, the dentigerous plates of which have been described, for the sake of convenience, after those of the Glossodus, &c., belong to the Halecoid family, although this is probable as regards the Pisodus.

small hemispherical tubercles. The jaw-teeth of the *Pœcilia* are also minute, but somewhat stronger than those of the *Anableps*. Those of *Lebias* are characterized by their dentated margin. In the *Fundulus*, the anterior teeth in both the maxillary and premandibular bones are conical and recurved, while the hinder ones are villiform. In the genus *Cyprinodon* all the teeth are " en velours."(1)

The ordinary bones of the mouth in all the true Cyprinoid fishes, of which the carp and roach may be taken as types, are devoid of teeth; but in some species there may be perceived upon the alveolar border of the jaws, as along the intermaxillaries in the barbel, a band of minute, close-set and pretty firm papillæ, which may be regarded as the uncalcified analogues of a series of villiform teeth, like those of the Cyprinodonts. The only true teeth, however, in the present division of the family are situated on the inferior pharyngeal bones, which work against each other, or against a very hard upper pharyngeal dental plate, which is fixed in a depression on the inferior surface of the basilar bone, and may thus be regarded as an occipital tooth.

The dentigerous pharyngeals are a pair of arched bones which may be regarded as the last of the lateral branches of the hyoid apparatus, or as a fifth pair of branchial arches supporting teeth instead of gills. They are smaller, stronger, and more curved than the true branchial arches which are anterior to them; they bound the sides and lower part of the pharynx; their anterior and inferior extremities are connected together by ligaments, allowing a yielding motion; but I have found them sometimes anchylosed together in old carp(2); their posterior and superior extremities are attached by ligaments and muscles to the occipital region of the skull.

Besides the movements backwards and forwards, the pharyngeals admit of being approximated and divaricated, and these movements are produced by very powerful muscles. One of these muscles, (*b*, Pl. 57, fig. 1, in which the armed pharynx of the barbel is represented as seen when looking down upon the base

(1) Cuvier, Loc. cit. p. 354.

(2) A portion of the left pharyngeal, so anchylosed to the right, is represented at Pl. 57, fig. 7

of the skull), arising from the outer margin of the anterior and inferior moiety of the pharyngeal bone, passes inwards below the pharynx and expands to meet its fellow at a strong median raphé. This muscle, which is more especially developed in the barbel, gudgeon, and those Cyprinoids which have the teeth formed for piercing and lacerating, besides approximating the pharyngeal bones at the median line, at the same time draws them forwards. The antagonist muscle (*c*) arises from the descending spine of the basi-occipital bone, and passing outwards and forwards, expands to be inserted along the outer margin of the posterior half of the pharyngeal bone; this muscle while it draws back the pharyngeal bones, at the same time, from the mode of attachment of the bones to the skull, slightly divaricates them.

The teeth are attached to the inner side of the pharyngeal bones by a confluence of their basis with the osseous substance. It might be supposed that the food of the leather-mouthed fishes, as the Cyprinoids without maxillary teeth are commonly termed, would be so nearly the same, that the few teeth which were lodged in the fauces would present much sameness of form; but this is by no means the case, as the selection of pharyngeal teeth from the Cyprinoid genera figured in plate 57 demonstrates. The laniary type is best shown in the barbel (fig. 1 & 2) and the molary type in the carp (fig. 6 & 7); indeed, the large lower pharyngeal tooth of this species exhibits, before it is too much worn, the most complicated triturating surface of any single tooth in the osseous fishes, and one which most closely resembles that of the molars of certain herbivorous mammalia.(1)

The barbel (*Barbus vulgaris*), which feeds on slugs, worms and small fishes, requires teeth so shaped as to pierce and lacerate the skin of its prey, and to tear them into fragments capable of passing the narrow œsophagus: in this species they accordingly are elongated, conical, slightly and somewhat irregularly bent, arranged in three rows, and increasing in number and size from the innermost to the outermost row; the teeth in this row are generally five in number, separated by interspaces, so as to interlock, when the pharyngeal bones are approximated, as represented in plate 57, fig. 1; the probe (*a*) shows their relative

(1) "In the carp, the crowns of the teeth are observed to be so worn down as to have the appearance of the crowns of the molar teeth of the hare."—Yarrell, l. c. Introduction, p. xix.

position to the entry of the œsophagus, and it may be seen how the teeth must sift and lacerate the alimentary substances in their passage through the pharynx.

In the Gudgeon, (*Gobio*), which feeds on worms, aquatic larvæ and small mollusca, the pharyngeal teeth are conical, slightly curved at the extremity and arranged in two rows. In the *Acanthopsis*, the pharyngeal teeth are sharp-pointed and placed in a single row. In the Loach, (*Cobitis*), which feeds on aquatic larvæ and worms, the pharyngeal teeth are slender and are chissel-shaped at the extremity. The same scalpriform type is seen in the teeth of the genus *Rhodeus*.

In the genus *Schizothorax* lately established by the laborious Ichthyologist I. J. Heckel for certain Cyprinoid Fishes from Cachmir, the pharyngeal bones have three rows of teeth, two in the first, three in the middle, and five in the third or posterior row, which last are the strongest, all somewhat elongated, oblique, and with the extremity slightly curved. The outer row of pharyngeal teeth are figured *in situ*, on the right pharyngeal bone of the *Schizothorax esocinus*, Heck. (fig. 4) where they exhibit the shape most common in the genus: in *Schizothorax curvifrons*, Heck. the pharyngeal teeth resemble long inverted cones, the expanded, but originally pointed summits being soon worn down so as to appear truncated.

In the *Cyprinus Nasus*, L., similarly shaped teeth are arranged in a single row, nine in number, on each pharyngeal bone; the inferior ones being somewhat larger, with a narrow but flat triturating surface, supported upon a slender pedicle.

In most of the species of *Leuciscus*, as the ide, the chub,(1) the dobule, the dace, the minnow, and the roach, (fig. 4) the pharyngeal teeth are subconical, slightly curved at the apex, and more or less truncated, in an oblique direction: their food, which includes the softer parts of aquatic herbs with worms and insects in different stages, corresponds with this approximation to the molar type. Some species of *Leuciscus*, however, as the *L. Scardinius*, Bonap. have the pharyngeal teeth slightly dentated along the internal margin. The *Leuciscus erythrophthalmus* has two rows of seven teeth on each pharyngeal bone;

(1) A friend informs me that the larger chub take the spinning minnow and gudgeon freely, and mash them out of all shape.

the five outer ones are the largest and have the triturating surface very elegantly dentated.

The bream (*Brama*) has five pharyngeal teeth in a single row on each side; they are moderately large, compressed and obliquely bevelled to a cutting edge, which works against the occipital tooth above. The teeth of the tench (*Tinca*) are similar to, but relatively broader than those of the bream: their oblique triturating surface is produced internally into a slightly hooked point, as represented in Pl. 57, fig. 5; they are arranged in a single row, four or five on each side of the pharynx, and work against a thick and dense triangular superior pharyngeal plate (*a*) imbedded in the basi-occipital bone. Similar pharyngeal teeth have been found to characterize two extinct species of tench, viz. *Tinca leptosoma* and *micropygoptera*, Agass.

Both the tench and carp combine a large proportion of vegetable matter, derived from aquatic plants, with worms and the larvæ of insects, for their ordinary food; but the carp, (*Cyprinus Carpio*), from the nature of its dentition ought to be the most herbivorous species of the family. In this species, the pharyngeal teeth are arranged in two or three rows; the innermost represented by a single tooth, the second having sometimes two teeth of larger size; and the outer row including three or four, which are the largest and most complicated, especially the middle one. The anterior and inferior tooth of this row has a round crown, with the centre raised into a small point; the rest are terminated by a flattened grinding surface, sculptured with transverse undulating furrows. These are not very deep, so that they disappear, as shown in Pl. 57, fig. 6, when the tooth is moderately worn down. Fig. 7, exhibits the grinding surface on a tooth recently anchylosed to the pharyngeal bone, and fig. 8 shows the inferior surface of the furrowed crown of an incompletely formed tooth as seen on looking into the wide and open pulp-cavity. The incudeal triangular dental plate, implanted in the occipital bone, is extremely dense, and presents a clear transparent amber-colour in the carp as in the tench; but its contour is more equilateral in the carp, and the surface which receives the appulse and friction of the pharyngeal molars is flatter.

It is sufficiently obvious from an inspection of the powerful

muscles which work the pharyngeal bones, that the teeth, whether adapted for piercing or lacerating aquatic animals, or for triturating vegetable substances, must be used with such force as soon to be rendered unserviceable, and to require renewal. I had formerly made sections of the dried pharyngeal bones of our common Cyprinoid fishes, under this conviction, in quest of the hidden germs of the replacing teeth, but without success. A subsequent acquaintance with the place of development of the successors to the maxillary teeth in certain fishes, as already described in the pike, alepisaur, &c., led me to renew the search in the substance of the thick and soft mucous membrane of the pharynx surrounding the pharyngeal bones, and I soon detected the germs of the successional teeth in this situation.(1) The primitive papilla first developed from the surface very soon sinks into the substance of the mucous membrane, and becomes inclosed by a complete capsule. I have not been able to detect in the carp or tench an enamel-pulp developed from the surface of the capsule covering the crown of the contained tooth: this adheres only to the dentinal pulp, and by means of its base to a part of the circumference of the capsule. The hollow cap of dentine of a half-formed tooth is easily displaced from the formative pulp in consequence of its dense structure presently to be described; but the surface so exposed when viewed by a strong reflected light, with a $\frac{1}{4}$ inch focus, is clearly seen to be an artificial and lacerated surface: it is minutely honey-combed, by the rupture of the calcified from the uncalcified portions of the nascent calcigerous tubes; and the subjacent and still unconfluent cells, are seen torn from the substance of the pulp, and scattered irregularly over its surface. When the pulp of the crown of the tooth is completely calcified, the margin of its base begins to assume a ligamentous density, and attaches itself to the margin of the pharyngeal bone, near the base of the tooth about to be displaced. I have not observed any further stage in the singular process of transference of the loosely imbedded tooth from its mucous capsule to the bone with which it is destined to form a common and continuous part.

In this process of union, which is analogous to that of the separated portions of a fractured bone, the question suggests itself, by what

(1) See Pl. 57, fig 6, in which a young tooth *c* is exposed by a reflection of part of its mucous capsule, *b*.

means does nature ensure in the often repeated process, that the detached osseous parts in the fish should always be well set, and the tooth transferred, not only to its right place in the series, but to its right relative position upon the bone? The marvel is not diminished when we consider that immobility is quite impracticable during the uniting process, that the fish must eat with the teeth that remain fixed, and that the bone to which the new tooth is in process of becoming anchylosed must be daily rotated backwards and forwards.

The pharyngeal bones in the Cyprinoids have rarely the thickness adequate to the lodgment of the matrix of a tooth beneath the one in place; in this respect they differ materially from those of the Labroid fishes: they are, on the contrary, in general, so thin that they are perforated on the side opposite the anchylosed base of the teeth in place, and the nerves and vessels of the remaining pulp pass by these orifices directly into the cavities of the teeth.

In all the Cyprinoid fishes the pulp-cavity of the pharyngeal tooth is extensive, and traverses almost the whole of the tooth in the barbel and other species, where the teeth present the elongated laniary form. The whole of the dentine is composed of fine calcigerous tubes, analogous to the structure of that of the simple mammalian teeth: these tubes in the barbel radiate from the narrow and elongated pulp-cavity, with a general course at right angles to the surface of the tooth, and consequently to the axis of the tooth: their diameter is $\frac{1}{16,000}$th of an inch at their origin with interspaces of thrice that diameter; they proceed with a slightly but regularly undulating course, branching dichotomously, but not frequently; and the branches, after slightly diverging are continued nearly parallel with each other, and in the direction of the trunk, until they approach the peripheral and denser portion of the tooth; here they diverge and decussate each other, and present a general inclination towards the base of the tooth. In plate 58, fig. 1 is shown the origin of a portion of the calcigerous tubes from, and in connection with, the uncalcified portion of the formative pulp, magnified 600 linear diameters; the honeycombed surface of the pulp, from which some of the calcified tubes have been displaced is shown at the lower part of the figure. The clear calcified walls of the tubes are scarcely, if at all, discernible in sections, which, like the present, are taken parallel with their axis; and the calcifying

cell or nascent tube appears to project from the surface of the pulp in a pyramidal form at the base of each tube, and to pass by a contracted apex into its cavity; this is, however, a deceptive appearance, for its walls are in continuity with the transparent calcified walls of the dental tube, and the more opake cavity of the cell alone communicates with the corresponding cavity of the calcified tube. The true diameter of the calcigerous tube, including its transparent parietes with its sub-opake cavity, nearly equals that of the superficial elongated cell, at the expense of which it is about to be developed.

From the circumstance of the section, here figured, including two or three layers of the calcigerous tubes, their interspaces are made to appear smaller and their decussation to commence sooner and to be more frequent than is really the case in any given layer.

In fully formed teeth calcification proceeds in the ligamentous basis of the pulp from the circumference towards the centre; the union of the tooth to the pharyngeal bone takes place in the laniariform teeth, as in those of the barbel, by numerous slender, wavy, subcylindrical processes, corresponding with the former fasciculi of the ligamentous substance; these calcified processes are implanted, like piles, into the subjacent bone, slightly diverging as they penetrate it, and gradually exchanging in it their dentinal for an osseous texture. The centripetal course of calcification proceeds more rapidly at the basis than in the body of the tooth, and the pulp-cavity thus becomes closed below, (excepting at a small central aperture for the passage of the nerve and vessels), while it remains widely open in the body of the tooth. A section of part of the base of a pharyngeal tooth of the barbel, exhibiting the numerous roots or fangs by which it is anchylosed to the bone, and the widely open pulp-cavity at the base of the projecting body of the tooth, is represented, as seen by a moderately magnifying power (1 inch focus of Ross's compound achromatic) in plate 58, fig. 2: the figure is in the situation of the pulp-cavity: opposite the right hand is a portion of the thin dentinal wall of the base of the exserted part of the tooth, in which the transverse course of the calcigerous tubes is indicated.

TRACHINOIDS.

59. The dental system of the fishes of the family of Trachinoids offers few particulars deserving attention: and I shall briefly allude to the modifications which are exemplified in two of the genera referable to this group.

In the Weevers (*Trachini Draco, et Vipera*) the intermaxillary, premandibular, palatine, vomerine and pharyngeal bones are beset with minute villiform teeth: they are arranged in two longitudinal bands upon the palatines, and form a single transverse band in front of the vomer. The tongue is edentulous.

In the Star-gazer, (*Uranoscopus scaber*), an exotic species of Trachinoid fishes, the intermaxillaries, pharyngeals and vomer, have their masticatory surfaces roughened like a rasp by numerous small, but more strongly developed teeth: those on the palatines are still larger: and the premandibulars support eleven strong canines separated by intervals, and placed behind a small patch of villiform teeth near the symphysis.

In microscopic structure and mode of reproduction the teeth of the Weevers resemble those of the Pike.

LOPHIOIDS.

60. In this singular family of fishes in which the pectoral fins are developed into terrestrial locomotive organs, the peculiarities of the dental system will be principally illustrated by a description of the teeth of one of the largest species, which is at the same time a native of our own coasts.

The Angler, (*Lophius piscatorius*), has teeth on the intermaxillary, premandibular, palatine, vomerine, and pharyngeal bones. They are of an elongated, conical, sharp-pointed, and slightly incurved form, presenting merely differences of size, degree of curvature, and mode of fixation, but all bespeaking the predatory and carnivorous habits of the species.

In the upper jaw, the teeth are congregated in three or four irregular rows at the median or upper third part of each intermaxillary bone, and form a single and regular series along the lower two-thirds.

These latter, which may be termed the serial teeth, are from fifteen to eighteen in number, short, strong, pointed and incurved ; of nearly equal size and placed at regular distances from each other.(1) The two outer irregular rows of the median intermaxillary teeth are somewhat larger and are directed forwards ; the inner rows at this part contain the longest teeth and their points are turned back ; but they are moveably connected with the bone by a mechanism which will be described when treating of those of the lower jaw.

The premandibular teeth can hardly be said to form a regular series, but are scattered along the alveolar margin of the lower jaw in an irregular quincuncial disposition ; being three, four, and five deep towards the middle and anterior part of the lower jaw, in full grown specimens. The largest teeth in the mouth of the Lophius are the innermost and median ones of the premandibular bones ; they decrease in size as they are situated more laterally. The transverse section of the body of these laniariform teeth is nearly circular, but at their broad and expanded base it is triangular with one of the angles directed outwards. The palatine teeth form a single row, near the outer edge of the bones, the median ones being the largest ; the cluster of two or three teeth on each side of the expanded anterior extremity of the vomer seem to terminate the palatine series.

The superior pharyngeal teeth are arranged in three groups upon as many separate bones on each side ; each group describes a curve with the convexity turned forwards ; the teeth of the posterior bone are the smallest. The inferior pharyngeal bones are two in number, and have the teeth arranged in a double alternate row along each margin.

The pharyngeal, palatine, and vomerine teeth are fixed by anchylosis to their respective bones ; this is also the case with most of the intermaxillary teeth, and with the exterior teeth of the lower jaw ; but the remainder, and especially the large posterior fangs of the lower jaw, are attached by means of elastic ligaments to the margins of slightly elevated alveolar processes. These ligaments are prin-

(1) In the *Lophius Upsicephalus* the corresponding serial intermaxillary teeth are described as being short, delicate and cylindrical, by Dr. A. Smith in his excellent " Zoology of South Africa."

cipally inserted into the inner straight margin of the base of the tooth, from which their glistening fasciculi radiate to be implanted into the jaw. The rest of the base of the tooth is connected at its circumference with more lax and yielding fibrous bands, and with the mucous membrane of the mouth, which covers the alveolar tract in the interspaces of the teeth. To any attempt to bend these teeth outwards resistance is offered by the internal ligaments above described, and by the pressure of the anterior angle of the base of the tooth against the alveolar process or raised tubercle on which it rests; but the tooth readily yields to a force acting in the opposite direction, and the largest and most prominent teeth can be bent inwards and backwards so as to point to the gullet when the hand is pressed over them in the direction a body would take when drawn into the mouth to be swallowed: the moment, however, this force ceases to act, the teeth recoil to their erect position, as if operated on by a spring. If every thing attached to the base of the tooth, excepting the internal pyramidal band of ligamentous fibres, be removed, the tooth, after being bent down, returns with the same force to the erect position; it is, therefore, to this band that its resilience is due.

The teeth of the Lophius exhibit, as stated in the first chapter, the higher type of dental structure: such as characterizes the teeth of sauroid fishes and of most reptiles and mammals. The fully-formed teeth are constituted by a single system of calcigerous tubes, radiating from a single sub-central pulp-cavity: this is widely open at the base of the tooth, but soon diminishes by the convergence of its sides, which arch inwards and meet at the basal third of the tooth, whence the pulp-cavity is continued as a mere line to near its apex. The course of the calcigerous tubes is unusually uniform, throughout the entire length of the tooth. On leaving the pulp-cavity they ascend obliquely and then incline in a graceful curve to the side of the tooth, to the exterior of which they are continued, in the greater part of their course in a straight line, and nearly at a right angle to that surface. This description applies to what I have termed the primary curvature of the calcigerous tubes; the secondary curvatures that each tube exhibits throughout its whole course consist of undulations, which are coarser, more angular, and less regular than

in ordinary mammalian dentine. The tubes divide and subdivide dichotomously four or five times in their progress to the perhiphery; their diminution of diameter is not proportionate to their degree of subdivision: their diameter at their origin is $\frac{1}{20,000}$th of an inch; at their terminations it is $\frac{1}{28,000}$th of an inch: their interspaces equal three or four of their diameters. The small lateral branches given off at the angles or sharp bends of the secondary undulations into the clear uniting substance are unusually conspicuous. A very small proportion of the calcigerous tubes proceeds from the apex of the linear pulp-cavity in the axis of that cavity. The apex of the entire and newly-developed tooth is coated with a thin, dense, white layer of an enamel-like substance, which is soon lost. A line of dentinal tissue, more opake than the rest, runs parallel with the pulp-cavity through the dentine about half way between the cavity and the external surface; this line, analysed with a sufficiently deep power, is seen to result from an unusual number of lateral branches sent off from a certain extent of the calcigerous tubes along the same parallel line, which branches anastomose together and dilate into small opake cells in the interspaces of the tubes from which they are given off.

Owing to the extent of the secondary inflections of the calcigerous tubes, and the difficulty, if not impossibility of obtaining a section which does not include three or more layers, they exhibit in every part of the tooth the appearance of an universal plexiform interweaving; this character, in combination with their general transverse course and the length of the linear pulp-cavity, might serve to distinguish the tooth of the Lophius from that of a reptile or mammal which it otherwise might most nearly resemble in general form and texture.

The new or successional teeth are found recumbent in different stages of development, some inclosed in their capsules, others with their apices projecting more or less from the lax gelatinous mucous membrane covering the broad alveolar margin of the jaws. When this membrane is stript off, the successional teeth and their matrices are brought away with it; their basis being inserted into its substance, just as the quills of the porcupine are attached to the skin. In the

exterior teeth, ossification extends along the ligamentous base of the matrix and they are thus fixed, as in the pharyngeal teeth of the barbel and many other fishes, by continuous anchylosis to the substance of the supporting bones; but it is peculiar to the Lophius to have this process arrested in certain teeth, which continue to be attached by elastic fibres instead of osseous piles, whereby the ordinary prehensile and destructive armature of the mouth is rendered still more effective by the additional mechanism of a spring-trap.

An exterior view of the maxillary teeth *in situ* is given by Mr. Yarrell, at p. 274, vol. 1, of his excellent work on British Fishes; I have figured a portion of the anterior part of the left premandibular bone and teeth, of the natural size, viewed from within, at Pl. 56, fig. 1; the second tooth of the inner row is represented as bent backwards, and the elastic ligaments at the inner side of the base are shortened and curved by the pressure; the dotted line shows the ordinary position to which the tooth is returned by the resiliency of the ligaments when the bending force is removed. Some of the shorter, inflexible exterior teeth are shown at *a a;* and the larger, moveable, inner teeth at *b b.*

The smaller species of Lophioids, forming the genera *Antennarius*, *Malthæa* and *Halieutæa*, have the teeth reduced to the rasp-like or villous character, and in the latter genus, which includes the *Lophius muricatus* of Shaw, the palatines and vomer are smooth and edentulous.

BLENNIOIDS.

61. The fishes of this family, like those of the preceding, have no common condition of the dental system. The Blennies (*Blennius*, Cuv.) present a close-set single row of long, fixed teeth, of which one is commonly more developed than the rest, and stands up, like a canine tooth, at the posterior extremity of each semi-circular series: there are no palatal or lingual teeth; those of the pharyngeal bones are similar to the maxillary teeth, but are moveable and disposed in two pectinated rows. In the *Blennechis ancylodon* the number of

elongated maxillary teeth is greater than in the true Blennies. In the *Chasmodes*, the teeth of the maxillary row, which extends along only the anterior part of the jaws, are of equal size. The maxillary teeth of the *Salarias*, with the exception of the single canine which terminates each end of the dental series of the lower jaw, are extremely thin and slender, and are hooked at the extremity; but they are chiefly remarkable in being attached, like the teeth of the Squaloids, to the gum only, or membrane covering the intermaxillary and pre-mandibular bones, so that they readily yield to pressure; there are about two hundred of these teeth in each jaw. The palatine and lingual bones are edentulous. In the genus *Clinus* there are always teeth on either the vomer or palatine bones, in addition to those supported by the jaws; the latter are of two kinds, an outer close-set row of longer pointed teeth, and behind these a band of villiform teeth. The *Myxodes* are devoid of palatal teeth; and have only a single row of teeth on the jaws, the largest being in the middle, and not at the ends of the row, as in the true *Blennies*. The butter-fish, (*Gonellus vulgaris*), has a row of conical, but rather blunt teeth on each jaw, and behind the middle of that of the upper jaw there is a second short row. There are some very small teeth in front of the vomer; the membrane covering the tongue and palatine bones is beset with firm papillæ, but the calcifying process has not converted them into teeth.

The viviparous Blenny, (*Zoarces*), has conical teeth arranged in two or three rows at the middle of the upper and lower jaws, and in a single row at their sides: the vomer, palatine, lingual and branchial bones are edentulous.

In the *Opistognathus*, the teeth are villiform and arranged on a narrow band in each jaw; the exterior ones are a little stronger and more separated than the rest. Of the other bones of the mouth, the pharyngeals alone have teeth, which are '*en cardes*.'

But the chief subject of interest to the anatomist in the present family of fishes is the singular and powerfully developed dental system of the Wolf-fish (*Anarrhichas Lupus*.) The general character and physiological relations of the teeth in this species had not escaped the attention of Hunter. In his paper on the Gillaroo trout

read before the Royal Society, in 1774,(1) he observes that the teeth of fishes which subsist chiefly on animal matter must vary according as their food may be common soft fish or shell-fish. "Such fish as live on the first kind have, like the carnivorous quadrupeds and birds, no apparatus for mastication, their teeth being intended merely for catching the food and fitting it to be swallowed. But the shells of the second kind of food render some degree of masticatory power necessary to fit it for its passage either into the stomach or through the intestines; and accordingly we find in certain fish a structure suited to the purpose. Thus the mouth of the wolf-fish is almost paved with teeth, by means of which it can break shells to pieces, and fit them for the œsophagus of the fish, and so effectually disengage the food from them, that though it lives upon such hard food, the stomach does not differ from that of other fish."

But in order to secure the capture of the shell-fish, the teeth of the wolf-fish are not all crushers; some present the laniary type, with the apices more or less recurved and blunted by use, and consist of strong cones spread abroad, like grappling hooks, at the anterior part of the mouth. A description of these teeth, illustrated with figures, is given by Mr. André in a volume of the Philosophical Transactions(2) subsequent to that in which they are noticed by Hunter; and a diminished view of the mouth of the Wolf-fish will be found in Mr. Yarrell's British Fishes.(3)

The oral dentigerous bones, viz: the intermaxillaries, premandibulars, palatines and vomer, are figured of their natural size, in their natural relative position and separately, in Plates 60 & 61 of the present work. The pharyngeal bones support much smaller conical and pointed teeth.

The intermaxillary teeth, (Pl. 60, fig. 1, and Pl. 61, fig. 2 *a a*) are all conical, and arranged in two rows; there are two, three or four in the exterior row, at the mesial half of the bone, which are the largest; and from six to eight much smaller teeth are irregularly arranged behind. There are three large, strong, diverging laniaries at the anterior end of each premandibular bone, (Pl. 61, fig. 1), and immediately behind these an irregular number of shorter and smaller

(1) Philos. Trans. vol. lxiv, p. 310. (2) Ib. vol. lxxiv, p. 274. (3) Vol. 1, p. 248.

conical teeth which gradually exchange this form for that of large obtuse tubercles ; these extend backwards, in a double alternate series, along a great part of the alveolar border of the bone, and are terminated by two or three smaller teeth in a single row, the last of which again presents the conical form. Each palatine bone, (Pl. 61, fig. 2, *b b*) supports a double row of teeth ; the outer ones being conical and straight, and from four to six in number ; the inner ones, two, three or four in number and tuberculate. I have seen a specimen where the inner row was wanting on one side. The lower surface of the vomer, *c*, is covered by a double irregularly alternate series of the same kind of large tuberculate crushing teeth as those at the middle of the premandibulars. All the teeth are anchylosed to more or less developed alveolar eminences, like the anterior teeth of the *Lophius*. The periphery of the expanded circular base of the large anterior grappling teeth is divided into processes indicative of the original ligamentous fasciculi at the base of the pulp by the ossification of which their anchylosis is effected.(1)

When such anchylosed teeth and the supporting bone are divided by a vertical section, as in Pl. 60, fig. 2, there may be generally discerned a faint transverse line indicating the original separation between the tooth and the bone, and more clearly defining the dental from the osseous structure than in the anchylosed teeth of other fishes. From the enormous development of the muscles of the jaws, and the strength of the shells of the whelks and other testacea which are cracked and crushed by the teeth, their fracture and displacement must obviously be no infrequent occurrence, and most specimens of the jaws of the wolf-fish exhibit some of the teeth either separated at this line of imperfect anchylosis, or, more rarely, broken off above the base, or, still more rarely, detached by fracture of the supporting osseous alveolar process.

Cuvier(2) describes the basal portion of the teeth themselves as osseous epiphyses, attached by a kind of suture to the jaw, and forming the medium by which the true teeth are fixed to

(1) Cuvier has given an accurate view of the plaited structure of the base of one of these teeth in Pl. 32, fig. 7, of his Leçons d'Anatomie Comparée, 1805, where it is described as the base of the osseous tubercle which supports the true tooth.

(2) Ib. tom. iii, p. 113.

the jaw. Retzius(1) has disproved at some length this supposed peculiarity in the mode of attachment of the teeth to the jaw; he observes that, ' at a short distance from the line of attachment of the teeth, there is a margin resembling an alveolar edge;' (it is clearly shown in Pl. 60, fig. 1, below the tuberculate teeth in the right premandibular bone): ' the portion of the jaw bone intervening between this margin and the teeth consists of a peculiar porous osseous substance,(2) and has on both sides small furrows corresponding with the interstices of the teeth, and giving to the basilar substance the appearance of being divided into as many processes as there are teeth:' this appearance is still more increased by the small openings, one at the end of each vertical furrow nearest the quasi-alveolar edge, which openings lead, according to Retzius, to cavities containing the germs of the successional teeth.

The dentigerous or alveolar processes of the jaw-bone are still more distinct at the anterior border of the premandibulars and intermaxillary bones, but these are not more developed in the wolf-fish than they are in the angler, the cod and other fishes with anchylosed teeth. The line of union of the tooth is situated at the summit of these processes; it is at this line that they are commonly detached; and not by a separation of the alveolar process from the rest of the jaw, either by interstitial absorption, analogous to that which causes the shedding of the antler of the deer, or by any other natural process.

In reference to the structure of the teeth of the wolf-fish Mr. André rightly observes " that they are formed of a hard bony matter not covered with enamel as in some animals," and Retzius confirms this statement in reference to the fully developed and fixed teeth; but he states that in the germs of the teeth contained in the alveoli of reserve there is a small portion of enamel, which in the conical teeth constituted the summit, and in the tubercular ones formed a white elevation, one third of a line in breadth, upon the centre of the flattened grinding surface. " It is no wonder," says Retzius, " that a fish which uses its teeth for bruising thick shells, as those of whelks,

(1) Müller's Archiv. 1837, p. 529.

(2) I find it however not to differ in texture from the remaining peripheral dense part of the jaw-bone, as shown in Pl. 60, fig. 2.

and cockles, lobsters, sea-urchins, &c., should soon wear off these small enamel points, which cannot therefore have much functional importance. These transitory summits, which are composed in reality of a fine tubular dentine, were supposed by Cuvier to be the true teeth, and to be peculiar to the young wolf-fish: he gives a figure of one of them in Pl. 32, fig. 6, *a*, of the Leçons d'Anatomie Comparée, vol. v, 1805.

The calcification of the dentinal pulp proceeds in nearly parallel lines from the summit to the base of the tooth; it is this peculiarity in the wolf-fish that occasions the solidity of the teeth, and the general straight course of the medullary tubes; most of these run parallel to each other and to the axis of the tooth; but the tubes nearest the sides of the tooth slightly diverge towards that surface. Tracing the medullary canals from the basis of the tooth, they divide dichotomously into finer and parallel branches, which form numerous reticular anastomoses together and terminate in fine loops at the periphery of the tooth. The medullary canals are occupied by processes of a vascular pulp; they were seen and described by both Cuvier and Von Born, who conceived them to be the channels of the nutrient vessels and nerves, and they were rightly compared by the latter anatomist to the similarly conspicuous tubes which traverse the teeth of the Orycterope; but the structure of both teeth is much more complicated than that of the horn of the rhinoceros, or of the baleen of the whale. The minuter or calcigerous tubes which traverse the firm substance occupying the interspaces of the medullary canals were not perceived in either case, by the above-cited anatomists; they are extremely minute in the Anarrhichas, and do not form by their parallel and straight course a distinct enamel-like outer layer, as in the pike, except at the apex of the recently formed teeth, but are confined to the fine and inextricable reticulate anastomoses at the periphery of the tooth as well as in the interspaces of the medullary canals.

GADOIDS.

62. The dental system maintains a greater uniformity in the Cod-tribe than in most of the other natural families of the class of

fishes. In every subgenus teeth are present on the intermaxillary, premandibular, vomerine, branchial and pharyngeal bones, but not on the hyoid or palatine bones; and in all, the teeth are simple, conical, and sharp-pointed; varying only in regard to size and degree of curvature.

They are distributed over a broad band upon the upper jaw, and over a narrower band along the lower jaw in the cod (*Morrhua vulgaris*), the haddock (*Mor. Merlangus*), the dorse (*Mor. callarias*), in which the exterior row is the largest in the upper teeth and the interior row in the lower ones. In the pout (*Morrhua lusca*), the ling (*Lota Molva*), and the whiting (*Merlangus vulgaris*), there is only a single row of long and large teeth in the premandibulars. The exterior row of larger intermaxillary teeth are more distinctly separated from the smaller posterior teeth of the same bones in the haddock, in order to receive in their interspace the points of the single row of premandibular teeth when the mouth is closed; but in the ling the upper teeth are numerous and of small size. In the hake (*Merlucius vulgaris*), there is a single row of slender and sharp teeth in both the upper and lower jaws. The tadpole-fish (*Raniceps trifurcata*), has two rows of sharp teeth in the premandibular bones, and numerous smaller, but not serial teeth in the intermaxillaries. In the coal-fish (*Merlangus carbonarius*), the torsk (*Brosmius vulgaris*), and the rock-ling (*Motella 5-cirrata*), the teeth are small and ranged in a band along both jaws. The vomerine teeth in all the cod tribe are usually arranged in a transverse crescent on the expanded anterior part of the bone.

All the teeth are less firmly attached to the bones in the Gadoids than in other osseous fishes with laniariform teeth. In the cod-fish the gelatinous conical pulp, after having formed the body of the tooth, is continued in an uncalcified state, but condensed into ligamentous firmness, from the base of the tooth to the alveolar margin of the jaw: ossification then proceeds from the jaw along the ligaments towards the base of the tooth, which, however, rarely become anchylosed to the ossified ligaments. The teeth, therefore, are generally detached in the course of macerating the head of the cod, and the broad alveolar margin of the dentigerous bones is then covered by the ossified dental ligaments

in the form of truncated cylinders of various sizes, the largest being most external in the intermaxillary and the reverse in the premandibular bones. A group of smaller but similarly shaped cylindrical processes for supporting the teeth are arranged in the form of a chevron across the anterior extremity of the vomer in the cod, after similar maceration. The branchial teeth are more firmly attached, being anchylosed in small groups upon the short obtuse processes of the branchial arches; there is a double series of these dentigerous tubercles along the concave margin of the second and third arches. The upper and lower pharyngeal bones are beset with small recurved laniary teeth, which are also more firmly fixed than those on the vomer and jaws.

Retzius compares the dentigerous processes of these bones to epiphyses, but I find that ossification is continued from the supporting bone into them, and have never observed them in a detached state, like the teeth themselves: he correctly describes their texture as being, in the ling, intermediate between that of the bone and tooth. In this species he describes the teeth as being "semi-transparent, with a covering of enamel upon the extreme points of such as are not too much worn. This little covering of enamel is disposed upon the tooth like the shoe of iron upon a spade, being continued from a transverse edge forwards and backwards, but being in some produced into a sharp point; the whiteness of the teeth is due to this substance."(1)

The pulp-cavity of the fully-formed tooth in the cod is continuous with the cavity of the supporting osseous cylinder to which it is attached; it varies in size according to the age of the tooth, and is, at length, reduced to a linear cavity extending along the middle of the axis of the tooth. Processes of the pulp are conveyed by medullary canals which diverge from all parts of the main central cavity into the substance of the dentine; these are about $\frac{1}{600}$th of an inch in diameter at their origin, but they quickly divide, and their branches form anastomoses with those of the neighbouring tubes; the loops, thus formed by the smaller terminal branches, constitute a well-defined boundary between the coarse central and the fine external dentine. In this latter layer the calcigerous tubes, which

(1) Loc. cit. p. 268.

are about $\frac{1}{15,000}$th of an inch in diameter, proceed, as usual, parallel to each other, and parallel to the axis of the tooth at its apex, but transversely to that axis at its sides.

The germs of the successive teeth are developed, as in the pike, in the mucous membrane covering the dentigerous surface of the jaws.

MURÆNOIDS.

63. The teeth in this predatory family of apodal fishes are generally sharp at the point and cutting at the edge; in the few species which have certain teeth approaching the molar type, these are always placed far back in the mouth, according to the usual law of the position of the teeth that give the final comminution to the food.

The teeth are numerous, of uniform shape and small size in the true eels (*Anguilla*): they are arranged in a narrow band along both jaws in the sharp-nosed eel (*Anguilla acutirostris*): the teeth are more numerous and form a broader band on the jaws in the broad-nosed eel (*Anguilla latirostris*) Pl. 56, fig. 3; the anterior part of the series in the upper jaw is formed by the vomerine teeth, Pl. 56, fig. 2. In the conger (*Conger vulgaris*, Cuv.) the teeth are relatively larger, especially at the anterior part of the vomer and maxillary bones; the larger teeth form a regular close-set row in each premandibular bone; the smaller teeth are almost concealed at their basal interspaces, except at the fore part of the bone, where they are larger and more numerous.

The dentition of the *Muræna* is generally of a more formidable character than that of the *Anguillæ*. Cuvier,(1) makes mention of their savage bite in allusion to the cruelty of *Vedius Pollio*, who is said to have caused his offending slaves to be cast into his fish ponds for the purpose of fattening the *Muræna*. The crime which brought this barbarity to light was the breaking of a crystal cyathus. The slave grasped the knees of Augustus who was the guest, in supplication. The Emperor heard his prayer that he might not be thrown to the fishes, discovered the horrid habit of the house, bade the slave rise up a freeman, ordered all the crystal vases to be broken,

(1) Règne Animal, vol. ii, p. 352.

and commanded that the abominable fish-ponds should be filled up.(1)

All Muræna have an external set of teeth, in one or more rows, on each side of the upper jaw, which may be termed 'maxillary,' as being opposed to corresponding series on the premandibular bones; and, in most species there is a median series of teeth in the upper jaw, supported by the vomer.

In the common Mediterranean species, (*Muræna Helena*, Linn.), Cuvier(2) describes the dentition as consisting of a single row of acute teeth on each jaw; and a short row upon the vomer, commencing by a single large tooth.

In the *Muræna anguiceps*, (Pl. 56, fig. 4), there is also a row of slender sharp-pointed teeth along the middle of the vomer in addition to the single series of similarly shaped maxillary and premandibular teeth. The anterior part of the external series in the upper jaw is supported by the expanded anterior extremity of the vomer: the first, fifth and tenth teeth of this row are much longer than the rest, and resemble canine teeth. The first two teeth of the median series are longer than the maxillary canines, and are situated one behind the other on the middle of the expanded part of the vomer: the rest of the series, which is confined to the narrow posterior part of the vomer, includes very small teeth. The anterior tooth on each premandibular bone is a long canine; the rest are short and recurved.

The *Muræna grisea* has two rows of acute teeth, on each side of the upper jaw, besides a single row on the vomer.

The lateral teeth are round and arranged in a single row in the *Muræna nebulosa*; the vomerine teeth are in two rows, and present a conical form at the anterior part of the bone.

In the *Muræna Zebra* the lateral teeth are also round, but in

(1) Quemadmodum, inquit, fecit Divus Augustus, quum cænaret apud Vedium Pollionem. Fregerat unus ex servis ejus crystallinum. Rapi eum Vedius jussit, nec vulgari quidem periturum morte, Murænis objici jubebatur, quas ingens piscina continebat.... "Evasit e manibus puer: nihil aliud petiturus, quam ut aliter periret, nec esca fieret. Motus est novitate crudelitatis Cæsar: et illum quidem mitti, crystallina autem omnia coram se frangi jussit, complerique piscinam." Seneca, de Ira, Lib. iii, c. 40.

(2) Leçons d'Anatomie Comparée, Ed. 1835, tom. iv, p. 330.

two rows on each side, while the vomerine teeth are in four rows. The teeth of the *Muræna Saga* are small and numerous, and may be said to be arranged 'en carde.'

In the skull of the *Muræna tigrina*, figured in Pl. 56, fig. 5, of which the jaws are upwards of four inches in length, they are armed with a pretty close-set row of strong conical teeth, *b*, with the base extended transversely and firmly anchylosed to the alveolar margin of the jaw, and the apex narrowed off to a pointed and somewhat trenchant edge set lengthwise; on the outside of this row there is an irregular series of small conical teeth, and in the inside a broader stripe of small granular teeth. At the extremity of the lower jaw two of the conical teeth are developed to a size much exceeding the rest; they are surrounded by smaller conical teeth which spread out like the prongs of a grappling-iron. These large terminal teeth of the lower jaw are opposed to four similar large, conical, sharp-pointed, divergent fangs on the expanded anterior extremity of the vomer. A longitudinal oval plate on the vomer supports twelve large and strong conical teeth, anchylosed by transversely extended bases; these teeth are arranged in alternate pairs in the middle of the group, but the rest form a single longitudinal row, decreasing in size as they are placed anteriorly. The whole dentition presents a most formidable armature for seizing and lacerating a resisting prey. The vomerine teeth are indicated by the letter *a*. In the great *Oxyrhynchus* the crowns of the teeth are sub-compressed laterally and have an anterior and posterior dentated edge.

LEPIDOSIREN.

64. At the extreme limit of the class of fishes, and connecting that class with the reptiles, stands the very remarkable genus of which the name is placed at the head of the present chapter, and the dental system is figured in Pl. 59. This consists of two small, slender, conical, sharp-pointed and slightly recurved teeth, which project downwards from the intermaxillary bone, and of strong trenchant dental plates anchylosed with the alveolar border of the

upper and lower jaws, in each of which the plate is divided at the middle or symphysial line so as to form two distinct lateral teeth.

The intermaxillary bone is represented by a single, horizontal, triangular plate, the base of which is attached by ligamentous union with the frontal and ascending process of the palatine bones, upon which it enjoys a slight vertical movement; the rounded apex forms the anterior extremity of the skull, and it is at the under surface of this part that the two laniariform teeth are attached by ligaments proceeding from their base, so as to admit of a yielding motion in every direction for a small extent, but most resisting inflection outwards. Their office is to pierce and retain the nutritive substance which is afterwards divided and comminuted by the strong maxillary dental plates.

The upper pair of these plates is supported by the anterior part of a strong arch of bone which combines the characters of the superior maxillary, palatine and pterygoid bones: the superior maxillary is represented by the external process which projects outwards and backwards and terminates in a free point on each side of the anterior part of the arch; the palatine portion constitutes the median and anterior part of the roof of the mouth; the pterygoid portion is indicated by its fulfilling the usual function of an abutment extended between the palatine portion of the upper jaw and the articular pedicle of the lower jaw: the upper dental plates are confined to the first two parts of the arch and do not extend upon the pterygoid portion; the lower dental plates are anchylosed to the premandibular bone. Viewing the upper pair of plates as a single tooth, it may be described as being indented at its outer surface by five vertical angular notches, penetrating inwards through half the breadth of the supporting bone, and dividing the plate into six angular processes, which, from the direction and varying form and breadth of the entering notches, radiate from the posterior part of the median line or division of the tooth (Pl. 59, fig. 3). The inferior dental plate is similarly notched on its outer side, but the proportions of the angular indentations are such that they receive the processes of the upper dental plate when the mouth is shut; thus the median notch is wider than the two adjoining ones in the lower

dental plate, but is narrower in the upper one. The figures 1, 2 and 3, Pl. 59, which give respectively a side view, front view and the working surfaces of the teeth of the Lepidosiren, will convey a truer idea than can be given by words, of the form of the maxillary dental plates. The two anterior lobes or divisions of both upper and lower dental plates are the most produced in the vertical direction, and their anterior angle is pointed and adapted for piercing. The posterior divisions are most extended in breadth and least in height, and terminate in a sharp trenchant edge; the middle lobes present an intermediate structure.

These teeth, in their paucity, large relative size, and mode of adaptation to the jaws, resemble the dental plates of the Chimæroid and some of the extinct Hybodont cartilaginous fishes, as *Cochliodus* and *Ceratodus* Ag.; but they are unlike these in microscopic structure; approaching in this respect, as will be presently shown, nearer to the teeth of many osseous fishes. The maxillary armour of the Lepidosiren surpasses any known dental apparatus in the class of fishes in the modification of the working surface, by which a single tooth is at once adapted for piercing, cutting and crushing the alimentary substances. The strength of the jaws of the Lepidosiren and the bulk of the muscles which work them are proportionate to the size and nature of the maxillary dental plates.

In Pl. 59, fig. 4, is given a reduced representation of a magnified view of a vertical section of a lobe of the lower dental plate of the Lepidosiren. It consists, as in the cod and sphyræna, of a central mass of coarse osseous substance, traversed by large and nearly parallel medullary canals, and an external sheath of very hard enamel-like dentine. The medullary canals are continued from a coarse reticulation of similar, but wider canals, in the substance of the supporting bone, and advance forwards, nearly parallel with each other, and with the plane of the upper surface of the tooth; they anastomose together by short, curved, transverse canals, which intercept spaces increasing in length as the canals recede from the osseous basis. The canals themselves diminish in size in the same ratio, and when they have arrived near the dense outer layer, their divisions and inosculations become again more frequent, the peripheral loops form-

ing a well marked line of demarcation between the coarse-tubed and the fine-tubed dentine. The interspaces of the medullary canals are occupied by a clear substance and by moss-like reticulations of fine calcigerous tubes, which appear to be more sparing in number than in the teeth of the sphyræna or shark. The calcigerous tubes of the external dentine run nearly parallel to each other, and vertically to the external surface of the dental plate through about two thirds of the thickness of the external hard substance; they then bend and cross each other in a manner very similar to those of the external layer of dentine in the teeth of the Lepidotus, Phyllodus, &c.

In the process of attrition this external dense substance is worn away from the upper surface of the dental processes in the lower jaw, exposing the softer osseous, or medullary substance of the tooth; in this state the dental plate offers an analogy to the incisors of the rodents, a posterior softer substance being sheathed by an anterior, denser layer; and an external sharp edge is similarly kept up by the unequal wearing away of the two substances. The progressive waste at the upper surface of the dental plate would appear to be met by a corresponding addition of new material to its lower part.

In the structure here presented to our observation we have a condition of the dentine which has hitherto been met with only in the class of fishes; and the form, the extent, and the continuity of the dental armature excepted, this part of the Lepidosiren closely corresponds with that particular modification of the dental structure which we have seen to be most eminently characteristic of the class of fishes. The Sauroid character, for example, which as in the Lepidosteus, pervades the air-breathing organs, and which, as in the Polypterus, is traceable in the intestinal canal of the Lepidosiren, is not at all manifested by the dental system: and neither in the modified bone which forms the basis of the tooth, nor in that coarser bone of which the jaw is composed, is there the slightest trace of radiated cells or corpuscules; the other parts of the skeleton exhibit a similar ichthyic condition.

The test of the affinities of the present paradoxical genus, afforded by the microscopic examination of the teeth, gives additional confirmation to the views which I have already maintained from argu-

ments drawn from the rest of its organization,(1) that the Lepidosiren is in every essential point a member of the class of fishes.

SAURICHTHYS.

65. I terminate the description of the dental system of fishes with an account of the microscopic structure of the teeth of two extinct species of different genera, indicated as yet only by these detached organs, and respecting which, doubts have been entertained as to whether they be actually referable to the class of fishes or of reptiles.

To these doubts, however, in regard to the first genus, *Saurichthys*,(2) the microscopic test satisfactorily puts an end; but with respect to the other genus, *Dendrodus*, the modification of the dental tissue approaches so closely to a new and singular condition which will be shown to characterize the structure of the teeth of an extinct family of Batrachian reptiles, that I hesitate in absolutely pronouncing it to be that of a fish.

The teeth of the Saurichthys characterize the Bristol bone-bed and the German Muschelkalk; they are conical, rather slender, with a subelliptical transverse section, slightly bent, with the apex not very acute: about one fifth of the tooth next the apex is smooth and polished, the remainder of the outer surface is traversed by fine close-set longitudinal ridges: thus, to all outward appearance the tooth very closely resembles the form most common among Saurians.

The specimen here described, from the Bristol bone-bed, is seven lines in length, and two broad at the base. I have investigated its structure by a transverse section through its base, and by a longitudinal section through the middle of the remaining part.

This tooth is traversed by a slender, straight, longitudinal, conical, central pulp-cavity, occupied by a coarse cellular bone, and from which radiates a system of close-set, slightly and minutely undulating calcigerous tubes, covered by a thick layer of the enamel-like dense tissue, which coats the teeth in the Lepidotus,

(1) Linnæan Transactions, vol. 18, 1839. p. 350.

(2) The term *Saurichthys* (σαῦρος a lizard, ἰχθὺς a fish) was applied by M. Agassiz to the present genus, to express its transitional characters, but it is nevertheless regarded by that distinguished Palæontologist, as being essentially a member of the class of fishes.

Sparus, and many other fishes. The central linear pulp-cavity extends, as also in the conical teeth of many fishes, to the extreme apex of the dentine: the cells of the ossified pulp were occupied by an opaque substance in the tooth examined: at its periphery and through the whole of the base of the tooth were scattered numerous coarse cells. The true dentine presented a mahogany brown colour: the main calcigerous tubes of this substance radiate through it at right angles to the periphery of the tooth, and with a slight curvature, the concavity of which is turned towards the apex of the tooth. The tubes give off many small lateral branches, which are curved, with their concavity directed towards the pulp-cavity, or to the base of the stem: they diminish in size as they approach the external enamel-like substance, pass across the well-defined boundary which separates this substance from the dentine, and then are immediately resolved into fasciculi of the extremely fine and slightly diverging fibres or minute tubes which form the only appreciable structure in this enamel-like substance. These fine lines have a general direction at right angles to the periphery of the tooth, like that of the calcigerous tubes of the dentine, from which they are continued; but many of them are bent in different directions, so as to cross each other, in the manner described and figured in the corresponding clear external enamel-like substance of the tooth of the Lepidotus; they are, however, somewhat larger and diverge in straighter lines; they finally terminate in fine calcigerous cells at the periphery of the tooth.

The thickness and structure of the dense external enamel-like layer, the length and form of the pulp-cavity, and the texture of the ossified remains of the pulp with which it was filled, are decisive against the reptilian character of the Saurichthys. Its affinities to that class are manifested only in the outward form of the tooth, and the dense, minutely-tubed tissue of the dentine, a structure, however, which is common to the teeth of all the Sauroid fishes.

DENDRODUS.

66. *Dendrodus biporcatus*.—The teeth indicative of the genus, for which I have proposed the name of *Dendrodus*(1), occur sparingly and detached in

(1) δένδρον a tree, ὀδους a tooth; in reference to its internal dendritic structure.

the central or corn-stone division of the Old Red Sandstone. The three specimens here described are from Scat-crag, near Elgin. The largest of these is represented of the natural size at Pl. 62 A, fig. 1. It is conical, subcompressed, subincurved, with a round obtuse summit (*a*), and a sub-circular base, the margin of which, in the specimen, was rounded off or bent in, and the surface of the base was slightly depressed in the centre, and rough as if it had been detached from an anchylosed union with a shallow alveolar depression. On each side of the tooth, a little nearer the convex than the concave surface, there is a well marked longitudinal ridge, which gradually subsides a little below the summit. The position of these two ridges, and the degree of compression of the tooth at its middle part, are shown in the outline of the transverse section of the tooth by the side of the figure. The smooth surface of the tooth is traversed by very fine longitudinal linear impressions extending from the base to within one fourth of the rounded apex.

A transverse section taken one line above the base of this tooth, exhibited a dark irregularly dotted central part, and a lighter peripheral structure: it is represented at Pl. 62 B, fig. 1. A portion of the same section corresponding with that intercepted by the two lines in fig. 1, as viewed by transmitted light with a magnifying power of fifty linear dimensions, is represented on a reduced scale at fig. 2.

Thus magnified, a central pulp-cavity of relatively small size and of an irregular lobulated form is discerned, a portion of which is shown at *a*; this is immediately surrounded by the transverse sections of large cylindrical medullary or pulp-canals of different sizes; and, beyond these, there are smaller and more numerous medullary canals, which are processes of the central pulp-cavity. In the transverse section these processes are seen to be connected together by a net-work of smaller medullary canals belonging to a coarse osseous texture into which the pulp has been converted, and this structure occupies the middle half of the section. All the medullary canals were filled by the opaque matrix. From the circumference of the central net-work, straight medullary canals radiate at pretty regular intervals to the periphery of the tooth; most of these canals divide once, rarely twice, in their course; the division taking place sometimes at their

origin, in others at different distances from their termination, and the branches diverge slightly as they proceed. Each of the above medullary rays is continued from a short process of the central structure, which is connected by a concave line with the adjoining process, so that the whole periphery of the transverse section of the central coarse reticulo-medullary body of the tooth presents a crenate outline. From each ray and its primary dichotomous divisions, short branches are sent off at brief intervals, generally at right angles with the trunk, or slightly inclined towards the periphery of the tooth. These subdivide into a few short ramifications like the branches of a shrub, and terminate in irregular and somewhat angular dilatations, simulating leaves, but which resolve themselves into radiating fasciculi of calcigerous tubes. There are from fifteen to twenty-five or thirty-six of these short and small lateral branches on each side of the medullary rays.

In a section of the same tooth, one third from its obtuse summit (Pl. 62 B, fig. 3), the irregular central pulp-cavity was lost, and in its place there were a few large medullary canals connected by a fine network of smaller canals. This tissue occupied rather more than one third of the diameter of the section. From its periphery there was continued the same system of nearly straight, sparingly dichotomizing, medullary canals, radiating at regular distances from the central tissue to the periphery of the tooth. The radiating canals here also give off short lateral branches, but these do not terminate in such well marked dilatations as those observable at the base of the tooth: the transverse branches here generally spring from short alternate lateral bendings of the main stem. There are about forty radiating medullary canals in this part of the tooth, and about fifty in the section taken from the base of the tooth.

In both sections the angular dilated terminations of the small lateral branches of the medullary rays form, as has been said, the centres of radiation of as many systems of the most minute calcigerous tubes, each system constituting a lobe of the dentine, separated from the adjoining lobes by an extremely thin layer of cement. In the section nearer the apex of the tooth, the radiating systems of calcigerous tubes, forming similar lobes of dentine are given off

more frequently from the sides of the lateral branches, than from their terminal dilatations.

The peripheral extremities, also, of the medullary rays, and of such of their subdivisions or branches as are nearest to and directed towards the margin of the section, and consequently to the periphery of the tooth, are resolved into fasciculi of calcigerous tubes, which diverge in graceful curves from their point of origin: two of these peripheral lobes are figured at Pl. 62 B, fig. 4. The middle tubes are continued from the interspace of the diverging ones to the periphery of the tooth in a line parallel with that of the main medullary canal (*a*), which radiates from the central reticulation: the lateral tubes gradually diverge more and more from this line, and those which proceed from the sides of the extremity of the medullary canal run at right angles to its course. The lateral tubes terminate, together with those of the adjoining medullary canal, in a linear series of calcigerous cells; which line is continued inwards from the periphery of the tooth, like a process of the external capsule, inclosing and defining, as it were, each of these terminal square lobes or systems of calcigerous tubes. There is a slight indentation of the periphery of the transverse section at the line of the above described inflection of the cellular structure; and this indentation (*b*) is a section of one of the fine superficial longitudinal striæ already mentioned. The inflected line of minute cells may be traced, in most parts of both sections, to near the central reticulate system of medullary canals, sending off branches on each side, which bound in a similar manner the different lobes of dentine, or systems of radiated calcigerous tubes which are given off from the sides of the straight medullary canals. The external longitudinal fine grooves on the superficies of the tooth indicate, as above stated, the entering lines of the fine cellular cement, or the interspaces of the lobes of the dentine appended to the medullary canals which radiate from the central pulp-cavity or net-work.

The medullary rays, though for the convenience of description they have been termed canals—as they appear to be in the transverse section of the tooth, yet are not cylindrical tubes. For it must be obvious from the similarity of the structure of the two sections here described from nearly the two opposite extremities of the tooth, that

the radiating lines described as medullary canals are, more probably, sections of vertical fissures, or lamelliform processes of the pulp, radiating from the central body of the pulp to the periphery of the tooth, and co-equal with the longitudinal extent of the tooth; but decreasing in number as the tooth contracts towards its apex.

The species to which the tooth, exhibiting the beautiful and complicated structure just described, belonged, may be indicated by the name of *Dendrodus biporcatus*, in reference to the two opposite ridges by which the tooth is characterized.

Dendrodus strigatus.—A second and smaller tooth from the same formation and locality, differs from the preceding in its more elongated and slender conical form, with a nearly circular transverse section; it also differs in the absence of the two longitudinal ridges and in the presence of broader,deeper, and closer longitudinal impressions separated by intervening convex ridges. As those characters strongly indicate a specific difference in the animal to which it belonged, it may be convenient to attach to this tooth the name of *Dendrodus strigatus:* its microscopic structure, as shown by a fine transverse section, proves it to be generically allied to the *Dendrodus biporcatus.*

In the *Dendrodus strigatus* the central system of reticulate medullary canals occupies a larger proportion of the mass of the tooth. The radiated canals or processes of the pulp are shorter and more branched: the systems of calcigerous tubes which diverge from the numerous processes and branches are separated from each other by a fine and clear line, and terminate in a broader band of calcigerous cells. The appearances which the structure of the tooth thus presents in the transverse section, somewhat resemble those of the tooth of a Myliobates; but the lobes or systems of calcigerous tubes are less regular in form and size.

Dendrodus hastatus.—The third tooth presents a more compressed conical figure than the two preceding, and the opposite ridges which characterized the *Dendrodus biporcatus* here form, as it were, the margins of two cutting surfaces, and the opposite ends of the flattened elliptical transverse section of the tooth. The length of this tooth is eight lines, the longest diameter of its base three lines; the shortest diameter two lines. The tooth diminishes regularly from

its base to its sub-acute apex. The surface of the tooth is much smoother than in the *Dendrodus strigatus*. I took a transverse section from the base of this tooth, and finding the same essential radiated disposition and dendritic ramifications of the medullary canals, I made a longitudinal section of the rest of the tooth.

In this section eight principal medullary tubes were seen ; the four largest and closest together were situated in the centre; the others diminishing as they approached the side. The central canals run parallel to each other and to the axis of the tooth along the basal half; the two middle canals so continuing to the apex. The small lateral tubes bend outwards to the side of the tooth ; the third on each side sends off one or two primary branches in the same oblique direction and also finally terminates by bending towards the margin of the tooth. The primary divisions of the large medullary tubes run parallel, or nearly so, to the trunks, but begin slightly to diverge as they approach the apex. The primary divisions of the small lateral tubes are given off at different, but always acute angles. The smaller or secondary branches are given off frequently at right angles, and those from the primary branches sometimes retrograde to the main tubes. The plan of branching of the whole system of medullary canals which pervades the entire substance of the tooth is strikingly similar to that of certain forest trees, as the elm, but with the characteristic difference, which distinguishes in this, as in most other cases, the branching of an animal from a vegetable structure, namely, that the terminal branches anastomose, forming a coarse but elegant net-work, occupying with considerable regularity the whole of the interspaces of the longitudinal medullary tubes.

A transverse section of this tooth exhibits three-fourths of its central part occupied by a reticulo-medullary structure; and the peripheral portion traversed by medullary rays. In the central structure are seen the areæ of numerous, nearly equal sized and equi-distant medullary canals, around which the dentine is disposed in well-marked concentric layers, and from which the calcigerous tubes radiate as in the Myliobate and Orycterope; but these tubes are relatively fewer and less parallel in their course, and form more decided reticulations in that course. The shape of each component

denticle, thus seen in transverse section, is more rounded and less regular than in either of the two above-cited instances. The cellular cement which separates each denticle is relatively thicker. The diameter of the central medullary canal is generally equal to two thirds the diameter of the laminated and tubular wall of the denticle, of which it forms the axis. In the peripheral structure, the radiated trunks are shorter in comparison with the central cellular part than in the preceding species. They are relatively wider apart from each other, are less parallel in their course, their primary divisions diverge at a more open angle, and their lateral branches are longer.

The branches of the radiating canals, after dichotomising, are resolved at their extremities into radiated systems of calcigerous tubes terminating in a thin stratum of calcigerous cells. This stratum forms the boundary of each system and thus describes an undulating line on each side of the radiated canals, which is very similar to the anfractuous inflected layer of the external cement in the Labyrinthodon. In the transverse section of the *Dendrodus hastatus* the calcigerous tubes seem to form, towards their extremities, a fine net-work with open meshes, and to be fewer and at a greater relative distance from each other than in the first described species.

It is obvious that the plan of structure, as exhibited in the longitudinal section of the tooth of the Dendrodus, bears considerable analogy to that in the shark, and Scomberoid fishes, as the Sphyræna, Dictyodus, &c.; but one cannot fail to recognize a greater amount of parallelism in the medullary tubes in the Dendrodus, and the systems of calcigerous tubes which diverge from the medullary canals still more strikingly exhibit the difference which depends upon their straighter and more parallel course, and which indicates the higher type of structure in the teeth of the Dendrodus. These tubes, in fact, instead of forming the inextricable moss-like reticulations, which occupy the median interspaces of the medullary canals in the Shark and Sphyræna, here run at right angles to the sides of the tube from which they are continued, and parallel to each other, as far as the middle of the interspace; there they meet the extremities of the opposite series of calcigerous tubes and are lost in minute cells. The differences above manifested in the dental structure of the

extinct Dendrodus, as compared with that hitherto known to characterize true fishes, is strikingly manifested both in the extent and regularity of the radiating medullary processes, and more especially in the straight course of the fine and close-set calcigerous tubes which form the intervening dentine. Nevertheless I should most probably have referred these teeth without hesitation to the class of Fishes, if so close an analogy had not been traceable between their singular dental structure, and that still more remarkable modification which will be shown to characterize the extinct Batrachian genus *Labyrinthodon*.

If, however, as seems most probable, the Dendrodus be a true fish, we may speculate, from the similarity alluded to, upon its having approached in its general organization, like the Lepidosiren, most closely to the lower confines of the reptilian class: and as this existing annectent genus is allied to the perennibranchiate Batrachians, so the Dendrodus may have linked some extinct group of the class of Fishes with the equally extinct family of Sauroid Batrachians which we have termed Labyrinthodonts.

PART II.

DENTAL SYSTEM OF REPTILES.

CHAPTER I.

GENERAL CHARACTERS OF THE TEETH OF REPTILES.

67. Teeth, properly so called, do not exist in all reptiles; they are absent in the whole order of *Chelonia*, in the *Coluber scaber*(1) among the *Ophidia*, and in the toads among the *Batrachia*. In the latter edentulous reptiles there is no compensating structure; but in the *Coluber scaber*, the inferior spinous processes of certain of the cervical vertebræ are unusually prolonged, and penetrate the coats of the œsophagus; their extremities, which are thus introduced into the alimentary canal, are coated with a layer of hard dentine, and form substitutes for the teeth, which, if not always entirely absent, are merely rudimental in the ordinary situations in the mouth.(2)

In the tortoises and turtles the jaws are covered, as is well known, by a sheath of horn, which in some species is of considerable thickness and very dense; its working surface is trenchant in the carnivorous species, but variously sculptured and adapted for both cutting and bruising in the vegetable feeders.

The development of the continuous horny maxillary sheath commences, as in the parrot-tribe, from a series of distinct papillæ, which sink into alveolar cavities, regularly arranged (in *Trionyx*) along the margins of the upper and lower jaw-bones: these alveoli are indicated by the persistence of vascular canals long after the originally separate tooth-like cones have become confluent and the horny sheath completed.

The teeth of the dentigerous Saurian, Ophidian and Batrachian reptiles, are, for the most part simple and adapted for seizing and

(1) Hence called *Anodon typus* by Dr. Smith.

(2) Dr. Jourdan, in Cuvier, Leçons d'Anatomie Comparée, Ed. 1835, tom. 1, p 340, tom. 4, p. 617.

holding, but not for dividing or masticating their food. The Siren alone combines true teeth with a horny maxillary trenchant sheath like that of the Chelonian reptiles.

68. *Number.*—In no reptile are the teeth reduced to so small a number as in certain mammals and fishes, nor are they ever so numerous as in many of the latter class. Some species of Monitor (*Varanus*) with sixteen teeth in the upper and fourteen in the lower jaw, afford examples of the smallest number in the present class, and certain Batrachians, with teeth 'en cardes' at the roof of the mouth, or which have upwards of eighty teeth in each lateral maxillary series, present the largest number. It is rarely that the number of teeth is fixed and determinate in any reptile so as to be characteristic of the species.

69. *Situation.*—The teeth may be present on the jaws only, as in the Crocodiles and many Lizards; or upon the jaws, and roof of the mouth, and here either upon the pterygoid bones as in the Iguana and Mosasaur, or upon both palatine and pterygoid bones as in most serpents, or upon the vomer as in most Batrachia, or upon both vomerine and pterygoid bones, as in the Axolotl, or upon the vomerine and sphenoid bones, as in the *Salamandra glutinosa*, Maclure. With respect to the marginal or jaw-teeth, these may be absent in the intermaxillary bones, as in many serpents; or they may be present in the upper and not on the lower jaw, as in most frogs; or in both upper and lower jaws, as in the tailed Batrachians; and among these they may be supported, upon the lower jaw, by the premandibular or dentary piece as in the Salamanders, Menopome, Amphiume, Proteus; or upon the opercular piece, as in the Siren; or upon both opercular and premandibular bones as in the Axolotl. The palatine and pterygoid teeth may, in the Batrachians, be arranged in several rows, like the 'dents en cardes' of fishes: the sphenoid and opercular teeth are always so arranged in the few species that possess them; the intermaxillary, maxillary and premandibular teeth are serial or in one row, with the exception of the Cæcilia and the extinct Labyrinthodon, which have a double row of teeth at the anterior part of the lower jaw.

70. *Form.*—The teeth of reptiles, with few exceptions, present a

simple conical form, with the crown more or less curved, and the apex more or less acute. The cone varies in length and thickness: its transverse section is sometimes circular, but more commonly elliptical or oval, and this modification of the cone may be traced through every gradation, from the thick round tooth of the Crocodile (Pl. 62 A, fig. 9) to the sabre-shaped fang of the Varanus, the Megalosaur (ib. fig. 6) and the Cladeiodon (ib. fig. 4). Sometimes, as in the fully-formed teeth of the Megalosaur, one of the margins of the compressed crown of the tooth is trenchant, sometimes both are so; and these may be simply sharp-edged, as in the Varanus of Timor or finely serrated, as in the great Varanus (Pl. 68, fig. 3.), the Megalosaur and the Cladeiodon.

The outer surface of the crown of the tooth is usually smooth; it may be polished, as in the Leiodon (Pl. 72, fig. 1), or impressed with fine lines, as in the Labyrinthodon (Pl. 63, 1), or raised into many narrow ridges as in the Pleiosaur and Polyptychodon (Pl. 72, figs. 3 and 4), or broken by a few broad ridges as in the Iguanodon (Pl. 70, fig. 1), or by a single longitudinal furrow, as in some serpents.

The cone is longest and its apex sharpest in the Serpents; from these may be traced, chiefly in the lizard tribe, a progressive shortening, expansion of the base and blunting of the summit, of the tooth, until the cone is reduced to a hemispherical tubercle, or plate, as in the Thorictes (Pl. 66, fig. 6) and Cyclodus (ib. fig. 7).

In the Pleiosaur, (Pl. 68, fig. 5), the dental cone is three sided, with one of the angles rounded off. The posterior subcompressed teeth of the alligator present a new modification of form; here they terminate in a mammilloid summit, supported by a slightly constricted neck (Pl. 75, fig. 3). In the tooth of the Hylæosaur (Pl. 62 A, fig. 8.) the expanded summit is flattened, bent, and spear-shaped, with the edges blunted. But the expansion of the crown is greatest in the subcompressed teeth of the Iguanas (Pl. 70, figs. 6 and 7 and Pl. 66, fig. 5), which are further complicated by having the margins notched. The extinct Iguanodon has the crown of the tooth expanded both in length and breadth, and combining marginal dentations with longitudinal ridges, presents the most complicated external

form as yet discovered in the class of reptiles. In no reptile does the base of the tooth ever branch into fangs.

71. *Attachment.*—As a general rule, the teeth of reptiles are anchylosed to the bone which supports them. When they continue distinct, they may be lodged either in a continuous groove, as in the Ichthyosaur, or in separate sockets, as in the Plesiosaur and Crocodilians. The base of the tooth is anchylosed to the walls of a moderately deep socket in the extinct Megalosaur and Thecodon. In the Labyrinthodons and Cæciliæ among the Batrachians; in most Ophidians; and in the Geckos, Agamians, and Varanians, the base of the tooth is imbedded in a shallow socket and confluent therewith(1). In the Scincoidians, Safe-guards (*Tejus*), in most Iguanians, in the Chameleons and most other Lacertian reptiles, the tooth is anchylosed by an oblique surface extending from the base more or less upon the outer side of the crown to an external alveolar plate of bone, as shown in Plate 67; the inner alveolar plate not being developed. In the frogs, the teeth are similarly but less firmly attached to an external parapet of bone. The lizards which have their teeth thus attached to the side of the jaw are termed 'Pleurodonts.' In a few Iguanians, as the Istiures, the teeth appear to be soldered to the margins of the jaws, these have been termed 'Acrodonts.' In some extinct Lacertians, as the Mosasaur and Leiodon, the tooth is fixed upon a raised conical process of bone, as shown in Plate 68, fig. 1 and Plate 72, fig. 2.

These modifications of the mode of attachment of the teeth of reptiles are closely adapted to the destined application of those instruments and to the habits of the species; we may likewise perceive that they offer a close analogy to some of the transitory conditions of the human teeth. There is a period, for example,(2) when the primitive dental papillæ are not defended by either an outer or an inner alveolar process, any more than their gigantic calcified analogues in the extinct Mosasaur. There is another stage(3) in which the groove

(1) Pl. 63 A, fig. 8. *a a*, sockets of the anchylosed teeth in *Varanus varius*.

(2) At the sixth month, see Mr. Goodsir, On the development of the Human Teeth.—Edinburgh Medical and Surgical Journal, No. 138.

(3) At the seventh or eighth week.—Ibid.

containing the dental germs is defended by a single external cartilaginous alveolar ridge: this condition is permanently typified in most existing lizards. Next there is developed an internal alveolar plate, and the sacs and pulps of the teeth sink into a deep but continuous groove, in which traces of transverse partitions soon make their appearance: in the ancient Ichthyosaur the relation of the jaws to the teeth never advanced beyond this stage. Finally, the dental groove is divided by complete partitions,(1) and a separate socket is formed for each tooth, and this stage of development is attained in the highest organized reptiles, as in the crocodile.

72. *Substance.*—This may be four-fold, and a single tooth may be composed of dentine, cement, enamel and bone; but the dentine and cement are present in the teeth of all reptiles.

In the Batrachian and Ophidian reptiles a thin layer of cement invests the central body of dentine, and as usual, follows any inflections or sinuosities that may characterise the dentine. Besides the outer coat of cement, which is thickest at the base of the teeth, a generally thin coat of enamel defends the crown of the tooth in most Saurians, and the last remains of the pulp are not unfrequently converted into a coarse bone, both in the teeth which are anchylosed to the jaw, and in some teeth, as those of the Ichthyosaur, which remain free. The only modification of the dentine, which could at all entitle it to be regarded in the light of a new or distinct substance, is that which is peculiar, in the present class, to the teeth of the Iguanodon, and which will be described in the following section.

73. *Structure.*—The varieties of dental structure are few in the reptiles as compared with either fishes or mammals, and its most complicated condition arises from the interblending of the dentinal and other substances rather than from modifications of the tissues themselves. In the teeth of most reptiles the intimate structure of the dentine corresponds with that which has been described as its fourth type or modification in the teeth of fishes, and which is the prevailing structure of mammalian dentine, viz: the radiation of a system of minute calcigerous tubes from a single pulp-cavity, at right angles to the external surface of the tooth. The most essential modification of this structure

(1) At the sixth month.—Edinburgh Medical and Surgical Journal, No. 138.

is the intermingling of cylindrical processes of the pulp cavity, in the form of medullary canals, with the finer tubular structure.(1) Another modification is that in which the dentine maintains its normal structure, but is folded inwardly upon itself, so as to produce a deep longitudinal indentation on one side of the tooth: it is the expansion of the bottom of such a longitudinal deep fold that forms the central canal of the venom-fang of the serpent; but a glance at Pl. 65 A, will show that, notwithstanding the singularly modified disposition of the dentine (*b*), its structure remains unaltered: and although the pulp-cavity (*a*) is reduced to the form of a crescentic fissure, the calcigerous tubes continue to radiate from it, according to the usual law. By a similar inflection of many vertical longitudinal folds of the external cement and external surface of the tooth, at regular intervals, around the entire circumference of the tooth, and by a corresponding extension of radiated processes of the pulp-cavity and dentine into the interspaces of such inflected and converging folds, a modification of dental structure is established in certain extinct reptiles, which, by the various sinuosities of the interblended folds of cement and processes of dentine, with the partial dilatations of the radiated pulp-cavity, produces the most complicated structure that has yet been met with in the teeth of any animal, (Pl. 64 A). But this complication is nevertheless referable to a modification of form or arrangement rather than of structure of the dental tissues: the calcigerous tubes in each sinuous lobe of dentine, in the most complex tooth of the Labyrinthodon, exhibit the same general disposition and course as in the fang of the Serpent and in the still more simple tooth of the Saurian.

In the Iguanodon (Pl. 71) the fine-tubed dentine is traversed by medullary canals which run at pretty definite intervals through the dentine, parallel with the calcigerous tubes, as in that coarser kind of dentine which characterizes the teeth of the sloth and megatherium, and which, in connection with the complex form of the teeth of the Iguanodon, peculiarly adapted that gigantic reptile for a vegetable diet.

The cement is simply and minutely cellular upon the crown of the tooth, but it exhibits the radiated cells at the base of the tooth in the anourous Batrachians, and Saurians. The enamel is subtransparent,

(1) Transactions of the British Association, 1838, p. 144.

dense, and minutely fibrous in all the reptiles which have their teeth defended by this substance.

74. *Development.*—The teeth of reptiles are never completed, as in certain fishes, at the first or papillary stage; but the pulp sinks into a follicle, and becomes inclosed by a capsule: the process of development, however, never offers the eruptive stage, in the sense in which this is usually understood, as signifying the extrication of the young tooth from a closed alveolus.

The completion of a tooth is soon followed by preparation for its removal and succession: the faculty of developing new tooth-germs seems to be unlimited in the present class, and the phenomena of dental decadence and replacement are manifested at every period of life: the number of teeth is generally the same in each successive series, and the difference of size presented by the teeth of different and distant series is considerable.

The new germ is always developed, in the first instance, at the side of the base of the old tooth, never in the cavity of the base; the crocodiles form no exception to this rule. The poison-fangs of serpents succeed each other from behind forwards; in almost every other instance, the germ of the successional tooth is developed at the inner side of the base of its predecessor. In the frog, the dental germ makes its appearance in the form of a papilla developed from the bottom and towards the outer side of a small fissure in the mucous membrane or gum that fills up the shallow groove at the inner side of the alveolar parapet and its adherent teeth: the papilla is soon enveloped by a capsular process of the surrounding membrane: there is a small enamel pulp developed from the capsule opposite the apex of the tooth; the deposition of the earthy salts in this mould is accompanied by ossification of the capsule, which afterwards proceeds *pari passu* with the calcification of the dentinal papilla or pulp: so that, with the exception of its base, the surface of the uncalcified part of the pulp alone remains normally unadherent to the capsule.

As the tooth acquires hardness and size it presses against the base of the contiguous attached tooth, causes a progressive absorption of that part, and finally undermines, displaces and replaces its predecessor. The number of nascent matrices of the successional teeth is so great in the frog, and they are crowded so close together, that it

is not unusual to find the capsules of contiguous tooth-germs becoming adherent together as their ossification proceeds. After a brief maceration the soft gum may be stripped from the shallow alveolar depression and the younger tooth-germs in different stages of growth are brought away with it.

The mode of development of the teeth of serpents does not differ essentially from that of the teeth of the Batrachian above described, except in the relation of the papillæ of the successional poison-fangs to the branch of the poison duct that traverses the cavity of the loose mucous gum in which they are developed.

The situation in which the successional teeth are developed in the Varanus is shown in Pl. 63 A, fig. 9: their relative position to, and the mode in which they affect, the adherent teeth, by pressing upon the inner side of their bases, is shown in the upper and lower jaws of the Cyclodus (Plate 66, fig. 7 *b*): the phenomena of dental development in these and other lizards closely correspond with those described in the frog. In the Acrodont lizards, and those in which the teeth are anchylosed to the summits of bony processes, the successional teeth are in like manner developed at the inner side of the supporting processes, gradually penetrate them as their growth proceeds, and finally undermine and displace the tooth and become in their turn anchylosed to new bony eminences of the alveolar tract. The jaws of the gigantic Mosasaur exhibit on a large scale different stages of this mode of shedding and replacement, which is so general in the class of reptiles.

In the Ichthyosaurus, in which, by the development of an internal as well as an external alveolar plate, the teeth are lodged in a deep continuous groove, the successional germs were also developed in this extinct reptile at the inner side of their predecessors, and, from the solidification of the implanted base of the fully formed tooth, occasioned an extensive absorption of its inner side, before it finally yielded to the lateral pressure.

In the Crocodile, the tooth-germ is developed from the vascular membrane covering the base of the internal wall of the socket; it is soon invested by a capsule, and by its pressure causes the formation of a shallow recess, or secondary alveolus, in the contiguous bone (Pl. 75, fig. 4). In this alveolus, however, it never becomes inclosed like the

successional teeth in most mammalia; for, exerting equal pressure against the fang of the contiguous tooth, which, from being incompletely formed, has a wide pulp-cavity with very thin walls, the nascent tooth soon penetrates that cavity, and quits the recess in the alveolar plate in which it was originally situated. Thus the stage of development corresponding with the 'eruption' of the tooth in the mammalia is immediately followed by the 'inclusion' of the new tooth in the pulp-cavity of its predecessor. Further details of the development and succession of the teeth of the Crocodiles will be given in the chapter appropriated to the description of the dental system in that family; but I may here observe that the rapid succession of tooth-germs, which stamps the impress of decay upon their predecessors often before the growth of these is completed, though common to many reptiles, is most strikingly manifested in the Crocodiles, in which three and sometimes four generations of teeth, sheathed one within the other, are contained in the same socket.

CHAPTER II.

TEETH OF BATRACHIANS.

75. The variations which the dental system presents in the Batrachian order of Reptiles are more conspicuous in the number, situation, and structure of the teeth, than in their form or mode of attachment. Certain Batrachians are edentulous, as the genus *Hylaplesia*, among the tree-frogs, and the *Bufonidæ* or family of Toads, some of the species of *Bombinator* excepted.

The teeth when present are generally numerous, simple, of small and equal size, and close-set, either in a single row or aggregated like the teeth of a rasp.

It is not without interest to observe that a characteristic condition of the dental system in fishes, viz: the absence of teeth on the superior maxillary bone, is continued in those genera of perenni-

branchiate Batrachians which stand at the lowest step of the Reptilian Class, and not only the superior maxillary teeth, but the bones themselves are absent in the Siren, Menobranchus and Proteus.

76. *Siren.*—In the Siren (*Siren lacertina*, Linn.) the lower margin of the intermaxillary bones, and the sloping anterior and upper margin of the lower jaw are trenchant, and are each encased in a sheath of firm albuminous, minutely fibrous tissue, harder than horn, (Pl. 62, fig. 1). The bones thus armed slide upon each other like the blades of a pair of curved scissors, when the mouth is closed, and are well adapted for dividing the bodies of small fish, aquatic larvæ, worms, &c. The horny substitute for teeth on the lower jaw is supported by the bony element corresponding with the premandibular of the lepidosiren and other fishes. A second osseous piece, applied to the inner surface of the ramus of the jaw, and representing the splenial or opercular element in the jaw of the crocodile, is beset with numerous minute pointed teeth, arranged in short oblique rows, and directed obliquely backwards. The palatal surface of the mouth presents on each side two flat, thin and moderately broad bones, forming an apparently single oblique oval plate, which converges to meet its fellow at the anterior part of the palate, so as conjointly to constitute a broad rasp-like surface in the form of a chevron, (Pl. 62, fig. 2).

The anterior long plate on each side, which may be regarded as the representative of the divided vomer, supports six or seven oblique rows of small pointed retroverted teeth ; the smaller posterior plate, probably the homologue of the pterygoid, is beset with four rows of similar teeth : there being thus ten or eleven rows on each side of the palatal chevron. The number of denticles in the middle rows is eleven or twelve ; they become fewer in the anterior and posterior rows : they are all of similar size and form, corresponding with those of the lower jaw to which they are opposed.

The condition of the dental system in this, the lowest of the class of reptiles, is not without interest independently of the absence of the superior maxillary teeth, and of the presence of the palatal and inferior maxillary ' dents en cardes.' If, for example, the dense sheath of the trenchant anterior parts of the upper and lower jaws had

been completely calcified and converted into hard dentine, the correspondence between the siren and the lepidosiren would have been very striking in this part of their structure; but the maxillary sheaths of the siren being composed of horn, and being, moreover, easily detached from the subjacent bones, much more closely resemble the deciduous mandibles of the tadpoles of the higher Batrachians.(1)

77. *Axolotl.*—The ichthyic character of rasp-like teeth, aggregated in numerous series, is manifested also in the Axolotl upon the palatal region of the mouth, and upon the splenial or opercular element of the lower jaw; but the superior maxillary bones are here developed and support teeth (Pl. 62, fig. 4). The premandibular and the intermaxillary bones (*a*), instead of presenting the larval condition of the horny sheath, have their alveolar border armed with a single row of small, equal, fine, and sharp pointed denticles, which are continued above, along the maxillaries (*b*); thus establishing the commencement of the ordinary batrachian condition of the marginal teeth of the buccal cavity. The dentigerous bones of the palate consist of two plates on each side, as in the siren; the anterior pair, or vomers, (*c*), converge and meet at their anterior extremities; the minute denticles which they support are arranged quincuncially: the posterior pair of bones, (*d*), are continued backwards, according to the usual disposition of the pterygoids, to abut against the tympanic or quadrate bones; the denticles are confined to the anterior part of their oral surface and resemble in their arrangement and anchylosed attachment those of the palatal series of which they form the posterior termination.

78. *Menobranchus.*—Although in this genus the superior maxillaries and their teeth are wanting, an advance to a higher type of dentition

(1) "Leur bord est tranchant et garni dans l'animal frais d'une gaîne presque cornée, qui se détache aisément de la gencive, et qui a son analogue dans les têtards de grenouille."—Cuvier, Ossem. Foss. Ed. 1837, x, p. 341. The combination of trenchant with lacerating rasp-like dental instruments in the jaws of the Siren was recognized by Ellis, who has given a figure of them in the 56th volume of the Philosophical Transactions, Pl. IX. c. He says, "The mouth is small in proportion to the body; but its palate and inside of the lower jaw are well provided with many rows of pointed teeth; with this provision of nature, added to the sharp exterior bony edges of both the upper and under jaw, the animal seems capable of biting and grinding the hardest kind of food."

is made by the arrangement of the teeth in a single row both upon the roof and at the margins of the mouth. The intermaxillary bones are produced backwards, and the single series of small pointed teeth which they support is opposed to a similar series upon the premandibular bones below; to which elements of the lower jaw the teeth are henceforth confined in the class of reptiles. The palatal teeth form a single row on each of the broad bones, which correspond with those described by Cuvier as the divided vomer in the higher Batrachians, and extend backwards upon the pterygoids, which support a few teeth.

79. *Proteus.*—The *Proteus anguinus*, (Pl. 62, fig. 3.) though retaining like the three preceding genera its external gills, offers a further advance to the dental characters of the higher Batrachians, especially of the amphiuma. The alveolar border of each intermaxillary bone is armed with a row of eight or ten minute and fine sharp-pointed teeth: each premandibular bone supports a greater number of similar but larger teeth, likewise arranged in a single row. The palatine bones, or the two vomers of Cuvier, support a row of denticles, similar and parallel to the intermaxillary crescentic series: but the horns of the palatal dental crescent are continued much further back, and terminate as in the menobranchus, on the anterior part of the pterygoid bones: each half of the crescentic, or chevron shaped series, contains twenty-four teeth. The superior maxillary bones are represented in the proteus by mere cartilaginous rudiments.

80. *Amphiuma.*—The Amphiume, like the proteus, presents the batrachian disposition of the teeth in a single close-set series along the alveolar border of both upper and lower jaws; but the upper series is extended along well developed maxillary, as well as intermaxillary bones; and in the extent of the maxillary and palatal series of teeth, especially in one species of amphiume (*Amph. tridactylum*), there may be discerned the indication of a character which is of much interest in regard to the affinities of an extinct race of gigantic Batrachians with biconcave vertebræ. The palatal teeth in the amphiume are arranged in a single close-set row along the lateral margins of the vomer, meeting at an acute angle at its anterior part, from which the series extends backwards on either side nearly longitudinally and

parallel with the maxillary teeth. All the teeth are conical, pointed, slightly curved backwards and inwards; their points glisten with a yellow metallic lustre, whence the name of *Chrysodonta* proposed for this genus by Dr. Mitchell.(1)

The *Amphiuma means* has twenty teeth on each side of the upper jaw, of which fifteen or sixteen are attached to the superior maxillary and four or five to the intermaxillary bones: it has sixteen teeth on each side of the lower jaw. There are fourteen or fifteen teeth in each of the vomerine series.

The *Amphiuma tridactylum* (Pl. 62, fig. 7) has four intermaxillary and thirty-one or two maxillary teeth on each side of the upper jaw, and twenty-four teeth on each side of the lower jaw. It has twenty-six to twenty-eight teeth in each vomerine series.

81. *Menopoma.*—The Menopome (Pl. 62, fig. 5 and 6), exhibits the same essentially batrachian condition of the teeth as the amphiume, but in their disposition, and in the division and form of the vomer, it makes a nearer approach to the caducibranchiate group, and allies itself most closely with the gigantic newt of Japan, (*Sieboldtia*, Bonap.) and with that equally gigantic extinct species of newt, so noted in palæontology, as the *Homo diluvii testis* of Scheuchzer.(2) In the persistence of the branchial apertures, and the more complex structure of os hyoides, the menopome, however, manifests its generic distinctness from the Sieboldtia. The single close-set series of small, equal, conical and slightly recurved teeth describes a semicircle on both the upper and lower jaws: the row of similar but smaller teeth on the anterior expanded border of the divided vomer runs parallel with, and at a short distance behind the median part of the maxillary series, (Pl. 62, fig. 6). The premandibular teeth are received into the narrow interspace between the two rows in the upper jaw when the mouth is closed. The teeth of the menopome as of the amphiume are anchylosed by their base and part of its outer side to a slightly elevated external alveolar ridge.

82. *Sieboldtia.* — The perennibranchiate or fish-like Batrachians—'doubtful reptiles' as they have been termed—lead by

(1) Medical Recorder, July, 1822.

(2) Philosophical Transactions, xxxiv, (1726), p. 38.

so easy a series of transitions to the caducibranchiate group, in which all external trace of the branchial apparatus is lost, that the artificial nature of such a division of the order is evident, and some Naturalists have even hesitated whether to separate, generically, the last of the perennibranchians from the species, *Sieboldtia gigantea*, with which the description of the dental system in the higher division of Batrachians is here commenced. As regards the teeth, the difference between the great aquatic salamander of the volcanic mountains of Japan and that of the Alleghanies is very slight and merely specific; the form, disposition and attachment of the teeth is the same in *Sieboldtia* as in *Menopoma;* they differ slightly in relative size, those of the Japanese newt having the advantage in this respect, with a somewhat deeper implantation of their anchylosed base; and the alveolar parapet of the intermaxillary bones is higher and is slightly incurved. There are fourteen teeth in each intermaxillary, seventy-two in each superior maxillary, and sixty-four teeth in each vomer of the *Sieboldtia gigantea*.

83. *Andrias*.—The disposition, form and attachment of the teeth in the great fossil newt or salamander, (*Andrias Scheuchzeri*, Tschudi), are the same as in the menopome and Sieboldtia; but they appear to have been relatively smaller than in the latter genus, are less compressed, and present more conspicuous basal grooves.(1)

84. *Triton*.—All the caducibranchiate Batrachians with tails, as the newts and land salamanders, have teeth on the inferior maxillary and vomerine bones, as well as on the intermaxillaries and superior maxillaries. In the common newts, as *Tr. palustris*, *cristatus*, and other allied species of the old world, the teeth are confined to the bones above mentioned; they are equal, subcompressed, fine, sharp-pointed cones,

(1) Cuvier being desirous of obtaining additional evidence of the truth of his opinion of the real nature of the pretended Anthropolite of Scheuchzer, obtained permission, while at Harlaem, to excavate the stone containing the celebrated fossil. "Nous avions placé," he says, "devant nous un dessin du squelette de la Salamandre, et ce ne fut pas sans une sorte de plaisir, qu'à mesure que le ciseau enlevait un éclat de pierre, nous voyions paraître au jour quelqu'un des os que ce dessin avait annoncé d'avance. C'est ainsi que cette table de schiste, gravée et regravée vingt fois depuis un siècle comme elle l'est, Pl. 253, fig. 2, fut mise dans l'état où on la voit, Pl. 254, fig. 2. Et d'abord nous avons trouvé autour de la rotondité, à droite et à gauche, une double rangée de petites dents; ce qui nous a fait voir que cette rotondité était produite par les mâchoires et non par la crâne."—Ossemens Fossiles, Ed. 1837, tom. x, p. 372. M. Tschudi

arranged in a single close-set row along the upper and lower margins of the mouth, and extending far back upon the roof of the mouth in a single row along the outer margins of each vomer: these vomerine teeth are extremely minute, (Pl. 62, fig. 9).

Most of the North American newts have a fourth locality for teeth, which reminds us of a peculiarity of the dental system of some of the highly organized Clupeoid fishes of the South American rivers, viz: upon the under surface of the sphenoid bone(1): there are four series of these sphenoid teeth in the sub-genus *Pseudotriton;* and in the *Salamandra glutinosa* of Maclure, (*Plethodon*, Tschudi), they are aggregated, ' en brosse,' to the number of three hundred and upwards, upon both the basi-sphenoid and basi-occipital bones (Pl. 62, fig. 12, *e*): there is a single row, set nearly transversely across the posterior margin of each vomer *c*, and the marginal teeth of the mouth of which the intermaxillary ones are shown at *a* and the maxillaries at *b*, are arranged as usual in a single row both above and below.

85. *Salamandra.*—In the land salamanders, (*Salamandra*, Laur.) the teeth are proportionally larger than in the newts: there are about sixty in each lateral series of both upper and lower jaws; and forty teeth, forming a sigmoid row on each side of the palate, in the *Salamandra maculata.*

86. *Rana.*—The frogs have no teeth on the lower jaw, but in some species the alveolar edge of this bone is finely notched or dentated, as in the horned frogs, (*Ceratophrys*). The intermaxillary and maxillary bones, support a long, close-set, single series of small, conical, hollow teeth of which the apices only project beyond the external alveolar ridge to which they are attached. A short transverse row of similar but smaller teeth extends along the posterior border of each vomer, except in the slender-armed frogs (*Leptobrachium*) and in some of the tree frogs, as the *Euchnemis*, in which the roof of the mouth is edentulous. The teeth are relatively most developed in the *Ceratophrys:* they are anchylosed by their basis, and outer

has added further details respecting the dental system of this interesting Batracholite, which prove its close alliance with the Salamandroid genera cited in the text. See his *Classification der Batrachier*, 4to. 1838.

(1) M. Tschudi, l. c. p. 11.

surface near the base, to a continuous alveolar groove defended by an external wall of bone. In the common frog (*Rana temporaria*), there are about forty of these teeth on each side of the upper jaw, of which eight are supported by the intermaxillary bones. In the *Rana esculenta*, (Pl. 62, fig. 8), there are the same number of intermaxillary, but a greater number of maxillary teeth. In the great bull-frog, (*Rana pipiens*) there are ten or twelve intermaxillary teeth, followed by between sixty and seventy maxillary teeth (Pl. 62, fig. 10). The largest teeth are placed in the anterior third of the series, whence they progressively diminish in size towards the two extremities. The vomerine bones each support a short transverse row of four or five small teeth. The base of the teeth, besides being confluent with the bone, are, from their close contiguity, frequently anchylosed to one another: they are sometimes thus conjoined to near the apex. Where the larger teeth are situated, the alternate ones are commonly found to be displaced. The germs of the successional teeth are developed in a groove of the mucous membrane of the mouth which covers the inner side of the basis of the teeth; as they increase in size they press upon and cause absorption of the contiguous surface of the base of the old teeth, and thus finally displace them and become in their turn anchylosed to the bone, then undermined and shed. As a general rule the toads (*Bufonidæ*) are edentulous, but among the *Bombinatores*, or those species which are termed 'earless,' from having the tympanum concealed under the skin, the subgenus *Hyladactylus* has teeth upon the vomer and *Sclerophrys* has teeth on both the intermaxillary and maxillary bones.(1)

In microscopic structure, the teeth of the existing Batrachians like those of most Saurians, correspond with the simple mammalian teeth.

If a longitudinal section of the tooth of a frog, including a portion of the alveolar plate to which it is anchylosed, be examined by transmitted light under a half-inch objective, a narrow transverse line will be seen inflected inwards from both the external and internal side of its base, defining the limits of the tooth and bone. Below this line the bone is characterized by numerous large, oblong, radiated cells,

(1) M. Tschudi, l. c. p. 3.

having their long axis vertical, or in the direction of the axis of the tooth: these cells do not extend into the substance of the tooth itself. The dentine is composed of fine calcigerous tubes and the intermediate clear substance, the minute cells of which are unusually conspicuous and abundant. In a completely formed tooth no trace of a pulp-cavity is discernible in the prominent crown. The calcigerous tubes are continued into the body of the tooth at once from the subjacent bone, in the interspace of the transverse fissure first mentioned. The tubes nearest the external and the internal periphery of the base of the tooth incline with a gentle curve towards those surfaces; but the greater number proceed vertically, and nearly parallel with each other, to the convex line anterior to the inflected apex of the tooth, where their extremities are slightly bent outwards, except in a few of the tubes nearest the apex which follow its inward curvature. The secondary undulations and branches of the calcigerous tubes are very elegant and conspicuous: the terminal branches of these tubes end in a rich border of calcigerous cells. The dentine is not complicated with medullary canals or inflected folds of the external cement. The convex margin of the upper half of the tooth is coated with a layer of enamel. The concave border and the basal half of the opposite margin exhibit a thin layer of cement. The enamel, viewed by transmitted light, presents the same dull brownish tint as that of the saurian and mammalian teeth; and has a minutely undulating fibrous texture.

LABYRINTHODONTS.

87. The dental system in the extinct genus *Labyrinthodon* is more formidable than that of any existing Batrachian: and principally differs, as regards its more obvious characters, in the implantation of the teeth in distinct sockets, and in the development of certain of the anterior teeth of both jaws into large and formidable tusks.

A close-set series of subequal teeth extends along the alveolar border of both upper and lower jaws, and along the anterior part of the outer margin of each broad vomerine bone: two or three canine-shaped teeth, at least three times the size of the serial teeth, are placed in the intermaxillary bones and at the anterior and external angle of

each vomer, at the fore part of both the outer and inner rows of the smaller teeth in the upper jaw; and two or three similar tusks are implanted, somewhat irregularly, behind the anterior extremity of the series of smaller teeth in each ramus of the lower jaw. This allocation of teeth in a double series on the premandibular bone is peculiar, among Reptiles, to the Cecilia and the present almost equally aberrant form of Batrachian. It is a common dental character in the class of fishes, and its repetition in the Labyrinthodon betrays a tendency to the ichthyic type which is manifested by some other of the extinct reptiles, as the *Ichthyosaurus*, although this genus in its general organization is essentially related to a higher order than that to which the *Labyrinthodon* belongs.

The first discovered fossils belonging to this genus were certain detached teeth from the Keuper sandstone (Alaunschiefer) of Wirtemberg, of which the largest is figured at Pl. 63, fig. 1, from the "*Fossile Reptilien in Wurtemberg*," 4to. 1828, of Prof. Jaeger, by whom the name *Mastodonsaurus* was applied to these teeth under the impression that they were the remains of some gigantic Saurian reptile.(1)

Other fossil fragments of jaws and teeth, or casts of teeth, also from the Keuper formation, (Dolomitsandstein), on which Prof. Jaeger has founded his genus *Phytosaurus*, I believe to belong to the same genus and most probably to the same species as the preceding teeth. The most remarkable of these fossils is described as the palatal surface of the upper jaw, measuring one foot and a half in length, nine inches in breadth at the posterior part and between two and three inches across the narrower anterior part of the fragment. On one side of this fragment there was a series of twenty-seven, and probably of thirty sockets, with very narrow and not quite equal interspaces. The anterior portion containing eighteen of these serial sockets, and probably the fractured bases of the teeth, is copied from Prof. Jaeger's work, at Pl. 63, fig. 3. At a short distance anterior to the series of smaller teeth, there is a portion of the socket, *a*, or

(1) The genus *Mastodonsaurus* is placed in the Saurian system of M. Hermann v. Meyer, in the Crocodilian family, intermediate between *Steneosaurus* or *Macrospondylus* and *Crocodilus*: the species on which the genus is founded is termed, after its discoverer, *Mastodonsaurus Jaegeri*. Palæologica, 8vo. 1832, p. 107.

cavity for the reception of one of the great tusks. The tooth, indicated by the letter *b*, is described as exhibiting a pulp-cavity, and the adjoining tooth, *c*, as showing a new tooth rising into the pulp-cavity, in progress of displacing the old tooth, after the manner of succession in the teeth of the crocodile. Pl. 63, figs. 2 and 4, represent the fossils on which Prof. Jaeger has founded respectively his species denominated *Phytosaurus cubicodon* and *Phytosaurus cylindricodon*, but it is doubtful whether they are teeth or casts of the sockets of most probably conical teeth, of which they exhibit only the shape of the implanted base: the real teeth that have been discovered in the same quarry as that which yielded the preceding casts have the form represented in fig. 5: these, like the teeth of *Mastodonsaurus Jaegeri*, are conical and are marked by fine striæ extending from the base to the middle of the crown: they bear the same relative proportions to the large tusk (Pl. 63, fig. 1) as do the serial teeth of the British species of *Labyrinthodon* to their anterior tusks.(1)

A third remarkable and characteristic fossil discovered in the Keuper sandstone (alaunschiefer) and described by Prof. Jaeger, (loc. cit. p. 38, pl. v, figs. 1 and 2), consists of the occipital portion of the cranium with two large and separate condyles, as in the batrachian reptiles: on this fossil the Professor founded his species called "*Salamandroïdes giganteus*."(2) Now the teeth of the extinct Batrachians from the New-Red Sandstone in Warwickshire correspond with those of the so-called *Mastodonsaurus*, in presenting a highly characteristic and peculiar structure (Pl. 64 B, fig. 2), which has suggested for the genus to which they belong the name of *Labyrinthodon:* and as the great teeth of the so called *Mastodonsaurus* correspond in size with the cranial fragment with the batrachian condyles above mentioned, it is highly probable that they belong to the same species of reptile as that fragment. But it is certain that the teeth of this gigantic Keuper reptile belong

(1) The genus *Phytosaurus* in the Saurian system of H. von Meyer is placed between *Mosasaurus* and *Saurocephalus*. I have already proved the latter to belong to the class of fishes, and, if the *Phytosaurus* be identical with *Mastodonsaurus*, they must both be expunged from the Saurian order.

(2) The *Salamandroides giganteus* of Jaeger, is placed in the system of H. von Meyer, between the *Salamandra gigantea* and the *Triton noachicus*, in the order *Batrachia*: it belongs, however, to a distinct family in that order.

to the same genus as the Batrachians of the Warwick Sandstones, and, therefore, I shall hereafter describe the German species under the name of *Labyrinthodon Jaegeri.*

As the circumstances which led me to detect this generic identity strikingly illustrate the value of the microscopic structure of teeth as a distinctive and available test of the nature and affinities of an extinct species, expecially in the absence of any other character, I shall here premise the account of these investigations as communicated by me to the Geological Society of London.(1)

A question was at issue whether the light coloured sandstone of Warwick was the equivalent of the Keuper or the Bunter division of the New-Red Sandstone formation as developed in Germany, and its decision had been set by one of the contending geologists upon the issue of organic remains, more especially of the supposed Saurian fossils of the strata in question. "If it could be shown," said the able supporter of the 'Bunter' theory, "that the fossils which we have pointed out as characterizing the upper sandstone occurred also in the lower, and that the fragments of Saurians formed in the sandstone of Guy's Cliff and Warwick really belonged to the species peculiar to the Keuper, then, indeed, we should willingly allow that the lower sandstone also must be grouped with that formation."

"In respect to the Saurian of Guy's Cliff, which we have had no opportunity of examining, it is sufficient to state, that Dr. Buckland himself does not contend that it is either of the species of the *Phytosaurus* (Jaeger) of the German Keuper; and he hesitates even to refer it to that genus. Now the mere existence of a Saurian in the Warwick sandstone proves nothing; for Geologists are well aware that various species of the family occur in all the formations, from the lias down to the magnesian lime-stone inclusive."(2)

The reptilian remains figured by the authors above quoted from the lower or Warwick sandstone were a few teeth or rather fragments of teeth, and a portion of a vertebra: and these were the fossils to be compared with the reptiles peculiar to the German Keuper.

(1) Proceedings of the Geological Society, January 20th, 1841. No. 74, p. 257.

(2) "On the Upper Formations of the New Red Sandstone System in Gloucestershire, Worcestershire and Warwickshire, &c., by R. I. Murchison, Esq. V.P. G.S., and H. E. Strickland, Esq., F.G.S."—Geological Transactions, vol. v, 2d Series, p.p. 345, 346, Pl. 28 and 29.

Of such reptiles the least ambiguous and most characteristic remains were the occipital bone of the *Salamandroïdes giganteus* of Prof. Jaeger: and the teeth of the so called *Mastodonsaurus* and *Phytosaurus*. On the other hand, the reptilian remains of the Warwick sandstone were still more meagre: no portion of the skull whereby their batrachian character could be tested was then known; the vertebra, as figured in the Memoir cited, apparently presented the characters of those of the Saurian reptiles(1); and the teeth, therefore, appeared to be the only fossils on which any comparison likely to solve the question of the relationship between the reptiles of the German Keuper and of the Warwick sandstone could be founded.

Now it has been seen that the teeth of the *Mastodonsaurus* are of a simple and common form; that they are far from possessing those well-marked external characters whereby the anatomist can distinguish the teeth of the *Iguanodon*, *Megalosaurus* or *Pleiosaurus*.

Of the teeth which had been discovered in the Warwick sandstone, the specimen figured in Messrs. Murchison and Strickland's Memoir, and which was transmitted to me for examination together with a similar but larger tooth, most nearly resembled the teeth of the *Mastodonsaurus*, in its conical figure and longitudinal striation; but as these were the commonest characters of Saurian teeth no weight could be attached to them as proving a specific or generic identity, bearing upon a geological problem of so much nicety as the one which related to the Warwick sandstones.

There only remained, therefore, to resort to the test of the intimate structure of the teeth in question, and upon application to Prof. Jaeger of Stuttgard, I was favoured with some portions of the teeth of the *Mastodonsaurus Jaegeri* from which were prepared transverse and longitudinal sections for microscopical examination.

Hitherto in investigating the intimate texture of the teeth of the Saurian reptiles, as the Crocodile, Plesiosaur, Megalosaur, Monitor, and most recent Lacertians, I had found the dentine or body of the tooth to consist of the finest calcigerous tubes, radiating according to the usual law, from the pulp-cavity, at right angles to the external surface of the tooth, which is covered by a simple investment of enamel;

(1) Subsequent examination has proved this vertebra to have a concave articular surface at both ends of the body, and to agree in other characters with the Salamandroid type.

from the prevalence of this structure in the simple conical teeth of reptiles, I did not build any very strong hopes of detecting such modifications of dental structure in the similarly simple teeth of the so called *Mastodonsaurus* and of the tooth from the Warwick sandstone, as would be sufficiently marked and obvious to carry conviction of their generic, much less specific identity. But in this I was agreeably and unexpectedly deceived.

When I refer to figure 1 in plate 64 A, and state that the first transparent transverse section of the tooth of the *Labyrinthodon* (*Mastodonsaurus*) *Jaegeri* that was placed under the microscope and viewed by transmitted light, with a low magnifying power, presented the singularly complicated structure there exhibited, the anatomist, conversant with the known modifications of dental structure in the animal kingdom, may well conceive my surprize. It was not, indeed, until I had had sections made in various directions, from the portions of the tooth of the *Lab: Jaegeri* transmitted to me, and had studied them intently at several successive examinations, comparing the appearances they presented with those of numerous examples of the teeth of Saurians, Batrachians and other animals, that I at length comprehended the nature and principle of the singular cerebriform convolutions or sinuosities which pervaded every portion of the tooth of this most remarkable reptile of the Keuper sandstone.

A transverse section from the base of the tooth of the Ichthyosaurus gave the first clue to the structure of that of the Labyrinthodon. Before investigating the latter I had been accustomed to regard the tooth of the Ichthysaurus as presenting, at its base, the most complicated condition of dental structure in the class of reptiles; but it is simple as compared with the structure which pervades almost the entire tooth of the *Labyrinthodon Jaegeri.*

To render intelligible the plan of this structure, I may first refer to that of the base of the tooth of the *Ichthyosaurus communis* (Pl. 64 B, fig. 3). Teeth in general, as has been shown, vary in structure according to the number of substances which enter into their composition, and according to the disposition of those substances. In the ungulate mammalia, as the elephant, rhinoceros, horse, etc., in which the crown of the tooth consists of dentine, enamel and cement, vertical folds of the enamel and cement penetrate the body of the tooth, and

receive in their interspaces corresponding vertical processes of the dentine: the consequence of this disposition in maintaining a grinding surface of the tooth, by the unequal attrition of the edges of the interblended laminæ is well known.

The pattern, however, after which the folds of enamel and cement are inflected into the substance of the tooth in these and other herbivorous species, although determinate in and characteristic of each genus or species, is always more or less irregular and unsymmetrical: there is no instance in the mammiferous class of these folds converging at regular intervals all round the circumference of the tooth towards its centre. Such a disposition of the external substance of the tooth may be traced at the base of the tooth in a few fishes, but is more conspicuous in the fang of the tooth of the Ichthyosaur. Here, the external layer of cement (for the enamel ceases at the base of the crown) is inflected, at pretty regular distances round the circumference of the tooth, towards its centre; the vertical folds being straight or plane, and extending to a distance about equal to the breadth of their interspaces. These interspaces are occupied by corresponding processes of the dentine, which radiate, or diverge from the central mass of that substance.

If we could suppose the tooth of the Ichthyosaur to be worn down in the living animal by the masticatory uses to its complicated basis, then an eighth part of the diameter of the tooth, around its circumference, would present a series of ridges of the denser substance converging in straight lines from that circumference.

The plan and principle of the structure of the Labyrinthodon's tooth is the same as that of the tooth of the Ichthyosaur but it is carried out to the highest degree of complication. The converging folds of the external cement, instead of being arrested at one fourth of the distance from the circumference to the centre of the tooth, are continued close to that centre; and, instead of being simple, straight, or plane lamellæ, they are bent upon themselves in a series of sinuous folds, resembling the anfractuosities of the brain. The ordinary laws of the complication of dental structure are here, however, strictly adhered to, and every space intercepted by a convolution of the converging folds of the cement, is occupied by a corresponding

process of the diverging layers of the dentine, and thus is produced the singularly complicated appearance which a transverse section of the tooth of the Labyrinthodon or Mastodonsaurus exhibits.

The external longitudinal flutings of the base of the tooth of the Ichthyosaur are much coarser, and more indicative of the converging vertical folds of the cement, than are the corresponding longitudinal lines on the exterior of the tooth of the Labyrinthodon; which is owing to the layer of the inflected cement being much thicker in the Ichthyosaur. The external striæ of the Labyrinthodon's tooth are too little conspicuous to attract particular attention, or to indicate that they are the lines of inflection of a series of extensive vertical folds of the external substance. Accordingly Professor Jaeger describes the tooth of the Mastodonsaurus as being longitudinally striated on the superficies, noting where the striæ terminate their relative distances, and where they are most marked: the texture of the tooth, where it was exposed by fracture, he pronounces, as indeed it appears to the naked eye, to be uniform, homogeneous and compact(1), and he concludes his description by stating that the tooth resembles most closely that of the *Lacerta nilotica* and of some species of *Monitor*.

The teeth, however, of those species of *Varanus, Lacerta, Monitor*, and other Saurian genera which I have submitted to microscopic investigation, have all presented the usual structure of simple Saurian teeth.

The portion of the tooth of the *Labyrinthodon Jaegeri* from which the sections here described, were prepared, included about the middle third part of a tusk nearly as large as the one figured by Prof. Jaeger (2). That tooth is three inches and a half in length, and one inch and a half in breadth at the base, whence it gradually contracts, with a slight bend, towards the apex: this is obtuse, with a slightly depressed summit; it is three lines in diameter, and presents a small rising in the centre of the terminal depression. The external longitudinal striæ are regularly arranged with intervals of about a line at the base of the tooth; and they maintain nearly the same relative position throughout the lower three

(1) Jaeger, loc. cit. p. 36. (2) Loc. cit. tab. iv. fig. 4.

fourths of the tooth, by decreasing in number as the tooth diminishes in thickness; they finally altogether disappear about half an inch from the summit of the tooth: and at this part, from the analogy of other species of *Labyrinthodon*, it is to be presumed that the structure of the tooth of the *Lab. Jaegeri* may be more simple.

The dentine or body of the tooth is invested by only a very thin layer of cement, and it is a vertical fold or duplicature of this cement which penetrates the substance of the tooth at each of the striæ, which, as before observed, are arranged at intervals of about one line, around the whole circumference of the tooth. The inflected fold runs straight for about half a line, and then becomes wavy, the folds rapidly increasing in breadth as they recede from the periphery of the tooth; the first two, three, or four undulations are simple; then their contour itself becomes broken by smaller or secondary undulations; these become stronger as the fold approaches the centre of the tooth, when it slightly increases in thickness, and finally terminates by a slight dilatation or loop close to the pulp-cavity, from which the free margin of the inflected fold of cement is separated by an extremely thin layer of dentine. The number of the inflected converging folds of dentine is about fifty at the middle of the crown of the tooth, but it must be greater at the base. All the inflected folds of cement at the base of the tooth have probably the same complicated disposition with increased extent; but, as they approach their termination towards the upper part of the tooth, they also gradually diminish in breadth, and consequently penetrate to a less distance into the substance of the tooth. Hence, in such a section as is delineated, it will be observed that some of the convoluted folds, as those marked *c c* Pl. 64 A, fig 1, extend near to the centre of the tooth; others, as those marked *d d*, reach only about half way to the centre; and those folds, which, to use a geological expression, are 'cropping out', penetrate to a very short distance into the dentine, and resemble in their extent and simplicity the converging folds of cement in the fangs of the tooth of the Ichthyosaurus.

The disposition of the dentine in the tooth of the *Labyrinthodon Jaegeri* is still more complicated than that of the cement. It consists of a slender, central, conical column, excavated by a conical pulp-cavity

for a certain distance from the base, and radiating outwards from its circumference a series of vertical plates, which divide into two, once or twice before they terminate at the periphery of the tooth.

Each of these diverging and dichotomizing plates gives off throughout its course smaller processes which stand at right angles or nearly so to the main plate; they are generally opposite, but sometimes alternate: many of the secondary plates or processes which are given off near the centre of the tooth, also divide into two before they terminate; and their contour is seen, in the transverse section, to partake of all the undulations of the folds of cement, which invest and divide the dentinal plates and processes from each other.

The dental pulp-cavity is reduced to a mere line about the upper third of the tooth, but throughout its whole extent fissures radiate from it, corresponding in number with the radiating plates of dentine. Each fissure is continued along the middle of each plate, dividing where this divides, and extending along the middle of each bifurcation and process, to within a short distance of the line of cement. The pulp-fissure commonly dilates into a canal at the origin of the lateral processes of the radiating plates, before it divides to accompany and penetrate those processes.

The main fissures or radiations of the pulp-cavity extend to within a line or half a line of the periphery of the tooth, and suddenly dilate at their terminations into spaces, which, in transverse section are subcircular, oval or pyriform (Pl. 64, *b b*): the branches of the radiating lines, which are continued into the lateral secondary plates or processes of the dentinal lamellæ, likewise dilate into similar and generally smaller spaces. All these spaces or canals, in the living tooth, must have been occupied by corresponding processes of the vascular pulp: they constitute as many centres of radiation of the fine calcigerous tubes, which with their uniting clear substance constitute the dentine.

Throughout every part of this complicated tooth, the calcigerous tubes were found, in their course, to obey the usual law, radiating or converging, with primary curvatures and secondary undulations, at right angles or nearly so to the surface of the dentine which the cement invests. The number of these calcigerous tubes, which are themselves

the centres of minor ramifications, defies all calculation. Their diameter is $\frac{1}{7000}$th line, with interspaces equal to seven diameters of their cavities. Their general disposition is shown in a section of one of the simple lateral processes of the radiating plates of dentine (Pl. 64 A, fig. 2). The undulation and ramification of the extremities of two of the calcigerous tubes, magnified 650 diameters are figured at Pl. 64 A, fig. 3.

It has already been stated that among the few teeth, presumed to be saurian, from the lower Warwick sandstone, the small conical externally striated one, figured in Plate 62 A, fig. 2, bears the nearest resemblance to the teeth of the German Labyrinthodon; it is, however, much smaller, and the cone is broader and shorter, and the base of the tooth is more ventricose.

I subsequently received a larger tooth from Dr. Lloyd, which was discovered in the Warwick sandstone at the Coten-end quarry. This tooth (Pl. 64 B, fig. 1) presented a more simple and regular conical shape, and differed from the tusk of the great *Labyrinthodon Jaegeri* in being somewhat more compressed at the base, and less obtuse at the apex. Its external surface was similarly impressed with fine longitudinal striæ continued, with a very slight degree of convergence, towards the apex of the tooth, where the longest striæ terminated. The interspaces of the striæ were more prominent and convex than in the tooth of the *Lab. Jaegeri*. The apex of the tooth, though obtuse, was worn by attrition obliquely down one side, and did not present the depression and central eminence which Prof. Jaeger describes in the large tooth of his species; this difference might, however, be due to the mode in which the tooth had been used or worn down.

The main point to be determined was whether and to what extent the apparently simple conical tooth from the English sandstone would correspond with that of the German Batrachian in the complicated structure above described. I could perceive indications, at the fractured basis of the Warwick tooth of fissures leading from the external striæ into the substance of the tooth. Were these fissures continued to the same extent, or in the same sinuous course which they had presented in the tooth of the *Labyrinthodon Jaegeri*? This could not be ascertained by inspection of the fractured surfaces of the dense and opake tooth either by unaided vision or the use of the microscope by reflected light.

With the kind permission of Dr. Lloyd, I took a thin transparent transverse section from the middle of the tooth, corresponding with the place of the section from the German tooth above described: at Pl. 64 B, fig. 2, is shown the structure of the tooth of the British Labyrinthodon as seen by transmitted light in one half of the transverse section: the complication of the interblended laminæ of dentine and cement is as remarkable, and its plan is the same as in the tooth of the great Labyrinthodon of the German Keuper. All the peculiarities, indeed, of this most extraordinary type of dental structure are so closely preserved in the specimen from the Warwick sandstone, that generic identity, at least, may be predicated of the fossils from both localities.

The differences which require to be noticed are such as might be expected in distinct species of the same genus. The inflected folds of cement in the Warwick tooth are continued for a greater relative extent before the lateral sinuosities commence, than in the German reptile, and the inflections or anfractuosities are rather fewer in number; some of the inflected converging folds in the Warwick tooth, having nearly reached the central pulp-cavity, are reflected backwards for a short distance before they terminate.

The modifications of the complex diverging plates of dentine correspond with those of the tooth of the *Labyrinthodon Jaegeri*; but their terminal quadrilateral lobes, as seen in the transverse section, are relatively longer.

The number of the inflected folds of cement is equal to that in the *Lab. Jaegeri* and varies in the same degree at different parts of the tooth; thus the folds which reach longitudinally to near the apex of the tooth extend inwards to near its centre in the section figured, and the shorter folds are inflected to a less extent proportionate to their diminished length.

The dentine is composed of calcigerous tubes of the same relative size and disposition as in the *Labyrinthodon Jaegeri*. The base of the tooth appeared to have been similarly anchylosed to the osseous substance of the jaw.

After having adduced this evidence of the affinity of the fossils of the German and British sandstones, I concluded by stating

that the results of the comparison might be deemed to be decisive as to the existence of reptiles in the latter formation, which belong to the same natural genus as does one of the most peculiar of the extinct reptiles of the German Keuper.

So far, therefore, as the geological question, to which reference was made at the beginning of the present section, depends upon the determination of the generic identity of the reptilian fossils in these formations, it must be regarded as supporting the view entertained by Dr. Buckland of the correspondence of the Warwick and Bromsgrove sandstones with the Keuper sandstones of Germany. And if, on the one hand, geology has, in this instance, derived any benefit from microscopical investigations of animal tissues, on the other hand it must be admitted that in no instance has comparative anatomy been more directly indebted to geology than for the fossils, and the stimulus to their microscopic investigation, by means of which a knowledge has been obtained of the most beautiful and complicated modification of dental structure hitherto known, and of which no adequate conception could have been gained from investigations, however close and extensive, of the teeth of existing species of animals.

88. *Labyrinthodon leptognathus.*—When the results of this comparison of the microscopic structure of the tooth of the *Labyrinthodon Jaegeri* and of the smaller tooth of the Warwick sandstone were communicated to Dr. Lloyd, he transmitted for my inspection all the fossils from the same stratum which had been deposited in the local or private museums of Warwick and Leamington, with permission to apply the microscopic test to any of the teeth which these fossils might contain. I shall here briefly notice such of these fossils as throw additional light on the dental characters of the species to which they belonged.

The most valuable and characteristic fossil in this respect is the anterior part of one side of the upper jaw, including the nasal bones (Pl. 63 A, figs. 1 and 3). It shows that the maxillary or facial division of the skull was broad, much depressed and flattened, resembling in this respect the skull of the gigantic salamander and alligator, and having the outer surface of the bones strongly sculptured by depressions and furrows as in the crocodilian family.

The portion of the superior maxillary bone contains the anterior part of the single row of small teeth, and the base of one of the great anterior tusks, which ranges in the same line with the other teeth, but is directed obliquely backwards; the small serial teeth project more vertically from the alveolar margin of the jaws and are slightly inclined outwards. In a few places the contiguous teeth are present, but throughout the greater part of the series there is alternately a tooth and an empty socket. The sockets are shallow, and are so closely arranged, that, although the alveolar series in the present fragments is but two inches, three lines in extent, it contains thirty-one sockets. The large anterior fang is three times the size of the first of the serial teeth which succeeds it; and the rest gradually diminish as they recede backwards, so that the eighth tooth, counting the sockets from the first, is little more than half a line in diameter at its base; beyond this the teeth are of equal size. Each of the serial teeth is slender in proportion to its length, and gradually diminishes from the middle of the crown to the apex, which is not very acute where entire; a linear pulp-cavity is continued along the centre of the tooth nearly to the apex. The transverse section of the base is elliptical, its smallest diameter being in the axis of the jaw; that of the apical two thirds of the tooth is circular; the basal third is finely fluted, the rest of the tooth is smooth. The outer wall of the socket is very thin, and is confluent with the fluted base of the tooth. From the flatness and thinness of the maxillary bones, the sockets of the teeth are necessarily shallow. The length of the common sized serial teeth is about two lines, their greatest diameter one third of a line; the diameter of the base of the large anterior tusk is two lines and a half.

The whole of the under surface of the fossil was covered by the sandstone matrix, but the fractured margin, opposite the alveolar border, exhibited the edge of a thin plate of bone, uninterrupted in the longitudinal extent, and forming the floor of a wide and shallow nasal cavity, thus affording a strong indication that the *Labyrinthodon* breathed air like the higher reptiles. That the bony palate extended as far in the transverse as in the longitudinal extent was indicated by the projecting base of a fractured conical tooth, twice the size

of the large anterior fang of the maxillary series, and situated internal to the anterior small serial teeth. The crocodilian affinities of the *Labyrinthodon* we have just seen to have been manifested in the character of the bones forming the upper surface of the maxillary part of the cranium, and by the interception of a wide and shallow nasal cavity between two horizontal plates of bone. The main test of the value of this manifestation would be the actual condition of the bony palate, first in regard to the bones composing it, and secondly in relation to the dental system. In Crocodiles the floor of the nasal cavity is chiefly formed by the maxillary bones, in Batrachians by the divided and expanded vomer; in all Crocodiles the bones of the palate are edentulous, in most Batrachians they support teeth. There was evidence in the fossil in question of a large laniary tooth projecting from the palatal surface of the mouth, internal to the series of maxillary teeth; it remained to be determined whether this was supported upon the same bone which supported the serial teeth, viz. the superior maxillary, or whether it was a true palatal or vomerine tooth. A careful removal of the adherent matrix brought to light this very instructive part of the cranial anatomy of the Labyrinthodon, (Pl. 63 A, fig. 3). The palatal processes of the maxillary bones instead of extending to the middle line, as in the Crocodiles, are very narrow, as in the Batrachians. The osseous roof of the mouth is principally constituted by a pair of broad and flat bones analogous to those which Cuvier describes as a divided vomer in the Batrachians. These bones are, however, of greater relative extent than in any existing Batrachians; they defend the mouth with a more complete bony roof than is present in most Lacertian reptiles. Physiologically the Labyrinthodon in this part of its structure comes nearest to the crocodile, but the structure itself, morphologically, is essentially Batrachian; that is to say, the bony palate is formed by largely developed vomerine bones, situated, as in the Batrachians, at a part of the skull which is occupied solely by the maxillary bones in the crocodiles.

The divided vomer varies much in form in the Batrachians; that of the Menopome most resembles the vomer of the Labyrinthodon in its broad anterior extremity, and the large tooth (fig. 3, *c*) is

situated on the outer part of this expanded extremity of the vomer in the present species of Labyrinthodon. The corresponding part of the vomer in the Menopome and gigantic Salamander supports a transverse row of small teeth; and the large tooth of the Labyrinthodon is the outermost of a similar transverse row of teeth extending, five in number, across the anterior expansion of each lateral moiety of the vomer, the three median teeth being small and equal, the two outermost much larger. In the present fossil these teeth appear to have been alternately shed; that is the first, third, and fifth, counting outwards from the middle line are in place; the second and fourth are indicated by their empty sockets. This is analogous to the condition of the maxillary series of teeth; it is a course or order of shedding and renewal which is common in many fishes, where these processes succeed each other frequently and quickly, and by which the dental series is always kept in an efficient state. The outermost or fifth tooth is placed behind, as well as to the outer side of the socket of the fourth displaced tooth; and while it terminates the transverse row of the vomerine teeth, it forms the commencement of a longitudinal row of small and equal-sized teeth which is continued backward along the outer margin of each vomerine bone (fig. 3 *c*); the whole of the vomerine series of teeth thus describes a curve, nearly concentric and parallel with the external maxillary series of teeth; and the large fangs occupy corresponding situations in both the outer and the inner row of the teeth of the upper jaw.

In the Saurian reptiles, the examples of such an inner or palatal row of teeth are comparatively few, and the series, when it does exist, is very short, and is situated towards the back of the palate upon the pterygoid bones, as in the iguana, aporomera and mosasaur. In the Ophidians, the inner rows of teeth are situated on the palatine and pterygoid bones, and are never arranged transversely to the axis of the mouth. In the Batrachians this is the most common disposition of the palatal teeth; they form a short transverse series at the posterior part of the divided vomer in the frog, and at the anterior part of the vomer in the menopome and gigantic salamander; in the amphiume, the palatal teeth form a nearly longitudinal series, along

each outer margin of the long and narrow vomer; the extinct Labyrinthodon combines both these dispositions of the vomerine teeth.

The next fossil which I proceed to describe, and which, like the preceding one, is from the sandstone in the neighbourhood of Warwick, also throws much light upon the dental system and affinities of the present singular genus of extinct reptiles. It is the anterior dentigerous part of the ramus of the lower jaw, a portion of which is figured at Pl. 63 A, fig. 2. This ramus is slender, straight, and with its symphysial extremity abruptly bent inwards, the inner line of the symphysis here forming a regular and deep curve. The breadth of the bone at the posterior fractured part is ten lines; at the anterior part, behind the inflected symphysis, seven lines; the breadth of the anterior fractured portion is one inch. The structure of this long and straight ramus of the jaw presents almost as striking a batrachian character as any of those derived from the foregoing fossil; that is to say, the angular piece is of great breadth, and is continued forwards to near the symphysis, forming the whole of the inferior part of the ramus of the jaw extending upon the inner as far as upon the outer side of the ramus; the inner plate performing the function of the detached "os operculare" in the lower jaw of the Saurians. The dentary piece is supported upon a deep and wide groove, extending along the upper surface of the angular piece and looking obliquely outwards. The angular piece projects beyond the outer edge of the groove, so as to form a strong convex ridge on the external side of the jaw below the dentary piece; this character, which in the large bull-frog (*Rana pipiens*) is confined to the posterior part of the maxillary ramus is here continued to near the anterior extremity, and forms a conspicuous character of the jaw of the Labyrinthodon. The teeth in the present ramus are long and slender, and so closely correspond in size and shape with those in the upper jaw, just described, that they must be regarded as belonging to the same species.(1) There are not less than fifty sockets in a single linear series, and at the anterior inflected part of the jaw there is the base of the socket of a large tooth, six lines in diameter: the serial teeth gradually diminish in

(1) The specific name, *leptognathus*, relates to the slenderness of this long lower jaw.

size towards the anterior portion of the jaw; the posterior teeth, which are slightly compressed at their base in the antero-posterior direction, present at that part about a line and a half in diameter; the anterior ones measure half a line across the same part; the length of some of these small anterior teeth above the sockets is three lines, they are terminated by a sub-acute apex. The sockets do not lie between parallel lines; the alternate ones are placed a little more internally. The teeth were present chiefly in the more external sockets; but where they remained in both, the row of teeth presented the same slightly zig-zag disposition. The sockets of the teeth are more shallow in the present than in the preceding fossil; the outer alveolar wall is rather more developed than the inner, and the anchylosed bases of the teeth more nearly resemble in their oblique position those of the existing Batrachians. The teeth are directed slightly inwards, and are probably received, like those of the Menopome, into the interval between the maxillary and vomerine series of the upper jaw, when the mouth is closed.

The fine external striation and fluting is confined to the basal third of the tooth, as are also the labyrinthic inflections of the external cement. Above this part, the dentine consists of fine calcigerous tubes, radiating from the linear remains of the pulp-cavity at right angles to the surface of the tooth; being parallel with the axis of the tooth, where they form its apex, and gradually inclining outwards until they become transverse to that axis, which is their general disposition in the body of the tooth, between the apex and the commencement of the inflected vertical folds of the cement. At its apical part, therefore, the tooth of the *Labyrinthodon* resembles in the simplicity of its intimate structure that of the entire tooth of the ordinary Batrachia and of most reptiles. The vertical inflected processes of the cement are at first short and straight, occurring at pretty regular distances around the circumference of the tooth; so that here the tooth partakes of the structure which has already been said to characterize the base of the tooth of the Ichthyosaurus. Soon, however, the primitive inflected folds of cement sink deeper into the dentine and commence their undulating course, and as the tooth expands,

other processes, at first simple like the preceding, begin to penetrate the dentine at the interspaces of the primary folds; these likewise take on a sinuous course a little nearer the base of the tooth; the diverging plates of dentine send off lateral lobes or processes corresponding with these sinuosities, and a transverse section at this part of the tooth exhibits the modification of the labyrinthic structure exhibited in Pl. 63 B, fig 2.

The anchylosis of the base of the teeth to distinct and shallow sockets is a structure in which the Labyrinthodon resembles certain fishes, as the Sphyrena; I am disposed also to believe, from the absence of any excavation in the base of the fixed teeth, or of any trace of alveoli of reserve for the successional teeth, that these were developed, as in many fishes, in the soft mucous membrane or gum which covered the alveolar margin, and that they subsequently became fixed to the bone by anchylosis. Thus, notwithstanding the close resemblance to the Crocodilian type which the Labyrinthodon presents in the form and superficial sculpturing of the skull, it deviates widely in the mode of fixation and reproduction of the teeth. Nor is it extraordinary that the present extinct Batrachian genus should have its relations of affinity thus radiating in different directions, since we find in the extinct reptilian forms of a later epoch the combination of Saurian characters with Ichthyic vertebræ and extremities.

89. *Labyrinthodon pachygnathus.*—A second and larger species of Labyrinthodon is established upon certain fossils from the lower sandstones of Warwick, of which I shall here describe those that appertain to the dental system. The most instructive specimen is a well preserved and considerable proportion of the right ramus of the lower jaw, measuring nine inches and a half in length; the anterior extremity of this specimen is represented of the natural size at Plate 63 A, fig. 4 and 5. The bone is thick and rounded, one inch and a half deep, and one inch broad at the posterior fractured part, thirteen lines broad and eight lines deep at the anterior expanded and subdepressed end, which is curved inwards towards the symphysis of the jaw, and which supports two of the great cuspidate or laniary teeth, and the socket of a third. The structure of this lower jaw,

which was broken across into two nearly equal portions, was the first object of attention. On the inner side of the anterior moiety it appeared to be strengthened by an opercular piece in the form of a thin plate, gradually narrowing to a point, and terminating at the beginning of the inward curvature of the ramus (fig. 4). Two transverse fractures of this lower jaw display the relations of the external plate of the angular piece with the thin internal bony lamina; the two pieces are uninterruptedly confluent, and form a single broad and strong piece of bone, supporting the dentary piece upon a groove along its upper surface, and terminating anteriorly at the bend of the expanded premandibular or dentary element, which there receives the extremity of the angular bone in a notch; the batrachian character is thus as clearly established by the present as by the preceding fragment of the lower jaw. A similar portion of the lower jaw of a Saurian would have exhibited either the dentary element alone, or the anterior extremity of the opercular element in the form of a thin plate applied and limited to the inner side of the dentary piece. The continuation of the angular element alone, forming the lower half of the ramus, to near the symphysis, and supporting the dentary piece in a groove on its upper surface is as striking a Batrachian character in the fossil of the British sandstone, as that observed by Prof. Jaeger in the occipital bone of the great *Labyrinthodon* (*Salamandroïdes giganteus*) *Jaegeri* of the German Keuper.

The smaller serial teeth in the present portion of jaw are about forty in number, and their sockets are in close contact with each other; they very gradually diminish in size as they approach both ends of the series. Two of the smallest teeth (b^1) at the anterior part of the jaw are recumbent, in front of the great laniaries; they may have been incompletely developed teeth of replacement, not yet erected and anchylosed to the bone.

The alternate sockets are empty in a considerable portion of the posterior part of the series, agreeably with the order of shedding and renovation illustrated in the *Labyrinthodon leptognathus*, so that the teeth thus appear to be separated by wider intervals than they really are. The form of the teeth is conical, with the base slightly compressed in the direction of the axis of the jaw; the largest trans-

verse diameter of one of the posterior of these serial teeth, where it emerges from the socket, is three lines; the same diameter of the anterior serial tooth is one line and a half; its length, four lines and a half. The great laniary teeth (*a*) appear to be three in number in each symphysis, and the one nearest the symphysis is somewhat larger than the others, but they are probably not all in place and use at the same time. The greatest diameter of the sub-compressed base of the largest of these fangs is five lines; its length, judging from an entire tooth of the same species, must have been at least one inch and a half. The lines of the inflected cement form well marked longitudinal striæ around the basal half of the tooth, and the interspaces of the striæ form convex ridges, as in the large tooth, the labyrinthic structure of which was described at p. 201. These ridges are fewest near the termination of the striæ, being divided and multiplied by new longitudinal striæ, caused by new inflected folds of the cement near the basis of the tooth; the apical half of the tooth has a smooth and polished external surface; the pulp-cavity is continued of small size into the centre of this part of the tooth. In the serial teeth, which, except their less gradual diminution of size, correspond with the anterior larger tusks, the central pulp-cavity is more quickly obliterated; the texture of the teeth is dense and brittle.

I have examined the structure of the serial teeth in a small fragment of the upper jaw of the *Labyrinthodon pachygnathus*, from the same locality as the lower jaw; this fragment was three inches and a half in length, and included twenty-four sockets of the serial teeth, the alternate teeth being in place though broken. These teeth precisely corresponded in size and form with those of the lower jaw. The labyrinthic structure is confined to the basal half of the tooth, where it is indicated by the external striation, and becomes more complex as it approaches the base. The blending of the external layer of cement with the dentine, as exhibited by a transverse section of the tooth above this part, well illustrates the principle of the more complicated modifications of the labyrinthic structure first discovered. The processes of dentine which radiate from the pulp-cavity (Pl. 63 B, fig. 1, *a*), are twelve in number at the line of the section here described, but most of them divide in their course outwards; the corresponding pulp-fissures diverge in straight lines, bifurcate

where the lobes divide, and terminate each in a dilated cavity, or medullary canal, about half way between the centre and the circumference of the tooth. In like manner the inflected folds of cement (*b*, *b*), converging from the circumference of the section, proceed inwards in a straight line, half way or three fourths of the way to the central pulp-cavity; the commencement of the lateral inflection of one of the longest of these folds is shown at *b*. The inflected substance consists of a very thin layer of cement. The calcigerous tubes radiate according to the usual laws, and resemble in diameter, in the width of their interspaces, in their secondary undulations, their dichotomous bifurcations and small lateral branches, the same tubes in the complex labyrinthic structure of the tusk, figured in Plate 64 A. The exterior or first formed part of the basal portion of the tooth resembles the above described apical part in the comparative simplicity of the alternate folds of cement and processes of dentine; but the central mass of the basal moiety of the tooth presents the labyrinthic disposition of these tissues: it may be said that the simple exterior crust of the tooth incloses and is expanded by the more complicated structure. The thickness of the exterior more simple structure is nearly the same in the serial teeth and the large tusks, so that the proportion of the central labyrinthic mass is greater in the latter, and its structure is likewise more complicated. In the serial teeth of the *Lab. pachygnathus*, the structure of the basal half of the tooth resembles that of the same part in the *Lab. leptognathus*, which is figured as seen in transverse section at Pl. 63 B, fig. 2.

The alveoli, in both upper and lower jaws of the *Lab. pachygnathus* are large, moderately deep, but complete. The outer wall of the alveolar processes in the lower jaw of the *Lab. pachygnathus* is not higher than the inner wall. In this structure, therefore, as well as in the division of the alveolar groove into sockets, the Labyrinthodon manifests an affinity to the Crocodilian and Pleriosaurian reptiles; but, on the other hand, a similarly complete dental socket is present in certain Scomberoid and Sauroid fishes; and, as in these fishes, the base of the tooth is anchylosed to the socket in both the *Labyrinthodon pachygnathus* and *Lab. leptognathus*. A still more striking Ichthyic character is manifested by the *Lab. pachygnathus* in the continuation of the row of small teeth

anterior and external to the three larger teeth. For a double series of teeth, thus occasioned, does not exist in the maxillary or premandibular bones of any Batrachian or Saurian reptile; and, in the mammalia, the only instance of such a disposition of the teeth is the exceptional presence of the small incisors behind the dentes scalprarii of the hares and rabbits; but the location of large tusks in front or behind a row of smaller teeth is a character which has hitherto been met with only in the jaws of fishes. This, therefore, must be regarded as another of the Ichthyic characters which are retained in the lowest forms of reptiles, and which is thus manifested in a new way in the primeval Batrachians, whose dental characters and peculiarities we have been endeavouring to interpret.

CÆCILIA.

90. In the extinct family of the Labyrinthodonts the Batrachian type of organization was modified so as to lead directly from that order to the highest forms of reptiles, viz: the loricate or crocodilian Sauria; some of the existing edentulous genera of *Bufonidæ* connect the Batrachian with the Chelonian order; the family founded upon the Linnæan genus *Cæcilia* forms the transition to the Ophidian reptiles. The characters which retain the Cæciliæ in the Batrachian order are generally known, and may be briefly enumerated as the double occipital condyle, the biconcave vertebræ, the smooth mucous integument with minute and concealed scales, and the branchial apertures retained by the young some time after their birth. In the fixed tympanic pedicle and the anchylosed symphysis of the lower jaw the Cæciliæ are also far removed from the typical ophidian structures; but the teeth in their length, slenderness, sharp points, wide intervals and diminished number begin to exhibit the characters of the dental system of the serpent tribe (Pl. 65, figs. 1 & 2). They are implanted in a single row upon the maxillary, intermaxillary and palatine bones, the upper jaw being thus provided with two semi-elliptical and sub-concentric series; there are also two rows of equal-sized teeth on the premandibular bones of the lower jaw, in certain species; and the *Cæcilia* is the last example, in the ascending survey which we have taken of the dental

system, of this disposition of teeth, which was so common in the class of fishes.

There are twenty teeth in the anterior or outer premandibular row in the lumbricoid and white-bellied Cæciliæ, and ten or twelve, of much smaller size, in the second row. There are twenty teeth in the outer row of the upper jaw, of which six are supported by the intermaxillaries; and sixteen in the inner or palatine row. All these teeth are long, slender, acute and slightly recurved.

In the rostrated Cæcilia the first two teeth of the maxillary and premandibular series are longer and stronger than the rest; they are succeeded by small and recurved teeth; the median margins of the palatal bones are bristled with small teeth; the second row in the lower jaw is represented by two small recurved teeth on the internal border of the premandibular bones. In the modification of the dental system presented by this species may be perceived a retention of the Batrachian type.

The annulated Cæcilia (*Siphonops annulatus*, D. & B.) has the maxillary and palatine teeth strong, pointed and slightly recurved. In the glutinous and two-banded Cæciliæ, (*Epicrium*), the teeth are slender, acute and more inclined backwards, thus approaching nearer to the Ophidian type; in the latter species, (*Epicrium bivittatum*), the palatal series, instead of ranging concentrically with the outer row, is chevron-shaped with the angle turned forwards and rounded off.

The teeth of the Cæciliæ are sub-transparent; their intimate structure corresponds with that of the frog's tooth; but their mode of implantation resembles that of the teeth of the Labyrinthodonts, the base being anchylosed to the parietes of a shallow alveolus.

CHAPTER III.

TEETH OF OPHIDIANS.

91. The order Ophidia, as it is characterized in the system of Cuvier, requires to be divided into two sections according to the nature of the food and the consequent modification of the jaws and teeth. Certain species, which subsist on worms, insects, and other small invertebrate animals, have the tympanic pedicle of the lower jaw immediately and immoveably articulated to the walls of the cranium; the lateral branches of the lower jaw are fixed together at the symphysis, and are opposed by the usual vertical movement to a similarly complete maxillary arch above; these belong to the genera *Amphisbæna* and *Anguis* of Linnæus.(1) The rest of the Ophidians(2), which form the typical members and by far the greatest proportion of the order, prey upon living animals of frequently much greater diameter than their own; and the maxillary apparatus is conformably and peculiarly modified to permit of the requisite distention of the soft parts surrounding the mouth and the transmission of their prey to the digestive cavity.

The two superior maxillary bones have their anterior extremities joined, by an elastic and yielding fibrous tissue, with the small and single intermaxillary bone: the symphysial extremities of the lower maxillary rami are connected together by a similar tissue allowing of a still wider lateral separation. The opposite or posterior extremity of each ramus is articulated to a long and moveable vertical pedicle, formed by the tympanic or quadrate bone (Pl. 65, fig. 7, *e*), which is itself attached to the extremity of a horizontal pedicle formed by the mastoid bone (fig. 7. *f*.), so connected as also to allow of a certain yielding movement upon the cranium. The palatine (fig. 6 *c*) and pterygoid (*d*) bones have similarly loose and moveable articulations, and concur with the other dentigerous bones of the mouth in yielding to the pressure of the large bodies with which the teeth may have grappled.

(1) Pl. 65, figs. 3-5. (2) ib. fig. 6-15.

I shall first describe the dental peculiarities of the true Serpents, and afterwards notice those of the *Amphisbænæ* in connexion with the teeth of the *Anguis* and other serpentiform genera, which lead by a series of close transitions to the Saurian order.

All true serpents subsist on animal matter and swallow their food whole, whether they prey on living animals, as is the case in almost every species, or feed on the eggs of birds as in the *Deirodon scaber*, O., (*Coluber scaber*, Linn.)

With the exception of this and some congeneric species, in which the teeth of the ordinary bones of the mouth are so minute as to have been deemed wanting, the maxillary and premandibular bones in all true Ophidians are formidably armed with sharp-pointed teeth; there is on each side the palate a row of similar teeth supported by the palatine and pterygoid bones; in the great Pythons and some species of Boa the intermaxillary bone also supports teeth.

All the teeth, whatever be their position, present a simple conical form, the cone being long, slender and terminated by an acute apex, and the tooth is either straight, or, more commonly, bent a little beyond the base, or simply recurved, or with a slight sigmoid inflection. The teeth are thus adapted for piercing, tearing, and holding, and not for dividing or bruising. In some species certain teeth are traversed by a longitudinal groove for conveying an acrid saliva into the wounds which they inflict: in others two or more teeth are longitudinally perforated for transmitting venom; such teeth are called 'poison-fangs' and are always confined to the superior maxillaries, and are generally placed near the anterior extremity of those bones.

The serpents in which the teeth are all simple and solid, when the pulp which occupies the basal cavity is calcified, will be first noticed.

92. *Deirodon.*—In the genus *Deirodon*(1) the teeth of the ordinary bones of the mouth are so small as to be scarcely perceptible, and they appear to be soon lost, so that it has been described as edentulous. An acquaintance with the habits and food of this species has shown how admirably this apparent defect is adapted to its well-being. Its business is to restrain the undue increase of the smaller birds by

(1) Genus *Anodon* of Dr. A. Smith by whom the habits of the typical species have been well elucidated. The name *anodon* had been previously applied to a genus of Bivalves

devouring their eggs. Now if the teeth had existed of the ordinary form and proportions in the maxillary and palatal regions, the egg would have been broken as soon as it was seized, and much of its nutritious contents would have escaped from the lipless mouth of the snake in the act of deglutition; but, owing to the almost edentulous state of the jaws, the egg glides along the expanded opening unbroken, and it is not until it has reached the gullet, and the closed mouth prevents any escape of the nutritious matter, that the shell is exposed to instruments adapted for its perforation. These instruments consist of the inferior spinous processes of the seven or eight posterior cervical vertebræ, the extremities of which are capped by a layer of hard cement, and penetrate the dorsal parietes of the œsophagus; they may be readily seen, even in very young subjects, in the interior of that tube, in which their points are directed backwards. The shell being sawed open longitudinally by these vertebral teeth, the egg is crushed by the contractions of the gullet, and is carried to the stomach, where the shell is no doubt soon dissolved by the acid gastric juice.

93. *Boa.*—The simple teeth, 'dentes solidi' as they are termed in Erpetology, are of equal length in a few species of non-venomous serpents; in the Pythons, Boas and Lycodons they are larger towards the fore-part of the mouth; but in some Colubers and Tropidonotes the situation of the larger teeth is reversed. In *Dryophis* and *Psammophis* there are a few very long teeth at the middle, and again at the posterior part of the maxillary series. In *Xenodon*, *Coronella* and many species of *Homalopsis* the posterior part of each jaw is provided with a large and simple tooth, which is long and compressed in the *Xenodon*.

In the *Boa Constrictor*, the teeth are slender, conical, suddenly bent backwards and inwards above their base of attachment, with the crown straight or very slightly curved, as in the posterior teeth. The intermaxillary bone supports four small teeth; each superior maxillary bone has eight much larger ones, which gradually decrease in size as they are placed further back: there are eight or nine teeth of similar size and proportions in each premandibular bone. These teeth are separated by wide intervals, from which other teeth similar to those in

place have been detached. The base of each of the above teeth is extended transversely, compressed antero-posteriorly, and anchylosed to a shallow alveolus, extending obliquely across the shallower alveolar groove. An affinity to the Lizard-tribes is manifested by the greater development of the outer as compared with the inner wall of the alveolar furrow.

The palatine teeth, of which there are three or four in each palatal bone, are as large as the superior maxillaries, and are similarly attached: the pterygoid teeth, five or six in number, which complete the internal dental series on the roof of the mouth, are of smaller size and gradually diminish as they recede backwards. In the interspaces of the fixed teeth in both these bones, the places of attachment of the shed teeth are always visible, so that the dental formula, if it included the vacated with the occupied sockets, would express a greater number of teeth than are ever in place and use at the same time. In the smaller species of Boa the intermaxillary bone is edentulous.

94. *Python.*—The dentition of the great Java Python (*Python amethystinus*) is figured, after Cuvier, at Plate 65, fig. 6 and 7. The intermaxillary bone (*a*) is represented as supporting four teeth: the superior maxillary (*b*) as being armed with eighteen teeth, but of these the three which are situated on the inner side of the anterior part of the outer row are the successors of those teeth to which they are contiguous. No serpent has a double row of fixed and serviceable teeth implanted on the same bone.

The palatine bone, opposite to which is the letter *c* in fig. 6, supports six teeth; and the remaining eight teeth of the series are continued upon the pterygoid bone, *d*. The premandibular element of the lower jaw (fig. 7) is armed with eighteen teeth. In the tiger Python (*Python tigris*) the teeth are less numerous than in the great Python. The intermaxillary bone exhibits the places of attachment of four teeth, but I have rarely found more than two in place: these in their size and curvature resemble the posterior teeth of the maxillary series. There are about twelve teeth in each superior maxillary bone, which gradually diminish in size as they recede backwards; the number of sockets is eighteen. There are six sockets on each palatine bone, and generally four teeth in place; eight sockets on each pterygoid

bone, and five teeth in place: the mode of fixation of all these teeth corresponds with that in the Boa constrictor. Their direction prevents the escape of the prey in which they are once fixed; while the separate and independent movement of each half of both upper and lower jaw, and of the dentigerous bones of the palate, allows of the different series of teeth being successively withdrawn and implanted in a more advanced position in the prey, which is thus gradually drawn into the gullet, without the retaining force being unduly relaxed during any part of the engulphing process.

The teeth seem to be more numerous, or there is a greater number in place at one time in the young than the old individuals of the *Python tigris*: I have counted fourteen superior maxillary and fifteen premandibulars in place on each side of the mouth, in an individual of this species six feet in length.

The inner alveolar border is rather higher than the outer one in the palatine bones. The pterygoid teeth are continued along the middle of the inferior surface or towards the outer side of those bones, whilst in the smaller Colubriform serpents they are placed on the inner margin of the pterygoids.

The teeth of both the Python and Boa consist of a body of firm dentine coated by a layer of cement, which is extremely thin upon the crown, but becomes thicker towards the expanded and attached base of the tooth. The calcigerous tubes radiate according to the ordinary course from the central pulp-cavity to the periphery of the tooth: the superior and central tubes proceed in the axis of the tooth; those nearest to them incline outwards, deviating from the axis as they recede from the point of the tooth, until they run at right angles to the axis, which course they maintain throughout a great proportion of the tooth; hence a transverse section of the tooth, as magnified in Plate 65 B, fig. 1, exhibits the whole length of the calcigerous tubes. Their primary curvature is slight, with the concavity directed towards the base of the tooth: their secondary undulations are faint and regular through seven-eighths of their course, but the tubes become bent in stronger and less regular sinuous curves in the rest of their extent, where, alone, they divide dichotomously, the terminal branches frequently inosculating in loops, the convexity of which is

directed outwards, (Pl. 65 B. fig. 2). These sinuous terminations of the calcigerous tubes give a very peculiar appearance to the dentine of the Python, which, viewed by transmitted light in thin sections by a low power, seems, at first sight, to be invested by a thick layer of some distinct tissue, (fig. 1, *b*). Another character, which was detected by Retzius(1), is displayed by a longitudinal section of the dentine of the Python, when viewed by transmitted light with an objective of $\frac{1}{8}$th inch focus. It is the transmission from the lower or concave side of the main calcigerous tubes of numerous, minute, parallel and nearly straight branches, directed obliquely outwards and downwards. These minute branches are not only given off from the main calcigerous tube, but also from its primary branches, which differ from the dichotomous divisions of the calcigerous tubes in other teeth, in being much smaller than the main tube; they also run parallel with each other and are given off at an acute angle from the under side of the calcigerous tubes. The structure of the external layer of cement (*c c*, fig. 1, Pl. 65 B.) can only be examined in sections taken from near the base of the tooth, as its extreme thinness in the crown causes it to appear merely as a clear line bounding the peripheral loops of the calcigerous tubes. It appears to be more readily detached from the dentine where it is thickest at the base of the tooth than in other teeth: portions of it adhering to the section figured are shown at *c c*, fig. 1, Pl. 65, B. It is a clear substance in which the calcigerous cells are simple, very minute and inconspicuous.

95. *Coluber*.—The solid teeth of the smaller non-venomous serpents correspond in structure with those of the Python and Boa. In the *Erix turcicus* the largest and longest teeth are placed at the anterior part of the series, and they diminish as they recede backwards: this is the usual disposition. But in the common harmless snake (*Natrix torquatus*) the proportions of the maxillary teeth are reversed and the largest are at the posterior part of the series. In the *Coluber filiformis*, the teeth are equal and of small size.

The disproportionate length of the last maxillary tooth is characteristic of the colubrine genera *Dryinus*, *Dendrophis* and *Heterodon*; but the *Dryinus nasutus* has one tooth in the middle of the maxillary

(1) Loc. cit. p. 523, Pl. xxii, fig. 5.

series as long as that which terminates it. The colubers, like other true serpents, have two longitudinal rows of teeth on the roof of the mouth, extending along the palatines and pterygoids: the genus *Oligodon* appears to form the sole exception to this rule. In the *Dryinus nasutus* M. Duvernoy(1) has noticed a few small teeth on the transverse bone or external pterygoid, as well as on the internal pterygoid.

In certain genera of non-venomous serpents, as *Dryophis*, *Dipsas*, and *Bucephalus*, in which the superior maxillary teeth increase in size towards the posterior part of the bone, the large terminal teeth of the series are traversed along their anterior and convex side by a longitudinal groove. In the *Bucephalus capensis*(2) the two or three posterior maxillary teeth present this structure, and are much larger than the anterior teeth or those of the palatine or premandibular series; they add materially, therefore, to the power of retaining the prey, and may conduct into the wounds which they inflict an acrid saliva, but they are not in connection with the duct of an express poison-gland. The long grooved fangs are either firmly fixed to the maxillary bones or are slightly moveable according to their period of growth; they are concealed by a sheath of thick and soft gum, and their points are directed backwards. The sheath always contains loose recumbent grooved teeth, ready to succeed those in place.

In most of the *Colubri* each maxillary and premandibular bone includes from twenty to twenty-five teeth: they are less numerous in the genera *Tortrix* and *Homalopsis*, and are reduced to a still smaller number in the poisonous serpents, in the typical genera of which the short maxillary bone supports only a single perforated fang.

96. *Poisonous Serpents.*—The transition to these Serpents, which was begun in the *Bucephali* and allied genera with grooved maxillary teeth, is completed by the poisonous serpents of the genera *Pelamis*, *Hydrophis*, *Elaps*, *Bungarus* and *Hamadryas*, which latter genus, as

(1) Annales des Sciences Nat. tom. xxvi, p. 43.

(2) Having been favoured by Dr. A. Smith with specimens of the *Bucephalus Capensis* the results of my dissections are confirmatory of his own as regards the absence of a poison-apparatus in that snake: the ordinary salivary gland is large, especially at its posterior part which transmits its secretion by many pores into the sheath of the grooved fangs. The presence of a distinct poison-gland and duct communicating with the grooved posterior teeth requires to be established before the Serpents with these teeth can be ranked with the poisonous genera.

its cervical integument can be expanded into a hood, constitutes an immediate link between the *Bungarus* and *Naja*.(1)

The superior maxillary bone diminishes in length with the decreasing number of teeth which it supports: the transverse or external pterygoid bone elongates in the same ratio, so as to retain its position as an abutment against the shortened maxillary, and the muscles implanted into this external pterygoid style communicate, through it, to the maxillary bone the hinge-like movements backwards and forwards upon the ginglymoid articulations connecting that bone with the anterior frontal and palatine bones. As the fully developed poison-fangs are attached by the same firm basal anchylosis to shallow maxillary sockets, which forms the characteristic mode of attachment of the simple or solid teeth, they necessarily follow all the movements of the superior maxillary bone; when the external pterygoid is retracted the superior maxillary rotates backwards, and the poison-fang is concealed in the lax mucous gum, with its point turned backwards: when the muscles draw forward the external pterygoid, the superior maxillary bone is pushed forwards and the recumbent fang withdrawn from its concealment and erected.

In this power of changing the direction of a large tooth, so that it may not impede the passage of food through the mouth, we may perceive an analogy between the viper and the lophius; but in the fish the movement is confined to the tooth alone, and is dependent on the mere physical property of the elastic medium of attachment: in the Serpent the tooth has no independent motion, but rotates with the jaw, whose movements are governed by muscular actions. In the fish the great teeth are erect, except when pressed down by some extraneous force: in the Serpent the habitual position of the fang is the recumbent one, and its erection takes place only when the envenomed blow is to be struck.

The peculiar structure of the poison-fang was first described by Fontana as it exists in the viper(2), and subsequently received addi-

(1) Dr. Canter, Proceedings of the Zoological Society, 1838, p. 73.

(2) Fontana's description is as follows: "The tooth of the viper has a double pipe or tubule almost for its whole length, a circumstance hitherto entirely unknown to observers. These two

tional elucidation by Mr. Smith's careful examinations of the fangs of the Hydrus, Naja and Crotalus, and by Mr. Clift's illustrative drawings appended to Mr. Smith's Paper(1). A true idea of the structure of a poison-fang will be formed by supposing the crown of a simple tooth, as that of a Boa, to be pressed flat, and its edges to be then bent towards each other, and soldered together so as to form a hollow cylinder open at both ends. The flattening of the fang and its inflection around the poison-duct commences immediately above the base, and the suture of the inflected margins runs along the anterior and convex side of the recurved fang: the poison-canal is thus in front of the pulp-cavity. The basal aperture of the poison-canal is oblique and its opposite outlet is still more so, presenting the form of a narrow elliptical longitudinal fissure terminating at a short distance from the apex of the fang. The relative position of the two apertures of the poison-canal is shown in the figure of the fang of the large Cobra (Pl. 65, fig. 9), where a fine hair is represented as passing through the poison-canal: in figure 11, the relative position of the pulp cavity, *a*, to the poison-canal, *b*, *b*, is shown in the plan of a longitudinal section of a poison-fang.

The character most commonly adduced from the dental system as distinguishing the venomous from the non-venomous serpents is that the former have two, the latter four rows of teeth in the upper jaw: the two outer or maxillary rows being wanting in the venomous species and their place being supplied by the single poison-fang.(2)

canals or tubes do not communicate with each other, and are separated by a bony partition, very brittle towards the basis, but which becomes somewhat stronger in proportion as it advances towards the point. One of these tubes or canals, which I call the external one, because it is at the side of the convex part of the tooth, begins, as has been seen, at the basis of the triangular opening, and goes on enlarging by degrees to the middle of the length of the tooth, whence it gradually narrows, and ends at the elliptical opening of the point. The inner canal on the contrary, which is towards the concave part of the tooth, begins with a large opening at the basis, from whence it advances, closing by degrees, and terminates at length in a blind point above the middle of the tooth. The partition likewise that separates the two cavities is crooked, and its convex part is turned towards the hollow of the canal it terminates. The blind canal communicates with the socket in which the tooth is fixed, and receives vessels and nerves."—Fontana, On Poisons, Part I. Treatise on the Venom of the Viper, &c., translated by Skinner, 8vo. 2d Ed. 1795, p. 10. (The original Treatise was published in Italian, in 1765.)

(1) Philos. Trans. 1818.

(2) Compare figure 13, Naja, with fig. 6, Python, in Plate 65: the letter *b* shows the

The exceptions to this rule are, however, too numerous for its value as a distinguishing character in a question of such practical moment as the venomous or non-venomous properties of a serpent. In all the family of marine serpents the poison-fang is only the foremost of a row of fixed maxillary teeth: in the *Hydrophis striatus* (Pl. 65, fig. 14) there are four teeth, and in *Hydrophis schistosa* (fig. 15) five teeth, behind the venom-fang, of rather smaller size than it; the two-coloured sea-snake (*Pelamys bicolor*) has also five maxillary teeth in addition to the perforated one. The poison-fang, in this genus, is relatively smaller than in the venomous serpents of the land, but presents the same peculiar structure. The poison-gland presents a correspondingly small development; it is pyriform, and its structure, according to Dr. Canter(1), is minutely cellular; it is covered by the aponeurotic expansion of the *articulo-maxillaris* (Pl. 65, fig. 15, *e*, *f*), and transmits a straight duct horizontally to the basal opening of the venom-fang. It is a curious fact that the smaller non-venomous teeth of the poisonous serpents all present a trace of the structure of the functional venom-fang, being more or less deeply grooved along the convex anterior side;(2) and in the Hydrus this groove commences by a depression analogous to the oblique basal aperture of the poison-canal in the true fang.

The colubriform poisonous serpents of the land have comparatively short venom-fangs, but they are larger than those of the pelagic serpents; and behind the venom-fangs there are likewise some smaller grooved teeth in the maxillary bones: there are three such teeth in the *Bungarus Pama*, and five in the *Bungarus annulatus*. In the *Hamadryas* or great hooded poisonous tree-snake of India, the venom-fang is relatively as large as in typical poisonous serpents, but three or four smaller grooved teeth are implanted behind it on the maxillary bone.

In the most deadly venom-snakes, as the viper (*Berus*), the puff-

maxillary, and *c d* the palato-pterygoid series of teeth in both species. In the Naja the maxillary series is reduced to a single fang.

(1) Zool. Transactions, vol. ii, p. 304.

(2) The presence of similar grooved teeth in Serpents which are not armed with venom-fangs has already been noticed: such teeth are never found in the Boas and Pythons.

adder (*Vipera*), the asps or hooded-snakes (*Naja*), the rattle-snakes (*Crotalus*), the cophias and fer-de-lance (*Trigonocephalus*), the poison fangs acquire their largest size, and are associated only with their successors : these are clustered in greater or less number behind them, presenting the same structure, but of a size proportionate to their degree of development, and further differing in being loosely imbedded in the thick and wide mucous gum, which likewise conceals the fixed and functional fang in its ordinary position of retraction and repose. This fang is more strongly curved backwards than the ordinary teeth, but its acute and slender apex is frequently bent slightly in the contrary direction, as in the rattle-snake, (Pl. 65, fig. 8, *b*).

The mechanism by which the short maxillary bone and the poison-fang are rotated backwards and forwards upon the ginglymoid joint that connects the maxillary with the præfrontal and palatine bones has already been noticed, and, as some description of the secreting apparatus to which the peculiar modification of the venom-fang is subservient might here be expected, I have selected for its illustration the accurate figure which Prof. Muller has given of the salivary and poison-glands in the *Trigonocephalus lanceolatus* in his great work on the Glandular System.(1)

The poison-glands (Pl. 65, fig. 12, *a*) occupy the sides of the posterior half of the head ; each consists of a number of elongated narrow lobes, extending from the main duct which runs along the lower border of the gland, *a*, upwards and slightly backwards : each lobe gives off lobules throughout its extent, thus presenting a pinnatified structure ; and each lobule is subdivided into smaller secerning cæca, which constitute the ultimate structure of the gland. The whole gland is surrounded by a double aponeurotic capsule, *b*, *b*, of which the outermost and strongest layer is in connection with the muscles by whose contraction the several cæca and lobes of the gland are compressed and emptied of their secretion. This is then conveyed by the duct, *c*, in the course of the dotted line, *c*, to the basal aperture of the poison-canal of the fang. We may suppose, that as the analogous lachrymal and salivary glands in other animals are most active during particular emotions, so the rage which stimulates the venom-snake to use its deadly weapon

(1) De Glandularum Secernentium Structura Penitiori, fol. tab. vi, fig. 1, p. 55.

must be accompanied with an increased secretion and great distension of the poison glands; and as the action of the compressing muscles is contemporaneous with the blow by which the serpent inflicts its wound, the poison is at the same moment injected with force into the wound from the apical outlet of the perforated fang.(1)

The duct which conveys the poison, although it runs through the centre of a great part of the tooth, is, nevertheless, as we have seen, really on the outside of the tooth, the canal in which it is lodged and protected being formed by a longitudinal inflection of the parietes of the pulp-cavity or true internal canal of the tooth. This inflection commences a little beyond the base of the tooth, where its nature is readily appreciated, as the poison-duct there rests in a slight groove or longitudinal indentation on the convex side of the fang; as it proceeds it sinks deeper into the substance of the tooth and the sides of the groove meet and seem to coalesce, so that the trace of the inflected fold ceases, in some species, to be perceptible to the naked eye; and the fang appears, as it is commonly described, to be perforated by the duct of the poison-fang.

From the real nature of the poison canal it follows that the transverse section of the tooth varies in form in different parts of the tooth; at the base it is oblong, with a large pulp-cavity of a corresponding form, with an entering notch at the anterior surface; farther on, the transverse section presents the form of a horse-shoe, and the pulp-cavity that of a crescent, the horns of which extend into the sides of the deep cavity of the poison-fang, (Pl. 65, fig. 10): a little beyond this part the section of the tooth itself is crescentic, with the horns obtuse and in contact, so as to circumscribe the poison-canal; and along the whole of the middle four-sixths of the tooth the section shows the dentine of the fang inclosing the poison cavity, and having its own centre or pulp-canal, in the form of a crescentic fissure,

(1) The nasal salivary gland is shown at *d*, the labial gland at *e*: it is an enlargement of the posterior part of this gland in the Serpents with large posterior grooved maxillary teeth that has been mistaken (as in the *Bucephalus*) for a poison-gland. Besides the preceding glands the lachrymal glands placed behind the eye are often largely developed, and, by a direct course of their duct to the palatal region of the mouth, contribute likewise their secretion to the lubricating stream which is so much wanted and for so long a time in the difficult and gradual process of deglutition in the Serpent tribe.

situated close to the concave border of the inflected surface of the tooth. It is such a section of which a magnified view is given in Pl. 65 A. The pulp-cavity disappears, and the poison-canal again assumes the form of a groove near the apex of the fang, and terminates on the anterior surface in an elongated fissure.

If the end of each inflected fold of cement in the tooth of the *Labyrinthodon* were dilated sufficiently to contain a tube, that tooth might convey the ducts of fifty poison-glands deeply imbedded in its substance and yet all of them actually on the outside of the tooth itself: it is the existence of a single fold of the same kind, but more simple, inasmuch as it is straight instead of wavy, which forms the complication of the viper's fang subservient to the completion of its peculiar offensive weapon.

The venom-fangs of the viper, rattle-snake and fer-de-lance are coated only with a thin layer of a subtransparent and minutely cellular cement: the disposition of the calcigerous tubes is obedient to the general law of verticality to the external surface of the tooth; it is represented as seen in a transverse section from the middle of the fang in Plate 65 A. Since the inflected surface of the tooth can be exposed to no other pressure than that of the turgescent duct with which it is in contact, the tubes which proceed to that surface, *d*, while maintaining their usual relation of the right angle to it, are extremely short, and the layer of dentine separating the poison-tube from the pulp-cavity is proportionally thin. The calcigerous tubes that radiate from the opposite side of the pulp-cavity to the exposed surface of the tooth, are disproportionately long.

The pulp-cavity following the form of the tooth itself, presents in a transverse section of this part the form of a fissure describing four-fifths of a circle: the fissure is widest at the middle and at the two extremities: the exterior calcigerous tubes, in quitting the pulp-cavity, form a graceful curve, the convexity being turned towards the nearest horn of the crescent: at the middle of the pulp-fissure the tubes proceed straight to the opposite surface; and at the two extremities of the crescent the central tubes are nearly straight, while the lateral ones radiate in graceful curves which become bolder as they diverge from the central and straighter tubes. Throughout the greater

part of the tooth the calcigerous tubes describe their various inflections in a plane transverse to the axis of the tooth; but towards the apex they begin gradually to rise from that plane; and as the pulp-cavity re-assumes, with the tooth itself, the simple conical form beyond the termination of the poison-canal, the calcigerous tubes extend to equal distances from the linear remnant of the pulp-cavity, which has again passed to the centre of the tooth, and those tubes which are continued from its continued extremity, pass to the apex of the fang in a line parallel with the axis of the tooth. The calcigerous tubes present secondary curvatures of a slightly wavy character, which become more marked and irregular near their termination. In whatever part of the section an entire tube could be clearly traced to its termination, it formed an anastomotic loop at the periphery of the dentine with an adjoining tube. The calcigerous tubes present a diameter of the $\frac{1}{18,000}$th of an inch, and they are separated by interspaces equal to four of their own diameters. Each calcigerous tube gives off many primary branches in its course, but is rarely seen to divide dichotomously until it begins to form its irregular sinuosities near the periphery of the tooth. In the transverse section figured, the primary branches were sent off from the concave side of the tube, at an acute angle with the trunk: the secondary smaller and more numerous branches proceed from the same side of the main tube or of its primary branches, at a less acute angle, into the clear uniting substance; they are remarkably parallel with each other and straight. In old poison-fangs the pulp-cavity or fissure is obliterated by ossification of the remains of the pulp.

The external layer of cement is very thin where it covers the crown of the tooth; it is best seen at the line of union of the coadapted margins of the inflected tooth *c*. At this part the cement is more abundant in the viper's tooth, and its transparency permits a bristle inserted into the poison-canal to be seen through it. The layer which coats the inflected surface of the fang is thinner than the outer one, which, from its transparency, has been regarded as enamel.(1)

(4) " I should observe," says Mr. Smith, " that the poison-tube is not coated with enamel, for the capsule in which the tooth is formed, and from the inner surface of which it is well known that the enamel is deposited, does not pass between the edges of the slit into the poison tube; as,

There is, however, no trace of true enamel upon the teeth of the poisonous serpents any more than upon those of the innocuous species. The cells of the cement are more minute and inconspicuous in the poison-fang, than in the simple teeth of the Python and Boa.

The teeth of all Ophidians are developed and completed in the original seat of the tooth-germs in all animals; viz. the mucous membrane or gum covering the alveolar border of the dentigerous bones. This gum presents the same lax tissue and is as abundantly developed as in the Pike, Lophius, and many other fishes, in which it likewise serves as the nidus and locality for the complete development of the teeth.

The primitive dental papilla in the common harmless snake very soon sinks into the substance of the gum and becomes inclosed by a capsule. As soon as the deposition of the calcareous salts commences in the apex of the papilla, the capsule covering that part becomes ossified and adherent to the dentine, and the tooth begins to pierce and emerge from the gum, before its mould, the pulp, is half completed. Fresh layers of cells are successively added to the base of the pulp, and converted by their confluence and calcification into the tubular dentine, until the full size of the tooth is attained, when its situation in the gum is gradually changed and its base becomes anchylosed to the shallow cavity of the alveolar surface of the bone.

In the posterior part of the large mucous sheath of the poison-fang, the successors of this tooth are always to be found in different stages of development; the pulp is at first a simple papilla, and when it has sunk into the gum the succeeding portion presents a depression along its inferior surface, as it lies horizontally, with the apex directed backwards; the capsule adheres to this inflected surface of the pulp. But how the cylindrical cavity of the dilated fold is occupied in the loose growing poison-fang, and by what contrivance it is

however, it passes over that slit, it will cover it with enamel and in some cases by that means alone the edges become soldered together."—Philos. Trans. 1818, p. 473.

The author appears here to have been misled by the prevalent doctrines of dental development; no tissue of a tooth is *deposited from a surface:* a distinct convertible matrix or mould is as essential to the formation of enamel, as of cement or dentine, and unless such organ be developed from the inner surface of the capsule, no enamel can be formed.

brought into the same relation with the severed duct of the poison-gland as the displaced fang which it succeeds, is not yet clearly understood.

CHAPTER IV.

TEETH OF SAURIANS.

OPHISAURIANS.

97. There are several genera of reptiles which, like the true snakes, are externally devoid of locomotive extremities or have them indicated only by minute rudiments, but are covered by small uniform scales, and resemble the Saurians much more than the Ophidians in their anatomical structure, especially in the fixed condition of the jaws, which cannot be divaricated laterally or rotated backwards and forwards upon a moveable tympanic pedicle: these snake-lizards have always intermaxillary as well as maxillary teeth.

Amphisbænians.—In these snake-like reptiles there are, as in the true Saurians, both acrodont and pleurodont species: the greater number belong to the latter category and have their teeth applied against the internal surface of an external alveolar wall; but in the *Trogonophis*, the teeth are blended by their whole base with the alveolar ridge, and are so closely arranged, as to cohere together. They are unequal, conical, subcompressed and obtuse. The intermaxillary teeth are in unequal number, the middle azygos tooth being longer than the rest.

The teeth of the Cheirotes (*Lacerta lumbricoides*, Shaw,) are slightly curved, simple and nearly equal, excepting the azygos intermaxillary tooth which is longer than the rest: these are very small at first, but increase as they are placed backwards.

In the true *Amphisbænæ* the teeth present the form of short and stout cones, (Pl. 65, figs. 3 & 4): five are attached to the intermaxillary bone, of which the middle tooth is the longest; there are five teeth

on each superior maxillary, and eight on each premandibular bone; of these the first is short, and the second and third teeth are the longest.

Anguians.—The typical blind-worms have only maxillary and not palatine teeth. In the *Anguis fragilis* the first five of the upper teeth on each side are small, with cutting edges, and are situated on the intermaxillaries; the eight following teeth are much larger, pointed and recurved; they are separated by intervals: the teeth of the lower jaw correspond with those above. In general form, therefore, the teeth of the true *Anguis* adhere to the Ophidian type: but in the *Ophiomerus*, or miliary blind-worm, and in the *Acontias* they are conical, obtuse and straight: the teeth are likewise simple and conical in the sub-genera *Lerista*, *Ablepharus*, *Hysteropus*, *Dibamus*, *Typhlinus*, and the rest of the family of blind-worms.

The *Pseudopus Pallasii* has sixteen teeth on each side of the upper and twelve teeth on each side of the lower jaw; the latter form a continuous series; but a median interval separates the two lateral series in the upper jaw. In both jaws the anterior teeth are conical and obtuse, the hinder ones present a hemispherical triturating crown. The palate, in this genus, is armed with teeth which are small, conical and simple; and are arranged in one moderately long row on each side.

The glass-snakes (*Ophisaurus*) have both jaws provided with a close-set row of small simple teeth; and very remarkably repeat a dental character observable in certain Batrachians, especially the newts of the same continent to which these Ophisaurs are peculiar, viz. in having teeth at the roof of the mouth disposed in several rows, here chiefly supported by the pterygoids, and, in a small proportion, by the palatine bones. The teeth composing this palatal pavement are short and conical; the maxillary teeth are subcylindrical and simple. There are about twenty teeth on each side of the upper, and eighteen teeth on each side of the lower jaw, (Pl. 65, fig. 5).

In the *Pantodactylus* the palatal teeth have not been detected; and the maxillary teeth are slightly compressed, with a tricuspid crown. The intermaxillaries are conical and simple. These teeth are close-set and equal.

The *Ecpleopus* has a similar dentition to the *Pantodactylus*, ex-

cept that the maxillary teeth are unequal, and terminate in a simple obtuse summit. In the Monodactyle or Anguine Lizard (*Lacerta monodactyla*, Shaw, *Chamæsaurus*, D. & B.), these teeth are subcylindrical and obtusely pointed: like the two preceding genera the palatal teeth are absent. In the heterodactyle Chalcis the maxillary teeth are slightly compressed, straight and divided into two or three obtuse points. Those of the annulated Chalcis are conical and terminate in a simple obtuse summit. In both species the teeth are not implanted in sockets, but are applied to the inner margin of the alveolar ridge.

The common Zonure (*Zonurus griseus*,) has about twenty equal, conical, or subcylindrical obtuse teeth, on each side.

In *Tribolonotus* and *Saurophis* the intermaxillary teeth are conical; the maxillaries straight, subcylindrical and with obtuse summits. These genera are devoid of teeth on the roof of the mouth.

In the *Gerrhosauri* the intermaxillary and anterior maxillary teeth are conical as in the *Tribolonoti*, but the posterior teeth are compressed and terminate in a bilobed summit; and the Gerrhosaurs further differ in having a row of small conical teeth on each pterygoid bone.

The *Gerrhonoti* have the posterior maxillary teeth simply obtuse at the summit, and the pterygoid teeth are in smaller number.

The teeth in the genus *Bipes* (*Scelotes*, Fitzinger), are confined to the jaw-bones, and are conical and simple. The same dentition characterizes the genus *Seps*: the teeth of the *Seps chalcides* are very small, their obtuse apex just protrudes above the gum at the anterior part of the mouth; but they gradually increase in size as they are placed farther back.

SCINCOIDIANS.

98. Most of the Scincoid or smooth-scaled lizards have small mouths and slender sharp teeth, fitted apparently for merely insect food.

In the *Tropidophorus* the teeth are straight, cylindrical, simple, and slightly compressed at the summit: they are confined to the jaws. In the true Scinks (*Scincus*, D. & B.) of which the officinal Scink of ancient pharmacy is the type, the palate is also armed; four or five small obtuse teeth being placed on each pterygoid bone: the

maxillary teeth of this genus are conical, obtuse, and sometimes slightly incurved.

In the short-footed Scinks (*Sphenops*, Wagler), the palate is unarmed; and the maxillary teeth are conical, straight, pointed, and smaller and more numerous than in the common Scink. The Gallywasps (*Diploglossus*) have the jaws armed with equal, close-set, simple, conical teeth, sometimes subcompressed at the crown. The palate is edentulous. The teeth are compressed, with cuneiform crowns in most of the species of *Gongylus*, D. & B. In the sub-genus *Eumeces*, they are equal, conical and only slightly compressed at the summit. In the carinated scink, and its congeners (*Euprepes*) the pterygoids are armed with teeth: these are particularly numerous in the golden Scink (*Euprepes cyprius*), in which each pterygoid supports two rows of short, straight, strong conical teeth; the maxillary teeth resemble those of the other *Euprepes*. Cuvier(1) figures the cranium of a large species of Scink, allied by its short tail to the *Lacerta Scincoïdes* of Shaw, in which the maxillary teeth have expanded crowns with a dentated margin, (Pl. 66, fig. 5, 5*a*): the pterygoid teeth are wanting.

Cyclodus.—The present genus of Australian Scincoid lizards differs from the rest of the tribe in the subhemispherical form of the teeth, which resemble tubercles instead of more or less pointed cones, and the species manifest a corresponding difference in their habits and the nature of their food.

The dentition of the *Cycl. nigroluteus* is figured in Plate 66, fig. 7. The intermaxillary bone has depressions for twelve teeth, of which only the alternate ones are usually in place: they are of very small size, with the fang compressed laterally, and the crown antero-posteriorly, so as to resemble a true incisor in form, the summit sloping to an edge from behind forwards, with the middle of the cutting surface a little produced. Each superior maxillary bone has depressions for fourteen teeth; they quickly increase in size and exchange their conical for a sub-hemispherical crown: the eighth to the thirteenth inclusive are the largest teeth, they are set obliquely, and pretty close together. In the lower jaw there are two small incisors at the anterior part of each premandibular bone corresponding with

(1) Ossem. Foss. 8vo. 1836, t. x, p. 56.

those of the intermaxillary; these are succeeded by five or six conical teeth, and the rest correspond in size and form with the tuberculate molars of the upper jaw.

All the teeth are attached, after the pleurodont type, by their base and outer margin to shallow depressions on the outer side of the external alveolar parapet.

The germs of the successional teeth (*b b*, fig. 7), are developed at the inner side of the base of their predecessors, which they excavate, undermine, and displace in the usual manner.

I have not seen any specimens of this genus which had the branches of the lower jaw anchylosed at the symphysis. The pterygoid bones present a rugous surface at the place where they ordinarily support teeth.

CHAMELEONS.

99. The dental system, though by no means formidable, in the Chameleons, indicates a more substantial diet than the poets have assigned to these singular reptiles.

The teeth are conical, compressed, trenchant, with the summit simple or terminating in three points, arranged in the same longitudinal line: in most species the teeth gradually increase in size, and become wider apart as they are situated farther back upon the jaws. The teeth in place are so completely confluent with the alveolar plate as to appear, externally, to be mere processes of that border of the jaw; but their true nature is evident, when viewed from the inner side of the jaw.

The common Chameleon (*Ch. vulgaris*), has eighteen or nineteen teeth on each side of both jaws: and the five posterior ones have a tricuspid crown.

The two-horned Chameleon (*Ch. bifurcus*, Pl. 66, fig. 3), has about sixteen teeth on each side of both jaws, and they offer a marked disparity of size at the two extremes of each series: figure 3, gives a magnified view of one of the middle teeth, showing the mode in which it is anchylosed to the alveolar plate, and the contour of the transverse section of its base.

AGAMIANS.

100. The Agamoid Lizards, which are grouped together under the

generic name of *Uromastyx*, (Pl. 66, fig. 1) resemble the Chameleons in their dentition, which seems at first sight to consist of a merely notched or dentated margin of the jaw. These processes are, however, true teeth, developed originally as independent parts, and afterwards becoming confluent by their base and a great part of their outer side with the alveolar parapet of bone.

In the young of the Uromastyx there are from two to four anterior or intermaxillary teeth which subsequently become anchylosed together, so as to appear like one lobated tooth. In the lower jaw the crown of this complex tooth is received into a wide interspace between the two anterior teeth. The molar teeth are triangular or subcylindrical, with rather obtuse and subcompressed summits: they are approximated, and increase in size as they recede backwards. Pl. 66, fig. 1, shows the form of the teeth, as seen from the inside of the jaw, and the section below the figure demonstrates the thinning off of the base of the tooth produced by its oblique adhesion to the alveolar bony plate.

In the common Stellio most of the teeth, sixteen or seventeen on each side, are triangular, with a small cusp in front and behind; and there are two larger, conical teeth, like canines, at the anterior part of the upper and lower maxillary bones. The intermaxillary bones support two small conical teeth, which have no corresponding ones in the lower jaw. The little flying Dragons (*Draco*), have proportionally longer canines than the Stellios, but in other respects the dentition is the same.

The mutable Agamæ (*Trapelus*), resemble the Stellios in having two conical teeth longer than the rest commencing the series in the lower jaw and superior maxillary bones; but they have four small conical intermaxillary teeth, without corresponding teeth below; seventeen triangular teeth succeed the canines in the lower jaw and fifteen in the upper jaw in the *Trapelus ater*. The dentition of the *Agama orbicularis* resembles that of the Trapeli, except that the molar teeth behind the canines are more conical.

The inferior maxillary dental series commences in the common Calotes with four simple conical teeth, and in the upper jaw with six, of which the middle smaller ones might pass for incisors, and the

external ones for canines: behind these there is a series of molar teeth with compressed triangular and tricuspid crowns, the median cusp being much the largest of the three: these teeth increase in size towards the back part of the jaws.

GECKOTIANS.

101. In this family of nocturnal insectivorous Lizards the teeth are more pointed, more slender, more equable and more numerous than in the preceding group. The summit of the tooth is always simple: the base is obliquely soldered to the internal surface of an outer alveolar parapet.

In the smooth Gecko (*Thecadactylus lævis*, Pl. 66, fig. 4), there are about thirty-five such teeth, forming a close-set series on each side of both jaws; the first five or six above being supported on the intermaxillary bones, and being rather longer than the rest. In most of the posterior teeth the crown is slightly expanded, with a trenchant margin, as shown in fig. 44′; its transverse section is given below. In the flat-headed Gecko (*Ptyadactylus fimbriatus*, Cuv.) there are from seventy to seventy-four teeth on each side. In the House-Gecko (*Ptyadactylus Hasselquistii*) the teeth are slightly recurved. In the common Indian Gecko (*Ptyadactylus guttatus*, Cuv.) the teeth, with the exception of a few anterior ones, are rather cylindrical than conical, and are terminated by obtuse summits. None of the Geckos have teeth on the roof of the mouth.

IGUANIANS.

102. The lizards of this family are characterized like the preceding groups by a short contractile tongue, slightly notched at its extremity; but are distinguished for the most part by having teeth on the pterygoid bone, and also by the complicated form of the crown of the maxillary teeth in the typical genera, the species of which subsist chiefly on vegetable substances.

In most of the Iguanians the teeth are lodged in a common shallow oblique alveolar groove, and are soldered to excavations on the inner surface of the outer wall of the groove. MM. Dumeril and Bibron enumerate the following genera as exhibiting the pleurodont type of dentition, and as possessing likewise pterygoid teeth: viz.

Polychrus, *Urostrophus*, *Anolis*, *Corythophanes*, *Basiliscus*, *Aploponotus*, *Amblyrhynchus*, *Iguana*, *Metopoceros*, *Cyclurus*, *Brachylophus*, *Leiosaurus*, *Hypsibates*, *Proctotretes*, *Ecphymotes*, *Stenocercus* and *Oplurus*.

The following pleurodont genera of Iguanians have no pterygoid teeth, *Hyperanodon*, *Tropidolepis*, *Phrynosoma*, *Callisaurus*.

The Acrodont Iguanians include the genera *Istiurus*, *Calotes*, *Lophyrus*, *Otocryptis*, and *Chlamydosaurus* in all of which the maxillary teeth may be divided into anterior laniary and posterior molary teeth.

In the crested *Istiurus* of Amboina the four anterior simple conical teeth in both upper and lower jaws are very small and represent incisors; the six following teeth, three on each side, are larger, more sharply pointed and incurved; they are followed by thirteen molars with compressed, triangular, trenchant, but undivided crowns, which gradually increase in size as they are placed backwards; the posterior ones being strong teeth, separated by intervals.

In the blue *Calotes* may be distinguished five incisors in the intermaxillary bone, a median and two shorter ones on each side; a single long laniary and eighteen or nineteen tricuspid molars on each side of the upper jaw. In the lower jaw there are two canines on each side.

The molars are more close-set and numerous in the *Lophyri*, there being sometimes twenty on each side, these are obtusely tricuspid.

In the Otocrypt (*Otocryptis bivittata*) the intermaxillary bones each support a single tooth, which is conical and straight; the third in succession, in the superior maxillary bone, is a very large laniary, with a slightly recurved point. Of the twelve molars which succeed these, the anterior are small, simple and compressed; they increase in size and complexity as they recede backwards, the large posterior molars having three lobes, but the series is terminated by teeth of small size and simple form.

The *Chlamydosaurus* presents a similar dentition, but the teeth are relatively larger, and a greater proportion terminates in simple and pointed summits.

In the pleurodont Iguanians the teeth never present the true laniary form; and if simply conical, as at the extremes of the maxillary

series, the cone is more or less obtuse ; but in general it is expanded, more or less trilobate, or dentated along the margin of the crown.

In the *Polychrus*, the anterior score of teeth are simple, slightly recurved and obtuse; the remainder are straight, compressed and tricuspid. The pterygoid teeth form a single row on each bone, and are short and conical.

In the *Urostrophus Vautieri* (D. and B.) the upper jaw has forty-six, or forty-eight teeth ; the lower jaw forty or forty-two teeth : the anterior ten or twelve are conical with obtuse apices in both jaws ; the rest are tricuspid. The pterygoid teeth are six or eight in number in each bone, and present the form of moderately wide cones.

The Anolians have the same anterior conical, and posterior compressed tricuspid teeth as in the previous genera ; but the latter are relatively fewer in many of the species : in *Anolis loysiana*, for example, out of fifty-four teeth in the upper jaw only the eight or nine posterior ones are distinctly compressed and tricuspid : and this form is restricted to the hinder six or seven of the forty premandibular teeth. In the *Anolis chloro-cyaneus* fourteen of the sixty maxillary and twenty of the fifty-six premandibular teeth are tricuspid ; these are as usual at the posterior part of the series.

In the *Anolis Carolinensis* four or five of the posterior tricuspid teeth are sensibly larger than the rest. In the *Anolis alligator* (*Lacerta bimaculata*, Shaw), there are three or four short but strong teeth on each pterygoid bone. The *Anolis chamæleonoides* resembles the chameleons not only in external appearance, but in its dentition, in so far as that none of the teeth present the tricuspid form : the thirteen anterior ones are pointed, the others simply obtuse : there are sixty two upper and fifty lower teeth in this species.

The genus *Chamæleopsis* (*Corythophanes*, Boié) has the posterior teeth tricuspid as in the ordinary Anolises.

The dentition of the Basilisks differs little from that of the Anolis ; the posterior teeth are rather trilobate than tricuspid : the anterior ones are small, circular, pointed and slightly curved : there are generally from five or six conical teeth on each pterygoid bone, but in the Mitred Basilisk there are twelve teeth in each of these rows.

In the *Aploponoti*, the pterygoid teeth are arranged in two series on each side.

The *Amblyrhynchus*, a genus which is somewhat remarkable for the marine habits of at least one of the species, (*Amblyrhynchus ater*) whose diet is sea-weed,(1) has the tricuspid structure well developed in the posterior teeth, and these teeth are somewhat thicker than in the preceding Iguanians.

The typical genus of the present family of Saurians is characterized by the crenate or dentated margin of the crown of the maxillary and premandibular teeth, a few of the anterior small ones excepted; the pterygoid teeth are arranged in two or three irregular rows, resembling somewhat the ' dents en cardes' of fishes.

In the full-grown *Iguana tuberculata* there are from forty-seven to forty-nine teeth in both upper and lower jaws: the number is less in young subjects. The double row of pterygoid teeth are in close order on each side.

In the horned Iguana (*Metopoceros cornutus*, D. & B., Pl. 70, figs. 6 and 7) there are about fifty-six teeth in both the upper and lower jaw, of which the four first are conical and slightly recurved; the twelve succeeding teeth are somewhat larger in size, with more compressed and expanded crowns; the rest are triangular, compressed, with dentated margins. The inner surface of the crown of the tooth is simply convex and smooth, the outer surface traversed by a median longitudinal broad obtuse ridge.

There is a single row of small teeth implanted in each pterygoid bone (Pl. 68, fig. 2, *d*). No Iguanian lizard has teeth on the palatine bones.(2)

The teeth of the *Cycluri* differ from those of the *Iguanas* in being trilobate or bilobate and not crenate at the margin: the pterygoid teeth are in a single row.

In the *Iguana cyclura* of Cuvier there are thirty-six teeth in the

(1) This species, and probably all the known *Amblyrhynchi* or blunt-nosed Iguanæ, inhabit the islands of the Gallopagos group; their habits have been well elucidated by Mr. Darwin, (Voyage of the Beagle, vol. iii. p. 466): in specimens which he dissected he found the stomach loaded with minced sea-weed.

(2) For the purposes of zoology the expression ' palatine teeth' serves in general sufficiently to denote their existence, whether they be vomerine as in the Batrachia or pterygoid as in the Saurians; it is in this sense doubtless that the learned authors of the *Erpétologie Générale*, describe the teeth of the Iguana and other Lacertians as being situated on the ' os palatines.'

upper jaw and thirty on the lower jaw in full-grown individuals; but in a half-grown specimen M. Bibron found only twenty-six teeth both above and below, and in a still younger individual only twenty above, and eighteen below. The pterygoid teeth in this species are nine or ten on each side; small, slender, rounded, and they appear not to be constant, at least in young specimens.

The spiny-tailed Cyclurus has more numerous teeth; from fifty to fifty-six in each jaw.

The banded Iguana, which is the type of the genus *Brachylophus* of Cuvier, has between thirty-five and forty teeth in both the upper and the lower jaw, most of which are compressed and tricuspid: there is a slightly curved row of short and pointed teeth on each pterygoid bone.

The dentition of the allied genus *Enyalus* differs only in the larger proportion of simple pointed anterior teeth.

The Iguanoid *Hyperanodon*, as its name implies, has no pterygoid teeth.

Most of the maxillary teeth of the *Proctotreti* are equal, compressed, and trilobate, a few of the anterior ones being pointed. The pterygoid teeth are still smaller and are pointed.

The dentition of the Tropidolepes and of the toad-like Phrynosomes differs from that of the Proctotretes only in the absence of pterygoid teeth.

In the *Callisauri* all the maxillary teeth are simple, nearly equal and conical; here likewise there are no pterygoid teeth.

The insectivorous Ecphymotes have pterygoid teeth.

In the Doryphorus the dentition begins to exhibit a little more variety: the palate is edentulous; but in the upper jaw there may be distinguished eight incisives, three laminaries, and about fourteen molars on each side. The laniaries are a little longer than the others, rounded and slightly curved; both these and the incisors are separated by intervals: the molars have compressed, tricuspid crowns with the middle cusp longer than the rest.

The most strictly vegetable feeding reptiles are the true *Iguanæ* and the *Amblyrhynchi;* yet the size of the teeth, their mode of implantation and the limited motions of the jaws permit only an imperfect

comminution of the food by these instruments; and their summits are rather chipped off than ground down by use. The appearance of abrasion is greatest in the posterior teeth, especially in the *Iguana cornuta*, in which the crowns of the teeth are thicker than in the *Iguana tuberculata*, and make a nearer approach to the very remarkable form of tooth that characterizes the gigantic Iguanodon.

Before, however, proceeding to describe the teeth of this extinct lizard, I shall offer a few observations on the microscopic structure of the teeth of the existing Iguana. In both the common and horned species, the teeth consist of a body of simple compact dentine, with the crown covered externally by a thin layer of enamel, and the fang with an investment of cement. The dentine, viewed by transmitted light in a thin horizontal section, exhibits minute calcigerous tubes in a clear substance, radiating from a simple conical pulp-cavity, which is widely open at the base of the tooth and continues in a linear form into the crown of the tooth: the calcigerous tubes at the base of the tooth proceed in an irregular sinuous course at right angles to the axis of the tooth: above this part they sweep outwards in a graceful curve, with the concavity turned towards the base of the tooth: as they approach the summit of the tooth they gradually incline towards it, and those from the apex of the pulp-fissure proceed directly in the axis of the tooth: throughout their course the calcigerous tubes are disposed in minute undulations, and they send off from the concave side of the primary flexures numerous short parallel branches at an angle of 45°: these branches rise less regularly the nearer the main tube is to its origin from the pulp-cavity. The diameter of the calcigerous tubes is $\frac{1}{25,000}$th of an inch: their interspaces are equal to between three or four of their diameters.

In general they do not divide until within a short distance from the periphery of the tooth, near which they subdivide frequently; the terminal branches of the different layers decussate each other. The tubes at the base of the tooth divide nearer their origin and more frequently; which, with the large oblique branches, and the stronger undulations of the main tubes occasions the interwoven appearance represented at Pl. 65 B., fig. 3.

The pulp-cavity in old teeth becomes occupied by a coarse bone,

characterized by large irregularly shaped calcigerous cells, and the interspaces are filled with irregular moss-like reticulations of tubes, (ib. *a*). Branches of the pulp-cavity are never continued in the form of medullary canals into the substance of the dentine in the existing Iguanæ.

The arrangement of the tubes, as seen in a transverse section at the middle of the tooth is represented at Pl. 69, fig. 1; *b* is the tubular dentine, *c* the enamel. The secondary curves and terminal divisions of the calcigerous tubes are shown in fig. 3, but the small oblique secondary branches are not accurately expressed in this figure.

The germs of the successional teeth are developed from the mucous membrane covering the inner side of the base of those in place. The apex of the dentated crown is first formed; by its pressure it excites absorption of the base of the fixed tooth and soon undermines it, and then occupies the recess in the alveolar plate in the interspace of the two adjoining fixed teeth. After the crown is completed, the rest of the tooth forms a contracted and elongated fang, which at first is hollow, then becomes consolidated by ossification of the remaining pulp, and afterwards a second time excavated by the pressure of a new tooth.

IGUANODON.

103. The value of a knowledge of the comparative anatomy of the teeth, and especially of their external characters in the cold-blooded classes of animals, has never, perhaps, been placed in so striking a point of view as in the leading steps to the discovery of the present most extraordinary and gigantic reptile; these, therefore, I shall recount in the words of Dr. Mantell, to whom is due this splendid accession to the riches of Palæontology.

After noticing the ordinary organic remains which characterize the sandstone of the Tilgate forest, and his discovery, in the summer of 1822, of other teeth distinguished by novel and remarkable characters, the indefatigable explorer of the Wealden proceeds to state,

" As these teeth were distinct from any that had previously come under my notice, I felt anxious to submit them to the examination of

persons whose knowledge and means of observation were more extensive than my own. I therefore transmitted specimens to some of the most eminent naturalists in this country and on the continent. But although my communications were acknowledged with that candour and liberality which constantly characterizes the intercourse of scientific men, yet no light was thrown upon the subject, except by the illustrious Baron Cuvier, whose opinions will best appear by the following extract from the correspondence with which he honoured me.

" Ces dents me sont certainement inconnues ; elles ne sont point d'un animal carnassier, et cependant je crois qu'elles appartiennent, vu leur peu de complication, leur dentelure sur les bords, et le couche mince d'émail qui les revêt, à l'ordre des reptiles. A l'apparence extérieure on pourrait aussi les prendre pour des dents de poissons, analogues aux tétrodons, ou aux diodons : mais leur structure intérieure est fort différente de celles-là. N'aurions-nous pas ici un animal nouveau, un reptile herbivore ? et de même qu'actuellement chez les mammifères terrestres, c'est parmi les herbivores que l'on trouve les espèces à plus grande taille, de même aussi chez les reptiles d'autrefois, alors qu'ils étaient les seuls animaux terrestres, les plus grands d'entr'eux ne se seraient-ils point nourris de végétaux ? Une partie des grands os que vous possédez appartiendrait à cet animal unique, jusqu'à présent, dans son genre. Le temps *con*firmera ou *in*firmera cette idée, puisqu'il est impossible qu'on ne trouve pas un jour une partie de la squelette réunie à des portions de machoires portant des dents. C'est ce dernier objet surtout qu'il s'agit de rechercher avec le plus de persévérance."

" These remarks," Mr. Mantell proceeds to say, " induced me to pursue my investigations with increased assiduity, but hitherto they have not been attended with the desired success, no connected portion of the skeleton having been discovered. Among the specimens lately collected, some however were so perfect, that I resolved to avail myself of the obliging offer of Mr. Clift, (to whose kindness and liberality I hold myself particularly indebted) to assist me in comparing the fossil teeth with those of the recent lacertæ in the Museum of the Royal College of Surgeons. The result of this examination

proved highly satisfactory, for in an Iguana which Mr. Stutchbury had prepared to present to the College, we discovered teeth possessing the form and structure of the fossil specimens.

" Like the teeth of the recent Iguana, the crown of the tooth is acuminated; the edges are strongly serrated or dentated; the outer surface is ridged, and the inner smooth and convex; and, as in that animal, the secondary teeth appear to have been formed in a hollow in the base of the primary ones which they expelled as they increased in size.

" From the appearance of the fangs in such fossil teeth as are in a good state of preservation, it seems probable that they adhered to the inner side of the maxillæ, as in the Iguanæ, and were not placed in separate alveoli, as in the crocodile. The teeth appear to have been hollow in the young animals, and to have become solid in the adult. The curved teeth probably occupied the front of the jaw; and those which are nearly straight the posterior part." (1)

A subsequent discovery by Dr. Mantell(2) of a portion of the lower jaw of the *Iguanodon* confirmed the previous inference as to the mode of attachment of the teeth, and approximates the extinct gigantic species to the Pleurodont section of Iguanians; whence it may also be inferred that the teeth were all of nearly uniform size and shape, at least not divisible into laniaries and molars as in the Acrodont Iguanians.

The portion of jaw alluded to, which is now in the British Museum with the rest of the Mantellian Collection, shows that the Iguanodon differed from the Crocodile not only in the lateral adhesion of the teeth to an alveolar wall, but in their arrangement in a close-set series.

Besides the opportunity of studying this unique fossil and the extensive series of detached teeth in the British Museum, I have availed myself of the kindness of Dr. Mantell and Mr. Dixon of Worthing to examine the specimens in their private collections, and I have been favoured by both these gentlemen with Iguanodon's teeth from which I have had sections prepared for microscopical examination.

(1) Philos. Trans. 1825, Mr. Mantell, Notice on the Iguanodon.

(2) Wonders of Geology, vol. 1, p. 393.

The teeth of the Iguanodon, though resembling most closely those of the Iguana, do not present an exact magnified image of them, but differ in the greater relative thickness of the crown, its more complicated external surface, and, still more essentially in a modification of the internal structure, by which the Iguanodon equally deviates from every other known reptile.

As in the Iguana, the base of the tooth is elongated, contracted and subcylindrical; the crown expanded, and smoothly convex on the inner side; when first formed (Pl. 70, fig. 5) it is acuminated, compressed, its sloping sides serrated, and its external surface traversed by a median longitudinal ridge, and coated by a layer of enamel, but beyond this point the description of the tooth of the Iguanodon indicates characters peculiar to that genus. In most of the teeth that have hitherto been found, three longitudinal ridges traverse the outer surface of the crown, one on each side of the median primitive ridge; these are separated from each other and from the serrated margins of the crown by four wide and smooth longitudinal grooves. The relative width of these grooves varies in different teeth; sometimes a fourth small longitudinal ridge is developed on the outer side of the crown as in the small anterior Iguanodon's tooth in Plate 62 A, fig. 5, *a*.

The marginal serrations, which, at first sight, appear to be simple notches, as in the Iguana, present under a low magnifying power the form of transverse ridges, themselves notched, as shown in Pl. 62 A., fig. 5 e.(1) so as to resemble the mammillated margins of the unworn plates of the elephant's grinder: slight grooves lead from the interspaces of these notches upon the sides of the marginal ridges. These ridges or dentations do not extend beyond the expanded part of the crown: the longitudinal ridges are continued farther down, especially the median ones which do not subside till the fang of the tooth begins to assume its subcylindrical form.

The tooth at first increases both in breadth and thickness; it then diminishes in breadth, but its thickness goes on increasing (as shown

(1) This figure, and those numbered 5, 6, 8, 9 and 10, Pl. 62 A., are zincographed from drawings by Mr. Dinkel kindly communicated to me by Dr. Mantell for the present work.

in fig. 5, *c*); in the larger and fully formed teeth, the fang decreases in every diameter, and sometimes, as in the tooth fig. 5 *d*, tapers almost to a point. A fracture of this tooth shows that the pulp was not entirely solidified, but that its cavity had continued open at the thickest part of the tooth.

The apex of the tooth soon begins to be worn away, and it would appear, by many specimens like that in Pl. 70, fig. 3, that the teeth were retained until nearly the whole of the crown had yielded to the daily abrasion. In these teeth, however, the deep excavation of the remaining fang, represented in profile in the figure (ib. fig. 3) plainly bespeaks the progress of the successional tooth prepared to supply the place of the worn out grinder.

At the earlier stages of abrasion a sharp edge is maintained at the external part of the tooth by means of the enamel which covers that surface of the crown; the prominent ridges upon that surface give a sinuous contour to the middle of the cutting edge, whilst its sides are jagged by the lateral serrations (Pl. 70, figs. 1 & 2): the adaptation of this admirable dental instrument to the cropping and comminution of such tough vegetable food as the Clathrariæ and similar plants, which are found buried with the Iguanodon, is pointed out by Dr. Buckland with his usual felicity of illustration in his Bridgewater Treatise; Vol. i, p. 246.

When the crown is worn away beyond the enamel, it presents a broad and nearly horizontal grinding surface, and now another dental substance is brought into use to give an inequality to that surface; this is the ossified remnant of the pulp, which, being firmer than the surrounding dentine, forms a slight transverse ridge in the middle of the grinding surface: the tooth in this stage has exchanged the functions of an incisor for that of a molar, and is prepared to give the final compression, or comminution, to the coarsely divided vegetable matters(1).

The marginal edge of the incisive condition of the tooth and the median ridge of the molar stage are more effectually established by the

(1) A tooth, presented to me by Mr. Dixon of Worthing, exhibits this modification of its grinding surface.

introduction of a modification into the texture of the dentine, by which it is rendered softer than in the existing Iguanæ and other reptiles, and more easily worn away: this is effected by an arrest of the calcifying process along certain cylindrical tracts of the pulp, which is thus continued, in the form of medullary canals, analogous to those in the soft dentine of the Megatherium's grinder, from the central cavity, at pretty regular intervals, parallel with the calcigerous tubes, nearly to the surface of the tooth. The medullary canals radiate from the internal and lateral sides of the pulp-cavity, and are confined to the dentine forming the corresponding walls of the tooth: their diameter is $\frac{1}{1,250}$th of an inch: they are separated by pretty regular intervals equal to from six to eight of their own diameters; they sometimes divide once in their course. Each medullary canal is surrounded by a clear space: its cavity was occupied in the section described by a substance of a deeper yellow colour than the rest of the dentine.

The calcigerous tubes present a diameter of $\frac{1}{25,000}$th of an inch, with interspaces equal to about four of their diameters. At the first part of their course, near the pulp-cavity, they are bent in strong undulations, but afterwards proceed in slight and regular primary curves, or in nearly straight lines to the periphery of the tooth. When viewed in a longitudinal section of the tooth, the concavity of the primary curvature is turned towards the base of the tooth: the lowest tubes are inclined towards the root, the rest have a general direction at right angles to the axis of the tooth; the few calcigerous tubes, which proceed vertically to the apex, are soon worn away, and can be seen only in a section of the apical part of the crown of an incompletely developed tooth. The secondary undulations of each tooth are regular and very minute. The branches both primary and secondary of the calcigerous tubes are sent off from the concave side of the main inflections; the minute secondary branches are remarkable at certain parts of the tooth for their flexuous ramifications, anastomoses, and dilatations into minute calcigerous cells, which take place along nearly parallel lines for a limited extent of the course of the main tubes. The appearance of interruption in the course of the calcigerous tubes occasioned by this modification of

their secondary branches is represented by the irregularly dotted tracts in the figure (Pl. 71). This modification must contribute, with the medullary canals, though in a minor degree, in producing that inequality of texture and of density in the dentine, which renders the broad and thick tooth of the Iguanodon more efficient as a triturating instrument.

The enamel which invests the harder dentine forming the outer side of the tooth presents the same peculiar dirty brown colour when viewed by transmitted light as in most other teeth: very minute and scarcely perceptible undulating fibres, running vertically to the surface of the tooth, is the only structure I have been able to detect in it.

The remains of the pulp in the contracted cavity of the completely formed tooth are converted into a dense but true osseous substance, characterized by minute elliptical radiated cells, whose long axis is parallel with the plane of the concentric lamellæ, which surround the few and contracted medullary canals in this substance.

The microscopical examination of the structure of the Iguanodon's teeth thus contributes additional evidence of the perfection of their adaptation to the offices for which their more obvious characters had indicated them to have been destined.

To preserve a trenchant edge, a partial coating of enamel is applied: and, that the thick body of the tooth might be worn away in a more regularly oblique plane, the dentine is rendered softer as it recedes from the enamelled edge by the simple contrivance of arresting the calcifying process along certain tracts of the inner wall of the tooth. When attrition has at length exhausted the enamel, and the tooth is limited to its function as a grinder, a third substance has been prepared in the ossified remnant of the pulp to add to the efficiency of the dental instrument in its final capacity. And if the following reflections were natural and just after a review of the external characters of the dental organs of the Iguanodon, their truth and beauty become more manifest as our knowledge of their subject becomes more particular and exact.

"In this curious piece of animal mechanism, we find a varied adjustment of all parts and proportions of the tooth, to the exercise of

peculiar functions, attended by compensations adapted to shifting conditions of the instrument, during different stages of its consumption. And we must estimate the works of nature by a different standard from that which we apply to the productions of human art, if we can view such examples of mechanical contrivance, united with so much economy of expenditure, and with such anticipated adaptations to varying conditions in their application, without feeling a profound conviction that all this adjustment has resulted from design and high intelligence."—Buckland's *Bridgewater Treatise*, vol. 1, p. 249.

HYLEOSAURUS.

104. Dr. Mantell has discovered, in the limestone of the Tilgate forest the remains of a second gigantic reptile generically distinct from the Iguanodon and for which he has proposed the name of *Hyleosaurus:* of this species he observes " the teeth are unknown; but in the quarries where the bones of that reptile were discovered, I have found teeth of a very peculiar form, which appear to have belonged to a reptile, and are entirely distinct from those of the Megalosaurus, Iguanodon, Crocodile and Plesiosaurus, whose remains occur in the Tilgate strata."(1)

One of these teeth, which may be referred with much probability to the *Hylæosaurus*,(2) is figured of the natural size in Pl. 62 A. fig. 8. The fang of the tooth is subcylindrical, subelongate, smooth; the crown expanded, compressed, slightly incurved, with the narrow sides straight and converging at a slightly acute angle to the apex. In all these teeth which I have seen, these sloping sides show the effects of attrition: the enamel being worn away and the dentine exposed.

The tooth consists of a body of dentine covered by a thick coating of clear structureless enamel, and surrounding a small central column of true bone, consisting of the ossified remains of the pulp, which presents the

(1) Wonders of Geology, vol. 1, p. 403.

(2) They unquestionably do not belong, as has been supposed, to the Keuper genus *Cylindricodon* of Jaeger.

usual characters of the texture of the bone in the higher reptiles. The dentine differs, like that of existing Lacertians, from the dentine of the Iguanodon in the entire absence of the numerous medullary canals which form so striking a characteristic of the more gigantic Wealden reptile. The main calcigerous tubes are characterized by the slight degree of their primary inflections; they are continued in an unusually direct course from the pulp-cavity to the outer surface of the dentine, at nearly right angles with that surface, but slightly inclined towards the expanded summit of the tooth. They are chiefly remarkable for the large relative size of their secondary branches, which diverge from the trunks in irregular and broken curves, the concavity being always turned towards the pulp-cavity. In most parts of the tooth, the number of these branches obscures even the thinnest sections.

The ossified pulp exhibits the parallel concentric layers of the ossified matter surrounding slender medullary canals and interspersed with irregular elliptical radiated cells.

LACERTIANS.

105. The genera of the typical family of the squamate Saurians are arranged in two subfamilies by MM. Dumeril and Bibron, the chief characteristics of which are derived from the dental system.

In the first group, the teeth are solid, or without any internal cavity, and are very firmly anchylosed by their base to the alveolar groove upon the inner side of the jaw; so that the extremity of the tooth is slightly directed outwards: the species which present this character are called 'pleodont' Lacertians.(1)

In the second group, the teeth are excavated by a sort of canal, and are less firmly fixed to the jaws, being applied vertically, like piles or buttresses, against the outer alveolar parapet, but not adhering by their base: this group is called 'Cœlodonts.'(2) The group of Pleodonts includes the genera *Crocodilurus*, *Thorictes*, *Neusticurus*, *Aporomera*, *Monitor*, *Ameiva*, *Cnemidophora*, *Dicrodon*, *Acrantus* and *Centropyx*.

The Cœlodont Lacertians comprise the genera *Tachydromus*,

(1) πλεος, full. (2) κοιλος, hollow.

Tropidosaurus, *Lacerta*, *Ophiops*, *Calosaurus*, *Eremias*, *Scapteira*, *Acanthodactylus* and *Psammodroma*.

In the genus *Crocodilurus*, the intermaxillary bone supports eleven small, conical, simple teeth; behind which there are, on each side, from fifteen to seventeen maxillary teeth; these are of larger size, compressed, the first four or five pointed and slightly recurved; the rest straight and with the summit tricuspid, at least in young individuals: these hinder teeth have the form of rounded tubercles in old specimens. The teeth of the lower jaw resemble those above: there are about twenty-two on each side.

The intermaxillary teeth of the bicarinated Lizard (*Thorictes Dracœna*, D. & B.) are nine in number, conical, slightly compressed from before backwards: there are about ten superior maxillary teeth and twelve inferior maxillaries on each side: the first four or five in both jaws are conical, but with obtuse summits, the posterior ones present the form of very large tubercles, (Pl. 66, fig. 5).(1)

The intermaxillary teeth of *Neusticurus* are twelve in number, of a simple conical form: there are twenty-two maxillary teeth on each side, compressed, all obtusely tricuspid. The lower jaw supports thirty-five teeth on each side: the first five or six being conical, and all the others flattened laterally, and divided into three obtuse cusps.

In the *Aporomera*, the intermaxillary teeth are small pointed cones slightly recurved: the maxillary teeth and the corresponding teeth of the lower jaw are long, strong, separated, pointed, arched

(1) "Il est très-probable qu'à une époque moins avancée de leur vie les Thorictes, de même que les Sauvegardes, chez lesquelles l'âge rend les dents maxillaires postérieures tuberculeuses, ont *ces mêmes dents*, plus ou moins comprimées et divisées à leur sommet, soit en deux soit en trois points mousses, (p. 52, tom. v., Dum. and Bib. Erpetology). That the same tooth should change a bicuspid or tricuspid for an obtuse crown through the attrition to which they are subject during life, and thus exhibit a tubercular character in age might be conjectured with great probability of a mammiferous animal, as, indeed, such a circumstance not unfrequently occurs in that class, in which the teeth are replaced in vertical succession but once, and the second series are long retained: but that such change of form and function should take place in the same tooth seems incompatible with the physiological laws of dental decadence and reproduction in the cold-blooded animals. No doubt the young *Dracœnæ* have their teeth fitted for insect food; but these are probably shed, and the molar type gained by a succession of new teeth.

and compressed transversely to the axis of the jaw; the anterior ones are simple, the posterior have a notch on their anterior margin near their apex. There are two rows of four or five pretty strong conical teeth, one on each pterygoid bone bordering the posterior nasal aperture.

In the *Apor. ornata* (*Ameiva ornata*, D'Orb.) there are four or five strong teeth on each pterygoid bone.

In the genus *Cnemidophorus*, of which the *Ameiva murina*, Cuv. is the type, the intermaxillary teeth are generally ten in number, the maxillaries vary from eighteen to twenty-two on each side, the premandibulars from twenty-two to thirty, the posterior being tricuspid, the others simple and compressed; the pterygoids are dentigerous.

In an allied species of *Ameiva* the maxillary teeth, instead of being compressed and tricuspid, are slightly flattened in the axis of the jaw, and their summits are bifid: whence it has been proposed to separate it generically under the name of *Dicrodon*.

The maxillary teeth of the *Acrantus* have a similar form: their large crown is excavated by a longitudinal furrow continued from the interspace of the cusps: but the pterygoids support teeth, which have not been found in *Dicrodon*. In the green Ameiva (*Acrantus viridis*, D. & B., *Tejus viridis*, Merrem) the pterygoid teeth are arranged two or three in number, on each side the posterior palatal fissure: they are small, conical and straight. The teeth, in some species of this genus, are finely dentated in the young individuals, whence Wagler proposed the name of *Ctenodon*, supposing the character to be peculiar to and permanent in them.

The intermaxillary teeth are ten in number in the Teguixin (Grande Sauvegarde d'Amérique, Cuv.); the maxillary teeth are thirteen or fifteen on each side, and gradually increase in size as they are situated further back in the jaw: the posterior teeth are tricuspid in young individuals and present the form of simple tubercles in the old. The inferior maxillary teeth, fifteen to eighteen on each side, correspond in size and form to those above.

In the common or side-streaked Ameiva (*Ameiva vulgaris*, Lichtenstein) there are twelve intermaxillary teeth, slightly separated; eighteen to twenty-four maxillary teeth on each side; and twenty to

twenty-eight premandibular teeth. All the teeth save the eight or ten anterior ones have their summit divided into three points, which in the earlier teeth are sharper than in the later ones.

In the genus *Centropyx* some species, as the *Centr. striatus*, have a few small pterygoid teeth on each side the palatal fissure: the maxillary and intermaxillary teeth resemble those of the genus *Cnemidophorus*.

In the cœlodont group of Lacertians the 'Swift Lizards' (*Tachydromus*) have the pterygoid bones armed with very small teeth, more easily felt than seen: there are ten small, pointed, slightly recurved intermaxillary teeth: twenty-six maxillaries on each side, and about thirty premandibular teeth. The teeth in both jaws are closely arranged, and the posterior ones are tricuspid.

The dentition of the Tropidosaurs resembles that of the Tachydromes: some species, as the *Algira*, have small pterygoid teeth. The true Lizards, like the other Cœlodonts, have two kinds of teeth, the anterior small, conical and recurved, the posterior larger, subcompressed and bi-or tricuspid: the pterygoid teeth are occasionally present, but are not constant either in the species of the genus or the individuals of the species. There are commonly eight or ten intermaxillary teeth; from thirty to thirty-six maxillary teeth on each side, and about forty teeth in each premandibular bone.

The viviparous Lizard (*Zootoka crocea*) has no pterygoid teeth: the common Lizard (*Lacerta agilis*) has about twelve conical pterygoid teeth on each side of the palatal opening. In this species may be counted from eleven to thirteen intermaxillary teeth; forty teeth in each superior maxillary bone, and fifty teeth in each premandibular bone.

The *Lacerta ocellata* and the *Lacerta Galloti* both have twelve small conical obtuse pterygoid teeth on each side of the palatal fissure.

The remaining subgenera of cœlodont Lacertians have teeth on the jaws like those of the preceding species; but they have no pterygoid teeth.

MOSASAURUS.

106. One gigantic extinct species of Saurian Reptile has been found to agree with many of the species above cited in the Lacertian, Iguanian, Anolian and Scincoid families of existing Saurians in having the pterygoid bones armed with teeth: but the maxillary teeth combine the pleodont with the acrodont characters; and the skeleton indicates a special adaptation for swimming and a marine life.

The true affinities of the Mosasaur, the extinct reptile in question, which was at least twenty-four feet in length, and the remains of which characterize the chalk-formations, were first determined by Cuvier, who places it in the Lacertine group of Saurians between the Iguanæ and Monitors. Its dentition exhibits in an eminent degree the acrodont character; the teeth being supported on expanded conical bases anchylosed to the summit of the alveolar ridge of the jaws: no existing Saurian exactly parallels this mode of attachment of the teeth, either in regard to the breadth of the alveolar border, or in the relative size of the osseous cones to the teeth which they support. A shallow socket is left where the tooth and its supporting base are shed. The form of the teeth is likewise different from that hitherto observed in any existing Saurian: they are pyramidal, with the outer side nearly plane, or slightly convex, and separated by two sharp ridges from the remaining surface of the tooth which forms a half-cone; the transverse section of the tooth near its attachment to the osseous base presenting the contour given at Pl. 72, fig. 5. All the teeth are slightly recurved and their peripheral surface is smooth. The teeth are implanted upon the intermaxillary, maxillary and premandibular bones; a series of similarly shaped but much smaller teeth are placed upon the pterygoid bones. The superior maxillary bone in the great cranium preserved in the Parisian Museum—the most celebrated fossil of the present species—contained eleven teeth: Cuvier calculates that the intermaxillary bone may have contained three teeth; meaning probably three on each side: the premandibular element of the lower jaw supported fourteen teeth: the number of the teeth thus approximating to that which characterizes the *Varanus Nilo-*

ticus. They are arranged in a pretty close and regular series. There appear to have been eight teeth on each pterygoid bone.

In the mode and place of development of the successional teeth, the Mosasaurus resembles the Iguanæ and most other Lacertians. In the great cranium above mentioned germs of new teeth in various stages of growth are lodged in hollows of corresponding degrees of depth on the inner side of the bases of the adherent teeth, and have evidently owed the commencement of their formation to the mucous membrane which originally covered those supporting cones of the teeth in place. The attention of Camper was particularly arrested by the observation of this fact, which appeared the more singular to him as this mode of dental succession, which is common in reptiles and osseous fishes, was not then known.

" The dentition is so singular," he says, " in these fossil jaws that it deserves a particular description. A small secondary tooth is formed complete with its enamel and solid root in the osseous substance of the temporary tooth: in the progress of its growth it seems gradually to form a cavity of corresponding size in the osseous root of the primitive tooth; but it is impossible for me to decide what next befalls it, or in what manner it is shed."

The crown of the tooth consists of a body of simple and firm dentine, invested with a moderately thick coat of enamel; the expanded base is composed of a more irregular mass of dentine which, by its progressive subdivision into vertical columnar processes, assumes a structure resembling that of true bone: this part is covered with a layer of cement, which is continued as an extremely thin coat upon the enamel.

The pulp-cavity generally remains open at the middle of the base of the crown of the tooth; irregular processes of the cavity extend, as medullary canals into the conical base of the tooth; but no processes of the pulp-cavity are continued, as in the Iguanodon, into the substance of the coronal dentine. This substance consists, as in the Crocodile, of fine and close set calcigerous tubes, arranged according to the usual law; and much resembling that of the tooth of the varanian Monitor figured in Pl. 67: the calcigerous tubes have a diameter of $\frac{1}{16,000}$th of an inch: with interspaces equalling about four of these dia-

meters : their secondary curvatures and branches resemble those in the tooth of the Varanus : the commencement of the subdivision of the mass of dentine, by the divergence of the calcigerous tubes from secondary centres, after quitting the main pulp-cavity, is shown in the reduced figure of a magnified view of the half of a transverse section taken from near the base of the enamelled crown at Pl. 69, fig. 3, at the lobe marked *b*, and the adjoining lobe: the curvilinear diverging extremities of the calcigerous tubes terminate in fine cells. The fibrous structure of the enamel is very conspicuous in the tooth of the Mosasaur, the lines to which this structure is due seem to be continued from the peripheral cells of the dentine ; and they bifurcate repeatedly as they traverse the enamel.

This subdivision of the pulp-cavity, and multiplication of centres of radiation for the calcigerous tubes increase until the piles of dentine can be scarcely distinguished from the Haversian canals of the bone of the jaw with which the root or base of the tooth is confluent. The gradual transition from the simple structure of the compact crown to the multifid dentine of the anchylosed base of the tooth was not known to Cuvier, otherwise he could not have supposed that the crown and the base of the tooth of the Mosasaurus were formed by vital processes of so dissimilar a nature as to forbid him considering them as parts of one and the same body. Cuvier had originally described the expanded base of the tooth of the Mosasaur as the root of the tooth ; but afterwards observing that the corresponding base became anchylosed by ossification of the remains of the pulp with the jaw, he conceived it to be incorrect to regard it as a part of a body which he believed to be an inorganic product, and the result of excretion. " The tooth," he observes, in correcting his first account of the Mosasaurus, " has no true root, but it adheres strongly to that pulp which has secreted it and it is further held in connection with it by the remains of the capsule which has furnished the enamel, and which by becoming ossified also, and uniting itself to the maxillary bone and the ossified pulp, implants or rivets the tooth with additional force."(1)

(1) La dent n'a point de vraie racine, mais elle adhère fortement à ce noyau qui l'a sécrétée, et elle y est encore retenue par le reste de la capsule qui avait fourni l'émail, et qui, en

The necessity under which Cuvier felt himself compelled to regard the crown and the base of the tooth of the Mosasaur as two distinct parts, is at once banished by the recognition of the principle, that the processes of calcification are essentially the same at every part of a tooth, whether it be free or anchylosed; and that they are modified only, as I have shown in my Memoir on the formation of the teeth of the shark,(1) according to the density of the part to be produced.

107. *Leiodon.*—In the English chalk-formations a few vertebræ have been found which are generically, if not specifically related to the Maestricht Mosasaur; but as yet the only teeth which approach in form to those of this genus are those from the Norfolk-chalk alluded to by Dr. Mantell in his "Wonders of Geology," (vol. 1, p. 339) as belonging to an unknown reptile or to a sauroid fish. The portion of the jaw to which they were attached exhibits the mode of attachment of the teeth, which so closely corresponds with that of the Mosasaur as to leave scarcely any doubt of their near relationship: it is by no means improbable that this fragment of jaw and teeth may belong to the same species as the vertebræ above alluded to; for these essential parts of the organization would retain their generic characters little if at all altered in a species of Mosasaurus that might be distinguished from the Maestricht fossil and be characterized by well marked modifications of the form of the teeth. Until, however, this conjecture be refuted or confirmed, the reptile, to which the teeth in question belonged, may be indicated by the name of *Leiodon*(2), in reference to the smooth and polished surface of the teeth. The fossil to which the foregoing observations refer is figured, of the natural

s'ossifiant aussi et en s'unissant, et à l'os maxillaire et au noyau devenu osseux, enchâsse et sertit la dent avec une nouvelle force." Cuvier proceeds to remark, "On conçoit très bien que ce noyau, identifié avec l'os maxillaire puisse, subir les mêmes changemens que lui; que l'alvéole de la dent de remplacement puisse pénétrer sa solidité; que la compression puisse le détacher, soit en le cassant, soit en oblitérant les vaisseaux qui le nourrissent; en un mot, qu'il soit exposé à des révolutions analogues, comme je l'ai dit, à celle du bois des cerfs, mais très différentes de celles qu'éprouve la dent qui est toujours un corps devenu étranger à l'animal qui l'a sécrété, ainsi que je l'ai démontré, après Hunter, dans mon chapitre sur les ossemens d'éléphans."—Ossem. foss. Ed. 1836, vol. x, p. 136.

(1) Comptes Rendus, Dec. 16, 1839.

(2) λειος, smooth; ὀδους, a tooth.

size, at Pl. 72, fig. 1 & 2. The teeth are about one half the size of those of the *Mosasaurus Hoffmanni;* they differ in having their outer side as convex as the inner side, the transverse section of the crown being elliptic with the ends of the ellipse pointed as in fig. 1, the points corresponding with two opposite longitudinal ridges, which separate the outer from the inner side of the tooth: the tooth is very slightly incurved; the line of its anterior margin is convex, that of the posterior one is nearly straight. The teeth are well adapted, by their form, for piercing and cutting; their summits are sharp-pointed, and their margins trenchant: the anterior edge is most produced. The crown of the tooth is compressed but gradually expands, so that its base is circular, as represented at fig. 1, *b*. This is supported, as in the *Mosasaurus*, upon a round hillock of bone resting upon the broad alveolar surface of the jaw. The close arrangement of the supporting bases of the teeth in this acrodont reptile gives a crenate outline to the margin of the jaw.

The teeth, in the state in which they have come under my observation, exhibit very strikingly the lamellar decomposition of the dentine, upon which one of the arguments for the excretion-theory has been founded(1). Fig. 2 shows the concentric arrangement of these lamellæ at the base of the crown of a fractured tooth, the centre of which contains a wide pulp-cavity, occupied by the chalk matrix: this structure is also exhibited at fig. 1, *b*; it probably depends upon the immature state of the tooth's formation.

The crown of the tooth is defended, as in the Mosasaur, by a coat of enamel.

108. *Geosaurus.*—The teeth of an extinct reptile, whose large eyes, defended by broad sclerotic plates, indicate the sea to have been its abode, but which has received the name of *Geosaurus* from Cuvier, resemble those of the large Varanian lizards in their com-

(1) According to the Report in the Literary Gazette, 1839, Sept. 21, p. 598, this argument, founded upon the appearances presented by the mammoth's tusks when in a state of lamellar decomposition, was brought forward by the author of the paper on the structure and development of teeth communicated to the British Association at Birmingham, in refutation of Dr. Schwann's hypothesis of the formation of ivory by ossification of the pulp. The fallacy of the argument was shown in my memoir in the 'Comptes Rendus' of the December following.

pressed sub-recurved crown, with a trenchant anterior and posterior edge, which likewise presents a fine and close dentation. In the best preserved cranial fragment of this reptile, (which is now in the British Museum), fourteen or fifteen of these teeth may be counted in the left upper maxillary bone; and a fragment, apparently belonging to the same jaw, exhibits three additional teeth: the posterior of these teeth, which, extend below the orbit, are smaller than the rest. The fragment of the premandibular bone contains five teeth.

The crown of the teeth is covered by a coat of remarkably smooth and polished enamel, which presents the same brown tint as that of the glossopetræ or fossil shark's teeth. Soemmering conjectured that the Geosaurus might be a young individual of the Mosasaurus, but Cuvier justly observes that the teeth of the Mosasaurus differ from these of the Geosaurus in their greater breadth, especially from side to side; and in the non-dentated character of the ridges which divide the internal convex from the external flattened side of the crown.

The form of the vertebræ of the *Geosaurus* indicates its near affinity to the crocodilian group, and the Argenton fossil crocodile presents the same subcompressed teeth with dentated trenchant margins, as does the Geosaurus.

VARANIANS.

109. The Varanian family of squamate Saurians, which includes the Monitors of the old world, and in which some of the species approach nearest in size to the Crocodiles, manifests its affinity to that group in the absence of pterygoid teeth, and in the number of successive tooth-germs which may be observed at the same time behind the fixed and functional teeth.(1) Besides these characters the Varanians must excite our interest from exhibiting in some species a form of tooth which most nearly resembles that which characterizes the Megalosaurus and other very remarkable extinct terrestrial species of gigantic squamate Saurians.

In a small species of extinct Lizard, referable to the present family, from the gault and chalk-formations, the teeth were awl-

(1) Pl. 63 A, fig. 9, *Varanus variegatus.*

shaped, i. e. slender, round, slightly incurved, and sharp-pointed: about three lines in length above the alveolar border, close-set, and equal sized. Their rounded base is anchylosed to the alveolar groove, and their outer side attached to a well developed external alveolar wall. I have proposed for the new genus of Lizard indicated by these remains the name of *Raphiosaurus*.

The following are the principal varieties which the existing Varanians exhibit in the form of the teeth.

The teeth of the *Heloderm* are slender, almost straight, sharp-pointed, and with a deep fissure.

In the monitor of the Nile (*Varanus niloticus* Pl. 68, fig. 4) there are four teeth in each intermaxillary and eleven in each maxillary bone: in the lower jaw there are eleven teeth in each premandibular bone. The posterior of these are obtuse tubercles in old specimens, but all the other *Varani* have trenchant teeth, often with dentated margins. The teeth are always obliquely bevelled off at the root, which is lodged in a common groove with the internal border slightly developed.

In the land Monitor (*Varanus arenarius*) the teeth are of moderate size, slightly compressed and a little curved backwards.

In the *Varanus Timoriensis* there are about thirty teeth adhering to the internal margin of the upper jaw and from twenty to twenty-two in the lower jaw: they are well spaced, compressed, pointed, slightly curved, trenchant but not dentate.

The teeth of the Dracæna lizard of Shaw (*Varanus bengalensis*, D. & B.), are neither trenchant nor dentate, but moderately compressed; short and strong, the anterior ones especially. There are thirty of these teeth in the upper jaw and twenty-four in the lower jaw.

The teeth of the double-banded Monitor (*Varanus bivittatus*) are all much compressed, with finely dentate trenchant margins: except the small intermaxillary teeth, which are conical, pointed and incurved. There are eight intermaxillary teeth, eleven maxillary teeth on each side, and twelve teeth in each premandibular bone, where one or two of the anterior teeth are conical, corresponding with the intermaxillaries above.

The variegated lizard (*Varanus variegatus*) presents the most compressed form of teeth: in specimens preserved in spirits they are

transparent, and their fine tubular structure may be discerned with the due microscopic power without cutting the tooth into slices. I find nine small conical sharp-pointed teeth in the anchylosed intermaxillaries, the middle azygos incisor being the smallest; and seven large, compressed, recurved, sharp pointed and trenchant teeth in each maxillary bone. In the lower jaw there are two small conical incisors at the fore-part of each premandibular series, succeeded by nine or ten long compressed teeth corresponding with the maxillaries above. These teeth are more convex on the inner than on the outer side; their margins are finely crenate. They are separated by moderately wide and irregular intervals, in which are contained the successional teeth, the apices of the largest of these appearing above the outer alveolar ridge.

These successional teeth are developed at the inner and posterior side of the base of their predecessors: and groups of three and sometimes four teeth, placed one a little behind the other and successively diminishing in size from the tooth in place to its third successor, are arranged in the alveolar groove, as shown in Pl. 63 A, fig. 9. The old teeth are not so much damaged by the growth of their successors as in other Saurians; and the young teeth are at no period inclosed in a cavity in those which they succeed.

In the great crocodilian Monitor (*Varanus crocodilinus*, Pl. 68, fig. 3), the large fixed compressed teeth, of which there may be about seven in each upper maxillary bone and six in each premandibular, are anchylosed by the whole of their base and by an oblique surface leading upwards on the outer side of the tooth to a slight depression on the oblique alveolar surface, as in the *Var. striatus*, Pl. 63 A, fig. 8 *a*. The base of the tooth is finely striated, the lines being produced by inflected folds of the external cement, as in the Ichthyosaur and Labyrinthodon, but being short and straight as in those of the former genus. The alveolar channel or groove has scarcely any depth; but the anchylosed base of the tooth is applied to an oblique surface, terminating in a sharp edge, from which the outer side of the free crown of the tooth is directly continued. The great Varanus, like the variegated species, manifests its affinity to the Crocodilians in the number of successive teeth which are in progress of growth to

replace each other: but from the position in which the germs of the successional teeth are developed, the more advanced teeth in this species, as in the *Var. variegatus*, do not exhibit the excavation that characterize the same parts of the teeth of the Enaliosaurs and Crocodiles.

THECODONTS.

110. We have already seen that among the inferior or squamate Saurians there are two leading modifications in the mode of attachment of the teeth, the base of which may be either anchylosed to the summit of an alveolar ridge, or to the bottom of an alveolar groove and supported by its lateral wall: these modifications were indicated by the terms 'acrodont' and 'pleurodont.' A third mode of fixation is presented by some extinct Saurians, which, in other parts of their organization, adhere to the squamate or Lacertine division of the order; the teeth being implanted in sockets, either loosely, or confluent with the bony walls of the cavity: these may be termed the 'thecodont'(1) Lacertians: the most ancient of all Saurians belong to this group.

111. *Thecodontosaurus.*—In the dolomitic conglomerate at Redland near Bristol, a formation considered to belong to the oldest or lowest division of the new-red-sandstone series, remains of reptiles have been discovered by Dr. Riley and Mr. Stutchbury(2) which are allied, in the form of their teeth to the typical Varanian monitors, but differ in having the teeth imbedded in distinct sockets: to this condition, however, the Varani, among the squamate saurians, make an approach, in the shallow cavities containing the base of the teeth along the bottom of the alveolar groove.

In the ancient extinct genus in question the sockets are deeper, and the inner alveolar wall is nearly as high as the outer one: the teeth are arranged in a close-set series, slightly decreasing in size towards the posterior part of the jaw; each ramus of the lower jaw is supposed to have contained twenty-one teeth. These are conical,

(1) θηκη, a sheath; οδους a tooth.

(2) Geol. Transactions, 1836, p. 349.

rather slender, compressed and acutely pointed, with an anterior and posterior finely serrated edge, the serratures being directed towards the apex of the tooth; the outer surface is more convex than the inner one: the apex is slightly recurved: the base of the crown contracts a little to form the fang, which is subcylindrical. The pulp-cavity remains open in the base of the crown.

In microscopic structure, the teeth of the Palæosaurus closely correspond with that of the teeth of the Varanus, Monitor and Megalosaurus. The body of the tooth consists of compact dentine, in which the calcigerous tubes diverge from the open pulp-cavity at nearly right angles to the surface of the tooth; they form a slight curve at their origin, with the concavity directed towards the base of the tooth, then proceed straight, and at the periphery bend upwards, in the contrary direction. The diameter of the calcigerous tube is $\frac{1}{30,000}$th of an inch: the breadth of the interspaces is $\frac{1}{8000}$th of an inch. The crown of the tooth is invested with a simple coat of enamel.

This examination, which I have been enabled to make by the kindness of Mr. Stutchbury, satisfactorily establishes the distinction between the Saurian of the Bristol conglomerate and the reptiles of the later member of the new-red-sandstone system in Warwickshire, already described under the name of *Labyrinthodon*.

112. *Palæosaurus*.—In the same formation as contained the jaw and teeth of the *Thecodontosaurus*, two other teeth were separately discovered, differing from the preceding and from each other; the crown of one of these teeth, measuring nine lines in length and five lines in breadth, is represented at Pl. 62 A, fig. 7. It is compressed, pointed, with opposite trenchant and serrated margins, but its breadth, as compared with its length, is so much greater than in the *Thecodontosaurus*, that Dr. Riley and Mr. Stutchbury have founded upon it the genus *Palæosaurus*,(1) and distinguish it by the specific name of *platyodon*, from the second tooth which they refer to the same genus under the name of *Palæosaurus cylindrodon*. The portion of the tooth of the *Pal. cylindrodon* which has been preserved, shows that the crown is sub-compressed and traversed by two opposite finely-serrated ridges, its length is five lines; its breadth at the base two lines.

(1) Loc. cit. p. 352.

113. *Cladeiodon.*(1)—In the new red sandstone (Keuper?) of Warwick and Leamington, detached teeth occur of the size and form represented in Pl. 62 A, fig. 4, *a* & *b*; they have been found in the same quarries as those containing the remains of the *Labyrinthodon.* In their compressed form, anterior and posterior serrated edges, sharp points, and microscopic structure, these teeth agree with those of the Saurian reptiles of the Bristol conglomerate. In their breadth, as compared with their length and thickness, they are intermediate between the *Thecodontosaurus* and the *Palæosaurus platyodon;* they are also larger and more recurved, and thus more nearly approach the form characteristic of the teeth of the *Megalosaurus.* From these teeth, however, they differ in their greater degree of compression, and in a slight contraction of the base of the crown; I propose, therefore, to indicate the genus, of which, as yet, only the teeth are known, by the name of *Cladeiodon,* and for the species from the Warwickshire sandstones the name of *Cladeiodon Lloydii,* in testimony of the friendly aid of Dr. Lloyd of Leamington, to whose exertions I owe the materials for the description of the teeth of the present genus, and the still more remarkable ones of the British species of Labyrinthodon, with which the teeth of the Cladeiodon are associated.

PROTOROSAURUS.

114. In the pyritic schists of Thuringia, which, like the dolomitic Breccia near Bristol, rank as the oldest member of the new-red-sandstone system, the fossil remains of a small species of Saurian reptile have long been known to occur; and it is from the individual specimen of this ancient extinct species, first described by Spener as a sort of crocodile in the Miscellanea Berolinensia for the year 1710, that the observations on the dental system are here taken.

It is well known that Cuvier, after an elaborate comparison of the figures and descriptions of the Thuringian fossil Saurian by Spener, Link, Swedenborg and Wachsmann, arrived at the conclusion that the species was to be referred to the Monitors or Tupinambis.(2)

(1) χλαδευω, to prune; ὁδες, a tooth; from the resemblance of the tooth to a pruning-knife.

(2) On ne comptera donc plus les animaux de Spener et de Link parmi les crocodiles, ou

M. Hermann V. Meyer has proposed the name of *Protorosaurus Speneri* for the Thuringian Monitor, but he has not added any new fact relative to its organization.

This name I shall retain, because the species in question actually differs from the existing Monitors and other Lacertians by the same character which distinguishes the *Thecodontosaurus*, viz: the implantation of the teeth in distinct sockets. Of these sockets, the dislocated ramus of the lower jaw in Spener's specimen exhibits fourteen, which are of a square shape with the angles rounded off, close-set and sub-equal. The teeth, of which eighteen may be counted in the upper jaw, are relatively longer, more slender, and more cylindrical than in the Thecodon; they are more or less broken; the most perfect of them measure three lines in length, and two-thirds of a line across the base; they are of a jet-black colour, and, being imbedded in a dark matrix, have not enabled me to determine whether the *Protorosaurus*, like the equally ancient reptiles of the Bristol conglomerate, had the teeth armed with serrated ridges(1).

MEGALOSAURUS.

115. The compressed varanian form of tooth, with trenchant and finely dentated margins, which characterized the ancient Palæosaur and Cladeiodon, is continued in the comparatively more recent and gigantic species of terrestrial lizard, of which the remains were discovered by Dr. Buckland in the oolite of Stonesfield. The characters and peculiarities of the jaws and teeth have been so accurately and graphically described by their discoverer, that an apology would be due rather for suppressing, than for here reproducing them.

"From these," says Dr. Buckland, "we learn that the animal was a reptile, closely allied to some of our modern lizards, and viewing the teeth as instruments for providing food to a carnivorous creature of enormous magnitude, they appear to have been admirably

celui de Swedenborg parmi les guenons ou les sapajous; mais on les rangera tous parmi les monitors ou tupinambis. Ossem. fossiles, 4to. vol. v, p. 306.

(1) Besides the thecodont type of dentition, the *Protorosaurus* differs from all recent Saurians, and resembles the Pterodactyle in the great relative size of the cervical vertebræ, and the ossified tendons of the muscles of that region of the spine; it differs from all reptiles, except the extinct *Racheosaurus* in the bifurcate superior spines of the caudal vertebræ.

adapted to the destructive office for which they have been designed. Their form and mechanism will be best explained by reference to the figures.

" The outer margin of the jaw (Pl. 70, fig. 8, *b*) rises nearly an inch above its inner margin, forming a contiguous lateral parapet to support the teeth on the exterior side, where the greatest support was necessary, whilst the inner margin throws up a series of triangular plates of bone (*c, c,*) forming a zig-zag buttress along the interior of the alveoli. From the centre of each triangular plate, a bony partition crosses to the outer parapet, thus completing the successive alveoli. The new teeth (*a, a*) are seen in the angle between each triangular plate, rising in reserve to supply the loss of older teeth, as often as progressive growth, or accidental fracture, may render such renewal necessary, and thus affording an exuberant provision for a rapid succession and restoration of these most essential implements. They were formed in distinct cavities, by the side of the old teeth, towards the interior surface of the jaw, and probably expelled them by the usual process of pressure and absorption, insinuating themselves into the cavities thus left vacant. This contrivance for the renewal of teeth, is strictly analogous to that which takes place in the dentition of many species of existing lizards.

" In the structure of these teeth (Pl. 70, figs. 9 & 10), we find a combination of mechanical contrivances analogous to those which are adopted in the construction of the knife, the sabre, and the saw. When first protruded above the gum, the apex of each tooth presented a double cutting edge of serrated enamel. In this stage, its position and line of action were nearly vertical, and its form, like that of the two-edged point of a sabre, cutting equally on each side. As the tooth advanced in growth, it became curved backwards, in the form of a pruning-knife, and the edge of serrated enamel was continued downwards to the base of the inner and cutting side of the tooth, whilst on the outer side a similar edge descended, but to a short distance from the point (fig. 10) and the convex portion of the tooth became blunt and thick, as the back of a knife is made thick, for the purpose of producing strength. The strength of the tooth was further increased by the expansion of its sides (as represented in the

transverse section, fig. 11). Had the serrature continued along the whole of the blunt and convex portion of the tooth, it would, in this position, have possessed no useful cutting power; it ceased precisely at the point beyond which it could no longer be effective. In a tooth thus formed for cutting along its concave edge, each movement of the jaw combined the power of the knife and saw; whilst the apex in making the first incision, acted like the two-edged point of a sabre. The backward curvature of the full-grown teeth, enabled them to retain, like barbs, the prey which they had penetrated. In these adaptations, we see contrivances, which human ingenuity has also adopted, in the preparation of various instruments of art."(1)

The teeth of the Megalosaur consist of a central body of dentine, with an investment of enamel upon the crown, and of cement over all, but thickest upon the fang. The marginal serrations are formed almost entirely by the enamel, and when slightly magnified are seen to be rounded, and separated by slight basal grooves (Pl. 62, A, fig. 6, *c*); the smooth and polished enamel upon the sides of the crown presents a finely wrinkled appearance; the remains of the pulp are converted into a coarse bone in the completely formed tooth.

The dentine consists of extremely fine and close-set calcigerous tubes, without admixture of medullary canals; they radiate from the pulp-cavity at right angles with the external surface of the tooth; the primary curvatures correspond with those of the calcigerous tubes in the monitor's tooth (Pl. 67) but are less marked, so that the tubes appear straighter. They present a diameter of $\frac{1}{28,000}$th of an inch; with interspaces varying between two and three times that diameter; they dichotomize sparingly, but the number of minute secondary branches sent off into the intermediate substance is very great. These secondary branches proceed at acute angles from the primary tubes; the divisions of the tubes become very frequent near the periphery of the dentine and the terminal branches dilate into, or inosculate with a stratum of calcigerous cells, which separates the dentine from the enamel. The microscopic characters of the tooth of the Megalosaur are represented in Pl. 70 A, in part of a transverse sec-

(1) Bridgewater Treatise, vol. i, p. 237.

tion of the middle of the crown, including the pulp-cavity and its ossified contents; the natural size of the section is given at fig. 1; a reduced figure of the same, magnified sixty diameters, at fig. 2, and a more highly magnified view of the terminations of the calcigerous tubes, at fig. 3, *a*; the marginal cells being shown at *b*, and the enamel with its thin coat of cement at *c*.

The highly organized nature of a tooth is well illustrated in this example of one of the simplest of Saurian teeth; in which, in addition to the tubular and cellular modifications of the dentine, there is also enamel, cement, and an internal coarse kind of bone.

The dentition of the Megalosaurus, besides exemplifying, on a large scale, the mechanical advantages of the varanian form of tooth, exhibits an interesting transitional character between the squamate and loricate types of Saurians, the distinct sockets making the approach to the crocodiles, while the raised external alveolar wall shows the retention of the lacertine structure.

THAUMATOSAURUS.

116. In a great extinct species of Saurian, whose remains have been discovered in the oolitic formation at Neuffen, in Wurtemberg, and which has received the name of *Thaumatosaurus oolithicus* from M. Hermann von Meyer, the teeth were conical, slightly curved, straighter on the inner side of the crown; implanted by a long and strong root rather obliquely in a deep socket. The base and basal portion of the crown presents a nearly circular transverse section; the wide pulp-cavity in this part of the tooth presented an elliptical transverse contour; the tooth becomes slightly compressed towards the apex.

The broadest part of the tooth is its implanted base; the breadth of the crown is to its height as one to three; the crown is invested with a thin layer of enamel, the basal half of which is marked by longitudinal striæ; these striæ seem to consist of folds of the enamel, which do not extend into the dentine.

The successional teeth penetrate into the interior of the fixed teeth in the progress of their development.

ISCHYRODON.

117. The teeth of the *Ischyrodon*, a gigantic reptile from the Jura limestone of the Canton of Aargau, somewhat resemble those of the *Thaumatosaurus*, but the external longitudinal striæ of the crown of the tooth are sharper and more elevated, and between the striæ the enamel is roughened by irregular linear risings.

PŒCILOPLEURON.

118. The teeth of the *Pœcilopleuron* (Deslongchamps), a gigantic reptile whose remains occur in the oolitic beds at Caen, according to the single tooth referred to that genus, has a more compressed crown than the teeth of the *Thaumatosaurus*; the striæ are also wider apart, and the two diametral ones are developed into ridges which extend to the apex of the tooth.

PTERODACTYLUS.

119. The true affinities of this the most extraordinary of all the ancient animals which Comparative Anatomy has brought to light, were, when much conflicting evidence was apparently given by other parts, pointed out most distinctly by the dental system. Cuvier, after discussing the various opinions which had been promulgated respecting the nature of the remains of the extinct volant animal in question, says:—"The teeth, by which the examination of an animal ought always to be commenced, here present nothing equivocal. They are all simple, conical and nearly alike, as in the crocodiles, the monitors and other lizards."(1) Their disposition in the jaws with wide interspaces, and their separate implantation in distinct sockets are characters in which the Pterodactyle approximates to the extinct Saurian genera, *Thecodon*, *Megalosaurus*, *Plesiosaurus*, and the Crocodilians.

In the *Pterodactylus longirostris* the teeth are of moderate and equal size, slender, conical, sharp-pointed, recurved, with pretty

(1) "Les dents, par où il faut toujours commencer l'examen d'un animal, ne présentent ici aucune équivoque. Elles sont toutes simples, coniques, et à peu près semblables entre elles comme dans les crocodiles, les monitors et d'autres lézards." Cuvier adds, "Tout le monde sait que les dauphins seuls, parmi les mammifères, pourraient présenter quelque chose de comparable."—Ossem. foss. Ed. 1836, tom. x, p. 225.

regular interspaces, slightly increasing as the teeth are placed further back. In the specimen described by Soemmering there are on the preserved side of the head nineteen teeth in the lower jaw ; and eleven in the upper jaw, which is probably only a portion of this series, but at least gives sixty teeth in all. There is an orifice in the jaw at the inner side of the base of each tooth, whence Cuvier supposes the teeth of replacement to issue.(1)

In the *Pterodactylus crassirostris* (Pl. 63 A, fig. 6) the teeth are relatively fewer, more unequal, but for the most part much larger than in the previous species, and the jaws are correspondingly shorter and stronger. The teeth are long, slender, very acute, sub-compressed and slightly curved ; they have been described as arranged or approximated in pairs, but this is the case with a few only, and the hinder tooth is always the smallest ; whence I conclude that it was a successional tooth, which has been developed in the same relative position to its predecessor as in the great Varanus, (compare figs. 6 & 9, Pl. 63 A). The intermaxillary bone, in the specimen figured, contains four teeth on one side, of which the first three are of small size ; there are seven teeth in the maxillary bone of the same side, of which the hinder ones, that extend beneath the orbit, are the shortest ; the corresponding ramus of the lower jaw contains six teeth ; the supposed successional teeth are included in the preceding enumeration.

In the *Pterodactylus medius* the base of the teeth have been stated to be hollow, as in the teeth of the crocodile, and to contain the germs of their successors ;(2) the right half of the lower jaw contains sixteen teeth, of nearly equal size, the hinder ones becoming smaller. They are simple, conical, slightly recurved, compressed and smooth.

In the *Pterodactylus Munsteri* the teeth are slender, recurved,

(1) " On en voit de tout semblables dans le sauvegarde, et surtout dans la dragone (*Thorictes dracæna*)." I have not observed in any existing reptile this mode of emergence of the successional teeth, as in Mammalia, by an outlet distinct from the socket of the previous tooth. In the great safe-guard (*Varanus*), the successional teeth rise from the alveolar groove behind those which they succeed, as shown in Pl. 63 A, fig. 9. In the *Pterodactylus medius* the germs of the young teeth have been observed in the basal cavities of the old, as in the crocodile.—See Munster, Nova Acta, Nat. Cur. t. xv, p. 63.

(2) Munster, loc. cit.

pointed, laterally compressed, but not trenchant, varying in size; their number is nine on each side of the upper jaw and seven on each side of the lower jaw; none of them are implanted in the intermaxillary bone.

The teeth figured in Pl. 63 A, fig. 7, are referred by Dr. Buckland to the large species of Pterodactyle (*Pter. macronyx*), discovered by him in the lias at Lyme Regis; they are implanted like the teeth of other species of the genus in separate sockets, but in the breadth and shortness, lateral compression, and trenchant anterior and posterior margins of the protruded crown, they much more closely resemble the teeth of certain Scomberoid fishes, which are similarly implanted in the jaws. M. H. Von Meyer observes that the jaw of a Pterodactyle from the lias at Banz, which he refers to the species *macronyx*, contains the sockets of only fourteen teeth, whilst the fragment of jaw with the Sphyrenoid teeth from Lyme Regis above mentioned, must have contained a much greater number.

Some portions of the skeleton of a large Pterodactyle have been discovered by Dr. Buckland in the oolite at Stonesfield. A few teeth from the same formation, in the collection of the Earl of Enniskillen, bear the same proportion to these bones, as do the teeth of the *Pter. crassirostris* to its skeleton; they are long, slender, conical, slightly curved, and sharp-pointed; their base is smooth, the enamelled crown is marked with fine striæ, converging obliquely upwards to a longitudinal line on the convex side of the tooth. These teeth vary from nine to fourteen lines in length, and are one line or one line and a half across the base.

I have not had the opportunity of examining the microscopical structure of an undoubted tooth of a Pterodactyle.

ENALIOSAURS.

120. *Ichthyosaurus.*—The teeth of the *Ichthyosauri* have a simple, more or less acutely conical form, with a long and, usually, expanded or ventricose base, or implanted fang. They are confined to the intermaxillary, maxillary and premandibular bones, in which they are arranged in a pretty close and uninterrupted series, and are of nearly equal size. They consist of a body of unvascular dentine, invest-

ed at the base by a thick layer of cement, and at the crown by a layer of enamel, which is itself covered by a very thin coat of cement; the pulp-cavity is more or less occupied in fully-formed teeth by a coarse bone.

The external surface of the tooth is marked by longitudinal impressions and ridges, but the teeth vary both as to outward sculpturing and general form in the different species.(1)

The teeth present the largest size in the *Ichthyosauri platyodon* and *communis*, and they are smallest and most slender in the *Ich. tenuirostris*.

Ich. communis, (Pl. 73, fig. 4). This species is characterized by teeth which have a cylindrical, sometimes sub-ventricose base, and a round, conical, slightly aduncate crown, tapering more rapidly and less regularly to the apex than in the other species; the apex is not very acute. The crown is traversed by moderately fine and close-set longitudinal furrows, and the base is sculptured by coarse and deep grooves which separate longitudinal convex ridges.

There are from forty to fifty teeth on each side of the upper jaw, eighteen of which are implanted in the superior maxillary bone; in the lower jaw there are on each side between twenty-five and thirty teeth. The fine coronal grooves are abruptly divided from the coarse basal ones at the terminal line of the enamel. The basal ridges are sometimes transversely scored in large teeth, and bifurcate and progressively diminish in breadth as they approach the contracted extremity of the tooth; the base of such teeth sometimes resembles a small contracted pentacrinite.

Ich. platyodon (Pl. 73, figs. 3 & 6).—The teeth of this species present a ventricose base, and a conical, sub-compressed, subincurved crown, the outer and inner sides of which meet at two opposite sharp edges, which terminate above at the acute apex of the crown, which is thus adapted for both piercing and cutting.

The basal longitudinal grooves and ridges of the tooth are as

(1) Pl. 73, 73 A & 74.

(2) The principal varieties of the form of the teeth, and the species thereby indicated were first observed by M. Delabeche, and are described by Mr. Conybeare in his beautiful memoir in the Geol. Trans. vol. vi, p. 108.

coarse as, but more regular than those of the tooth of the *Ich. communis;* the surface of the crown is smoother and more polished, and the longitudinal lines are due to slightly developed angular ridges dividing narrow flattened tracts, like those of a polyhedron.

I have not observed more than forty-five teeth on each side of the upper, and forty teeth on each side of the lower jaw. The crowns of the teeth are more frequently found to be snapped off in this than in the smaller species of Ichthyosaurus, a circumstance which is indicative of the greater force with which they had been used.

Ich. lonchiodon(1) (Pl. 73, fig. 2).—The teeth are more slender in this gigantic species than in the two preceding ones, and they are straighter than in any other species. Their base is cylindrical and regularly fluted; a smooth boundary divides it from the crown; this is conical and is traversed by finer and more numerous grooves, which are minutely and irregularly undulated, but converge with a general longitudinal course to the apex of the tooth. The transverse section of the crown is nearly circular; the crown tapers gradually to its apex, which is nearer the posterior line than the central axis of the tooth.

Ich. tenuirostris (Pl. 73, fig. 5).—The teeth are more slender, in proportion to their length, in this than in any other species; and they are also more numerous; their base is cylindrical, and their crown conical, gradually tapering to an acute apex, and slightly recurved: the basal grooves are regular and longitudinal; the coronal striæ are extremely fine. I have found between sixty-five and seventy teeth on each side of the upper jaw; of these the posterior third part, or about twenty-five of the teeth, are implanted in the slender maxillary bones, the rest being supported by the disproportionately long intermaxillaries. In the lower jaw there are about sixty teeth on each side. The teeth are directed more obliquely backwards in this than in the preceding species.

Ich. intermedius (Pl. 73, fig. 1).—Mr. Conybeare (2) thus characterizes this species:—"The upper part of the teeth is much more acutely conical than in the *Ich. communis,* and the striæ less

(1) λογχη, spear; οδους, tooth.

(2) Loc. cit. p. 108.

prominent, yet they are less slender than in the *Ich. tenuirostris.*" They are also much fewer in number; I have not found more than forty teeth on each side of the upper jaw, or than thirty-five on each side of the lower jaw.

In the *Ich. acutirostris* the teeth differ from those of the *Ich. tenuirostris* in having a somewhat wider base in proportion to their length: in the specimens which I have examined the teeth likewise present less regularity of size, and they are fewer in number; in a fragment of jaw, three inches in length, which included twenty-four teeth, their exserted crowns presented a regular alternation of three and five lines in length. In an entire head there are about fifty teeth on each side of the upper jaw, and about forty teeth on each side of the lower jaw.

I have investigated the microscopic structure of the teeth of the Ichthyosaurus in the species *platyodon* and *intermedius*(1).

The dentine has the same simple compact structure as in the teeth of existing carnivorous Saurians. The calcigerous tubes present a diameter of $\frac{1}{20,000}$th of an inch, with interspaces of $\frac{1}{8000}$th of an inch. They radiate from the pulp-cavity, and form a line continued from its upper end to near the apex of the tooth, according to their usual course, towards the periphery of the tooth; they describe at their origin a graceful curve, the concavity of which is directed towards the base of the tooth, and then proceed in straight lines at right angles to the periphery of the tooth(2). The secondary curvatures or undulations of the tubes are more regular, more numerous, and more marked than in the crocodile's tooth; the tubes divide dichotomously many times during their course, and send off lateral branches obliquely into the clear intermediate substance, and principally from their concave side; the terminal divisions of the calcigerous tubes (*a*, fig. 2) become less regular, and appear to decussate and communicate at their extremities, either directly with one another by inosculating loops, or through the medium of minute cells.

The enamel (*b*) is a clear dense substance presenting faint traces

(1) Trans. Brit. Assoc. 1838, p. 144.

(2) The disposition of the calcigerous tubes, as seen in a longitudinal slice of the apical part of the crown of the tooth, is figured in Plate 73, A.

of a fibrous structure, the lines being vertical to the surface of the tooth.

The coronal cement appears only as a line of substance more opaque than the enamel which it invests; it augments in thickness at the base of the tooth, where the radiated corpuscles or cells that characterize its structure are very conspicuous; the cement is inflected at each of the basal grooves in the form of a short, straight and simple vertical fold into the substance of the dentine. The peripheral portion of the basal dentine is thus divided, to the extent represented in Pl. 64 B, fig. 3, into a corresponding number of processes; fissures of the pulp-cavity radiate to their bases, becoming there the centres of divergence of as many series of calcigerous tubes, which obey in their course the usual law of verticality to the external surface of the dentine. This structure can be seen only in a transverse section of the base of the tooth: its correspondence with that of the apex of the crown of the teeth of the Labyrinthodon will be obvious on comparing fig. 3, Pl. 64 B, with fig. 1, Pl. 63, B, and, as has been already stated, it gave the key to the nature and principle of the complicated labyrinthic interblending of dentine and cement, which was first observed in the great tusk of the *Labyrinthodon Jaegeri*.

The remains of the pulp, after the formation of the due quantity of dentine, became converted, as in the pleodont lizards, by a process of coarse ossification into a reticulate fibrous or spongy bone(1); but it continues open at the crown after the basal part of the tooth is thus consolidated, as shown in the longitudinal section (Pl. 73, fig. 8), wherein *a* is the pulp-cavity filled with crystallized spath, *b* the ossified pulp at the base of the tooth. The radiated cells or corpuscles are very conspicuous in both this bone and the external cement.

The chief peculiarity of the dental system of the Ichthyosaur is the mode of implantation of the teeth; instead of being anchylosed to the bottom and side of a continuous shallow groove, as in most Lacertians, or implanted in distinct sockets, as in the Thecodon, Megalosaur or Pterodactyle, they are lodged loosely in a long and

(1) "The tooth in these genera becomes completely solid, its interior cavity being filled up by the ossification of the pulpy substance."—Conybeare, loc. cit. p. 106.

deep continuous furrow, and retained by slight ridges extending, between the teeth, along the sides and bottom of the furrow (Pl. 73, fig. 9), and by the gum and the organized membranes continued into the groove and upon the base of the teeth.

The germs of the new teeth are developed at the inner side of the base of the old ones. Mr. Conybeare has given a figure of a transverse section across the jaw-bone, (reproduced at Pl. 73, fig. 7), in which the new tooth (*c*) has penetrated the osseous substance of the base of the old tooth (*b*), and its point has nearly entered the remains of the pulp-cavity which has continued open in the crown of the tooth(*a*).

From the circumstance of the consolidation of the base of the teeth in the Ichthyosaur Mr. Conybeare infers that they were retained longer in the jaw than are the hollow teeth of the crocodiles; but the analogy of other Saurians, and the observation of two new teeth at successive stages of formation at the base of an old tooth, prove that the succession of new sets of teeth was repeated more than once, though probably not so frequently as in the crocodile.

121. *Plesiosaurus.*—The teeth of the Plesiosaur are conical, long, slender, curved and sharp-pointed; they appear to retain their internal cavity, as in the teeth of a crocodile; they have a very long round fang or implanted base, which, in old teeth, contracts, as it sinks into the jaw, and terminates almost in a point.

The chief distinction, which the dental system offers between the present and the preceding genus of Enaliosaur, is the loose implantation of the teeth of the Plesiosaur in separate alveoli. In thus deviating from the Ichthyosaur, the Plesiosaur proportionally approximates to the crocodilian type, and this affinity is likewise manifested in the unequal size of the teeth, and the development of some of the anterior ones into large tusks.

The teeth are composed, as in the Ichthyosaur, of a body of hard and simple dentine, covered at the crown by a coat of enamel, and, at the base, by a coat of cement; but the latter is relatively thinner than in the Ichthyosaur, and is not inflected into the substance of the dentine. The crown is characterized by well-defined narrow

elevated longitudinal ridges, terminating abruptly at different distances from the apex, to which, however, none of them extend.

In the lower jaw of the *Ples. macrocephalus* there are twenty-six teeth on each premandibular bone: the crown of one of the large anterior tusks, in a lower jaw, ten inches in length, measured one inch and a half in length and one third of an inch in breadth; its transverse section was nearly circular. The premandibular piece of the lower jaw of the *Ples. arcuatus* contains fifty-four teeth, or twenty-seven on each side, the six anterior teeth on each side being larger and longer than the rest. In the lower jaw of the *Ples. dolichodeirus* there are twenty-five teeth on each side, the four anterior of which are the largest.

The disposition of the calcigerous tubes is shown in a longitudinal section of the apical third part of a tooth of the *Plesiosaurus Hawkinsii* in Pl. 74. In their general course they bear a considerable resemblance to the same parts in the *Ichthyosaurus*, but the primary curvature presents a more graceful sigmoid line, from the inclination of the peripheral extremities of the tubes towards the apex. The diameter of the tubes near their origin is $\frac{1}{26,000}$th of an inch; their interspaces equal five or six of their diameters; the secondary undulations are relatively wider than in the Ichthyosaurus, and the secondary branches are longer and more bent; the tubes divide dichotomously several times in their course; the divisions, after a slight divergence proceeding in the same parallel line with each other and with the main stem. The finer secondary branches dilate into extremely minute cells along tracts which run parallel with the contour of the tooth itself, and occasion the apparent alternation of opaque and clear layers observable in the section by transmitted light, as represented in the figure; the mode of termination of the calcigerous tubes is shown at fig. 2, Pl. 74. The enamel presents the same fine fibrous structure as in the *Ichthyosaurus*.

The mode of succession of the teeth of the Plesiosaur differs from that of the Ichthyosaur in the growing tooth being developed in a cell at the inner side of the old socket, and affecting by its pressure the bone of the jaw, rather than the tooth about to be displaced.

Notwithstanding the approximation to the crocodilian type which the teeth of the Plesiosaur make in their persistent pulp-cavity, there is not more than a single successional tooth in progress of development at the base of the tooth in use at any period; and the dentition of the Plesiosaur further differs from that of the crocodile, inasmuch as the new tooth, instead of emerging from the pulp-cavity of the old tooth, or even from the same socket, protrudes its apex through a distinct foramen at the inner side of the alveolus of its predecessor.

PLEIOSAURUS.

122. Large, simple, conical teeth, with the enamelled crown traversed by well-defined and abruptly terminated longitudinal or oblique ridges, as in the Plesiosaur, have not unfrequently been discovered in the Kimmeridge clay formation. These teeth differ from those of the Plesiosaur in their greater relative thickness as compared with their length and in the subtriedral shape of their crown; the outer side is slightly convex, sometimes nearly flat; it is separated from the two other facets by two sharp ridges; these are more convex, and the angle dividing them is often so rounded off, that they form a demi-cone, and the shape of the tooth thus approximates very closely to that of the Mosasaur, with which it is equal in size. It may readily be distinguished, however, even when the crown only is preserved, by the ridges which traverse the inner or convex sides; the outer flattened surface alone being smooth: but an entire tooth of the present extinct reptile presents a long fang, which at once removes it from the acrodont group, and allies it with the thecodont reptiles, among which it approaches nearest, in the superficial markings of the crown, to the Plesiosaurus. The known parts of the skeleton of the gigantic extinct reptile, to which the teeth in question belong, confirm this approximation; but the vertebræ of the neck are so modified that the peculiarly elongated proportion of this part of the spine, which characterizes the typical *Plesiosauri*, is exchanged for one that much more nearly approaches the opposite condition of the cervical region in the *Ichthyosauri*; this abrogation of the main characteristic of the *Plesiosauri*, combined with the more crocodilian proportions of the teeth in the present reptile, have

induced me to found a sub-genus for its reception under the name of *Pleiosaurus*.

In the collection of Prof. Buckland, at Oxford, a considerable proportion of both upper and lower jaws of a gigantic specimen of the *Pleiosaurus brachydeirus* is preserved from the Kimmeridge clay formation at Market Raisin. The teeth are arranged in separate sockets, in a close and regular series, along the alveolar borders of the intermaxillary, maxillary and premandibular bones. Twenty-six sockets may be counted on the most perfect side of the upper jaw, but the series is evidently incomplete posteriorly. An interspace not quite equal to the breadth of a socket divides the fourth from the fifth tooth, counting backwards, and the jaw is slightly compressed at this interspace; the four anterior teeth, thus marked off, occupy the slightly expanded anterior extremity of the upper jaw, but do not present the disproportionately large size which characterizes the anterior teeth in the true Plesiosaurs. After the fifth tooth the sockets progressively increase in size to the twelfth tooth, and, from the fourteenth they begin gradually to diminish in size; becoming, beyond the twentieth tooth, smaller than those at the fore part of the jaw.

The alveolar septa are narrow and are thinned off to an edge, which is lower than either the outer or inner walls of the sockets: these walls are equally developed. A line drawn transversely across any of the twelve anterior sockets would be transverse to the jaws, but in the remaining sockets it would incline obliquely from without, inwards and backwards. The transverse diameter of the thirteenth socket is one inch, six lines; its antero-posterior diameter is one inch, eight lines. The extent of the alveolar series is nearly three feet; the breadth of the palate at the twenty-sixth tooth is nearly one foot; the breadth of the upper jaw at the third tooth is four inches and three lines; the breadth of the socket of that tooth is one inch, three lines.

In the lower jaw of the specimen in the Oxford Museum the posterior extremity of the dental series is complete, but not the anterior one; thirty-five teeth are present in each premandibular bone. The first, from its large size, I conclude to have been received into the slight concavity at the side of the

upper jaw where the diastema separates the fourth and fifth teeth; there are probably, therefore, thirty-eight teeth on each side of the lower jaw; counting backwards, on this supposition, the teeth begin to diminish in size beyond the fifteenth, and at the posterior extremity of the series the sockets are less than half an inch in diameter; in their close arrangement and position they correspond with those of the upper jaw.

The teeth which are preserved in this magnificent cranial fragment present the characters described at the commencement of this section; the outer smooth surface of the crown of a tooth of the lower jaw is represented at Pl. 68, fig. 5; the inner surface of two of the teeth of the upper jaw is represented at 5′ and 5″: the inserted fang of each of these teeth is four inches and a half in length, the entire tooth being thus seven inches in length. The ridges which divide the outer from the inner surfaces of the tooth subside at the base of the crown; the fang is smooth; it assumes a sub-circular form, gradually expands for about half its length, and then contracts to its termination, but this is always less pointed than in the fully-formed teeth of the true Plesiosaur. In the old teeth with the elongated fang, the pulp-cavity remains open, as in the Plesiosaurian teeth; it presents at the expanded part of the fang, a narrow elliptic transverse section. In a tooth of the present species, six inches and a half in length, from the Kimmeridge clay at Shotover, the diameter of the persistent pulp-cavity was thirteen lines. In this tooth the flattened surface is polished, but marked with minute shallow wrinkles; one of the ridged surfaces, which stood at right angles to the preceding, was traversed by eleven well-marked linear ridges, of unequal length, separated by smooth interspaces of about three times the breadth of the ridges; the third surface which formed an acute angle with the smooth outer surface was traversed by twelve ridges. These ridges on the inner surfaces of the tooth slightly incline towards the rounded angle dividing these surfaces; they terminate abruptly; some cease half-way from the apex of the crown; about ten are continued to within half an inch of the apex, which is smooth; the two ridges which divide the flat or smooth side from the ridged surfaces of the tooth are alone continued to the sub-acute apex of the tooth.

The teeth of the Pleiosaur present varieties of form as well as of size; the rounding off of the angle between the ridged surfaces has been already alluded to; the smooth outer surface is sometimes so convex, that the transverse section of the tooth is more elliptical than triangular. All the teeth of the Pleiosaur are slightly bent inwards and backwards, but the smaller posterior teeth are most recurved, and have the sharpest apex; in the crown of these teeth, also, the ordinary rounded or elliptical form of the cone is most nearly attained; but the distinction of the smooth external surface, and the ridged internal surfaces of the crown of the tooth is retained, and would suffice to characterize any of these teeth if found detached.

The teeth of the Pleiosaur consist, like those of the Plesiosaur and Crocodile, of a central body of compact dentine, with a coronal investment of enamel, and a general covering of cement; of extreme tenuity upon the crown, but thicker upon the base of the tooth.

The dentine consists of fine calcigerous tubes, without admixture of medullary canals; the arrangement, division, secondary undulations and branches of the calcigerous tubes correspond so closely with those of the teeth of the Plesiosaur, as to render a particular description of them unnecessary.

The germs of the successional teeth are developed at the inner side of the bases of the old teeth, but do not penetrate these teeth; the apices of the new teeth make their appearance through foramina situated at the inner side, and generally at the interspace of the sockets of the old teeth. Here, therefore, as perhaps also in the Pterodactyle, the growing teeth may be included in closed recesses of the osseous substance of the jaw and emerge through tracts distinct from the sockets of their predecessors; but this is an exceptional condition of the reproduction of the teeth in Reptiles.

CROCODILIANS.

123. The ancient writers on Natural History appear to have been much struck with the great number of teeth in the crocodile: and their descriptions were exaggerated to the tone of the impressions thus produced. According to Achilles Tatius the crocodile had as many teeth as there were days in the year: Alkazuin assigns it two

hundred teeth; Abuhamed was more reasonable and allowed eighty.(1)

How many teeth a crocodile may develope through the whole course of its life in uninterrupted succession will never perhaps be determined; they, then, would doubtless far exceed in number the liberal allowance of Tatius; but with regard to those teeth which are in use in the jaws at any given time the number is now well established, e. g. the Crocodile of the Nile has $\frac{19-19}{16-16} = 68$; that of the West Indies (*Crocodilus acutus*) has $\frac{17-17}{16-16} = 66$; the common Alligator (*Alligator lucius*) has $\frac{2020}{18-18} = 76$. The great Gavial or Garrhial (*Gavialis gangeticus*) has $\frac{30-30}{29-29} = 118$. Thus the different species and genera of Crocodiles differ from each other in the number of teeth, and also the individuals differ within small limits, as will be presently shown.

The best and most readily recognizable characters by which the existing Crocodilians are grouped in appropriate genera are derived from modifications of the dental system.

In the *Caimans*, (Genus *Alligator*), the teeth vary in number from $\frac{18-18}{18-18}$ to $\frac{22-22}{22-22}$: the fourth tooth of the lower jaw, or canine, is *received into a cavity* of the palatal surface of the upper jaw, where it is concealed, when the mouth is shut; in old individuals the upper jaw is perforated by these large inferior canines, and the fossæ are converted into foramina.

In the Crocodiles, (Genus *Crocodilus*), the first tooth in the lower jaw perforates the palatal process of the intermaxillary bone when the mouth is closed; the fourth tooth in the lower jaw is *received into a notch* excavated in the side of the alveolar border of the upper jaw, and is visible externally when the mouth is closed.

In the two preceding genera the alveolar borders of the jaws have an uneven or wavy contour and the teeth are of unequal size.

In the Gavials, (Genus *Gavialis*), the teeth are nearly equal in size and similar in form in both jaws, and the first as well as the fourth tooth in the lower jaw, passes into a groove in the margin of the upper jaw, when the mouth is closed.

In an extinct species, the 'Crocodile d'Argenton' of Cuvier,(2)

(1) These authors are quoted by Tiedemann and Oppel in their Naturgeschichte der Amphibien, fol. 1817, p. 39.

(2) Ossem. Fossiles, 8vo. 1836, tom. ix, p. 330.

the crown of the teeth is compressed, subincurved, and terminated by an anterior and posterior trenchant and finely serrated edge, as in the Varanian and many of the Thecodont Saurians. In the *Crocodilus cultridens* of the Wealden strata (Pl. 62 A, fig. 10) the crown of the teeth is thicker than in the Argenton species, and the anterior and posterior edges are unbroken; a few longitudinal ridges traverse the crown of the tooth of this species, which makes the transition to the ordinary crocodilian teeth.

In all the genera of *Crocodilians* the teeth of the upper and lower jaws are so placed that their points, instead of meeting, interlock.

In all the species of each genus, the teeth are present in the intermaxillary, superior maxillary and premandibular bones, and are confined to those bones, the palate being edentulous. The teeth are relatively larger and stronger in the Alligators and Crocodiles, than in the Gavials; they are almost always conical, and slightly recurved; the crown has generally a sharp border before and behind, and it is longitudinally striated.

The *Alligator palpebrosus* has nineteen teeth on each side of the upper jaw and twenty-one teeth on each side of the lower jaw, making eighty teeth in all. The second, third, seventh and eighth teeth are the largest in the upper jaw; and the first and fourth are the largest in the lower jaw. This dental character will be expressed by the following formula, which, to save space and prevent repetition of words, will be used to express the dental characters in all the other species of Crocodilians.

Alligator palpebrosus, $\frac{19-19}{21-21}=80.\ \frac{2,3,7,10,}{1,\ 4,}=$largest.

The first ten or eleven teeth in this species are more pointed and compressed than the rest, and are slightly curved, while the others are straight.

Alligator lucius, $\frac{20-20}{20-20}=80\ \frac{4,\ 5,\ 8,\ 9,\ 10}{1,\ 3,\ 4,\ 11,\ 12,\ 13}=$largest.

Alligator sclerops, $\frac{18-18}{18-18}=72.\ \frac{4,5,10}{1,4}=$largest.

The teeth in this species are less unequal than in the Alligator lucius: the fourth lower canines pierce the upper jaw in old specimens.

Alligator cynocephalus, $\frac{19-19}{18-18}=74\ \frac{3,4,\ 9}{1,\ 4}=$largest.

The fourth or great tooth below does not pierce the upper jaw in this species.

Alligator trigonatus,(1) $\frac{20-20}{21-21}=82\ \frac{2,3,6,\ 7\ \&\ 8}{4,5,\ 11\ \&\ 12}$=largest.

Alligator niger, $\frac{18-18}{19-19}=74\ \frac{3,4,\ 5\ \&\ 9}{1,4,11\ \&\ 12}$=largest.

In almost all, if not all of these species of Alligator from eight to ten of the posterior teeth are straight, sub-compressed, and terminated by an obtuse mammilloid crown.

Crocodilus rhombifer, $\frac{17-17}{15-15}=64\ \frac{2,\ 7,}{4,\ 10,}$=largest.

Crocodilus Gravesii, $\frac{18-18}{15-15}=66\ \frac{2,7,\ 8,\ 9}{4,9,10,11,}$=largest. This species exhibits, besides the notch for the fourth lower tooth or canine, a remarkable emargination for the elongated crowns of the ninth, tenth, and eleventh teeth.

Crocodilus vulgaris, $\frac{18-18}{15-15}=66\ \frac{3,\ 9,}{1,4,\ 11,}$=largest.

Crocodilus biporcatus, $\frac{18-18,\text{ or }19-19}{15-15}=66$ or $68\ \frac{2,3,8,9}{1,4}$=largest.

Crocodilus acutus, $\frac{18-18}{15-15}=66\ \frac{4,\ 10,}{4}$=largest. In this species the first ten teeth, counting from the anterior part of each side of both jaws are pointed and slightly recurved: the rest are straight and obtusely conical.

Crocodilus intermedius. The name of this species indicates the gradational character between the Crocodiles and the Gavials, which it manifests in the increase of the longitudinal over the transverse diameter of the cranium and in the comparative slenderness of its jaws: the alveolar border is less deeply sinuous in both jaws, and the rami of the lower jaw are united along the anterior fourth part of their length. The teeth are relatively smaller than in the preceding Crocodiles; the dental formula is $\frac{18-18}{15-15}=66\ \frac{1,5,10}{1,4.}=$ largest.

The transition, of which the first steps were made by the *Crocodili acutus* and *intermedius* is completed by the *Gavialis Schlegelii*, in which the head is more elongated and contracted, the teeth smaller and more equal, and the anterior pair of the lower jaw received, like the fourth pair, in notches at the outside of the intermaxillary bone, between the first and second teeth of the upper jaw.

The first, second, third and ninth teeth of the upper jaw, are larger than the rest, the ninth is the largest, and the superior max-

(1) *Champsa trigonata* Natterer.

illary bones are slightly expanded at the insertion of this pair of teeth. The first, fourth, eleventh and fifteenth pairs are the largest teeth in the lower jaw, but the anterior tusks do not perforate the intermaxillary bones.

In the foregoing gavial-like Crocodile the narrowing of the skull to form the jaws is gradual, but in the true Gavials the cranium suddenly contracts into the prolonged upper jaw. In this subgenus the two jaws together form a long, straight, narrow, and four-sided column, with the angles rounded off, terminating in an expansion something like that of the beak of the spoon-bill. The terminal expansion of the upper jaw is indented by four vertical notches, which receive the crowns of the first and second pairs of the inferior teeth when the mouth is closed. The number of teeth is always greater in the Gavials than in the Crocodiles or Alligators. The formula of the common Gavial(1) (*Gavialis gangeticus*) is $\frac{29-29}{27-27} = 112$. The first five pairs of teeth above, are supported by the intermaxillary bones; the first, third, and fourth teeth of the upper jaw, and the first, second, and fourth of the lower jaw are the longest. The eight or nine posterior teeth are nearly conical, the rest are sub-compressed antero-posteriorly and present a trenchant edge on the right and left side, between which a few faint longitudinal ridges traverse the basal part of the enamelled crown.(2) The position of the opposite sharp ridges and the direction of the flattening of the crown are thus reversed in the Gavial and in the extinct Crocodile (*Croc. cultridens*), before-mentioned, which in other respects most nearly resembles the Gavial in the form of the teeth.

In most of the extinct species of Crocodilians, the teeth are characterized by more numerous and strongly developed longitudinal ridges upon the enamelled crown than in the recent species, and they are commonly longer, more slender and sharper-pointed. But in one of the Crocodiles with sub-biconcave vertebræ (*Goniopholis crassidens*), from the Wealden formation and Purbeck limestone, the teeth

(1) Pl. 75*a*, fig. 3. This word ought to be written "Gharrial"; but the universal adoption of the erroneous orthography in European scientific works, and its conversion into a Latin generic name (*Gavialis*), render an alteration undesirable.

(2) Plate 75, fig. 2.

have crowns which are as round and as thick in proportion to their length as in the recent Crocodiles or Alligators. Some of the teeth of this species are even shorter and more obtuse, as are those figured in Pl. 62, A. fig. 9, *a* and *b*. The crown is traversed by longitudinal ridges, which are more numerous, more close-set, and more neatly defined than in the *Croc. cultridens* (*Suchosaurus*) from the same formation. Two of the ridges, larger and sharper than the rest, traverse opposite sides of the crown ; but are placed as in the Gavial, on the right and left sides, midway between the convex and concave lines of the curve of the tooth. These ridges are confined to the enamel ; the cement-covered cylindrical base of the tooth is smooth.

The more ancient Crocodiles from the Oolite and Lias, called *Steneosauri* and *Teleosauri* had jaws like those of the modern Gavials, but sometimes longer and more attenuated, and armed with more numerous, equal, and slender teeth, adapted for the capture of fishes, which appear to have been the only other vertebrate animals existing at those periods in numbers sufficient to yield subsistence to carnivorous Saurians.(1)

In a specimen of *Teleosaurus Chapmanni* I have counted one hundred and seventy-eight teeth, thus arranged, $\frac{46-46}{48-48}$: the *Teleosaurus latifrons* had one hundred and forty-two teeth, viz, $\frac{36-32}{38-38}$. The *Tel. Egertoni* had $\frac{39-39}{38-38}$. (Pl. 75*a*, fig. 4.) Cuvier calculates the number of teeth in the *Teleosaurus* of the Caen Oolite, which is a distinct species from the two above-mentioned, to be one hundred and eighty, viz. $\frac{45-45}{45-45}$. The enumeration will differ within small limits in different individuals of the same species, in consequence of the uninterrupted and irregular shedding and replacement of the teeth. The foregoing numbers indicate those of the sockets, some of which are almost always empty. In the *Teleosaurus priscus* (*Crocodilus priscus*, Soemmering) the teeth appear to have been shed and renewed in a more regular alternate order than in other species.(2)

In all the *Teleosauri* the teeth are more slender, less compressed and sharper pointed than in the Gavial ; they are slightly recurved, and the enamelled crown is traversed by more numerous

(1) Buckland's Bridgewater Treatise, i, p. 250.

(2) Whence the term *Aelodon* proposed for the species by M. H. v. Meyer.

and better defined ridges, two of which, on opposite sides of the crown, are larger and more elevated than the rest. The fang is smooth, cylindrical, and always excavated at the base. The teeth of the *Steneosauri*, or extinct Crocodiles with long and slender jaws and with vertebræ subconcave at both extremities, but with subterminal nostrils, differ from those of the *Teleosauri* in being somewhat thicker in proportion to their length, and larger in proportion to the jaws.

A distinct genus of extinct Crocodile (*Marmarosaurus*) is indicated by a form of tooth differing from that of the *Steneosaurus* in being subcompressed, and in having the ridges on the basal two-thirds of the crown shorter, more frequently interrupted, irregularly alternating, and slightly wavy; the two opposite stronger ridges are not developed. Teeth of this kind, with crowns fifteen lines in length, and six lines across the long diameter of the base, occur in the Forest-marble, Pl. 75 *a*, fig. 5.

A more remarkable and almost heart-shaped form of tooth, is presented by the extinct Crocodilian genus denominated, from this character, *Cardiodon*. The crown of the tooth suddenly expands above the neck, as in the Caiman, but is more flattened transversely and is broader antero-posteriorly, terminating in an edge before and behind, and contracting to a point above, which is generally more or less abraded. The enamel is roughened by wavy longitudinal ridges, with more minute rugæ in their interspaces. The fang of the tooth is smooth and cylindrical, Pl. 75 *a*, fig. 7.(1)

Structure.—The teeth of both the existing and extinct Crocodilian Reptiles consist of a body of compact dentine, forming a crown covered by a coat of enamel, and a root invested by a moderately thick layer of cement. The root slightly enlarges, or maintains the same breadth, to its base, which is deeply excavated by a conical pulp-cavity extending into the crown, (as indi-

(1) These teeth are likewise from the secondary rock, called Forest-marble, near Bradford, Wilts, and I am indebted to Mr. Channing Pearce of that town, for the opportunity of examining them. The teeth from the Wealden, supposed to belong to the *Hylæosaurus*, very closely resemble those of *Cardiodon* in the superficial markings, and approach them in the shape of the crown.

cated by the dotted line in plate 75, fig. 1), and is commonly either perforated or notched at its concave or inner side.

The calcigerous tubes in the crown of a fully-developed tooth form short curvatures at their commencement at the surface of the pulp-cavity, and then proceed nearly straight to the periphery of the crown; they very soon bifurcate, the divisions slightly diverging; then continuing their course with gentle parallel undulations, they subdivide near the enamel, and terminate in fine and irregular branches, which anastomose generally by the medium of cells.

The calcigerous tubes send off from both sides, throughout their progress, minute branches into the intervening substance, and terminate in the dentinal or calcigerous cells. These cells are subhexagonal, about $\frac{1}{800}$th of an inch in diameter, and are traversed by from ten to fourteen of the dentinal tubes: they are usually arranged in planes parallel with the periphery of the crown, near which they are most conspicuous and towards which their best defined outline is directed:(1) they combine with the parallel curvatures of the calcigerous tubes to form the striæ, visible in sections of the teeth by the naked eye or a lower power, which cause the stratified appearance of the dentine, as if it were composed of a succession of superimposed cones. The diameter of the calcigerous tube before the first bifurcation is $\frac{1}{12000}$th of an inch; both the trunks and bifurcations of the calcigerous tubes have interspaces equal to four of their respective diameters.

The enamel, viewed in a transverse section of the crown, presents some delicate striæ parallel with its surface; whilst the appearance of fibres, vertical to that surface, is only to be detected, and there faintly, on the fractured edge. It is a very compact and dense substance; the dark brownish tint is strongly marked in the middle of the enamel when viewed by transmitted light.

The cells with which the fine calcigerous tubes of the basal cement communicate are oblong, about $\frac{1}{2000}$th of an inch across their long axis, which is transverse to that of the tooth; the intercommunicating tubes, which radiate from the cells, giving them a stellate figure.

(1) "Report of British Association," 1838, p. 144.

Development.—In the black Alligator of Guiana the first fourteen teeth in the lower jaw are implanted in distinct sockets, the remaining posterior teeth are lodged close together in a continuous groove, in which the divisions for sockets are faintly indicated by vertical ridges, as in the jaws of the Ichthyosaurus.(1)

A thin compact floor of bone separates this groove, and the sockets anterior to it, from the large cavity of the ramus of the jaw; it is pierced by blood-vessels, for the supply of the pulps of the growing teeth and the vascular dentiparous membrane which lines the alveolar cavities.

The tooth-germ is developed from the membrane covering the angle between the floor and the inner wall of the socket. It becomes in this situation completely enveloped by its capsule, and an enamel organ is formed at the inner surface of the capsule before the young tooth penetrates the interior of the pulp-cavity of its predecessor.

The matrix of the young growing tooth affects, by its pressure, the inner wall of the socket, as shown in fig. 4, Pl. 75, and forms for itself a shallow recess: at the same time it attacks the side of the base of the contained tooth, as shown in fig. 3: then, gaining a more extensive attachment by its basis and increased size, it penetrates the large pulp-cavity of the previously formed tooth either by a circular or semi-circular perforation.

The size of the calcified part of the tooth-matrix which has produced the corresponding absorption of the previously-formed tooth on the one side, and of the alveolar process on the other, is represented in the second exposed alveolus of fig. 4, the tooth *a* having been displaced and turned round to show the effects of the stimulus of the pressure: the size of the perforation in the tooth and of the depression in the jaw, proves them to have been, in great part, caused by the soft matrix, which must have produced its effect by exciting vital action of the absorbents, and not by mere mechanical force. The resistance of the wall of the pulp-cavity having been thus overcome, the growing tooth and its matrix recede from the temporary alveolar depression, and sink into the substance of the pulp contained in the cavity of the fully-formed tooth. As

(1) Pl. 75, fig. 3.

the new tooth grows, the pulp of the old one is removed; the old tooth itself is next attacked, and the crown, being undermined by the absorption of the inner surface of its base, may be broken off by a slight external force, when the point of the new tooth is exposed, as in the figs. 5 and 7, Pl. 75.

The new tooth disembarrasses itself of the cylindrical base of its predecessor with which it is sheathed, by maintaining the excitement of the absorbent process, so long as the cement of the old fang retains any vital connexion with the periosteum of the socket; but the frail remains of the old cylinder, thus reduced, are sometimes lifted out of the socket upon the crown of the new tooth, as in fig. 4, *b*; when they are speedily removed by the actions of the jaws. This is, however, the only part of the process which is immediately produced by violence: an attentive observation of the more important previous stages of growth, teaches that the pressure of the growing tooth operates upon the one to be displaced only through the medium of the vital absorbent action which it has excited.

Most of the stages in the development and succession of the teeth of the Crocodiles are described by Cuvier with his wonted clearness and accuracy; but the mechanical explanation of the expulsion of the old teeth, which Cuvier(1) adopts from M. Tenon, is opposed by the disproportion of the hard part of the new tooth to the vacuity in the walls of the old one, and by the fact that the matter impressing—viz., the uncalcified part of the tooth-matrix—is less dense than the part impressed.

No sooner has the young tooth penetrated the interior of the old one, than another germ begins to be developed from the angle between the base of the young tooth and the inner alveolar process, or in the same relative position as that in which its immediate predecessor began to rise, and the processes of succession and displacement are carried on uninterruptedly, throughout the long life of these cold-blooded carnivorous reptiles.

From the period of exclusion from the egg the teeth of the Crocodile succeed each other in the vertical direction; none are added from behind forwards like the true molars in Mammalia.

(1) Ossemens Fossiles, ed. 1836, Tom. ix. p. 182.

It follows, therefore, that the number of the teeth of the Crocodile is as great when the animal first sees the light as when it has acquired its full size; and, owing to the rapidity of their succession, the cavity at the base of the fully-formed tooth is never consolidated.

The fossil jaws of the extinct Crocodilians demonstrate that the same law regulated the succession of the teeth at the ancient epochs when those highly organised reptiles prevailed in greatest numbers, and under the most varied generic and specific modifications, as at the present period when they are reduced to a single family, composed of so few and slightly varied species, as to have constituted in the system of Linnæus a small fraction of the genus *Lacerta*.

PART III.

DENTAL SYSTEM OF MAMMALS.

CHAPTER I.

GENERAL CHARACTERS OF THE TEETH OF MAMMALS.

124. The class *Mammalia*, like that of *Pisces* and *Reptilia*, includes a few species which are entirely devoid of teeth; these are the Ant-eaters, forming, when clothed with hair, the genus *Myrmecophaga;* when defended by scales, the genus *Manis;* and when armed with spines, the genus *Echidna*. A few Mammals have the jaws provided with horny substitutes for teeth, as the Whalebone-whales (*Balæna* and *Balænoptera*), and the Ornithorhynchus; in the rest of the class true teeth are present. In the Feline tribe the epithelium of the tongue is thickened at the fore-part of its dorsum, and invests the papillæ there with hard sheaths, like prickles, which are analogous to the lingual teeth of certain Fishes and Batrachians. The back part of the dorsum of the tongue in the Echidna is provided with a plate of horny denticles, which bruise its food against the hard and prickly epithelium covering the palate. Horny processes, analogous to the palatal teeth of Fishes and Reptiles, are likewise developed upon the roof of the mouth of the great Bottle-nose Dolphin, thence termed *Hyperoodon* by Lacépède.

125. *Number.*—In the last-named Cetacean, the true teeth are two in number, whence its specific name, *bidens:* the Narwhal likewise has but two teeth, both of which are concealed in the substance of the jaws in the female, whilst only one is ordinarily visible in the male: but this grows to an unusual length. The *Delphinus griseus* has five teeth on each side of the lower jaw; but they soon become reduced to two on each side. Amongst the Marsupial

animals, the genus *Tarsipes* is remarkable for the paucity as well as minuteness of its teeth. The Elephant has never more than one entire molar, or parts of two, in use on each side of the upper and lower jaws, to which are added two tusks, more or less developed in the intermaxillary bones. Some Rodents, as the Australian Water-rats, (*Hydromys*), have two grinders on each side of both jaws; which, added to the four cutting teeth in front, make twelve in all: the common number of teeth in this order is twenty; but the Hares and Rabbits have twenty-eight teeth. The Sloth has eighteen teeth. The number of teeth, thirty-two, which characterises Man, the Apes of the old world, and the true Ruminants is the average one of the Class *Mammalia*. The examples of excessive number of teeth are presented, in the order *Bruta*, by the Priodont Armadillo, which has ninety-eight teeth; and, in the Cetaceous Order, by the Cachalot, which has upwards of sixty teeth, though most of them are confined to the lower jaw,—by the common Porpoise, which has between eighty and ninety teeth,—by the Gangetic Dolphin, which has one hundred and twenty teeth, and by the true Dolphins (*Delphinus*), which have from one hundred to one hundred and ninety teeth, yielding the maximum number in the class Mammalia.

126. *Form.*—Where the teeth are in excessive number, as in the species above cited, they are small, equal, or sub-equal, and of a simple conical form: pointed and slightly recurved in the common Dolphin; with a broad and flattened base in the gangetic Dolphin (*Inia*); with the crown compressed, and broadest in the Porpoise; compressed, but truncate, and equal with the fang in the Priodon. The simple dentition of the smaller Armadillos, of the Orycterope, and of the three-toed Sloth presents a difference in the size, but little variety in the shape of the teeth, which are sub-cylindrical with broad triturating surfaces: in the two-toed Sloth, the two anterior teeth of the upper jaw are longer and larger than the rest, and adapted for piercing and tearing. In almost all the other Mammalia particular teeth have special forms for special uses; thus, the front-teeth, from being commonly adapted to effect the first coarse division of the food, have been called cutters or incisors, and

the back-teeth which complete its comminution, grinders or molars; large conical teeth, situated behind the incisors, and adapted by being nearer the insertion of the biting-muscles to act with greater force, are called holders, tearers, laniaries, or more commonly canine teeth, from being well developed in the Dog and other Carnivora, although they are given, likewise, to many vegetable feeders, for defence or combat.

The names 'incisors,' 'laniaries,' 'molars,' are not, however, always indicative of the shape of the crowns of the teeth which occupy the relative positions above mentioned. In some Carnivora, for example, the front teeth have broad tuberculate summits adapted for nipping and bruising, while the principal back teeth are as admirably shaped for cutting, and work upon each other like the blades of shears. The front teeth in the Elephant project, from the upper jaw, in the form and direction of long pointed horns; in the extinct Dinothere the lower incisors had a similar form and development, but were bent down from the end of the jaw. Hence, therefore, shape alone has been found insufficient to characterize the analogous teeth in the Mammalia, and it has been necessary to consider the position, and also the mode of succession of the teeth, in order to their definition and classification.

Comparative Anatomists, by common consent, now apply the term '*incisor*,' arbitrarily, to those teeth which are implanted in the intermaxillary bones and in the corresponding part of the lower jaw. When the tooth which succeeds the incisors, or the first of the upper maxillary bone, is conical, pointed, and longer than the rest, it is called a *canine*, as is also its analogue in the lower jaw, which always passes in front of it when the mouth is closed. Of the remaining teeth, those which are shed and replaced vertically, or which have successors descending into their place in the upper, and ascending in the lower jaw, are called '*premolars*,' or false molars, and in Human Anatomy 'bicuspides'; the remaining teeth, which are not displaced by vertical successors, but which follow each other from behind forwards, in both jaws, are called *molars*, or true molars.

Naturalists have availed themselves of the degree of constancy

with which the foregoing kinds of teeth are recognizable in the Mammalian genera, to indicate them by an abbreviated formula of the initial letters, or first syllables of their respective denominations; thus, *I* or *in.* signifies incisor; *c* or *can.* canine; *p* or *prem.* premolar; *m* or *mol.* molar: succeeding numerals, according to their relative position to added lines, give the number of these several kinds of teeth on the right and left sides of the upper and lower jaws. For example, the dental formula of the genus *Homo* is :—

$$\text{Incisors } \frac{2-2}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{2-2}{2-2};\ \text{molars } \frac{3-3}{3-3}:\ =\ 32.$$

which expresses that, on each side of both upper and lower jaws, there are two incisors, one canine, two premolars, and three true molars; thirty-two in all.

The last upper premolar and the first lower true molar in the Carnivora are termed, from their peculiar form, 'sectorial' or 'carnassial' teeth, 'molaires carnassières' of Cuvier. Teeth of an elongated conical form, projecting considerably beyond the rest, and of uninterrupted growth are called 'tusks;' such are the incisors of the Elephant and Dugong, the canines of the Boar and Walrus: the long and large incisors of the Rodents have been termed from the shape and structure of their cutting edge, scalpriform or chisel-teeth, 'dentes scalprarii.' The inferior incisors of the Flying Lemurs, (*Galeopithecus*), have the crown deeply notched, like a comb, and are termed 'dentes pectinati.' The canines of the Baboons are deeply grooved in front, like the poison-fangs of some serpents. The compressed conical crowns of the molar-teeth of the small-clawed Seals, (*Stenorhynchus*), are divided either like a trident, into three sharp points, or like a saw, into four or five points, 'dentes serrati.' Molar teeth, which are adapted for mastication, have either tuberculate, or transversely ridged, or flat summits, and usually are either surrounded by a ridge of enamel, or are traversed by similar ridges arranged in various patterns. Certain molars in the Dugong, the Mylodon and the Zeuglodon, are so deeply indented laterally by opposite longitudinal grooves, as to appear to be composed of two cylindrical teeth cemented together, and the transverse section of the crown is bilobed. The teeth of the Glyptodon were fluted by two analogous grooves on each side. The large molars

of the Capybara and Elephant have the crown cleft into a numerous series of compressed transverse plates, cemented together side by side.

The ordinary teeth of the Mammalia have so much more definite and complex a form, than those of Fishes and Reptiles, that three parts are usually recognized in them, viz., the fang, the neck, and the crown. The fang or root (*radix*) is the inserted part, the crown (*corona*), the exposed part, and the constriction which divides these is called the neck, or *cervix*. The term, 'fang,' is properly given only to the implanted part of a tooth of restricted growth, which gradually tapers to its extremity; those teeth which grow uninterruptedly have not their exposed part separated by a neck from their implanted part, and this generally maintains to its extremity the same shape and size as the exposed crown.

It is peculiar to the class Mammalia to have teeth implanted in sockets by two or more fangs; but this can only happen to teeth of limited growth, and generally characterizes the molars and premolars.

127. *Attachment.*—In no mammiferous animal does anchylosis of the tooth with the jaw constitute a normal mode of attachment. Each tooth has its particular socket, to which it firmly adheres by the close co-adaptation of their opposed surfaces, and by the firm adhesion of the alveolar periosteum to the organized cement, which invests the fang or fangs of the tooth: but in some of the *Cetacea*, at the posterior part of the dental series, the sockets are wide and shallow, and the teeth adhere more strongly to the gum than to the periosteum: in the Cachalot I have seen all the teeth brought away with the ligamentous gum, when it has been stript from the sockets of the lower jaw.

True teeth implanted in sockets are confined, in the present class, to the maxillary, intermaxillary, and lower maxillary bones, and to a single row in each. They may project only from the intermaxillary bones as in the Narwhal; be apparent only in the lower maxillary bone, as in the Cachalot; or be limited to the superior and inferior maxillaries, and not present in the intermaxillaries, as in the true *Pecora*, and most *Bruta* of Linnæus; in general, teeth are situated in all the bones above mentioned. In Man, where the intermaxillaries early coalesce with the maxillary bones, where the jaws

are very short, and the crowns of the teeth are of equal length, there is no interspace or 'diastema' in the dental series of either jaw, and the teeth derive some additional fixity by their close apposition and mutual pressure. No inferior Mammal now presents this character; but its importance, as associated with the peculiar attributes of human organization, has been somewhat diminished by Cuvier's discovery of a like contiguous arrangement of the teeth in the jaws of the extinct *Anoplotherium*.

128. *Substance*.—The teeth of the Mammalia usually consist of hard or unvascular dentine, defended at the crown with an investment of enamel, and everywhere surrounded by a coat of cement. The coronal cement is of extreme tenuity in Man, Quadrumana and terrestrial Carnivora; it is thicker in the Herbivora, especially in the complex grinders of the Elephant, and is thickest in the teeth of the Sloths, Megatherioids, Morse, and Cachalot. Vertical folds of enamel and cement penetrate the crown of the tooth in the Ruminants, and in most Rodents, and Pachyderms, characterizing by their various forms the genera of the two last orders: but these folds never converge from equidistant points of the circumference of the crown towards its centre. The teeth of the quadrupeds of the order *Bruta*, (*Edentata*, Cuv.), have no true enamel; this is absent, likewise, in the molars of the Dugong, the Zeuglodon and the Cachalot.(1) The tusks of the Narwhal, Walrus, Elephant, Mastodon, and Dinotherium, consist of modified dentine, which, in the large proboscidian animals, is properly called 'ivory,'(2) and is covered by cement.

The central part of the fully-formed tooth in man and most other animals contains an irregular kind of osseous substance, which is most abundant in the Cachalot,(3) and forms around foreign bodies which may gain admission to the pulp-cavity of tusks. A fifth substance which, from the number and regular position of the vascular canals

(1) M. Fr. Cuvier divides the teeth of Mammalia, according to their composition, into four classes: the first consist of ivory, (dentine), enamel and cement; the second of ivory and enamel; the third of ivory and cement; the fourth of ivory only. '*Dents des Mammifères*,' p. xxi. I have met with no Mammalian teeth, in which cement is absent, and believe that the second and fourth of the above-cited classes of teeth, have no existence in Nature.

(2) "*Hoc solum est ebur*," Plinius, Hist. Nat. lib. xi. c. 37.

(3) Pl. 89, fig. 2, c.

in it, I have termed the 'vascular dentine,' forms the body or axis of the tooth in the Sloth-tribe,(1) and is present in smaller proportion in the centre of the teeth of the Armadillos. The teeth of the Orycteropus consist of congeries of long and slender prismatic columnar denticles, each consisting of a body of dentine, with a coating of cement, by which they are united together to form a composite tooth, as in some of the Cartilaginous Fishes.

129. *Structure.*—In most Mammals the body of the tooth consists of a gelatinous animal basis and calcareous earth, combined and arranged according to the plan which characterizes the tissue called "unvascular dentine."(2) The compartments of the basal substance, which I have called 'calcigerous' or 'dentinal cells,' and which contain the hardening salts in their densest state, are sub-circular (Pl. 95), or sub-hexagonal (Pl. 70). The calcigerous and nutrient tubes varying from $\frac{1}{10,000}$ to $\frac{1}{20,000}$th of an inch in diameter, and placed with intervals equal to from two to six of their own diameters, proceed, at first with strong, and then with gentle curves from the pulp-cavity to the outer surface of the dentine, their general direction being always more or less nearly at right angles to that surface: those tubes which proceed from the apex, and from the basal third-part of the pulp-cavity are the straightest. They are nearly parallel to one another, both in their general course and curvatures; but, as the outer surface of the tooth exceeds the inner one in extent, the tubes slightly diverge in their course and divide, decreasing in diameter to their peripheral extremities, and rapidly so near their termination where they become irregularly flexuous and often interlaced. The dichotomizing calcigerous tubes send off from their sides much more minute branches, which quickly divide and sub-divide in the interspaces of the trunks, and penetrate the dentinal cells. In the unvascular dentine of all Mammalian teeth the tubes present the "primary curvatures," and "secondary gyrations" described in the Introduction.(3) These curvatures are strongest and least regular in the dentine of the Elephant's grinders. In that of the tusks of the Elephant and Mastodon, the form, extent, and parallelism of the secondary curvatures of the dentinal tubes, cause the peculiar appearance of the decussation of curved lines, like the ornamental work called

(1) Pl. 82, fig. 1. (2) Introduction, p. iii, & iv. (3) P. xvi.

'engine-turning,' upon the surface of transverse or oblique sections or fractures of the tusk, which is characteristic of true 'ivory.'

In the incisors of certain Rodents, and in the molars of the Sloths and Megatherioids, or the large extinct phyllophagous *Bruta*, more or less of the dentine is modified by the persistence of certain tracts of the pulp-cavity, forming vascular or medullary canals; the characters of this "vascular dentine" will be described in the sections devoted to the dentition of the species possessing it.

The dentine of the long and slender prismatic denticles which are aggregated to form the compound tooth of the Orycterope(1) is unvascular, and is characterized chiefly by the frequent division and wide angles at which the branches of the bifurcating calcigerous tubes diverge, before resolving themselves into their minute wavy terminations.

The cement, which, with the dentine, is present in all teeth of mammalian animals, is characterized, except where it forms an extremely thin layer, by the radiated calcigerous cells.(2) These are usually arranged in lines or layers parallel with the surface of the cæmental coat and with each other; they average a diameter of $\frac{1}{1000}$th of an inch in Man; they are rather smaller in the true Carnivora; proportionally larger in some of the Pachyderms; but present their most minute size in some of the Ruminants, as the Giraffe and Ox. The radiated forms of these cells arises from the numerous minute tubes continued from or opening in them, and which are analogous to the more parallel calcigerous tubes of the dentine, with which they communicate.

In the thick radical cement of the Seal's teeth, and in both the radical and coronal cement of the teeth of most Herbivora, very conspicuous vascular canals are present in addition to the calcigerous tubes and cells. These canals in the cement of the molars of the Megatherium are numerous and constant, take a course parallel with each other and transverse to the outer plane of the cement, and anastomose by loops close to the dentine, towards which the convexity of the loops is directed.(3)

(1) Pl. 78. (2) *Corpuscula Purkingii*. (3) Pl. 84, *b*, *b*.

The structure of the enamel presents fewer varieties than in the lower classes of Vertebrata, and in all the Mammalian genera in which it exists, it manifests its most distinctive and elaborate condition. It consists of more or less curved or wavy prismatic fibres, averaging about $\frac{1}{4000}$th of an inch in diameter, and having a general direction vertical to the plane of the dentine; some of the fibres extend through the thickness of the enamel, others are shorter and are wedged in their interspaces; the fibres of the thick enamel of the molars of the large Pachyderms are most curved and interwoven; they are so arranged, however, as always to have one end directed towards the outer surface of the tooth, and the other end to that by which the enamel is attached to the dentine: the outer, or peripheral end of the fibre is sensibly larger than the inner one. In Man and Quadrumana the fibres are transversely striated: I have not detected this character in the Herbivorous Quadrupeds. The fine horizontal lines on the exterior surface of the enamel(1) are usually most conspicuous in the teeth of Mammals.

130. *Development.*—The teeth in this, as in the foregoing classes, are formed by superaddition of the hardening salts to pre-existing moulds of animal pulp or membrane, organized so as to insure the arrangement of the earthly particles according to that pattern which characterizes each constituent texture of the tooth. The complexity of the primordial basis, or matrix, corresponds, therefore, with that of the fully-formed tooth, and is least remarkable in those conical teeth which consist only of dentine and cement. The primary pulp, which first appears as a papilla rising from the free surface of the alveolar gum, is the part of the matrix which by its calcification constitutes the dentine; it sinks into a cell and becomes surrounded by a closed capsule, in every Mammiferous species, at an early stage of the formation of the tooth; and, as the cement is the result of the ossification of the capsule, every tooth must be covered by a layer of that substance. In those teeth which possess enamel, the mould or pulp of that constituent is developed

(1) Introduction, p. xxvi.

from the capsule covering the coronal part of the dentinal pulp. In the simple teeth the secondary or enamel-pulp covers the crown like a cap; in the complex teeth it sends processes into depressions of the crown, which vary in depth, breadth, direction, and number, in the numerous groups of the Herbivorous and Omnivorous quadrupeds. The dentinal pulp, thus penetrated, offers corresponding complications of form; and, as the capsule follows the enamel-pulp in all its folds and processes, the external cavities or interspaces of the dentine become occupied by enamel and cement; the cement, like the capsule which formed it, being the outermost substance, or having the enamel interposed between it and the dentine. The dental matrix presents the most extensive interdigitation of the dentinal and enamel pulps in the Capybara and Elephant. The processes of formation and calcification of the several constituents of Mammalian teeth have been already described in the Introduction(1).

The matrix of the Mammalian tooth sinks into a furrow and soon becomes inclosed in a cell in the substance of the jaw-bone from which the crown of the growing tooth extricates itself by exciting the absorbent-process, whilst the cell is deepened by the same process and by the growth of the jaw, into an alveolus for the root of the tooth. When the formative parts of the tooth are reproduced indefinitely to repair by their progressive calcification the waste to which the working surface of the crown of the tooth has been subject, the alveolus is of unusual depth, and of the same form and diameter throughout, except in the immature animal when it widens to its base. In teeth of limited growth, the dentinal pulp is reproduced in progressively decreasing quantity after the completion of the exterior wall of the crown, and forms by its calcification one or more roots or fangs, which taper more or less rapidly to their free extremity. The alveolus is closely moulded upon the implanted part of the tooth; and it is worthy of special remark that the complicated form of socket which results from the development of two or more fangs is peculiar to animals of the class Mammalia(2).

(1) P. xli.

(2) On the strength of this generalization I have established the Mammalian nature of the

In the formation of a single fang, the activity of the reproductive process becomes enfeebled at the circumference, and is progressively contracted within narrower limits in relation to a single centre, until it ceases at the completion of the apex of the fang; which, though for a long time perforated for the admission of the vessels and nerves to the interior of the tooth, is, in many cases, finally closed by the ossification of the remaining part of the capsule.

When a tooth is destined to be implanted by two or more fangs, the reproduction of the pulp is restricted to two or more parts of the base of the coronal portion, around the centre of which parts the sphere of its reproductive activity is progressively contracted. The intervening parts of the base of the coronal pulp adhere to the capsule, which is simultaneously calcified with them, covering those parts of the base of the crown of the tooth with a layer of cement. The ossification of the surrounding jaw being governed by the changes in the soft, but highly organized dental matrix, fills up the spaces unoccupied by the contracted and divided pulp, and affords, by its periosteum, a surface for the adhesion of the cement or ossified capsule covering the completed part of the tooth(1).

huge extinct animal called *Basilosaurus* by Dr. Harlan, and have advocated the claims of the diminutive *Amphitherium* and *Phascolotherium* of the oolite slate of Stonesfield, to be admitted into the same high class, against the objections raised by Dr. de Blainville. See Comptes Rendus de l'Acad. des Sciences, Oct. 22, 1838. The bifid base of the teeth of certain Sharks not being implanted in a socket, forms no true exception to the rule enunciated in the text. Geological Transactions, 2nd Series, vol. vi. p. 66.

(1) Cuvier ascribes the formation of the fangs of teeth partly to phenomena which are real, but merely concomitant, partly to conditions of the pulp which have no existence. He observes: "La production des racines est due à ce que le noyau pulpeux n'adhère pas au fond de la capsule, par la totalité de sa base, mais seulement par certains endroits, qui peuvent être dès lors considérés comme des pédicules très courts. Les lames osseuses arrivées au bas du noyau, se glissent entre ces pédicules, et les entourent eux-mêmes d'une enceinte tubuleuse qui, s'alongeant toujours, force aussi les pédicules pulpeux à s'alonger, et produit ainsi les racines." Leçons d'Anat. Comp. ed. 1836, tom. iv. p. 215.

If the molar of an Ox be examined at the period when the outer crust of the crown is completed, and the fangs have begun to be formed, the capsule will be found adhering to the base of the pulp at their interspaces as well as to their circumference. A vertical slice of such a molar, when it is fully developed, exaimned with a magnifying power of 300 linear dimensions, displays a layer of cement covering the concave interspaces of the base of the fangs; this layer is as distinct in character from the dentine as that which

The matrix of certain teeth does not give rise during any period of their formation to the germ of a second tooth, destined to succeed the first; this, therefore, when completed and worn down, is not replaced: all the true Cetacea are limited to this simple provision of teeth. In the Armadillos, Megatherioids, and Sloths, the want of germinative power, as it may be called, in the matrix is compensated by its persistence, and by the uninterrupted growth of the teeth. In other Mammalia the matrix of the first developed tooth gives origin, as described in the Introduction, to the germ of a second tooth, which sometimes displaces, sometimes takes its place by the side of its predecessor and parent. All those teeth which are displaced by their progeny are called temporary, deciduous, or milk teeth: the mode and direction in which they are displaced and succeeded, viz., from above downwards in the upper, from below upwards in the lower jaw, in both jaws vertically, are the same as in the Crocodile; but the process is never repeated more than once in any Mammiferous animal. A considerable proportion of the dental series is thus changed; the second, or permanent teeth having a size and form as suitable to the jaws of the adult as the displaced temporary teeth were adapted to those of the young animal. The permanent teeth, which assume places not previously occupied by deciduous ones, are always the most posterior in their position, and generally the most complex in their form.

The successors of the deciduous incisors and canines differ from them chiefly in size; the successors of the deciduous molars may differ likewise in shape; in which case they have always less

invests the rest of the fangs, and could not have existed if the dentinal pulp had been detached from the bottom of the capsule in the interspaces of the fangs. The elongation of the pulpy pedicles by the mechanical constriction of the surrounding bone, is an hypothetical cause founded on the same imperfect conception of the vital, and especially the absorbent forces, as that which led Cuvier to ascribe the destruction of the conical base of the Crocodile's old tooth to the mechanical pressure exerted upon it by the apex of the new tooth. The primary branches of the artery of the dentinal pulp correspond in number with the future fangs, at least when the formation of these has begun; but this condition of the supplying channels may be more justly regarded as a concomitant effect of the modified assimilative and formative processes to which the formation of the fangs is due, than as the efficient cause of such changes in the progressive calcification of the pulp.

complex crowns than their predecessors(1). The bicuspides, in Human Anatomy, and the corresponding teeth, called 'premolars,' in the lower Mammals, illustrate this law.

The first true molar owes the germ of its matrix to a vegetation or bud, separated by the fissiparous process from the matrix of a pre-existing tooth; but the backward elongation of the jaw affords space for its development by the side of its progenitor, during which process it may in like manner give origin to a second, and this to a third molar, succeeding each other from before backwards or horizontally. In this successive germ-production we find repeated the multiparous property of the dental matrix of the Crocodile; but the concomitant growth of the jaw allows the second, third, and sometimes fourth generation of true molars to co-exist, and come into place side by side. In the Unguiculate and most of the Ungulate species of the Placental division of the Mammalian class, the fissiparous reproduction of horizontally succeeding teeth stops at the third generation; in other words, they have not more than three true molars on each side of the upper and lower jaws. In the Marsupial series the same process extends to a fourth generation of true or horizontally succeeding molars(2); and in most of the species the four true molars are in use and place at the same time; but in the Kangaroos the anterior ones are shed before the posterior ones are developed. This successive decadence is still more characteristic of the grinding teeth of the Elephant, which consist exclusively of true molars.

(1) "C'est une règle générale, que les molaires de remplacement ont une couronne moins compliquée que celles auxquelles elles succèdent; mais cette couronne compliquée se trouve reportée sur les molaires permanentes qui viennent plus en arrière." This generalization was established by Cuvier. Leçons d'Anat. Comp. ed. 1805, vol. iii. p. 135.

(2) This characteristic extension of the reproductive power of the matrices of the true molars in the Marsupials, is an approximation to the peculiar activity and of persistence of the same power in the vertically succeeding teeth of the cold-blooded Ovipara, and is associated with many other instances of the same affinity in more important parts of the organization of the implacental Mammals.

CHAPTER II.

HORNY TEETH.

MONOTREMES.

131. In entering upon the special consideration of the teeth in the Mammalian class, we meet, at its lowest step, as in Reptiles and Fishes, with horny substance in the place of teeth, properly so called. In the Myxines these dental substitutes were of a conical form, like canine teeth; in the Siren the horny matter sheathed the fore-part of the jaw-bones with a trenchant or incisive plate; in the Ornithorhynchus it assumes the form of both incisive and molar teeth. These bodies, in the paradoxical Mammal, have been admitted by M. F. Cuvier amongst the "Dents de Mammifères," with good figures and descriptions of their outward form. Heusinger has accurately described their intimate texture, and an affirmative reply has been given, by the common consent of all Anatomists and Naturalists who have treated of the Ornithorhynchus, to the remarkable anticipatory remark with which Hunter concludes one of his philosophic generalizations on the dental organs:— "We may call," he writes in 1792, "everything *teeth* fitted for the purposes before mentioned, (viz., holding or retaining, dividing, cracking, and grinding the food), which is composed of an animal substance and calcareous earth, called bone: how far horny substance may be so shaped as to deserve the name of teeth, I do not yet know." Within ten years after the decease of Hunter, Mr. Home was enabled to describe the most conspicuous of the horny teeth of the Ornithorhynchus as follows:—"The teeth, if they can be so called, are all grinders; they are four in number, situated in the posterior part of the mouth, one on each side of the upper and under jaw, and have broad flattened crowns. In the smaller specimens before examined, each of these large teeth appeared to be made up of two smaller ones, distinct from each other. The animal, therefore, most probably sheds its teeth as it increases in size. They differ from common teeth very materially,

having neither enamel nor bone, but being composed of a horny substance only embedded in the gum, to which they are connected by an irregular surface, in the place of fangs. When cut through, which is readily done by a knife, the internal structure is fibrous, like nail; the direction of the fibres is from the crown downwards." Philos. Trans. 1802, p. 71. Pl. ii. fig. 2. These constituent vertical fibres are rightly described by Heusinger as hollow tubes, forming a texture closely similar to that of Baleen and Rhinoceros-horn(1).

In the figure which is appended to Home's description, two other horny teeth are accurately represented "in situ," in the lower jaw, and the corresponding teeth of the upper jaw have been subsequently figured and described by F. Cuvier(2). The horny teeth of the Ornithorhynchus are, in fact, eight in number: the anterior tooth in the upper jaw is situated on the slender anterior termination of the upper maxillary bone; it is much extended from behind forwards, and pointed at each extremity, but is low, very narrow, and four-sided: the broadest side forms the base of attachment, and is slightly concave and unequal: the outer and inner exposed facets converge to a serrated edge in the young Ornithorhynchus, but this becomes worn down to a flattened surface, which forms the fourth side of the tooth in the old animals. The corresponding tooth in the lower jaw(3) is rather narrower, and retains longer its trenchant edge: these teeth hold the position of the canines and premolars in the normal Mammalia.

At a distance behind the anterior tooth equal to its own length, is situated the horny molar, consisting of a flattened plate, of an oblong subquadrate figure, bounded by a convex outline externally, and a straight line internally, with the inner and anterior angle slightly produced: a slightly raised margin includes two large concave surfaces a little elevated above the intervening part of the grinding surface. The corresponding tooth of the lower jaw(4) is narrower in proportion to its antero-posterior extent, with a convex inner border, and has the two concave surfaces a little more elevated. These surfaces, in both upper and lower molars,

(1) Histologie, 4to. 1822, p. 197.—Pl. 76, fig. 1, *a* and *b*. F. Cuv.
(2) Loc. cit. Pl. 83, p. 202. (3) Pl. 76, fig. 2, *a*. (4) Ib. fig. 2, *b*.

are, prior to abrasion, the most prominent parts of the grinding surface: they are, also, the first-formed parts of the molar, as are the tubercles of the crown in true grinding teeth: like these tubercles also, they are connected together at an early period of the growth of the tooth, only by the vascular matrix, and in dried specimens are separate and distinct. The subsequent conversion of this apparently double into a bituberculate single grinder, is produced by the progressive extension and confluence of the bases of the tubercles, not by a process of sheding and the formation of a new tooth, as Home conjectured.

According to the analysis of Lassaigne, 99·5 parts of the dental tissue of the Ornithorhynchus has the composition of horn, which is hardened by 0·3 parts of the earthy matter of bone.

The account of the horny dental apparatus of the Ornithorhynchus cannot be completed without a notice of the two short and thick conical processes which project from the fore-part of the raised inter-molar portion of the tongue, and which, like the before-mentioned more numerous spines on the corresponding part of the tongue of the Echidna, represent in these low organized Mammals the lingual teeth of Fishes.

132. Those Cetaceous Mammals which are properly called Whales have no teeth, but horny substitutes in the form of plates ending in a fringe of bristles, a peculiarity first pointed out by Aristotle.(1) Of these plates, called "Baleen" and "Whalebone," the largest, which are of an inequilateral triangular form, are arranged in a single longitudinal series on each side of the upper jaw, situated pretty close to each other, depending vertically from the jaw, with their flat surfaces looking backwards and forwards and their unattached margins outwards and inwards, the direction

(1) The passage occurs in the 12th Chapter of the 3rd Book of the "Historia Animalium," and has given rise to much speculation and controversy amongst the Commentators. "Mysticetus etiam pilas in ore intus habet vice dentium, suillis setis similes." To a person looking into the mouth of a stranded whale, the concavity of the palates would appear to be beset with coarse hair. The species of *Balænoptera* which frequents the Mediterranean might have afforded to the Father of Natural History the subject of his philosophical comparison.

of their interspaces being nearly transverse to the axis of the skull. The smaller subsidiary plates are arranged in oblique series internal to the marginal ones. The base of each plate is hollow, and is fixed upon a pulp developed from a vascular gum, which is attached to a broad and shallow depression occupying the whole of the palatal surface of the maxillary and of the anterior part of the palatine bones, the Whale being thus, like the Echidna, an example of a Mammalian animal which may be said to have palatal teeth. The base of each marginal plate is the smallest of the three sides of the triangle; it is unequally imbedded in a compact sub-elastic substance, which is so much deeper on the outer than on the inner side, as, in the new-born Whale, to include more than one-half of the outer margin of the baleen-plate. These margins, which are shown at *a*, fig. 4, Pl. 76, are continued downwards in a line dropped nearly vertically from the outer border of the jaw; the inner margin of each plate(1) slopes obliquely outwards from the base to the extremity of the preceding margin; the smaller plates decrease in length to the middle line of the palate, so that the form of the baleen-clad roof of the mouth is that of a transverse arch or vault, against which the convex dorsum of the thick and large tongue(2) is applied when the mouth is closed. Each plate sends off from its inner and oblique margin the fringe of moderately stiff but flexible hairs(3), which projects into the mouth.

In a new-born Whale (*Balæna australis*) in which the longitudinal extent of the baleen-matrix was two feet three inches, I found the number of the large marginal plates to which it gave origin to be one hundred and ninety. The breadth of the base of each of the principal plates of baleen was two inches, the length of the oblique and fringed margin three inches, that of the vertical external margin three inches and a half, of which two inches were embedded in the elastic substance or gum. The thickness of the plate at the free part of this margin is one-third of a line, and the plate becomes a little thinner at the opposite or fringed margin. The direction of the plates is not quite transverse at every part of the series; the inner border is turned rather forwards in the

(1) Pl. 76, fig. 4, *b*. (2) Pl. 76, fig. 4, *c*. (3) Pl. 76, fig. 5, *c*.

anterior and obliquely backwards in the posterior plates, and the inner margin at the basal part of the posterior plates is slightly curved towards the back part of the mouth, to which the bristly terminations of these parts of such plates are directed, thus presenting an additional obstacle to the escape of the small marine animals(1), for the prehension and detention of which, this singular modification of the dental system is especially adapted.

The interspaces of the free extremities of the baleen-plates, which, from the oblique position of their fringed internal margins, are only visible by raising the large lip and looking on the outer part of the series, are in general equal to five or six times the thickness of the plates themselves; the external line of the plate is broken by the outward projection(2) of the base of the free portion of each plate, at least in the dry subject. In the specimen above alluded to, the pulp-cavity at the base of each principal tooth presented the form of a narrow, transversely-elongated fissure, from four to five lines in depth in the larger plates. The bases of the baleen-plates do not stand far apart from one another, but the anterior and posterior walls of the pulp-fissure are respectively confluent with the contiguous divisions of the bases of the adjoining plates at their thin and extreme margins, which by this confluence close the basal end of the interspace of the baleen-plates, which interspace is occupied more than half-way down the plate, by the cementing substance or gum. Thin layers of horn in like manner connect the contiguous plates, and may be traced extending in parallel curves with the basal connecting layer across the cementing substance, as shown in the diagram, Pl. 76, fig. 6, *c*.

The baleen-pulp (indicated by the dotted line, at *a*) is situated in a cavity at the base of the plate, like the pulp of a true tooth; whilst the external cementing material maintains, both with respect to this pulp and to the portion of the baleen-plate which it de-

(1) *Clio borealis*, *Limacina*, and small pelagic *Crustacea*. Before the naturalists of the Arctic expeditions had determined the nature of the food of the true *Balænæ*, John Hunter had stated "I do suppose the fish they catch are small when compared with the size of the mouth." On the Structure and Economy of Whales, Phil. Trans. 1787, p. 397.

(2) The letter *a* is placed near the line of termination of the baleen matrix in fig. 4, called the "beard," by Hunter, Phil. Trans. 1787, p. 397.

velopes, the same relations as the dental capsule bears to the tooth. According to these analogies, it must follow, that only the central fibrous or tubular portion of the baleen-plate is formed, like the dentine, by the basal pulp, and that the base of the plate is not only fixed in its place by the cementing substance or capsule, but must also receive an accession of horny material from it, as Hunter first indicated; this material answers to the cement of true teeth.

The baleen-plates are smallest at the two extremities of the series: in the *Balæna australis* they rapidly increase in length to the thirtieth, then very gradually increase in length to about the one hundred and fortieth, from this they as gradually diminish to the one hundred and sixtieth, and thence rapidly slope away to the same small size as that with which the series commenced. Besides the external and, as they may be termed, the normal plates, which have just been described, there are developed from the inner part of the palatal gum, in *Balæna australis*, a series of smaller fringed processes progressively decreasing in size as they recede from the large external plates; the small plates clothe the middle region of the palate with a finer kind of hair, against which the surface of the tongue more immediately rests; they are also arranged in longitudinal series, which, however, are not parallel with the external one, but pass from the inner margin of that series in oblique lines inwards and backwards. The baleen-processes in each of these oblique series gradually but progressively diminish in size as the series tends backwards; the shape of the base of the smaller median baleen-teeth is rhomboidal or sub-circular; and, from the parallelism of the oblique series, the pulps present the same quincuncial arrangement as that of the feathers of birds; we may say, indeed, that such is the disposition of all these corneous productions on the roof of the Whale's mouth, but that the pattern is obscured by the disproportionate size and lamellar form of the external series of plates.

In the *Balæna mysticetus*, the baleen-plates which succeed the large ones of the outer row, are more numerous, and are relatively longer and larger than in the *Bal. australis*: Mr. Scoresby, who in

his account of the *Balæna mysticetus*, notices only the large marginal plates, states that they are about two hundred in number on each side: the largest are from ten to fourteen feet, very rarely fifteen feet in length, and about a foot in breadth at their base. These plates are overlapped, and concealed by the under lip when the mouth is shut.(1) In the *Balænopteræ*, or Fin-backed Whales, the baleen-processes internal to the marginal plates, are fewer and smaller than in the *Balænæ:* the marginal plates are more numerous, exceeding three hundred on each side:(2) they are broader in proportion to their length, and much smaller in proportion to the entire animal: they are also more bent in the direction transverse to their long axis.

Each plate of baleen consists of a central coarse fibrous substance, and an exterior compact fibrous layer: but this reaches to a certain extent only, beyond which the central part projects in the form of the fringe of bristles. John Hunter first expressed a belief, that the part of the baleen, which was formed by the core or pulp was the hair: and that this received the compact layers on the outside, from the dense but vascular substance between the bases of the plates; which substance he well describes to act as abutments to the whalebone, like the alveolar processes of the teeth, keeping them firm in their places. And he further observes: "As both the whalebone and intermediate substance are constantly growing, and as we must suppose a determined length, necessary, a regular mode of decay must be established, not depending entirely on chance, or the use it is put to. In its growth three parts appear to be formed; one from the rising core, which is the centre; a second on the outside; and a third being the intermediate substance. These appear to have three stages of duration; for that which forms on the core, I believe, makes the hair, and that on the outside makes principally the plate of whalebone; this, when got a certain length breaks off, leaving the hair projecting, becoming at the termination very brittle; and the third or intermediate substance, by the time it rises as high as the edge of the skin of the

(1) Wernerian Trans: vol. i. p. 579.

(2) Hunter, loc. cit. p. 307, & Neill, Wernerian Trans. vol. i. p. 202.

jaw, decays and softens away like the old cuticle of the sole of the foot when steeped in water"(1).

A thin transverse section of baleen, viewed with a low magnifying power, demonstrates that the coarse fibres, as they seem to the naked eye, which form the central substance, are hollow tubes(2), with concentric laminated walls. When a high magnifying power is applied to such a section, the concentric lines are shown not to be uniform; but interrupted here and there by minute elliptical dilatations, which are commonly more opake than the surrounding substance, and which, like the calcigerous cells of true bone, are probably remains of the primitive cells of the formative substance: similar long elliptical opake bodies or cells, are dispersed irregularly through the straight parallel fibres of the dense outer laminæ of the baleen plate.

The chemical basis of baleen, according to Brande, is albumen hardened by a small proportion of phosphate of lime.

HYPEROODON.

133. Before leaving the consideration of the horny teeth of the Mammalia, it seems proper to notice in the present chapter the hard horny pointed processes which are said to project from the palate of the Bottle-nose Dolphin, thence called *Hyperoodon*, by Lacepede; which processes may be regarded as analogous to the baleen-plates in true Whales, but I regret that no opportunity has occurred to me of examining them.

RYTINA.

134. The singular armature of the palate and lower jaw, in the *Rytina*, or Arctic Dugong, likewise falls within the present category. According to Steller(3), this marine animal has no true teeth, but only two large whitish dental masses, one adhering to the palate, the other to the opposed part of the lower jaw: they are not implanted by gomphosis, but adhere by numerous pores to corresponding papillæ of the membrane covering the palate and lower jaw; besides which, the palatal tooth is fixed at the sides of

(1) Loc. cit. p. 397. (2) Heusinger Histologie, p. 198, pl. ii, fig. 3.
(3) Nova. Comment. Petropolit. tom. ii. p. 294, 1751.

its anterior part to furrows in the lining membrane of the thick lip. The free surface of the dental mass is sculptured by undulating grooves and risings, adapted to corresponding inequalities in the opposite mass.

Dr. Brandt(1) has shown by later and more minute examination of the problematical teeth of the *Rytina*, deposited by Steller in the Petersburgh Collection, that their texture is horny, consisting of minute hollow fibres, placed vertically to the plane of the grinding surface of the tooth, but of unusual density. Thus the dentition of the Rytina closely resembles that of the Ornithorhynchus in both the texture and implantation of the teeth, which will probably be found to contain a similar or greater proportion of osseous matter. M. F. Cuvier(2) has suggested, that the above described plates may be analogous in position, as in texture, to the horny covering of the opposed surfaces of the deflected portions of the upper and lower jaws in the Dugong.

CHAPTER III.

TEETH OF BRUTA, (EDENTATA, Cuv.)

ORYCTEROPUS.

135.—The Orycterope, or Cape Ant-eater, differs from the edentulous Ant-eaters of South America, in having teeth in both jaws(3). These teeth are of a simple form, but peculiar structure; their common number in the mature animal is $\frac{7.7}{6.6} = 26$; they all belong to the molar series. The anterior teeth are very small, and are not unfrequently wanting, or are concealed by the gum, especially the first in the upper jaw: the second tooth of the upper jaw is small, compressed and obtuse; it opposes a similar one in the lower jaw: the third and fourth molars increase in size, have an elliptical transverse section, and a triturating surface of two facets: the fourth and fifth molars are the largest in the upper jaw, are of equal size, and have a longitudinal depression in their internal

(1) Mém. de l'Acad. Imp: de Pétersb. vi. ser. t. ii. p. 103.

(2) Histoire des Cétacés, 8vo. 1836 p. 736.

(3) Pl. 76, fig. 89.

and external sides, giving their transverse section a bilobed or hour-glass figure: the seventh molar is smaller, and has the same simple figure as the fourth.

The first molar in the lower jaw is similar in size and shape to the second of the upper jaw to which it is opposed; in one of the specimens examined by me, it was shed, and every trace of its alveolus effaced, leaving only five molar teeth in the lower jaw. In this bone, which measured eight inches in length, the molar series occupied an extent of two inches, commencing about three inches and a half from the anterior extremity of the ramus: the dentigerous part of the bone is slightly expanded, both laterally and inferiorly. The antepenultimate and penultimate molars of the lower jaw are indented, like those above, by a longitudinal groove upon both their outer and their inner sides, which grooves sink rather deeper into the substance of the tooth, as they approach the base.

The proportions of these teeth, the depth of their sockets, and their structure, as viewed in longitudinal section with the naked eye, are shown in Plate 76, Fig. 10. The teeth are continued solid, and of the same dimensions, to the bottom of the socket, and terminate by a truncated and undivided base. M. F. Cuvier and other Comparative Anatomists have noted the distinction which the teeth of the Orycteropus present, as compared with those of all other animals, in the absence at every period of their growth of a pulp-cavity at the base. But this difference is more apparent than real; it could only be predicated of the teeth in question, if each was what it seems, a single tooth, and not as it really is an aggregate of teeth. When viewed in the latter light, it will be found that each component denticle has its base excavated by a conical pulp-cavity, as in other animals, and which is persistent, as in the rest of the order *Bruta*. The wide inferior apertures of these pulp-cavities constitute the pores observable on the base of the compound tooth of the Orycterope, and give to that part a close resemblance to the section of a cane (1): the canals to which these pores lead, are the centres of radiation of the calcigerous tubes of the denticle,(2)

(1) Pl. 76, fig. 11.

(2) Report of the British Association, vol. vii. 1838, p. 145.

and not the orifices of simple canals resembling, as it was supposed, those of baleen or Rhinoceros-horn.(1)

The compound tooth of the Orycterope consists of a congeries of very long and slender prismatic denticles commonly six-sided, more rarely five or four-sided, cemented together laterally, slightly decreasing in diameter, and occasionally bifurcating as they approach the grinding surface of the tooth. The medullary or pulp-canal of each denticle is widest at its base (Pl. 77, *a*, *a*,) diminishes at first rapidly, then very gradually, and divides where the denticle divides, to continue along the centre of each division. The walls of the denticle consist of hard unvascular dentine, into which the minute calcigerous tubes are sent from every part of the circumference of the medullary canal (Pl. 78). The calcigerous tubes are $\frac{1}{700}$th of a line in diameter at their origin; but rapidly diminish as they proceed, dichotomously sub-dividing, towards the interspace which separates them from the contiguous denticles: their general course is transverse to the axis of the denticle, and they give off numerous branches, which form near the boundary space a moss-like reticulation of extremely minute tubes. Nearly the whole extent of the medullary canal is occupied by a vascular pulp, and the base of each denticle is surrounded by a delicate vascular capsule, which becomes ossified about a line above the base, and forms the cementing substance of the congeries of denticles. The vascular pulp, likewise, becomes ossified near the grinding surface of the tooth, and consequently a transverse section taken from this part, presents the centres of the radiation of the calcigerous tubes filled up with bone.

From the preceding account of the minute structure of the compound tooth of the Orycterope, it will be seen to resemble the teeth of the Myliobates and Chimæroids, among fishes, rather than any true teeth in the Mammalian class, in which it offers a transitional step from the horny substitutes of teeth, above described to the true teeth.

The teeth of the *Orycteropus*, when rightly understood, offer, however, no anomaly or exceptional condition in their mode of

(1) Cuvier, Leçons d'Anat. Comp. ed. 1836, t. iii. p. 205. Heusinger Histologie, 1823, p. 198.

development(1). Each denticle is developed according to the same laws, and by as simple a matrix, as those larger teeth in other Mammalia which consist only of dentine and cement. The dentine is formed by the centripetal calcification of the pulp, and the cement by ossification of the capsule: both pulp and capsule continue to be reproduced at the bottom of the alveolus, *pari passu* with the attrition of the exposed crown; and the mode and time of growth being alike in each denticle, the whole compound tooth is maintained throughout the life of the animal. The augmentation in the size of the whole tooth, during the growth of the jaw, is effected by the development of new denticles, and a slight increase of size in the old ones, at the base of the growing tooth, which in the progress of attrition and growth, becomes its grinding surface.

ARMADILLOS.

136. It has been a subject of regret to most Naturalists that the great Reformer of Zoology should have substituted the name *Edentata* for that of *Bruta*, applied by Linnæus to the order of Mammals which he had characterized by the absence of incisors. The subsequent discoveries of Naturalists have much augmented the *Edentata* of Cuvier, and have shown that out of the great number of species contained in this order, two only are without teeth, whilst almost all are destitute of incisors. The exceptions to the Linnæan character occur in the family of Armadillos, in which the species of the existing subgenus *Euphractus*, and of the extinct genera *Glyptodon* and *Chlamydotherium* have teeth in the intermaxillary bones.

(1) M. Fred. Cuvier, at the close of his description of the teeth of the Orycterope remarks: "Les machelières de l'orycterope ont une structure qui leur est tout-à-fait particulière; leurs racines ne diffèrent point de leur couronne, mais elles ne présentent point de cavité pour la capsule dentaire, comme font toutes les espèces de dents chez les mammifères; elles semblent présenter un nouveau mode de développement pour ces organes. Comme toutes les dents dépourvues de racines proprement dites, elles paraissent croître constamment; mais, au lieu d'être formées de couches successives et toujours renaissantes, elles le sont, en apparence du moins, de fibres longitudinales, pentagones, et dont le centre serait percé, ou rempli d'une substance de couleur plus foncée que ces fibres." Dents de Mammifères, p. 209.

The present knowledge of the dental system of the Orycterope strikingly exemplifies the manner in which anomalies disappear as we gain a deeper insight into structure.

The teeth are more numerous in the *Priodon*, the largest of existing Armadillos, than in any other land Mammal, but they are of very small size and simple form, and are all referable to the molar series(1). They vary in number from twenty-four to twenty-six in each upper jaw, and from twenty-two to twenty-four on each side of the lower jaw, amounting to from ninety-four to one hundred in total number. They are compressed laterally, most so where they are smallest at the anterior part of the series, increasing in size, and especially in breadth, as they recede backwards, with oblique or horizontal flat grinding surfaces, and continued of the same size and form to their implanted extremity, which is excavated by a large conical pulp-cavity. This absence of roots and the undivided hollow base, indicative of the constant growth of the tooth, are common, as has been before stated in the general observations on Mammalian dentition, not only to the teeth of the Armadillos, but to those of all the known species of the order *Bruta*. In the Priodont the teeth, though so unusually numerous, are separated by slight intervals ; those of the lower jaw oppose their outer sides to the inner sides of the upper teeth when the mouth is shut.

In the subgenus *Tatusia* of F. Cuvier, which includes the 7-banded, 8-banded, and 9-banded Armadillos, the upper teeth are also confined to the maxillary bones, but are much fewer in number and larger than in the Priodon. In the species whose dentition is figured and described by M. F. Cuvier(2), there are eight molars on each side of the upper jaw, and nine on each side of the lower jaw (Pl. 85, fig. 2). It agrees, therefore, with the *Dasypus octocinctus* of Linnæus (*Das. uroceras*, Lund.), a species with a tail somewhat shorter than the body, and a native of Central Brazil and Paraguay, where it is called "Tatu-verdadeiro." In both jaws the teeth progressively increase in size from the first to the penultimate, the last suddenly decreasing in size: those of the lower jaw alternate in position with the upper teeth, and it results from this reciprocal position that the grinding surface is worn down into two sloping facets. The *Dasypus novem-cinctus* L., (*D. longicaudus*, Max.) has

(1) Pl. 85. fig. 1, *a—d*.

(2) Loc. cit. Pl. lxxx.

seven molars on each side the upper jaw, and a tail as long as the body; it inhabits Cayenne and the northern parts of Brazil. The *Das. septem-cinctus.* L., (*D. hybridus*, Desm.)(1) has likewise seven molars on each side of the upper jaw, and a tail much shorter than the body.

The Armadillos of the subgenus *Euphractus*, Wagler, to which the term *Dasypus* is restricted by F. Cuvier, are distinguished by having the anterior tooth, which is shaped like the succeeding molar, implanted in the maxillary bone. The species of which the dentition is figured by M. F. Cuvier(2), is the *Dasypus sex-cinctus* of Linnæus, the Weasel-headed Armadillo of Grew. It has $\frac{9-9}{10-10} = 38$ teeth. Those of the upper jaw gradually increase in size to the sixth, and diminish from the seventh to the ninth: they present an elliptical, transverse section, which is narrowest in the small anterior teeth. The two anterior teeth of the lower jaw being in advance of the intermaxillary tooth, are, with it, arbitrarily held to be incisors: they are compressed, but are terminated by obtuse crowns: the rest of the series, from which the incisors are not separated by any remarkable interval, gradually increase in size to the penultimate molar: they have the same alternate position and obliquely worn grinding surfaces as in the *Tatusiæ*.

Among the extinct species, that forming the type of the genus called by M. Lund *Euryodon* is distinguished from all existing Armadillos by having the teeth compressed from before backwards, instead of laterally; but the grinding surface consists, as usual, of two facets, which meet at a more or less acute angle in a transverse ridge(3).

In a second extinct genus, *Heterodon*, Lund, the teeth exhibit much less conformity in shape and size than in the existing Armadillos. Both the anterior and posterior molars are small and conical; while the penultimate and ante-penultimate are much larger, the former being oval, the latter heart-shaped in transverse section.

(1) This species occurs only in the extra-tropical part of S. America.

(2) Loc. cit. Pl. lxxix.

(3) Blik paa Brasiliens Dyreverden För Sidste Jordomvæltning, af Dr. Lund, Kjöbenhavn, 4to. p. 7.

In the *Chlamydotherium*, Lund, there are eight teeth on each side of the upper, and nine on each side of the lower jaw: of these the two anterior ones in the upper jaw, and the three anterior ones in the lower jaw, are incisors by position. The latter are shaped like small cylinders, with a more or less reniform transverse section, while the molars are very large and compressed, so that their section resembles an elongated kidney: their sides are marked with several canaliculate impressions, and their grinding surface presents two projections, the effect of the action of the teeth of the opposite jaw; elsewhere the surface is flat, and a little hollowed in the middle. The size of the species (*Chlam. Humboldtii*), of which the dentition is here described, was six feet, or double that of the *Priodon*, which is the largest of existing Armadillos; but the *Chlam. giganteum* equalled in bulk the Rhinoceros.

The extinct *Glyptodon*(1) seems to have surpassed the Rhinoceros in size: and its dentition(2) was more complicated, more adapted to a vegetable diet, than that of the Chlamydothere. The total number of teeth in the Glyptodon has not yet been determined. A fragment of the anterior part of the lower jaw shows that the teeth extended close to the symphysis, and, therefore, indicates their presence in the intermaxillary bones above. The single tooth, on which the generic character of the Glyptodon was founded, is long, rootless, as in the existing Armadillos, but compressed laterally, and divided by two deep, angular, longitudinal, and opposite grooves on each side, into three plates, which give the grinding surface the form of as many rhomboidal lobes. The alveoli on the fragment of jaw above mentioned, indicate the anterior teeth there to have had the same form, and, from the allusion which Dr. Lund(3) makes to the teeth in the *Hoplophorus* (Glyptodon) of the Brazilian Caverns, it would seem that the complicated form just described, pervaded the whole dental series.

The teeth of the Armadillo-tribe are harder than those of

(1) Sir W. Parish's Buenos Ayres, 8vo. 1839, Geol. Trans. 2nd series, vol. vi. p. 81—85.

(2) Pl. 86. fig. 1 and 2.

(3) "Its teeth are shaped like the molars of the Capibara, but have a different structure, inasmuch as they are simple, and not composed of laminæ." Loc. cit. p. 10.

any other species of the order *Bruta*, but, as in all that order provided with teeth, they are wholly devoid of enamel: it is not true, however, that they have no cement, as Retzius believed. They consist, in both existing and extinct Armadillos, of three distinct substances, of which the unvascular dentine is present in greatest proportion, and forms the main body of the tooth: but it includes a small central axis of vascular dentine, and is surrounded by an extremely thin coating of cement.

The calcigerous tubes of the dentine are continued from the vascular or Haversian canals of the central bone: in the *Dasypus sex-cinctus*(1) they present strong curvatures at their commencement, except the few which arise from the summit of the central axis: these ascend vertically to the grinding surface; the surrounding tubes rapidly diverge like the outer streams of a fountain; and throughout the rest of the body of the tooth the calcigerous tubes bend outwards, and direct their course at right angles to the axis of the tooth, but with a slight convexity directed towards the grinding surface. The diameter of the calcigerous tube, where the parallel course and moderate and regular curve begins, is $\frac{1}{16,000}$th of an inch; the interspace of two tubes equals four of their diameters. The interstitial branches are not easy of detection, but the terminal ones are sufficiently obvious: they are numerous, often irregularly curved; many appear to anastomose, either directly or by intermediate cells, close to the cement(2); others are directly continued into that substance, and terminate in its cells.

The central axis of the solid part of the tooth is occupied, as already stated, by a hard substance, closely resembling bone,(3) in which the last traces of the dentinal pulp appear as the vascular occupants of the medullary canals: these canals are few in number, have not a regular or parallel arrangement, and do not anastomose by loops: some of them are continued, along with short processes of the osseous substance a little way into the dentine: a rich pencil or brush of calcigerous tubes radiates in strong irregular curves from the obtuse ends of these processes, before falling into the common parallel course.

(1) Pl. 85, fig. 4, *b*. (2) Ib. fig. 4, *c*. (3) Ib. fig. 4, *a*.

In the *Glyptodon* the vascular osseous texture(1) occupies a larger proportion of the centre of the tooth than in the small Armadillos: it is harder than the dentine or cement, and rises upon the grinding surface(2) in the form of a ridge extending along the middle of the long axis of that surface, and in three shorter ridges at right angles to the preceding, at the middle of each of the three rhomboidal divisions of the tooth. The medullary canals are surrounded by fine compact concentric strata, but are wider than in true bone, and the calcigerous cells are fewer and less conspicuous: the canals bend towards the dentine, but without any regular or parallel arrangement. The calcigerous tubes(3) assume their parallel and regular course sooner than in the Armadillos: they have the same relative diameter, arrangement, and terminal ramification. The outer coat of cement(4), though not exceeding $\frac{1}{10}$th of a line in thickness, is relatively thicker than in the Armadillos; a large proportion of the terminal branches of the calcigerous tubes is continued into it, and these branches anastomose with the plexiform tubes which surround the calcigerous cells. These cells, which generally present an oblong form, are about $\frac{1}{2,560}$th of an inch in their long diameter.

Although the teeth of the largest of the extinct loricated *Bruta*, present so much more complicated a form than do those of the small existing species, their intimate texture and composition are essentially the same, and very distinct from what has been described in the Orycteropus and will subsequently be shown to characterize the dentition of the family of the Sloths. Nevertheless, the modification in regard to the proportions of the constituent textures of the molars of the Glyptodon, which produce the inequality in the grinding surface of the crown, coincide with the more complicated form of that surface, in adapting the tooth for a more strictly vegetable diet than is indicated by the more simple molars of the existing Armadillos. It is interesting to find that the herbivorous character of the dentition of the Glyptodon was associated with a descending process of the malar bone(5), which, in the Sloths, affords the masseter muscle, a more extensive and

(1) Pl. 86, fig. 3, *a*. (2) Ib. fig. 2. (3) Ib. fig. 3. *b*, *b*. (4) Ib. fig. 3, *c*.
(5) Geol. Trans. 2nd series, vol. vi. p. 86.

favourable attachment for producing the horizontal triturating movements of the lower jaw.

With reference to the diet of the existing Armadillos, Dr. Lund states, that those which he kept in his house manifested an extraordinary predilection for putrid flesh, as well as a remarkable skill in managing it; and, that he always found in the stomachs of the wild Armadillos numerous remains of insects, particularly of beetles and centipedes, whence he concludes, that the recent Armadillos are insectivorous and carnivorous. The maintenance of the dental series in both the existing species and the great extinct phytiphagous Armadillos is effected, as the wide conical persistent basal pulp-cavity demonstrates, by constant renovation of the matrix, which, by its calcification produces the different dental substances.

SLOTHS.

137.—Of the leaf-eating species of the order *Bruta* very few, and these the most diminutive of the tribe, now exist. They are called Sloths, Tardigrades, and Bradypodes, from their inability to move otherwise than slowly and with difficulty on the ground; but they are excellent climbers, for which their organization especially befits them.

If we restrict our survey of the dental system to existing Mammals, that of the Sloths appears anomalous, both as respects the number, the form and the intimate composition of the teeth. But when the bradypodal dentition is viewed in connection with that of the extinct phyllophagous *Bruta*, the repetition of all its essential characters, under various minor modifications, in the already known species and genera of those once numerous and gigantic quadrupeds, gives it as important a place in the classification of the Mammalian teeth, as that of the dentition of the proboscidian Pachyderms or Ruminants.

The following are the common and constant characters of the dentition of the phyllophagous *Bruta*, both recent and extinct:—*Teeth* implanted in the maxillary, never in the intermaxillary bones; few in number, not exceeding $\frac{5-5}{4-4}$ (1); composed of a large central axis of vascular dentine, with a thin investment of hard

(1) Unless the Megatherium had ten molars in the lower as in the upper jaw.

or unvascular dentine, and a thick outer coating of cement. To these, of course, may be added the dental characters common to the order *Bruta*: viz. uninterrupted growth of the teeth, and their concomitant implantation by a simple, deeply excavated base, not separated by a cervix from the exposed summit or crown.

In the mature Ai, (*Bradypus tridactylus*, Linn.) the teeth(1) are small, of a simple columnar form, presenting, for the most part, a sub-elliptical transverse section, sub-equal, and separated from each other by short intervals. The grinding surface has a central depression, with a raised margin, worn unequally into one or two points. The first tooth in the upper jaw is the smallest, the second is the largest; both approach the trihedral form. The first in the lower jaw is more curved than the rest, and is compressed from before backwards, the posterior surface forming a slight angle, and bevelled down obliquely from the anterior margin, which is trenchant, and sometimes notched: the fourth or last molar of the lower jaw is subtetragonal, and rather larger than the rest. The teeth of the upper and lower jaw are not opposite; but subalternate when the mouth is closed.

The dental formula of the genus *Bradypus* is

$$\text{Inc. } \tfrac{0}{0}, \text{ Canini } \tfrac{0}{0}, \text{ Molares } \tfrac{5-5}{4-4} = 18.$$

Dr. Brant(2) has described and figured the skull of a young Ai, in which a very small tooth preceded the compressed one on each side of the lower jaw, rendering the number of teeth equal to that in the upper jaw. The remains of the alveoli of these teeth are visible in the jaw of a young Ai in the Hunterian Museum, but they are soon shed; and, if constant in the species, are confined to the immature period.

In the two-toed Sloth or Unau, (*Cholæpus didactylus*, Illig) the teeth(3) offer a greater inequality of size than has yet been observed in any other genus of *Bruta*; the first of each series, in both jaws, which in the rest of the Order is the smallest, here so

(1) Pl. 81, fig. 1.

(2) Dissertatio Zoologica inauguralis de Tardigradis, 4to. figs 5 & 6. 1828. p. 31, pl. 2. In the fœtal Ai examined by Dr. Harlan, these small deciduous teeth were, perhaps, not developed. See this Author's Medical and Physical Researches, p. 549.

(3) Pl. 81, figs. 3, 4, 5.

much exceeds the others, as with its peculiar form, to have received the name of a canine. The Unau is the only species of *Bruta*, which derives a weapon of offence and defence from the dental system; and, instead of affording the type(1) of the dentition of its particular family, ought rather to be regarded as manifesting the exceptional modification.

The so-called canines of the Unau are separated by a marked interval from the other teeth, especially in the upper jaw; so that those above play upon the anterior part of those below, contrary to the relative position, and mutual action of the true canine teeth in the *Quadrumana* and *Carnivora*. They are of a triedral form, (fig. 5. *a*,) with the margins of the oblique abraded surface leading to the point, trenchant. The sockets containing the long excavated base of each of these laniiform molars, projects beyond the level of the outer surface of the jaw. The second tooth (*b*) of the upper jaw is the smallest of the series, it has an elliptical transverse section, and its grinding surface slopes from before and behind to a sub-median transverse ridge. The third (*c*), and fourth (*d*) molars, are a little larger, and have two abraded surfaces, which converge to the median ridge. The fifth molar (*e*), is the smallest, and has an oblique grinding surface. In each tooth the ridge is formed by the hard dentine, and is interrupted in the middle by an excavation of the soft dentine. The second, third, and fourth teeth of the lower jaw correspond with the third and fourth above; and like the small upper molars, are separated by short intervals: the last is the smallest and most curved.

The large laniiform molars are three-sided; the upper one has one of its sides turned outwards; the lower, one of its angles: the latter resembles the laniiform premolar in the lower jaw of the slow Lemur, in working against the posterior surface of the upper canine, which is an interesting analogy. The wedge-shaped summits of the three lower small molars fit into the interspaces of those of the four upper small molars, when the mouth is closed.

The teeth of the Sloths consist of a central axis of vascular

(1) Dr. Blainville, Ostéographie des Paresseux, (pp. 32, 33.)

dentine, occupying rather more than half the thickness of the tooth, which is enclosed by a wall of unvascular dentine, and this, by one of cement, of less thickness than the layer of hard dentine: but this description applies only to the teeth of the mature animals; and the large anterior laniiform molars of the Unau have a very thin coating of dark coloured cement. Before the teeth are abraded by use, they all present a conical form, and consist chiefly of the hard dentine, which is covered by cement, and has its cavity lined by a layer of the unvascular dentine. Their resemblance at this stage, to the ordinary cuspidate teeth, only wants the interposed layer of enamel, between the coronal cement and the hard dentine to be complete. The cement is soon abraded from the protruded apex, and the exposed hard dentine is worn into a hollow; the magnified section of the tooth of the young *Bradypus* figured in Plate 82, shows its structure at this stage of growth. Whilst abrasion of the summit proceeds, the base elongates by progressive addition of the three constituent substances; and, when it has attained the diameter of the adult tooth, these continue to be added without variation of their respective thicknesses; the complex matrix alone preserving its conical form, and filling the cavity at the base of the tooth. When the coronal hard dentine is worn away, this constituent is afterwards added only to the vertical surface of the central axis of vascular dentine, which henceforward constitutes the central and deepest part of the grinding surface of the tooth.

The intimate structure of the vascular dentine resembles that of the entire tooth in *Psammodus*, *Ptychodus*, and some other Cartilaginous fishes, and that of the inner half of the dentine in the *Iguanodon*: it is perforated by vascular or medullary canals, from $\frac{1}{600}$th to $\frac{1}{1000}$th of an inch in diameter, with intervals of twice or thrice that breadth; which canals proceed in a slightly undulating and sub-parallel course from the internal surface connected with the pulp, to the hard dentine, at right angles, for the most part, with the plane of the pulp-surface, and obliquely to that of the hard dentine: those vascular canals proceeding from the summit of the pulp are parallel, or nearly so, with the axis of the tooth,

whilst those from the base of the pulp are transverse to the same axis: the intermediate canals have an intermediate course Processes of the vascular pulp are continued along these canals, which consist essentially of tracts of the primitive pulp, which have remained uncalcified. The medullary canals are cylindrical; but not of equal diameter throughout, sometimes presenting alternate expansions and constrictions: they everywhere give off minute calcigerous tubes, which have a wavy course, and the finest branches of which terminate in the minute cells of the intertubular tissue. The medullary canals occasionally bifurcate, and also, but more rarely, anastomose together by loops, the convexity of which is turned towards the hard dentine. Their usual termination, in *Bradypus*, is by splitting into a pencil of smaller wavy branches, close to the hard dentine, the calcigerous tubes of which, are formed by the ultimate sub-division of those branches, as shown in Plate 82, fig. 2, on the left hand-side of the section figured.

The hollow cylinder, or thin layer of hard dentine, resembles very closely that of the human tooth in structure: it consists of a clear substance permeated by the calcigerous tubes given off from the penicillate terminations of the medullary canals: the calcigerous tubes have a diameter of $\frac{1}{1,300}$th of a line, and their interspaces are equal to about twice that diameter. At the sides of the tooth, they proceed in beautiful sigmoid curves parallel with each other, and almost transverse to the cement, but a little inclined towards the summit of the tooth: their first curve is convex towards the same part, their second curve concave, and they then proceed straight to the cement, in which they terminate, either by immediately penetrating, or by sending into it their finer sub-divisions. In a few instances, I have detected looped anastomoses of the peripheral ends of the calcigerous tubes. With a magnifying power of 600 linear dimensions, the minute branches sent off by the calcigerous tubes into their clear interspaces may be discerned. The axis of vascular dentine is not conformable with the conical pulp; but, in the molar of the young Ai examined by me, (the third of the lower jaw) expanded at its summit, which is bifid. The calcigerous tubes of the hard dentine sent off from this part of the vascular dentine,

do not present the curvatures observable in the lateral layer, but pass almost in a straight line to the grinding surface of the tooth, slightly converging and decussating each other at the middle, and slightly diverging near the margin of the crown. The coronal portion of the hard dentine, which is originally nearly three times the thickness of the cylindrical or parietal portion, is worn away almost before the Sloth reaches maturity; and, as the pulp, when once it has taken on the incomplete process of calcification which produces the vascular cement, is never afterwards subject to the primitive and more complete process, the coronal hard dentine is never reproduced. The depressed centre of the grinding surface is then formed by the vascular dentine only; that surface having its inequality maintained by the edge of the cylinder of hard dentine, in place of enamel, and being thus adapted to the comminution of the softer vegetable substances, as the leaves and tender buds of trees.(1)

The external coat of cement has an average thickness of $\frac{1}{4}$th of a line; it gradually thins off to the sharp margin of the pulp-cavity, forming the inserted base of the tooth. It is principally characterized by the numerous calcigerous cells, represented by the dark or opake dots in Plate 82, fig. 1. These present a more or less oblong form, with the long axis parallel with that of the tooth: those next the hard dentine making the nearest approach to the circular form. Their average diameter is $\frac{1}{3000}$th of an inch in the long-diameter, and $\frac{1}{5000}$th in the short diameter; but the extremely numerous minute tortuous tubes, which open into every part of their circumference, give the cells a greater apparent size than they present when viewed by a sufficiently deep power for the clear analysis of the rich and minute tubular system, with which they are everywhere connected. The principal trunks of this system, which, nevertheless, do not exceed the diameter of the calcigerous tubes of the hard dentine, affect a parallel course in many parts of the cement, at nearly right angles to its surface. They are most conspicuous at that part of the cement, which is in contact with

(1) *Cecropia peltata* and *Achra sapota* have been particularized as affording nutriment to the Sloths; but, probably, few of the trees forming the denser forests of tropical America are exempt from their attacks.

the dentine. They communicate freely with the dentinal tubes, and, by their fine sub-divisions, with the calcigerous cells. I have not observed any canal or vessel in the cement of the Sloths' tooth, capable of carrying red blood. It is, therefore, harder than the vascular dentine, but softer than the unvascular dentine, and wears away, so as to form a bevelled edge at the circumference of the grinding surface.

The structural appearances of the Sloth's tooth, with unaided vision, are, as might be expected from its unusual composition, different from those presented by ordinary teeth. Cuvier was misled by these appearances to describe the teeth of the Sloths as "being of the most simple structure imaginable. A cylinder of bone enveloped by enamel, and hollow at both ends; at the outer end by attrition, at the inner end by default of ossification, and for lodging the remains of the gelatinous pulp which has served for their nucleus. "Voilà," he concludes, "toute leur description." Cuvier, however, adds, that "it may be further remarked that the plates which compose their osseous substance are but imperfectly united to each other. In sawing a tooth longitudinally, these plates are seen to be all distinct, piled one upon another like pieces of money or draughtmen in a tube: which tube is formed by the enamel(1)."

The parallel and nearly equi-distant vascular canals occasion the appearance of intervals separating distinct layers of vascular dentine. M. F. Cuvier(2) describes the substance surrounding the central axis as being "analogous to, but less hard than enamel." Dr. Richard Harlan(3) appears to have first distinguished the cemental constituent of the Sloth's tooth; "in which tooth," he says, "there exists first, a central cylinder of bone which is surrounded by enamel, which itself is surrounded or enveloped by a regular layer of cement." The intimate structure of the Sloth's tooth was first accurately described by Retzius(4).

(1) Ossemens Fossiles, tom. v. part 1, p. 84.

(2) Dents de Mammifères, 1825, p. 193.

(3) Medical and Physical Researches, 8vo. 1835, p. 315.

(4) Mikroskopiska undersökningar öfver Tändernes struktur, 8vo. 1827, p. 23.

MEGATHERIOIDS.

138. The larger leaf-devouring species of the order *Bruta*, being too bulky to obtain their food by climbing, were compensated by such colossal proportions and Herculean strength as enabled them to uproot and prostrate the trees on which they fed; certain toes on each foot were modified for support and progression of the body by hoofs on level ground; all the known species had complete clavicles, closed zygomatic arches, and a powerful tail as long as the hind-legs, ancilliary to the support of the enormous hinder parts. Every member of this most extraordinary family of quadrupeds, which was peculiar to the American continents, is now extinct; their teeth, which governed their diet, closely resembled those of their nearest existing congeners, the Sloths.

Megalonyx.—The teeth of the species of this genus correspond most nearly, in form, with those of the existing Sloths, and, in their relative size, with those of the Ai, there being no large anterior laniiform molar, at least, in the lower jaw. Here, on the contrary, the first tooth is the smallest: the second and third teeth are laterally compressed, presenting an ovate transverse section, with the great end turned forwards: the form of the last tooth of the lower jaw, which appears from the mutilated socket in the jaw under consideration, to have been the largest, is not known(1). The tooth (Pl. 80, fig. 6), ascribed by Cuvier to the *Megalonyx*, presents a somewhat irregular, elliptical, transverse section; and, like those in the lower jaw, has the grinding surface hollowed out in the middle. A tooth (Pl. 80, fig. 7), found with certain bones of a Megalonyx in a cavern in Kentucky, presents, in transverse section, a longer and narrower ellipse than the tooth described by Cuvier: there is, also, an irregularity of one side of the ellipse; the middle prominence of that side which is formed by a longitudinal ridge, being stronger, and having a slight concavity or channel on each side: it may probably be, as Dr. Harlan, who has described these interesting remains, conjectures, an upper molar

(1) See my description of the Fossil Mammalia in the Zoology of the Voyage of the Beagle, 4to. p. 99, Pl. xxix.

of the Megalonyx. the entire tooth presents a double curvature, its anterior and external sides being slightly convex, its posterior and internal ones concave(1). This tooth consists, like the one described by Cuvier, of a central body of vascular dentine, surrounded by a thin layer of hard dentine, called enamel by Cuvier and Dr. Harlan, and with an exterior coating of cement: the central less dense axis is worn, as in the Ai's molars, into a hollow; but the hard boundary is uniformly obtuse, not raised into points.

Mylodon.—In this genus of extinct phyllophagous *Bruta* the teeth are eighteen in number, disposed, as in the dental formula of the Sloths, $\frac{5-5}{4-4}$, or five on each side of the upper jaw, four on each side of the lower jaw. They are, as usual, long, and of the same thickness from the exposed to the implanted end: the latter is excavated by a deep conical pulp-cavity, the exposed surface is worn into a shallow depression, with a raised obtuse margin. In the *Mylodon robustus*,—a species about the size of a Rhinoceros, but in some dimensions equalling the Elephant,—the first tooth of the upper jaw is separated by a marked interval from the rest, and it is also more curved, the convexity being turned forwards: its transverse section is subtriedal, with the angles rounded; it measures not more than ten lines across its longest diameter, and is rather more than three inches in length, with a very small portion protruding from the socket. The second molar has an elliptical transverse section, with the long axis parallel with that of the skull: it is of the same size as the first. The remaining upper molars are triedral, indented along the side which looks inwards; the last, of rather larger size than the others, having its longest diameter from behind forward, the other two with theirs transversely: the four posterior molars have short interspaces. In the lower jaw the first molar resembles that above in its size and curvature, but it is nearer the second tooth, and has an oval transverse section; it plays upon the posterior part of the upper tooth, like the inferior canine-shaped molar in the Unau. The second tooth is bent outwards, but less so than the first; its inner surface presents a longitudinal

(1) Harlan's Medical and Physical Researches, 8vo. 1835, pp. 323, 324, Pl. xii. figs. 7, 8, 9.

indentation; its transverse section is triangular, and the posterior and inner angle is produced. The third molar presents a subquadrate transverse section, placed obliquely in the jaw: it is of the same size as the second. The fourth and last molar is the largest, and has the most complex form of any in the series: it is slightly bent lengthwise with the convexity turned inwards, and by the longitudinal channels which traverse its outer and inner surfaces, the transverse section or grinding surface is made bilobed: the inner channel is oblique and much deeper than the outer one; the anterior surface of the anterior lobe of the tooth is also impressed by a shallow channel. The grinding surface of all these teeth is nearly flat; with the slight central depression bounded by an obtuse margin: the small anterior teeth, which, by their more advanced position and curvature, are analogous to the large laniariform molars of the Unau, are rather obliquely worn. The teeth of the *Mylodon Harlani*, very closely resemble those of the *Myl. robustus* in figure: the last molar of the lower jaw presents the most characteristic difference: it has two shallow longitudinal channels along its outer side, the anterior one being the deepest: and the deep and broad longitudinal channel on the inner side of the tooth is angular, and not rounded as in the *Myl. Robustus*. In the *Mylodon Darwinii*, a third species of this extinct genus, the posterior molar of the lower jaw is relatively smaller than in either of the other species, and is impressed with a single longitudinal channel, on both the outer and inner sides; both penetrate the tooth obliquely, but in opposite directions; and both are equally deep: the anterior lobe is not impressed by any channel. The penultimate molar in the same species has the inner side longitudinally indented; but not the anterior side, as in the *Mylodon Harlani*: the second molar is less deeply indented along the inner side(1).

I have investigated microscopically the structure of the teeth in the last two species of Mylodon, and have given illustrations of that of the *Myl. robustus* in the description of the skeleton of that species published by the Royal College of Surgeons(2). Each tooth consists, as in the Sloth, of a central axis of vascular dentine, enclosed by a

(1) Pl. 80, fig. 5. (2) Memoir on the *Mylodon*, &c., 4to. 1842, Pl. xxiv. figs. 2 and 3.

sheath of hard unvascular dentine, about one line and a half in thickness, with an exterior covering of cement, about half a line in thickness. The vascular dentine is permeated, as in the Sloth, by long, nearly straight and parallel vascular canals, proceeding, for the most part outwards, and with a slight inclination, to the grinding surface; this inclination is least at the base, and greatest at the summit of the tooth, where the vascular canals are parallel with the axis of the tooth. They have a slightly undulating course; a diameter of $\frac{1}{700}$th of an inch, which they preserve throughout with little variation; and have intervals of about twice that diameter. They differ chiefly from the vascular canals in the Sloths, by anastomosing together in regular loops, turned towards, and close to the inner surface of the hard dentine. Very fine calcigerous tubes are given off into the interspaces of the vascular canals, from every part of their course; but the most abundant penicilli of these tubes proceed from the convexity of the loops, and there diverge to enter the hard dentine, through which they then proceed in a parallel course, forming the calcigerous tubes of that substance. These tubes are almost as minute as in the Sloth, having a diameter of $\frac{1}{8000}$th of an inch, but have a straighter course; throughout the greater proportion of the hard dentine, they run at right angles to the plane of the cement. In the teeth of the *Mylodon Darwinii*, I observed in the hard dentine a few small vascular canals, which had an irregular course, occasionally anastomosing together, and branching at acute or right angles; their diameter equalled that of five or six of the calcigerous tubes: they were more numerous near the central part of the hard dentine, were filled with dark carbonaceous matter, and, being continued from the larger vascular canals of the soft dentine, established a communication between them and the vascular canals of the cement. In the Sloth, no vascular canals have been detected in the hard dentine or in the cement; in the Mylodon a few of these canals, of larger diameter than those of the hard dentine, are present in the cement(1). They are directed towards the plane of the dentine, and are most conspicuous near that substance; but do not form a series of loops, like the vascular canals of the central substance.

(1) Memoir on the Mylodon, pl. xxiv. fig. 3, *d*.

and are fewer in number. The radiated calcigerous cells are as numerous as in the cement of the Sloth's molar, but offer more conspicuously the elongated form; their long axis being parallel, as in the Sloth, with that of the tooth itself. They measure $\frac{1}{2000}$th of an inch in the long diameter. The cement, in the Mylodon, is traversed likewise by numerous and close-set calcigerous tubes, continued from those of the dentine, with a general direction transversely to the surface of the cement; but with a more wavy and less parallel course, with more frequent bifurcations and more numerous branches, the sub-divisions of which form a rich plexus around each calcigerous cell. The dentinal cells are unusually conspicuous, presenting the appearance of a network in a thin section of the hard dentine of these fossil teeth: they present a sub-hexagonal form, and a diameter of $\frac{1}{1000}$th of an inch; and are figured with the few dispersed vascular canals of the hard dentine in Plate 79.

Scelidotherium.—The genus *Scelidotherium* includes three known species, which resemble the *Mylodon* more nearly than the *Megalonyx*, but differ from both those genera, not only in the form of the teeth but in that of the astragalus, and in the structure of the knee-joint. The dental formula is the same as in the Sloth and Mylodon, viz. $\frac{5-5}{4-4}$.(1) The sockets of the upper jaw are much closer together than in the Mylodon, and the first is not separated by a wider interval from the rest: they occupy an antero-posterior extent of three inches, seven lines, in the *Scelidotherium leptocephalum*, and, in the *Mylodon robustus*, one of five inches, four lines: yet the first and second molars in the Scelidothere exceed those in the Mylodon in size; but the rest are of inferior size in the Scelidothere, and the last is the least of those in the upper jaw, contrary to its proportions in the Mylodon. The four teeth of the lower jaw are also in closer order than in the Mylodon; the length of the alveolar series is three inches, ten lines in the *Scel. leptocephalum*, and five inches in the *Myl. robustus*, but the longest transverse diameter of the first tooth in the Scelidothere exceeds that in the Mylodon, whilst that of the last tooth is half an inch shorter than in the

(1) Plate 80, figs. 1 and 2. The name *Scelidotherium* has been left out, by mistake, at the foot of this plate, in reference to the above figures.

Mylodon robustus; but the difference is less, as compared with the lower molars in the *Mylodon Darwinii.* The two series of upper molar teeth are separated by a narrower palate in the Scelidothere than in the Mylodon. The first molar in the upper jaw, (Pl. 80, fig. 1), is trihedral, and much less curved, and more compressed than in the Mylodon. The second molar is also three-sided, and its transverse section is triangular instead of elliptical; and two of its sides are slightly indented: it resembles the antepenultimate molar in the *Myl. robustus.* The third and fourth molars of the Scelidothere are more compressed, and the long axis of their transverse section is oblique, whilst in the Mylodon it is transverse to the line of the jaw. The fifth molar, besides being relatively smaller, has a trihedral figure with the broadest side turned outwards, and is slightly excavated lengthwise.

In the lower jaw, the differences in the form of the teeth are of the same degree: a comparison of figure 2 with figure 5, in Plate 80, will demonstrate their nature in the *Scel. leptocephalum,* and *Mylodon Darwinii.* The lower molars of the *Myl. robustus* and *Myl. Harlani* differ still more, especially in the last species, from those of *Scelidotherium.*

The composition of the teeth closely resembles that in the genus *Mylodon,* but the central axis of vascular dentine is relatively smaller: it is traversed, however, as in the Mylodon by medullary canals, which, at the periphery of the axis anastomose by loops, from the convexity of which the calcigerous tubes are given off, which penetrate and constitute so large a proportion of the hard dentine. This substance is about one line and a half in thickness, and is invested by a coat of cement, not exceeding one third of a line in thickness. The teeth of the Scelidothere are thus calculated to offer more resistance than those of the Mylodon, having a larger proportion of the hard unvascular dentine, by which they approach nearer to the structure of the teeth in the Armadillo tribe.

Megatherium.—The teeth of this most gigantic of the extinct quadrupeds of the Sloth-tribe are as small in proportion to the size of the animal as in the Mylodon; they are five in number on each side of the upper jaw, and, probably, four on each side of

the lower jaw: they are more closely arranged, are longer, and more deeply implanted than in the smaller Megatherioids; they present a more or less tetragonal figure, and have the grinding surface traversed by two transverse angular ridges. Plate 83 exhibits a longitudinal section of the five molars of the upper jaw, in situ; and demonstrates the great extent of the persistent pulp-cavity; the natural length of the series is ten inches.

The first or anterior molar is the second in point of size, the last being the least, as in the Scelidothere. The first molar is eight inches and a half in length; the pulp-cavity extends five inches from the base: it presents two slight curvatures, one having the convexity turned forwards, and the other inwards. The transverse section gives an irregular semicircle, with the convexity turned forward, and the flat side next the second tooth; the angles at which this side joins the curve are rounded; the outer angle is somewhat produced, and the outer side of the curve is flattened. The central axis of the tooth, formed by the vascular dentine, is irregularly tetragonal, the cement is thick on the anterior and posterior surfaces, thin on the sides of the tooth.

The second molar is the largest of the upper series; it exceeds nine inches in length, is of a tetragonal form, with two slight curvatures, as in the first molar. The posterior and broadest side is nearly flat, the anterior side somewhat convex, the outer and narrowest side is concave, the inner side is sinuous, having a median longitudinal eminence between two longitudinal concavities. The central axis of vascular dentine is more compressed from before backwards, than in the preceding tooth, and its posterior surface is concave; the two transverse ridges of the grinding surface of the tooth are nearly equal; but the sloping side formed by the dentine, is larger than that formed by the cement.

The third tooth is of nearly the same size and form as the second; but is somewhat narrower, the anterior or outer angle is less rounded off, and the external longitudinal depression is deeper.

The fourth molar is smaller than the two preceding, but of nearly equal length, viz. eight inches and a half, and is distinguished from all the other teeth, by being curved in only one direction,

and that in a very slight degree, the concavity looking, as in the other teeth, outwards: the central axis of the tooth is, in reference to the anterior and posterior planes of the skull, quite straight: the anterior and posterior layers of cement decrease in thickness as they approach the base of the tooth, so as to describe a slight curve, the convexity of which is turned, on both sides, towards the adjoining tooth. The fourth molar is tetragonal, and with more equal sides than the two preceding teeth; the outer and inner sides are concave, the anterior and posterior ones convex, the angles rounded, and the anterior and inner one more produced than the rest. The grinding surface presents two equal transverse ridges, the contiguous sides of which are the longest.

The fifth molar is five inches in length, one inch two lines in transverse, and ten lines and a half in antero-posterior diameter: its principal curvature presents its concavity forwards, or towards that of the anterior tooth; the curve in the transverse axis of the skull is scarcely appreciable. The transverse section of this tooth is rhomboidal, with the angles rounded, and with the longest diameter intersecting the anterior internal, and the posterior external angles. The dentinal axis is transversely quadrilateral, with the posterior angles entire, and the posterior surface concave: the layer of cement which covers this surface is the thickest, and is convex: those which cover the outer and inner sides of the tooth are, as in the rest, the thinnest; the anterior layer is less than one third the thickness of the posterior layer. I have not been able to extricate the grinding surface of this molar tooth from the hard conglomerate in which it is imbedded; but from the disposition of the cement it is obvious that the two transverse ridges must be unequal, and the anterior one the smallest, if not almost obsolete.

No distinctly recognizable part of the lower jaw of the Megatherium has yet reached England, and our knowledge of the number and kind of teeth of that jaw is derived from the descriptions and figures of the Madrid Megatherium. These are wanting in the requisite detail, and we have seen how little they can be trusted, even in relation to the number and mode of implantation of the teeth of the upper jaw. Four teeth, of similar size and shape to the large

ones in the upper jaw, have been assigned to each half of the lower jaw of the Megatherium, by Garriga,(1) Pander and D'Alton,(2) and Cuvier.(3) One cannot suppose, that the figures in the celebrated works of these Authors err in the general form and proportions of the four lower molars, which in a side view are not concealed by the ascending ramus of the jaw: but, since we have proof, that a small molar, posterior to the corresponding teeth in the upper jaw has been overlooked, the same oversight may have been committed in regard to a corresponding small tooth in the lower jaw.(4)

In the Collections of Megatherian remains, brought to this country by Sir Woodbine Parish and Mr. Darwin, the following teeth, which differ from those of the upper jaw, may with more probability be referred to the lower jaw than to a distinct species of Megatherium.

That which most closely corresponds with the first molar in the upper jaw, I have referred to the same part of the lower series of molar teeth. The anterior surface is so much less convex than in the first upper molar, that the entire tooth presents a tetragonal rather than a semi-cylindrical figure; the anterior facet, however, being only two-thirds the breadth of the posterior one, by which it differs from all the tetragonal teeth of the upper jaw. Both the inner and outer sides which converge to the anterior surface are slightly concave, whilst the inner side in the first upper molar is convex: it has the same double curvature and transverse diameter as the first upper molar.

A molar tooth of a tetragonal form, but with the anterior facet relatively broader and flatter than in the preceding tooth, and narrower than in any of the tetragonal teeth of the upper jaw, may be the second molar of the lower jaw.

A third tetragonal molar resembles the third in the upper jaw,

(1) Description del Esqueleto de un Quadrupedo muy corpulento y raro, &c. fol. 1796.

(2) Das Riesen-Faulthier, *Bradypus giganteus*, abgebildet, beschrieben, &c. fol. 1821.

(3) Ossemens Fossiles, 4to. 1825, vol. v. pt. i.

(4) Professor Daubeny kindly undertook, at my request, to examine the jaws of the celebrated skeleton of the Megatherium at Madrid during his recent visit to Spain, with a view to determine the actual number of teeth: but he found the specimen so inclosed in its glazed case, as to prevent any examination of the interior of the mouth, and to exhibit only those teeth that are obvious in the published figures. This may account for the oversight of the fifth superior molar. Permission to open the case for a nearer inspection could not be obtained.

in its slight and single curvature: its anterior and posterior sides are convex; the outer and inner ones concave.

Another molar tooth of a Megatherium is preserved with its own and a portion of the adjoining socket, showing it to be the last of its series, and less than half the size of the teeth which preceded it. It is, in fact, as small as the last molar of the upper jaw; but differs in being straighter, and in the smaller antero-posterior diameter compared with the transverse diameter: the posterior surface is flatter, and the angles dividing the four surfaces are more marked.

The fragment of the jaw connected with this tooth is insufficient to determine whether it be part of the upper or lower jaw: if of the upper, the tooth clearly indicates a distinct species of Megatherium from that of which the upper molar series is figured in Pl. 83; if of the lower jaw, then the tooth in question may be a fifth molar, and the two last molars in the upper jaw will be opposed by a fourth and fifth in the lower jaw, instead of by a larger and more complicated fourth molar, as in the other known Megatherioid genera.

Each molar tooth of the Megatherium is excavated by an unusually extensive conical pulp-cavity, (Pl. 83, *c*) from the apex of which a fissure is continued to the middle concavity of the grinding surface of the tooth. The central axis of vascular dentine, (Pl. 83, *b*, *b*) is surrounded by a thin layer of hard or unvascular dentine, and this is coated by the cement, (ib. *a*, *a*.) which is of great thickness on the anterior and posterior surfaces; but is thin where it covers the outer and inner sides of the tooth. As the outer layer of the vascular dentine is first formed by the centripetal calcification of the pulp, the thin crust of that substance at the base of the tooth includes a space equal to that of the vascular dentine at the crown of the tooth: the contraction of the base of the tooth is due to the progressively diminishing thickness of the cement, as it approaches that part; the intervening vacancy in the socket indicating the primitive thickness of the capsular basis of the cement.

The vascular dentine (Pl. 84, *a*, *á*) is traversed throughout by medullary canals, measuring $\frac{1}{1500}$th of an inch in diameter, which are continued from the pulp-cavity, and proceed, at an angle of 50°,

to the plane of the hard dentine, parallel to each other, with a slightly undulating course, having regular interspaces, equal to one diameter and a half of their own area, generally anastomosing in pairs by a loop, (*á*, *á*,) the convexity of which is turned towards the origin of the tubes of the hard dentine, forming a continuous reflected canal. The loops are situated near, and for the most part close, to the hard dentine. In a few places one of the medullary canals may be observed to extend across the hard dentine, and to anastomose with a corresponding canal in the cement. The interspaces of the medullary canals of the vascular dentine are principally occupied by calcigerous tubes, which have an irregular course, form reticulate anastomoses, and terminate in very minute cells, at least one hundred times smaller than the calcigerous radiated cells of the cement.

The more regular and parallel calcigerous tubes, which traverse the thin layer of unvascular dentine, are given off from the convexity of the terminal loops of the medullary canals. The course of these tubes is more directly transverse to the axis of the tooth than is that of the medullary canals from which they are continued. They run parallel with each other, but with fine undulations throughout their course. They have a diameter of $\frac{1}{10,000}$th of an inch, and have interspaces of about twice that diameter. As the calcigerous tubes approach the cement, they divide and subdivide, and become more wavy and irregular: their terminal branches take on a bent direction and form anastomoses, dilate into small cells, and many are seen to become continuous with the radiating tubes of the cells of the contiguous cement. The dentinal cells are less distinctly defined than in the Mylodon, and of a more elliptical form: their average diameter is $\frac{1}{900}$th of an inch, and they are traversed by from nine to twelve of the dentinal tubes.

The cement, which enters so largely into the composition of the grinders of the Megatherium, is characterized in that extinct animal by the size, number, and regularity of the vascular or medullary canals which traverse it. They present the diameter of $\frac{1}{1200}$th of an inch, are separated by intervals equal to from four to six of their own diameters, commencing at the outer surface of the cement, they traverse it in a direction slightly inclined from the transverse axis towards the crown of the tooth

running parallel with each other: they divide a few times dichotomously in their course, and finally anastomose in loops, the convexity of which is directed towards, and in most cases is in close contiguity with the layer of hard dentine. Fine calcigerous tubes are sent off, generally at right angles, from the medullary canals, which quickly divide and sub-divide, form anastomosing reticulations, and communicate freely with the similar tubes that radiate from the calcigerous cells. These are dispersed throughout the dentine, and present an oblong form, with the long axis transverse to that of the tooth, measuring $\frac{1}{2000}$th of an inch in diameter. The cavity of the cell, which is not quite occupied by their opake contents, is often very clearly demonstrated. The calcigerous tubes, which radiate from the cells nearest the hard dentine, and from the terminal loops of the vascular canals, intercommunicate freely with the calcigerous tubes of the hard dentine.

The tooth of the Megatherium thus offers an unequivocal example of a course of nutriment from the dentine to the cement, and reciprocally. Professor Retzius has observed, with respect to the human tooth, that "the fine tubes of the cœmentum enter into immediate communications with the cells and tubes of the dentine (zahnknochen), so that this part can obtain from without the requisite humours, after the central pulp has almost ceased to exist." In the Megatherium, however, those anastomoses do not relate to the performance of a vicarious office, since the pulp is maintained in its full size and functional activity during the whole period of the animal's existence.

In the structure which the fossil teeth of the Megatherium and its extinct congeners clearly demonstrate, we have striking evidence of their rich organization, and that they were once pervaded by vital activity. All the constituents of the blood freely circulated through the vascular dentine and the cement, and the vessels of each substance intercommunicated by a few canals continued across the hard or unvascular dentine. With respect to those minuter tubes, the more important as being more immediately engaged in nutrition, which pervade every part of the tooth, characterizing by their difference of length and course the three constituent substances, and which are derived, like the

hypothetical "vasa lymphatica" of the old physiologists, from the ultimate blood-vessels, they form one continuous and freely intercommunicating system of strengthening and reparative vessels, by which the plasma of the blood was distributed throughout the entire tooth for its nutrition and maintenance in a healthy state.

The grinding surface of the close-set molars of the Megatherium differs, on account of the greater thickness of the cement on their anterior and posterior surfaces, from those of all the smaller Megatherioids, in presenting two transverse ridges; one of the sloping sides of each ridge being formed by the cement, the other by the vascular dentine; whilst the unvascular dentine, as the hardest constituent, forms the summit of the ridge, like the plate of enamel between the dentine and cement in the Elephant's grinder. The great length of the teeth and concomitant depth of the jaws, the close set series of the teeth, and the narrow palate are also strong features of resemblance between the Megatherium and Elephant in their dental and maxillary organization. In both these gigantic phyllophagous quadrupeds provision has likewise been made for the maintenance of the grinding machinery in an effective state; but the fertility of the Creative resources is well displayed by the different modes in which this provision has been effected: in the Elephant, it is by the formation of new teeth to supply the place of the old when worn out; in the Megatherium, by the constant repair of the teeth in use, to the base of which new matter is added, in proportion as the old is worn away from the crown. Thus, the extinct Megatherioids had both the same structure and mode of growth and renovation of their teeth, as are manifested in the present day by the diminutive Sloths.

CHAPTER IV.

TEETH OF CETACEANS.

139. *Balænidæ.*—In this, as in the preceding order, the dental system presents little fixity of character, and its variations extend in some cases to anomalies. Surveyed in the true or carnivorous *Cetacea*, it seems, on the whole, to be of a grade inferior to that

of the *Bruta*, since the teeth are all of a more or less simple, conical form, and none of them present flat or ridged crowns like true molars: nevertheless we here first, in the ascensive survey of Mammalian dentition, find enamel entering into the composition of the teeth, the sharp crowns of those of the predaceous Dolphins being tipped or sheathed by this hard substance.

The main anomaly of the dental system in the family *Balænidæ* has already been treated of in the chapter on Horny teeth. But the great Whales, before they acquire their peculiar array of baleen plates, manifest in their fœtal age a transitory condition, a true dental system, which, though abortive and functionless, beautifully typifies that which is normal and persistent in the majority of the order.

In an open groove, which extends along the alveolar border of both the upper and the lower jaws, there is a series of minute, conical, acute, or obtuse denticles, with hollow bases inclosing the uncalcified remains of a vascular pulp. These were first noticed by the philosophical anatomist, Geoffroy St. Hilaire, and have subsequently been described and figured by Prof. Eschricht. The subject examined by the latter Author was the fœtus of a *Balænoptera*, the jaws of which were about four inches in length. The unclosed alveolar groove of the upper jaw contained twenty-eight denticles(1), that of the lower jaw forty-two. The anterior denticles in both jaws were the smallest; but they increase in size more gradually, and maintain a greater regularity of form in the lower jaw, where they are also most numerous, and in which the typical dentition of the carnivorous Cetaceans first manifests its plenary development in the great Cachalot. In the upper jaw of the fœtal Whale some of the denticles are double, two adhering together side by side(2), and they offer in their varying extent of confluence, no unapt resemblance to the stages of the fissiparous multiplication of an infusorial Monad: there can be little doubt, indeed, that these literally 'double-teeth' have resulted from a spontaneous fission of the primordial pulp-cell; the divisions of which growing to a certain size, have again coalesced in the progress of their calcification like the two primitively detached summits of the Ornithorhynchus's grinder. We cannot avoid recognising in these bicuspid denticles

(1) Pl. 90, fig. 1. (2) Ib. figs. 5 and 6.

the representatives of the molars of the gigantic extinct Cetacean, called 'Zeuglodon,' and they also call to mind the similarly shaped ultimate molar in the Dugong.

These small teeth and their matrices entirely disappear before birth: yet the fœtal Whale comparatively long retains and palpably exemplifies the earliest stage of dental development in the higher Mammals, viz., the open fissure, which in these is so rapidly closed, especially in the Human subject. But beyond this stage the true dentition of the *Balænidæ* is not destined to proceed; and they thus manifest, agreeably with the general laws of unity of organization, their closest relations to the typical characters of their order at the early periods of development, divesting themselves of part of the more general type, in order to assume their special and distinctive characters, as they advance towards maturity.

140. *Hyperoodon.*—The great bottle-nose or bident Whale offers a beautiful transitional grade between the true Whales and the typical *Delphinidæ:* the palate is beset with small, unequal, pointed, callous processes, which Cuvier conjectures to be rudimental baleen-plates; whilst to balance, as it might seem, this arrest of the development of the typical garniture of the Whale's jaws, the fœtal denticles do not all perish, but two or three of the anterior pairs acquire a large size, as compared with their transitory representatives in the *Balænidæ*, and one of these pairs is long retained in the lower jaw, though functionless and hidden by the gum.

These teeth are figured of the natural size at the extremity of the lower jaw of an immature *Hyperoodon*, in Pl. 88, fig. 1. They are conical, slightly curved, with an unusually sharp and slender apex, tipped by enamel. Though loose in their sockets, they project so little from them, and have such wide bases that they are retained in situ, and do not fall out in the dried jaw: two smaller cavities in front, and the remains of a larger socket in the alveolar groove, behind the retained teeth, attest the former presence of other teeth.

141. *Monodon.*—In the Narwhal two of the primitive dental germs at the fore part of the upper jaw, proceed in their deve-

lopment to a greater extent than those in the lower jaw of the Hyperoodon; but every other trace of teeth is soon lost. The two persistent matrices rapidly elongate, but in the retrograde direction, forming a long fang rather than a crown; each tooth sinks into a horizontal alveolus of the intermaxillary bone, or rather at the junction of the intermaxillary with the maxillary, and soon, by the forward growth of these bones becomes wholly inclosed, like the germs of the teeth of the higher Mammalia at their second stage of development. In the female Narwhal the pulp is here exhausted, the cavity of the tooth is obliterated by its ossification, further development ceases, and the two teeth remain concealed, as abortive germs, in the substance of the jaws for the rest of life; so that in the skeleton a section of the skull must be made in order to display them, as in Plate 87, fig. 2. In the male Narwhal, the matrix of the tooth in the left intermaxillary bone continues to enlarge; fresh pulp-material is progressively added, which by its calcification elongates the base and protrudes the apex from the socket, and the tusk continues to grow, until it acquires the length of nine or ten feet, with a basal diameter of four inches. This is that famous so-called horn, which figures on the forehead of the heraldic Unicorn, and so long excited the curiosity and conjectures of the older Naturalists, until Olaus Wormius made an end of the speculative and fabulous 'monocerologies' by the discovery of the true nature of their subject; whilst Anderson(1) in the year 1736, took advantage of the accident of the stranding of a Narwhal at the mouth of the Elbe, to communicate to the Zoological world, an accurate figure of the animal which bore the supposed single horn. The exterior of this tusk is marked by spiral ridges, which wind from within forwards, upwards, and to the left: about fourteen inches of the tusk is implanted in the socket; it tapers gradually from the base to the apex. The pulp-cavity is continued nearly to the extreme point, but is of variable width; at the base it forms a short and wide cone, is then continued forwards, as a narrow canal along the centre of the implanted part of the tooth, beyond which, the cavity again expands to a

* Cited by Cuvier, Ossem. Foss. v, pt. 1. p. 319.

width equalling half the diameter of the tooth; and again, but gradually, contracts to a linear fissure near the apex; Plate 87, fig. 4.

Thus the most solid and weighty part of the tooth is that which is implanted in the jaw,(1) and nearest the centre of support, whilst the long projecting part is kept as light as might be compatible with the uses of the tusk as a weapon of attack and defence: the portion of pulp in which the process of the calcification has been arrested, receives its vessels and nerves by the fissure continued from the basal expansion of the pulp-cavity.

The small abortive tusk of the right side of the male Narwhal (Plate 87, fig. 1) has a few slight longitudinal indentations on its basal half, and is smooth on the rest of its exterior; it is solid and closed, generally by a bulbous accumulation of cement, at its base; the apex is truncated with a rough prominence from its centre: the ordinary length is between eight and nine inches. The two concealed tusks of the female Narwhal are of a similar size and shape.

Sometimes both tusks are so developed as to project from their sockets in this sex; Mr. Scoresby records such an example in his Voyage to Greenland.(2) Cuvier saw at Hamburg the skull of a Narwhal with two tusks projecting, which he ascribes to the male sex, probably on account of their length; and he cites two other instances, one figured in the *Ephemerides Naturæ Curiosorum* for 1700, p. 351, the other in Albers' Icones ad illustrand. Anat. Comp. Pl. 2 and 3.

In the cranium of the Narwhal figured by Albers, the right tusk projects only six inches from the socket, is proportionally slender, and is smooth. With regard to the paper in the 'Ephemerides,' or 'Miscellanea curiosa,' (1702, p. 350), though it is entitled "De Unicornu Marino duplici," it gives an account, not of two projecting tusks, but of the discovery by the author, Dr. Reisel, of the small concealed tooth in the right maxillary bone of an ordinary male Narwhal, the tooth being eight

(1) M. F. Cuvier appears to have been misled by ordinary analogies, in describing the Narwhal's tusk as "creuse dans une grande partie de sa longeur, mais surtout dans sa partie alvéolaire," Hist. de Cetacés, 8vo. 1836, p. 237.

(2) It would be interesting to know the condition of the ovaria in such an instance.

inches in length, and exposed by the laying open of the narrow socket ('rima'), in which it was lodged. Two very accurate views of this abortive tusk are given in the figures 23 and 24 of the Plate which illustrates the paper, and the Author conjectures that it may serve to supply the place of the large left tusk should this be either broken away by violence, or shed naturally in process of time. The normal tusk in the skull of the Narwhal, '*Cete Narhual*' the subject of his observation, was inserted fourteen inches deep, and projected nearly four feet from the socket, but its extremity had been broken off. It is figured in the Plate, together with two views of the skull from which the tusks are removed, the fissure, or alveolus of the abortive tusk being shown in Fig. 21. The plate bears no number, but is marked p. 35. I doubt whether Cuvier had ever read this paper: it has the priority of Tichonius' often cited Dissertation "Monoceros piscis haud monoceros," by four years, having been printed in 1702.

The skull of a Narwhal, with two long exserted tusks, formed part of the collection of the late Joshua Brookes; in this specimen the alveolus of the right tusk appeared to have been artificially enlarged, and the tusk was unquestionably cemented in its place; but the circumstance which most militated against its authenticity was the direction of the spiral lines which corresponded with, instead of opposing those of the left tusk.

With regard to the conjectured ulterior use of the concealed tusk in the male as a substitute in the event of the loss of the large tusk —a conjecture more than once repeated since first proposed by Reisel, —the solidity of the concealed tusk and its distorted and generally closed base evince that the term of its growth has expired.

142. *Delphinidæ*. In the *Delphinus griseus* the dentition of the upper jaw is transitory as in the Hyperoodon, but at least six pairs of teeth rise above the gum, and acquire a full development at the fore-part of the lower jaw: the crowns of these teeth soon become obtuse; and even their duration is limited, for the specimen described by M. F. Cuvier(1) had but two teeth on each side of the lower jaw. A Dolphin, perhaps an aged individual of this species, has lately been described with the dentition reduced to two teeth

(1) Dents de Mammifères, p. 243. It was eleven feet in length, and captured at Brest.

in the lower jaw(1). The permanent or mature dentition of the Beluga (*Delphinus leucas*, Pall.) is more normal though scanty, nine teeth being retained on each side of the upper jaw, and eight in each ramus of the lower jaw; they present the form of straight, subcompressed, obtuse cones. The *Delphinus globiceps*, which has $\frac{14-14}{12-12} = 52$ strong, conical and pointed teeth in the vigour of its age, begins soon after to lose them, and in aged individuals none remain in the upper jaw, and not more than eight or ten are preserved in the lower jaw; those at the anterior part of the jaws last longest and their summits are received in cavities in the upper jaw, or the gum covering it, when the mouth is shut.

The most formidable dentition is that of the predaceous Grampus (*Phocæna Orca*) whose laniariform teeth are as large in proportion to the length of the jaws, as in the Crocodile; they are in number $\frac{13-13}{12-12} = 50$, all fixed in deep and distinct sockets, separated by interspaces which admit of the close interlocking of the upper and lower teeth when the mouth is closed. The longest and largest teeth are at the middle of the series, and they gradually decrease in size as they approach the ends, especially the posterior one; the shortness of the anterior teeth is in great part due to the wearing down of the sharp summits, which are best preserved in the small posterior teeth; the position of the bruising and piercing teeth being the reverse of what commonly obtains. An analogy to this circumstance in the dentition of the great predatory Dolphin, is however, manifested by the typical carnivorous quadrupeds in which the incisors are shaped more like grinders than the back teeth.

In the great or Bottle-nose Dolphin (*Delphinus tursio*) the teeth are fewer and larger in proportion to its size than in the common *Delphinus delphis*; but proportionally less developed and more numerous than in the Grampus, the dental formula being $\frac{23-23}{22-22} = 90$ with a variation of three or four more or less in each jaw; the teeth are conical, sub-obtuse, the posterior ones smaller and sharpest. In the common Dolphin the number of teeth amount to 190, arranged in equal numbers above and below. They have

(1) Proceedings of the Acad. of Philadelphia, 1842, p. 127.

slender, sharp, conical, slightly incurved crowns, and diminish in size to the two extremes of each dental series; the acute apices are longer preserved than in the foregoing species. In Pl. 88, fig. 2, the teeth of the upper jaw of an immature Dolphin are exposed *in situ*, and both the extent of their implanted base and that of their pulp-cavity is displayed.

The teeth of the common Porpoise *(Phocæna vulgaris)*, are arranged in equal number on each side of both upper and lower jaws, and are from 80 to 92 in number; the crown is slightly expanded and compressed, and the fully-formed fang is recurved and enlarged at its extremity.

The gangetic Dolphin *(Platanista gangetica)* differs from the rest of the *Delphinidæ* scarcely less in the form of its teeth than in that of the jaws; both the upper and lower maxillary bones are much elongated and compressed; the symphysis of the lower jaw is co-extensive with the long dental series, and the teeth rise so close to it that those of one side touch the others by their bases, except at the posterior part of the jaw; the lateral series of teeth are similarly approximated in the upper jaw at the median line of union, which line is compelled by the alternate position of the teeth, to take a wavy course.

There are thirty teeth on each side of the upper jaw, and thirty-two on each side of the lower jaw(1); in the young animal they are all slender, compressed, straight, and sharp-pointed, the anterior being longer than the posterior ones, and recurved. Contrary to the rule in ordinary Dolphins, the anterior teeth retain their prehensile structure, while the posterior ones soon have their summits worn down to their broad bases. The most remarkable change that occurs in the progress of growth is the antero-posterior expansion as well as elongation of the implanted base of the tooth, which likewise has its outer surface augmented by longitudinal folds or indentations, analogous to, but weaker than those in the base of the teeth of Sauroid fishes. Sometimes the posterior tooth of the *Platanista* has the base divided into two short fangs,—the sole example of such a structure which I have met with in the existing

(2) Pl. 90, fig. 7.

Carnivorous Cetacea. Sir E. Home in a Paper published in the Philosophical Transactions(1) descriptive of the teeth of the Platanista, *(Delphinus gangeticus)*, says of their structure that "the perfect tooth has a tolerably sharp enamelled point, and the lower portion has no enamel." This part which forms the implanted base, is thickly coated by cement; and the pulp-cavity is obliterated. The summits of the teeth are worn or broken off rather suddenly, beyond the tenth in the upper, and beyond the eleventh tooth in the lower jaw; these anterior teeth are worn by mutual attrition, the upper ones on the posterior and inner part of the crown, the lower ones on the anterior and outer sides.

143. *Physeter.*—The outward and visible dentition of the great Sperm-whale or Cachalot *(Physeter macrocephalus)* is confined to the lower jaw, the symphysis of which is co-extensive with four fifths of the entire dental series. This series in the male Cachalot consists in each ramus of twenty-seven subincurved conical, or ovoid teeth, according to their state of development and usage; the smallest teeth are at the two extremes of the series (Pl. 89, fig. 1). In the young Cachalot they are conical and pointed; usage soon renders them obtuse, whilst progressive growth expands and elongates the base into a fang, which then contracts, and is finally solidified and terminated obtusely.

In the lower jaw of a female Cachalot in Dr. Buckland's Museum, the first and the last teeth have the pulp-cavity solidified; in the rest it is widely open, and the lower margin of the tooth forming the base of the conical cavity is very sharp. From the last or hindmost, the teeth gradually increase to the tenth, then continue of equal size to the nineteenth, and again gradually diminish to the twenty-second, counting forwards, that being the total number in each ramus. My friend Mr. Broderip possesses a tooth of a male Physeter, with the base open and uncontracted, which measures nine inches and a half in length and nine inches in circumference and weighs three pounds.(2)

The teeth are separated by intervals as broad as themselves. In

(1) 1818, p. 417.

(2) An ingenious whale-fisher has carved in his leisure moments the chief incidents of his

respect of their mode of implantation in the jaw they offer in the Cachalot a condition intermediate between that of the teeth of the extinct cetaceous-like Ichthyosaurus and the piscivorous Delphinus; they are lodged in a wide and moderately deep groove, imperfectly divided into sockets, the septa of which reach only about half-way from the bottom of the groove. These sockets are both too wide and too shallow to retain the teeth independently of the soft parts, so that it commonly happens, when the dense semi-ligamentous gum dries upon the bone and is stripped off in that state, that it brings away with it the whole series of the teeth, like a row of wedges half-driven through a strip of board. A firmer implantation would seem unnecessary for teeth which have no opponents to strike against, but which enter depressions in the opposite gum when the mouth is closed. That gum, however, conceals a few persistent specimens of the primitive fœta series; these are always much smaller and more curved than the functional teeth of the lower jaw. One of the upper concealed teeth, which was removed by Mr. F. W. Bennett from the gum of a large female Cachalot, is figured of the natural size in Pl. 89, figs. 3 and 4; the latter shows a smooth surface at the convex side of the crown-end which seems to have been produced by contact with the end of the opposite large lower tooth. The fang is contracted and the pulp-cavity closed in the rudimental upper teeth. In two mature Cachalots which Mr. Bennet examined he found eight of these teeth on each side of the upper jaw; they had a very slight attachment to the bone.

There is a well-marked sexual distinction in the size of the jaws of the *Physeter macrocephalus*, those of the mature female being relatively shorter by full one third than in the male. There are

exciting and dangerous occupation on one side of this very fine tooth; the other side bears the following inscription:—

"The Tooth of a Spermatic Whale,
That was caught by the Ship Adam's Crew,
of Albemarle Point, and made 100 bls. of Oil.
in the Year 1817."

Below this inscription are two excellent figures of the Cachalot, one spouting, the other dead and marked for flensing.

usually twenty-three teeth in each ramus of the lower jaw of a full-sized female Cachalot.

The first-formed extremity of the tooth in the young Cachalot may be tipped with enamel, but as yet no authentic example has come under my notice. In all that I have examined, the summits of the crown have been more or less abraded, and the tooth has consisted of a hollow cone of dentine coated by cement, and more or less filled by the ossified pulp. Irregular masses of this fourth substance have been found loose in the pulp-cavity of large teeth; one of those which I divided had no foreign substance as a nucleus. The external cement is thickest at the junction of the crown and base, which are not divided by a neck. The laminated appearance of the dentine is very conspicuous in the surface of polished sections, such as that exhibited in Pl. 89, fig. 2; the cause of that appearance will be described in the next section; in this figure *a* is the cement, *b* the dentine and *c* the osseo-dentine or irregularly ossified pulp.

144. *Structure.*—The dentine of the teeth of the Carnivorous Cetacea is chiefly remarkable, as Retzius first observed, for the number of calcigerous cells in it, arranged generally in planes parallel to the superficies of the tooth and giving rise, in vertical sections, to the appearance of concentric layers of dentine; it is also characterised by the free communication of the dentinal tubes, either immediately or by their branches with these cells, and through their minute prolongations, with the radiated cells of the cement. The early closure of the pulp-cavity in the teeth of the Cetacea may relate to this free communication of the minute canals adapted to circulate the liquor sanguinis through the dental tissues, and to maintain their vital connection with the rest of the organism. The Cetacea in which I have studied the microscopic structure of the teeth are the *Delphinus Tursio*, the *Platanista* and the *Physeter macrocephalus*. The dentinal tubes from the upper part of the pulp-cavity, in the *Delphinus*, ascend and curve, even with slight convergence, towards the apex, then begin to diverge, and lower down the tooth they pass out at right angles to the surface: thus far their course is nearly parallel with one another, but in the fang they assume more considerable and irregular curves. In the Cachalot

the direction of the dentinal tubes at the extremity of the crown of the tooth is represented in Pl. 89, *a*, fig. 1; here they sooner begin to diverge in graceful curves from the vertical tubes which pass to the apex. The diameter of the main tubes in the Cachalot is $\frac{1}{12,000}$th of an inch, in the *Platanista* and *Dolphin* it is less. The interspaces of clear substance equal from four to five of the diameters of the tubes. The tubes divide dichotomously several times in their course, and send off very conspicuous lateral ramuli; they terminate at the periphery of the dentine in numerous and very minute irregularly tortuous tubes which partly anastomose together, partly are lost in the contiguous cells; the minutely undulating course, the bifurcations, lateral branches, and terminal anastomoses of the dentinal tubuli, and part of the peripheral layer of cells of the dentine in the Cachalot's tooth is represented in Pl. 89 A, fig. 2, *a*, *b*. As the dentine of the cetaceous tooth approximates to cement by the size and number of the calcigerous cells, so the cement resembles the dentine in the number and parallelism of the fine canals, which run from its outer surface towards the dentine, in the interspaces of the cells. The parallel tubes differ from those which traverse the cement of the Megatherium's tooth in being too minute to convey the red particles of the blood; they scarcely surpass the origins of the dentinal tubes in diameter; the cement is, however, sparingly traversed in the Cachalot by vascular or medullary canals, about $\frac{1}{2,000}$th of an inch in diameter. In this species the radiated or calcigerous cells of the cement are very abundant and are arranged mostly in layers parallel with the surface, having an irregularly angular outline; a few are roundish, but most are of an oval form, about $\frac{1}{3,000}$th of an inch in the short diameter, and $\frac{1}{1,800}$th of an inch in the long diameter, which is parallel to the plane of the layer, (Pl. 89 A, fig. 2, *c*.) The canals which radiate from the cells, ramify and anastomose with those from contiguous cells and with the branches of the parallel cemental tubes. In some parts of the cement, especially near the dentine, the ramifications of the tubuli are so numerous and dense, along lines parallel with the contour of the dentine, as to give the appearance of white lines to the naked eye, and almost to in-

tercept the light even in very thin sections, when examined in the microscope by transmitted light.

In the Cachalot I have usually found the cement thickest at the middle of the tooth, as represented in Pl. 89, fig. 2, *a*. The cement is thickest in the Dolphins at the end of the fang of the old teeth, where it usually blocks up the pulp-cavity; this is similarly closed in the expanded and compressed bases of the teeth of the Gangetic Platanista.

The formation of the ordinary dentine ceases, in the teeth of the Platanista, at the base of the crown, the entire expanded fang being composed of tubular cement and a narrow central plate of irregularly ossified pulp. A few medullary canals remain in this vertical layer for the passage of the red blood into the tooth, whence the supply of plasma is derived for the system of minuter tubes in the dentine and cement; there are no other remains of the pulp-cavity and the entire fang seems one solid mass of bone to the naked eye.

The transition from the central osseo-dentine to the cement is imperceptible; the former is distinguishable only by the grouping of the concentric layers of calcigerous cells around detached vascular centres and by the presence of the vascular canals. In the cement these appear to be extremely few; I saw but one in the whole extent of a transverse section from the middle of the broad base of a large posterior tooth of the Platanista.

The calcigerous cells of the cement are elliptical, with the extremities pointed in most, in many produced; the long axis being in the direction of the stratum; they chiefly indicate the concentric disposition of the layers of cement which follow the undulations of the section or surface of the fang. The cement is characterised, as in other Cetacea, by the number and parallelism of the minute tubuli, which traverse it, like the tubes of the dentine, in a direction vertical to its planes or layers of growth: these tubes are opake and calcigerous; are generally grouped in fasciculi with clearer interspaces in which the ordinary irregular reticulating rays of the elliptic cells are best seen. In each of the large or primary bundles the tubuli are grouped together in smaller fasciculi; and

every tube has a minutely wavy course. The cemental tubuli are rather smaller and give off more numerous lateral branches than the dentinal tubuli; these branches everywhere anastomose extensively with the radiated tubes of the calcigerous cells. The cemental tubes are rather less and the cells larger and more elongated in the cement of the Platanista than in that of the Cachalot.

145. *Development.*—The primitive seat of development of the tooth-matrix in the vascular membrane or gum, lining an open groove on the alveolar border of the maxillary bones, is maintained much longer in the Cetacea than in the higher organized Mammalia; a greater proportion of the tooth is, also, developed before the matrix sinks into or is surrounded by a bony alveolus, and, with the exception of the rudimental tusks in the Narwhal, is at no period entirely inclosed in a bony cell; in which respect the Cetacea offer an interesting analogy to true fishes. In a preparation of the jaw of a young Porpoise(1), which I added to the Hunterian Series of Comparative Anatomy in 1832, the half-formed posterior teeth are shown imbedded in the gum only, the growth of the jaw not having yet attained their level. Hunter, whom none of the peculiarities of the Cetaceous organization had escaped, was aware of this circumstance in their dental development; but, not having carried his researches on this subject into the earlier periods of fœtal life in man and mammalia, when the aid of a microscope is needed, he believed the phenomena of the papillary and open follicular stages to be peculiar to the Cetacea; thus he says, "The situation of the teeth, when first formed and their progress afterwards, as far as I have been able to observe, is very different in common from those of the quadruped. In the quadruped the teeth are formed in the jaw, almost surrounded by the alveoli, and rise in the jaw as they increase in length, the covering of the alveoli being absorbed. The alveoli afterwards rise with the teeth covering the whole fang; but in this" (the whale-) "tribe the teeth appear to form in the gum upon the edge of the jaw, and they either sink in the jaw as they lengthen, or the alveoli rise to inclose them; this last is most probable, since the depth of the jaw is

(1) No. 325 A.

also increased(1)." A deeper insight into the phenomena of the growth of teeth in the class Mammalia proves this to be no exceptional case, but one of beautiful and harmonious concordance with the general laws of organic development. The Cetacea permanently represent that early embryonic stage when no cervical constriction divides the large head from the trunk, and when the rudimental limbs offer no outward marks of joints or digits; they likewise retain a preponderating proportion of brain, and manifest for a long period, and on a magnified scale, the first stages in the development of the teeth.

When by the increasing depth of the jaw and the reciprocal elongation of the tooth its base or fang becomes supported by bone, a longer time than usual elapses before the alveolus is completed by the development of transverse partitions between the outer and inner walls of the open groove, and in the meanwhile the teeth are lodged like those of the *Ichthyosauri* in a common and continuous bony channel. In the *Delphinidæ* the teeth are successively developed from before backwards, and pass through all their stages of growth in that order of position, the anterior ones having their fangs and alveoli completed, whilst the posterior teeth are lodged in a common groove, or may be supported at the back part of the series by the gum only. When the formation of the entire series of teeth approaches its completion, the Dolphin resembles the Alligator in having the anterior teeth lodged in sockets and the posterior teeth in an alveolar groove. In the Cachalot the large middle teeth of the series are the last to have the fang solidified.

The calcification of the dentinal pulp in the Dolphin proceeds so that the pulp-cavity extends to near the apex of the tooth for a longer period than in the simple teeth of quadrupeds; for a certain time the teeth continue widely open at their base, and of a simple conical form, as in the Crocodiles; but, not being subject to displacement by successors pushing them vertically from their sockets, the calcification of the remaining pulp proceeds to close the basal opening, and to form a fang which, with the exception

(1) On Whales, Philos. Trans. 1787, p. 398.—The abortive tusks of the Walrus are the sole exceptions to this rule in the true Cetacea.

of the teeth of the Platanista, contracts in every direction and gives the tooth the form of "a double cone," as described by Hunter, one point being exserted the other having the reverse direction and inserted. The conversion of the last remnant of the pulp produces the irregular bone-like deposit in the centre of the tooth, and closes up the lower aperture, one or two minute canals for the nutrient vessels being usually left. The mass of this fourth central substance is greatest in the Cachalot, in which the process sometimes commences at an independent centre and proceeds centrifugally as in ordinary ossification, giving rise to the detached stalactitic masses occasionally found loose in the unclosed pulp-cavity of large teeth.

146. *Zeuglodon.*(1) The remains of a gigantic animal, discovered in a tertiary formation in the state of Louisiana, and originally interpreted to belong to the class of Reptiles with the name of *Basilosaurus*,(2) presented in portions of both upper and lower jaws, teeth implanted by a double fang in deep sockets. This anatomical peculiarity of a mammiferous species, though its occurrence in the supposed *Basilosaurus* has been cited in depreciation of the value of the character of the two-fanged tooth in the determination of fossil remains,(3) has had its importance established by the result of a closer examination of the remains of the supposed gigantic Reptile, which has proved their mammalian and cetaceous character.(4)

The crowns of the teeth in the largest portion of the upper jaw which has hitherto been obtained are more or less perfect, and are contiguous to each other; but they are placed rather obliquely so that the inner surface of the anterior part of the crown of the hinder tooth is on the same line as the outer surface of the posterior part of the tooth next in front.

The crowns are sub-compressed and conical, with an obtuse apex:

(1) Ζευγλη, a yoke, *οδους*, a tooth, expressive of the peculiarity of certain teeth of this genus resembling two teeth linked or yoked together.

(2) Dr. Harlan, Medical and Physical Researches, 1835, pp. 337, 369.

(3) Dr. Grant, in Thomson's British Annual, 1838, p. 265.

(4) See my Paper on the *Zeuglodon*, Geological Transactions, IInd Series, vol. vi. p. 69.—An almost entire skeleton which has been since brought to light has fully confirmed the deductions therein recorded.

the antero-posterior diameter of the middle one is three inches, the transverse diameter of the same is one inch two lines; the height above the alveolar process two inches and a half, the total length of the tooth about four inches and a half. Later and more perfect specimens demonstrate the upper part of the crown to have had its anterior and posterior margins obtusely serrated. The crown is contracted from side to side in the middle of its base, so as to give its transverse section somewhat of the hour-glass form (Pl. 90, fig. 2,); and the opposite wide longitudinal grooves, which produce this form, become deeper as the crown approaches the socket, and at length meet, and divide the root of the tooth into two separate fangs. The anterior teeth have a single root and are somewhat smaller than the posterior ones; the crown is sharp-pointed, conical, slightly recurved and laterally compressed, the transverse section of the base forming an ellipse. The length of the anterior teeth, including the root is five or six inches, and the longest diameter nearly two inches. In the last discovered remains of the Zeuglodon it is stated that "the enamel of the teeth is retained(1). Besides the teeth implanted in the jaws as above described, there is a fragment of a tooth imbedded in the matrix containing the above pieces, and consisting of the base of the crown and beginning of the fangs. The crown of this tooth, which is equal in size to the posterior one in place, and was probably a tooth of the same jaw, is partly worn down and partly broken, but is so blended with the matrix, that its exact form could not be determined. Of this tooth I had a transverse section made near to the base of the crown, which presents the figure represented in Pl. 90, fig. 1, and is that form which we may reasonably suppose would be characteristic of the old and worn-down hinder teeth of the Zeuglodon. The crown is here divided into two irregular rounded portions or lobes, placed one before the other and joined by a narrow neck or isthmus. The anterior lobe is the broadest, its grinding surface is sub-ovate, and placed obliquely: it measures one inch three lines in the long diameter, one inch in the short diameter; the posterior lobe is narrower, more regularly ovate, with the long diameter (which is

(1) Silliman's American Journal, vol. xliv, p. 411.

one inch, three lines), placed parallel with the axis of the jaw. The isthmus is about three lines in breadth, and two in length; but the breadth diminishes while the length increases as the tooth descends in the socket, until it finally disappears, and the two portions take on the character of separate fangs.

The mode of completion of the teeth in this extinct Cetacean is different from and conforms to a higher type than that of any of the existing carnivorous genera. It is evident that the pulp which, from the form and structure of the crown, was originally simple, becomes afterwards divided into two parts, and that its calcification then proceeds towards two distinct centres, which are each separately surrounded by concentric striæ of growth. The *cavitas pulpi*, which is very small in the crown of the tooth, becomes contracted as the fangs descend, and is almost obliterated near their extremities.

Of the fragment of the lower jaw of the *Zeuglodon* there is a plaster cast in the Museum of the Geological Society. It contains four teeth of which the two posterior are nearly contiguous; the next is separated from them by an interval of an inch and a-half, and the most anterior is placed at a distance of two inches from the preceding. The anterior tooth is here of smaller size, and apparently of more simple form than those behind, and it is described by Dr. Harlan as a canine. This interesting fragment is preserved in the Museum of the Philadelphian Academy: it confirms the evidence afforded by the fragments of the upper jaw, viz:—that the teeth in the *Zeuglodon* were of two kinds, the anterior being smaller, more simple in form and more remote from each other, than those behind.

The summits of the crown of the teeth of the *Zeuglodon* were most probably sheathed with enamel; their base exhibits an investment of a thin layer of cement which augments in thickness where it surrounds the fangs.

In a fine transverse section taken from below the middle of the exposed crown, I found this cement presenting the same microscopic characters as that in the Cetacea; being traversed by numerous transverse parallel tubuli. The Purkinjean cells are scattered in some places irregularly, in others arranged in parallel rows;

they are about $\frac{1}{200}$th of a line in diameter, generally of an oval form, but with very irregular outlines; the tubes radiating from the cells are wider than usual at their commencement, but soon divide and sub-divide, forming rich reticulations on the interspaces and communicating with the branches of parallel larger tubes. These are placed, as in the Dugong, perpendicularly to the superficies of the tooth, but are less regularly arranged than the calcigerous tubes of the dentine, with which, however, they form numerous continuations. There is a greater proportion of the cement at the isthmus of the bilobed base of the crown than at its circumference.

The dentine consists of fine calcigerous tubes, radiating in the section examined from two centres, one in each lobe, without any intermixture of medullary tubes. The breadth of the calcigerous tubes in the *Zeuglodon* is equal to one-eighth of the diameter of an ordinary human blood-disk or globule; they present a regular undulating course, and like the calcigerous tubes of the Cetacea exhibit plainly the primary dichotomous bifurcations, and the subordinate lateral branches, which are given off at acute angles. Upon the whole the microscopic characters of the texture of the teeth of the *Zeuglodon* are strictly of a mammiferous character, and its minor modifications agree with those in the Cetacea.

If the crowns of the teeth be at no period, which is unlikely, tipped with enamel, yet the presence of fangs, proving their restricted time of growth, shows the *Zeuglodon* not to have been a member of the order *Bruta*, and the microscopic structure displays no vascular dentine which enters so largely into the composition of the teeth of the gigantic extinct Sloths. The outer cement is much thinner in proportion to the dentine than in the Cachalot, and there is a much less quantity of the irregularly ossified pulp in the centre: the teeth, moreover, were developed in both the upper and lower jaws of the *Zeuglodon*. The two fangs distinguish in a marked degree the *Zeuglodon* from any of the true Cetacea, among which, however, we have seen that the *Platanista* makes an approach to this structure in the hindmost teeth. The obtusely serrated margins of the crowns also form a peculiar character in the present order, but which is

present in the dentition of some species of seal.(1) In the so-called herbivorous Cetacea, whose dentition will next be described, the two-fanged structure is fully established in the Manatee, whilst in the Dugong we shall find the near resemblance to the Zeuglodon in the composition and the intimate structure of the molar teeth. The vertebræ of the Zeuglodon prove it, however, to be a true or carnivorous Cetacean; its size is estimated at near seventy feet; it accordingly affords a very interesting addition to the history of the dental system in the Cetaceous order, and approximates the typical group by an additional step to the Dugongs and Manatees which are more essentially related to the Pachyderms.

147. *Halicore.*—Two marks of inferiority in the dental system of the carnivorous Cetacea, which they have in common with many of the order *Bruta*, viz :—uniformity of shape in the whole series of teeth, and no succession and displacement by a second or permanent set, disappear when we commence the examination of the dentition of those apodal pachyderms which have been called the herbivorous Cetacea. In the Dugong, (*Halicore Dugong*) for example, we find *incisores* distinguished by their configuration as well as position from the *molares*, and the incisive tusk is deciduous, displaced vertically and succeeded by a permanent tusk: both these characters are shown in Pl. 92.

Of the incisors of the Dugong only the superior ones project from the gum in the male sex, and neither upper nor lower ones are visible in the female(2). The superior incisors are two in number in both sexes; in the male they are moderately long, subtriedral, slightly and equally curved, of the same diameter from the base, which is deeply excavated to the apex, which is obliquely bevelled off to a sharp edge, like the scalpriform teeth of the Rodentia. The form and extent of the persistent pulp-cavity of this tooth are shewn in the figure of its longitudinal section, two-thirds the natural size, in Pl. 93, fig. 4. Only the extremity of this tusk projects from the jaw, at least seven-eighths of its extent being lodged in the socket, the parieties of which are entire and the

(1) A fossil carnivorous Cetacean with serrated teeth has been indicated by M. Grateloup, under the hybrid name of 'Squalodon,' in Leonhard and Bronn, Jahrbuch für Mineralogie, 1841, p. 330.

(2) Proceedings of the Zool. Society, 1838, p. 41.

exterior of the great intermaxillary bones presents an unbroken surface. In the female Dugong the growth of the permanent incisive tusks of the upper jaw is arrested before they cut the gum, and they remain throughout life concealed in the intermaxillary bones; the tusk is solid, is about an inch shorter and less bent than that of the male; it is also irregularly cylindrical, longitudinally indented, and it gradually diminishes to an obtuse rugged point; the base is suddenly expanded, bent obliquely outwards and presents a shallow excavation.

It is remarkable that the external wall of the socket is always deficient opposite the expanded and distorted base of the tusk of the female, and this vacuity occurs even in the young Dugong of this sex, when the base of the growing tusk is near the lower extremity of the deflected portion of the intermaxillary bone; but, as the base of the tooth ascends (or rather seems to ascend in consequence of the elongation of the bone and the tooth), the vacuity also ascends and becomes situated in the adult at the upper part of the exterior of the deflected portion of the intermaxillary bone.

The solid tusks of the female Dugong were supposed by Sir E. Home to be the deciduous or 'milk tusks' and to be the predecessors of those of the male, which he held to be the permanent tusks, and he suggested that the use of these projecting scalpriform tusks was to detach sea-weeds—the food of the Dugong—from the rocks: one can hardly, however, assign any important function in relation to nutrition to parts which we now know to be limited to the male sex. This hypothesis of Sir E. Home was first called in question by Dr. Knox(1), who, having detected the supposed deciduous tusks in the head of a nearly full-grown Dugong, rejected the idea that they were deciduous teeth, observing that no evidence had been given to prove the existence of deciduous tusks at all in the Dugong(2). I have, however, discovered

(1) Edin. Phil. Trans. vol. xi, p. 389.

(2) "The milk-tusks of the Dugong have never been seen by any one; that is, I have not heard of the existence of any preparation showing the germs of the milk or permanent teeth, together or in succession." Dr. Knox, loc. cit. p. 398.—Sir E. Home seems, however, to have observed the true milk-tusks, without recognising their nature, in the young female Dugong whose dissection he describes in the Philosophical Transactions for 1820, for he

in the recent specimens, which I have dissected at the Zoological Society, the true deciduous incisors of the upper jaw co-existing with the permanent ones. They are much smaller than the permanent tusks of the female, and are loosely inserted by one extremity in conical sockets immediately anterior to those of the permanent tusks, adhering by their opposite ends to the tegumentary gum, which presented no outward indication of their presence. When this gum was stripped off the bone, the deciduous tusks came away with it; and this may account for their absence in dried crania of immature Dugongs, in which their alveoli are sufficiently conspicuous. The deciduous tusk (Pl. 92, *a*) is two inches in length, slightly curved, sub-cylindrical, tapering to both extremities, the fang-end being the smallest; it was perforated, in the specimen figured, by an aperture leading to the extremely contracted cavity in which the remnant of the exhausted matrix was lodged.

True permanent incisors are not developed in the lower jaw of the Dugong, those which are occasionally found there are abortive remnants of the first or deciduous series, which are not destined at any time to rise above the gum.

The sloping truncated surface at the anterior part of the lower jaw presents a coarse and loose reticulate structure, and is excavated on each side by four wide irregular sockets. The first is the shallowest, the third the deepest. Sir E. Home discovered a small tooth(1) in this socket on each side of the jaw of a young female Dugong. I have also found in the third socket of the left side of the jaw of a full-grown male Dugong, a similar abortive incisor, or rather the fang of an incisor with the crown irregularly eaten away by the absorbent process. This imperfect tooth measured 10½ lines in length 2½ lines in breadth, and two lines in thickness; it was slightly bent, with a shallow impression along the middle of the convex side, and with the fang abruptly diminishing to a point at its extremity, which was quite closed; its surface was rougher than in ordinary teeth, and presented two or three small vascular perfora-

says, "It has two incisors in the upper jaw immediately before the two milk-tusks, these are more advanced in the gum than the tusks and, therefore, would appear before them." p. 315.

(1) Pl. 93, fig. 3.

tions. The socket containing this functionless tooth showed the influence of the stimulus of its presence by its greater depth and smoother parietes, as compared with the other sockets, in which the corresponding teeth had been wholly absorbed. The crown-end of the latent incisor adheres to the thick gum in which it is buried: this adhesion Sir E. Home describes as "gubernacula for the incisors not yet completely formed:" he says, "these incisors enable the young Dugong to crop the tender plants, but are no longer wanted when the animal grows up;" and adds, "this is a curious fact, and is so far an approach to ruminating animals, whose incisors are only in the lower jaw," loc. cit. p. 154. But the solidity, the exhaustion of the formative matrix, and commencing destruction of the lower incisors in the sockets of the lower jaw, which in Sir E. Home's specimen had not cut the gum, prove that they were never destined to come to use; and the same thing must be inferred of those which had disappeared.

The truly remarkable instances already recorded in the Cetacea of the manifestation and subsequent disappearance of the germs of teeth, lead us to view without surprise this indication of allegiance to a more general type, by which alone the phenomena of latent teeth seem explicable.

A comparison of the jaws of many specimens of different sex and age has assured me of the accuracy of Cuvier's conjecture, that not more than twenty molar teeth are developed in the Dugong; viz., five on each side of both upper and lower jaws: but these are never simultaneously in use, the first being shed before the last has cut the gum. In the skull of a male Dugong measuring fourteen inches in length, having the deciduous and permanent upper tusks in place, the first molar of the left side, lower jaw, was shed, and the fang of those in place had suffered from absorption: the second, third, and fourth molars were in use, but the last presented its primitive obtuse tuberculate summit, and had not penetrated the gum. In a female Dugong, whose skull was fourteen inches eight lines long, and in which the deciduous tusks were shed and the sockets obliterated, the last molars were in place, and the conical summit worn down to the beginning of the transverse

constriction: the first molar was lost in both jaws, and the second was shed on the right of the upper jaw. A male Dugong, with a skull fourteen inches and half in length, with the sockets of the deciduous tusks obliterated, and the permanent tusks protruded to the usual extent and worn by use, had the molar teeth reduced to two on each side of both jaws, the grinding surface of the last presenting the hour-glass shape, analogous to that of the worn posterior grinders in the Zeuglodon; but the fang of this tooth does not become divided in the Dugong.

The period when the molar series can be viewed in its most complete state in the Dugong is that represented in Pl. 92. These teeth increase very regularly in size: the fang of the first *c*, and of the second *d*, is soon completed and solidified; that of the third *e* is more elongated and retains its basal cavity longer; but it becomes at length contracted to a point, solidified, partially absorbed, and the tooth is then shed: the crown presents an irregular oval shape in transverse section. The fourth molar tooth, when fully formed, resembles a slightly bent cylinder with a nearly smooth outer surface; the crown is flat, or slightly depressed at the centre. The opposite extremity of the tooth is excavated by a regular conical cavity, lodging the remains of the pulp (Pl. 93, fig. 5). With age, however, the fang contracts, takes on an irregularly fluted and tuberculate surface, and is at last closed at its extremity. The matrix of the last molar tooth expands as the crown is forming and manifests a tendency to divide into two fangs; but, having acquired the size and form exhibited in fig. 6, Pl. 93, the pulp is maintained in a wide basal pulp-cavity to supply the waste of the crown according to that pattern.

The molar teeth of the Dugong consist of a large body of dentine, a small central part of osseo-dentine, and a thick external investment of cement. The disposition of the calcigerous tubes, as displayed in a transverse section near the base of the crown of the first molar, is shown in the reduced figure of a highly magnified view in Pl. 94. They have a sinuous course for a certain extent from the pulp-cavity, in which they frequently bend in opposite instead of parallel curves, and here and there form loops, convex towards

the periphery of the tooth. Beyond this part the tubes proceed with the usual gentle parallel primary curvatures to the periphery of the dentine. The cells of the dentine become more conspicuous, their boundaries being more opake, in the outer part of the dentine: and the analogy which this structure presents to that of the dentine in *Platanista* and *Delphinus* is interesting in connexion with the outward cetaceous form of the Dugong; the dichotomous divisions and the minute lateral branches of the dentinal tubuli are not less conspicuous in the Dugong than in the carnivorous Cetacea. The clear dentinal cells present an imbricated arrangement when viewed in vertical section, and have a diameter of $\frac{1}{1000}$th of an inch.

The calcigerous cells of the cement closely resemble in their size, form, and disposition those in the *Platanista*.

The communications between the tubes of the cement and those of the dentine are clearly discernible in several parts of the circumference of the latter substance, and the whole system of tubes adapted to circulate the plasma of the blood through the solid tissues of the tooth is, perhaps, in no animal better seen than in the molar of the Dugong. The small portion of osseo-dentine in the centre of the tooth is permeated by a few vascular canals, which are derived from the remains of the pulp-cavity.

The calcigerous tubes of the incisive tusks radiate from the subcentral pulp-fissure with a well-marked double curvature, at first convex, then concave, towards the extremity of the tusk. In a transverse section, taken within an inch of the extremity of the tusk, the dentinal tubes are grouped in fasciculi where they are so crowded as to intercept the light, with narrow intervals where the tubuli are fewer, but the unusual density of the dentine depends on the clear and compact earthly salts combined with the animal matter in the dentinal cells.

In the female Dugong the whole of the extremity of the tusk is surrounded by a thin coat of true enamel, which is covered by a thinner stratum of cement.

In the male's tusk the enamel (Pl. 95, fig. 1, *e*), though it may originally have capped the extremity, as in the female's, yet, in the body of the tusk, it is laid only upon the anterior convex and on the lateral

surfaces, but not upon the posterior concave side of the tusk; which is thickly coated with cement (fig. 1, *c*). This side accordingly is worn away obliquely when the tusk comes into use whilst the enamel maintains a sharp chissel edge upon the anterior part of the protruded end of the tusk.

The dentinal cells are of a subcircular form, with an average diameter of $\frac{1}{800}$th of an inch: they seem to form an unbroken network, and in sections taken parallel with the course of the calcigerous tubes present an imbricated character, as in Plate 95, fig. 1, the free convex border of each compartment or cell being turned towards the periphery of the tooth, near to which the cells diminish in size and increase in number. The interspaces or outlines of the cells (fig. 2, *b*) are dark or clear, as the change of focus causes them to intercept or transmit the rays of light reflected from the mirror of the microscope. In a section taken transversely to the course of the tubes and parallel with the plane of the layer of cells, the reticulated takes the place of the imbricated character: the dark extremities of from ten to fourteen calcigerous tubes whose diameter is $\frac{1}{10,000}$th of an inch, may be seen included in the area of a single dentinal cell, as in Plate 95, fig. 2.

The presence of abortive teeth concealed in the sockets of the deflected part of the lower jaw of the Dugong, offers an interesting analogy with the rudimental dentition of the upper jaw in the Cachalot and of both jaws in the fœtal Whales: the arrested growth and concealment of the upper tusks in the female Dugong, and the persistent pulp-cavity and projection of the corresponding tusks in the male, are equally interesting repetitions of the phenomena manifested on a larger scale in the singular dental system of the Narwhal; but the habitual abrasion to which the tusks of the male Dugong are subject prevents their closer resemblance to the male Narwhal's tusk in regard to length.

The simple implantation of the molar teeth and their composition are paralleled in the teeth of the Cachalot: their difference of form, and the more complex shape of the hindmost tooth are repetitions of characters which were present in the dentition of the extinct Zeuglodon.

The coexistence of incisive tusks with molar teeth, and the successive displacement of the smaller and more simple anterior ones by the advance of larger and more complex grinders into the field of attrition, already, as it were, sketch out characteristics which become normally established and attain their maximum in the Proboscidian family (Elephants and Mastodons) of the Pachydermal order.

148. *Manatus.*—The transition from the cetaceous to the pachydermal type of dentition is effected by the Manatee, (*Manatus*, Scopoli, Cuv.) especially by the modification of the molar series.

The deflected anterior extremities of the intermaxillary bones each support a single deciduous tusk in the young Manatee (Pl. 96, fig. 1, *a*), but this is not succeeded by a permanent one in either sex. No germs of incisors have been detected in the corresponding part of the lower jaw. The molars of the American Manatee, according to Daubenton and Cuvier(1), are thirty-six in number, nine on each side of both jaws, but they are never simultaneously in place and use. Their crowns in the upper jaw are square, and support two transverse ridges with tri-tuberculate summits, having also an interior and posterior basal ridge: each tooth is implanted by three diverging roots, one on the inner and two on the outer side; they increase in size, very gradually, from the foremost to the last. The crowns of the anterior molars of the lower jaw resemble those above, but the posterior ones have a larger posterior tubercle; they are all implanted by two fangs, which enlarge as they descend and bifurcate at the extremity, Pl. 96, fig. 3.

In the Manatee of Senegal ten molars are developed on each side of both jaws.

The molars consist of a body of dentine, a coronal covering of enamel and a general investment of cement, very thin upon the crown, and a little thicker upon the fangs.

All the grinding teeth of the Manatee belong to the true

(1) Ossemens Fossiles, 4to. vol. v. Pl. 1, p. 250. But in the "Règne Animal," Cuvier assigns $\frac{8-8}{8-8}$—32. The number of teeth ordinarily in use at the same time is that represented in Pl. 96, fig. 1, where the first molar has been shed and the two last have not come into place: in the lower jaw seven molars are usually in use in the adult: fig. 2 shows the socket of the first which has been shed and the crown of the last, the growth of which is still incomplete.

molar series, none of them being displaced by vertical successors: in this respect it manifests, like the Dugong, a cetaceous character, and the more strongly, inasmuch as the number of molars successively developed from before backwards is greater. The anterior teeth are, however, displaced before the posterior ones are developed, although they have no vertical successors, which circumstance is also characteristic of the Elephant: the shape, the structure, and the mode of implantation of the molars of the Manatee quite accord with the pachydermal type, and herein more especially with the Dinotherium and Tapir.

149. *Halitherium*(1).—An extinct herbivorous Cetacean has been discovered in the miocene tertiary deposits which resembles the Dugong in many parts of its skeleton, and in having permanent tusks in the upper jaw: but which has complex, ridged, enamelled and many-rooted molars as in the Manatee. The grinding surface of these teeth offers a slight modification of form; the superior molars when first found detached were referred by Cuvier to the *Hippopotamus dubius:* the lower molars to the *Hippopotamus medius.* The latter, Pl. 97, fig. 5, have three tuberculate ridges, the posterior one the smallest; when worn down the crown of the tooth presents three pairs of rounded lobes, and its margins are deeply festooned. The upper molars (fig. 4) are more square-shaped, and the third tubercular ridge is almost obsolete.

In a second species of the same or a nearly allied genus (*Halitherium Brochii*) the crowns of the teeth are more rounded, and beset with tuberculated mammiliform eminences. The entire series on the left upper jaw is shown in Pl. 97, fig. 1, and a similar series of three molars in the left ramus of the lower jaw of the *Halitherium Cuvieri* (fig. 2). The ultimate discovery and restoration of a great part of the skeleton of one of the species (*Halitherium Cuvieri*), and the determination of the small number of molar teeth in both species, have established a very interesting intermediate genus between *Halicore* and *Manatus*, and, at the same time, one which pushed its infinities much nearer than either of the existing genera towards the pachydermal aquatic genus *Hippopotamus.*

(1) *Metaxytherium*, Christol, *Cheirotherium*, Bruno.

CHAPTER V.

TEETH OF MARSUPIALIA.

150. *Sarcophaga*(1).—There is no toothless genus in the present Order, unless the Monotremes or implacental Edentata be regarded as modified Marsupials. Molar and incisor teeth are present in both jaws in every true Marsupial species, but are relatively smaller in *Tarsipes* and *Myrmecobius*, than, perhaps, in any other mammiferous quadruped; the canines are but feebly represented in many, as the Phalangers and Petaurists, are wanting in the lower jaw in the Potoroos and Koala, and in both jaws of the Kangaroos and Wombat. The grinders, on the other hand, present their most complicated structure in these last cited herbivorous genera.

The Dasyures and Thylacine offer the carnivorous type of the dental system, but differ from the corresponding group of the Placental Mammalia in having the molars of a more uniform and simple structure, and the incisors in greater number; which number, however, is different in the different predaceous genera, as is expressed in the dental formulæ.

That of the *Thylacinus*, or Dogheaded Opossum (Pl. 98, fig. 1), is as follows:

$$\text{Incisors } \frac{4-4}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{4-4}{4-4}: = 46.$$

The incisors are of equal length and regularly arranged in the segment of a circle with an interspace in the middle of the series of both jaws. The external incisor on each side is the strongest. The laniary or canine teeth are long, strong, curved, and pointed, like those of the dog tribe; the points of the lower canines are received in hollows of the intermaxillary palatal plate when the mouth is closed, and do not project, as in the carnivorous Placentals, beyond the margins of the maxillary bones. The spurious molars (*p*)

(1) By this name I first defined the present Tribe of Marsupial Animals in order to avoid the confusion that might have arisen from the use of the word 'Carnivora' usually applied to the corresponding group in the Placental series of Mammalia.—*Zoological Transactions*, vol. ii, p. 315.

in this as in all other Marsupials have two roots; their crown presents a simple compressed conical form, with a posterior tubercle which is most developed on the hindmost. The true molars (*m*) in the upper jaw are unequally triangular, the last being much smaller than the rest; the exterior part of the crown is raised into one large pointed middle cusp and two lateral smaller cusps obscurely developed; a small strong obtuse cusp projects from the inner side of the crown. The molars of the lower jaw are compressed, tricuspidate, the middle cusp being the longest, especially in the two last molars, which resemble closely the sectorial teeth (*dents carnassières*) of the dog and cat.

The dental formula of the genus *Dasyurus*, is :

Incisors $\frac{4-4}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{2-2}{2-2}$; molars $\frac{4-4}{4-4}$: = 42.

The eight incisors of the upper jaw are of the same length and simple structure, and are arranged in a regular semicircle without any medium interval. The six incisors of the lower jaw are similarly arranged, but have thicker crowns than the upper ones. The canines present the same or even a greater relative development than in the Thylacine: in an extinct species of *Dasyurus*(1) they had the same form and relative proportions as in the Leopard. The spurious molars (*p*) have a pointed compressed triangular crown with a rudimental tubercle at the anterior and posterior part of its base. The grinding surface of the true molars (*m*) in the upper jaw is triangular; the first presents four sharp cusps, the second and third each five; the fourth, which is the smallest, only three. In the lower jaw the last molar is nearly of equal size with the penultimate one, and is bristled with four cusps, the external one being the longest: the second and third molars have five cusps, three on the inner and two on the outer side; the first molar has four cusps: these are all sharply pointed in the young animal, in which the posterior tubercle of the posterior molar in the lower jaw is divided into two small cusps.

The carnivorous character of the above dentition is most strongly

(1) *Dasyurus laniarius*: the fossil remains of this species were discovered with those of two gigantic species of Kangaroo in the bone-caves of Wellington Valley, by Major, now Lieut.-Col. Sir Thomas L. Mitchell.

marked in the Ursine Dasyure or *Devil* of the Tasmanian Colonists, the largest existing species of the genus, and the dentition of which is represented in Pl. 98, fig. 2.

In some of the smaller species of the carnivorous group, as the *Phascogales*, the canines lose their great relative size, and the molar teeth present a surface more cuspidated than sectorial: there is also an increased number of teeth, and as a consequence of their equable development they have fewer and shorter interspaces. Thus the *Phascogale penicillata* may be said, in Hunter's words to have "a mouth full of teeth," and these are adapted for the capture and mastication of insects and other small and low organized animals.

The genus *Phascogale* (Pl. 98, fig. 3) is characterized by:

Incisors $\frac{4-4}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{4-4}{4-4}$: = 46.

In this dental formula may be discerned a step in the transition from the Dasyures to the Opossums, not only in the increased number of spurious molars, but also in the shape and proportions of the incisors. In the upper jaw the two middle incisors are longer than the rest, and separated from them by a brief interval; they are more curved and project more forward. The three lateral incisors diminish in size to the outermost. The middle incisors of the lower jaw also exceed the lateral ones in size, and project beyond them but not in the same degree, nor are they separated from them by an interval, as in the upper jaw. The canines are relatively smaller than in the Dasyures. The spurious molars present a similar form, but the third in the lower jaw is smaller and simpler than the two preceding ones. The true molars resemble those of the Dasyures.

The general character of the dentition of these small predatory Marsupials approximates to the insectivorous type, as will be exemplified in the Shrew, Hedgehog, &c. among the placental Mammalia, and corresponds with the food and habits of the species which thus lead from the predaceous or Sarcophagous to the Entomophagous tribes.

The interval is further diminished by a lost Marsupial genus

which forms one of the ancient Mammalia that have rendered the oolitic formations at Stonesfield so celebrated. This genus, which I have called *Phascolotherium*, presents the same numerical dental formula as in *Phascogale*, viz.:

Incisors $\frac{?-?}{3-3}$ or $_{4-4}$; canines $\frac{?-?}{1-1}$; premolars $\frac{?-?}{3-3}$; molars $\frac{?-?}{4-4}$.

But the incisors and canines are separated by vacant interspaces, and occupy a large proportional space in the dental series (Pl. 99, fig. 4). The transition from the false to the true molars is more gradual: the latter are more compressed than in the Opossum; they present a large middle cusp with a smaller one in front and behind it, and with a basal ridge, which, projecting a little beyond both the anterior and posterior smaller cusps, gives a quinque-cuspid character to the crown of the tooth.

151. *Entomophaga*.—This is the most extensive and varied of the primary groups of the Marsupial order. In the system of Cuvier, the species of this tribe are united with those of the preceding to form a single family characterized by the presence of long canines and small incisors in both jaws: but in most of the Entomophagous genera of the present classification, the canines present a marked inferiority of development, and the species are consequently unable to cope with animals of their own size and grade of organization, but prey, for the most part, upon the smaller and weaker classes of invertebrate animals. Their intestinal canal is complicated by a moderately long and large cæcum; and while, in the *Sarcophaga*, the feet are constructed upon the plan of those of the ordinary placental Digitigrades, they offer in the present tribe a variety of well-marked modifications, according to which the species may be arranged into gressorial, saltatory, and scansorial groups.

a. GRESSORIA.

Genus *Amphitherium*(1).—This, which includes the oldest known Mammalian inhabitants of our planet, is founded upon fossil remains of jaws and teeth discovered in the Oolite slate at Stonesfield in

(1) See Geological Transactions, 2nd Series, vol. vi, and History of British Fossil Mammalia, 8vo. 1844.

Oxfordshire, of which the most instructive specimens are represented in Pl. 99, figs. 1, 2, and 3. The first figure illustrates the dental formula, which is remarkable for the number of the molars:

$$\text{Incisors } \frac{?-?}{3-3};\ \text{canines } \frac{?-?}{1-1};\ \text{premolars } \frac{?-?}{6-6};\ \text{molars } \frac{?-?}{6-6}.$$

The incisors (*i*) are small, simple, and separated by intervals as in the existing Marsupial genus *Myrmecobius:* the canine (*l*) appears by its socket to have had a similar size and form. The shape of the crowns of the premolars (*p*) and molars (*m*), is shown in the specimens of the larger species (*Amphitherium Broderipii*, fig. 3); their implantation of the jaw, each by two long slender roots, is demonstrated by one of the specimens of the smaller species (*Amphitherium Prevostii*, fig. 2).

Genus *Myrmecobius*.—The only known existing representative of this family is the animal described by Mr. Waterhouse, which constitutes the type of his genus *Myrmecobius*, and of which the following is the remarkable dental formula, (Pl. 98, fig. 4):

$$\text{Incisors } \frac{4-4}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{6-6}{6-6}: = 54.$$

From this formula it will be seen that the number of true and false molars, eighteen in both jaws, exceeds that of any other known existing Marsupial, and nearly approaches the peculiar dental formula of the extinct *Amphitherium*, as also that which characterizes some of the existing Armadillos. The resemblance to the genus *Dasypus* is further carried out in the small size of the molar teeth, their separation from each other by slight interspaces, and their implantation in sockets, which are not formed upon a well-developed alveolar ridge or process. The molars (*m*), however, present a distinct multicuspidate structure, and both the true and false ones possess two separate fangs, as in other Marsupials. The inferior molars are directed obliquely inwards, and the whole dental series describes a slight sigmoid curve. The false molars (*p*) present the usual compressed triangular form with the apex slightly recurved; and the base more or less obscurely notched before and behind. The canines are very little longer than the false molars; the incisors are minute,

slightly compressed and pointed; they are separated from each other and the canines by wide intervals.

The Myrmecobians are insectivorous,(1) and shelter themselves in the hollows of trees, frequenting most, it is said, those situations where the Port-Jackson willow abounds. In the structure and proportions of its hinder feet, *Myrmecobius fasciatus* resembles the Dasyurine family; and in the slightly developed canines, the smooth external surface of the skull, the breadth between the zygomata, and the absence of the interparietal ridges, as well as in its general external form and bushy tail, it offers an especial approximation to the genus *Phascogale*.

β. SALTATORIA.

Genus *Perameles*, (Bandicoots).

Incisors $\frac{5-5}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{4-4}{4-4}$: = 48.

This dental formula characterizes a number of Marsupials commonly known in Australia by the name of *Bandicoots*; the hind legs are longer and stronger than the fore, and exhibit in a well marked manner the feeble and slender conditions of the second and third digits counting from the inside, and the sudden increase in length and strength of the fourth and fifth, or two outer toes, which are chiefly subservient to locomotion. In consequence of this inequality in length in their extremities, the mode of progression in the Bandicoots is by bounds, the hind feet being moved together, and alternately with the fore feet, as in the hare and rabbit, and the crupper is raised higher than the fore-quarter. The teeth which offer the greatest range of variation in the present genus are the external or posterior incisors and the canines: the molars, also, which originally are quinque-cuspidate, have their points worn away, and present a smooth and oblique grinding surface in some species sooner than in others.

The Bandicoots which approach nearest to the *Myrmecobius* in the condition of the incisive and canine teeth, are the *Perameles Obesula* and *P. Gunnii*. There is a slight interval between the first

(1) Mr. Gould informs me that they feed exclusively on ants.

and second incisor, and the outer or fifth incisor of the upper jaw is separated from the rest by an interspace equal to twice its own breadth, and moreover presents the triangular pointed canine-like crown which characterizes all the incisors of *Myrmecobius*; but the four anterior incisors are placed close together, and have compressed, quadrate, true incisive crowns. From these incisors the canine is very remote, the interspace being equally divided by the fifth pointed incisor, which the canine very slightly exceeds in size. In *Per. nasuta* the incisor presents the same general condition, but the canines are relatively larger. In *Per. Gunnii*, the outer incisor is closer to the others, which it also more nearly resembles in form than in the preceding species; but in *Per. lagotis* (Pl. 98, fig. 5), it is not separated from the rest by a wider interval than that which intervenes between the first and second incisor. In both the preceding Bandicoots the canines are long and well developed, but the true molars (*m*) have the grinding surface worn down flat in the full-grown specimens which I have had the opportunity of examining.

Genus *Chœropus*.—The singular animal on which Mr. Ogilby has founded this genus differs from the true *Perameles* in having but two toes on each fore-foot; its dental formula is:

$$\text{Incisors } \frac{4-4}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{4-4}{4-4};\ = 46.$$

All the teeth are of small size; the upper incisors are conical, the lower ones truncated and the hindmost is notched; the canines are conical, compressed, the upper one simple and remote from the incisors, the lower one near the incisors and notched anteriorly; the spurious molars are separated by intervals, as in *Myrmecobius*; they are tricuspid, except the first in the upper jaw which resembles the canine. Each true molar consists of two triangular prisms, those of the upper jaw being broader than those below, and with their base turned outwards contrary to those in the lower jaw. The genus would seem by its dentition to rank between *Myrmecobius* and *Perameles*. Its digital characters are anomalous and unique among the Marsupialia, but are evidently a degeneration from the Saltatorial or Bandicoot type.

γ. SCANSORIA.

Genus *Didelphys*, (Opossums).—These Marsupials are now exclusively confined to the American Continents, although the fossil bones and teeth of a small species attest their former existence in Europe contemporaneously with the *Pelæothere*, *Anoplothere*, and other extinct *Pachyderms*, whose remains characterize the Eocene strata of the Paris basin.

The dental formula of the Genus *Didelphys* (Pl. 98, fig. 6) is:

Incisors $\frac{5-5}{4-4}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{4-4}{4-4}$: = 50.

The Opossums resemble in their dentition the Bandicoots more than the Dasyures; but they closely resemble the latter in the tuberculous structure of the molars. The two middle incisors of the upper jaw are more produced than the others, from which they are also separated by a short interspace. The canines are well developed; the upper being always stronger than the lower. The false molars are simply conical, but are more compressed than in the Carnivorous Marsupials. The posterior false molar is the largest in the upper jaw; the middle one is the largest in the lower jaw: the anterior is the smallest in both jaws. The true molars are beset with sharp cusps which wear down into tubercles as the animal advances in age. The crowns of the upper molars present a triangular horizontal section; the base of the triangle is turned forward in the posterior molar; and obliquely inwards and backwards in the rest. In the lower jaw the true molars are narrower and of more equal size than in the upper jaw: there are five tubercles on each, four placed in two transverse pairs, the anterior being the highest, and a fifth forming the anterior and internal angle of the tooth: the anterior and external angle seems as if it were vertically cut off.

The canines still exhibit a superior development in both jaws adapted for the destruction of living prey, but the molars have a conformation different from that which characterizes the true flesh-feeders, and the Opossums consequently subsist on a mixed diet, or prey upon the lower organized animals.

The smaller species of *Didelphys*, which are the most numerous, fulfil in South America the office of the insectivorous Shrews of the old Continent. The larger Opossums resemble in their habits, as in their dentition, the carnivorous *Dasyures*, and prey upon the smaller quadrupeds and birds, but they have a more omnivorous diet, feeding on reptiles and insects and even fruit. One large species, (*Did. cancrivora*) prowls about the sea-shore and lives, as its name implies, on crabs and other crustaceous animals. Another species, the *Yapock*, frequents the fresh waters, and preys almost exclusively on fish. It has all the habits of an Otter; and, in consequence of the modifications of its feet, forms the type of the sub-genus, *Chironectes*, Ill. Its dentition, however, does not differ from that of the ordinary Opossums.

152. *Carpophaga.*—In this tribe the teeth, especially those at the anterior part of the mouth, present considerable deviations from the previously described formulæ; the chief of which is a predominating size of the two anterior incisors, both in the upper and lower jaws. Hitherto, we have seen that the dentition in every Marsupial genus has participated more or less in a carnivorous character; henceforth it will manifest a tendency to the Rodent type.

Genus *Tarsipes.*—The dental formula of this genus has not been accurately determined; the molars soon begin to fall, the small canines are also deciduous, the two long, procumbent incisors of the lower jaw remain the longest; besides these only one small molar was present in each ramus, in the first specimen described. The inferior incisors are opposed to six minute incisors above, which are succeeded by a small canine and some small molars, but these were reduced to a single tooth on each side in M. Gervais' specimen. This was kindly submitted by that acute observer, the founder of the present Genus, to my examination, and the transparency of the dental tissue permitted the tubular structure to be examined by the microscope with transmitted light: it resembled in the degree of divergence of the tubuli calcigeri the dentine of the Mole and other small Insectivora.

The Genus *Tarsipes* seems, in fact, to link the *Myrmecobius*

and *Perameles* of the preceding tribe with the small insectivorous Phalangers.

Genus *Phalangista*.—The Phalangers are so called from the phalanges of the second and third digits of the hinder extremity being inclosed in a common sheath of integument and they have the innermost digit modified to answer the purposes of a thumb.

In the skull of a *Phalangista Cookii*, of which the dental formula is given in Pl. 100, fig. 2, there are both in the upper and lower jaws four true molars on each side, each beset with four three-sided pyramidal sharp-pointed cusps ; thus these essential and most constant teeth correspond in number with those of the Opossum: but in the upper jaw they differ in the absence of the internal cusp, which gives a triangular figure to the grinding surface of the molars in the Opossum; and the anterior single cusp is wanting in the true molars of the lower jaw. Anterior to the upper grinders in this Phalanger there are two premolars of similar shape and proportions to those in the Opossum ; then a third premolar, too small to be of much functional importance, separated also, like the corresponding anterior premolar in the Opossum, by a short interval from those behind.

The canine tooth but slightly exceeds in size the contiguous premolar, and here consequently occurs the first great difference between the Phalangers and Opossums; it is, however, but a difference in degree of development; and in the Ursine and other Phalangers, as well as in the Petaurists (fig. 4), the corresponding tooth presents more of the proportions and form of a true canine.

The incisors, which we have seen to be most variable in number in the Carnivorous section, are here three instead of five on each side of the upper jaw; but their size, especially that of the first, compensates for their fewness.

In the lower jaw there is the same number of molars and functional premolars as in the Opossums ; the three very minute and functionless teeth, which form part of the same continuous series, represent the two small premolars and the canine of the upper jaw; and anterior to these there is one very large procumbent incisor on each side. From this analysis it appears that

the difference in the number of teeth between the Phalanger and the Opossum resolves itself into the former being minus certain incisors in the upper and lower jaws, the great development of the lower incisor producing an atrophy of all the rest.

The interspace between the functionally developed incisors and molars in both jaws always in the Phalangers contains teeth of small size, of little apparent use, and variable not only in their proportions but their number. The canines are constant in regard to their presence, but variable in size; they are always very small in the lower jaw.

With respect to the functional premolars $\frac{1-1}{1-1}$, separated by the dotted line from the true molars in figs. 1 and 2, Pl. 100, these are always in contact with the molars, and their crowns reach to the same grinding level; sometimes a second premolar is similarly developed in the upper jaw, as in the *Phal. Cookii*, (fig. 2) and as in the great flying Phalanger (*Petaurus Taguanoides*), but it is commonly absent, or replaced by a very minute tooth, shaped like a canine: so that in the upper jaw, between the posterior or functional premolar and the incisors, we may find three teeth, as in *Phal. Cookii* and *Phal. cavifrons*; or there may be only two teeth, the first representing the canine, as in *Phal. ursina* and *Phal. vulpina* (fig 1), and the species which M. Fr. Cuvier has selected as the type of the dentition of the Genus.

In the lower jaw similar varieties occur in these small and unimportant teeth; thus, there may be between the procumbent incisors and the posterior premolar either three teeth, as in *Phal. Cookii* and *Phal. cavifrons;* or two, as in *Phal. ursina*, *Phal. maculata*, *Phal. chrysorrhoos;* or finally one, as in *Phal. vulpina* and *Phal. fuliginosa*. The most important modification is presented by the little *Phal. gliriformis* of Bell (Pl. 100, fig. 3), which has only three true molars (*m*) on each side of each jaw, and has the last and penultimate premolars below shaped like canines.

The Phalangers, being provided with hinder hands and prehensile tails, are strictly arboreal animals, and have a close external resemblance to the Opossums, by which name they are generally known in Australia and the Islands of the Indian Archipelago, where

alone they have hitherto been found. They differ from the Opossums chiefly in their dentition: and in accordance with this difference their diet is more decidedly of a vegetable kind(1). The Australian Phalangers feed chiefly on the tender buds and the leaves of *Eucalypti*: but according to Temminck(2), the Indian Phalangers are omnivorous, and combine insects with fruits and leaves. Mr. Ogilby(3) states that both "the *Phalangers* and *Petaurists* display so decided a preference for live birds, as to make it probable that these constitute a main portion of their food in a state of nature." I find, however, that the intestinal canal, and especially the cæcum, offers so great an additional development in length, as, with the corresponding predominance of the incisors, and atrophy of the canines, to indicate clearly a natural and constant tendency in the Phalangers to a vegetable diet.

Genus *Petaurus*.—There are many species of Marsupialia limited to Australia and closely resembling, or identical with, the true Phalangers in their dental characters and the structure of the feet. I allude to the Petaurists or Flying Opossums: these, however, present an external character so easily recognizable, and influencing so materially the locomotive faculties, as to claim for it more consideration than the modifications of the spurious molars which we have just been considering in the *Phalangers*. A fold of the skin is extended on each side of the body between the fore and hind legs, which, when outstretched, forms a lateral wing or parachute; but which, when the legs are in the position for ordinary support or progression, is drawn close to the side of the animal by the elasticity of the subcutaneous cellular membrane, and there forms a mere tegumentary ridge. These delicate and beautiful Marsupials have been separated generically from the Phalangers under the name of *Petaurus*: they further differ from the Phalangers in wanting the prehensile character of the tail, which, in some species of *Petaurus*, has a general clothing of long

(1) In the stomach and intestines of specimens sent to me in spirits from Australia, I have never found any other alimentary substances but those of a vegetable nature.

(2) Monographies de Mammalogie, p. 3.

(3) Mag. Hist. Nat. 1837, p. 458.

and soft hairs, whilst in others, the hairs are arranged in two lateral series.

In the Petaurists, however, there is as little constancy in the exact formula of the dentition as among the Phalangers. The largest species of Petaurus (*Pet. Taguanoides*), for example, is almost identical in this respect with the *Phalangista Cookii*, which M. Fr. Cuvier has therefore classed with the *Petauri*. Those teeth of *Pet. Taguanoides* which are sufficiently developed and so equal in length as to exercise the function of grinders, are six in number on each side of the upper jaw, and five on each side of the lower jaw. The four posterior molars in each row are true, and bear four pyramidal cusps, excepting the last tooth in the upper jaw, which, as in *Ph. Cookii*, has only three cusps. In the upper jaw the space between the functional false molars and the incisors is occupied by two simple rudimentary teeth, the anterior representing the canine, but being relatively smaller than in *Ph. Cookii;* the crowns of the two anterior incisors are relatively larger. In the lower jaw the sloping alveolar surface between the functional molars and large procumbent incisor is occupied, according to M. Fr. Cuvier, by two rudimentary minute teeth; but I have not found any trace of these in the two skulls of *Pet. Tagua-noides* examined by me.

In *Petaurus sciureus* and *Petaurus flaviventer* (Pl. 100, fig. 4) the dentition more nearly resembles that of *Phalangista vulpina*. In the upper jaw the functional molar series consists of five teeth on each side; the four hinder ones being, as in *Pet. Taguanoides*, true tuberculate molars, but diminishing more rapidly in size as they are placed further back in the jaw; the hinder tooth has three tubercles, the rest four: the apices seem to be naturally blunter than in *Pet. Taguanoides*. Between the functional premolar and the incisors there are three teeth, of which the representative of the canine is relatively larger than in the *Pet. Taguanoides;* the second false molar is also larger and has two parts; the first, which is functional in *Pet. Taguanoides*, is here very small. The first incisor is also relatively larger and more produced. In the lower jaw the functional series of grinders consists of the four true tuberculate molars only, of which the last is relatively smaller, and the first of a more triangular form than in

Pet. Taguanoides. The space between the tuberculate molars and the procumbent incisor is occupied by four small teeth, of which the one immediately anterior to the molars is large, compressed, pointed, and has two roots; the remaining three are rudimentary and have a single fang; the anterior of these corresponds to the one regarded as a canine in the upper jaw.

Among the species exhibiting this dental formula, viz.

$$\text{Incisors } \frac{3-3}{1-1};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{4-4}{4-4} := 40.$$

are *Pet. sciureus, Pet. flaviventer*, and *Pet. macrurus.*

The *Pigmy Petaurist* differs from the preceding and larger species, in having the spurious molars large and sharp-pointed; and the true molars bristled each with four acute cusps. This tendency in the dentition to the insectivorous character, with the modification of the tail, induced M. Desmarest to separate the Pigmy Petaurist from the rest of the species, and constitute a new sub-genus for its reception under the name of *Acrobates*(1). Mr. Waterhouse first pointed out that the Pigmy Petaurist had but three true molars on each side of each jaw instead of four. (Pl. 100, fig. 5). There seems, therefore, to be better reason for accepting this sub-generic section, although we evidently perceive a transition to this condition in the small size of the hinder or fourth molars in the Sciurine Petaurist and its congeners.

The description of the dentition of the Pigmy Petaurist in the 'Règne Animal,' besides the omission of this remarkable particular, is not quite exact in other respects. In four adult specimens, two of which were males, and two females with young in the pouch, I find the following dental formula to be constant:

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{3-3}{3-3} := 36.$$

The three quadricuspid grinders of the upper jaw are preceded by three large premolars, each of which has two fangs, and a compressed triangular sharp-pointed crown, slightly but progres-

(1) Ακρος, *summus*, βαινω, *gradior*, as frequenting the summits of trees.

sively increasing in length as they are placed forward. An interspace occurs between these and the canine, which is long, slender, sharp-pointed, and recurved. The first incisor is longer than the two behind, but is much shorter than the canine. In the lower jaw the true molars are preceded by two functional false ones, similar in size and shape to the three above the anterior false molar, and the canine are represented by minute rudimental simple teeth; the single incisor is long and procumbent as in the other Petaurists.

With these differences of dentition approaching more or less to one or other of the modifications of the dentition in the group of Phalangers, the Petaurists may nevertheless be readily discriminated from those Phalangers which they most resemble; for example, the *Petaurus Taguanoides* may be distinguished from the *Phalangista Cookii* by the greater relative length in the latter of the nasal and maxillary portion of the skull; while in most of the other species of *Petaurus*, the facial part of the skull is relatively shorter than in the *Pet. Taguanoides*.

Genus *Phascolarctus*.—The absence of anomalous or functionless premolars and of inferior canines appears to be constant in the only known species of this genus. The dental formula (Pl. 100, fig. 6.) in three examples of the Koala (*Phasc. fuscus*, Desm.) is

Incisors $\frac{3-3}{1-1}$; canines $\frac{1-1}{0-0}$; premolars $\frac{1-1}{1-1}$; molars $\frac{4-4}{4-4}$: = 30.

The true molars are larger in proportion than in the Phalangers: each is beset with four three-sided pyramids, the cusps of which wear down in age, the outer series in the upper teeth being the first to give way; those of the lower jaw are narrower than those of the upper. The spurious molars are compressed and terminate in a cutting edge; in those of the upper jaw there is a small parallel ridge along the inner side of the base. The canines slightly exceed in size the posterior incisors; they terminate in an oblique cutting edge rather than a point; their fang is closed at the extremity; they are situated as in the Phalangers close to the intermaxillary suture. The lateral incisors of

the upper jaw are small and obtuse; the two anterior or middle incisors are twice as long, broad, and thick as the posterior incisors; they are conical, slightly curved, sub-compressed, bevelled off obliquely to an anterior cutting edge, but differing essentially from the *dentes scalprarii* of the *Rodentia* in being closed at the extremity of the fang. The two incisors of the lower jaw resemble those of the upper, but are larger and more compressed; they are also formed by a temporary pulp, and its absorption is accompanied by a closure of the aperture of the pulp-cavity, as in the upper incisors. The Koala, therefore, in regard to the number, kind, and conformation of its teeth, closely resembles the Phalangers, with which it also agrees in its long cœcum and the general conformation of its digestive organs. It has also the extremities similarly organised for prehension; each is terminated by five digits; the hind feet are provided with a large thumb, and have the two contiguous digits enveloped in the same tegumentary fold; the anterior digits are divided into two groups; the thumb and index being opposed to the other three fingers. We have already noticed a structure approaching to this in some of the small Phalangers. The Koala, however, differs from the Phalangers and Petaurists in the extreme shortness of its tail, and in its more compact and heavy general form. It is only known to feed on the buds and leaves of the trees in which it habitually resides.

153. *Poephaga.*—The present tribe includes the most strictly vegetable feeders in the Marsupial order; all the species have a complex sacculated stomach, and a long simple cœcum.

Genus *Hypsiprymnus*. Potoroos.—Guided by the modifications of the teeth we pass from the Koala to the Potoroos and Kangaroos —animals of widely different general form. The Potoroos, however, present absolutely the same dentition as does the Koala, some slight modifications in the form of certain teeth excepted. The premolars (Pl. 100, fig. 7, *p*) in their longitudinal extent, compressed form, and cutting edge, would chiefly distinguish the dentition of the *Potoroo;* but the Koala evidently offers the transitional structure between the Phalangers and Potoroos in the condition of these teeth, of which one

only is retained on each side of each jaw in the Potoroos as in the Koala.

The dental formula of *Hypsiprymnus*, the generic name of the Potoroos, is

Incisors $\frac{3-3}{1-1}$; canines $\frac{1-1}{0-0}$; premolars $\frac{1-1}{1-1}$; molars $\frac{4-4}{4-4}$: = 30.

The two anterior incisors are longer and more curved, the lateral incisors relatively smaller than in the Koala. The pulps of the anterior incisors are persistent. The canines are larger than in the Koala; they always project from the line of the intermaxillary suture; and while the fang is lodged in the maxillary bone, the crown projects almost wholly from the intermaxillary. In the large *Hypsiprymnus ursinus* the canines are relatively smaller than in the other Potoroos, a structure which indicates the transition from the Potoroo to the Kangaroo genus. In the skeleton of this species in the Leyden Museum, the canines have a longitudinal groove on the outer side.

The characteristic form of the trenchant premolar has just been alluded to: its maximum of development is attained in the arboreal Potoroos of New Guinea *(Hypsiprymnus ursinus* and *Hyps. dorcocephalus)*, in the latter of which its antero-posterior extent nearly equals that of the three succeeding molar teeth. In all the Potoroos the trenchant spurious molar is indented, especially on the outer side and in young teeth, by many small vertical grooves. The true molars each present four three-sided pyramidal cusps; but the internal angles of the two opposite cusps are continued into each other across the tooth, forming two angular or concave transverse ridges. In the old animal these cusps and ridges disappear, and the grinding surface is worn quite flat.

Genus *Macropus*. Kangaroos.—In the genus *Macropus* (fig. 8,) the normal condition of the permanent teeth may be expressed as follows:—

Incisors $\frac{3-3}{1-1}$; canines $\frac{0-0}{0-0}$; premolars $\frac{1-1}{1-1}$; molars $\frac{4-4}{4-4}$: = 28.

The main difference, as compared with *Hypsiprimnus*, lies in

the absence of the upper canines as functional teeth; the germs, however, of these teeth are always to be found in the young mammary fœtus of the *Macropus major*, and I have seen them present, but of very small size, and concealed by the gum, in the adults of some small species of Kangaroos, as *Macropus rufiventer*, Ogilby, and *Macr. psilopus*, Gould. This, however, is a rare exception; while the constant presence and conspicuous size of the canines will always serve to distinguish the Potoroo from the Kangaroo. But there are also other differences in the form and proportions of certain teeth. The upper incisors of the Kangaroo have their cutting margins in the same line, the anterior ones not being produced beyond that line, as in the Potoroos: the third or external incisor is also broader in the Kangaroos, and is grooved and complicated by one or two folds of the enamel, continued from the outer side of the tooth obliquely forward and inward. In most species the anterior fold is represented by a simple groove: the relative size of the outer incisor, the extent and position of the posterior fold of enamel, and consequently the proportions of the part of the tooth in front or behind it, vary more or less in every species of *Macropus*: there are two folds of enamel near the anterior part of the tooth in *Macr. major*, and the posterior portion is of the greatest extent, and the entire crown of the tooth is relatively broadest in this species. The middle incisor is here also complicated by a posterior notch and an external groove. These modifications of the external incisors of the Kangaroos were first noticed by M. Jourdan, and subgeneric distinctions, have been subsequently based upon them.

M. Fr. Cuvier has proposed a binary division of the genus *Macropus*, as here defined, founded on the absence of permanent spurious molars, and a supposed difference in the mode of succession of the true molars in certain species of Kangaroo, combined with modifications of the muzzle or upper lip, and of the tail.

The dental formula which I have assigned to the genus *Macropus* is restricted in its application by that Naturalist to some small species of Kangaroo, grouped together under the term *Halmaturus*,

originally applied by Illiger to the Kangaroos generally(1). The other Kangaroos are characterised by M. Fr. Cuvier under the generic term *Macropus*, by the following dental formula :—

$$\text{Incisors } \frac{6}{2}; \text{ molars } \frac{4-4}{4-4} : = 24.$$

The truth, however, is, that both the *Halmaturi* and *Macropi* of M. Fr. Cuvier have their teeth developed in precisely the same number and manner: they only differ in the length of time during which certain of these teeth are retained(2). In the great *Kangaroo*, for example, the permanent premolar which succeeds the corresponding deciduous one in the vertical direction, is pushed out of place and shed by the time the last true molar has cut the gum: the first true molar is soon afterwards extruded; and I have seen a skull of an old *Macropus major* in the Museum at Leyden, in which the grinders were reduced to two on each side of each jaw by this yielding of the anterior ones to the *vis a tergo* of their successors.

Remains of gigantic Kangaroos have been discovered in the same caves in Australia which contained the teeth and jaws of the large extinct *Dasyurus laniarius*, and they probably formed the prey of that species and of its contemporary the Thylacine, which has equally become extinct in the continent of Australia.

Portions of the lower jaw and teeth of two of these extinct species of Kangaroos are figured of the natural size in Plate 101. They are

(1) *Prodromus Systematis Mammalium et Avium*, 8vo. 1811. The dental character which this excellent naturalist gives, accurately expresses the condition of the canine or laniary teeth, "Laniarii aut nulli, aut superiores 2 ambigui, minuti, in medio inter primores et molares collocati," p. 80; but there are never more than five molars in place on each side of each jaw in the Kangaroo.

(2) M. Fr. Cuvier was aware that a deciduous false molar existed in the great Kangaroo and other species of his subgenus *Macropus*, but he believed that it was peculiar to an early period of life, and then existed only in a rudimental state, or "en germe;" and that instead of being displaced and succeeded in the vertical direction by a permanent false molar, as in the *Halmaturi*, it was displaced by the true molars, which are developed from behind forwards. I have, however, detected the crown of the permanent false molar in the jaws of the *Macropus major* in a concealed alveolus, and have observed it completely formed and in place in an individual which had nearly attained its full size.—See M. Fr. Cuvier's account of the *Halmaturus Thetis* in the "Histoire des Mammifères" folio.

principally distinguished from one another by the different size and shape of the permanent premolar tooth, or that which displaces and succeeds the deciduous molars in the vertical direction. This tooth is displayed in its closed alveolus in both specimens(1) in which situation, notwithstanding their superiority of size over the largest existing Kangaroos, I was led to seek for it, by observing the sharp, unworn summits of the crowns of the molar teeth and other signs of immaturity in the fossil specimens.

The total number of molar teeth successively developed in the great extinct Kangaroos is the same as in the existing species, viz: two deciduous molars, one premolar, and four true molars: and the permanent series of five appears to have been longer retained than in the large existing species.

The true molars of the upper jaw in the *Macropus Titan* differ from those of the *Macr. Atlas* and of all the existing species in having a well-developed ridge at the back part of the base of the crown in addition to the two principal transverse eminences and the anterior basal ridge. In the *Macropus Atlas* the posterior basal talon of the upper molars is much smaller, the crown broader, especially its anterior division, and the ridge connecting the two transverse eminences is shorter and more simple. In the lower jaw the molars likewise present modifications characteristic of the two species: those of the *Macropus Titan* have no posterior basal ridge, but the anterior one is longer, as is also the ridge connecting the two chief transverse eminences; and the antero-posterior extent of the crown is greater in proportion to its breadth, than in the *Macropus Atlas:* these characters are shown in the figure of the left penultimate molar, Pl. 101, fig. 2; the greater thickness of the transverse ridges is shown in fig. 1.

In the lower molars of *Macropus Atlas* the posterior talon exists in the same rudimental state as in the upper jaw, and the anterior talon is shorter than in the *Macr. Titan*, as is shown in the right penultimate molar in Pl. 101, fig. 4. The upper premolar of the

(1) They are now preserved in the Museum of the Geological Society, and were originally described by me in Sir T. Mitchell's "Expeditions into Australia." 8vo. 1838, Vol. ii, p. 361, Pl. 29.

Macr. Atlas has the same remarkable size as the lower one displayed in fig. 3, Pl. 101 ; the anterior end of the crown is irregularly notched, the inner surface uniform, and its margin entire ; the outer surface is obliquely indented, forming a notched lobe posteriorly. The outer surface of the lower premolar is more equally divided by an oblique vertical fissure into two lobes. The relative size of this tooth to the true molars is not only greater than in the *Macropus Titan*, but also than in the existing true Kangaroos, (*Macropus*), and clearly indicates a subgeneric type connecting these with the Potoroos, (*Hypsiprymnus*). The large procumbent flattened inferior incisor displays the characteristic form of that tooth in the existing Kangaroos, and has the same strengthening ridge along its inner size, fig. 5.

154. *Rhizophaga.*—In this tribe, the stomach is simple in outward form, but complicated within by a large cardiac gland ; and the cœcum, which is short and wide, is furnished with a vermiform appendage.

Genus *Phascolomys*, (Pl. 100, fig. 9.)—In its heavy shapeless figure, large trunk, and short equably developed legs, the Wombat offers as great a contrast to the Kangaroos as does the Koala, which it most nearly resembles in its general outward form and want of tail. But in the more important characters afforded by the teeth and intestinal canal, the Wombat differs more from the Koala than the latter does from either the Phalangers or Kangaroos.

The dental system presents the extreme degree of that degradation of the teeth, intermediate between the front incisors and true molars, which we have been tracing from the Opossum to the Kangaroos : not only have the functionless premolars and canines now totally disappeared, but also the posterior incisors of the upper jaw, which we have seen in the Potoroos to exhibit a feeble degree of development as compared with the anterior pair ; these in fact are alone retained in the dentition of the Wombat, which is thus reduced to that of the true Rodentia.

$$\text{Incisors } \frac{2}{2}\text{; canines } \frac{0}{0}\text{; premolars } \frac{1-1}{1-1}\text{; molars } \frac{4-4}{4-4}\text{: } = 24.$$

The incisors, moreover, are true *dentes scalprarii* with persistent

pulps, but are, especially in the lower jaw, shorter and less curved than in the placental *Glires;* they present a subtriedral figure, and are traversed by a shallow groove on their mesial surfaces.

The spurious molars present no trace of that compressed structure which characterizes them in the Koala and Kangaroos, but have a wide oval transverse section; those of the upper jaw being traversed on the inner side with a slight longitudinal groove. The true molars are double the size of the premolars: the superior ones are also traversed by an internal longitudinal groove, but this is so deep and wide that it divides the whole tooth into two prismatic portions, with one of the angles directed inwards. The inferior molars are in like manner divided into two triedral portions, but the intervening groove is here external, and one of the facets of each prism is turned inwards. All the grinders are curved, and describe about a quarter of a circle: in the upper jaw the concavity of the curve is directed outwards; in the lower jaw, inwards. The false and the true molars like the incisors, have persistent pulps, and are consequently devoid of true fangs, in which respect the Wombat differs from all other Marsupials, and resembles the extinct *Toxodon*, the dentigerous *Bruta*, and many of the herbivorous *Rodentia*. The incisors and the first molar tooth are shed when the animal is young; the latter is superseded by the premolar tooth and the four true molar teeth succeed each other from before backwards.

In all the placental Rodents, which have more than three molars in each lateral series, the additional ones are placed at the anterior part of the row, and are subject to displacement by a permanent successor in the vertical direction, and consequently are essentially "premolars," or spurious molars; the Wombat strikingly manifests its marsupial character in having four true molars on each side of both jaws.

155. *Diprotodon.*—The ossiferous caves and the superficial alluvial or pleistocene deposits of Australia have yielded evidences of still more gigantic and extraordinary forms of the Marsupialia than the Titanic Kangaroos. Amongst the fossils from Wellington valley, first brought to England by Sir Thomas, then Major Mitchell, I recognised in a large incisive tusk such marks of similarity to

that of the Wombat, as to encourage me to indicate the former existence of a Marsupial apparently as large as a Rhinoceros, and for which I proposed the provisional generic name of *Diprotodon*,(1) ranking it with the Wombat in the family '*Phascolomyidæ*.'(2) I have subsequently obtained further evidence of the marsupial nature of the Diprotodon in the inflected angle of the lower jaw, and of its affinities to the *Phascolomys* in the form and extent of the symphysis of the jaw, and in the peculiar construction of the os calcis ;(3) but at the same time, with proof that these characters of *Phascolomys* were combined with molar teeth shaped like those in the genus *Macropus*. The great incisive tusk(4) extends forwards and slightly upwards, its socket being close to the symphysis in each ramus of the lower jaw ; it is sub-compressed, measuring in one specimen, an inch and a half in vertical diameter, and nearly one inch in transverse diameter ; in another specimen the same admeasurements giving respectively one inch two lines and ten lines. This incisor has a partial covering of enamel, which is laid upon its lower and a considerable part of its outer surfaces ; the whole being invested by cement which is thickest on the upper and inner surfaces of the dentine, where there is no enamel. In three specimens of this tusk from the different localities of Wellington Valley, Moreton Bay, and the district of Melbourne, the protruded extremity had been broken off ; but this may be concluded to have been chisel-shaped from the partial deposition of the dense enamel.

The molar teeth(5) are five in number in each ramus of the lower jaw, as in the Wombat ; but they are implanted each by two fangs, and the crown is divided into two principal transverse wedge-shaped eminences, with an anterior and posterior basal ridge or talon. The two principal eminences are slightly curved, with the concavity directed forwards : they are higher and more compressed from behind forwards than in the Kangaroo, Dinothere, Tapir, or Manatee, which present the same type of molar tooth ; and there

(1) Mitchell's Expeditions into Australia, 1838, vol. II, p. 362, Pl. 31, figs. 1 and 2.

(2) 'On the Classification of the Marsupialia,' Zoological Transactions, vol. II, p. 332.

(3) See the Catalogue of the Fossil Mammalia in the Museum of the Royal College of Surgeons, pp. 294, 303.

(4) Pl. 90, fig. 1, *i*.

(5) Pl. 90, fig 1, *m m*.

is but a very feeble indication of that median basal connecting ridge which forms so characteristic a feature of the molars of the Kangaroo. The two fangs are long, and the surfaces which are turned towards each other are impressed by a longitudinal groove, as in the Tapir, Dinothere, and Kangaroo. The molars progressively increase in size from the first to the last: in a jaw, the symphysis of which anterior to the molar series is four inches, the narrow toothless margin between the incisor and the first molar is eight inches in extent: the series of five molars occupies an extent of from ten to eleven inches. The enamel of both molars and incisors is remarkable for its reticulate and punctate exterior, as if worm-eaten; the holes being seen at the fractured margins of the enamel to lead to smooth pits in that substance.

156. *Nototherium.*—A second genus of large Pachydermoid Marsupial has molar teeth resembling in form, mode of implantation, and relative size, those of the preceding genus, Diprotodon, but apparently four in number on each side of the lower jaw, and their crowns covered with smooth enamel;(1) the *Nototherium* is more especially distinguished by the total absence of incisors in the lower jaw, and the much smaller size of the symphysis.

Like the Diprotodon the Notothere had no canines, and being also devoid of defensive tusks, I have called one species *Nototherium inerme.* In a ramus of the lower jaw of this species, twelve inches in length, the series of four molars, which commences within two inches of the anterior end of the jaw is six inches in extent; the antero-posterior diameter of the last tooth is one inch nine lines, and is situated internal to the base of the coronoid process. In a rather larger species the *Nototherium Mitchelli*, the last molar tooth is in advance of the base of the coronoid.

157. *Structure.*—The dentine, enamel, and cement of the teeth of the Marsupial animals present the usual microscopic characters of these tissues in the Mammalia.

The dentinal tubuli of the small molars of the *Phascogale*, *Myrmecobius*, and *Petaurus* have very short trunks, and are relatively larger and fewer in number as compared with the size of

(1) Pl. 91, fig. 4.

the teeth than in the Thylacine, the Wombat or the Kangaroo: the trunks resolve themselves into penicilli of minute radiating branches, which interlace and form a rich net-work at the boundary line between the dentine and enamel.

In the large lower incisors of the Kangaroo (Pl. 102, Fig. 1, *d d.*) the dentine is very compact, and the tubuli extremely minute: their diameter is $\frac{1}{13,000}$th of an inch, and their intervals equal three of these diameters. The tubes radiate with elegant secondary undulations, from the central pulp-cavity to the periphery. The dichotomous divisions of the tubuli are sparing until they approach their terminations: the extremity of one of the tubes magnified 600 diameters, is represented at Pl. 102, fig. 2: the lateral branches are unusually minute, numerous, and short, giving the tubuli a pilose appearance when brought into view by an adequate magnifying power. The terminal branches of the tubuli open into minute irregular cells, forming a thin boundary layer between the dentine and enamel. The fibres of the enamel which invest the crown of the large lower incisor, are likewise unusually minute; viewed in transverse section, as in Pl. 102, *e e*, they describe an abrupt curve at their commencement, and then proceed in a nearly straight course to the outer surface; but at the trenchant margins of the tooth their general course is curved, and they decussate one another as represented in the figure; some of the enamel lines at this part seem as fine as the dentinal tubes. An extremely thin layer of cement may be traced over the basal half of the enamelled crown; it is soon worn away from the remainder; the cement increases in thickness where it invests the fang.

The dentine of the scalpriform incisor of the Wombat is characterized by a few short medullary canals continued from the long conical vascular pulp. The dentinal tubuli are rather larger than in the procumbent incisor of the Kangaroo, but are separated by still narrower interspaces; they dichotomize very sparingly, but send off many fine branches from the side of the primary curve of the tube which is directed towards the crown of the incisor. The boundary layer of cells, in which the terminal branches of the tubuli open, is thicker than in the Kangaroo. The layer of

enamel is situated upon the anterior and outer part of the incisor, forming, by the abrasion of the dentine, the cutting edge of the tooth; its fibres are larger than in the Kangaroo, and their transverse striæ more plainly visible, the enamel is covered by a layer of cement continued from the thicker layer upon the back part of the tooth.

The tubular structure of the dentine of the molars is figured in Pl. 103, fig. 2, *d d*, as seen in part of a section near the base of the crown; in this is likewise shown the lower boundary of the investment of enamel, (*e e*,) and the continuation of the coronal layer of cement, (*c c*,) from the fang, upon the enamel of the crown. There are no parallel tubuli nor vascular canals in the cement; but the radiating tubuli from the calcigerous cells are very numerous, and form rich plexuses in the interspaces. The outer part of the cement is dense and devoid of radiated cells.

CHAPTER VI.

TEETH OF RODENTIA.

158.—We have traced in the Marsupialia a progressive diminution in the number and size of those teeth which intervene between the anterior incisors and the true molars, until the dentition assumed in both jaws the condition expressed by the formula of the genus *Phascolomys*, p. 393. This condition of one large curved incisor on each side, separated by a wide interval from a short series of molars, characterizes the whole order of Rodents: the rule being proved by the single exceptional family (*Leporidæ*) of Hares, Rabbits, and Pikas, or tail-less Hares of Siberia, which retain a second minute incisor behind each of the normal 'dentes scalprarii' of the upper jaw.

The incisors(1) are always regularly curved, the upper ones des-

(1) Pl. 104, figs. 2 & 3, *i*.

cribing a larger segment of a smaller circle, the lower ones a smaller segment of a larger circle; these are the longest incisors and usually have their alveoli extended below or on the inner side of those of the molars to the back part of the lower jaw.(1) Like the molars of the Megatherium and other teeth of unlimited growth, the implanted part of the long and large incisors retains the form and size of the exposed part or crown, to the widely open base, which contains a long conical persistent dentinal pulp, and is surrounded by the capsule in a progressive state of ossification as it approaches the crown, an enamel pulp being attached to the inner side of that part of the capsule which covers the convex surface of the curved incisor. The matrix is here noticed in connexion with the tooth, because it is always found in full development and activity, to the time of the Rodent's death. The calcification of the dentinal pulp, the deposition of the earthy salts in the cells of the enamel pulp, and the ossification of the capsule, proceed contemporaneously; fresh materials being added to the base of the vascular matrix as its several constituents are progressively converted into the dental tissues in the more advanced part of the socket. The tooth thence projecting consists of a body of compact dentine, sometimes with a few short medullary canals continued into it from the persistent pulp-cavity, with a plate of enamel laid upon its anterior surface, and a general investment of cement, which is very thin upon the enamel, but less thin, in some Rodents, upon the posterior and lateral parts of the incisor. The substances of the incisor diminish in hardness from the front to the back part of the tooth; the enamel consisting of two layers, of which the anterior and external is denser than the posterior layer, and the posterior half of the dentine being by a modified number and arrangement of the calcigerous tubes less dense than the anterior half.(2)

The abrasion resulting from the reciprocal action of the upper and lower incisors produces accordingly an oblique surface, sloping from a sharp anterior margin formed by the dense enamel, like that which slopes from the sharp edge formed by the plate of hard

(1) Pl. 104, fig. 1, *i*. (2) Pl. 106.

steel laid upon the back of a chisel; whence the name, 'dentes scalprarii,' given to the incisors of the Rodentia.(1)

The varieties to which these incisors are subject in the different Rodents are limited to their proportional size, and to the colour and sculpturing of the anterior surface. Thus in the Guinea-pig, Jerboa, and Squirrel, the breadth of the incisors is not half so great as that of the molars, whilst in the Coypu they are as broad, and in the Cape Mole-rats, (*Bathyergus* and *Orycteromys*), broader than the molars.

In the Coypu, Beaver, Agouti, and some other Rodents, the enamelled surface of the incisors is of a bright orange or reddish brown colour. In some genera of Rodents as *Orycteromys*, *Otomys*, *Meriones*, *Gerbilla*, *Hydrochœrus*, *Lepus* and *Lagomys*, the anterior surface of the upper incisors is indented by a deep longitudinal groove. This character seems not to influence the food or habits of the species; it is often present in one genus and absent in another of the same natural family: in most Rodents the anterior enamelled surface of the scalpriform teeth is smooth and uniform.

The molar teeth are always few in number, obliquely implanted and obliquely abraded, the lateral series converging anteriorly in both jaws; but they present a striking contrast to the incisors in the range of their varieties, which are so numerous that they typify almost all the modifications of form and structure which are met with in the molar teeth of the omnivorous and herbivorous genera of other orders of Mammalia.

In some Rodents the molar teeth are rootless, like those of the Wombat, the Toxodon and Elasmothere; some have short roots tardily developed, like the molars of the Horse and Elephant; and some soon acquire roots of the ordinary proportional length.(2)

(1) John Hunter grouped together the quadrupeds composing this order under the name of 'Scalpris-dentata;' but the large curved, chisel-shaped incisors, though common to all the Rodents, are not peculiar to that order: we have seen them in the Wombat amongst the Marsupials; they are present in the Cheiromys amongst the Lemurine group of Quadrumana, and in the Toxodon amongst the Pachyderms; some of the Shrews have the anterior incisors restricted in number and developed in bulk, almost to their proportions in the Rodentia.

(2) Prof. Erdl has given a tabular arrangement of the molars of the Rodentia, according

The Rodents which have rootless molars, comprise the families of the Hares,(1) Chinchillas,(2) Chili-rats,(3) and Cavies(4), most of the Voles,(5) the Houtias (*Capromys*), and the Cape Jerboa (*Helamys*).

The genera which have molars with short or incomplete roots, developed late, are *Castor* (Beaver), *Hystrix* (Porcupine),(6) *Cœlogenys* (Spotted Cavy), *Dasyprocta* (Agouti), *Spalax* (Blind-rat), *Myopotamus* (Coypu), *Euryotis*, *Ascomys*, and *Aplodontia*.

The families of the Squirrels, Dormice, Rats, and Jerboas have rooted molars.

The differences in the mode of implantation of the molar teeth relate to differences of diet. The Rodents which subsist on mixed food and which betray a tendency to carnivorous habits, as the true Rats, or which subsist on the softer and more nutritious vegetable substances, as the oily kernels of nuts, suffer less rapid abrasion of the molar teeth; a minor depth of the crown is therefore needed to perform the office of mastication during the brief period of existence allotted to these active little Mammals; and, as the economy of nature is manifested in the smallest particulars as well as in her grandest operations, no more dental substance is developed after the crown is formed, than is requisite for the firm implantation of the tooth in the jaw.

Rodents that exclusively subsist on vegetable substances, especially the coarser and less nutritious kinds, as herbage, foliage, the bark and wood of trees, wear away more rapidly the grinding surface of the molar teeth; the crowns are therefore larger, and their growth continues by a reproduction of the formative matrix at their base in proportion as its calcified constituents, forming the exposed working part of the tooth, are worn away. So long as this reproductive force is active the molar tooth is implanted, like the incisor,

to their modes of implantation, in his excellent Paper on the Teeth of that order, in the Munich Transactions, 'Abhandlungen der K. Bayerischen Akademie der Wissenschaften,' Bd. III. 1841, p. 529.

(1) *Lepus, Lagomys.*

(2) *Lagostomus, Lagotis, Chinchilla.*

(3) *Abrocoma, Octodon, Schizodon, Poephagomys, Ctenomys.*

(4) *Hydrochœrus, Dolichotis,* (Pl. 104, figs. 2 & 3), *Kerodon, Cavia.*

(5) *Lemmus, Arvicola,* except *A. riparia.*

(6) Pl. 104, fig. 1.

by a long undivided continuation of the crown; when the force begins to be exhausted the matrix is simplified by the suppression of the enamel organ, and the dentinal pulp continues to be reproduced only at certain points of the base of the crown, which, by their elongation, constitute the fangs. The Beaver and other Rodents in the second category of the order, according to the implantation of the molar teeth, exemplify the above condition; but in the Capybara, Dolichotis, (Pl. 104, figs. 2 & 3), and other Rodents with rootless molars, the reproduction of the molar like that of the incisor teeth, appears to continue throughout the animal's existence. The rootless and perpetually growing molars are always more or less curved; they derive from this form the same advantage as the incisors, in the relief of the delicate tissues of the active vascular matrix from the effects of the pressure which would otherwise have been transmitted more directly from the grinding surface.

The complexity of the structure of the crown of the molar teeth, and the quantity of enamel and cement interblended with the dentine, are greatest in the rootless molars of the strictly herbivorous Rodents. The crowns of the rooted molars of the omnivorous Rats and Mice are almost as simple as the tuberculate molars of the Bear or of the Human Subject, which they appear to typify. They are at first tuberculate, as shown in Pl. 105, fig. 9; when the summits of the tubercles are worn off, the inequality of the grinding surface is for a time maintained by the deeper transverse folds of enamel, the margins of which are separated by alternate valleys of dentine and cement, as shown in Pl. 105, fig. 10, 3 *a;* but these folds sinking only to a slight depth are in time obliterated, and the grinding surface is reduced to a smooth field of dentine with a simple border of enamel, as shown in the upper tooth of figure 10, 3. A similar change in the grinding surface, consequent on age and use, is shown in the molars of the Souslik, or Ground Squirrel, Pl. 105, fig. 3, *b*, and in those of the Gerbille, fig. 8, and is common to all that possess roots.

Examples of various forms assumed by the inflected folds of enamel in the molars of the Rodentia are given from the works of the Cuviers in Pl. 105. It will be seen that these folds have

a general tendency to a transverse direction across the crown of the tooth. Baron Cuvier has pointed out the concomitant modification of the shape of the joint of the lower jaw, which almost restricts it to horizontal movements, to and fro, in the direction of the axis of the head, during the act of mastication. When the folds of enamel dip in vertically from the summit to a greater or less depth into the substance of the crown of the tooth, as in those molars which have roots, the configuration of the grinding surface varies with the degree of abrasion, of which examples have already been cited; but in the rootless molars where the folds of enamel extend inwards from the entire length of the sides of the tooth, the characteristic configuration of the grinding surface is maintained without variation, as in the Guinea-pig, (fig. 16), the Capybara, (fig. 17), and the Patagonian Cavy, (Pl. 104, figs. 2 & 3).

The whole exterior of the molar teeth of the Rodentia is covered by cement, and the external interspaces of the enamel-folds are filled with the same substance. In the *Chinchillidæ* and the *Capybara* where the folds of enamel extend quite across the body of the tooth, and insulate as many plates of dentine, these detached portions are held together by the cement; such folds of enamel are usually parallel, as in the large posterior lower molar of the Capybara, which in shape and structure offers a very close and interesting resemblance to the molars of the Asiatic Elephant.

The partial folds and islands of enamel in the molars of the Porcupine (fig. 13), and Agouti, (fig. 14), typify the structure of the teeth of the Rhinoceros: the opposite lateral inflections of enamel in the molars of the Gerbille, (fig. 8), and Cape Mole-rat, (fig. 11), represent the structure of the molars of the Hippopotamus: the double crescentic folds in the Jerboa (fig. 7), sketch out, as it were, the characteristic structure of the molars of the Anoplothere and Ruminantia.

Although, as has been shown, the molar teeth in many Rodents are rootless and of unlimited growth as in the Edentata, in none is enamel absent or vascular dentine, as the chief constituent of the tooth, present: these essential differences characterise the molars of those Rodents which by use have their grinding surface reduced

to a simple depression bounded by a raised circular margin, as in the great Cape-mole: that margin being formed by true enamel, but in the Sloths by hard dentine.

159. *Structure.*—The proportions and relative positions of the dentine, enamel and cement which enter into the composition of the scalpriform incisors have already been mentioned; I have observed the modifications of the enamel, alluded to at p. 399, in the Rat, the Water-Vole, the Beaver, the Agouti and the Hare, and believe it to be common to the Rodentia: the difference in the tubular structure of the anterior and posterior halves of the dentine is more conspicuous in the Hare, Vole and Beaver than in the Agouti.

In the Agouti a longitudinal slice from the middle of the upper incisor shows the conical pulp-cavity extending through one half of the tooth, and a linear tract continued from its apex to the gnawing surface of the tooth: from this line, the end of which, in most Rodents, is perceptible on that surface, the calcigerous tubes diverge; those passing to the anterior margin of the tooth describe a sigmoid curve, first convex towards the cutting end, which may be called the crown, then concave: the tubes which proceed to the opposite margin describe a stronger and shorter curve convex towards the crown, and then proceed straighter and more transversely to their termination: the origin of these tubes is obscured by the cut ends of those which were proceeding towards the sides of the tooth: and which are chiefly formed by the posterior half of the pulp. The tubuli are $\frac{1}{12,000}$th of an inch in diameter and are very closely arranged, being separated by intervals of little more than their own diameter: so that the dentine is unusually firm and compact. The exterior clear and denser enamel forms about one-third the thickness of that layer and is coated by thin and well-defined brown-coloured cement.

The fibres composing the inner and more opake part of the enamel proceed obliquely, but almost transversely across that substance, with a gentle curve in the opposite direction to the last curve of the contiguous dentinal tubes; viz. with the convexity towards the crown: the fibres of the peripheral layer of the enamel make a slight bend towards the crown: these enamel-fibres are as thick as two of the dentinal tubes with their interspace: their ends are lost

in the clear peripheral substance to which the distinct apparently structureless brown layer of cement is attached, and to which the colour of the convex surface of the incisor is due.

In a transverse section of the incisor of the Water Vole (*Arvicola amphibia*), the thin colourless and apparently structureless layer of cement covering the concave surface of the tooth is distinctly traceable from the dentine at the sides of the tooth upon the anterior plate of enamel; and seems to be intimately blended with its exterior surface. The layer of cement becomes thinner at the margin of the enamel, where it is continued from the dentine upon that part, but soon increases in thickness, acquiring the bright brown tint, and separated by a well-defined line from the outer clear layer of enamel.

The delicate transverse or concentric lines of this substance are seen more distinctly in the transverse than in the longitudinal sections of the incisor. The faint outlines of the dentinal cells, and the traces of the concentric layers of the clear substance of the dentine are likewise best seen in the transverse section of the incisor. No vascular canals are continued from the pulp-cavity into the dentine of the incisors of the Water-Vole or Agouti.

In the incisors of the Hare and Rabbit the pulp-cavity terminates in a transversely extended fissure: the dentinal tubes proceeding to the anterior enamelled surface after forming the curve, convex towards the crown, proceed in a straighter transverse course to the enamelled surface than in the Agouti. The tubes which pass to the opposite or posterior surface of the tooth are less numerous, less parallel and less closely packed together: they send out more and larger branches, which decussate each other in an elegant arborescent manner. The dentinal tubes of the Hare, figured by Retzius (loc. cit. tab. v. fig. 2 *a* and *b*) appear to have been taken from the inner and less dense half of the dentine.

In the Beaver, as in the Hare, the tubes which are characterised by the great number and size of their branches, are confined to the posterior half of the incisor;(1) the tubes of the anterior half of the dentine(2) in the Beaver's incisor are more numerous, more parallel

(1) Pl. 106, *d*'. (2) Ib. *d*.

and less ramified, and thus produce a greater degree of density and resistance, which must favour the oblique wearing and the maintenance of the sharpness of the chisel-shaped extremity of the tooth. Short medullary canals (Pl. 106, *v v*), are continued from the end of the pulp-cavity into the central tract of the dentine.

The difference of structure of the anterior and posterior parts of the enamel-plate is very clearly shown in the Beaver's incisor. The fibres of that half of the enamel(1) next the dentine are nearly transverse, their diameter is equal to two dentinal tubes and their interspace; they describe a gentle sigmoid curve, and are distinctly, almost coarsely, defined: the fibres of the peripheral half of the enamel(2) are more minute, more oblique, and less distinctly defined; the substance being clearer and denser.

In a transverse section of the incisor the distinction between the two layers of enamel is still more obvious, and the fibres of the inner half being cut across, give the appearance of fine decussating oblique lines; while those of the outer half run transversely to the surface, and are crossed by the traces of the concentric layers. The coloured exterior layer(3) is as distinctly defined as in the incisors of the Vole; the fine fibres of the outer layer of enamel appear to penetrate it, but its continuation with the thin indubitable layer of cement upon the lateral and posterior parts of the incisor lead me to conclude that it is due to the calcification of the capsule, and that it is essentially what Mr. F. Cuvier supposed it to be, cement, but in too small a quantity to permit the development of the calcigerous cells. In a transverse section of a Beaver's incisor in my microscopical collection the cement is distinctly continued, retaining its peculiar colour, from the enamel, beyond the lateral boundary of that substance upon the dentine, for a short distance. Retzius' denial (loc. cit. p. 63) of the presence of any cortical substance or cement upon the Beaver's incisor appears be founded on a non-recognition of that substance where it is so thin as to be devoid of radiated or Purkingian cells.

In the molar teeth the enamel presents a uniform structure throughout its thickness, which is like that of the denser outer layer of the enamel of the incisor. It is distinctly coated by a layer of structureless dentine as thin as the coloured layer upon the enamel

(1) Pl. 106, *e*. (2). Ib. *e*^{1}. (3) Ib. *c*

of the incisor, and which, as it gradually augments in thickness to enter and fill the inflected folds of enamel acquires the radiated cells and also the medullary canals. This thin exterior layer is not represented in Prof. Erdl's figures of the microscopic structure of the molars of Rodentia, which, from their accuracy in other respects I have reproduced in Plates 107—109. The size of the calcigerous tubes is unavoidably exaggerated from the limited scale of the drawings; but their course is correctly given.

The structure of the rooted molar teeth with simple crowns is correspondingly simple: the dentine consists of calcigerous tubes radiating in the body of the tooth from a single pulp-cavity, with the primary curves rather stronger than usual, especially in the tubules which ascend vertically from the summit of the pulp-cavity. At the base of the crown, where the pulp-cavity divides in order to be continued into the fangs, the tubuli radiate from each division almost horizontally and a section at this part displays their entire course, as shewn in Pl. 107, fig. 1, in a molar tooth of the common Squirrel (*Sciurus vulgaris*).

The section of the crown of the molar tooth of the Rat, taken through the middle, shows the external coat of enamel, a small portion of the cement and enamel at the bottom of the fissures and depressions down which these substances are continued from the summit of the crown, and the disposition of the calcigerous tubes in relation to those depressions and to the external coat of enamel: the third molar—the lowest and largest in Pl. 105, fig. 10, 3—shows the crown naturally worn down almost to the degree corresponding with the section magnified in Pl. 108, fig. 1.

The vertical section of the molar of the Flying Squirrel, the crown of which has been worn down in a less degree, shows better the course of the dentinal tubuli relatively to the inflected cups of enamel upon the grinding surface. These cups or depressions, (Pl. 108, fig. 3, *e*, *e*, *e*). are filled by a brown-coloured cement (*c*, *c*, *c*). In a transverse section of the crown the inflected vertical folds of enamel appear, as on the naturally abraded surface, in the form of islands including the cement, whilst the lateral folds of enamel project like promontories into the substance of the crown.

The transverse section of the molar of the Water-Vole (*Arvicola*) (Pl. 168, fig. 3) shows only the latter form: that of the Beaver (Pl. 107, fig. 2) exhibits chiefly the islands with a single promontory of enamel.

The transverse section of the crown of the molar of *Lagostomus* displays not fewer than five islands of enamel, which hard substance is so thick that it enters more abundantly into the composition of the tooth than the dentine itself. The dentine of the crown closely adheres to the surface of all the inflected folds and cavities of enamel as well as to that of the outer investing layer; and in the complex molars, where the folds are numerous, the layer of dentine is in many parts thinner than that of the enamel. As the pulp-cavity sends narrower or wider fissures into each of the processes of dentine it assumes a very complicated form when seen in transverse section, as in the molar of the Beaver, Pl. 107, fig. 2, where the dark fissures in the substance of the tooth indicate the spaces which contained the vascular pulp (*v v*). The calcigerous tubes maintain at most parts of this complicated dentine (*d d*) their general course at right angles between the pulp-cavity and the enamel with the usual graceful flexuous sigmoid curves: but in some places, near the angles of the folds of dentine, the curves are stronger and less regular. The secondary minute undulations with the terminal bifurcations, anastomoses and loops of the dentinal tubuli are shown at Pl. 109, fig. 2. The cavities of the enamel-folds which open upon the exterior of the tooth are filled with cement; and where this is accumulated in sufficient quantity, as in the Beaver's molar (Pl. 107, fig. 2, *c*) or in that of the Water-Vole (Pl. 108, fig. 3, *c*), it presents not only the calcigerous cells but also medullary canals. Prof. Erdl has described and figured the concentric layers of the walls of these canals, and the minute dendritic tubuli which radiate from their cavities, and establish a communication between them and the calcigerous cells; doubtless for the conveyance of the nutritious colourless plasma transuded from the blood-vessels. The calcigerous cells are larger, more numerous and more angular in the cement of the Beaver's tooth than in ordinary bone.

The pulp, after the formation of a certain thickness of tubular dentine becomes converted into osseo-dentine in both the rooted and

rootless molars of the Rodents. This fourth substance is exhibited at *o* in the magnified transverse section of the Water-Vole's molar, (Pl. 108, fig. 3), which shows the four different dental tissues, viz. cement **c**, enamel *e*, dentine *d* and osseo-dentine *o*, entering in more equal proportions into the formation of the crown, than has, hitherto, been demonstrated in any other tooth. When the crown is worn by mastication down to the place of the section figured, the four substances appear in the same proportions on the grinding surface, contributing to its efficiency as a triturating organ by the inequalities consequent on their various degrees of density and resistance to the abrading forces.

The transverse section of the molar of the Hare, (Pl. 109, fig. 1), shows the single, but deep, lateral fold of enamel (*e*) extending almost across the entire breadth of the tooth, and followed as usual by the included layer of cement (*c*). In the Capybara the fold is carried quite across, and divides the anterior molars into two portions of a prismatic form, with the base turned outwards, and penetrated by a shorter fold of enamel: the posterior molar in the lower jaw is divided into ten or more portions of which only the anterior one is prismatic and indented on the outer side, the rest being simple, compressed plates, having a microscopic structure very similar to that in the lobes of the molar of the Hare. In this tooth the primary curvatures of the dentinal tubes are more flexuous than usual: the concentric layers of the clear basal substance may be more clearly perceived than in most other Rodents: the quantity of osseo-dentine which fills the remains of the pulp-cavity is very small. The enamel varies in its thickness both in the outer surface and the inflected fold in the Hare: this fold is elegantly undulated through a greater part of its extent.

It is peculiar to some of the Rodents with rootless molars to have the sockets of these long curved teeth open at both extremities, so that, in the dry skull, the base of the tooth protrudes as well as the grinding surface: the matrix in such instances adheres to the periosteum which covered the portion of bone absorbed from the bottom of the alveolus. The Jumping-Hare (*Helamys capensis*), when full-grown, offers a good example of this curious structure.

160. *Succession.*—The molars are not numerous in any Rodent; the Hare and Rabbit (*Lepus*) have $\frac{6-6}{5-5}$, i. e. six molars on each side of the upper jaw and five on each side of the lower jaw: the Pika (*Lagomys*), has $\frac{5-5}{5-5}$: the Squirrels have $\frac{5-5}{4-4}$: the families of the Dormice, the Porcupines, the Spring-Rats (*Echimyidæ*), the Octodonts, Chinchillas and Cavies, have $\frac{4.4}{4.4}$ molars: in the great family of Rats (*Muridæ*), the normal number of molars is $\frac{3-3}{3-3}$: but the Australian Water-rat, (*Hydromys*), has but $\frac{2-2}{2-2}$ molars, making with the incisors twelve teeth, which is the smallest number in the Rodent order: the greatest number of teeth in the present order is twenty-eight, which is exemplified in the Hare and Rabbit: but thirty-six teeth are developed in these species, six molars and two incisors being deciduous.

In all the Rodents, in which the number of molars exceeds three in a series, the additional ones are anterior to these and are premolars; i. e. they have each displaced a deciduous predecessor in the vertical direction, and are what Cuvier calls 'dents de remplacement.' This it is which constitutes the essential distinction between the dentition of the marsupial(1) and the placental Rodent; the latter, like the placental Carnivora, Ruminantia and ordinary Pachyderma having never more than three true molars. Thus the Rodents, which have the molar formula of $\frac{4-4}{4-4}$, shed the first tooth in each series, and this is succeeded by a permanent premolar which comes into place later than the true molars; later, at least, than the first and second, even when the deciduous molar is shed before birth, as was observed by Cuvier in the Guinea-pig, Pl. 104, fig. 4. In the Hare and Rabbit the three anterior teeth in the upper jaw and the two anterior ones in the lower jaw succeed and displace, in like manner, deciduous predecessors, and come into place after the first and second true molars are in use, and contemporaneously with the last molar.

It does not appear that the scalpriform incisors are preceded by milk-teeth, or, like the premolars of the Guinea-pig, by uterine teeth: but the second incisor was observed by Cuvier(2) to be so preceded in the genus *Lepus*, and he has figured the jaw of a young Rabbit, before

(1) See Dentition of the Wombat, p. 393.

(2) Ossemens Fossiles, tom. v, pt. i, p. 5.

that deciduous tooth was shed, when six incisors are present in the upper jaw.(1) This condition is interesting both as a transitory manifestation of the normal number of incisive teeth in the Mammalian Series, and as it elucidates the disputed nature of the great anterior scalpriform teeth. Geoffroy St. Hilaire contended that the scalpriform teeth of the Rodents were canines, because those of the upper jaw extended their fang backwards into the maxillary bone, which lodged part of their hollow base and matrix. But the scalpriform teeth are confined exclusively to the intermaxillary bones at the beginning of their formation, and the smaller incisors which are developed behind them in our anomalous native Rodents, the Hare and Rabbit, retain their usual relations with the intermaxillaries, and *d fortiori*, prove the tooth which projects anterior to them to be also an incisor.

The law of the unlimited growth of the scalpriform incisors is unconditional, and constant exercise and abrasion are required to maintain the normal and serviceable form and proportions of these teeth. When, by accident, an opposing incisor is lost, or when by the distorted union of a broken jaw the lower incisors no longer meet the upper ones, as sometimes happens to a wounded hare, the incisors continue to grow until they project like the tusks of the Elephant, and the extremities in the poor animal's abortive attempts to acquire food also become pointed like tusks: following the curve prescribed to their growth by the form of their socket, their points often return against some part of the head, are pressed through the skin, then cause absorption of the jaw-bone and again enter the mouth; rendering mastication impracticable and causing death by starvation. In the Museum of the College of Surgeons there is a lower jaw of a Beaver in which the scalpriform incisor has, by unchecked growth, described a complete circle: the point has pierced the masseter muscle and entered the back of the mouth, passing between the condyloid and coronoid processes of the lower jaw, descending to the back-part of the molar teeth, in advance of the part of its own alveolus which contains its hollow root. The upper jaw of a rabbit with an analogous abnormal growth of the scalpriform and accessory incisors is figured in Pl. 104. fig. 7.

(1) Pl. 104, fig. 5.

CHAPTER VII.

TEETH OF INSECTIVORA.

The dental system is here remarkable for the many varieties and even anomalies which it presents: almost the only characteristic predicable of it in the numerous small quadrupeds which constitute the Insectivorous order(1) being the presence of several sharp points or cusps upon the crowns of the true molar teeth, which are always broader in the upper than in the lower jaw. The teeth that intervene between these and the incisors are most variable in form and size, but are never absent: the incisors also differ in number, size, and shape in different species, the anterior ones approximating in some species to the character of the scalpriform teeth of the Rodents.

The Insectivora are divided into the families of Moles (*Talpidæ*), Shrews (*Soricidæ*), and Hedgehogs (*Erinaceidæ*), in which succession their dentition will be here described.

161. *Talpidæ*.—Of all existing Insectivora the Chrysochlore, or iridescent mole of the Cape, makes the nearest approach, by the number of its molar teeth, to that remarkable condition which was manifested in the most ancient period of mammalian existence by the extinct *Amphitherium* described in the chapter of Marsupialia. We must assign at least $\frac{6-6}{5-5}$ true molars to the Chrysochlore(2) according to their form, which, in the absence of the known order of vertical displacement and succession, is the only character by which the true and false molars can be defined. The anterior large laniariform tooth and the two succeeding small teeth are incisors, by virtue of their position in the intermaxillary bones; the next small

(1) Pallas points out succinctly some of the leading differential characters which distinguish the *Insectivora* from the *Carnivora* or true *Feræ* in his 'Zoographia Rosso-Asiatica' where (Vol. i. p. 119) he says "Continuitate etiam dentium, numero *incisorum* a Ferarum Ordine semper discordante, *caninis* minus elongatis, plerumque uno alterove spurio stipatis, pedum pentadactylorum structura multifaria et singulari, clavicularum perfectarum in sceleto præsentia, totoque indolis, morum, victus et habitus complexu, cuncta hæc genera à feris omnino discrepant, simul affinitate concatenata inter se successive cohærent." The *Insectivora* are further distinguished from the *Carnivora* by the absence of cerebral convolutions and by a discoid, instead of an annular, placenta.

(2) Pl. 110. fig. 1.

tooth with a simple compressed tricuspid crown is a premolar. The crowns of the true molars are thin plates, flattened from before backwards, with two notches on the working edge and a longitudinal groove along the outer and thicker margin, which divides the outer cusp into two as shown in the figure, where the middle cusp, which is the largest, is seen in the interspace of the bifid external cusp: the base of the lamelliform molar divides tardily into two short roots. The third internal simple cusp is not present in the anterior molar, and the posterior or sixth molar has a simple tricuspid crown. Another anomaly, more remarkable than that of the shape of the true molars, is their separation from each other by vacant intervals, as in many Reptiles. The crowns of the five lower true molars are compressed antero-posteriorly but are of unusual length, and have the thicker margin turned inwards, with the summit divided by a single notch, and the inner and lower division is subdivided into two. The anterior incisor is small and procumbent: the second has a larger laniariform crown; the third is small and resembles the two premolars which intervene between this and the first true molar. The lower molars are separated by wider intervals than those above; the crowns of the opposing series enter reciprocally the interspaces and interlock: in mastication the anterior margin of one tooth works upon the posterior margin of the opposite molar.

According to M. F. Cuvier(1) each series in the upper jaw of the Chrysochlore includes 1 incisor and 9 molars; and in the lower jaw 2 incisors and 8 molars. M. de Blainville, guided by the intermaxillary sutures in the young Chrysoclore, regards the first three teeth in each lateral series as incisors, the fourth as a canine, and the remaining six as molars in both upper and lower jaws. My views, as given in the foregoing description, are expressed by the following formula: *in.* $\frac{3-3}{3-3}$, *pm.* $\frac{1-1}{2-2}$, *m.* $\frac{6-6}{6-6}=40$.

In the Shrew-moles of America, (*Scalops*), the dentition makes an important step towards the normal mammalian condition by the restriction of the characters of the true molars to the three posterior teeth in each lateral series(2): between these and the large scalpriform incisor, in the upper jaw, there are six teeth, the first two

(1) Dents de Mammifères, p. 63. (2) Pl. 110, fig. 2.

of which must be regarded, by the analogy of the Chrysochlore, as incisors: the next tooth might pass for a canine; and the remaining three for premolars, of which the last is the largest and has a trihedral pointed crown: the true molars have large crowns, each with six cusps, four on the outer and two on the inner part of the grinding surface. In the lower jaw, the first incisor is small and procumbent, and the second large and laniariform, as in the Chrysochlore; the third is absent, and a vacant space separates the incisor from the three premolars, the crown of each true molar consists of two parallel three-sided prisms, each terminated by three cusps, and having one of the angles turned outwards and one of the faces inwards: the interspace between the angles makes the outer surface of the long molars of the *Scalops* appear grooved. The dental formula of this genus, according to the above description, is:

$$in\ \frac{3-3}{2-2},\ c.\ \frac{1-1}{0-0},\ pm.\ \frac{3-3}{3-3},\ m.\ \frac{3-3}{3-3} = 36.$$

The dentition of the common Mole *(Talpa europæa)*,(1) includes eleven teeth on each side of both upper and lower jaws. The first three in the upper jaw are very small, with simple incisive crowns, and are each implanted by a long and slender fang: these teeth, by analogy with the Chrysochlore, and by the position of the incisive foramen, must be regarded as incisors: the next tooth, by the size and shape of the crown, represents a canine, but it is implanted by two fangs like the three succeeding premolar teeth, and these teeth are of small size with compressed conical crowns; the fourth premolar has a larger three-sided conical crown, supported by three fangs: the crowns of the true molars are multicuspid, the middle one is the largest with five points and is usually supported by four fangs, the hindmost is the smallest, with a tricuspid crown and three fangs. In the lower jaw, the first four teeth on each side are small, simple and single-fanged, like the three incisors above: the fifth tooth has a large laniariform crown, supported by two fangs, being very similar to, but shorter than, the two-fanged canine above; but, as it passes behind that tooth when the mouth is shut, we must regard the fourth tooth below, notwithstanding its small size and similarity to the

(1) Pl. 110, fig. 3.

incisors, as the true inferior canine: the fifth tooth is then the first and largest of the series of four premolars, each of which has a small posterior talon at the base of the compressed conical crown. The three true molars are each implanted by two fangs and have quinquecuspid crowns, the middle molar being the largest.

The teeth of the Mole have been differently classified by different authors: the dental formula according to M. F. Cuvier(1) is:

$$in.\ \frac{3-3}{4-4};\ c.\ \frac{1-1}{0-0};\ pm.\ \frac{4-4}{4-4};\ m.\ \frac{3-3}{3-3}: = 44.$$

Prof. Bell, in his "History of British Quadrupeds,"(2) adopts the following:

$$in.\ \frac{3-3}{4-4};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{7-7}{6-6}: = 44.$$

Prof. de Blainville(3) prefers the formula:

$$in.\ \frac{4-4}{4-4};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{3-3}{3-3};\ m.\ \frac{3-3}{3-3}: = 44.$$

From which it will be seen that the difference turns mainly upon the determination of the canine teeth. M. F. Cuvier and Prof. Bell both regard the fourth large tooth of the upper jaw as a canine, notwithstanding it has two fangs. M. de Blainville(4) has assured himself that it is an incisor, in which case the double implantation would be still more anomalous. The position of the incisive foramen (Pl.110, 3 *a*), however, indicates that the double socket of this tooth is posterior to the intermaxillary suture, and that the number of incisors has been rightly determined by F. Cuvier. By this justly esteemed authority the canines are held to be wanting in the lower jaw of the Mole. Prof. Bell regards as lower canines the large fifth tooth on each side, although posterior to the canine above; and M. de Blainville, having assigned eight incisors to the upper jaw, gives the same number to the lower jaw, and calls the first premolar a canine. With regard to the fourth tooth above, if it be not developed in the intermaxillary bone, it claims to be regarded as a canine by the size and shape of the crown, and to be a premolar by virtue of its two fangs; but, since the fang of a tooth is subject to more variety than the crown, we

(1) Dents de Mammifères, p. 61.
(2) 8vo. 1837, p. 85.
(3) Ostéographie.
(4) Loc. cit.

should be guided by the more fixed character, and call the tooth in question a canine. The fourth tooth below, although so small, is the only one which has the true relative position of a canine, in advance of the one above, when the mouth is shut; and we shall find in the genus *Lemur* a similar conformity of size and shape between the lower canine and incisors as exists in the common Mole.(1) There is no difficulty about the other teeth, the canines being determined; thus, according to my view, the dental formula of the genus *Talpa* is: *in.* $\frac{3-3}{3-3}$, *c.* $\frac{1-1}{1-1}$, *pm.* $\frac{4-4}{4-4}$, *m.* $\frac{3-3}{3-3}$, = 44; the teeth are here equal in number, and the same in kind in both jaws; the true molars are reduced to the normal quantity in the Placental series, and the entire dentition is the least anomalous of any which is manifested in the family *Talpidæ*.

162. *Soricidæ*.—The transition from the Moles to the Shrews seems to be made by the Water-moles, (*Mygale*), and the *Solenodon*. The latter Insectivore combines the form of a gigantic Shrew with a dentition resembling that of the Chrysochlore.(2) Each intermaxillary bone contains three incisors, the first large, canine-shaped, grooved anteriorly with the point inclined backwards; the other two incisors small with simple conical crowns; these are succeeded by seven teeth, the two anterior having three-sided conical crowns, the other five bearing in addition an external tuberculate basal ridge. In the lower jaw, the anterior incisor is very small, and the second large and laniariform, as in the Scalops and Chrysochlore; but it is remarkable for a deep longitudinal excavation upon its inner side,(3) (Pl. 111, *b* and *c*,) apparently produced by the friction of the large upper incisors which are received into the interspace of the lower pair; the third lower incisor is small and simple; of the seven succeeding teeth the four last have multicuspid crowns like true molars.

The Pyrenean Water-mole, (*Mygale pyrenaica*), has eleven teeth on each side of both jaws; the first incisor above is relatively larger than in *Scalops*, trihedral and sharp-pointed; the second and third

(1) In the *Talpa moogura* Temm., the inferior canine is absent, as in the genus *Scalops*; in the *Condylure*, or Rayed-mole, it is present with the form and proportions of a canine.

(2) See Brandt, Acta Petropol; ii, 1835.

(3) The name of the genus, (σολην, a pipe, οδους, a tooth), relates to this structure.

incisors are very small; none of the succeeding teeth present the form and size of a canine; the last three teeth are multicuspid, and are true molars. In the lower jaw all the teeth anterior to the true molars are small and simple.

The teeth in the lower jaw of a species of Water-mole, as large as a Hedgehog, which has become extinct in England, present a close resemblance with those of the *Mygale;* the true molars have square, quinque-cuspid crowns, but are distinguished from the teeth of all known recent *Insectivora* by the presence of a minute tubercle at the bottom of the outer vertical fissure of the crown. I have called this extinct genus *Palæospalax*.(1)

The typical Shrews always manifest their Rodent analogy by the superior size of the anterior pair of incisors in both upper and lower jaws; in the latter the great incisor is uniformly succeeded by two small and three large multicuspid molars; but in the upper jaw the number of small premolars varies, and there is generally a fourth true molar of small size. The sub-genera of Shrews are chiefly based upon the form of the large incisors, and the numeral variations of the dentition of the upper jaw. In the common Shrew (*Sorex araneus* of Linnæus, Pl. 111, fig. 2) there are four true molars and three small teeth between these and the anterior incisor; this tooth has a pointed tubercle at the back of the base of the crown. The long procumbent incisor of the lower jaw has the trenchant superior margin entire. In the *Sorex* (*Amphisorex*) *tetragonurus* (Pl. 110, fig. 4) the edge of the lower incisor is notched; the large upper incisor appears bifurcate from the great development of the posterior talon; five small teeth progressively decreasing in size, intervene between the upper large incisor and the true molars. In the *Sorex* (*Hydrosorex*) *Hermanni* the trenchant edge of the lower procumbent incisor is entire; there are four small teeth between the large anterior incisor and the true molars in the upper jaw, as in the great *Sorex indicus*, but the three first are sub-equal and the fourth very minute; there is a fourth small true molar above. The enamelled tips of the teeth of the species of *Amphisorex* and *Hydrosorex* are stained

(1) "History of British Fossil Mammals," p. 25.

of a bright brown colour; the teeth of *Sorex* proper, as the common Shrew (*S. araneus*), are not so stained.(1)

In the progress of the formation of the large notched incisors, the summits of the tubercles are first formed as detached points, supported upon the common pulp, and do not coalesce until the centripetal calcification has converted the pulp into a common dentinal base. Some anatomists have regarded the large incisor so formed as an aggregate of two or three teeth: but in *Sorex* proper and *Hydrosorex*, the calcification of the lower incisor spreads from a single point; and the interpretation of the notched incisor of the *Amphisorex*, as the representative of these incisors,(2) might, by parity of reasoning, be applied to the human incisor teeth, the dentated margins of which are likewise originally three or four separate tubercles.

The determination of the small teeth between the large anterior incisors and the multicuspid molars depends upon the extent of the early anchylosed intermaxillaries; the incisors being defined by their implantation in those bones, the succeeding small and simple-crowned molars must be regarded as premolars, not any of them having the development or office of a canine tooth; their analogues in the lower jaw are implanted by two roots.

The thickness of the enamel in proportion to the body of dentine is unusually great in these small Insectivora, and the sharp points of the teeth long retain their fitness for the office of cracking and crushing the hard or tough teguments of insects. The capsule supporting the enamel-pulp of the lower incisors is so large as to overlap, in the young Shrew, the growing margin of the socket, so as to encase with enamel and cement, not only the crown of the tooth, but also the contiguous part of the jaw-bone.

Daubenton first drew attention to the close adhesion of the teeth of the Shrews to the jaw-bone; and M. Duvernoy in his excellent Memoir on these small Insectivores(3), affirms that the roots

(1) See the beautiful Monograph "Sur les Musaraignes," by Prof. Duvernoy, in the Mémoires de la Société d'Histoire Naturelle de Strasbourg, 4to. 1834.

(2) See Prof. de Blainville, "Ostéographie des Insectivores, p. 55.

(3) Loc. cit., 4to. 1831.

of the teeth become anchylosed to the jaw-bone,—a reptilian character offered by the *Soricidæ* alone in the Mammalian Class.

163. *Erinaceidæ*.—In the dentition of the Tupaias (*Glisorex*) we begin to trace characters intermediate between those of the dentition of Shrews and of Hedgehogs. The dental formula of the *Glisorex tana* is: *in.* $\frac{2-2}{2-2}$, *c.* $\frac{1-1}{1-1}$, *pm.* $\frac{3-3}{3-3}$, *m.* $\frac{3-3}{3-3}$:=36 : the upper incisors are small, simple, and wide apart in the upper jaw(1) ; the anterior incisor in the lower jaw is long and procumbent, but relatively smaller than in the Shrews ; the canines are small in both jaws ; the premolars increase in size and complexity as they approach the true molars ; the first two of these are sub-equal with six cusps in the upper and five cusps in the lower jaw, the last true molar is smaller and is tricuspid.

In *Macroscelis* (Elephant-mice of the Cape) and *Gymnura* each intermaxillary bone contains three teeth, which, in the former genus are succeeded by four premolars and three true molars, with the same number of teeth in the lower jaw. In *Gymnura*(2) the first tooth which succeeds the incisors has the form and size of a canine in both upper and lower jaws ; this is followed by four premolars, the last of which in the upper jaw is large and quadri-cuspid like the first and second of the true molars, which have square crowns : the last true molar is smaller and triangular. In the lower jaw of the Gymnura the fourth premolar has a compressed tri-cuspid crown. The dental formula of *Gymnura* is : *in.* $\frac{3-3}{3-3}$, *c.* $\frac{1-1}{1-1}$, *pm.* $\frac{4-4}{4-4}$, *m.* $\frac{4-4}{4-4}$: = 42.

The dentition of our common Hedgehog (*Erinaceus europæus*) shows greater inequality in the upper and lower jaws, the formula being :—*in.* $\frac{3-3}{3-3}$, *pm.* $\frac{4-4}{2-2}$, *m.* $\frac{3-3}{3-3}$, = 36.(3) The first incisor in both upper and lower jaws is larger and longer than the rest, and is very deeply implanted in the jaw : the tooth which follows the incisors is small in both jaws, but especially so in the lower, and it does not merit a distinction from the other premolars : the last premolar is the largest in both jaws ; above, it has a quadricuspid crown with three fangs ; below, a subcompressed tricuspid crown with two fangs. The true molars decrease in size from the first to the third in both jaws : the first and second have

(1) Pl. 111, fig. 3. (2) Pl. 111. fig. 4, 4*a*, 4*b*. (3) Pl. 110, fig. 5.

subquadrate four-pointed crowns above: below they are narrower, and the anterior and inner angle is produced into a fifth cusp.

The true molars of the tropical Hedgehogs, forming the subgenera *Echinops* and *Ericulus*, are more simple, and approach the form of those in the Chrysochlore, being compressed from before backwards, with two outer cusps and one inner cusp in the upper jaw, and with one outer and two inner cusps in the lower jaw. The number of incisors is $\frac{2-2}{2-2}$ in both subgenera, which are followed by $\frac{2-2}{2-2}$ small and simple premolars; but *Ericulus*(1) has $\frac{5-5}{5-5}$ compressed tri-cuspid molars, and Echinops only $\frac{4-4}{4-4}$(2).

The largest species of the present family, called Tenrecs(3) or tail-less Hedgehogs of Madagascar, combine the simple molars of the *Ericulus* with the most formidably developed canines which are to be met with in the whole order *Insectivora*. The incisors are two in number in the upper jaw and three in the lower jaw; very small and sub-equal in both: the canines are long and large, compressed, trenchant, sharp-pointed, recurved, and single fanged; thus presenting all the typical characters of those teeth in the Carnivora; they are separated, in both jaws, by a wide space from the premolars: the first premolar above is compressed, unicuspid, with a hinder talon, and two-fanged; the second has a larger prismatic tricuspid crown, and three fangs: of the four posterior teeth, which by their antero-posterior compression may be regarded as true molars, the first three have tricuspid crowns as in the *Echinops*, and have three fangs; the fourth is smaller, is bicuspid, and has two fangs: all the lower molars have two fangs. The Tenrecs prey more upon serpents and lizards than on insects, and thus approximate the true Carnivora in diet as well as dentition.

164. *Structure and Succession.*—The teeth of the Insectivora consist of a basis of hard dentine with a thick coronal investment of enamel, and an outer covering of cement. This third substance is very recognizable in the interspaces of the coronal cusps in microscopic sections of the molars of the larger species, as the Tenrecs and Macroscelles; and is always thick where it closes the extremity of

(1) Pl 111, fig. 6.

(2) See Mr. Martin's Memoir in the Zoological Transactions, vol. II, p. 249.

(3) Pl. 110, fig. 6.

the fangs; at which part it is commonly more highly organized, traversed by medullary canals which generally present concentric walls, and thus assumes the character of true bone: in the *Soricidæ* the cement is frequently continued into the substance of the jaw itself. The small proportion of dentine in comparison with the thick layer of enamel has been already alluded to in the Shrews, yet the dentinal tubuli are, at their commencement, very little inferior in diameter to those of the human incisors; the trunks, as Retzius has observed, are unusually short, and are resolved into radiated penicilli of undulating branches, which quickly subdivide, interlace, and anastomose together near the boundary line between the dentine and enamel. In most of the Insectivora, the secondary branches of the calcigerous tubes are very conspicuous, especially in the dentine forming the fangs. The dentinal cells are rarely well defined; in the large canines of the *Centetes* they are sub-hexagonal, and about $\frac{1}{6000}$th of an inch in diameter; but diminish in size towards the periphery of the dentine.

The calcigerous tubes in the anterior incisor of the Hedgehog (*Erinaceus europæus*) present, in a longitudinal slice of the tooth, the usual disposition, vertical in the middle of the crown, diverging obliquely at the sides, and gradually becoming transverse at the base, which course they maintain throughout the long fang to its slightly enlarged extremity, where the tubuli become irregularly and strongly curved, crossing each other, and forming a net-work. In the incisor here described the end of the fang was closed by cement, through which a single vascular canal passed to the pulp-cavity: this cavity was widely open in the rest of the fang, and extended more than half-way up the enamelled crown.

The dentinal tubes at the middle of the crown ascend without any primary curvature; they dichotomize earlier and more frequently than usual, and the secondary undulations of these sub-divisions of the main-tubes are irregular. The oblique tubes at the sides of the crown form a short but strong curve at their commencement, concave towards the summit of the tooth, then proceed in a straight and parallel course obliquely upwards, and bend gently down near the enamel, forming at the boundary line a rich reticulation by their

numerous minute branches. As the tubes become situated lower down the fang the number of their large curved lateral branches becomes more remarkable; and the reticulate or moss-like disposition extends over a greater proportion of the dentine. Numerous minute opake cells form the boundary line between the dentine and the cement which covers the fang. The minute transverse tubuli of the cement are present in the thinner part, where there are no Purkinjian cells; these cells are developed in great number, and present the usual irregular angular figure in the mass of cement closing the end of the fang.

The enamel fibres are disposed with a very slight curve, almost transversely to the plane of that substance, inclining towards the crown; they are crossed by other lines nearly parallel with the same plane, extending from its inner surface upwards and outwards; these lines are equi-distant, parallel with each other, with intervals equal to the breadth of two enamel fibres; they indicate successive and regular periods in the formation of the enamel; and, where they crop out upon the outer surface of the enamel, they form the fine transverse striæ which have been often noticed on that substance in larger teeth. I counted sixteen of these longitudinal lines in a section of the enamel, at the middle of the side of the crown of the incisor examined, where the enamel was $\frac{1}{60}$th of an inch in thickness.

Not any of the main calcigerous tubes are straight in the molars of the Hedgehog; those which ascend from the summit of the pulp-cavity to the middle of the grinding surface of the crown, rise with a wavy curve, which becomes stronger in the tubes that diverge to the angles of the crown. At the sides of the crown the tubes curve outwards, with the concavity turned towards the grinding surface, and then bend towards the enamel in the opposite direction; the latter curvature being lost in the transverse tubuli of the fangs, which have a single curvature convex towards the crown; near the end of the fang the tubuli bend down with irregular flexuosities, and here they present very conspicuously that rich ramification which Retzius has remarked: it is also beautifully seen in the tubuli of the dentine at the base of the crown between the origins of the fangs. The

tubes in the crown retain their almost parallel course and their character of undivided trunks, until they attain the usual proximity to the enamel.

This substance offers no noticeable peculiarity in the molar teeth. The fangs are invested with a layer of cement, which is sufficiently thick at their extremities and at the interspace of their origins to show the calcigerous cells; these cells present an irregular elongated form, with angular projections continued into the radiated tubes. The cement is likewise traversed by transverse minute parallel tubuli of the size of those in the dentine, which have a diameter of $\frac{1}{12,000}$th of an inch.

The deciduous teeth of the Moles and Shrews are uterine, *i.e.* are developed and disappear before birth; they are extremely small, and all of the most simple form. In the fœtal *Sorex araneus* calcification of the papillary exposed pulps of the teeth which are succeeded by the first and second premolars proceeds to a very slight extent, and these microscopic rudiments appear to be absorbed rather than shed; the deciduous incisors are further advanced before their displacement, and present the form of equal-sized dentinal spicula, tipped with enamel, attached by the opposite end to the gum, and not exceeding $\frac{1}{40}$th of an inch in length; the number of the uterine series of teeth is $\frac{4-4}{3-3}$.

In a fœtal Hedgehog, two inches and a half in length, the alveolar border of the upper jaw forms a smooth, convex ridge on each side, and those of the lower jaw are equally entire and edentulous, but less prominent; both are covered by a thick epithelium; the margin of the gum easily opens longitudinally, as if the dentiparous groove had been but recently closed, and the matrices of five deciduous teeth on each side are brought into view; the four first, representing the three incisors and the canine, are very minute and simple, the fifth tooth is quadrituberculate, and $\frac{1}{20}$th of an inch in breadth: calcification has commenced in the summits of the crown of this deciduous tooth, which is succeeded by permanent premolars of a more simple form. M. Duvernoy alludes to M. Laurillard's examination of the deciduous teeth of the Hedgehog, and states that he has himself determined their existence in the Tenrecs (*Centetes*), in which they are long

retained. He suspects that the Shrews have but one dentition: the minute size and rudimental state of the transitory teeth, and their disappearance before birth having caused them to escape the observation of the accomplished continuator of Cuvier's "Leçons d'Anatomie Comparée."(1)

CHAPTER VIII.

TEETH OF CHEIROPTERA.

165. The dental system presents more constancy in this than in the preceding Order, and the different kinds of teeth are more easily and unequivocally determinable.

The canines are always present in both jaws, of the normal form and with slightly variable proportions. The molar series never exceeds $\frac{6-6}{6-6}$, and is divisible into premolars and true molars, the latter presenting two types of grinding surface; in one of these the crowns are bristled with sharp points, as in the foregoing order, and this type characterizes the great bulk of the *Cheiroptera*, which may be called true Bats or volant Insectivores; the molars of the second type have flat crowns and characterize the large frugivorous Bats which constitute the aberrant genus *Pteropus*, and conduct towards the Quadrumanous Order.

The incisors are the most variable teeth in the *Cheiroptera;*

(1) See the posthumous edition of the Leçons, tom. IV, p. 242, where M. Duvernoy adds to the text: "J'ai lieu de penser que tous les *Insectivores* n'ont pas cette succession de dents. Je l'ai constatée, à la vérité, dans les *Tenrecs* qui perdent leurs dents fort tard, au contraire de certains Rongeurs les ayant trouvées encore, en partie, chez un individu dont la taille était à peu près celle de l'adulte. M. Laurillard l'a vue dans les *Chauve-souris* et les *Hérissons*. Mais dans les *Musaraignes* je suis porté à croire qu'il n'y a qu'une seule dentition." M. de Blainville goes further, and denies the existence of a deciduous series of teeth in the Mole, Hedgehog and Tenrec, (Ostéographie des Insectivores, p. 63); as, indeed, he likewise did with regard to the Bats, (Compte Rendu de l'Académie des Sciences, Sept. 1837, p. 420.) M. Rousseau, in his excellent "Mémoire sur la Chauve-souris commune," read to the Academy of Sciences, March 19th, 1838, described the deciduous dentition of that Cheiropter with all the requisite detail, and its existence is admitted by M. de Blainville in the "Ostéographie des Chéiroptères," published in June 1840. Similar proofs will be found, if nature be rightly consulted, that the other Insectivora, also, form no exception to the rule.

they may be entirely wanting, or be present in the numbers of 1—1 to 2—2 in the upper, and from 1—1 to 3—3 in the lower jaw; they are always very small, and in the upper jaw commonly unequal and separated by a wide median vacancy. Taking the common simple-nosed Bat(1) (*Vespertilio-murinus*) as a type of the Insectivorous group, we find its dental formula to be :—

$$in.\ \frac{2-2}{3-3};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{3-3}{3-3};\ m.\ \frac{3-3}{3-3}: = 38.$$

The first upper incisor (Pl. 112. fig. 1, *i*.) has a slightly expanded tri-dentate crown, separated by a basal ridge of enamel from a long, slender, slightly curved, fusiform fang; the second upper incisor has a sub-bifid crown. The three lower incisors (*i*) are tri-dentate, and the crown of the outermost has an additional tubercle. The crown of both upper and lower canines (*c c*) is sharp-pointed, and its inner surface is indented by two grooves; a basal ridge divides it from the long conical fang. The first premolar is very small, both above and below, and has a sharp-pointed simple crown with a basal ridge, and a single fang; the second premolar is still smaller: both are soon shed. The third premolar, as it may be called from its shape, though it has no deciduous predecessor, has a triangular pointed crown, with a basal ridge, and is implanted above by three fangs; in the lower jaw the crown is narrower, and is supported by two fangs (*p p*). The first and second upper true molars (*m*), have each a six-pointed crown supported by three fangs: the third molar is compressed from before backwards; its crown has three points or tubercles, and is supported by three fangs. The first and second true molars of the lower jaw have quinque-cuspid crowns, two of the largest points being on the outer and three small ones on the inner side, the crown is supported by two fangs; the last molar is the smallest, and is tri-cuspid. A well-developed ridge of enamel surrounds the base of the crown of each molar tooth both above and below.

(1) The insectivorous Cheiroptera are divisible into groups according to the modifications of the tactile dermal appendages of the nose; which may be wanting, as in the *Vespertilio murinus* and other *Leionycteridæ;* or be present in the form of a simple leaf, as in the Vampire-bat and other *Phyllonycteridæ;* or be developed into more complex forms, as in the Horse-shoe Bat and other *Lophonycteridæ* of Prof. de Blainville.

All the teeth of the lower jaw touch each other; in the upper jaw the incisors are separated by a wide interspace from the canine.

The dentition of the Long-eared Bat (*Plecotus auritus*) differs from the foregoing chiefly by the absence of one of the small premolars on each side of the upper jaw. In the Horse-shoe Bats (*Rhinolophus*, Pl. 112, fig. 5), the Barbastelles (*Barbastellus*), the Noctule (*Vespertilio Noctula*, Pl. 112, fig, 2), and the Pipistrelle (*Vespertilio pipistrellus*), the small premolars reduced to one on each side of both jaws, are extremely minute, and seldom visible from without. In the Serotine (*Vespertilio serotinus*, Pl. 112, fig. 3) the rudimental premolar is entirely wanting in the upper jaw, but remains in the lower; and this condition of the molar series also characterises the genera *Rhinopoma*, *Noctilio*, and many species of *Molossus* and *Nycticeus*. In the genus *Nycteris* (Pl. 112, fig. 6 and 7) the small premolars are absent in both jaws; and the molar series is reduced to the large premolar and three true molars, which are present on both sides of both jaws, in all the foregoing Bats.

The Bats with ciliated tongues, (*Glossophaga*, Pl. 112, fig. 4, 4[1]), have three premolars and three true molars on each side of both jaws, rather small and slender canines, and two minute incisors on each side of both jaws.

The following are examples of the variation in the number of incisive teeth: $\frac{0-0}{2-2}$ in *Taphozous perforatus*, Geoff. and the species of *Megaderma*: $\frac{1-1}{1-1}$ in *Molossus* and *Myoptera*: $\frac{1-1}{2-2}$ in *Nyctinoma*, *Rhinopoma*, *Rhinolophus* and *Dysopus*: $\frac{1-1}{3-3}$ in *Vespertilio lasiurus* and *V. paradoxus*: $\frac{2-2}{1-1}$ in *Noctilio*: $\frac{2-2}{2-2}$ in *Phyllostoma*, *Glossophaga* and *Mormoops*: $\frac{2-2}{3-3}$ in *Plecotus*, *Nycteris* (Pl. 112, fig. 6[11]), and in most species of the genus *Vespertilio*, as restricted by modern Naturalists.

The molar teeth have a more trenchant character and fewer points in the Leaf-nosed Bats (*Phyllostoma*) of South America, which are commonly called Vampyres; their canines also, which are remarkably long and strong, sharp-pointed and vertical in position, indicate a higher kind of animal diet than that of the ordinary insectivorous Bats. The premolar teeth are better developed than usual; in the *Phyllostoma hastatum* the first upper premolar has a strong, thick pointed crown,

with an internal and posterior talon; the second premolar is larger than the first, with a triedral crown, and an anterior and posterior talon at the base of the long, sharp middle cusp. The first and second true molars have sub-compressed quinque-cuspid crowns; the third molar is compressed from before backwards, and has a tri-cuspid crown. The first and second premolars below are simple and larger than those above, especially the first; the first and second true molars have two large external and three small internal cusps, and the last molar differs only by a slight inferiority of size.

The dentition of the true blood-sucking Vampire Bats, which form the genus *Desmodus* (Pl. 112, fig. 9) deviates, as might be anticipated, in a remarkable degree from that of the Insectivorous Bats: the crushing instruments required for the food of those species are not needed; and the true molars, with their bristled crowns, are entirely absent in the *Desmodus*. The teeth at the fore-part of the mouth are especially developed and fashioned for the infliction of a deep and clean triangular puncture, like that made by a leech. The incisors (*i*) are two in number above, closely approximated, one in each intermaxillary bone, with a very large, compressed, curved, and sharp-pointed crown, implanted by a strong fang which extends into the maxillary bone. The upper canines have similar large, lancet-shaped crowns, and their bases touch those of the incisors. In the lower jaw the incisors are two in number on each side, much smaller than the upper pair, and with bilobed crowns. The lower canines are nearly equal in size to those above. The molar series is reduced above to two very small teeth, each with a simple compressed conical crown, implanted by a single fang. The first two molars below resemble those above; but they are followed by a third which has a larger compressed and bilobed crown, implanted by two fangs; this tooth corresponds with the last premolar in the more normal genera of Insectivorous Bats. The dental formula of the true Vampire-bat (*Desmodus*) is thus reduced to:—

$$in.\ \frac{1-1}{2-2};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{2-2}{3-3}:\ =\ 20.(1)$$

The opposite extreme which the aberrant varieties of the

(1) The intestinal canal, like the dentition, is modified in conformity with the easily assimilated food, viz. the blood of living animals, on which the true Vampires habitually

Cheiropterous dentition attain, is manifested in the great frugivorous Bats, which have been sometimes, but erroneously, called Vampires; but which have never been met with in South America, the peculiar country of the true blood-sucking Bats.

The frugivorous species, sometimes called "flying-foxes" and by the French "Rousettes," include the largest animals of the order *Cheiroptera*, and constitute the genus *Pteropus*; their dental formula is:

$$in.\ \frac{2-2}{2-2};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{2-2}{3-3};\ m\ \frac{3-3}{3-3}: = 34.$$ (Pl. 112. fig. 10.)

The upper incisors are small, equal, contiguous, ranged in a semi-circle, with broad, sub-incisive crowns; the inferior ones are obtuse, the middle pair very small in some species; the number, shape, and disposition of the incisors manifest an approximation to the Quadrumanous type of dentition.(1) The upper canines are long, rather slender and sharp-pointed, but are sub-tetragonal, the four facets being separated by strong longitudinal ridges; a transverse ridge divides the inner side of the base of the crown from the fang; the lower canines are smaller, with an anterior and posterior longitudinal ridge, and an internal transverse basal ridge. A wide space separates the upper incisors from the canines; they almost touch below. The first premolar above is extremely minute, and sometimes wanting, as in *Pteropus Whitei* and the species figured (fig. 10); in some species it is situated in the middle of the diastema between the canine and second premolar, in other species it is close to the canine. In the lower jaw the first premolar is larger and more

subsist; it extends in almost a straight line from the stomach to the vent. The dentition of the so called "Vampire," minutely described by M. de Blainville in his "Ostéographie des Chéiroptères," p. 32, is that of an insectivorous species of *Phyllostoma*, in which the intestine is twice the length of the body.

The complex stomach of a Pteropus is described as that of a Vampyre Bat in the "Lectures of Comparative Anatomy," by Sir Everard Home, who thereupon infers that "the Vampyre-bat lives on the sweetest of vegetables; and all the stories related with so much confidence of its living on blood, and coming in the night to destroy people while asleep, are entirely fabulous," p. 160. The blood-thirsty habits of the true Vampires have been observed by more than one scientific traveller in South America. Dr. Spix calls one of these bats, which he discovered in Brazil, "*Sanguisuga crudelissima*"; and Mr. Darwin has recorded the attack of another species which fastened upon the withers of his horse, during a nocturnal bivouac in Chile. See "Voyages of the Adventure and Beagle," vol. III, p. 25.

(1) In some species of Roussette, as the *Pteropus Peronii*, only a single pair of incisors has been observed in both upper and lower jaws. See M. de Blainville *loc. cit.* p. 38.

constant, but always much less than the second premolar, and with a simple obtuse crown. The second premolar is the largest; the succeeding teeth diminish in size to the last true molar: the crown of each of these teeth is impressed by a longitudinal excavation, the outer border of which is produced into a long conical cusp, which in the second lower premolar resembles the crown of the canine, especially in certain African Roussettes, as *Pt. Whitei*, Bennett: this pointed lobe gradually subsides in the following teeth; it is a little higher than the inner boundary of the triturating depressed surface in the penultimate molars, is almost obsolete in the small posterior molar above, and quite lost in the still smaller one below. In *Pt. Whitei* and *Pt. macrocephalus* the last small molar would seem to be wanting in both jaws, according to Messrs. Ogilby and Bennett.(1)

166. *Structure and Succession.*—In the normal or Insectivorous Bats the teeth so closely resemble those of the small terrestrial Insectivores in composition and structure, as to render a particular description of them almost superfluous in the present work.

When the fangs of the long and slender incisors and canines are completed, the pulp-cavity contracts as it approaches the apex of the fang to a linear fissure, and is finally closed by the external cement. The calcigerous tubes descend almost vertically from the closed end to the lowest part of the dentine, in a direction diametrically opposite to that of the tubes which rise from the upper end of the pulp-cavity to the summit of the crown. Through a great extent of the middle part of the tooth the tubuli, forming a slight bend as they leave the pulp-cavity, pass transversely to the outer surface. In the crown the tubuli gradually bend upwards until they acquire a vertical direction at the middle; at the opposite termination of the fang, the tubuli gradually bend downwards from the transverse to the vertical direction. The primary curve of the tubuli at the base of the crown presents its concavity towards the fang; that of the tubuli near the end of the fang is concave towards the crown: in both, the concavity is towards the centre of the tooth. The short trunks of the dentinal tubes are $\frac{1}{12,000}$th of an inch thick: in the fang they seem to be grouped in fasciculi. The dentinal cells are well defined near the periphery of the crown; they present a diameter of $\frac{1}{5000}$th

(1) Zool. Trans. vol. II, p. 34.

of an inch. The fibrous structure of the enamel is very conspicuous; at the side of the crown the fibres make a short curve on leaving the dentine concave towards the grinding surface, and then make a longer bend in the opposite direction. This structure may be clearly seen in the canines of the *Rhinolophus ferrum-equinum*.

The microscopic structure of the teeth of the frugivorous Bats appears worthy of a fuller notice. I have examined it more particularly in the canine and molar teeth of the Great Roussette (*Pteropus edulis*).(1) The crown of the canine has an entire investment of enamel; the fang is covered by clear cement, thickest at its extremity but without radiated cells. The tubuli of the dentine are $\frac{1}{10,000}$th of an inch in diameter at their origins, and are there about the same distance apart; they slightly diverge from one another as they proceed from the summit of the pulp-cavity, in the usual radiated direction; the primary curves of the tubes which proceed to the sides of the crown being gently concave towards the summit in the greater part of their course, with both extremities slightly bent in the opposite directions; at the beginning of the fang they pass outwards, and gradually acquire a curve convex towards the crown; lower down they are more irregularly bent, and near the apex of the fang, again present the curve concave towards the crown. The tubuli in the crown rarely dichotomize, and accordingly by their divergence leave wider interspaces of the clear basal substance, which receive the small lateral branches that are sent off from both sides of the tube, subalternately, throughout its course. The tubes diminish in size, like arteries after division, and near the enamel are resolved into fine ramuli, which anastomose or dilate into minute opake cells. The secondary undulations are extremely faint in the crown; they become stronger as the tubes descend into the fang, crossing each other and producing, with the side-branches, a rich arborescent, and interlaced appearance, which becomes more complex as the tubes approach their termination near the cement, into which they push many terminal ramuli: in this clear substance they dilate into minute opake cells; but, as has been already observed, there are no normal radiated Purkingian cells in the cement of the canine tooth.

The tubuli of the dentine of the crown of the molar tooth differ

(1) Pl. 113, 113A.

from those in the fang in the minor degree of secondary undulation; being, in fact, much straighter than the coronal tubuli of the human tooth, which they rather exceed in size at their origin: they diminish more rapidly in size as they approach the enamel, and give off more numerous and conspicuous lateral branches;(1) presenting a stellate appearance in transverse or oblique section. The median tubuli rise vertically to the summit of the crown, the lateral ones diverge with a graceful curve convex towards the summit; at the neck of the tooth they rather abruptly take the opposite curvature, still proceeding transversely outwards; but gradually incline downwards as they approach the ends of the fangs.(2) In the thick cement at this part of the molar teeth a few of the cells assume the angular form, and approach the size of the ordinary Purkingian cells; in the rest of the fang the clear cement is studded with more minute and simple opake cells.

The boundaries of the dentinal cells,(3) which were scarcely discernable in the canine tooth, are very conspicuous in the molars, especially near the periphery of the crown. They are of unusually large size in proportion to the whole tooth, being absolutely larger than the dentinal cells of the human tooth, and their interspaces dilate here and there into semi-opake streaks. In vertical sections of the molar teeth the part of the boundary of the cells next the periphery of the crown was most conspicuous, forming a semicircular line, clear or opake, according to the focus, convex towards the periphery, arching across from ten to twelve of the dentinal tubuli: the whole producing the appearance of an imbricated structure. In transverse sections the whole contour of the dentinal cells is visible:(4) they are irregular in form and size as seen in a section exposing them on the same plane, where they are probably cut through at different levels, some of the largest present an irregular hexagonal figure, and a diameter of $\frac{1}{3000}$th of an inch.

The enamel of the teeth of the Pteropus is unusually opake,

(1) Pl. 113, fig. 2, *d*.
(2) Ib. fig. 1.
(3) Ib. fig. 1, and Pl. 113 *a*, fig. 2, d^1, d^1,.
(4) Pl. 113 *a*, fig. 1.

dark-coloured, and its fibrous structure ill defined.(1) In the canine the fibres are $\frac{1}{6000}$th inch in diameter; they are directed at the sides of the crown, almost perpendicularly to the surface of the dentine, with a slight convex bend towards the summit of the tooth; the layers of growth proceed very obliquely from without, downwards and inwards; I counted eleven layers in a transverse section of the enamel at the middle of the crown of the canine.

The succession of the teeth in the order of Volant Mammals has received the most satisfactory elucidation from the careful and minute researches of M. Rousseau on the *Vespertilio murinus*.(2) The deciduous teeth make their appearance above the gum in Bats, as in Shrews, before birth; but they attain a more completely developed state, and are retained until a short time after birth, when they are shed. The series consists of *in.* $\frac{2-2}{3-3}$, *c.* $\frac{1-1}{1-1}$, *m.* $\frac{2-2}{2-2}$, $=22$: magnified views of the deciduous teeth *in situ* of the common Bat are given in Pl. 112, fig. $1^{\cdot\cdot}$, and of both the deciduous and permanent teeth detached on the right hand of figs. 1 and $1^{\cdot\cdot}$. The deciduous incisors (*i*) have slightly expanded tridentate crowns; the anterior and longest does not exceed $\frac{1}{10}$th of an inch in length: the lower deciduous incisors are shorter, but of a similar form. The canines ($c^{\cdot\cdot}$) very slightly exceed the incisors in length, but are a little more deeply implanted, and the middle cusp of the tridentate crown is longer and more conical. The upper deciduous molars ($p^{\cdot}$) resemble the incisors, but are broader in proportion to their length, which scarcely equals one line; the lower deciduous molars are more slender. No tooth has been observed to precede the third tooth of the permanent molar series, (*p*) which, by its shape should be regarded as a premolar: if this tooth be classed, from the circumstance of its not displacing any predecessor, amongst the true molars, these will then be four in number on each side of both jaws, as in the *Marsupialia*.

In the fœtus of a species of *Pteropus* so far advanced as to

(1) Pl. 113, fig. 2, *e*.

(2) "Mémoire zoologique et anatomique sur La Chauve-souris commun, dite 'Murin,'" Magazin de Zoologie, 1839.

have acquired a slight covering of hair, and of which the head was an inch and a half in length, I found the whole of the deciduous series in place, in number as follows:

$$\text{Incisors } \frac{2-2}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{2-2}{2-2} = 20.$$

The representatives of the molars were not quite one line in length, slender, and with simple and very slightly enlarged crowns; the canines were larger and more curved.

CHAPTER IX.

TEETH OF QUADRUMANA.

In entering upon the study of these organs in the extensive group of mixed-feeding placental Quadrupeds, associated together by the common character of the opposable thumb on the hind-foot, and to which Cuvier has applied the name *Quadrumana*, (though this name be strictly applicable only to the old-world *Simiæ* of Linnæus), we are met at the outset by two very singular and anomalous conditions of the dental system in the genera *Galeopithecus* and *Cheiromys*.

167.—The Colugos (*Galeopithecus*) resemble the Bats in the great expanse of their parachute, formed by the fold of integument extending on each side from the fore to the hind extremity; but they appertain by the essential characters of their organisation to the *Lemuridæ*: the dental formula of the genus (Pl. 114, fig. 1, 1*a*, 1*b*.) is:

$$\text{Incisors } \frac{2-2}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{2-2}{2-2};\ \text{molars } \frac{5-5}{3-3}: = 34.$$

The two anterior incisors of the upper jaw are separated by a wide interspace: in the Philippine Colugo they are very small, with simple sub-bilobed crowns; but, in the common Colugo (*Lemur volans*, Linn. *Galeopithecus Temminckii*, Wat.) their crown is an expanded plate with three or four tubercles; the second upper incisor, which is unquestionably supported by the

intermaxillary bone, presents the peculiarity of an insertion by two fangs in both species of *Galeopithecus;* its crown is a compressed triangular plate, with a small talon at the anterior and posterior part of the base in *Gal. Philippinensis*, and with two anterior and three posterior dentations in *Gal. Temminckii.* The upper canine (*c*) very closely resembles the second incisor, and is also implanted by two fangs. The first upper premolar (*p*) has a trihedral crown, more simple and compressed in *Gal. Temminckii* than in *Gal. Philippinensis*, in which the crown supports two triangular prisms, with one side turned outwards and one angle inwards; the crown of the second premolar has, besides the two prisms, a pointed talon at the base of the internal space between the prisms. In the true molars (*m*) the internal talon is relatively larger, and when the prisms are worn down to its level they present a broad triturating surface.

In the lower jaw the crowns of the first two incisors (*i*) present the form of a comb, and are in this respect unique in the class *Mammalia:* one is figured of the natural size in Pl. 115, fig. 1, and magnified at fig. 1*g*. This singular form of tooth is produced by the deeper extension of the marginal notches on the crown, analogous to those on the edge of the new-formed human incisor; the notches being also more numerous as well as deeper: each of these broad pectinated teeth is implanted by a single conical fang.(1) The third incisor, viewed through the analogy of the Lemurs seems to be a canine, but in nature its crown is in advance of the last intermaxillary tooth above: the margin of the crown is broad, horizontal, and is indented by shallow notches which are four in number in the Philippine Colugo; in both species this tooth is supported by a single fang. The lower canine (*c''*) nearly resembles the upper canine, has two fangs, but has a rather shorter crown, which passes before that of the upper canine when the mouth is shut: its oblique margins are dentated in the *Galeopithecus Temminckii*, and entire in *Gal. Philippensis.* The first premolar resembles the canine, but has a thicker and a lower

(1) The Colugos have a large cœcum, and are said to feed on the leaves of the Nanka or Jack-fruit: they may also derive part of their diet from small birds or insects; but the mode in which the crowns of the molar teeth are abraded by mastication indicates the preponderance of vegetable food. The pectinated lower incisors may serve to trim the fine fur with which they are clothed.

crown: the second premolar, like the three true molars, has a broad, oblong quinque-cuspid crown, four cusps being in two transverse pairs, and the fifth at the anterior and internal angle of the tooth.

In the broad pectinated incisors of the Galeopithecus the pulp-cavity divides at the base of the crown into as many canals as there are divisions of the crown, one being continued up the centre of each to within a short distance of its apical extremity. The calcigerous tubes which radiate from these canals have a diameter at their origin of $\frac{1}{15,000}$th of an inch: they quickly divide and subdivide dichotomously with rather large and irregular secondary undulations, sending off many fine branches and resolving themselves into numerous smaller ramifications which interlace irregularly near the enamel. The tubuli in the body of the tooth have longer trunks, but present a very similar character: the section figured in Pl. 115, being taken a little on one side of the central pulp-cavity shows the diverging tubuli cut almost transversely across in the middle of the body of the tooth, and the longitudinal course of the wavy ramifying tubes at the margins of the section. The medullary canal or branch of the pulp-cavity is shown in some of the divisions of the crown, at *m*. Each division of the crown has its proper investment of enamel, which substance is continued for a short distance upon the common base.

The deciduous teeth appear not to cut the gum before birth, as they do in the true Bats. In a fœtus of *Galeopithecus Temminckii*, with a head one inch and a half in length, I found the calcification of the first incisor just commenced in the closed alveolus; the second incisor and the rest of the deciduous series being represented by the vascular uncalcified matrices. The upper milk teeth (Pl. 114, fig. 1*b*) consist of two incisors, a canine, and two molars; which latter are displaced and succeeded by the two premolars. The deciduous teeth are six in number in the lower jaw; the incisors being pectinated, but much smaller than their successors. The true molars are developed and in place before the deciduous teeth are shed.

168. *Cheiromys*.—In this genus of Lemurine animals, as in *Desmodus* amongst the Bats, and *Sorex* amongst the Insectivores,

the dentition is modified in analogical conformity with the Rodent type, to which, in the present instance, it makes a very close approximation, the canines being absent and a wide vacancy separating the single pair of large curved scalpriform incisors in each jaw from the short series of molars.(1)

The upper incisors are compressed, presenting a narrow oval transverse section, with the long diameter from before backwards; they are curved in the segment of a circle, and deeply implanted; the short exserted crowns touch one another; their simple, widely excavated fangs diverging as they penetrate the substance of the jaw. The short crowns project obliquely forwards and do not extend vertically downwards as in the true Rodentia.

The lower incisors are more compressed, and of greater breadth from before backwards, than the upper ones; they are more curved than in the Rodentia, describing a semicircle, two thirds of which are lodged in the socket, which extends backwards beyond the last molar tooth to the base of the coronoid. The anterior edge of the oblique cutting surface does not rest against a posterior ridge of the surface of the tooth above, whence M. de Blainville infers that these large scalpriform teeth were put to a different use from that to which the same teeth of the Rodents are habitually applied. He conjectures, that they served the Cheiromys rather as a pair of cutting pincers to remove the bark and perhaps the wood of trees in search of larvæ or insects, which, however, the smooth, flat crowns of the molars would not indicate to have been the staple food of the Cheiromys. The most important character by which the incisors of this anomalous Lemur differ from those of the Rodentia is the entire investment of enamel, which is, however, thicker upon the front than upon the back part of the tooth.

The molar teeth are four on each side of the upper jaw,

(1) Pl. 114, fig. 2. M. de Blainville, who first pointed out the affinity of the *Cheiromys* to the Quadrumana, has made the observation that the edentulous margin of the jaw between the incisors and molars is sharp, as if it had lodged some small teeth that had been shed; whilst in the true Rodentia it is always broadly rounded off and smooth.

and three on each side of the lower jaw, implanted vertically and in parallel lines.(1) The molars are of simple structure, with a continuous outer coat of enamel, and a flat sub-elliptic grinding surface: the upper ones are of unequal size, the first being the smallest, and the second the largest: in the lower jaw the inequality is less, and the last molar is the least. The first and last molars above have but one root: the second and third have each three roots. The first lower molar has two roots, the second and third have each a single root.

169. *Lemuridæ.*—The Indris (*Lichanotus*, Illiger) are small tail-less Lemurs, which, when full-grown, have but two incisors in the lower jaw, of larger size than in other Lemurs, especially in the species (*Lich. Diadema*) on which the sub-genus *Propithecus* has been founded. The dental formula in the *Lichanotus Indri* and *Lich. laniger*, is :—

$$\text{Incisors } \frac{2-2}{1-1};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{2-2}{2-2};\ \text{molars } \frac{3-3}{3-3}:\ = 30.$$

In the common Indri the upper incisors, especially the anterior one, are proportionally larger than in the higher *Lemuridæ*, in the woolly Indri (Pl. 114, fig. 6) they are very small. In both species the canine has a trihedral straight compressed conical crown; the premolars have shorter compressed crowns: the first and second molars have square, four-lobed crowns; the last molar is triangular and of smaller size. The lower canine (*c*) is directed obliquely forwards parallel with the incisor, which it closely resembles in the *Lichanotus laniger;* in the common Indri it is longer and larger. The premolar and molar teeth resemble those above, but the last supports five tubercles.

The dentition of the Malmags or Spectre-Lemurs (*Tarsius*) offers a more insectivorous character;(2) the formula is :—

$$\text{Incisors } \frac{2-2}{1-1};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{3-3}{3-3}:\ = 34.$$

The first upper incisor, as in the Shrews, is longer than the canine. The inferior canines (*c'*) are characterised, as in other *Lemuridæ*,

(1) In the general characters of the teeth of the Rodentia, p. 400, the convergence of the molar series is noticed.

(2) Pl. 114, fig. 3.

by their crowns passing in front of the upper canines; but they here present more of the laniariform shape and proportions and have, therefore, been recognised as canines by those Comparative Anatomists, M. F. Cuvier for instance, who have regarded the analogous teeth as incisors in the Indris and the higher *Lemuridæ*. The premolars in the *Tarsii* are conical, and slightly increase in size as they approach the true molars: these have the lobes of the crown, especially the outer ones, produced into sharp points.

The Galagos (*Otolicnus*) resemble the Malmags in the insectivorous character of the crowns of the true molar teeth, but have an additional pair of incisors and smaller canines in the lower jaw. The dental formula in these, as in the Slow Lemurs (*Stenops*) is :—

$$\text{Incisors } \frac{2-2}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{3-3}{3-3} : = 36.$$

In the *Stenops tardigradus*(1) the first upper incisor is larger than the second, as in the genus *Tarsius*.

The true Lemurs or Makis (*Lemur*, Geoff.) have the same number and kind of teeth as the Slow Lemurs. The inferior canines, Pl. 114, (fig. 5, c'), first recognized as such by Geoffroy, are compressed and procumbent like the incisors, but are a little larger. In the upper jaw the two incisors are small and vertical, with short, expanded crowns: the two on the right side are separated by a wide space from the two on the left. The canine (*c*) is long, curved, compressed, sharp-edged and pointed. The three premolars have the outer part of the crown prolonged into a compressed pointed lobe, whilst the inner part forms a tubercle, which is largest in the second and third. In the true molars the inner division of the crown is so increased as to give it a quadrate form: the outer division being divided into two pointed lobes. The first of the true molars is the largest in both jaws.

The first premolar above is implanted by two connate fangs: in the second and third they are distinct, and a third inner fang is developed to support the inner lobe of the crown. Each upper molar is supported by three short and thick fangs. In the lower

(1) Ib. fig. 4.

jaw both premolars and molars are severally implanted by two fangs; the canines and incisors, in both jaws have each a single fang, according to the normal mode of implantation of these teeth, which is henceforth not departed from in the Mammalian Class.

The deciduous series of teeth in the genus Lemur is:—

$$\text{Incisors } \frac{2-2}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{3-3}{3-3}:= 24.$$

170. *Platyrhines.*—All the Quadrumana of America are distinguished from the Apes and Monkeys of the old world by certain well-marked external characters: of these, the position of the nostrils at the sides of the broad nose, whence their collective name, is the most conspicuous; but they have a more important dental distinction in the superior number of the premolars, which are $\frac{3-3}{3-3}$, instead of $\frac{2-2}{2-2}$; whereby the American Monkeys manifest their closer affinity to the Lemurs, and their inferior position in the zoological scale.

The small and delicate platyrhine Monkeys commonly known in this country by the name of 'Marmosets,' and forming the genera *Hapale* and *Midas*, have but two true molar teeth on each side of both jaws, their dental formula (Pl. 114, fig. 8.) being:—

$$\text{Incisors } \frac{2-2}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{2-2}{2-2}: = 32.$$

In the Jacchus Marmoset (*Hapale Jacchus*) the crowns of the upper incisors are broad and trenchant, the first being the largest; but the lower incisors continue, as in the Lemurs, to be long and pointed like the canines, to which they are but little inferior in size. The upper canines present a character which is peculiar among Mammalia to the Quadrumana, viz: a longitudinal groove along the fore-part of the crown. The shape of the crowns of the premolars is shewn in fig. 8, *p*: they are each implanted by a single fang. The first true molar above has three roots, that below has two; the second molar has a single root in both the upper and lower jaws. A vacant interspace separates the upper canine from the incisors; the teeth of the lower jaw form a continuous series, as in Man.

The lemurine character of the long, narrow, inferior incisors continues to be manifested by the Sakis (*Pithecia*, Illig.), which, like the larger species of Platyrhines called Howlers, Capuchins, and Spider-Monkeys, have the normal number of true molar teeth in the Quadrumanous Order, their dental formula being:—

Incisors $\frac{2-2}{2-2}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{3-3}{3-3}$: = 36.

The Capuchin Monkeys, (*Cebus*, Pl. 114, fig. 9) have the four lower incisors (*i*) with broad, thick, wedge-shaped trenchant crowns; a form which these teeth retain with slight modifications throughout the rest of the Quadrumanous Order. In the Howlers, (*Mycetes*), the incisive margin of the lateral lower incisors is more produced; these are larger than the middle incisors, the proportions of the upper incisors are reversed. The canines (*c*) are strong and well-developed in both jaws; those above being marked by the deep anterior groove; there is also a second longitudinal groove on the inner surface of the crown near its posterior margin. The canines are relatively stronger than in the Marmosets; especially in the male Capuchins. The upper premolars (*p*) have their crown divided into two trihedral pointed cusps on the same transverse line, the outer one the longest and largest: the transverse diameter of these teeth exceeds their antero-posterior diameter. The first premolar below differs in form from the rest, a short trenchant ridge being continued forwards from the outer cusp, and opposing itself to the inner surface of the canine tooth above: the two cusps of the second and third premolars are less unequal than those above, and the inner one is the most produced. The true molars (*m*) decrease in size from the first to the third, which is tricuspid below, the rest being quadri-cuspid. In the Spider-monkeys (*Ateles*) the second true molar below is larger than the first; and in the Howlers (*Mycetes*) both the second and third lower molars exceed the first in size, and the middle one is the largest above, (Pl. 114, fig. 10). In the attrition of the crowns by mastication, the inner tubercles of the upper molars, and the outer ones of the lower molars, are the first to yield; but the sub-trenchant

first premolar below continues longest prominent, and resembles a small canine.(1)

The premolars are implanted by two connate fangs, those above becoming separate, and diverging near their extremities. The first and second true molars above have three fangs; the last has two in *Mycetes*, and one in *Cebus*. Each of the lower true molars is implanted, in *Mycetes*, by two fangs; but the last has only one fang in *Cebus*.

All the platyrhine Monkeys have four more teeth in their first dentition than the catarhine or old-world Quadrumanes possess; the deciduous formula being:—

$$\text{Incisors } \frac{2-2}{2-2}; \text{ canines } \frac{1-1}{1-1}; \text{ molars } \frac{3-3}{3-3}: = 24.$$

171. *Catarhines.*—In this division of the Order the first or deciduous dentition consists, as in Man, of:—

$$\text{Incisors } \frac{2-2}{2-2}; \text{ canines } \frac{1-1}{1-1}; \text{ molars } \frac{2-2}{2-2}: = 20.$$

The milk molars are displaced and succeeded vertically by the bicuspid premolars, and are followed(2) horizontally by three true molars on each side of both upper and lower jaws; the permanent formula in all the old-world Quadrumanes being:—

$$\text{Incisors } \frac{2-2}{2-2}; \text{ canines } \frac{1-1}{1-1}; \text{ premolars } \frac{2-2}{2-2}; \text{ molars } \frac{3-3}{3-3}: = 32.$$

If a speculative morphological view were to be given in explanation of the transition from the Platyrhine to the Catarhine type of dentition, it might be said that the third premolar of *Cebus* had been developed into a true molar, and the last true molar reduced so low as to be confluent, as a fifth posterior tubercle, with the second molar, now become the last true molar, in order to form the dentition of the Baboons and Semnopitheques, at least of the lower jaw (Pl. 116, fig. 2, *m.* 3): the small size of the first true molar in the Baboons, (ib. fig. 2, *m.* 1) would seem to give further countenance to such an hypothesis; but this tooth, like the other true

(1) Duvernoy in Cuvier's Leçons d'Anat. Comp. t. IV, (1836) p. 297.

(2) This word refers to position in the jaw, not to time of appearance.

molars, has no deciduous predecessor.(1) In the true Monkeys (*Cercopitheci*), the Gibbons, and the Orangs, the last molar of the lower jaw has a square quadri-tuberculate crown like that above.

The incisors have always a shape conformable to their name, but are very strong and thick; in the upper jaw the middle are larger than the lateral ones, and both are larger than those below. In the Baboons, the Monkeys, and the Semnopitheques, the lower incisors (*Pl. 116, fig. 2, i*) are sub-equal, or the middle ones are larger than the lateral ones in the Gibbons (ib. fig. 6), and the Orangs, (Pl. 117, Pl. 119, fig. 1), the middle lower incisors are the smallest, as in Man. The lateral inferior incisors of the Baboons (Pl. 116, fig. 4', *i*) and Semnopitheques (ib. fig. 5)are further distinguished by the oblique truncation of the outer angle of the crown. Both series of incisors describe a deeper curve in the Baboons and Monkeys than in the Orangs, in which they approach the rectilinear arrangement which characterize these teeth in the Human subject.

The canines are conical, pointed, with trenchant posterior margins, always longer than the adjoining teeth, and acquiring in the males of the great Baboons and Orangs, the proportions of those teeth in the true Carnivora. The Mandrills, (*Cynocephalus maimon*,) have these dental weapons most formidable for their size and shape; especially the upper pair, which descend behind the crowns of the lower incisors, and along the outside of the first lower premolars, (Pl. 116, fig. 4', *p*) the crowns of which seem as if bent back by the action of the upper canines: the anterior longitudinal groove of these canines (ib. fig. 4) is very deep, their posterior margin very sharp. A long diastema divides the upper canine from the incisors, a short one separates it from the premolars: these and the three true molars are arranged in a straight line. Each premolar supports a large external and a small internal cusp; the true molars have four prominent, sharp-pointed cusps, with an anterior and posterior basal ridge; they progressively increase in size from the first to the third in all the Baboons. The first premolar of the lower jaw is

(1) In the private collection of the Baron Van der Capella, near Utrecht, I saw, in the year 1838, a variety in the dentition of an adult *Simia Satyrus*, vix: six molar teeth on each side, but only two of these had the characters of premolars.

remarkable for the anterior prolongation of the base of the crown, which is worn to a sharp edge by the action of the upper canine; the second premolar has a quadri-cuspid crown. The crowns of the lower molars are narrower and longer than those above, especially the last, in which the posterior ridge is developed into a fifth lobe or tubercle. The premolars and molars of the upper jaw are implanted each by three fangs; those of the lower jaw by two fangs.

The smaller Baboons, of the genus *Macacus*, repeat on a smaller scale the dental characters of the Mandrils; but in most of them the posterior tubercles of the second inferior premolar are reduced to a talon or basal ridge (Pl. 116, fig. 1 & 2). In fig. 3 a view is given of two of the fossils from an eocene tertiary formation in Suffolk, which have revealed the former existence of a species of *Macacus*, in our latitudes, at that ancient period.(1)

In the Semnopitheques (Pl. 116, fig. 5) the lower incisors are more equal in size: the canines are smaller, and the upper ones less deeply grooved than in the Baboons: the base of the first lower premolar is less extended anteriorly: the first true molar is equal to the second, and the last is narrower anteriorly in proportion to its length. These dental differences, however, are very slight as compared with those in the structure of the stomach, by the expansion and sacculation of which the ordinary Semnopitheques, as well as the long-nosed species (*Nasica*) and the thumbless species (*Colobus*), differ from the Macacques and Mandrils.(2)

In the long-tailed Monkeys with a simple stomach (*Cercopithecus*), the dentition differs from that of the Semnopitheques in the last lower molar being quadri-tuberculate, and of equal size with the rest. In the long-armed tail-less Apes, or Gibbons, (*Hylobates* Pl. 116, fig. 6) the true molars (*m*) are sub-equal, the lower ones being rather narrower than those above; the crowns have a more rounded contour than in the inferior Quadrumana; the upper molars support four tubercles, the lower ones five, three being placed along the outer curve. In the skull of an old *Hylobates syndactylus*, I find these outer tubercles of the lower molars worn into three deep depressions,

(1) See my "History of British Fossil Mammalia," p. 1 & 16.

(2) See Trans. Zool. Society, vol. 1. pp. 70, and Proceedings of the Zool. Society, 1841, p. 84.

which are stained black; the two inner tubercles are polished flat by attrition, but retain their enamel: in the upper molars the outer tubercles are in the latter state, the inner half presents a deep excavation of the dentine, which is stained black.

In the great Orang-utan (*Simia Wurmbii*, Pl. 117, fig. 1 & 2) the median incisors of the upper jaw are of unusual size and strength; the thickness (antero-posterior diameter) of the base of the crown almost equals the breadth of the same; and they are double the size of the lateral incisors (*i* fig. 2). The abraded surface of the front incisors in the old Orang forms a broad tract extending obliquely from the cutting edge to the back part of the base of the crown; the lateral incisors are more pointed, the outer angle being obliquely truncated: a vacant space of their own breadth divides them from the canines. These, in the male of the great (Wurmb's Pongo, *c*) have a long and strong slightly curved crown, Orang extending below the alveolar border of the under jaw when the mouth is shut, with a moderately sharp posterior margin, but without an anterior groove: the crown is convex externally, with a slighter convexity between two longitudinal depressions on the inner surface. In the female Orang (fig. 3) the canines are smaller; the crowns extend only a short distance beyond the level of the adjoining molars. The male of the smaller and more anthropoid species of Bornean Orang, which I have called *Simia Morio*, (fig. 4) has the canines less developed in proportion to those of the female.(1) In both species of Orang the two cusps of the first premolar are rather more produced than those of the second, as is likewise the outer and anterior angle of the base of the crown. The first and second true molars are rather larger than the third; they have each four cusps, but less developed, and with shallower interspaces than in the Baboons and Monkeys. The

(1) Zool. Trans. vol. II, p. 1655, Pl. 33, Oct. 1836. Mr. Brooke, the enterprising traveller in Borneo, has transmitted skulls of both sexes of *S. Morio* to the Zoological Society, and fully confirms my determination from cranial evidence of the two distinct species of that island. He says, "The natives of the north-west coast of Borneo are all positive as to the existence of two distinct species." "The *Mias Pappan* is the *Simia Wurmbii* of Mr. Owen, having callosities on the side of the face. The *Mias Kassar* or *Simia Morio*, is the same colour as the *Mias Pappan*, but altogether smaller and devoid of callosities either on the male or female adults."—Proceedings of the Zoological Society, 1841, p. 55.

enamel covering the grinding surface is finely wrinkled before abrasion. In the upper jaw both premolars and molars are implanted by three diverging fangs, two external and one internal; the anterior external fang of the first premolar is the longest and strongest. In the lower jaw the median incisors are a little larger than the lateral ones, in which the outer angle is usually rounded off; the crowns of the canines are less robust than those above. The outer part of the first premolar rises to a sub-acute point, from which three ridges descend, one to the fore part of the grinding surface, the other to the back part, and the third to the inner part, which is developed into a slight tubercle. In the second premolar this tubercle rises almost to an equality with the outer one. The first and second true molars have three cusps along the outer curve of the grinding surface, and two upon the inner side, the anterior being the highest. The last molar has two external cusps, and the posterior inner one is almost obsolete. The premolar and molar teeth are each inserted by two strong diverging fangs. The series of grinders forms a straight line in both jaws.

The dentition of the Chimpanzee (*Simia Troglodytes*), though in all its most prominent characters strictly Quadrumanous, yet, in the minor particulars in which it differs from that of the Orang, advances towards the human type. In the upper jaw the middle incisors (Pl. 118, fig. 1, *i*) are smaller, the lateral ones larger than those of the Orang; they are thus more nearly equal to each other; nevertheless the proportional superiority of the middle pair is greater than in Man. Each incisor has a prominent posterior basal ridge, and the outer angle of the lateral incisors is rounded off, as in the Orang. The diastema between the incisors and canine is narrower than in the Orang. The crown of the canine (ib. *c*.), passing outside the interspace between the lower canine and premolar, extends a little below the alveolar border of the under jaw when the mouth is shut; it is conical, pointed, more compressed than in the Orang, and with a sharper posterior edge; convex anteriorly, flattened at the posterior half of the outer surface, concave on the corresponding part of the inner surface, which is traversed by a shallow longitudinal impression: a feeble ridge divides this from the convex anterior surface, which bears a linear longitudinal

impression. Both premolars (ib. *p.*) are bicuspid, the exterior cusp of the first is the largest and most produced. The true molars (ib. *m*) are quadri-cuspid, relatively larger in comparison with the bicuspids than in the Orang: the last is the smallest by the feeble development of the two hind cusps. The premolars as well as molars, are severally implanted by one internal and two external fangs, diverging, but curving towards each other at their ends, as if grasping the substance of the jaw.

In the lower jaw the lateral incisors are broader than the middle ones, but have their outer angle rounded off; they are all much larger and less vertically implanted than in Man (Pl. 119, fig. 1, *i.*). The lower canines (ib. *c*) are two inches in length including the root; the enamelled crown is three fourths of an inch in length, and two thirds across the base; it is conical, trihedral, the outer surface convex, the other two surfaces flattened or sub-concave, and converging to an almost trenchant edge, directed inwards and backwards; a ridge separates the outer convex from the anterior surface: both this and the posterior surface, show slight traces of a longitudinal rising. The canine almost touches the incisor, but is separated by a diastema one line broad, from the first premolar. This tooth (ib. *p.*) is larger than the second premolar, and is twice the size of the human first premolar; it has a subtrihedral crown, with the anterior and outer angle produced forwards, still indicating the peculiar feature of the same tooth in the Baboons; the summit of the crown terminates in two sharp trihedral cusps, the outer one rising highest, and it has a well developed ridge at the inner and posterior part of its base. The second premolar has a sub-quadrate crown, with the two cusps developed from its anterior half, and a third smaller one from the inner angle of the posterior ridge. Both the lower premolars are implanted by two antero-posteriorly compressed, divergent fangs, the anterior one the largest.(1) The three true

(1) M. de Blainville, in his "Ostéographie des Primates" expresses himself somewhat obscurely on the mode of implantation of the molar teeth of the Chimpanzee and Orang, and although he alludes to faint indications of the two external holes for the premolars, leaves the impression that these superior Apes differ from the inferior ones in the structure of the alveoli of the teeth. "Du reste, si les quatre parties de la couronne ne sont pas aussi nettement dessinées que dans les Singes inférieures, certainement il n'y a aucune indice des mammelons accessoires des Gibbons." (See, however, a demonstration of the

molars (ib. *m.*) are almost equal, the first being smaller or not larger than the last; which is the only molar equalling in size the corresponding tooth in the black varieties of the Human subject (Pl. 119, fig. 2, *m.*), in which the true molars attain their largest dimensions. The four principal cusps, especially the two inner ones, of the first molar of the Chimpanzee are more pointed and prolonged than in Man: a fifth small cusp is developed behind the outer pair as in the Orangs and the Gibbons but is less than that in Man. The same additional cusp is present in the second molar, which is seldom seen in Man: the crucial groove on the grinding surface is much less distinct than in Man, not being continued across the ridge connecting the anterior pair of cusps in the Chimpanzee. The crown of the third molar is longer antero-posteriorly, from the greater development of the fifth posterior cusp, which, however, is rudimental in comparison with that in the Semnopitheques and Macacques. All the three true molars are supported by two distinct and well-developed, antero-posteriorly compressed, divergent, fangs, longitudinally excavated on the sides turned towards each other. The molar series in both jaws forms a straight line, with a slight tendency in the upper jaw to bend in the opposite direction to the well-marked curve which the same series describes in the Human subject.

172. *Succession and Structure.*—The deciduous dentition includes in all the catarhine Quadrumana, twenty teeth, viz:

$$\text{Incisors } \frac{2-2}{2-2};\quad \text{canines } \frac{1-1}{1-1};\quad \text{molars } \frac{2-2}{2-2}: = 20.$$

The second deciduous molar is quadri-cuspid, and is succeeded by a permanent premolar with a bicuspid crown; the first deciduous molar is bicuspid, and in the lower jaw of the Baboons it has

contrary in Pl. 119, fig. 1, m.) He proceeds—"Quant aux alvéoles des dents de ces Singes supérieures, il est aisé de voir qu'elles doivent présenter quelques différences concordantes; ainsi à la mâchoire supérieure, à peine si les deux trous externes sont indiqués pour la première et surtout pour la seconde des avant molaires, aussi bien chez le Chimpanzée que chez l'Orang-Outang. Les différences sont moins marquées pour les autres molaires et surtout à la mâchoire inférieure," p. 47. If there ever was an anatomical comparison deserving a deeper and more decisive examination it is that regarding the mode of implantation of the teeth of the Chimpanzee and Orang, which bears so imme-

a small anterior tubercle, which feebly indicates the great extension of that part of the crown of its successor. The deciduous canines have short, straight, conical crowns; differing in form and still more in size from the formidable sub-compressed curved, piercing and trenchant teeth which succeed them: especially in the male sex, which in this respect diverges farther from the immature type than does the female. The permanent incisors are also much larger than the deciduous ones, and especially so in the Chimpanzee and Orang in which I shall here describe the order of development and succession of the permanent teeth; reserving the special comparison of their deciduous teeth with those of the Human subject for the following Chapter.

The deciduous teeth are shown *in situ* in Pl. 120, in the young of both these highly organised Apes, at the period when the first permanent true molar (*m* 1) has cut the gum, on each side of both jaws. The next permanent teeth that appear are the middle incisors of the lower jaw, the corresponding deciduous teeth being the first that are shed. Then the two large middle upper incisors (*i* 1) come into place: these, in the living Orang of the Zoological Gardens(1) occasioned the displacement not only of the middle but the lateral milk incisors; whilst in the skull of the young Orang, which I have described and figured in the Zoological Transactions,(2) the middle permanent incisors and the lateral deciduous ones are both in place in the upper jaw. The next permanent tooth that cuts the gum is the second true molar of the lower jaw, which is followed by the corresponding tooth of the upper jaw (*m* 2). In about eight months after the lateral inferior incisors make their appearance above the gum, and then those of the upper jaw (*i* 2). The bicuspids (*p.* 1 and *p.* 2) are the next teeth which come into place. They are followed by the third true molar teeth. The great canines (*c*) are the last of the permanent series which

diately upon the question of distinction between Man and the Ape: I have, therefore, devoted two plates (118 and 119) to the illustration of the striking difference which the lowest as well as the highest races of the Human species present as compared with the Chimpanzee, in the insertion of the premolar teeth in both jaws.

(1) Zoological Proceedings, 1843, p. 123.

(2) Vol. ii, p. 166, pl. 30.

acquire their full development and functional position. In the female the point of the canines sometimes pierces the gum before the last molar has come into place.

The concomitant change which takes place not only in the size but shape of the jaws is so considerable, and gives rise to such remarkable modifications in the exterior of the cranium and the facial angle, that the mature and immature states of the *Simia Wurmbii* were for some time regarded by Naturalists as distinct species, under the names of Orang (*Simia Satyrus*, Linn.) and Pongo (*Papio Wurmbi*, Latr.). Nor is it surprising that the transition from the Orang to the Hottentot should seem to be so gradual and easy, the cranial characters of the supposed adult anthropoid Quadrumane being those of a young animal with a full-sized brain and with deciduous teeth. Had the skull of the mature Chimpanzee been transmitted from Africa at the period when Wurmb's Pongo was placed in the Mammalian Systems of Cuvier,(1) Fischer,(2) and other Naturalists, as a distinct species, far below the *Simia Satyrus*, it would most probably have been mistaken for that of a lower, baboon-like Quadrumane. But its first description was accompanied by a demonstration of the concealed germs of the permanent teeth in the jaws of the young Chimpanzee, which established the true nature of the adult cranium; the paternal relation of the great Pongo of Wurmb to the young Orang being demonstrated by the same evidence.(3)

The jaws of these highly organized *Simiæ*, during the acquisition of the large permanent series of teeth, not only rapidly increase, but a considerable change takes place in the extent of origin of the temporal muscle: this leaves a well-marked impression near the vertex in the Chimpanzee, and in the male Orang meets its fellow at the vertex and stimulates the growth of a strong osseous crest. The mastoid ridge also shifts its place, and retreats by progressive absorption and deposition nearer to the plane of the occipital region

(1) Règne Animal, Ed. 1817, p. 111.

(2) Synopsis Mammalium, 1829, p. 32. Fischer thus concludes his description of the *Simia Wurmbii*:—"Sunt, qui hanc speciem pro *S. Satyro* adultâ ducant. Permulta tamen sententiæ isti repugnare videntur." He does not cite any of the grounds of opposition.

(3) See Zoological Transactions, vol. i, p. 343.

of the skull. The capacity of the cranial cavity undergoes no change, but the parietes are thickened, especially at the line of the lambdoidal suture, preparatory to the development of the great occipital ridge, which diverges from the end of the sagittal crest. The zygomatic arches are strengthened and expanded, the superior maxillaries produced, while the intermaxillaries having given passage to the crowns of the large permanent incisors, appear to have fallen in. In the Orang the intermaxillary bones at this period have become anchylosed to the maxillaries: in the Chimpanzee that confluence is completed before the deciduous teeth are in place.

The microscopic structure of the teeth of the Quadrumana is conformable throughout the platyrhine and catarhine groups, and closely resembles that which Purkinje, Retzius, Müller, and myself have described in the Human subject. As this structure will be more particularly elucidated in the chapter on the Human teeth I shall here merely mention the most obvious differences which the teeth of the Quadrumana present, and which are manifested not only in the Baboons and Monkeys but in the most anthropoid Ape, viz: the Chimpanzee(1). In the incisor and canine the general direction of the calcigerous tubes agrees with that figured in Fraenkel's Thesis, fig. 1, B, and by Retzius in his "Mikroskopiska undersökningar" Pl. *i* (*iv*), fig. 1, in the corresponding Human teeth. The tubes(2) in the Chimpanzee describe the same primary curvatures, but less strongly; and the secondary gyrations are longer and more feebly marked: they are $\frac{1}{10.000}$th of an inch in diameter, and the interspace between two tubes on the same plane equals the width of two tubes, when viewed in transverse section near the pulp-cavity, as in Pl. 119a, fig. 2; nearer the enamel the interspaces are wider; but in general they are more closely arranged and relatively more numerous, besides being straighter than in the Human subject. They maintain the same diameter through three-fourths of their course; divide sparingly, except close to the enamel boundary and the periphery of the fang: in this part of the tooth the minute lateral branches are most numerous. The calcigerous cells of the dentine(3) are most conspicuous, as usual, near the periphery of the crown, where their well-defined semi-circular contour is seen

(1) Pl. 119 *a*, fig. 1 & 2. (2) Ib. fig. 1, *t*, *t*. (3) Ib. fig. 1, *d*, *d*.

with its convexity next the enamel: from ten to twelve dentinal tubes on the same plane are included in the diameter of a peripheral calcigerous cell: the cells decrease in size and increase in number, and become less definable as they become situated nearer the pulp-cavity. The enamel fibres(1) are more wavy, even, than in the human teeth: they are $\frac{1}{6000}$th of an inch in thickness, and manifest the striated indication of their cellular origin as distinctly as in the human teeth. The vertical fibres ascending from the summit of the crown of the canine of the Chimpanzee described twenty acute-angled undulations in their course. In the section examined, the bend in one direction transmitted more light than in the opposite, and gave an appearance of waves upon the cut surface of the enamel. This is the character attempted to be shown by Fraenkel in fig. 4, of his Thesis, and which Retzius says he had not succeeded in observing in human enamel. The lines of growth or strata of the enamel were best displayed in transverse sections of the incisors and canines. The cement is thickest at the apex of the fang; the Purkingian cells are traceable to near the neck of the tooth, over which the clear basis of the cement is continued upon the enamel: the tubuli continued from the cells are most numerous on the side next the dentine: they form likewise rich anastomotic plexuses in the interspaces of the cells, besides communicating with peripheral ramifications of the tubuli of the dentine: their diameter is $\frac{1}{25,000}$th of an inch.

CHAPTER X.

TEETH OF BIMANA.

173. HAVING reached in the Chimpanzee the highest step in the series of the brute creation, our succeeding survey of the Human dental system, expanded by retrospective comparisons, becomes fraught with peculiar interest, since every difference so detected establishes the true and essential characteristics of that part of Man's frame.

(1) Pl. 119 *a*, fig. 1 *e*, *e*.

The human teeth are the same in number and in kind as those of the Chimpanzee and Orang, nor does Man differ in this respect from any of the inferior catarhine Quadrumanes. The human dental formula is therefore :—

Incisors $\frac{2-2}{2-2}$; canines $\frac{1-1}{1-1}$; premolars $\frac{2-2}{2-2}$; molars $\frac{3-3}{3-3}$: = 32.

That is to say, there are on each side of the jaw, both above and below, two incisors,(1) one canine,(2) two premolars,(3) and three true molars.(4) They are more equal in size than in the Quadrumana; no tooth surpasses another in the depth of its crown; and the entire series, which describes in both jaws a regular parabolic curve, is uninterrupted by any vacant space. The incisors (Pl. 118, 119, fig. 2 and 3, *i*) are much smaller in proportion to the molars than in the Chimpanzee and Orang; in the upper jaw the first exceeds the second in breadth, but in a less degree than in the Chimpanzee. The posterior basal ridge is less prominent and distinct in the middle incisor; it is wanting in the lateral incisor, the outer angle of which is entire, and touches the crown of the canine: its fang is longer in proportion to the median one than in the Chimpanzee; in both incisors the fang is long, slender, and subcompressed. The most marked distinction between the dentition of Man and that of the highest Quadrumanes is the absence of the interval between the upper lateral incisor and the canine, and the comparatively small size of the latter tooth (ib. *c*): but its true character is indicated by the conical form of the crown, which terminates in an obtuse point, is convex outwards and flat or sub-concave within, at the base of which surface there is a feeble prominence: the conical form I find best expressed in the Melanian races, especially the Australian(5): the canine is more deeply implanted, and by a stronger fang than the incisors; but the contrast with the Chimpanzee is sufficiently manifest, as is shown in Pl. 118. There

(1) *Dentes incisores, primores.*

(2) *Dentes canini, cuspidati.*

(3) *Dentes molares anteriores, seu minores, s. spurii, s. bicuspidati.*

(4) *Dentes molares posteriores, seu majores, s. veri, s. multicuspidati.*

(5) Pl. 118, fig. 2, *c*. It is also very well marked in the dentition of the Mozambique Negro, figured by F. Cuvier, 'Dents de Mammifères,' Pl. 1.

is no sexual superiority of size, either of the canine or any other single tooth in the human subject.

Both upper and lower premolars (ib. *p.*) are bicuspid; they are smaller in proportion to the true molars than in the Chimpanzee and Orang: in the upper premolars a deep straight fissure at the middle of the crown divides the outer and larger from the inner and smaller cusp: in the lower premolars the boundary groove describes a curve concave towards the outer cusp, and is sometimes obliterated in the middle by the extension of a ridge from the outer to the inner cusp, which cusp is smaller in proportion than in the upper premolars. These teeth in both jaws are apparently implanted each by a single, long, sub-compressed, conical fang: but that of the upper premolars is shown by the bifurcated pulp-cavity to be essentially two fangs, connate, and which, in some instances, are separate at their extremities.

The crowns of the true molars (ib, *m.*) are larger in proportion to the jaws, are a little larger in proportion to the bicuspids, and still more so in proportion to the canine and incisor teeth, than in the Chimpanzee and Orang: the contour of the grinding surface is more rounded, and we have seen that the higher Quadrumana already approximate to this character by the angles of the crown being less marked than in the lower Quadrumana. The first and second true molars of the upper jaw support four trihedral cusps; the internal and anterior one is the largest and is connected with the external and posterior cusp by a low ridge extending obliquely across the grinding surface, with a deep depression on each side of it, the anterior groove extending to the middle of the outer surface, the posterior one to the inner surface. The enamel is first worn away by mastication from the anterior and internal or largest tubercle: a line of enamel extending from the outside to the middle of the crown is the last to be removed before the grinding surface is reduced to a field of dentine with a simple ring of enamel.(1) It is worthy of remark that by the time when the permanent teeth have come into place the first true molar in both jaws is much more worn, as compared with the second and third molars, than it is in the Chimpanzee

(1) Pl 120, fig. 3, *m.* 1.

or Orang, owing to the slow attainment of maturity characteristic of the Human species, and the longer interval which elapses between the acquisition of the first and the last true molars, than in the highest Quadrumanes. In the last true molar, called from its late appearance, the "dens sapientiæ" or wisdom-tooth, the two inner tubercles are blended together, and a fissure extends, in many instances, especially in the Melanian varieties, from the middle of the grinding surface, at right angles to that dividing the two outer cusps, to the posterior border of the tooth.

The first upper molar is always implanted by three diverging fangs, two external and one internal. The second molar is usually similarly implanted, but the two outer fangs are less divergent, are sometimes parallel (Pl. 118, fig. 2), and occasionally connate (ib. fig. 3); this variety appears to be more common in the Caucasian than the Melanian races. The two outer fangs of the last molar tooth are more commonly connate or confluent, and sometimes also the inner fang is blended with them into one simple root, in the Caucasian race: but I have never seen these varieties in the Melanian races; and in the Australians the wisdom-tooth has always presented the same three-fanged implantation as in the Chimpanzee and Orang.

The crowns of the inferior true molars are quinque-cuspid, the fifth cusp being posterior and connected with the second outer cusp: it is occasionally obsolete in the second molar. The four normal cusps are defined by a crucial impression, the posterior branch of which bifurcates to include the fifth cusp; this bifurcation being most marked in the last molar where the fifth cusp is most developed. In the first molar a fold of enamel extending from the inner surface to the middle of the crown is the last to disappear from the grinding surface in the course of abrasion.(1) The wisdom-tooth is the smallest of the three molars in both jaws, but the difference is less in the Melanian than the Caucasian races. Each of the three lower molars is inserted by two sub-compressed fangs, grooved along the side turned towards each other: this double implantation appears to be constant in the Melanian, especially the Australian race, in which the true molars

(1) Pl. 120, fig. 4, *m.* 1.

are relatively larger than in the Caucasian race. In Europeans it is not unusual to find the fangs of the second and third inferior molars connate along a great part or the whole of their extent, as in Pl. 119, fig. 3.

With respect to the reciprocal apposition of the teeth of the upper and under jaw it is interesting to observe that the crown of the lower canine is, as usual, in advance of that above, and fits into the shallow notch between that and the lateral incisor. The inferior incisors are so small that their anterior surface rests against the posterior surface of the upper ones, when the mouth is closed: the other teeth are opposed crown to crown, the upper teeth extending a little more outwardly than the lower ones.

Hunter remarks that the supernumerary teeth happen oftener in the upper than the under jaw, and he believed them to be always incisors or canines. I have seen a skull of a male Hindoo in which there were two well-formed canine teeth placed side by side in the left upper jaw, the series being very regular and even. The wisdom-tooth is sometimes not developed; but I never saw a supernumerary premolar or molar tooth.

174. *Comparison of the deciduous teeth of the Orang, Chimpanzee, and Human Subject.*—The deciduous series of teeth in the Human subject (Pl. 121) consists of *in.* $\frac{2-2}{2-2}$, *c.* $\frac{1-1}{1-1}$, *m.* $\frac{2-2}{2-2}$: = 20. I shall here describe them in immediate comparison with the same teeth in the Chimpanzee and Orang; because the differences, though less in number and degree are more expressive of original specific distinction, in proportion to the immaturity of the subjects of comparison in which they may be detected.

The upper milk incisors of the Chimpanzee (Pl. 120, fig. 1.) are relatively larger than in Man, especially the middle pair; but the disproportionate size of these is still more manifest and characteristic of the Orang (ib. fig. 2.) and the outer angle of the lateral incisors is more rounded off in this Quadrumane. The crown of the canine is longer, and more pointed in the Chimpanzee than in Man; still more so, and farther apart from the incisor in the Orang. The first molar is as large in the Human subject as in the Chimpanzee, and its crown is divided into two principal cusps, but the outer and larger one has a small sub-

division notched off posteriorly, and the inner cusp is relatively larger than in the Chimpanzee: the first upper molar of the Orang is simply bicuspid, but is larger than in the Chimpanzee. The second molar of the Human child could scarcely be distinguished from that of the young Chimpanzee: both are quadricuspid, and the same oblique ridge crosses the grinding surface from the antero-internal to the postero-external tubercle; but the pointed summits of the two outer cusps are a little more produced in the Chimpanzee. The second molar of the Orang besides its larger size, has the four tubercles better defined, and the oblique ridge less developed.

The lower deciduous incisors of the anthropoid Apes differ from those of the Human subject in their superior size, greater relative thickness, and the lateral incisor more particularly by the rounding off of the outer angle. The lower canine of the Chimpanzee has a larger, longer, and more pointed crown with a sharp posterior edge: this is less marked in the canine of the Orang, which is larger and thicker than in the Chimpanzee: the crowns of the upper and lower canines are more obliquely opposed, the lower one being more advanced in those Apes than in the Human subject. The first lower deciduous molar of the Human subject has four tubercles and a small anterior ridge, and is larger than that of the Chimpanzee, which supports a single large pointed cusp, and a posterior ridge: the first molar of the Orang has a similar simple crown, but is as large as that of the child. The second molar is of equal or superior size in the Human to that in the Chimpanzee, but it supports three outer and two inner cusps, while in the Chimpanzee it has but four cusps: in the Orang the fifth external and posterior tubercle is feebly indicated. The deciduous molars of the Human subject, as in the Chimpanzee and Orang, have each three fangs in the upper and two in the lower jaw.

The differences brought out by the foregoing comparisons, though less striking than those exhibited by the permanent teeth, will be appreciated by the philosophical Anatomist as yielding more certain evidence of the essential distinction of the Bimanous species: he will perceive that they are not due to mere adaptive developments, but are

manifested at a period when the subjects of comparison are far from having attained the pre-ordained term of deviation from the common primordial type, and antecedent to those changes in the dental system itself, which more broadly characterise the species, and, in the Orang and Chimpanzee, proceed further to mark the different sexes.

175. *Succession.*—The primary development of the matrices of both the deciduous and permanent Human teeth has been described in the 'Introduction'. Calcification of the permanent series commences first in the pulp of the first true molar, and very soon after, if not simultaneously in that of the anterior incisor, about five or six months after birth. The first true molar (Pl. 121, *m* 1) comes into place and use between the sixth and seventh year(1): the first permanent incisor (ib. *i* 1) between six years and a half, and eight years: the calcification of the pulps of the lateral incisor (*i* 2) and canine, (*c*) commences about eight or nine months after birth, and they cut the gum, the canine quickly following the incisor, between the seventh and ninth years. Calcification of the first premolar (*bicuspis*, *p* 1) begins at, or soon after, the second year, that of the second about a year later, and both premolars have displaced the deciduous molars, and come into use between the eighth and tenth years. The pulp of the second molar (*m* 2) begins to be calcified about the fifth or sixth year, and it cuts the gum from about the twelfth year to the fourteenth year; but always later than the permanent canines and premolars. The third molar or *dens sapientiæ*, begins to be calcified about the twelfth year, and usually comes into place at or after the twentieth year.

Both earlier and later periods of the development of the permanent teeth have been observed and recorded; but such varieties rarely affect the general order of succession. I have described this order as it occurs in the lower jaw, the teeth of which usually appear earlier than the corresponding ones above. It will be seen, therefore, that the Human subject differs from the Chimpanzee and Orang in the order of progression of the permanent teeth. John Hunter, after indicating the first incisor and the first molar as

(1) Hunter says it cuts the gum about the twelfth year of age; but this must be a rare exception, if it is not a mistake. See "Natural History of the Human Teeth," 4to. p. 84.

the earliest of the adult teeth that are formed, rightly observes, "The teeth between these two points make a quicker progress than those behind."(1) In the Quadrumana the progress is slower, the second molar preceding the bicuspids, and the last molar, the canines. We may readily suppose that the larger grinders are sooner required by the frugivorous Orang, than by the higher omnivorous Bimanous species; but the more immediate condition of the earlier development of the canines and premolars in Man is their smaller relative size.

176. *Microscopic Structure.*—The progressive steps in the acquisition of the knowledge of the intimate structure of the Human teeth have been pointed out in the 'Introduction,' pp. v—xvi. The body of the tooth consists of hard or unvascular dentine (Pl. 122, *d*); the exserted part or crown is invested by enamel (ib. *e*); the whole tooth is coated by cement, (ib. *c*), but this attains the thickness requisite for the development of its characteristic radiated cells only upon the fang or fangs. Every tooth has an internal cavity (Pl. 122, *v*), which contains the remains of the vascular dentinal pulp, and is thence termed 'pulp-cavity': it is progressively diminished in size as the dentine is completed; remains widest at the base of the crown, and contracts as it descends along the fang or fangs, dividing according to the number of these; and, when they are connate and form apparently a simple root, the pulp-cavity indicates by its division into linear fissures, continued from the coronal dilatation, the number of fangs which compose such undivided root. After the pulp-cavity has been reduced by the completion of the dentine, it is further diminished by the conversion of part of the residuary pulp into a layer of osseo-dentine (ib. fig. 4 *a*, 5 & 8 *o*). The cement, which is thickest at the end of the fangs, sometimes penetrates the pulp-cavity, and blending with the osseo-dentine closes the aperture, except where two or more minute canals perforate it for the passage of capillary blood-vessels, and nerve-filaments.

The pulp-cavity of the front incisor, when exposed by a longitudinal section through the breadth or transverse axis of the tooth, (ib. fig. 9) presents the form of a long and narrow inverted cone; the base being concave and next the crown, the apex

(1) Op. cit. p. 82.

prolonged to the extremity of the fang: a linear fissure is continued from each angle of the base towards the corresponding angle of the crown. The same cavity, exposed by a longitudinal section through the thickness or antero-posterior cavity of the crown (ib. fig. 2), is fusiform, its coronal end contracting to a linear fissure which is continued towards the middle of the summit of the crown. The pulp-cavity of the canine (ib. fig. 3), is relatively wider in its coronal portion. In the upper premolars (ib. fig. 4), the coronal dilatation sends a short and wide process to the base of each cusp, and is continued from the opposite end in the form of two linear fissures, one near the external, the other near the internal part of the compressed apparently single fang. In the true molars (ib. fig. 7) a short and wide process of the common coronal cavity is continued towards the base of each tubercle of the grinding surface, and as many linear prolongations as there are fangs, extend from the opposite side of the cavity. In the broad fangs of the lower molars the pulp-fissure commonly divides into two in each fang; and in the last or wisdom-tooth, which has frequently, at least in the Caucasian races, a single implantation, the pulp-cavity always indicates by its divisions the number of connate fangs that form such undivided base.

Every part of the surface of the pulp-cavity is pierced by microscopic pores, about $\frac{1}{10,000}$th of an inch in diameter, which are orifices of tubes radiating from the pulp-cavity to the periphery of the dentine with a general direction vertical to that surface; these are the dentinal or calcigerous tubes. In the lower incisor and canine teeth, those from the middle of the summit of the pulp-cavity ascend vertically to the enamel-covered surface of the dentine at the summit of the crown; the tubes on each side of these gradually incline outwards; those which go to the angles of the crown forming an angle of 45° with the middle vertical tubes: at the sides of the crown the tubes incline still more outwards until in the middle of the fang they become horizontal, and still lower, bend downwards.(1) The vertical tubes are nearly

(1) Pl. 122, fig. 1—3, *d*.

straight; but, as soon as they begin to incline from the perpendicular, they become bent into two or, more commonly, three gentle wavy curves; at the sides of the crown and along the upper half of the fang the tubes form a short bend concave towards the crown, then a longer bend in the opposite, and finally a third bend in the first direction; the general curve being concave downwards: in the lower half of the fang the first curvature with the concavity upwards is the principal one. These 'primary curves' are on the same plane or nearly so. The 'secondary curves,'(1) of which two hundred may be counted in an extent of $\frac{1}{10}$th of an inch of the length of a tube, are not on the same plane, but form slight gyrations through the whole course of the tube. Both the primary and secondary curves of adjacent tubes are parallel; and occasionally the tubes make a short bend along a line parallel with the outer contour of the crown, giving rise to the appearance which may be called 'contour lines;'(2) the parallelism of the entire tubes being affected only by the amount of their divergence in radiating from the pulp-cavity. As a general rule the tubes are nearly perpendicular to the surface of the dentine, and take an almost direct course from the pulp-cavity to that surface. Thin sections of dentine taken across the tubes, viewed by transmitted light with a five hundred times linear magnifying power, show the clear area of the tube more or less occupied by a dark subgranular opake calcareous substance,(3) and a clear border(4) to the area, neatly defined from the intertubular substance,(5) and indicating the proper parietes of the tube. The addition of dilute muriatic acid dissolves the opake contents of the tube and clears the whole circular area: it dissolves, at the same time, the finer particles of lime in combination with the animal basis of the intertubular substance and parietes of the tubes, which latter then cease to be distinguishable. This shows that either the lime-particles have a peculiar arrangement in the parietes of the tubes, or are more abundant there than in the intermediate substance, since the parietes can be distinguishable only whilst those particles are present: the appearance can scarcely be an optical deception because

(1) Pl. 122 *a*, fig. 5. Pl. 122 *a*, fig. 1. (2) Pl. 122, fig. 7, *l*.
(3) Pl. 124 *a*, fig. 4. (4) Ib. *b*. (5) Ib. *i*.

the thickness of the parietes of the dentinal tubes, in relation to their area, varies in different animals; it is twice as great, for example, in the incisor of the Dugong as it is in that of Man. In viewing the dentinal tubes lengthwise, a third is usually more faintly seen in the interspace of any two that are in focus(1); it is on a different plane, and the tubes on different planes are commonly alternate in position; viewed in transverse section(2) their arrangement appears quincuncial, yet not regularly so throughout; so viewed, the distance between each two tubules does not exceed, and often does not equal, the width of one, its parietes and lumen being included. The distance between two tubes viewed longitudinally on the same plane is generally equal to the width of two; but, if the distance between the opake area of two parallel tubes be estimated, irrespective of the proper tunics of the tubes, it more than equals the width of three such opake areæ. Professor Retzius appears to have calculated the relative width of the tubes and their interspaces in the latter mode, and his results have been generally copied by subsequent writers on microscopic anatomy. The method though easy, and applicable to the detection of differential characters in the dental structure of different animals, is inexact in reference to the actual distance between the tunics of the dentinal tubes. The true distance is nearly the same throughout the course of the tubes; for, as they diverge, they divide and sub-divide dichotomously, maintaining the same diameter to within one fourth or one fifth of their terminations. If the tubes were described according to the order of their formation, the peripheral extremities would be their beginnings, and the dichotomous divisions would rather be the anastomoses of the more numerous and smaller tubes as they gradually converged to terminate, by fewer and wider extremities, in the pulp-cavity. The tubes also send off into the intertubular space very minute branches which divide, and passing into the next interspace, are lost

(1) Pl. 123. This is well shown in Retzius' Treatise, Pl. 2, (v), fig. 1 *b*.

(2) In some parts of the dentine the tubes are occasionally observed to be collected into small groups or bundles.

there, anastomosing, or terminating in the calcigerous or dentinal cells.(1)

The lateral ramuli are more numerous in the fang than in the crown; here the finer branches are most abundant at the peripheral extremities of the tubes, which frequently appear to end abruptly, as if truncated; sometimes dividing and sub-dividing quickly; the terminal divisions diverge widely, and appear to end in the stratum of fine cells which divides the dentine and enamel: here and there I have seen a tube bending back to form an anastomotic hoop with an adjoining tube. The peripheral stratum of minute cells receiving the terminal ramifications of the calcigerous tubes and forming the boundary between the dentine and enamel, is the most sensitive part of the dentine: it is not, however, so distinct a tissue as to merit a special name.(2)

In the bicuspids(3) a larger proportion of the tubes proceeding from the summit of the pulp-cavity are vertical than in the canines or incisors, and a still greater proportion in the broad-crowned molars.(4) The tubes going to the apex of each cusp or tubercle are the most vertical, and the surrounding tubes begin to incline from the perpendicular in proportion as they terminate nearer the base of each cusp: in the interspaces of the cusps, therefore, the tubes incline towards each other. At the early stage of the calcification

(1) Pl. 123, fig. 1, d^1. These cells, defined in my Report to the British Association in 1838, (vol. VII, p. 144) as "calcigerous cells, which form numerous layers generally arranged parallel with the contour of the cavity of the pulp, and most numerous at the circumference of the ivory," are untruly indicated by the exaggerated expression that 'the intertubular substance is cellular'; they would be sought for in vain as cells, in the interspaces of the tubes. The true dentinal or calcigerous cells include many tubes and intertubular spaces, and it is much more exact to say that those cells include a tubular structure, than that the intertubular space is cellular. The unprejudiced microscopical observer will find the tissue in the intervals of these dentinal tubes, for the most part clear and structureless, as Purkinje and Retzius have rightly described. Dr. Henle has stated that when deprived of the hardening salts it tears into fibres, whose course is parallel to the tubes: this is not a satisfactory indication of original structure. *Sömmering, von Baue des Mensch. Körp.* 8vo. 1841, p. 855-856.

(2) M. Duval, who has well described the vital properties of this part of the dentine, and rightly states it to be the seat of the commencement of caries, has proposed to call it 'dictyodonte.'—"Observations Anatomiques sur l'Ivoire," 8vo. 1839, p. 14.

(3) Pl. 122, fig. 4. (4) Ib. fig. 6 and 7.

of the dentinal pulp, when the cusps are yet distinct from each other, they constitute so many distinct radiating systems of dentinal tubes, and the crown of a molar seems to be formed by the basal confluence of three, four or five simple teeth. At the circumference of the crown of both premolar and molar teeth, the tubes incline more and more towards the horizontal direction as they approach the fangs. In the upper premolars in which the pulp-cavity divides and is continued in the form of two linear fissures along the connate fangs,(1) each fissure is the centre of divergence of radiating tubes, having the same primary and secondary curvatures, as in the single fang of the incisor and canine. When a molar is implanted by only two broad and compressed fangs the pulp-cavity usually divides in each; and when the last molar is implanted by an undivided root, the dentinal tubes of that part radiate also from two distinct pulp-canals. In the base of three-fanged and four-fanged molars there are as many radiating systems of dentinal tubes. The terminations of the tubes in the fangs are more frequently resolved into fine branches than in the crown, and the communications between these branches and the analogous minute tubes from the radiated cells of the cement are numerous and plain.

The dentinal cells of the human tooth(2) are sub-circular, about $\frac{1}{3000}$th of an inch in diameter; they seem most numerous from being most conspicuous, near the periphery of the dentine, as originally described by me in the dentine of the Crocodile.(3) They are best seen in sections of the crown of a permanent tooth before it has come into place. In a longitudinal section the peripheral boundary of the cell, or that next the enamel, is most conspicuous; it describes a slight curve: the lateral boundaries form a very open angle: the posterior boundary is formed generally by the convex curve of the posterior cell which appears slightly to over-lap the one in front, and in this view of the cells their transverse diameter exceeds the longitudinal one. In a transverse section of the dentine the cells' boundaries are, for the most part hexagonal, with the angles feebly marked. From the differences

(1) Pl. 122, *v'*, *v'*. (2) Pl. 123, fig. 1, *d'*, *d'*.

(3) Report of British Association, 1838, p. 144.

observable in the two views of the cells, that surface of the cell which is next the periphery of the tooth is shown to be more rounded and convex, than the other surfaces. Viewed by transmitted light, the cell-boundaries are usually opake ; but by a slight alteration of focus the dark lines become clearer and brighter than the surrounding substance : in parts of the dentine near the periphery, the boundaries are occasionally seen to be irregularly widened ; as if contiguous cells were separated by depositions of lime-salts in a sub-granular state : these thickened and less regular boundaries are always opake, and when viewed by reflected light are white. As the dentine approaches the pulp-cavity the indications of the cells gradually decrease in size, and their boundaries usually become fainter and less complete ; viewed in longitudinal section the peripheral margin is the last to disappear.

After noticing the cells and tubes of the dentine, the third and least important appearance, which relates rather to the course of formation than to the essential structure of the dentine, is that produced by the lines, which from their parallelism with the vertical outline of the crown I have termed 'contour-lines.' These are the lines, or striæ of the dentine, which, in sections of the larger teeth of many of the inferior Mammalia, are visible by the naked eye, through the action of a short parallel bend of the dentinal tubes, along the course of the contour line, upon the rays of light. These lines are not equally conspicuous in every tooth ; I have usually found them most so in the molars of the human subject, where, without being regularly equi-distant, they have presented intervals of about $\frac{1}{100}$th of an inch, commencing at thrice that distance from the periphery of the dentine(1).

The enamel of the human teeth(2) consists of long and slender solid, prismatic, for the most part hexagonal, fibres of phosphate, carbonate, and fluat of lime, in the proportions mentioned in the 'Introduction' : they are essentially the contents of extremely delicate membranous tubes, originally sub-divided into minute depressed

(1) Pl. 122, fig. 7, *l*. The dentine in fossil teeth commonly breaks up along these lines into conical or superimposed strata.

(2) Pl. 122, fig, 1—7, *e*.

compartments or cells, of which membranes scarcely a trace can be detected in fully-formed teeth. The fibres are arranged closely together, side by side, with occasional narrow angular fissures, or interspaces, which are most common between the ends nearest the dentine; their general direction is perpendicular to the surface of the dentine, where the ends of the prisms are fixed in shallow depressions; the opposite and larger ends form the exposed surface of the enamel: the fibres proceeding to the horizontal masticating surface are, therefore, vertical; the greater number, which are directed to the circumference of the crown, are horizontal or nearly so; every fibre, as a general rule, having, like the tubes of the dentine, that direction which is best adapted for resisting either the external force of mastication or the effects of lateral pressure. Besides the minute pits corresponding with the inner ends of the enamel fibres, the outer surface of the dentine sometimes presents larger depressions, as shown at e', fig. 1, pl. 123. The enamel-fibres describe a flexuous course, the curves being much stronger and shorter than the primary curves of the dentinal tubes(1). The parallelism of the fibres continues over a much smaller extent of any part of the enamel than that of the calcigerous tubes in the dentine: in some parts of the enamel they curve in opposite directions to one another, like the vane of a feather. Sometimes the fibres may be traced through the entire thickness of the enamel; where they fall short, and where the larger fibres diverge from each other, shorter complemental fibres fill up the interspaces. Each fibre is $\frac{1}{5000}$th of an inch in thickness, and is marked throughout its entire course by faint, close-set, transverse striæ(2). When a section of enamel includes several fibres in its thickness, certain of the overlapping curves intercept a portion of light, and occasion the appearance of dusky, brownish waves. Another appearance, more immediately related to the formation of the enamel, is produced by lines crossing the enamel-fibres, parallel with the outer margin of the enamel, but not always parallel with that attached to the dentine. These lines are not of equal clearness, but are very nearly equi-distant, being about $\frac{1}{2000}$th of an inch

(1) Pl. 122, *a*, fig. 1 & 2.

(2) Ib. fig. 3. Pl. 123, fig. 1, *e*.

apart; they are more plainly seen in transverse sections of the crown than in longitudinal sections, and they have the same relation to the fibres of the enamel which the contour-lines of the dentine bear to the calcigerous tubes. Without doubt they indicate, in like manner, strata of segments of the fibres and stages in the formation of the substance. Where these strata, which are arranged very obliquely to the vertical surface of the dentine, crop out upon that surface they occasion those wavy transverse annular delicate markings which Leeuwenhoek(1) noticed upon the exterior of the enamel, and which he supposed to indicate successive stages in the protrusion of the tooth through the gum, in taking its place in the dental series. The various conditions of the enamel at different periods of its formation have been mentioned in the description of the development of the tooth.(2)

The cement in the human tooth,(3) as in other simple teeth, is confined to the exterior surface, with the exception of a small portion which, in old teeth, is usually reflected into the entry to the pulp-cavity and sometimes closes it up. This third substance is thinnest upon the crown and very gradually increases in thickness as it approaches the end of the fang: it is only on the implanted part of the tooth that the radiated cells, which demonstrate the close analogy between cement and bone, exist; elsewhere the clear basis of the cement alone is present, and this is soon worn away from the enamel of the crown. There are no vascular canals in human cement, except when it happens to be abnormally thickened; in which case, as in the naturally thickened masses of that substance in the teeth of Herbivora, it acquires also this additional feature of resemblance to true bone. The chemical constitution of both the animal basis and earthy salts of this dental tissue and of bone is identical; the hardening particles are chiefly blended in the finest state of sub-division with the clear basis, a portion being contained in a coarser state in the cells; it is this which occasions their milk-white colour when viewed by reflected light.(4) The cemental cells are generally oblong, sometimes cir-

(1) 'Select Works' by Hoole, 4to. 1800, p. 115.

(2) Introduction, p. xlvi. (3) Pl. 122, *fig.* 1—7, *c*.

(4) The calcareous matter does not occupy the whole of the cavity of the cell; space is left as in the dentinal tubes, for the transit of fluids. Mr. Smee, (Med. Gazette,

cular, more rarely fusiform: they average about $\frac{1}{3000}$th of an inch in the long diameter: their contour is broken by the numerous fine tubes which radiate from them, with wide angular beginnings, but quickly contracting to the minute size of $\frac{1}{20,000}$th of an inch. In transverse sections of the fang, the cells are generally seen to be arranged in parallel concentric lines; their long axis being in the direction of the lines, which vary in clearness of definition, like the concentric striæ of enamel; and, like these, indicate stages of formation in the cement. The radiating tubuli anastomose together either directly or by their numerous fine branches; which latter also communicate with the terminal ramifications of the dentinal tubes, either directly or through the medium of the fine granular cells dispersed through the boundary line between the dentine and cement. In the deciduous teeth the cement is relatively thinner and the cells fewer and less regularly arranged. The thickened cement near the end of the fang of old permanent teeth is occasionally perforated by a vascular canal, conveying capillary vessels to the osteo-dentine and the small remnant of the pulp. An increase beyond the usual thickness is usually accompanied by the formation of vascular canals in the cement; and it is the existence of this most highly organized of the dental tissues which explains the possibility of engrafting teeth upon vascular parts.(1)

In my Report to the British Association in 1838, which contains the first announcement of some of the observations described in detail in the present Work, I stated, with respect to the component structures of a tooth, "that in addition to those usually described and admitted, there were other substances entering into the composition of teeth and presenting microscopic characters equally distinct both from ivory, enamel and cement,

Nov. 20th. 1840), succeeded in injecting them with Canada balsam, and I have generally found in fossil teeth that the mineral matter had penetrated into the cells and tubes of the cement, as well as into the tubes of the dentine.

(1) Retzius rightly points out the cement as the seat of the abnormal growths called 'exostosis,' to which the fangs of teeth loosened by the scurvy or mercurial medicines are more particularly liable. One of his figures of the thickened cement on the fang of the tooth of an aged person is given in Pl. 122, fig. 8.

and from true bone, and as easily recognizable."(1) Of these is the tissue, there first defined and which I have since called 'osteo-dentine,' from its combining the vascular concentric-coated canals of the osseous tissue, with a development of the fine tubes resembling those of true dentine, but with stronger and less regular curvatures. This substance is found lining the pulp-cavity of old teeth; and sometimes forms the middle part of the grinding surface of much worn molars: but the conversion of the remains of the pulp into the osteo-dentine is constant in human teeth after the age of twenty years.(2)

To ascertain what modifications of structure the dental tissues might present in teeth which are sometimes developed, with hair and portions of bone, in the human ovarium, I examined microscopically one of those ovarian teeth, of which a longitudinal slice, taken through the middle, is figured in Pl. 124. The intimate structure of the dentine *d*, enamel *e*, and cement *c*, was essentially identical with those of the ordinary maxillary teeth. The dentinal cells and tubes presented the same dimensions: the primary and

(1) "One of these substances is characterised by being traversed throughout by numerous coarse canals, filled with a highly vascular medulla or pulp, sometimes anastomosing reticularly—sometimes diverging and frequently branching,—sometimes disposed nearly parallel with one another, and presenting more or fewer dichotomous divisions. The canals in many cases are surrounded by concentric lamellæ, and thus resemble very closely the Haversian canals of true bone; but the calcigerous tubes which every where radiate from them are relatively much larger. The highly organized tooth-substance just described differs from true osseous substance, and from cœmentum, in the absence of the Purkingian corpuscles or cells." Trans. Brit. Assoc. 1838. p. 137.

(2) Lintott 'On the structure of the Human teeth.' 1843. John Hunter appears first to have called attention to this process which prevents the exposure of the pulp-cavity when the crown is worn low down; he calls the substance 'new matter' and says "it may be easily known from the old, for when a tooth has been worn down almost to the neck a spot may always be seen in the middle, which is more transparent and at the same time of a darker colour, and generally softer than the other." Hunter's success in injecting vessels in the cavities of the teeth in very old people is explained by the existence of vascular canals in the osteo-dentine and their communication with similar canals perforating the thickened cement. I have already noticed the abundance of this substance in the teeth of the Cetacea, and its centrifugal development from detached centres in the substance of the pulp of the Cachalot, forming there sometimes detached masses (p. 360). A modification of osteo-dentine forms, as we have seen, the main body of the teeth of the Sloths and Megatheroid quadrupeds; but the transition from the normal hard dentine to its vascular modification is more gradual in the Human teeth.

secondary curves of the tubes were equally present, but the direction of the former somewhat different, the principal bend in the upper and lower tubes being turned rather from, than towards, the centre of the tooth; but the general principle of arrangement, perpendicular to the tooth's surface equally prevailed. The lower end of the pulp-cavity was quite closed by dentine, the tubes of which descended vertically; the pulp-cavity forming a centre from which the dentinal tubes radiated on all sides. The normal part of the dentine was developed, as in a premolar, into two cusps, and the pulp-cavity *v* was single as in a bicuspid of the lower jaw. The enamel was unusually thick, and the cusps were divided by a cleft extending nearly to the dentine. The enamel fibres had the usual form, structure, and direction. The cement became unusually thick at the closed end of the fang and there formed the medium of adhesion between the dentine and a small portion of true bone. Three or four vascular canals (*b*) were detected perforating the cement and dentine which closed the pulp-cavity, and communicating with similar canals in a mass of osteo-dentine (*o*) which almost blocked up the cavity of the tooth. The thin layer of non-cellular coronal cement was conspicuous over the whole outer surface of the enamel, and presented no increase in thickness in the abnormal median cleft.

The presence of all the beautiful prospective arrangements of the minutest particles of an organ, by which it is adapted to its office, in an example of the same organ developed abnormally under conditions unfitting it for the exercise of its proper office, affords no argument against the contrivance, but, rightly considered, enlarges our conceptions of the liberal provision of the contriver. The matrix of a tooth, wherever it may chance to be formed, must so operate in the disposition of the hard building materials of the tooth as to ensure the utmost strength and power of resistance in all those directions in which such tooth would have been acted on, if it had been developed in its proper position.

Of the four substances composing the human tooth that which is most exposed to outward influences, and which is first

to operate upon the food in preparing it for deglutition, is the hardest, the most solid, the least organized. We have seen that every fibre of the enamel is so disposed, by the preliminary disposition of the cells in which it was moulded, as to give it the utmost strength and power of resistance of which such a tissue could be capable. The polished surface, the pearl-white colour of this dense and brittle substance, adds ornament to use. In the second and principal substance of the tooth, the dentine, we have traced an equally beautiful arrangement of the earthy salts in directions which best resist both vertical and lateral pressure, but with the additional economy of the substitution of the hollow column for the solid prism. The saving of material is however, the least of the benefits gained by this tubular structure of the dentine: the vitality of the tissue, which Hunter recognized so forcibly, but which, being equally convinced of the non-vascularity of the tissue, he was unable to explain,—willing rather to enunciate an apparent paradox, or be taunted with dilemma, than yield one iota of either of his convictions,(1)—is explicable by the possible and highly probable fact of a circulation of the colourless plasma of the blood through the dentinal tubes. That some elementary prolongations of nerve may also be continued into these tubes, who may confidently deny? Whoever has felt the pang produced by contact of a probe with the recently exposed surface of the dentine, must at least allow the tubes to be most efficient conductors of the impression to the sentient pulp. Nature has suffered no part of the dentine to be exposed: its organization and vital powers are adequate to its own support in health, and to control that stimulus which, when the dentine is dead and truly 'an extraneous body', operates detrimentally upon the surrounding more highly organized parts: but the vitality of the dentine is insufficient for the reproduction of its tissue, or for the arrest or repair of decay. The third substance which is chiefly developed around the implanted part of the tooth is more highly organized than the dentine, more analogous to bone, and accordingly better adapted for vital connexion with the vascular

(1) See Prof. Bell's preface to his Edition of 'Hunter on the Teeth,' p. xiii.

membrane of the alveolus. It is the cement which renders a living tooth 'capable of uniting with any part of a living body' as Hunter proved by his ingenious experiments.

When the tooth performs its function throughout a long life, free from any destructive influence but that of ordinary mastication, a compensating provision would seem to have been intended against the decay of the alveoli in old age by the final substitution of a more highly organized substance, the osteo-dentine, for the ordinary dentine which has been worn away. Nor can we help admiring the analogy which this acquisition of a more vascular organization, with the weakening of the alveolar implantation, presents to the condition of the teeth in many of the lower vertebrate animals.

177. *Adaptation of the teeth to the food and nature of Man.*— Whether Man was originally designed by nature to be herbivorous or carnivorous is a question which some authors have supposed might be absolutely determined from his dentition. If we had to judge only by fossil remains we should be warranted in concluding from the human teeth that the species was not intended, under all circumstances and in all places, to subsist upon either animal or vegetable food exclusively. It would be obvious at the first glance that they were intermediate in character between the typical carnivorous and the typical herbivorous dentitions: the presence of canines and the absence of the complex structure arising from the interblending of vertical plates of the different dental tissues in the molars, would prove that the food could not have been the coarse uncooked vegetable substances for which complex molars are adapted; and on the other hand the feeble development of the canines and the absence of molars of the sectorial shape and opposed like scissor-blades, would equally show that the species had been unfitted for obtaining habitual sustenance from the raw quivering fibre of recently killed animals.

The Apes and Monkeys which Man most nearly resembles in his dentition, derive their staple food from fruits, grain, the kernels of nuts, and other forms in which the most sapid and nutritious tissues of the vegetable kingdom are elaborated; and the close resemblance between the Quadrumanous and Human

dentition shows that Man was, from the beginning, more especially adapted 'to eat of the fruit of the trees of the garden.'(1)

But the Quadrumana are not exclusively frugivorous. Some are known to seek the eggs and callow-brood of birds. The African Baboons pass whole hours in turning up great stones in quest of insects. The young Chimpanzees and Orangs in our menageries manifest no repugnance to cooked meat, and the avidity with which they will pluck and devour a sparrow leads us to suspect that their vegetable diet is occasionally varied by the capture of a live bird.

The formidable development of the canine teeth in the Orangs and Baboons seems, at the first glance, to relate to the predominance of animal food in their regimen; but the sexual difference in the development of those teeth might have indicated that they had other subserviences than to the acquisition of daily sustenance, if observation had not shewn them to have been given to the males for the purpose of combat and defence. The molar teeth are those which form always the best and sometimes the sole guides to a knowledge of the diet of a mammiferous animal: and these clearly indicate the frugivorous and mixed regimen of the Quadrumana and Man.(2)

We have seen that the most striking characteristic of the human dentition is the absence of any disproportionate development of particular teeth, and the concomitant continuity of the series in both jaws: the more immediate comparison with the Quadrumanous dentition, while it demonstrates the close similarity of the molar teeth, and supports the consequent deduction of an omnivorous diet, brings to light the very interesting difference in the proportions and disposition of the incisive and canine teeth, by which we may appreciate the adaptation of the human dentition to Man's peculiar and higher attributes. His reason furnishes

(1) This is the conclusion to which my friend Prof. Bell has arrived in his 'Physiological Observations on the Natural Food of Man, deduced from the characters of the Teeth.' On the Teeth, 8vo. 1829, p. 33.

(2) John Hunter in considering the question, "Under what class do the Human Teeth come?" concludes by stating, "He, (Man) ought, therefore, to be considered as a compound, fitted equally to live upon flesh and upon vegetables." Nat. Hist. of Human Teeth, 4to. 1771, p. 120.

him, in the lowest condition of savage life, with weapons more formidable than sharp and long canine teeth, and his mastery over fire, the prime element of cookery, enables him to dispense with strong and prominent incisors in the reduction of the tough, raw, and indigestible parts of vegetable or animal food.

But the moderate and equable development of the anterior teeth, and the graceful continuous curve which they form with the molar series, have not merely a negative relation to the substitutes which Man's inventive faculty provides for the absence of the large and strong incisors and canines of the Orangs. The smooth and equable posterior surface of the incisors, their vertical position and their close arrangement in a gentle curve with the canines, offer the best conditions for reacting upon the tongue in the various applications of that organ to the teeth during speech. The appearance of the teeth in the mouth is contemporaneous with the child's power of forming articulate sounds; and the clearness of utterance is affected both by the temporary deficiency of the incisive series during the change of dentition, and in a still greater degree by the final loss of the teeth and their sockets in old age.

Lastly, the vertical symphysis of the human jaw not only affords the most favourable position to the incisors in relation to speech, but is accompanied in the highest races with a prominence of the lower border forming the chin, which is wanting in every inferior animal: and this remarkable feature, with the short jaws proportioned to the small incisors and canines, harmoniously combine with the capacious forehead in stamping the head of Man with the impress of his intellectual superiority.

NAWAB SALAR JUNG

CHAPTER XI.

TEETH OF CARNIVORA.

178.—Having completed in Man the survey of the dental system of Omnivorous Mammalia, I next proceed to consider the stronger-featured modifications of those preparatory digestive organs

in the Orders which are more strictly limited to one kind of aliment, and to which such modifications are more immediately and decidedly related.

In this point of view it has seemed to me that the teeth of the Carnivora present a higher grade of development than those of any of the mixed or insect feeders, and, in their more essential relationship to the digestive system, their preparatory operations are much more extensive and important than in Man: the teeth of the Carnivora being adapted not only to comminute but obtain the food, to seize and kill the victim, to divide it when killed, and to separate the nutritious from the inedible parts of the prey.

Had I been guided in this ascensive survey of the dental system by the general perfection of the species, I must have ended with that of Man; but viewing its modifications and complexities irrespective of the rest of his organization, it must be admitted that, notwithstanding the admirable adaptation of the human teeth to the nature and faculties of Man, they are far from manifesting the most complex structure of those organs. This must be sought for in the herbivorous Mammalia—the Pachyderms, the Ruminants and especially the gigantic Proboscidian quadrupeds, —with which, therefore, the present Treatise on the Comparative Anatomy of the Dental System will conclude.

The predaceous Mammalia offer various kinds and degrees of deviation from the typical carnivorous dentition, as exemplified in the genus *Felis*. Throughout the Order the incisors are six above and below; few are the exceptions in which they fall short of that number, in none of the Carnivora do they exceed it: the canines are always present and largely developed, with long conical sharp-pointed and often trenchant crowns: the variations from the type are played upon the molar teeth; and herein the Carnivora offer a marked contrast with the *Insectivora*, in which we found much constancy in the bristled molars but extreme diversity in the incisors and canines. In most Carnivora one molar tooth on each side of both jaws has its crown modified, either wholly or in part, for reacting upon the opposite tooth, like the blades of scissors, in express relation to the division of flesh:

whence Cuvier has applied to this tooth the name of 'Dent carnassière,' which I have rendered 'dens sectorius,' sectorial, or scissor-tooth.(1) The compressed trenchant part of this tooth has a sharp edge, more or less deeply cleft by one or two notches, and with its divisions more or less pointed or produced in different genera: this part of the crown of the sectorial tooth I call the 'blade;' it is usually combined with one or more basal tubercles. The blade of the upper sectorial always plays upon the outside, and a little in advance of the lower sectorial. The upper permanent sectorial succeeds and displaces a deciduous tubercular molar in all Carnivora, and is, therefore, essentially a premolar tooth: the lower sectorial comes up behind the deciduous series and has no immediate predecessor, it is, therefore, a true molar and the first of that class. By these criteria the sectorial teeth may always be distinguished under every transitional variety of form which they present in the Carnivorous series, from *Machairodus* in which the crown consists exclusively of the 'blade' in both jaws, to *Ursus* in which it is wholly tubercular: the development of the tubercle bearing an inverse relation to the carnivorous propensities of the species.

The leading modifications of the Carnivorous dentition will be described as they are presented in the families typified respectively by the Dog, the Civet, the Hyæna, the Tiger, the Stoat, the Bear and the Seal.

179. *Canidæ*.—The normal dental formula of the genus *Canis* is:—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{4-4}{4-4};\ m\ \frac{2-2}{3-3}:\ =42.$$ (Pl. 125. fig. 1 & 2.)

The incisors (fig. 1) form a continuous series, describing the segment of a circle in both jaws, and progressively increase in size from the first to the third: the trenchant margin of the crown is divided by two notches into a large middle and two small lateral lobes: in the large external incisor the inner lobe is obsolete, the outer

(1) 'Fleisch-Zahn' of the German Naturalists; the term 'lacerator' is more applicable to the canine than to the trenchant molar, to which it has been applied by some English Authors. See Gardens and Menagerie of the Zoological Society, vol. i. p. 14.

one situated near the base, and the middle lobe is produced into a strong conical laniariform crown. The canines (*c*) are curved, sub-compressed; the enamelled pointed crown forms nearly half the length of the tooth, is smooth, without any groove; it has a slight internal depression and a posterior, not very sharp, ridge in the upper tooth. The premolars (*p*) have strong sub-compressed conical crowns gradually enlarging from the first to the third in the upper, and to the fourth in the lower jaw, and acquiring one or two accessory posterior tubercles as they increase in size. The fourth upper premolar presents a sudden increase with the sectorial form: its blade is divided into two cones by a wide notch, the anterior cone being the strongest and most produced; the tubercle is developed from the inner side of the base of this lobe. The first and second upper molars (*m*) are tuberculate; each supports two external cusps, and has a broad, internal, subtuberculate basal talon; but the second is very small, less than half the size of the first molar. The first true molar below is modified to form the opposing blade to the sectorial tooth above; retaining the tuberculate character at its posterior half (fig. 3, 1): the blade is divided by a vertical linear fissure into two cones, the posterior being the largest: behind this the base of the crown extends into a broad, quadrate, trituberculate talon. The second molar has two anterior cusps on the same transverse line, and a posterior broad flat talon: the last lower molar is the smallest of all the teeth; it is sometimes bituberculate, as in the Wolf, Dog, and Jackall, sometimes presents an additional talon, as in the *Canis lagopus*, and is sometimes entirely wanting, as in the *Canis primævus*.

The incisors, canines, and first premolars (*p* 1) in both jaws have each a single fang: the next two premolars above, and all the others below have two fangs, which are usually connate in the second of the lower jaw: the upper sectorial premolar has three fangs, two anteriorly on the same transverse line, and a large and strong one behind: the first true molar has four fangs, three slender external, and one strong internal: the last molar has three fangs. The lower sectorial and second molar teeth have each two fangs; the last molar has but one fang.

The normally developed deciduous molars are :—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{3-3}{3-3}: = 28.$$

The predecessors of the first permanent premolars in both jaws are seldom calcified, and generally disappear after being transitorily manifested in the papillary stage; the second, third, and fourth milk-molars which are developed and in use by the young animal, are those only which are enumerated in the deciduous formula. The incisors appear about the third week after birth, the middle ones first cutting the gum, and the other teeth following in the order of their position; the last molar is in place before the end of the sixth week. In the Dog, at three months old the successors of the deciduous teeth present the development represented in Pl. 125, fig. 4. The deciduous incisors (*i*) and canines (*c*) differ from their successors chiefly in their smaller size; the crowns of the canines are more recurved. The first molar (*d* 1) is conical with two widely diverging fangs, in both jaws: the second in the upper jaw (*d* 2) is the sectorial tooth, and has a relatively shorter blade, and the tubercle is continued more nearly from the middle of the inner side, than in the permanent sectorial: the third upper molar (*d* 3) resembles the first permanent tubercular molar, but has a less tuberculate inner lobe. In the lower jaw the first deciduous molar resembles that above, but has the anterior and posterior basal tubercles better marked; the second is similar, but larger; the third is the sectorial tooth, in which the biconical blade is shorter in proportion to the posterior quadrituberculate broad lobe, than in the permanent sectorial.

The first permanent premolar (*p* 1) comes into place before any of the deciduous teeth are shed: its germinal predecessor disappearing before birth. The second upper premolar (*p* 2) resembles in form the first deciduous molar which it displaces. The third upper premolar (*p* 3) is a more simple tooth than the sectorial molar which it displaces: the upper permanent sectorial (*p* 4) displaces the deciduous tubercular molar. The two permanent true molars (*m* 1, *m* 2) succeed each other horizontally without displacing any teeth. In the lower jaw the second and third premolars have

thicker and more obtuse as well as larger crowns than the first and second milk-molars which they displace. The lower deciduous sectorial is succeeded by the fourth premolar, which, as usual, has a more simple crown than the deciduous tooth which it displaces. The permanent sectorial has no direct deciduous predecessor and therefore must be held to be a true molar tooth, according to the character assigned to those teeth in this work. The absence of a tuberculate molar in the lower jaw of the immature Dog brings the character of the deciduous dentition of the genus *Canis* much closer to that of the typical members of the Carnivorous Order, and affords an interesting illustration of the law that 'unity of organisation is manifested directly as the proximity of the animal to the commencement of its development.'(1) The succession of two tubercular molar teeth behind the permanent sectorial tooth in the adult or permanent dentition of the lower jaw carries the genus *Canis* farther from the type of its Order, and stamps it with its own proper omnivorous character: and this contributes to adapt the Dog for a greater variety of climate, food, and other circumstances, all tending in an important degree to fit that animal for the performance of its valuable services to man.

In no other genus of Quadruped are the jaws so well or so variously armed with dental organs: notwithstanding the extent of the series, the vacancies are only sufficient to allow the interlocking of the strong canines. These are efficient and formidable weapons for seizing, slaying, and lacerating a living prey: the incisors are well adapted by their shape and advanced position for biting and gnawing: the premolars, and especially the sectorials, are made for cutting and coarsely dividing the fibres of animal tissues, and the tuberculate molars are as admirably adapted for cracking, crushing, and completing the comminution of the food, whether animal or vegetable.

Amongst the aberrant species of *Canidæ* it is interesting to find in the *Proteles*, which presents the most anomalously simple dentition in the adult state, a much greater conformity with the common

(1) This Law is defined and exemplified in my 'Lectures on the Invertebrate Animals,' p. 368, 8vo. 1843.

type in the teeth of the immature period of existence. M. de Blainville describes the deciduous dentition as including, besides the usual number of incisors and canines, the same number and kind of molars, as in the other *Canidæ;* i. e. a premolar with two fangs, a sectorial and a complex molar each with three fangs,(1) (in the upper jaw?). These are succeeded, in both jaws by four small, simple, widely separated molars (Pl. 125. fig. 6): the first has a sub-compressed conical crown supported by a single fang; the second has a larger crown of similar shape supported by two fangs; the third molar has a shorter and broader crown supported by two fangs; the fourth molar is the smallest, with a subtriquetral crown above, and a simple compressed one below, where it is supported by a single fang. In this instance of arrested development of the molar series we may discern the retention of the more strictly carnivorous (feline) type, though feebly manifested.

In the Megalotis or Long-eared Fox (*Otocyon*, Licht.) the deviation from the typical dentition of the *Canidæ* is effected by excess of development; two additional true molars being present on each side of the upper, and one on each side of the lower jaw, in the permanent series of teeth; and an approach is made by the modified form of the sectorial molar and of some of the other teeth to the dentition of the genus *Viverra*.

The upper incisors are small, simple, the outer one separate from the rest and pointed; the under incisors are sub-bilobed, relatively smaller than in the Fox. The canines are shorter and less compressed than in the Fox. The first three premolars (Pl. 125, fig. 5, *p*. 1, 2, 3) have shorter and more conical crowns, especially the last; and the sectorial tooth (*p* 4) is more advanced; the trenchant portion of the sectorial is shorter and the inner tubercle larger than in the typical *Canidæ*, in which it retains more of the form of its deciduous predecessor. The first, second, and third true molars have the internal basal ridge more developed than in the tuberculate molars of the Fox: the last molar is disproportionately small, like that of the under jaw in the typical *Canidæ*. The lower premolars, like the upper ones, are more conical and shorter in proportion to

(1) Ostéographie de *Canis*, p. 56.

their height than in the Fox; and the posterior basal ridge is more developed: the fifth tooth or first true molar, which is the lower sectorial, approaches still nearer to that in the *Viverridæ*—the anterior part answering to the trenchant portion in the Fox is tri-cuspid, the inner cusp forming the most prominent point of the crown; the posterior bicuspid portion of the tooth is smaller than in the Fox. The second true molar is quadri-cuspid; the third and fourth resemble the last two in the Fox.

180. *Viverridæ*.—This family of Carnivora which comprehends the Civets, Genets, Ichneumons, Musangs, Surikates, and Mangues, is characterized, with few exceptions, by the following formula:—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{4-4}{4-4};\ m.\ \frac{2-2}{2-2}: = 40.$$

It principally differs from that of the genus *Canis* by the absence of a tubercular tooth on each side of the lower jaw: but, in thus making a nearer step to the typical Carnivorous dentition, the *Viverridæ*, on the other hand, recede from it by the less trenchant and more tubercular character of the sectorial tooth; as will be seen in the figures of the teeth of the *Viverra indica*, in Pl. 126, fig. 1, 2 & 3.

The canines are more feeble, and their crowns are almost smooth; the premolars, however, assume a formidable size and shape in some aquatic species, as those of the sub-genus *Cynogale*, (fig. 4) in which their crowns are large, compressed, triangular, sharp pointed, with trenchant and serrated edges, like the teeth of certain sharks, (whence the name *Squalodon*, proposed for one of the species), and well adapted to the exigencies of Quadrupeds subsisting principally on fish: the opposite or obtuse, thick form of the premolars is manifested by some of the Musangs, as *Paradoxurus auratus*. The upper sectorial tooth is a 'dent de remplacement,' and the last of the premolars; its inner tubercle is larger than in the Dog, and is bilobate in the *Bassaris astuta;* the middle conical division of the blade is thicker and the posterior one is smaller than in the genus *Canis*. This tooth advances to beneath the ant-orbital foramen in the Musangs (*Para-*

doxurus), it is situated farther back in the Civets and Genets, in which the blade of the sectorial is sharper. The first upper molar (fig. 1 & 2, *m* 1) has a trihedral crown, with two small external cusps and one low and large internal tubercle: this, in *Cynogael* (fig. 5, *m* 1) is more developed.

In the lower jaw the sectorial tooth (fig. 3, *m* 1) is the first true molar, as in the Dog, and manifests its proper character by the presence of an additional pointed lobe on the inner side of the two lobes forming the blade at the fore-part of the crown: the posterior, low, and large lobe of the tooth being also tri-tuberculate, as in the Dog. The last molar (fig. 3, *m* 2) has an oval crown with four small tubercles, resembling the penultimate lower molar in the Dog, with which it corresponds.

The deciduous dentition consists, in the Viverrine family of:

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{3-3}{3-3}: \ = 28.$$

If the first permanent premolar has any predecessor it must be rudimental and disappear early in both jaws; the second premolar displaces the first normally developed deciduous molar; the third upper premolar displaces and succeeds the deciduous sectorial, which has a sharper and more compressed blade, and a relatively smaller internal tubercle, than the permanent sectorial. This tooth displaces the last deciduous molar, which is a tubercular tooth, resembling in form the first of the two upper permanent tuberculars: these, coming into place without pushing out any predecessors, enter into the category of true molar teeth. In the lower jaw the third premolar displaces the deciduous sectorial, which has three trenchant lobes, and a relatively smaller posterior talon than the permanent sectorial. The fourth premolar displaces the third or tubercular milk-molar. The permanent sectorial and tubercular molars displace no predecessors and are therefore true molars.

The first permanent premolar, which has no deciduous representative, is not developed at any period in the Mangues (*Crossarchus*), the Suricates (*Ryzæna*), or the *Mangusta paludinosa*: these Viverrines, therefore, retain throughout life more of the immature features of the family, and in the same degree approach nearer

in the numerical characters of their dentition, to the more typical Carnivora.

The alternate interlocking of the crowns of the teeth of the upper and lower jaws, which is their general relative position in the Carnivora, is well marked in regard to the premolars of the *Viverridæ* (fig. 4): as the lower canine is in front of the upper, so the first lower premolar rises into the space between the upper canine and first upper premolar; the fourth lower premolar in like manner fills the space between the third upper premolar and the sectorial tooth (*p* 4), playing upon the anterior lobe of the blade of that tooth which indicates by its position, as by its mode of succession that it is the fourth premolar of the upper jaw. The first true molar below, modified as usual in the *Carnivora* to form the lower sectorial, sends the three tubercles of its anterior part to fill the space between the sectorial and the first true molar above. In the Musangs the lower sectorial is in more direct opposition to its true analogue, the first tubercular molar in the upper jaw; and these Indian *Viverridæ* (*Paradoxuri*) are the least carnivorous of their family, their chief food consisting of the fruit of palm-trees, whence they have been called 'Palm-cats.'

181. *Hyæna*.—The dentition of this genus presents a nearer approach to the strictly carnivorous type by the reduction of the tubercular molars to a single minute tooth on each side of the upper jaw, the inferior molars being all conical or sectorial teeth: the molar teeth in both jaws are larger and stronger, and the canines smaller in proportion than in the Feline species, from the formula of which the dentition of the Hyæna differs numerically only in the retention of an additional premolar tooth on each side of both jaws. The dental formula of the genus *Hyæna* (Pl. 126, fig. 6) is:—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{4-4}{3-3};\ m.\ \frac{1-1}{1-1}: = 34.$$

The crowns of the incisors form almost a straight transverse line in both jaws; the exterior ones, above, being much larger than the four middle ones, and extending their long and thick inserted base further back: the crown of the upper and outer incisor is strong,

conical, recurved, like that of a small canine, with an anterior and posterior edge, and a slight ridge along the inner side of the base. The four intermediate small incisors are divided by a transverse cleft into a strong anterior conical lobe, and a posterior ridge, which is notched vertically; giving the crown the figure of a trefoil. The lower incisors gradually increase in size from the first to the third; this and the second have the crown indented externally, but they have not the posterior notched ridge like the small upper incisors; the apex of their conical crown fits into the interspace of the three lobes of the incisor above. The canines have a smooth convex exterior surface, divided by an anterior and posterior edge from a less convex inner side: this surface is almost flat and of less relative extent in the inferior canines. The first premolar above (*p* 1) is very small, with a low, thick conical crown: the second presents a sudden increase of size with an additional posterior and internal basal ridge to the strong cone. The third premolar exhibits the same form on a still larger scale, and is remarkable for its powerful aspect. The posterior part of the cone of each of these premolars is traversed by a longitudinal ridge. The fourth premolar (*p* 4) is the carnassial tooth and has its long blade divided by two notches into three lobes, the first a small thick cone, the second a long and compressed cone, the third a horizontal sinuous trenchant plate: a strong trihedral tubercle is developed from the inner side of the base of the anterior part of the crown. The single true molar of the upper jaw (fig. 7, *m* 1) is a tubercular tooth of small size: it is transversely oblong in the *Hyæna vulgaris* and *H. fusca*; smaller and sub-circular in the *Hyæna crocuta*; still smaller and implanted by a single fang in the *Hyæna spelæa*: in all the existing species of Hyæna it has two fangs. The first premolar of the lower jaw (fig. 6, *p* 2) fits into the interspace between the first and second premolars above, and answers, therefore, to the second lower premolar in the *Viverridæ*: it is accordingly much larger than the first above; it has a ridge in the forepart of its cone, and a broad basal talon behind. The second (*p* 3) is the largest of the lower premolars, and has an anterior and a posterior basal ridge, with a vertical ridge

ascending upon the fore as well as the back part of the strong rounded cone: the third premolar (*p* 4) is proportionally less in the *Hyæna crocuta* than in the *H. vulgaris*; its posterior ridge is developed into a small cone. The last tooth (*m* 1) is the sectorial and consists almost entirely of a blade divided by a vertical fissure into two sub-equal compressed pointed lobes: the points are less produced than in the Felines, but the lower sectorial of the Hyæna is better distinguished by the small posterior basal talon, from which a ridge is continued along the inner side of the base, and is slightly thickened at the fore-part of the crown. According to the relative position of the crowns of the premolars, the third below ought to be the last, being analogous to the fourth in the *Viverridæ*, and the sectorial should be the first true molar: we shall find this view confirmed by the test of the mode of succession of the permanent teeth. But the mode of implantation of the premolar and molar teeth may first be noticed. The first upper premolar has but one fang; the second and third have each two; the sectorial tooth has three, the two anterior ones on the same transverse line, the inner one supporting the tubercle. The lower premolars and sectorial have each two fangs, there being none truly answering to the first above: the anterior root of the lower sectorial tooth is very strongly developed in the great extinct Cave-Hyæna.

The deciduous teeth approximate, as usual, to the typical dentition of the Carnivora; they consist of:—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{3-3}{3-3}: \quad = \quad 22.$$

The figure of the skull of the young *Hyæna crocuta* in the posthumous Edition of the 'Ossemens Fossiles,' 8vo. 1836, pl. 190, fig. 3, shows that stage when the correspondence with the formula of the genus *Felis* is completed by the appearance, in the upper jaw, of a small premolar in the interspace between the canine and first molar of the deciduous series: but this appearance is due to the apex of the first permanent premolar which cuts the gum before any of the normal deciduous teeth are shed: whether it is preceded, as in the Dog, by a deciduous germ-tooth in the fœtus I know not. The first normal deciduous molar is two-fanged, and has a more compressed and consequently more carnivorous crown

than that of the second permanent premolar by which it is succeeded. The second deciduous molar is the sectorial tooth: the inner tubercle is continued from the base of the middle lobe, and thus resembles the permanent sectorial of the Glutton (*Gulo*) and many other *Mustelidæ*; the deciduous tubercular molar is relatively larger than in the adult *Hyæna*, and offers another feature of resemblance to the permanent dentition of the Glutton. It is also worthy of remark that the exterior incisor of the upper jaw is not only absolutely, but relatively smaller in the immature than in the adult dentition of the Hyæna, giving another feature of resemblance to the more common type of dentition in the Carnivora.

The first and second deciduous molars below (Pl. 126, fig. 9) have more compressed conical crowns than their successors: the third deciduous molar (fig. 9, 3) is the sectorial tooth, and, again, as in *Gulo*, has a better developed hinder tubercle than the permanent sectorial; it is not displaced by this tooth, but, as in other Carnivora, by a premolar (p. 4) of more simple character. The permanent sectorial (*m* 1) is developed posteriorly and rises, like other true molars, without displacing a deciduous predecessor.

The permanent dentition of the *Hyæna*, as of other genera or families of the Carnivora, assumes those characteristics which adapt it for the peculiar food and habits of the adult and mark the deviation from the common type, which always accompanies the progress to maturity. The most characteristic modification of this dentition is the great size and strength of the molars as compared with the canines, and more especially the thick and strong conical crowns of the second and third premolars in both jaws, the base of the cone being belted by a strong ridge which defends the subjacent gum.(1) This form of tooth is especially adapted for gnawing and breaking bones, and the whole cranium has its shape modified by the enormous development of the muscles which work the jaws and teeth in this operation.(2) Adapted

(1) An eminent Civil-Engineer, to whom I showed the jaw of a Hyæna, observed that the strong conical tooth, with its basal ridge was a perfect model of a hammer for breaking stones for roads.

(2) "The strength of the Hyæna's jaw is such that, in attacking a Dog, he begins by biting off his leg at a single snap." Buckland, 'Reliquiæ Diluvianæ,' p. 23.

to obtain its food from the coarser parts of animals, which are left by the nobler beasts of prey, the Hyæna chiefly seeks the dead carcase, and bears the same relation to the Lion which the Vulture does to the Eagle. In consequence of the quantity of bones which enter into its food, the excrements consist of solid balls of a yellowish white colour, and of a compact earthy fracture. Such specimens of this substance, known in the old *Materia Medica* by the name of 'album græcum,' were discovered by Dr. Buckland in the celebrated ossiferous cavern at Kirkdale. They were recognised at first sight by the keeper of a menagerie, to whom they were shown, as resembling both in form and appearance the fæces of the spotted Hyæna; and, being analysed by Dr. Wollaston, were found to be composed of the ingredients that might be expected in fœcal matter derived from bones, viz.: phosphate of lime, carbonate of lime, and a very small proportion of the triple phosphate of ammonia and magnesia. This discovery of the coprolites of the Hyæna formed, perhaps, the strongest of the links in that chain of evidence by which Dr. Buckland proved that the cave at Kirkdale in Yorkshire had been, during a long succession of years, inhabited as a den by Hyænas, and that they dragged into its recesses the bodies of other animals, whose remains, splintered and bearing marks of the teeth of the Hyæna, were found mixed indiscriminately with their own.

182. *Felidæ*.—The dentition in the well-marked and circumscribed genus of Cats (*Felis*) might be recognised as the most typical of the order *Carnivora*, not only from its formidable simplicity and peculiar adaptation to the destruction of living animals and the mastication of their flesh; but because it is that to which the transitory dentitions of all the other digitigrade families and genera more or less closely approximate. The feline formula (Pl. 127, fig. 1) is:—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{2-2};\ \text{molars } \frac{1}{1}: = 28.$$

The six incisors in both jaws are closely arranged with their crowns in a transverse line; their fangs, for economy of space, are zig-zag, at least in the lower jaw: the outer incisor of the upper jaw is

not so large as in the Hyæna, but is conical, with a sharp ridge on the outer side, and a small tubercle on the inner side, in which the posterior basal ridge terminates: the smaller intermediate incisors have their broad and thick crowns indented by a transverse cleft, and the posterior ridge so defined, is sub-divided by a minute vertical notch, which is soon worn away. The lower incisors are smaller, especially the outer pair, which have an external basal tubercle, and have not the posterior ridge. The canines are very large and strong; the fang commonly thicker and longer than the enamelled crown: this is conical, sub-compressed, slightly recurved, sharp-pointed; convex anteriorly and externally; much less convex internally, almost flat here in the lower canines: the two surfaces are divided by a sharp ridge behind, where they meet at an acute angle and where feeble indications of a serrated structure may be discerned in the larger Cats, as the Lion and Tiger: both the outer and the inner surfaces of the crown are indented with one, or more commonly, two parallel longitudinal grooves, which are very characteristic of the canines of the typical *Felidæ;* they are faintly expressed in those of the Hunting Leopard, and are not present in the long, compressed and serrated canines of the very formidable extinct Feline sub-genus *Machairodus.*

The first upper premolar (marked *p* 2 in fig 1, as answering to the second in the Hyæna and Dog) is a very small tooth with an obtuse conical crown supported by a single fang, except in the *Felis planiceps* in which it retains its typical structure, and has two fangs: the opposite variety is manifested by the Short-tailed Lynxes, in which this small premolar is commonly wanting, as in the extinct *Machairodus.* The second upper premolar (*p* 3), of much larger size, has a sub-compressed conical crown, with a posterior, sometimes bilobed, basal tubercle, and a small anterior prominence; it has two strong diverging fangs. The third upper premolar (*p* 4) is the sectorial tooth; its extensive blade is divided into three lobes by two angular notches; the first and second lobes are conical, the latter the largest and with its point inclined backwards as in all strictly flesh-eating *Carnivora,* an obtuse ridge is continued from its inner side to the base of the internal tubercle; the third lobe is

flat on the inner side of the blade, and has a horizontal sinuous edge: the internal basal tubercle (fig. 2, *p* 4) is developed from the interspace between the first and second lobes of the blade: this is relatively smaller than in the Hyæna, and almost obsolete in the Hunting-Leopard (*Felis jubata*) and in a small allied extinct Feline animal of Brazil, which Dr. Lund, adopting the sub-generic name applied by Wagler to the Hunting-Leopard, calls *Cynailurus minutus*(1). In all the *Felidæ* the upper sectorial has three fangs, the two anterior ones being on the same transverse line. The small tubercular true molar (fig. 1 & 2, *m* 1) has a transversely extended elliptical or sub-trihedral crown.

The first lower premolar (marked *p* 3 as being the analogue of the third in the Dog) is implanted by two fangs which support a middle compressed cone and an anterior and posterior basal tubercle; its crown passing behind the first upper premolar shows it to answer to the second above. The second premolar below (*p* 4) is larger and has two posterior tubercles; its crown fits into the space between the second and the third or sectorial premolar above, opposing the anterior lobe of that tooth. The last molar below (*m* 1) is the sectorial tooth, the crown of which consists exclusively of the blade; this is divided into two equal, compressed, pointed lobes, with straight margins, very sharp except the anterior one of the first lobe; the contiguous margins of the two lobes meet at a right angle, from which a vertical fissure extends nearly half way down the crown. The outer surface of the crown presents an equable convexity from before backwards; the inner side is deeply excavated between the lobes (fig. 3). A transverse notch near the base of the posterior margin of this tooth indicates the rudiment of the talon or tubercle which distinguishes the corresponding tooth of the Hyæna; the indication being strongest in the aberrant species of Felis, as the Lynx and Hunting-Leopard(2). Although the lobes of the crown of the lower sectorial tooth are equal, the anterior fang is much larger

(1) Bilk paa Brasilien Dyreverden, &c., Kjöbenhavn, 4to. 1839, p. 35.

(2) M. de Blainville, by whom many interesting varieties manifested by specimens in the Cuvierian collection have been carefully noted, figures one, from the Canada Lynx, in which a small tubercular molar exists behind the lower sectorial tooth; thus presenting an analogy to the Stoat and other *Mustelidæ*. 'Ostéographie de Felis,' pl. 14, p. 57.

than the posterior one. It would be difficult to recognise this metamorphosed molar as the corresponding tooth to the small tubercular above, were we not assured of the fact by the constancy in the relative position of the crowns of the molar series in the Carnivora, where the lower ones are always in advance of the upper, and still more unequivocally by the relations of the permanent to the deciduous teeth.

The deciduous dentition in the genus *Felis* (Pl. 127, fig. 4) is:—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{3-3}{2-2}: = 26.$$

The incisors in the common Cat begin to appear above the gum when it is between two and three weeks old; the canines next, and then the molars follow, the whole being in place before the end of the sixth week. After the seventh month they begin to fall in the same order; but the lower sectorial molar rises above the gum before any of the deciduous molars are displaced. The longitudinal grooves are very faintly marked in the deciduous canines. The first deciduous molar in the upper jaw (*d* 1) is a very small and simple, one-fanged tooth; it is succeeded by the corresponding tooth of the permanent series, which answers to the second premolar of the Hyæna and Dog. The second deciduous molar (*d* 2) is the sectorial tooth; its blade is trilobate, but both the anterior and posterior smaller lobes are notched, and the internal tubercle, which is relatively larger than in the permanent sectorial, is continued from the base of the middle lobe, as in the deciduous sectorial of the Dog and Hyæna; it thus typifies the form of the upper sectorial in the permanent dentition of several Viverrine and Musteline species. The third or internal fang of the deciduous sectorial is continued from the inner tubercle, and is opposite the interspace of the two outer fangs. The Musteline type is further adhered to by the young Feline in the large proportional size of its deciduous tubercular tooth (*d* 3). In the lower jaw, the first milk-molar (*d* 1) is succeeded by a tooth (*p* 3) which is analogous to the third lower premolar in the Dog and Civet(1). The deciduous sectorial (*d* 2), which

(1) M. de Blainville states that the first lower deciduous molar in the *Felis maniculata* has an unusually thick crown supported by three roots, and hence derives an argument against the opinion of Temminck, that this Egyptian wild Cat was the source of our domestic

is succeeded by the second premolar (analogous to the fourth in the Dog), has a smaller proportional anterior lobe and a larger posterior talon, which is usually notched; thereby approaching the form of the permanent lower sectorial tooth in the *Mustelidæ*. We thus perceive that even the fierce Feline Carnivora recede in a slight degree, as they advance to maturity, from the more common type of the dentition of their order, by the suppression of a few characters retained in other genera; whereby they acquire a more decidedly destructive and carnivorous dentition, which more strongly marks their own peculiar predatory characters.

A single glance at the long and strong, sub-compressed, trenchant and sharp-pointed canines, closely interlocking, the lower in front of the upper, when the jaws are clenched, suffices to appreciate their peculiar adaptation to seize, to hold, to slay and lacerate a struggling prey. The jaws are strong, but shorter than in other Carnivora and with a concomitant paucity of the molar teeth: thus the canines are brought nearer to the insertion of the very powerful temporal and masseter muscles, which work them with proportionally greater force. The use of the small incisor teeth is obvious to any one watching a captive Lion or Tiger at its meals: they are applied to gnaw the soft cartilaginous ends of the bones, and to tear and scrape off the tendinous insertions of the muscles and the periosteum. The compressed trenchant blades of the sectorial teeth play vertically upon each other like the blades of scissors; and the form of the mandibular articulation almost limits the movements of the jaws to the vertical direction. The wide and deep zygomatic arches, and the high sagittal and occipital crests concur in completing the destructive character of the cranium of these most formidable of the Carnivora.

183. *Machairodus*(1).—This generic name was given by Dr. Kaup to the extinct animal which was armed with canine teeth, like that figured in pl. 127, figs. 5 & 6. Such teeth, long, compressed, falciform, sharp-pointed and with anterior and posterior finely-ser-

race, in which the first deciduous molar has the usual form and number of fangs, as in our own Wild Cat (*Felis Catus.*)

(1) From μάχαιρα *a sabre*, and ὀδὲς *a tooth.*

rated edges, but of larger size than the specimen figured (fig. 6) were first discovered in tertiary strata in Italy and Germany, and were referred by Cuvier to a species of Bear under the name of *Ursus cultridens;* but similar canines were afterwards discovered *in situ* with some of the molar teeth in the tertiary deposits of France,(1) which proved the animal to belong to the Feline family; and the same evidence is afforded by fossil specimens of both upper and lower jaws of other species of *Machairodus* from the tertiary deposits of the Sewalik mountain range in India, transmitted by Captain Cautley to the British Museum; as well as by remains discovered in the newer tertiary deposits of Buenos Ayres, and in the ossiferous Caves of Brasil.(2)

The dental formula of the present extinct genus of *Felidæ* is :—

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{2-2}{2-2}$; molars $\frac{1-1}{1-1}$: = 28.

Here, therefore the adult dentition closely approximates the deciduous formula of the genus *Felis*. In the lower jaw of the *Machairodus neogæus* in the British Museum the anterior premolar on each side the lower jaw is shed, and its dentition is thus rendered numerically identical with that transitory formula. The dental characteristic of the immature state of the existing Lion and Tiger was thus retained, in combination with a most remarkable modification of the canine teeth, in the extinct and more formidable Carnivore of the ancient world.

The middle incisors of the upper jaw, in the depth and width of the vertical notch bisecting the posterior ridge of the crown, more closely resemble those of the *Hyæna* than those of the *Felines;* they are more compressed, especially at their strong implanted base. The external incisor is as large as, and in some species appears to be larger in proportion to the intermediate incisors, than in the genus *Felis*. In the ancient British *Machairodus (M. latidens,)* the anterior convex part of the crown of the external incisor is

(1) Bravard, Monographie de deux Félis d'Auvergne, 1828.

(2) See my History of British Fossil Mammalia,' Part IV., 1844, p. 174. The remains of *Machairodus* from the Brazilian caves were first noticed by their discoverer Dr. Lund as indications of an extinct Hyæna, for which he proposed the name of *H. neogæa :* subsequently he recognised its distinctive characters, and proposed for it the generic name of *Smilodon :* the canine tooth figured in Dr. Lund's second Memoir, in the Copenhagen Transac-

divided from the posterior less convex surface by two finely serrated ridges, at the base of each of which there is a tubercle: the fang is longer and more compressed in *Machairodus neogæus* of S. America, than in *M. latidens*. The canine figured in Pl. 127, fig. 6, is one of a few specimens of similar form and size which have been found in ossiferous caves in England, associated with remains of a large Tiger and other extinct Mammals. The compressed crown presents no trace of the longitudinal impressions which characterise the canines of the true *Felis* but is provided with a double cutting edge of serrated enamel; the posterior concave edge is continued to the base of the crown, the anterior convex margin becomes thicker as it approaches the base, like the back of a knife, and the strength of the crown is further increased by the expansion of its sides. Thus in the *Machairodus*, as in the *Megalosaurus*, whose teeth the present canines most nearly resemble, each movement of the jaw combined the power of the knife and saw; the points of the teeth in making the first incision would act like a two-edged sabre, and their backward curvature would give them better holdfast. The first premolar of the upper jaw (ib. fig. 5, *p* 3) corresponds with the second in the genus *Felis*, and with the third in *Canis* and *Viverra*. The crown is elliptic, low, with a middle compressed cone trenchant before and behind, having a small blunt tubercle at the fore part of its base, and two tubercles behind, the first conical and pointed, the second obtuse. The succeeding tooth (ib. *p* 4) is the sectorial, and is larger in proportion to the preceding premolar than in *Felis*: it is, also, much more 'carnassial' to use the Cuvierian term, having no other indication of the internal tubercle than a slight basal thickening of the blunt ridge which descends along the inner side of the middle lobe of the blade: it is more like the deciduous than the permanent sectorial in the true Cats. The crown of the tooth consists of the antero-posteriorly elongated strong and trenchant blade: it is divided into three principal lobes; but the anterior and smallest differs from that in the permanent sectorial of the true Cats in being sub-divided into an an-

tions, 1842, Pl. 37, fig. 5, 6, 7. agrees with that of *Machairodus*, to which genus the extinct carnivore belongs by the number and structure of the molar teeth.

terior obtuse tubercle and a posterior larger compressed pointed portion: the second lobe resembles that in *Felis*; the third is relatively larger, equalling in some species, as *Machairodus neogæus*, half the antero-posterior extent of the crown; its trenchant edge being, however, as in the Cats, horizontally sinuous. The upper sectorial differs still more from that of the typical *Felidæ* in being supported by only two fangs. The tubercular tooth is small, with a more rounded crown than in *Felis*. The canines of the lower jaw are much shorter than those above, and form the outer teeth of the same transverse series with the incisors, like the lower canines of the Ruminants, whose true nature they serve to indicate. The fore-part of the lower jaw, which supports those teeth and the incisors is of unusual depth, for the purpose of affording a kind of defensive buttress to the long sabre-shaped crowns of the upper canines, when the mouth is closed. In this state the crown of the first lower premolar (ib. *p* 3) is applied to the fore-part of that above, and is therefore strictly its analogue, answering, like the first lower premolar in the true Felines, to the third premolar in the Dog. In *Machairodus neogæus* it is minute and simple; in the small *Machairodus* (*M. megantereon*), found fossil in France, it has a middle compressed principal cone, with one basal tubercle in front, and two behind. The second lower premolar (ib. *p* 4) is double the size, and its true relationship to the last premolar of the upper jaw is here manifested, not only by relative position, and mode of succession, but by the form of the crown: the anterior basal tubercle is developed into a sub-compressed cone, answering to the anterior lobe of the blade of the upper sectorial; the middle and largest compressed cone below repeats the form of the middle lobe of the sectorial blade above, whilst the sinuous edge of the posterior lobe of the upper sectorial is represented by the two better defined posterior basal cones of the lower last premolar tooth. The third tooth of the lower jaw of *Machairodus* (ib. *m* 1) which is a true molar, retains the peculiar sectorial modification of the crown, which characterises it in the normal Feline animals; but its trenchant and sharp-pointed lobes are more inclined backwards. The entire dentition of this most extraordinary and formidable of extinct predaceous animals

thus accords with the peculiarly destructive character of the upper canine teeth, and manifests permanently that super-carnassial character which is temporarily typified in the dentition of the cubs of the Lion and Tiger; and the Machairodus thus yields another example of a lost primæval form which retained throughout life structures that are transitory in the present races.

184. *Mustelidæ.*—Of this family the Stoats, Ferrets, and Weasels (*Putorius*) are the most carnivorous, predacéous and blood-thirsty: their canine teeth are long, slender, and very sharp-pointed; the incisors small, gradually increasing from the internal one, with the crowns in zigzag series in the lower jaw, the second incisor being posterior to the first and third. The dental formula of the genus *Putorius* is:—

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{1-1}{2-2}$: = 34.

The only diastema is in the upper jaw, between the incisors and canine. The first premolar is very small; the second is twice the size of the first, and the third twice the size of the second: in the sectorial tooth the blade consists chiefly of one compressed pointed lobe; the tubercle is small: the true molar is relatively larger than in *Felis*, and consists of an outer and an inner tubercle; the latter being the broadest. In the lower jaw the last premolar is twice the size of the first; the second is intermediate in size, as it is in position: but it has no inner tubercle to match that of the analogous tooth above; and in general the lower molars are narrower transversely than the upper ones. The first true molar below has a sectorial crown with a bilobed blade and a posterior tubercle; but no internal one: the second true molar has a small round obtuse crown. The Cape-Stoats (*Zorilla*) have an inner tubercle on the same transverse line with the posterior lobe of the blade of the lower sectorial tooth, which thus begins to deviate from the true Carnivorous type and to acquire the tubercular character which is proper to it as a true molar.

The Grison (*Galictis*) and the Taira (*Gal. Barbara*, Pl. 128, fig. 1.) repeat the characters of the dentition of the Zorille, with a greater

relative thickness of the crowns of most of the teeth, and a larger development of the tubercle of the upper sectorial tooth; ib. fig. 2. *p* 4 (1).

The Martin-Cats (*Mustela*, Cuvier), have an additional premolar at the beginning of each series, their dental formula being :—

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{4-4}{4-4}$; molars $\frac{1-1}{2-2}$: = 38.

The canines are shorter and stouter, and the upper true molar (Pl. 128, fig. 5, *m* 1) has a larger crown than in the Stoats. The inner tubercle also exists in the lower sectorial (ib. fig. 6, *m* 1) but is relatively smaller than in the Zorilles.

The Wolverenes and Gluttons, (*Gulo*, Pl. 128, fig. 7), have the same dentition, numerically, as the Martins, but have relatively stronger canines, and no inner tubercle on the lower sectorial tooth (ib. fig. 9, *m* 1): their habits answer to this resumption of a more carnivorous type of dentition.

The Skunks, (*Mephitis* and *Mydaus*,) with the exception of the *Mephitis Humboldtii*, (Pl. 128, fig. 11) which wants the first upper small premolar, have the same dentition, numerically, as the Stoats; but the internal tubercle of the upper sectorial (fig. 11, *p* 4,) is so much more developed that the crown assumes a triangular form: the true molar (fig. 11, *m* 1.) which follows, surpasses the sectorial in size, and has a broad, quadrate and quadrituberculate crown. In the lower jaw the omnivorous character is manifested by the assumption of a tubercular crown and the almost total loss of the sectorial form by the first true molar, which supports six small tubercles; three on the inner border, two on the outer border, and one behind.

The dental formula of the Otter (*Lutra*) is:—

in. $\frac{3-3}{3-3}$; *c.* $\frac{1-1}{1-1}$; *pm.* $\frac{4-4}{3-3}$: *m.* $\frac{1-1}{2-2}$; = 36. (Pl. 128, fig. 4.)

The first premolar, (*p* 1) very small and single-fanged, lies close upon the inner side of the strong canine, and is not visible from with-

(1) See the excellent description, by Prof. T. Bell, of the *Galictis vittata*, in the Trans. Zool. Soc. vol. II, p. 201, Pl. 35 & 36. He assigns, however, 2-2 premolars to the upper jaw, as M. F. Cuvier does in his dental formula of *Putorius*, regarding the upper sectorial as the corresponding tooth to the lower sectorial.

out: the second (*p* 2) almost touches the posterior surface of the canine, has a compressed conical, sharp-pointed crown, with an anterior and posterior talon: the third (*p* 3) is similar but larger: the fourth is the sectorial tooth, (fig. 4 & 5, *p* 4), with its blade divided into two lobes, each pointed and inclined backwards, and it has a small anterior talon, and a large, flat, semi-circular inner tubercle. The true molar (ib. *m* 1) has a large rhomboidal grinding surface, with two external cusps separated by a broad concave surface from two smaller internal tubercles. The first (fig. 4, *p* 2), second (*p* 3), and third (*p* 4) premolars of the lower jaw progressively increase in size, and have similarly shaped, compressed, pointed crowns; the last increasing in breadth posteriorly, and having the talon there more distinct. The first true molar (fig. 6, *m* 1) is essentially like that of the Zorille, but is relatively broader, with a greater development of the internal tubercle and posterior broad grinding surface: the sectorial blade forms an accessory, rather than a principal, part of the crown; it is divided into two pointed compressed lobes. The last true molar is relatively smaller than in the Civet, and has a round sub-tuberculate crown.

The Sea-Otter (Pl. 128, fig. 12.) has one molar less on each side of the upper jaw than the common Otter: the first small premolar is the absent tooth, and the posterior molars are so remarkably modified as to justify the sub-generic distinction proposed for the marine species by the name of *Enhydra marina*. There is nothing peculiar in the incisors or canines: the second premolar (*p* 3) has a strong obtuse conical crown with a posterior basal ridge, and is double the size of the first premolar (*p* 2): the third (*p* 4) is more than twice the size of the second, and represents the sectorial tooth most strangely modified; the two lobes of the blade are hemispherical tubercles, the first the largest; the crown of the tooth is much extended inwards and is developed into a third similar tubercle. The last upper tooth, which is the first true molar (*m* 1) has a rather larger crown than the sectorial, and of similar transversely extended triangular form; but the base is turned inwards, and the apex forms a hemispheric tubercle, the rest of the broad grinding surface being irregular. In the lower jaw the teeth are not sepa-

rated by any interspace: the first and second premolars have oblique obtuse conical crowns. The third premolar is more than twice the size of the second and supports a large anterior hemispheric protuberance with a small internal tubercle and a posterior basal ridge. The first true molar has an oblong quadrate crown with an anterior small tubercle, a larger and more prominent inner one, and the rest of the broad horizontal surface undulating. The second true molar has a transversely elliptical crown depressed in the centre. When the teeth are in apposition, the anterior third of the first true molar below is applied to the inner tubercle of the last premolar above; the rest of its crown plays upon that of its analogue the first true molar in the upper jaw, leaving a small part of that tooth to receive the appulse of the second true molar below, which has no corresponding tooth in the upper jaw.

The *Mustelidæ* present great constancy in regard to the number of their true or post-molar teeth; with one exception, (*Mellivora*), the lower molar series of which is figured at Pl. 128, fig. 10, showing the absence of the second true molar, they have one true molar on each side of the upper jaw, and two on each side of the lower jaw: the second of these has always a broad tubercular crown, like the one above. The upper true molar is supported by one inner, and sometimes by one (*Putorius*, *Gulo*), sometimes two (*Mustela*, *Lutra*, *Mephitis*), outer fangs. The second true molar below is also tubercular but has a single fang. The crown of the first true molar below offers many gradations from the sectorial type as manifested in *Putorius* and *Gulo*, to the tubercular type as in the Taira, Ratel (Pl. 128, fig. 10 *m* 1) and Sea-Otter (ib. fig. 12 *m* 1); it is usually supported by two fangs; a small intermediate supplemental root is occasionally developed, as in the example from the Otter figured by M. de Blainville, (*Ostéog. de Mustela*, Pl. XIII.) The principal varieties occur, as usual, in the comparatively less important premolars: in the Martins and Gluttons (Pl. 128, fig. 7) they are as numerous as in the Dog; the first, in both jaws, being implanted by a single fang; the rest by two, with the exception of the last above which has three roots. In the Otter (ib. fig. 4) we find the first premolar removed from the

lower jaw; and the second (now the first) shows its true analogies by its double implantation, as well as by the position of its crown behind the first in the upper jaw (*p* 1.) In the Stoats (fig. 1), Skunks and Ratels, the premolar series is further reduced by the loss of the anterior tooth in both jaws, and by the diminution of the size of the second, thus become the first in both jaws, and which is also now implanted by a single fang. In a South American Skunk (*Mephitis Humboldtii*, fig. 11), the second premolar disappears in the upper jaw, leaving there only the analogues of the third and fourth, which latter is always the sectorial in the *Mustelidæ*, as in other terrestrial *Carnivora*. This tooth, under all its modifications, retains the blade with the lobe, corresponding to the middle one in the feline sectorial, generally well developed and sharp pointed: the differences are principally manifested by the proportions of the inner tubercle, and the relative size of the third root supporting it. But the upper sectorial, being a premolar, and therefore requiring less modification of the crown to adapt it for its special functions, manifests a more limited extent of variety than the lower sectorial, which, being a true molar, requires greater modification of the typical form of its crown to fit it for playing upon the opposite blade of the flesh-cutting pair of teeth.

185. *Melidæ*.—In this sub-family I comprise the European Badger (*Meles*), the Indian Badger (*Arctonyx*), and the American Badger (*Taxidea*); which, with respect to their dentition, stand at the opposite extreme of the *Mustelidæ* to that occupied by the predaceous Weasel, and manifest the most tuberculate and omnivorous character of the teeth. The formula (Pl. 128, fig. 13, Pl. 129, fig. 1.) is:—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{4-4};\ \text{molars } \frac{1-1}{2-2}:\ = 30.$$

The canines (Pl. 129, fig. 2 and 5,) are strongly developed, well pointed, with a posterior trenchant edge: they are more compressed in *Arctonyx* than in *Meles*. The first lower premolar (*p* 1) is very small, single-fanged, and, generally, soon lost. The first above, (Pl. 128, fig. 13, Pl. 129, fig. 1, *p* 2) corresponding with the second in the Dog, is also small and implanted by two connate

fangs. The second upper premolar (ib. *p* 3) has a larger, but simple, sub-compressed, conical crown, and is implanted by two fangs: the third (ib. *p* 4) repeats the form of the second on a larger scale, with a better developed posterior talon, and with the addition of a tri-tuberculate low flat lobe, which is supported by a third fang: the outer pointed and more produced part of this tooth represents the blade of the sectorial and the entire crown of the antecedent premolars. The true molar in *Meles* (Pl. 129, fig. 1 & 3 *m* 1.) is of enormous size compared with that of any of the preceding Carnivora: it has three external tubercles, and an extensive horizontal surface traversed longitudinally by a low ridge and bounded by an internal belt, the *cingulum* of Illiger: this tooth has a similarly shaped, but relatively smaller crown in *Arctonyx* (Pl. 128, fig. 13, *m* 1). The second premolar below (ib. *p* 2) is commonly the first, through the early loss of the minute one in front: its fangs are usually connate, as in its analogue above. The third and fourth premolars slightly increase in size, have simple compressed conical crowns and two fangs each. The first true molar below (Pl. 128, fig. 13, *m* 1, Pl. 129, fig. 6, *m* 1) now retains little of its sectorial character, the blade being represented only by the two anterior small, compressed pointed lobes; behind these the crown expands into an oval grinding surface, narrower in *Arctonyx* than in *Meles*, supporting three tubercles and a posterior tuberculate ridge: it has generally two principal roots and a small intermediate accessory fang as in the Otter. The second molar (ib. *m* 2) which terminates the series below, is of small size and has a rounded flat crown, depressed in the centre and with two small external tubercles: its two short fangs are connate. In the Labrador Badger (*Taxidea*)(1) the last premolar has a larger relative size, the part

(1) Trans. Zool. Society, vol. II, p. 343, pl. 59. The genus *Meles* intervenes between *Lutra* and *Canis* in the description of the teeth of Mammalia by M. F. Cuvier. Mr. Waterhouse (Proceedings of Zool. Soc. 1837.) and Prof. Wiegmann (Archiv fur Naturgeschichte, 1838, p. 257.) have recognised the closer affinity of the Badgers to the *Mustelidæ* than to the *Ursidæ*. The value of the generic distinction of the European and Indian Badgers is very doubtful; that proposed by Mr. Waterhouse for the North American species is better supported by the dental and cranial modifications; but unnecessary multiplication of names is much to be deprecated.

corresponding with the blade of the sectorial is sharper and more produced, and the internal tubercle has two lobes: the succeeding molar tooth is reduced in size and its crown presents a triangular form. The first true molar below has its sectorial lobes better developed: these differences give the North American Badgers a more carnivorous character than is manifested by the Indian or European species.

186. *Sub-Ursidæ.*—In other allied genera, which, like the Badgers, have been grouped, on account of the plantigrade structure of their feet, with the Bears, a progressive approximation is made to the type of the dentition of the Ursine species. The first true molar below soon loses all its sectorial modification, and acquires its true tubercular character: and the last premolar above becomes more directly and completely opposed to its fellow in the lower jaw. The Racoon (*Procyon*, Pl. 129, fig. 7) and the Coati (*Nasua*, ib. fig. 8-13) present good examples of these transitional modifications; they have the complete number of premolar teeth, the dental formula being:—

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{4-4}{4-4}$; molars $\frac{2-2}{2-2}$: = 40.

The development of the inner part of the crown of the last upper premolar, which constitutes the tubercle of the sectorial tooth, now produces two tubercles on a level with the outer ones which represent the blade; (Pl. 129, fig. 7 & 8, *p* 4); and the opposite premolar below (fig. 11, *p* 4) which is the true analogue of the modified sectorial above, begins to acquire a marked increase of breadth and accessory basal tubercles. All the lower premolars, as well as the true molars, have two fangs; the three first premolars above have two fangs, the fourth has three, like the two true molars above.

The dental formula of the Indian Benturong (*Arctictis*) and Kinkajou (*Cercoleptes*) is:—

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{2-2}{2-2}$: = 36.

The Benturong (Pl. 129, fig. 14 & 15) differs from its South American analogue the Coati, not only in the absence of the anterior

premolar in both jaws, but by the smaller size and more simple structure of the true molar teeth, with the exception of the first below (fig. 15, *m* 1), which still indicates the sectorial character by the development of a sub-compressed pointed lobe on the outer side of the crown. In the small size of the last true molars the Benturong manifests its affinity with the *Viverridæ*. In the Kinkajou (Pl. 129, fig. 16, 17), the true molars more nearly approach in form and proportions those of the Coati and Raccoon: the two fangs of the first and second premolars in both jaws are connate.

187. *Ursidæ*.—The essential characteristic of the dentition of the true Bears is the development, in the lower jaw, of the true molar teeth to their typical number in the placental Mammalia, and their general manifestation, in both jaws, of a tuberculate grinding surface. The premolar teeth are so reduced both in size and number, that for the better understanding of the nature and analogies of the molar series, I shall commence by the description of the deciduous series of teeth.

The immature or transitory dentition of the Bear, consists of:

$$i.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{3-3}{3-3}: = 22.$$ (Pl. 130, fig. 1 & 2.)

The molars (*d*. 1, 2, 3) increase in size in a geometric ratio from the first to the last, which has a middle principal subcompressed cone and an anterior and posterior basal talon. The change of the teeth takes place at a very early period: before any of the deciduous teeth fall, the first small permanent premolar (*p*. 1) cuts the gum, as in the Dog, without any apparent predecessor. The second premolar (*p* 2) pushes out the first of the deciduous series and is itself soon shed, it has a single fang: the third premolar (*p* 3) is also small, simple, and single-fanged, like its deciduous predecessor; it is commonly retained longer than the second premolar. The fourth premolar (*p* 4) is developed for use, and is truly permanent; it displaces the last tricuspid deciduous molar, and though with a larger crown, yet has a more simple one viewed exteriorly; the anterior talon, for example, is wanting or very feebly indicated; the large middle and the smaller posterior subcompressed pointed cones repeat the proportions of those in the deciduous tooth and represent the

blade of the sectorial; the internal tubercle is developed from the whole of the inner side of the base of the blade; in the *Ursus arctos* it is of a triangular form and supports a single obtuse eminence; in the *Ursus maritimus* the internal tubercle is smaller and is developed from the posterior half of the inner base of the blade: the outer part of the fourth upper premolar is supported by two fangs, and a third short rudimental one is developed from the inner tubercle. The first upper true molar (ib. fig. 3 & 4, *m* 1) makes its appearance above the gum, as usual, before the deciduous molars are lost; it has a large oblong quadricuspid crown with smaller irregularities, and is supported by three roots. The second upper true molar (ib. *m* 2) has a large posterior lobe added to the quadricuspid principal part of the crown; from which a fourth fang is developed. In the more frugivorous bears of India and the Indian Archipelago, the four premolars are commonly retained longer than in the fiercer species of the Northern latitudes. M. de Blainville has figured the jaws of the *Ursus ornatus* in which they are all preserved in both jaws. I have seen the same condition in the *Ursus labiatus*, the third small premolar above and the second and third below having each two connate fangs: the fourth premolar above presents three subequal obtuse tubercles in this species. In the lower jaw as in the upper one, of all Bears, the first premolar of the adult dentition (ib. fig. 2, *p* 1) cuts the gum, close to the canine, before the deciduous teeth are shed; the second premolar displaces the first deciduous molar; the third displaces the second, and the fourth the third. The fourth premolar (ib. figs. 5 & 6, *p* 4) has a functionally developed crown, supported by two distinct fangs. It is the only one of the four lower premolars retained in the dentition of the great extinct *Ursus spelæus*: the first premolar coexists with it in the *Ursus priscus*, as also commonly in the *U. maritimus* and *U. Arctos*: in the latter I have seen likewise the small third premolar with the adult dentition. The second lower premolar is soon lost in the Bears of temperate and northern latitudes, but is longer retained in the tropical species called 'Sun-bears' (*Helarctos*, Horsefield). The first true molar (ib. fig. 5 & 6, *m* 1) has a longer and narrower crown than the one above; but,

like it, rises above the gum before the antecedent premolar has come into place. One may still trace in the single anterior tubercle, and the second pointed cusp in the outer side of the crown, the rudiment of the blade and last remnant of the sectorial character of this tooth. This representative of the blade, moreover, still plays upon the last premolar above, receiving upon its outer side the inner surface of the principal pointed lobe of that tooth; but the extensively developed tubercular posterior lobe of *m* 1 below is opposed to the similarly formed crown of the first molar above. The second true molar (*m.* 2, fig. 5 & 6) has a narrow oblong subquadrate tubercular crown; which, like that of the first true molar, is supported by two fangs. The crown of the third lower molar (*m.* 3, figs. 5 & 6) is contracted posteriorly, and supported by two connate fangs, it is relatively smallest in the Sun-bears and largest in the great *Ursus spelæus*.

Thus, guided by the important character of development and succession for the determination of the molar teeth, the permanent dental formula of the genus *Ursus*, is:

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{4-4}{4-4};\ \text{molars } \frac{2-2}{3-3}: = 42.\ (1)$$

It is essentially the same both in number and kind of teeth as in the genus *Canis*, but the individual or specific varieties which, in the Dog,

(1) The molar series of the Genus *Ursus* is classified by M. F. Cuvier as follows:—

fausses molaires $\frac{3-3}{4-4}$, carnassières $\frac{1-1}{1-1}$, tuberculeuses $\frac{2-2}{2-2}$: = 26.

and by M. de Blainville thus:—

avant-molaires $\frac{3-3}{3-3}$, principales $\frac{1-1}{1-1}$, arrière-molaires $\frac{2-2}{3-3}$: = 26.

In the first formula the carnassial or sectorial teeth are rightly indicated as those marked *p.* 4, fig. 3, and *m* 1, fig. 6, in Pl. 130; but M. F. Cuvier does not show that the sectorial character is a subordinate modification of teeth essentially belonging to two distinct categories, and an erroneous idea is thereby conveyed of the number of both premolars and true molars. In M. de Blainville's formula the number of true molars is correctly given; but the teeth specified as 'principales' have less claim to be so distinguished than the carnassials of Cuvier; and, owing to the absence of any natural character, different teeth are indicated as 'principales', in different animals, in the 'Ostéographie.' Thus, in the genus *Felis* the 'principales' are the teeth marked *p.* 3 in fig. 1, pl. 127. (See 'Ost: des *Felis*, p. 55); and, in the genus *Simia*, they are the first of the teeth marked *m* in fig. 1, pl. 117, Ost. des *Primates*, p. 43.) The principles of the classification and notation of the teeth of the molar series in the present Work will be explained more fully after the description of the examples selected from the Order *Carnivora*.

affect the true molar teeth, are confined, in the Bears, to the premolars. It would seem that in the genus *Ursus* the predominating size of the large tubercular true molars had tended to blight the development of the premolars.

Rarely are these teeth all manifested in the adult animal, save in some of the small frugivorous tropical Sun-bears. The second premolar is the first to fall in both jaws; the third next disappears; and the first and fourth only are most commonly found, separated by an interspace in which some traces of sockets are occasionally perceptible, as in the Grisly, the Polar, the Black and the Brown Bears. In the great extinct Bear of the Caves all the three anterior small premolars were early lost; and this appears to have been the case also with an equally large and formidable extinct species, whose remains have been discovered by Capt. Cautley and Dr. Falconer in the tertiary formations of the Sub-Himalayan Mountain range. In the last premolar of the upper jaw of this species (Pl. 131, fig. 1 & 2, *p.* 4) the anterior talon is more developed than in the typical *Ursidæ;* the internal tubercle is continued from the posterior half of the base of the crown. The first upper true molar (*m.* 1) has a quadri-tuberculate crown, but the two inner lobes are smaller than the two outer ones, and the transverse exceeds the antero-posterior diameter of the crown. The second upper true molar (*m.* 2) has a square crown, as broad as it is long, quadri-tuberculate, and thus resembling the form of that tooth in some of the small Sub-ursine plantigrade quadrupeds. Of the dentition of the lower jaw of the Sewalik Bear I know only the three true molar teeth; and the socket of the last premolar (*p.* 4, fig. 3 & 4), which was implanted by two fangs. The first true molar, (*m.* 1, fig. 3 & 4) which is the representative of the lower sectorial of the more carnivorous *Feræ*, has a simple compressed crown, with a middle conical lobe and a basal talon before and behind, but no internal tubercle. The second true molar (*m.* 2, fig. 3 & 4) has also a remarkably compressed crown, divided into two principal conical lobes; the posterior being the broadest. The last true molar repeats the compressed character, but is broader anteriorly; it has one principal conical obtuse lobe, with a basal talon before and behind. Each of the lower true molars is supported, as in the true *Ursi*, by two fangs.

The above remarkable modification of the crowns of the molar teeth of the lower jaw indicates this great extinct Bear to have been more 'carnassial' and ferocious than the *Ursus spelæus* or any of its existing congeners. It differs essentially from all the small Sub-ursine Plantigrades in the full complement of true molar teeth in the lower jaw; and is still more removed from the genus *Hyæna*, in which only the first true molar is present below and under its true sectorial form: the term *Hyænarctos sivalensis* has, however, been provisionally assigned by its Discoverers to the extinct species, which, from the modification of the molars, ought to be regarded as subgenerically distinct from the true *Ursi*.

188. *Phocidæ*.—We have seen a tendency to deviate from the ferine number of the incisors in the most aquatic and piscivorous of the Musteline quadrupeds, viz: the Sea-otter (*Enhydra*), in which species the two middle incisors of the lower jaw are not developed in the permanent dentition. In the family of true Seals, the incisive formula is further reduced, in some species even to zero in the lower jaw, and it never exceeds $\frac{3-3}{2-2}$. All the *Phocidæ* possess powerful canines; only in the aberrant Walrus are they absent in the lower jaw, but this is compensated by the singular excess of development which they manifest in the upper jaw. In the pinnigrade, as in the plantigrade, family of Carnivores we find the teeth which correspond to true molars more numerous than in the digitigrade species, and even occasionally rising to the typical number, three on each side; but this, in the Seals, is manifested in the upper and not, as in the Bears, in the lower jaw. The entire molar series usually includes five, rarely six teeth on each side of the upper jaw, and five on each side of the lower jaw, with crowns, which vary little in size or form in the same individual: they are supported in some genera as the Eared Seals (*Otariæ*), and Elephant Seals (*Cystophora* Pl. 132, fig. 7), by a single fang; in other genera (ib. fig. 1-4) by two fangs, which are usually connate in the first or second teeth: the fang or fangs of both incisors, canines and molars are always remarkable for their thickness, which commonly surpasses the longest diameter of the crown. The crowns are most commonly compressed, conical, more or less pointed, with the 'cingulum' and the anterior and posterior

basal tubercles, more or less developed; in a few of the largest species, they are simple and obtuse, and particularly so in the Walrus, in which the molar teeth are reduced to a smaller number than in the true Seals(1). In these the line of demarcation between the true and false molars is very indefinitely indicated by characters of form or position; but, according to the instances in which a deciduous dentition has been observed, the first three permanent molars in both jaws succeed and displace the same number of milk molars, and are consequently *premolars;* occasionally, in the Seals with two-rooted molars, the more simple character of the premolar teeth is manifested by their fangs being connate, and in the *Stenorhynchus serridens* the more complex character of the true molars is manifested in the crown. There is no special modification of the crown of any tooth by which it can merit the name of a ' sectorial ;' but we may point with certainty to the third molar above, and the fourth below, as answering to those teeth which manifest the sectorial character in the terrestrial Carnivora.

The coadaptation of the crowns of the upper and lower teeth is more completely alternate than in any of the terrestrial Carnivora, the lower tooth always passing into the interspace anterior to its fellow in the upper jaw. In the genus *Phoca* proper (*Calocephalus*, Cuv.) typified by the common Seal (*Ph. vitulina*), the dental formula is:

Incisors $\frac{3-3}{2-2}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{2-2}{2-2}$: = 34.

The forms and proportions of these teeth are shown in Pl. 132, fig. 1.

The first tooth above and below presents a complete confluence of the fangs; they are separated in the rest above; but below they sometimes do not become free before the fourth, and sometimes the two roots are distinct in the third and second molars. In the *Phoca anellata*, Nills: the principal cusp of the molar teeth is complicated with anterior and posterior smaller cusps, sometimes one in number in the upper molars; the anterior accessory cusp is sometimes wanting in the first, and is rudimentary in the rest; but usually

(1) The relation of *Trichechus* to the *Phocidæ* is analogous to that of *Machairodus* to the *Felidæ*, and also, in the simplification of the molars, to the relation of *Proteles* to the *Canidæ*.

there are two small cusps behind the principal one, and in the three or four posterior molars in the lower jaw there are sometimes two small cusps before and two behind the principal one.(1)

In the *Phoca caspica* the upper molars have commonly one accessory cusp before and one behind the principal lobe, the lower molars have one accessory cusp before and two behind the lower molars.

In the *Phoca grœnlandica* the upper molars have no anterior basal cusp and only one behind; the lower molars have two cusps behind and one in front, except the first which resembles that above and, like it, has connate fangs.

The condition of the molar teeth is nearly the same in the *Phoca barbata* (Pl. 132, fig. 2); but the crowns are rather thicker and stronger, and the three middle ones above have two posterior basal cusps feebly indicated, the same being more strongly marked in the four last molars below.

The following genera of Seals with double-rooted molars, (*Pelagius* & *Stenorhynchus*), have four incisors above as well as below, i. e. $\frac{2-2}{2-2}$. An upper view of the molar teeth in the Hooded Seal of the Mediterranean, *Pelagius monachus*, is given in Pl. 132, fig. 3, as when they are worn down in an old specimen; the crowns are thick, obtuse, subcompressed, with a well developed cingulum, a principal lobe and an anterior and posterior accessory basal lobule; the fangs are connate in the first tooth both above and below.

The allied sub-genus (*Ommatophoca*) of Seals of the southern Hemisphere has six molar teeth on each side of the upper, and five on each side of the lower jaw, with the principal lobe of the crown more incurved. The two first molars above are closely approximated; but this may prove to be a variety.

In the *Stenorhynchus* the jaws are more slender and produced, and the molar teeth are remarkable for the long and slender shape of the principal lobe and of the accessory basal cusps. The incisors have sharp conical recurved crowns, like the canines, and the exter-

(1) Nillson, in Wiegmann's Archiv. 1841, p. 313. I notice these varieties of the crown, in connection with analogous ones in the fangs of the teeth of the same species, to show the inadequacy of such characters as marks of subgeneric distinction.

nal ones in the upper jaw are intermediate in size between the canines and the middle incisors.

In the *Stenorhynchus leptonyx* each molar tooth in both jaws is trilobed, the anterior and posterior accessory lobes curving towards the principal one which is bent slightly backwards; all the divisions are sharp-pointed, and the crown of each molar thus resembles the trident or fishing-spear; the two fangs of the first molar in both jaws are connate. In *Sten. serridens* (Pl. 132, fig. 4) the three anterior molars on each side of both jaws are four-lobed, there being one anterior and two posterior accessory lobes; the remaining posterior molars (true molars) are five-lobed, the principal cusp having one small lobe in front and three developed from its posterior margin; the summits of the lobes are obtuse, and the posterior ones are recurved like the principal lobe. Sometimes the third molar below has three instead of two posterior accessory lobes. Occasionally, also, the second as well as the first molar above has its fangs connate; but the essentially duplex nature of the seemingly single fang, which is unfailingly manifested within by the double pulp-cavity, is always outwardly indicated by the median longitudinal opposite indentations of the implanted base. These slight and unessential varieties, presented by the specimens of the Saw-toothed Sterrink (*Stenorhynchus serridens*) brought home by the enterprising Naturalists of Sir J. Ross's Antarctic expedition, accord with the analogous varieties noticed by the best observers of the Seals of our neighbouring seas, as, for example, Nillson.(1)

The Grey Seal (*Halichœrus gryphus*) of our own Seas begins, by the extension of the connate condition of the two roots through a greater proportion of the molar series, to manifest a transition to the

(1) A diligent labourer, in what our plain-speaking German fellow-zoologists call the 'Gattungsmacherei' has seized upon the variable mode of implantation of the anterior premolars as ground for the generic distinction of Seals; and so by the following phrase, "*the 1st, 2d and 3d front upper, and the 1st front lower grinder single-rooted, the rest 2 rooted,*"(*a*) my *Stenorhynchus serridens* is tied as a synonym to the tail of '*Lobodon carcinophaga*, Gray.' Not a single additional fact does the writer find to add to those characters which I first pointed

(*a*) Zoology of Ross's Antarctic Voyage, Mammalia, p. 2, 4to. 1844.

family of Seals with true single-rooted molars; the formula of this genus, is:

$$\text{Incisors } \frac{3-3}{2-2};\quad \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{2-2}{2-2}: = 34.$$

The four middle upper incisors are close set, with pointed recurved crowns; the lateral incisors are much larger and laniariform: the canines have moderate crowns, with a sharp ridge before and behind. The crowns of the molar teeth (Pl. 132, fig. 5) are conical, subcompressed, longitudinally and finely grooved, with an anterior and posterior edge; those below have generally a slight notch at the fore and back part of the base. The first molars, both above and below, are the smallest, with a simple crown and a single ventricose fang; the second and third above, and the second, third, and fourth below, have two connate roots; the two roots are commonly distinct in the remaining posterior molars: all the roots are very thick.

In the genus *Otaria* (ib. fig. 6) the dental formula, is:

$$\text{Incisors } \frac{3-3}{2-2};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{3-3}{2-2} = 36.$$

The two middle incisors are small, subcompressed, with the crown transversely notched; the simple crowns of the four incisors below fit into these notches: the outer incisors above are much larger with a long pointed conical crown, like a small canine. The true canine is twice as large as the adjoining incisor, and is rather less recurved. The molars have each a single fang; the crown is conical, subcompressed, pointed; in the two last recurved, with a basal ridge or 'cingulum,' broadest within: in the *Otaria jubata*, with a pointed cusp developed from its fore-part, and in the last two molars also from its back part. In some species, as the *Otaria lobata*, (*Phoca*

out as distinguishing the *Sten. serridens* from the *Sten. leptonyx*, except the above-cited variety respecting the implantation of the premolars; and even this is misinterpreted, the supposed single root being essentially two roots connate. A re-examination of the specimens of *Sten. serridens*, in comparison with *Sten. leptonyx*, has only impressed more strongly the truth of the observation with which I concluded my description of that new species, "the modifications of the compressed and deep-cleft molars are not of sufficient importance to justify the introduction of a new generic name into the group of amphibious or pinnigrade Carnivora, which has already been overburthened in this way."(*a*)

(*a*) Annals of Nat. History, 1843, p. 331.

lobata, Fischer), the single molar is not developed in the upper jaw, and the outer incisors above are not so large: in this species a thick plicated cingulum belts the base of each molar, and developes a small tubercle from its fore part in the molars of the lower jaw; the crown of the last molar above is notched.

In the great proboscidian and hooded Seals (*Cystophora*, fig. 7) the incisors and canines still more predominate in size over the molars; but the incisors are reduced in number, the formula here, is:

$$\text{Incisors } \frac{2-2}{1-1};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{2-2}{2-2}: = 30.$$

All the molars are single-rooted and all the incisors are laniariform. The two middle incisors above and the two below are nearly equal; the outer incisors above are larger. The canines are still more formidable, especially in the males; the curved root is thick and subquadrate. The crowns of the molar teeth are short, subcompressed, obtuse; sometimes terminated by a knob and defined by a constriction or neck from the fang; the last is the smallest.

In the Walrus (*Trichechus rosmarus*) the phocal incisive formula is transitorily represented in the very young animal, which has three teeth in each intermaxillary bone and two on each side of the forepart of the lower jaw; they soon disappear, except the outer pair above, which remain close to the intermaxillary suture, on the inner side of the sockets of the enormous canines, and seem to commence the series of small and simple molars which they resemble in size and form. In the adult there are usually three molars on each side, behind the permanent incisor, and four similar teeth on each side of the lower jaw; the anterior one passing into the interspace between the upper incisor and the first molar, and therefore being the analogue of the molar. In a young Walrus's skull, with canine tusks eight inches long, I have seen a fourth upper molar, (fifth including the incisor), of very small size, about a line in breadth, lodged in a shallow fossa of the jaw, behind the three persistent molars. The crowns of these teeth must be almost on a level with the gums in the recent head; they are very obtuse and worn obliquely from above down to the inner border of their base. The molars of the lower jaw are rather narrower from side to side, than those above, and are convex or

worn upon their outer side. Each molar has a short, thick, simple and solid root.

The canines are developed only in the upper jaw, but are of enormous size, descending and projecting from the mouth, like tusks, slightly inclined outwards and bent backwards; they present an oval transverse section, with a shallow longitudinal groove along the inner side, and one or two narrower longitudinal impressions upon the outer side; the base of the canine is widely open, its growth being uninterrupted.

The food of the Walrus consists of sea-weed and bivalves: the molars are well adapted to break and crush shells; and fragments of a species of *Mya* have been found, with pounded sea-weed, in the stomach. The canine tusks serve as weapons of offence and defence, and to aid the animal in mounting and clambering over blocks of ice.

189. *Composition and microscopic structure.*—The teeth of the *Carnivora*, with the exception of the aberrant amphibious forms in which we have been last considering the outward modifications of the dental system, so closely correspond in their intimate structure, both with each other and with those of the *Quadrumana*, as to require here only a brief and general notice. They all enter into the category of 'simple teeth;' that is, the dentine or main body is not penetrated by folds of the other component tissues, but has an even exterior, covered at the part forming the crown with enamel, and having a general outer investment of cement, the coronal layer forming too thin a film to manifest any of the radiated cells. The dentine is of the kind called 'hard or unvascular': the tubuli are rather finer than in the human teeth; they have the same general direction from the pulp-cavity, but present stronger primary curvatures, more frequent dichotomous divisions, and more numerous minute lateral branches, which latter usually curve from the trunks at right angles. The dentinal cells are subhexagonal, about $\frac{1}{5000}$th of an inch in diameter, with the peripheral contour forming almost a regular curve. In the Seals the dentine forms usually a smaller proportion of the tooth than in the terrestrial Carnivora; the characteristic thickness of the roots in this family is principally due to the thick covering of

cement, and the pulp-cavity is generally closed by an unusual quantity of the osteo-dentine. The calcigerous tubes in the dentine of the Seal's molar describe very strong and irregular curves on leaving the pulp-cavity; but, when within a third of the distance to the outer surface, they fall into more parallel and regular undulations; they are $\frac{1}{12,000}$th of an inch in diameter, and the interspace between two tubes is about $\frac{1}{8000}$th of an inch in width. The tubes dichotomise less frequently and less regularly than in the teeth of the Dog or Hyæna, but send from both sides extremely numerous short branches, which bend almost transversely across the interspaces, and the sub-branches are continually sent off in greater abundance along lines parallel with the outer contour of the tooth, giving the appearance of opake striæ or concentric layers to polished sections of the dentine. The calcigerous tubes resolve themselves at their extremities into rich tufts of curved branches which terminate in a layer of minute cells at the crown, and in the root, communicate with the radiated cells of the cement.

In the molar teeth of the *Otaria jubata* the tubes proceeding in the long axis of the crown are pretty parallel on the peripheral half of the dentine; towards the side of the crown they proceed in more zigzag, almost angular curves and appear to cross each other, conspicuous branches being continued from the angles: the interspaces of the tubes were about $\frac{1}{8000}$th of an inch in width. The dentinal cells are more numerous and less regular than in the teeth of the ordinary *Carnivora*, and their contour is more obscured by the deeper curves and more numerous branches of the dentinal tubes.

The enamel of the teeth of the *Carnivora* is extremely dense and brittle, it consists of fibres similar to those in the Human teeth, but relatively smaller, as for example, in the large canines of the Tiger, and the molars of the Hyæna. The transverse striæ, moreover, are less distinct.

In the molar of the *Otaria* the enamel fibres were very distinct, placed at right angles to the plane of the crown, and less curved than in Man or the Quadrumana. Instead of the transverse striæ they presented a minute granular structure.(1)

(1) Retzius failed to detect any true enamel in the teeth of the *Phoca anellata*.

The cap of enamel with which the teeth of the Walrus are at first tipped is soon worn off, and, except at the abraded surface, the rest of the teeth, both tusks and molars, are thickly coated with cement. Retzius has left little to add to his detailed and exact account of the microscopic structure of both the canines and molars of the Walrus.(1)

The dentine, in this species, closely corresponds with that in the ordinary Seals; in the molar teeth the tubes present the same diameter, the same interspaces, and undulating curvatures; but their dichotomous divisions are more marked. In the canines the lateral branches terminate in minute opake cells, dispersed throughout almost the whole dentine, but most numerous and conspicuous near its periphery, where the dentine is defined by a distinct layer of these cells: only a third part of the periphery of the canine is composed of true dentine, the central thin part of the tooth is filled up by osteo-dentine, which, as in the teeth of the Cachalot, often projects in irregular rounded masses, like stalactites, into the short and wide basal pulp-cavity. The whole mass, indeed, of the osteo-dentine consists of numerous independent calcifications of the pulp, having as many distinct centres, usually hollow, and producing, when the substance is examined by the naked eye, the appearance which Cuvier has compared to 'pudding-stone.'(2) The central cavities are for

(1) Loc. cit. p. 35, 73.

(2) " L'ivoire des défenses du Morse est compact, susceptible d'un poli presque aussi beau que celui de l'hippopotame mais sans stries; la partie moyenne de la dent est formée de petits grains ronds placés pêle-mêle, comme le cailloux dans la pierre appelée *poudingue*; c'est ce qui le caractérise. Les dents molaires de cet animal ont leur axe composé des mêmes petits grains que celui des défenses. Elles n'ont aucun cavité dans leur intérieur." Cuvier, Leçons d'Anat. Comparée, tom. iii, (1805) p. 106. The cement of the Morse's teeth is distinguished from the osteo-dentine by its continuous uniform structure, by the absence of the detached centres and their concentric lines; but the radiated cells are disposed in regular layers concentric and parallel with the contour of the body of dentine. The radiating tubes from the cells forming the layer next the dentine communicate freely with the peripheral ramifications of the dentinal tubes and also with the proper cemental tubes which are dispersed vertically to the plane of the cement: indeed, the evidence of an intercommunicating system of canals, too minute for the gross fluid of the circulating system, is most striking and universal throughout the substance of both the tusks and small teeth of the Walrus. Vascular canals are, however, present in the cement as in the osteo-dentine, from the contents of which it may be presumed that the colourless plasma is elaborated, which meanders through the minuter systems of cells and tubes.

the most part associated together and with the pulp-cavity by medullary canals. The calcigerous tubes radiate from those central cavities, in all directions, with sub-parallel, diverging curvatures; dividing, subdividing and sending off numerous branches, which anastomose with those of the adjoining masses, and, where these are situated next the dentine, with the tubes of that tissue. In each lobe of the osteo-dentine the concentric rings parallel with the contour of the central medullary cavity, are well-marked. Myriads of minute calcigerous cells are dispersed throughout the osteo-dentine.

The pulp-cavity of the incisor and molar teeth of the Walrus is filled up by a smaller quantity of the osteo-dentine. Minute vascular canals convey the capillary blood vessels to this structure from the vascular membrane attached to the solid base of the molars, and, in the tusks, from the persistent pulp which fills the basal cavity.

190. *Classification and analogies of the molar teeth of the Carnivora.* —The various forms of the teeth composing the molar series and their concomitant diversity of function in the order *Carnivora* have led to their being divided into distinct groups, to which the Anatomists, who have more especially devoted themselves to the study of those organs, have generally assigned special names. The most commonly adopted classification and nomenclature of the molar teeth, especially, as they exist in the Carnivora, is that proposed by Mr. F. Cuvier in his celebrated work the 'Dents des Mammifères;' where, treating of the 'machelières,' cheek-teeth, or molar teeth, he says: "Ces dernières se partagent en trois divisions. La première se compose de deux à quatre dents qui viennent après les canines, dont l'usage est assez indéterminé, et qui sont '*des fausses molaires.*' La seconde ne se compose jamais que d'une dent qui est *la carnassière;* c'est en elle que réside essentiellement la faculté de couper les fibres de la chair. La troisième est celle des *dents tuberculeuses,* dont le nombre ne s'élève jamais au-delà de deux et qui paraissent avoir pour destination principale de broyer les alimens susceptibles de l'être." p. 77. The dentition of the different genera is numerically formulised, according to the foregoing classification: thus the genus *Felis* has: machelières $\frac{8}{6}$; dont $\frac{4}{4}$ fausses molaires, $+\frac{2}{2}$ carnassières, $+\frac{2}{0}$ tuberculeuses.

In the second edition of the 'Leçons d'Anatomie Comparée,' of G. Cuvier, tom. iv, 1836, the '*fausses-molaires*' are distinguished from the '*vraies-molaires*,' by their fewer roots and narrower crown: "par moins de racines et par une couronne moins large et conséquemment moins propre à broyer." (p. 246). And, in the Numerical Tables, the molar series is divided into '*fausses molaires rudimentaires, fausses molaires normales, vraies molaires carnassières*,' and '*vraies molaires tuberculeuses*:' the series in Man giving:

$$f.\ m.\ r.\ \frac{v-v}{0-0};\ f.\ m.\ n.\ \frac{2-2}{2-2};\ v.\ m.\ \frac{3-3}{3-3}.\ \text{(p. 254.)}$$

and that in the Lion or genus *Felis*:—

$$f.\ m.\ r.\ \frac{0-0}{0-0};\ f.\ m.\ n.\ \frac{2-2}{2-2};\ v.\ m.\ c.\ \frac{1-1}{1-1};\ v.\ m.\ t.\ \frac{1-1}{0-0}.\ \text{(p. 262.)}$$

Both these systems are rejected by M. de Blainville in his 'Ostéographie d'Animaux Vertébrés.'(1) In this beautifully illustrated Work the molar series is divided into premolars, principal, and true molars: '(avant molaires, principale et arrière-molaires,' t. i, p. 43); which are thus exemplified in the Human dentition: the five teeth of the molar series are divided into two *premolars*, one *principal*, and two true or *post-molars*, and, with the incisors and canine, are indicated by the following notation:—

"$\frac{2}{2}$ *i.* + $\frac{1}{1}$ *c.* + $\frac{5}{5}$ *m.* dont $\frac{2}{2}$ *av. m.* $\frac{1}{1}$ *pr.* $\frac{2}{2}$ *ar. m.*" (*l. c. p.* 43)

In order to determine the analogues of these kinds of molar teeth, and especially the 'principal' molar, in other animals, the Author gives the following definitions or characters: first, with respect to *form or shape*, he divides the molars of Mammalia 'en avant-molaires, en principale, et en arrière-molaires, qu'importe qu'elles soient simples ou complex, tranchantes, ou tuberculeuses.' (*l. c. p.* 43.)

As the so called principal molar of Man is not distinguished by the trenchant, or any other peculiar form, M. de Blainville next points out another character taken from its *position* in the jaw. In most cases, he says, we may easily recognise the principal molar, in the upper jaw, which is always the 'point de départ'

(1) "Nous avous été obligé d'abandonner cette classification des molaires des Mammifères et d'en établir une autre."—Ostéogr. des Mammifères, tom. i. p. 43.

for the signification of the teeth, by assuming that tooth to be such which is implanted below the root of the zygomatic process of the maxillary bone: 'en prenant pour telle' (la principale) 'celle qui se trouve implantée sous la racine de l'arcade zygomatique, ou mieux de l'apophyse zygomatique du maxillaire.' p. 43. Those teeth which are in front of the 'principale,' so recognised, are premolars, those behind it are true or post-molars. With regard to the lower jaw it will suffice to bring the teeth in their natural apposition with those above in order to learn their signification: that which shall cross in front of the upper 'principale' will be the lower 'principale'; whence one may readily determine the premolars and post-molars (*l. c. p.* 43).

To test the value of these characters as determining the natural species of molar teeth, and as guides to the representatives of each through different genera of Mammalia, let us take another example of the Author's application of them, viz: the dentition of the Lion. The molar formula of the genus *Felis*, according to M. de Blainville, (Ost. des Carnassiers, p. 69.) is: $\frac{1}{1} + \frac{1}{1} + \frac{2}{1}$. *i.e.* there are one premolar, one principal, and two true molars in the upper jaw; one premolar, one principal, and one true molar in the lower jaw. This view of the nature of the Feline molars differs from that which is given by M. Fred. and Baron Cuvier, and equal or greater discrepancies will be found between most of the determinations of the molar series in the work of M. de Blainville, and in those of the other distinguished French Professors. The high reputation of these Authors, and the character and value of the great Work in which M. de Blainville's views are promulgated, call for the present statement of the considerations which have compelled me to abandon them, much as I am impressed with the advantage of uniformity in the classification and nomenclature of natural objects.

To return, then, to the two examples cited from the 'Ostéographie' of M. de Blainville; the second of the molar series of the Lion (*p* 3, Pl. 127, fig. 1) is the representative of the third of the molar series in Man, (first of the three marked *m* in Pl. 118) in both jaws: that is to say, a tooth which displaces and succeeds

a milk tooth, and which is, therefore, a premolar according to my definition, in the Lion, is made the analogue of a tooth which rises above the gum without displacing any predecessor, and which is consequently a true molar, in Man. It will, I presume, be conceded that the teeth in the Lion, called 'principales' by M. de Blainville, in having smaller and more simple crowns than those behind them, and in being preceded by deciduous teeth which they replace, are more naturally analogous to the bicuspides or premolars in the Human Subject; and if so, it may be concluded that the characters which have conducted M. de Blainville to the opposite conclusion cannot be founded in nature.

These characters, moreover, seem in the instance cited, to have been as little applicable to the detection of the tooth in the lower jaw which is analogous to the 'principale' above, as to the discovery of the 'principales' in different Mammalia; and, indeed, M. de Blainville abandons one of his own criteria, viz: that founded on relative position, in selecting the second tooth of the Feline molar series below, as the analogue of the second tooth in the upper series, distinguished by him as the 'principale' in the preliminary observations on the Classification of the Carnassiers (p. 69). The same view of the analogies of the upper molar series is adopted in the detailed descriptions given in the subsequent Monograph on the genus *Felis*, but a different one is given of the lower molars: the first tooth (*p* 3, fig. 1, Pl. 127) is here described as the 'principale,' and the two succeeding teeth are both 'arrière-molaires'. (p. 55).

The relative value of the characters for the classification of the molar teeth proposed in the present work, and of those proposed by the Cuviers and by M. de Blainville, will be best tested by applying them to the same instances as have been cited above. According to my view the molar formula in Man is:—*p.* $\frac{2-2}{2-2}$, *m.* $\frac{3-3}{3-3}$; in the Lion it is:—*p.* $\frac{3-3}{2-2}$, *m.* $\frac{1-1}{1-1}$: that is to say, the last tooth in the series of both jaws of the Lion is the analogue of the first true molar in Man, whilst the others answer to the bicuspids, of which the Lion has one more in the upper jaw than Man possesses. Thus the permanent teeth, indicated as the corresponding true molars (*m* 1) in *Felis* and *Homo*, by their mode of succession,—neither

of them being 'dents de remplacement,'—also agree, in the upper jaw, in the tubercular character of the crown, and in the lower jaw, in their superior size as compared with the antecedent teeth; which characters, though they be of secondary importance, tend, when concurring, as they generally do, with the primary character, to vindicate its value. Moreover, according to my view, the second lower premolar in *Felis*, (M. de Blainville's 'principale' in the 'Classifications des Carnassiers, p. 69), is not the fellow of the second but of the third premolar above: and the last tooth below, although the greater part of its crown plays upon the third above, yet is not, as the Cuviers indicate, the fellow of that sectorial tooth, but being somewhat posterior to it, pairs strictly with the small tubercular tooth above. And it is important to observe that these teeth—the tubercular above and sectorial below,—notwithstanding the diversity in the form of their crown in the genus *Felis*, have the same developmental character; and that the first tooth (*m* 1) which follows the 'dents de remplacement' in the upper jaw, and the first tooth (*m* 1) which follows them in the lower jaw, do actually acquire, the one by progressive increase of size, the other by gradual acquisition of a broad tuberculate grinding surface, even in the Carnivorous series, almost as close a correspondence in structure, as they present in the Quadrumanous Order. It needs only to compare the dentition of the Cat, the Grison, the Badger, and the Bear, to appreciate the truth of this proposition and the respective accuracy of the following dental formulæ:

Genus *Meles* according to Cuvier:—

in. $\frac{3-3}{3-3}$; c. $\frac{1-1}{1-1}$; fausses m. $\frac{2-2}{4-4}$; carnassières $\frac{1-1}{1-1}$; vraies m. $\frac{1-1}{1-1} = 36$,

Genus *Meles*, as in the present work:—

in. $\frac{3-3}{3-3}$; c. $\frac{1-1}{1-1}$; pm. $\frac{3-3}{4-4}$; true m. $\frac{1-1}{2-2} = 36$. The last upper premolar, and the first lower true molar being indicated, in the text, as the analogues of the teeth which manifest the carnassial or sectorial character in the typical *Feræ*.

It will be seen that I have made no use of the term 'principale', in describing and discriminating the molar teeth of the Mammalia.

The character of form ('trenchant') in reference to this tooth, fails, as we have seen, in its first application: the character of relative position to the base of the maxillary zygomatic process has as little constancy or value; and, indeed, I never found any Comparative Anatomist, who, when asked to indicate the 'dent principale' by that character in the Lion's skull, did not point to the third premolar or 'carnassial' of Cuvier, instead of to the second premolar or 'principale' of M. de Blainville. The name 'principale' seems to refer to a character of size; and in the Human Subject, the tooth, so called by M. de Blainville, is larger than the third molar, and not less than the second; but before we quit the Quadrumanous series we find numerous examples in which, in the lower jaw especially, the last molar tooth is the principal one in point of both size and complexity of crown; and the 'principales' in the Feline dentition, according to M. de Blainville, are far from being the chief either in size or special adaptation to the carnivorous regimen.

It may be thought, perhaps, that the principles of the classification of the teeth, adopted by M. de Blainville, have been tested by extreme examples in selecting the dentition of Man and the Lion; let us take, therefore, a third instance of the Author's application of them from the Carnivorous order. In the *Paradoxurus* the upper molar series has a different relative position to the root of the zygomatic process from that in the Lion; and accordingly we find the upper carnassial tooth of Cuvier, or the last of my premolars, selected by M. de Blainville as the 'dent principale', leaving three premolars in advance of it; the tooth immediately anterior to the lower carnassial of Cuvier being selected as the corresponding 'principale' in the lower jaw. *Ostéogr. de Viverra*, p. 43. Here, again, therefore, we find that teeth which are 'dents de remplacement' in one Mammiferous animal, the Paradoxure, are selected as the analogues of true molar teeth rising posteriorly to the whole deciduous series in another, the Monkey, for example. The upper 'principale' in the Civet and Paradoxure not only displaces a milk-molar, but one which had a tubercular and more complex crown; and this is precisely what happens to the premolar which precedes the 'principale' in the Human and Quadrumanous dentition, but which

does not happen to the 'principale' in the same dentition as classified by M. de Blainville.

Passing next to the comparison of the dentition of Quadrupeds more closely allied, and of the same natural order, we find the upper 'principale' in the Lion thus described by M. de Blainville: "Celle-ci, bien plus grande et de forme triangulaire et subtriquètre à sa couronne, avec le sommet submédian et peu pointu, est pourvue en avant et un peu en dedans d'un tubercule basilaire peu marqué, et de deux en arrière, dont l'un, le postérieur, est une sorte de talon." *Ostéogr. de Felis*, p. 55. Then follows the description of the first 'arrière-molaire', which is rightly termed 'carnassière supérieure'. If we turn to M. de Blainville's account of the dentition of *Viverra* we find that "La principale d'en haut est aussi un peu moins carnassière par plus d'épaisseur du talon interne antérieure et par moins de largeur du lobe postérieur." '*Ostéogr. de Viverra*, p. 42.' The Author is comparing it with the premolar in front of it, which is, in fact, the analogue of his 'dent principale' in the Lion, the 'dent principale' in the *Viverra* being the analogue of the 'dent carnassière' in the Lion. Thus the characters adopted by M. de Blainville, not only fail in the determination of the analogous teeth in different orders but also in different genera of the same order, and, according to his first determination of the Feline formula,. even in the upper and lower jaws of the same species.

Neither is the author of the 'Ostéographie' more consistent with himself in a later portion of his great Work: in the Fasciculus on the 'Ostéographie de Hyæna,' (p. 25) he adopts a third formula for the molar series of the genus *Felis*, apparently from Daubenton, which differs both from that which is given in the 'Generalities on the Carnivora,' (p. 69), and from that described in detail in the 'Ostéographie de Felis' (p. 55): it is as follows:— $\frac{2}{1} + \frac{1}{1} + \frac{1}{1}$; *i.e.* two premolars, one principal, one true molar above; and one premolar, one principal and one true molar below; not any remark being made on its discrepancy with the other formulæ. But neither is this third view more true to nature, than the two views previously proposed by M. de Blainville in the same Work; for, according to the natural characters of the

molar series, the typical Felines have not two, but three premolars on each side of the upper jaw, and two premolars, instead of one, on each side of the lower jaw. I have come to the conclusion, therefore, after a long and patient series of researches upon both the deciduous and permanent dentition of the Mammalia, that a 'molaire principale' does not exist in nature, that its characters as defined by M. de Blainville are artificial, and that they utterly fail, or mislead, in their application to a philosophic determination of the analogous teeth in the different genera of placental and terrestrial Mammalia.

Having premised thus much in explanation of the grounds which have prevented my adopting the dental formulæ assigned to the genera of Mammalia, not only by M. de Blainville, but by the Cuviers, I have only to add an explanation of the principles of the formulæ substituted for them in the present work. As respects the molar teeth, I believe my classification to be founded on a more important, a more constant, and therefore a more natural character than those of 'form,' 'size,' or 'relative position.' According to the law of development the series of *true molars* begins with that tooth which rises into place behind the last of the deciduous series and includes all behind it; all the permanent molars in front of this series are *premolars*. I have already exemplified the application of this law to the determination of the analogous true-molar teeth in the Lion and Man, and I may observe that it is equally applicable to the identification of every tooth in the molar series. According to it, the first upper true molar tooth in the Human Subject, ('principale' of M. de Blainville), is the analogue of the last, or tubercular molar in the upper jaw of the Lion; the first lower true molar tooth in Man answers to the lower sectorial tooth in the Lion; the upper sectorial in the Lion is essentially the same tooth as the second superior bicuspid in Man; the second upper premolar of the Lion answers to the first upper bicuspis in Man; the first small premolar in the Lion has no analogue in the Human dentition; the two premolars in the lower jaw of the Lion correspond with the two inferior bicuspids in Man.

The natural character of the premolars as a distinct subdivision of the molar series is shown by a certain independence in their time of

development: its course is the same as that of the true molars, viz. from before backwards, and is nearly parallel in point of time, but a little anterior; the first and generally the second true molars being in place before the last premolar cuts the gum. I may further remark that, when either series falls short of the typical number, which in the placental Mammals, is four for the premolars and three for the true molars, the absent teeth are from opposite ends of the two series, being taken from the fore-part of the premolar, and from the back part of the true molar series.

No character is of less importance in the determination of the essential nature and analogies of teeth than mere shape of the crown: peculiar modifications have obtained peculiar names; the long, curved, pointed incisors of the Elephant, and the similarly shaped canines of the Walrus are called 'tusks,' or 'défenses:' the incisors of the Beaver and canines of the Hippopotamus are compared to the chisel, and called 'dentes scalprarii', from the partial disposition of the hard enamel, and the oblique bevelled cutting edge thence resulting: we must not be surprised, therefore, to find a premolar in one jaw and a true molar in the opposite jaw similarly modified to cut flesh, and so placed in the alternate disposition of the teeth of the 'Carcharodonta',(1) as to play in a greater or less proportion upon each other, like the blades of scissors. In retaining, then, the convenient and expressive term assigned by the Cuviers to these sectorial teeth, it must, at the same time, be borne in mind that they are not the analogous teeth in the two jaws, but, in these, respectively belong to two naturally distinct categories of the molar teeth. So, likewise, before we quit the Carnivorous series we find both molars and premolars taking on as complete a tubercular structure of the crown, and equally meriting the name of 'tuberculeuses';(2) and it is in restricting the terms 'sectorial' and 'tubercular' to secondary indications of the differences observable in the teeth composing the two natural primary divisions of true molars and premolars, instead of using them as characters for the primary division of the molar series, that I chiefly dissent from the classification adopted in the deservedly esteemed works of the CUVIERS.

(1) Aristotle's name for the modern '*Carnivora*.'

(2) See *Procyon* and other *Subursi*.

CHAPTER XII.

TEETH OF UNGULATA.

THE most complex and varied systems of dentition are to be found in the different Orders, Families and Genera of the great natural group of hoofed Quadrupeds. From this group it will suffice for the objects of the present Work to select certain examples to elucidate the leading modifications of the systems of complex teeth, and these examples will be taken from the typical species of the Isodactyle(1), the Anisodactyle(2), and the Proboscidian divisions of the *Ungulata*.

Although the structure of the molar teeth presents very different degrees of complication and is much modified in the Isodactyle *Ungulata*, it generally produces a more symmetrical form or pattern of the grinding surface than in the Anisodactyle division. I shall commence with the dentition of an extinct genus of the Isodactyle group.

191. *Anoplotherium.*—The Anoplothere was one of the earliest forms of hoofed quadrupeds introduced upon the surface of this earth, and it is characterized by the most complete system of dentition: it not only possessed incisors and canines in both jaws, but these were so equably developed that they formed one unbroken series with the premolars and molars, which character is now found only in the Human species.

The dental formula of the genus *Anoplotherium* is :—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ p.\ \frac{4-4}{4-4};\ m.\ \frac{3-3}{3-3}:\ =\ 44.$$ (Pl. 135. fig. 1—3.)

Those teeth which are transitorily manifested in the embryo-state

(1) Hoofed Quadrupeds with toes in even number, as two or four, and which have a more or less complicated stomach, with a moderate sized simple cœcum. *Ex.* Ox, Hog, Peccari, Hippopotamus.

(2) Hoofed Quadrupeds with toes, (on the hind-foot at least,) in uneven number, as one three, or five, the latter number being manifested by the Proboscidians. All these have a simple stomach and an enormous cœcum. *Ex.* Horse, Tapir, Rhinoceros, Elephant: but the last Pachyderm combines, with its proboscis, so many other peculiarities of structure, as to have been recognised as the type of a distinct group of *Ungulata*, most of the members of which group are now extinct.

of the Ruminant, as the upper incisors and canines(1) and the anterior premolars, were, in the ancient Anoplothere, retained and raised to proportional equality with the rest of the teeth. What is suppressed in the Ruminant Order is developed in excess in other Isodactyle Herbivora, as, for example, in the Hippopotamus and Babyroussa; and almost every kind and degree of variety, save that of increased number of teeth, has been superinduced in later and existing forms of hoofed Mammals upon the primitive Anoplotherian formula, which may therefore be regarded as the type or perfect standard of the dentition of the great natural group of *Ungulata*.

In the *Anoplotherium commune*(2) the upper mid-incisor has a semi-elliptic crown, very convex externally, with a large root expanded near the neck: the second and third incisors have the end of the crown slightly produced giving it a triangular form: all three have a small cusp at the outer border. The canine differs in the greater breadth and thickness, but not in the length of the crown; the middle part of which forms a low cone with well-marked basal angles. In the first upper premolar (Pl. 135, fig. 2, *p* 1) the anterior angle is more developed, and the principal lobe has an internal basal ridge: the outer surface is sinuous, convex in the middle, and the entire tooth is enlarged. In the second premolar (ib. *p* 2) the depression between the more developed inner basal ridge and the main lobe is deepened, and forms a long enamel-island when the crown is much worn: a second basal ridge is also developed below the former in this and the next premolar (ib. *p* 3), which, with the fourth (ib. *p* 4), progressively increase in size. The true molars (ib. *m*) have thicker square crowns which present the following characters: a transverse valley (*b*) extending, from within, two-thirds across, divides the crown into an anterior (*o*) and a posterior (*o'*) lobe which are continuous along the outer border of the tooth: an antero-posterior valley (*c*, *e*) crosses the termination of the first, penetrating

(1) Goodsir, Report of British Association, 1838.

(2) This animal was the size of an Ass, and, with the other species of the extinct genus, had a cloven-hoof, like the Ruminants, but the division extended through the metacarpus and metatarsus. The Anoplothere was an animal of aquatic habits and had a very long and strong tail which Cuvier conjectures to have been used like that of the Otter in swimming.

and sub-dividing each lobe with a bend convex inwards: but the peculiar characteristic of the Anoplotherian upper molar is the large conical tubercle (*p*) at the wide entry of the first valley. The outer side of the crown is impressed by two concavities, produced into points upon the grinding surface: these points are first worn by attrition; a double crescentic tract of dentine (*o d* & *i d*) is next exposed in each primary lobe, with a detached island upon the summit of the internal cone; this, from the minor depth of the valley at the fore part of its base, is finally blended with the anterior lobe, on which the crescentic enamel-fold (*e*) becomes first obliterated, as in fig. 2, *m* 1: thus the Ruminant pattern of the grinding surface is reduced to that which we shall afterwards find to characterize, with minor modifications, the upper molars of most anisodactyle Pachyderms. The three principal stages of attrition of the Anoplotherian molars are well shewn in the fossil upper jaw of the *An. commune* from the Montmartre gypsum, figured by Cuvier in the 'Ossemens Fossiles' 4to. 1812, tom. III., Supplement Pl. 8, fig. 2. The incisors and canines are severally implanted by a single fang; the first premolar by two fangs; the rest by three, two external and one internal; the true molars by four fangs.

In the lower jaw the first premolar is implanted by two connate fangs; the second to the penultimate molar inclusive by two fangs; the last molar by three fangs, the second and third being connate. The mid-incisor of the lower jaw is small, with a convex or flat border: the second and third have triangular crowns progressively increasing in size: the canine is a little larger, with the crown rather more pointed, and the hinder basal lobe and the two depressions on the inner side of the crown better marked.(1) The first premolar (Pl. 135, fig. 3, *p* 1) scarcely differs from the canine save by a slight increase of size. The rest (*p* 2, *p* 3, *p* 4) are divided into two lobes by an external vertical depression, each lobe being convex externally, and penetrated internally by a valley deepest at its termination, the posterior lobe having also a second

(1) The difference is so slight that Cuvier described the canines of the Anoplothere as incisors, in his original Memoir, in the 'Annales du Muséum,' tom. III. pp. 374, 376, and before later specimens had demonstrated the extent of the intermaxillary bone.

notch at its posterior and inner angle: the crown is sub-trenchant and tricuspid before it begins to be worn down. A progressive increase of size, and especially of transverse breadth, is combined with a similar form in the first and second true molars (*m* 1 & *m* 2); but the outer notch is deeper, and the two divisions (*o*, *o*) more convex, and swollen at their base; the third molar (*m* 3) has an additional small hind lobe. The unworn summits of the first and second true molars are produced into three points in the anterior, and into two points in the posterior lobe. The deep terminations of the folds penetrating the inner side of these semi-cylindrical lobes form crescentic islands of enamel at a certain stage of attrition, and thus typify the Ruminant character of the inferior molars; but these islands are soon obliterated and the pattern characteristic of the same teeth in the Rhinoceros and some other anisodactyle Pachyderms is produced. In some of the smaller species of *Anoplotherium*, separated subgenerically under the name of *Dichobune*, the Ruminant type of grinding surface is more closely adhered to, and is longer retained: in the lower jaw it is produced simply by the crescentic folds of enamel becoming more vertical and sinking into the crown from its summit, instead of penetrating it from the inner side.(1)

The constituent tissues of the teeth of these ancient Herbivora are the same in number, kind, and microscopic structure as those of existing Ruminants and ordinary Pachyderms. A dense, unvascular, fine-tubed dentine forms the basis; the crown is defended by a moderately thick coat of fibrous enamel; and the whole is invested by a cement, which is thickest on the fangs, and at the bottom of the inflected enamel folds of the teeth. The last portion of pulp in the centre of each tooth or tooth-lobe was converted into osteo-dentine, which forms the dark mark on the middle of the much-worn crowns of the teeth of old individuals. The diameter of the dentinal tubes of the canine tooth of the *Anoplotherium*

(1) From the close resemblance of these molars to those of the *Ruminantia* thus produced, it has happened that they have been sometimes referred to that Class: the fossil lower jaw of the species which I have called '*Dichobune cervinum*,' from the eocene tertiary beds in the Isle of Wight was originally described and figured as a species of Ruminant apparently closely allied to the Genus *Moschus*. See Geol. Trans. 2nd Ser. Vol. III, p. 451.

commune is $\frac{1}{12,000}$th of an inch: that of their interspaces, in the middle of the dentine is $\frac{1}{6000}$th of an inch. The diameter of the sub-hexagonal dentinal cells is $\frac{1}{5000}$th of an inch. The purkingian cells of the cement are for the most part oblong, $\frac{1}{4000}$th of an inch in largest diameter.

The vast abundance of Anoplotherian remains accumulated in the ancient lacustrine deposits which now form the gypsum-quarries at Montmartre, afforded Cuvier evidence not only of the changes produced in the form of the teeth by mastication, but also by the shedding and succession of the teeth. The deciduous formula of the Anoplotherium is:—

$$\text{Incisors } \frac{0-0}{3-3}\text{; canines } \frac{1-1}{1-1}\text{; molars } \frac{4-4}{4-4}\text{: } = 32.$$

The incisors and canines were replaced by teeth of similar form, but of larger size: the deciduous molars by teeth of more simple conformation; the deciduous molars typifying the structure of the permanent true molars, but the last in the lower jaw having the third posterior lobe of larger proportional size than in the last lower true molar. We cannot but recognize with much interest the constancy in the number of the true molar teeth under all their diversified forms in the existing *Ungulata* not proboscidian; but that interest is greatly heightened when we find that the same law both as regards the number of true molars, and the inferior complexity of the premolars to the deciduous teeth which they displace, has prevailed from the remote period when we first obtain evidence of hoofed Herbivora on the surface of this planet.

192. *Ruminantia.*—The essential character of the dentition of all Mammalia, which by the Ungulate modification of their locomotive extremities are deprived of one of the means of seizing a living prey, is the complex structure of the molar teeth, produced by an interblending of the dental tissues in the crown, whereby they are made more efficient instruments for the mastication of vegetable substances.

Different groups of *Ungulata*, not only Orders and Genera but even species, are characterised by the various patterns which result from the various forms, directions and proportions in which the

enamel and cement alternate with the dentine in the substance of the crowns of the complex molars. The pattern which characterises the Ruminantia, and which is remarkable for its degree of constancy in that Order, is shown in the upper and lower molar teeth in Pl. 133. The next dental characteristic in degree of constancy is the absence of incisors and canines in the upper jaw, and the seeming absence of canines in the lower jaw, where those teeth are so modified in shape and position as to resemble an external or fourth pair of incisors. Two remarkable exceptions to this character are, however, figured in Pl. 133; one in the genus *Moschus* fig. 1, the other in the *Auchenia*, fig. 2.

The ordinary dental formula of the Ruminantia is:—

$$\text{Incisors } \frac{0-0}{3-3};\ \text{canines } \frac{0-0}{1-1};\ \text{premolars } \frac{3-3}{3-3};\ \text{molars } \frac{3-3}{3-3}:\ =\ 32.$$

The Antelopes, the Sheep, the Ox, representatives respectively of the families *Antilopidæ*, *Ovidæ and Bovidæ*, which are collectively designated the 'hollow-horned' Ruminants(1), all present this formula. It likewise characterises many of the 'solid-horned' Ruminants(2) or the Deer-tribe (*Cervidæ*), the exceptions having canine teeth in the upper jaw in the male sex and sometimes also in the females, though they are always smaller in these. In the male Muntjak the upper canines protrude, like tusks, beyond the lips, descending a little beyond the lower jaw; and they had a like development in the extinct Dorcathere. The upper canines attain their greatest length in the small Ruminants called Musk-deer, and especially in the typical species *(Moschus moschiferus)* most famous for the preputial scent-secretion from which it takes its name: these teeth, indeed, in the male Musk, present proportions intermediate between those of the upper canines of the Machairodus and of the Morse. (Pl. 133, fig. 1. *c*). The inverse relationship in the development of teeth and horns exemplified by the total absence of canines in the Ruminants with persistent and typical horns, by their first

(1) From having persistent and commonly hollow bony processes of the skull supporting hollow cones of true horny material.

(2) From having solid bony processes undefended by horny sheaths, and which are annually shed and renewed.

appearance in the periodically hornless Deer, and their larger size in the absolutely hornless Musks, is further illustrated by the presence not only of canines, but of a pair of laniariform incisors in the upper jaw of the *Camelidæ*. In the Camel and Dromedary the upper canines are formidable for their size and shape, but do not project beyond the lips like the tusks of the Musk-deer; they are more feeble in the Llamas and Vicugnas (Pl. 133, fig. 2, *c*), and are always of smaller size in the females than the males. The inferior canines, moreover, retain their laniary form in the *Camelidæ*, and are more erect in position than in the ordinary Ruminants: they are separated by a short diastema from the incisors in the *Auchenia*, (ib. *c*). The true nature of the corresponding teeth in the ordinary Ruminants, in which they are procumbent and form part of the same series with the incisors, is always indicated by the lateness of their development, and often by some peculiarity of form: thus in the Moschus they are smaller and more pointed than the incisors, and in the Giraffe they have a much larger crown which is bilobed: their ordinary proportions and position, as presented by a large Antelope, the Gnu, is shown in Pl. 134, fig. 9, *c*. The laniariform tooth in the intermaxillary bone of the *Camelidæ*, which represents the upper and outer incisor, is smaller than the true canine which is placed behind it in the Camel and Dromedary: but in the Vicugna (Pl. 133, fig. 2, *i*.) it is as large as, or larger than the true canine. The lower incisors in the genus *Auchenia* (ib. *i*) have long and narrow crowns, directed straight forward and placed side by side: in *Camelus* the crowns of the lower incisors are oblong, depressed, spatulate or leaf-shaped, with a sinuous bend concave above; and they overlap each other, as shown in Pl. 134, fig. 8, the outer contour of the series describing half of an ellipse. In the Giraffe the incisors describe a semicircle. In most of the ordinary Ruminants the lower incisors are arranged in a transverse line at the extremity of the jaw. In these the first is the largest, and the second and third decrease in size, and to a greater degree in the Deer and Antelopes than in the Elk, the Sheep and the Ox: their crowns are trenchant and procumbent,

slightly diverging from the alveoli: they are opposed above by a callous gum, and are thereby better adapted for cropping or tearing the herbage and foliage on which the Ruminants subsist.

The true molars, three in number on each side of both jaws, are constant; the premolars are subject to some variety. They are essentially four in number in each series; but the first, in the true Ruminants, is feebly and transitorily represented by a rudimental matrix developed in the primitive dental groove at a short distance in advance of the second deciduous molar, and has no successor. The second deciduous molar, or that which is essentially such, is developed as the first of the functional molar series of the immature animal (Pl. 133, fig. 4, *d* 1), and is displaced by the tooth, marked *p* 1 in figs. 1 & 4, which is the first of the permanent molar series, and is here indicated and described as the first premolar, although it essentially corresponds with the second premolar of the typical dental formula of the *Ungulata*. In the Camel and Dromedary the actual first premolar is functionally developed and assumes the form of a small canine implanted by a single fang a little way behind the true canine; it is transitorily represented in the fœtus of the true Ruminants; and is retained only a little longer time in the Llama and Vicugna.(1) The second premolar soon disappears in all the *Camelidæ;* it is long retained in the true Ruminants, where, as above stated, it is described as the first premolar. The third premolar in the *Camelidæ*, marked *p* 2 in fig. 2, Pl. 123, as being that to which the second premolar in the true Ruminants answers, is relatively smaller than that analogue, and is earlier lost, especially in the lower jaw. The last premolar is persistent in the *Camelidæ*, but is smaller and more simple, especially in the lower jaw, than it is in the true Ruminants. The true molars in the Camel are larger in proportion to the size of the head than they are in the

(1) Cuvier believed the laniariform premolar of the Camel to be the analogue of the first permanent premolar in the true Ruminants, but altered in shape and position. See 'Ossemens Fossiles,' 4to. 1823, tom. III, p. 5. The normal number, viz. four premolars and three true molars, was functionally developed in an extinct species of the Deer-tribe, called by Dr. Kaup *Dorcatherium*, See 'Ossemens Fossiles de Darmstadt', 4to. p. 91.

ordinary Ruminants, and the two lateral series in the upper jaw converge anteriorly in a greater degree.

The characteristic complexity of the molar tooth of a Ruminant is manifested by most of the deciduous series; but, in the permanent series, only by the three posterior teeth of both upper and lower jaws, which are the true molars; the three first, or premolars, having more simple crowns than those which they displace. The complexity in question is the result of peculiar folds of the formative capsule, some of which are longitudinal or project inwards from the sides of the capsule and form peninsular folds of enamel upon the grinding surface of the tooth, whilst others depend vertically from the summit of the matrix into the body of the tooth, and form islands of enamel when the crown begins to be worn (Pl. 134). Of the longitudinal folds two, in the upper true molars, are external, broad but shallow, and often sinuous (fig. 1, *o*, *o*), and one is internal, narrow and deep (ib. *i*) extending quite across the summit of the crown of the tooth, as in figs. 6 & 7, and decreasing in depth towards the base of the crown; the corresponding fold of enamel in the completed tooth accordingly extends more or less across the crown, from within outwards, as the tooth is less or more worn. The crown of the tooth is thus divided into two lobes, placed one in front of the other; the inner side (*i i*, fig. 3) of each lobe being convex, the outer side (*o o*) concave but in a minor degree, and usually sinuous or with a convex prominence in the middle (fig. 3 & 4). The vertical folds of the capsule, two in number extend one into each lobe, and in the upper molars are concave towards the outer and convex towards the inner side of the lobe, which is thus divided into two semi-cylindrical bodies or lobules (*o*, *i*, fig. 6), with crescentic summits, as seen in a transverse section or on the grinding surface of the tooth; each lobule consisting of a middle body of dentine (*od*, *id*, fig. 5) and an outer coat of enamel and thin cement; the midspace between the lobules, answering to the centre of the vertical fold, is filled partly by cement, and commonly contains portions of the vegetable food; it is inclosed by a crescentic island of enamel (figs. 3 & 4, *e e*); the whole

circumference of this complex molar is also invested by a coat of enamel (fig. 8, *e*) and a thinner layer of cement (ib. *c*). In some Ruminants(1) a small vertical column (fig. 3, *p*), the analogue of the large conical one in the Anoplothere, is developed at the internal interspace of the two lobes of one or more of the upper true molars, varying in height, and rarely reaching the summit of the new formed crown. Different genera of Ruminants also differ in the depth and sinuosity of the two outer longitudinal folds, and in the depth and complexity of the two vertical folds, which likewise are united in some species by a longer common base than in others, producing thereby a continuity of the enamel and complete antero-posterior bisection of the grinding surface during a longer period of attrition. The upper molars also differ in their breadth or antero-posterior diameter as compared with their thickness or transverse diameter; but, as the summit of the crown is always relatively broader in proportion to its thickness, care must be taken to compare teeth of the different species that have been worn to the same extent, or to allow for the difference.

In the family of Sheep and Goats (*Ovidæ*, Pl. 134, fig. 1) the two outer depressions (*o o*) are broad and shallow with a very low middle convexity, and are bounded by well defined, narrow prominent longitudinal ridges, the posterior or third ridge being less developed than the other two: there is no internal accessory column: the breadth of the crown is greater in proportion to its thickness than in the *Cervidæ* or *Bovidæ*. The vertical crescentic folds of enamel forming the islands (*e e*) are narrow and simple: the Goat and Argali offer a rudiment of a secondary fold at the extremities of the insular crescents, which is rarely seen in the Sheep. The little Musk-deer differs from the Sheep, principally by the greater prominence of the middle longitudinal convexity on the outer side of the anterior lobe, and the crescents are more curved.

The *Antilopidæ* have the median convexity of the two outer shallow depressions of the upper molars more marked than in the *Ovidæ* and the crescentic enamel-folds are wider; in the Gnu

(1) Cuvier specifies the Ox, Deer, and Giraffe, loc. cit. p. 8.

(fig. 2, *e e*) they present a secondary fold or indentation at each end. The small internal accessory column is present in this species, but placed deeper in the substance of the tooth than usual, forming a circular island of enamel (*p*) when the crown is worn a short way down.

In the Ox (fig. 3) the outer contour of each lobe of the upper molars (*o*) is more sinuous than in the Antelope or Sheep, the middle convexity being more prominent and the lateral depressions deeper; the crescentic islands (*e e*) are not so wide as in the larger Antelopes (fig. 2), and the secondary terminal indentations are less marked at the fore-part of the island. The small internal accessory column (*p*) forms part of the periphery of the grinding surface at the inner interspace of the lobes, when the crown has been worn down about half an inch, from which part it decreases in size to the beginning of the fangs.

The upper molars of the Aurochs (*Urus*, fig. 4) are thicker in proportion to their breadth(1) and have a squarer grinding surface than in the Ox (*Bos* proper); the crescentic islands (*e*) are simple, with prolonged horns: the internal accessory column (*p*) is less developed, and is soon indicated by a slight bend of the enamel at the inner interspace of the lobes.

In the Deer (*Cervus*) the inner crescentic sub-division (*id*, fig. 5) of each lobe is thicker transversely than in the *Bovidæ*: in the great extinct Irish Deer (*Megaceros*, fig. 5) which has molar teeth as large as those of the Aurochs, the crescentic islands are simple, narrow, and more curved or bowed than in the Ox, and in consequence of the later division of the vertical fold of the capsule, the cemental cavity of each is continued into the other until a later period of the attrition of the crown, as shown in the upper molar of fig. 5.

In the Elk (Subgenus *Alces*, fig. 6) the central crescents are continuous for a still longer period, and the median transverse fold retaining its full breadth for a greater extent, the crown of the molar continues to be divided, during a longer period of attrition, by a crucial incision; the crescentic fold—ultimately

(1) Breadth is antero-posterior diameter, thickness is transverse diameter.

the island of the anterior lobe (*e*)—presents a small accessory fold at the inner side of its posterior horn: in the posterior lobe the fold is represented by a small circular island of enamel (*e'*) both are soon obliterated as the tooth wears down. There is an accessory column at the internal interspace of the lobes in *Alces* as in *Megaceros*, which is not present in the Rein-deer or Fallow-deer, but it is rudimental and confined to the base of the fissure. The anterior border of the outer concavity of each lobe is unusually produced.

In the Giraffe (fig. 7) the median convexity of the outer surface of the anterior lobe (*o*) is more prominent than the anterior border of the depression from which it rises, whilst the anterior border of the posterior lobe (*o'*) is more produced than the middle prominence: this distinctive character is well shown in the upper molars of the fossil Giraffe from the Sewalik Hills, noticed by Captain Cautley in the 'Journal of the Asiatic Society of Bengal,' Vol. VII, pp. 658-660, and figured in his joint communication with Dr. Falconer, in the 'Proceedings of the Geological Society,' No. 98, Pl. 2, fig. 3 & 4; the last and penultimate molars are specifically distinguished by an obtuse lobe at the bottom of the outer interspace of the two lobes. The crescentic enamel folds are continued into each other until the tooth is worn low down; but their outer boundaries are earlier completed than in the Elk: the two principal lobes are divided almost to the base of the crown: the internal column is reduced to a very small basal rudiment. The enamel of the Giraffe's molars is unusually rugose and resembles that of the Sivatherium.

The molars of the Camel (fig. 8), present the most simple condition of the ruminant type of these teeth: the transverse fold dividing the crown being short, the dentine of the two lobes forms a continuous tract: the common base of the crescentic vertical folds of the capsule being likewise short, the enamel islands are soon separated from each other: they include a shallow or narrow crescentic cavity, with a simple but slightly sinuous contour. The two outer shallow longitudinal depressions of the crown (*o o'*) have no middle rising; and there is no columnar process at the interspace

of the two inner convexities. Bojanus has well illustrated these characteristics of the upper molars of the Camel in his Memoir on the *Merycotherium*(1), a large extinct Cameloid genus of Ruminants founded on fossil remains discovered in Siberia, and he has extended the comparison to the Sheep, the Elk, and the Ox.

Cuvier compares the lower molars of the Ruminants to the upper ones reversed: in the lower true molars the single median longitudinal fold is external and divides the convex outer sides of the two lobes (fig 3*, *o o*): the base of the fold extends in some species across the molar for some depth, before it contracts towards the outer side, and the two lobes of the crown accordingly continue to be completely divided for a longer period, as in the Elk and Giraffe (figs. 6 & 7): the inner surface of the molar is gently sinuous, the concavities being rarely so deep as those of the outer surface of the upper molars: the lower molars are always thinner in proportion to their breadth than those above, and the crescentic islands are narrower and less bowed. The differences which the lower molars present in different genera of Ruminants are analogous to those in the upper molars, but are less marked: the accessory small column when present, as in *Bos*, *Urus*, *Meyaceros* and *Alces*, is situated at the outer interspace of the convex lobes, and nearer the base in the *Cervidæ* than in the *Bovidæ*: in the Giraffe it is present in the first, but not in the second or third true molars; it is not developed in the Antelopes, Sheep or Camel, and is wanting in most of the smaller species of Deer: other differences are expressed in Plate 134. The last true molar of the lower jaw is characterised in all Ruminants by the addition of a third posterior lobe: this is very small and simple in the Camel and the Gnu, is relatively larger in the *Bovidæ* and *Cervidæ*, presents in the *Megaceros* and *Sivatherium*(2) a deeper central enamel island or fold, which also characterises the

(1) Nova Acta Nat. Curios. 4to. 1824, tom. xii, pt. i, p. 265, tab. xxi.

(2) The last lower molar of this most gigantic of Ruminants is figured in Pl. 133, fig. 3. Cuvier (loc. cit. p. 5) describes the two lobes of the lower molars as being composed of two half-cylinders forming crescentic ridges on the grinding surface, and the last lower molar as having an additional half cylinder, and consequently a grinding surface of five crescents: the crescentic ridges are formed by the vertical descending fold, which divides the summit of the lobe, and the fact is that the third lobe of the last molar has also this fold; but it is shallower and the entire lobes are smaller. In most Ruminants the crescentic enamel island or fold is therefore soon obliterated in the third lobe; but in some species it is deeper and

smaller third lobe in the Giraffe. The lower molars of the genus *Auchenia* are peculiarly distinguished by the vertical ridge at the fore part of the anterior lobe (Pl. 133, fig. 2, *m*, 2 & 3), which does not exist in the Camels of the Old World.

In all Ruminants the outer contour of the entire molar series is slightly zigzag, the anterior and outer angle of one tooth projecting beyond the posterior and outer angle of the next in advance.

The premolars are smaller and more simple than the molars with which they form a continuous series in the true Ruminants; in the upper jaw they are not divided into two lobes by an internal cleft, but resemble a single lobe of the true molars, of greater breadth than thickness, with a single central crescentic island, and usually with an internal basal ridge. The central crescents have a more complex contour in *Megaceros* than in *Bos*, and the first premolar, which is always the smallest, is relatively larger in the Deer than in the hollow-horned Ruminants. In the small Musk-deer the crescentic enamel island is reduced to a small internal notch or fold, and the outer border of the crown is trenchant and pointed. In the lower jaw the premolars decrease in size from the third to the first, which has usually a compressed conical crown with a sinuous inner surface: the second and third premolars have two deeper notches on the inner side, and a small second hinder lobe slightly marked off by a vertical depression on the outer side of the crown. All the three lower premolars have compressed, sub-trenchant and pointed crowns in the small Musk-deer (*Tragulus*): the true Musk (*Moschus*) more resembles the ordinary Deer in its premolars. The aberrant *Camelidæ* deviate most from the Ruminant type in their premolar teeth. In *Auchenia* the first is soon shed; the second (Pl. 133, fig. 2, *p* 2) is unusually small and simple, and the third (*p* 3) does not surpass in breadth a single lobe of the true molars, in either jaw. In the Dromedary and Camel the second and third premolars bear the same proportions to the molars as in the Llama and Vicugna,

remains longer as in the last molar of the Giraffe, the great Irish Deer and the Sivatherium, which plainly shows that the additional lobe in the last lower molar is a reduced analogue not of half, but of a whole lobe, and that it is essentially composed of two half-cylinders, presenting as long as its central enamel fold remains, two crescentic ridges, but of smaller size than those in the two normal lobes which it succeeds. The essential distinction of the third lobe of the last lower molar is that it has not a distinct root.

but the first, which is placed further in advance of the molar series, is retained in the form of a small subcompressed, recurved, trenchant and sharp-pointed canine, implanted by a single root: the second premolar in the lower jaw is usually soon shed, the premolars are here indicated by numbers according to their appearance as functional teeth.

In the ordinary Ruminants, the upper premolars are implanted by three fangs, two outer and one inner: the upper true molars by four fangs, two outer and two inner. In the lower jaw both premolars and molars are implanted by two fangs, but the second fang in the last molar is very thick and consists of two connate fangs (Pl. 133, fig. 1). The crowns extend some way into the sockets before dividing into fangs; but these are always formed sooner than in the Horse, and increase in length with the age of the Ruminant.

193. *Microscopic Structure.*—In the true vegetable-feeding hoofed Mammalia, as in the small Rodents with a similar regimen, the crowns of the molar teeth are complicated by the interblending of layers of enamel and cement with the dentine or basal substance of the tooth: the microscopic structure of the several tissues does not essentially vary from that of the same tissues in the more simple teeth of the Mammalia; except that in the dentine of the incisors a few vascular canals are retained, and that the cement of the molars, being of great thickness, also presents vascular canals in addition to the minuter radiated cells. The calcigerous tubes of the dentine in the incisor of a Deer, maintain their parallelism best and are least bent, in the last half or third of their course, *i. e.* nearest the enamel; and fall into stronger and less regular curves as they approach the pulp-cavity, altering their curves somewhat abruptly, and along contour-lines indicated by the change of curve and by the numerous minor branches there given off, most of which communicate with or dilate into minute cells which likewise add to the distinctness of the contour lines. The dentinal tubes are most curved at their commencement from, or rather termination in the pulp-cavity, where in the incisor of the Red Deer, they present a diameter of $\frac{1}{11,000}$th of an inch, and are separated by interspaces of about $\frac{1}{6,000}$th of an inch in width. They soon begin to divide dichotomously into primary branches, and then to send off numerous fine ramuli whereby the more parallel and straighter continuations of the main tubes which form the peri-

pheral third part of the dentine are reduced to less than half the diameter of their beginnings: the primary curve of the terminal portions of the tubes in the crown is convex towards the upper margin; in the basal portion of the tooth it is concave towards the upper margin and sends off, as Retzius rightly describes in the Sheep, the most numerous ramuli from the concavity and directed towards the upper surface of the tooth. The white colour of the dentinal tubes, when viewed by reflected light, is well displayed in the figures of Dr. Erdl:(1) though they give an idea of the solidity of the tubes which is not accurate: the opacity is due to the particles of the lime salts which the tubes contain in a disgregated state; but the more important functions of the tubes are perforated by that part of the area which is left unoccupied by such salts, and through which the vital and nutritious plasmatic fluid meanders. In the portion of dentine of a Calf's molar, taken from the bottom of the pulp-cavity (Pl. 109, fig. 3) the undulations of the tubes, the stronger flexuosities of some of the terminal branches, and the occasional anastomotic loops which they form are shown.

The clear compartments of the basal substance are relatively smaller than in the dentine of carnivorous and mixed feeding Mammals: those in the peripheral third part of the Deer's incisor are $\frac{1}{5000}$th of an inch in diameter, of a subcircular figure, and with an overlapping or imbricated arrangement when viewed in a section taken in the axis of the tooth: they increase in size and lose their regularity of form nearer the pulp-cavity. In an antero-posterior longitudinal section of the incisor of the Ox, Sheep, and Deer, a linear tract of the orifices of medullary canals is seen continued from the summit of the pulp-cavity to the grinding surface: these canals extend towards the lateral borders of the crown and form loops at a short distance from the enamel.

In old teeth, especially the molars, the residue of the pulp is converted into osteo-dentine, forming the yellow-coloured nodules mentioned by Retzius, around which the dentinal tubes irregularly wind. The peripheral terminations of the tubes are resolved into rich plexuses of minute branches interspersed, close to the enamel, with minute opake cells.

(1) Abhandlungen der Akademie der Wissenschaften, Bd. iii. tab. ii.

The enamel extends to the beginning of the division of the crown of the tooth into fangs, and consequently for some distance into the socket in young Ruminants. The enamel covering the outer sides of the flattened crowns of the incisors is thicker than that upon the inner sides of the same teeth. The fibres are unusually slender, not exceeding $\frac{1}{8000}$th of an inch in diameter.

Retzius has accurately and clearly described both the coronal and radical cement in the teeth of Ruminants. He says, " I found only a thin layer on that part of the teeth which was covered by enamel: the cement was more thickly deposited round the ends of those roots which were nearly closed, and in the clefts or enamel-folds of the crown. Both the calcigerous cells and tubes were large and very irregularly formed. In the thin layer of cement covering the enamel, the cells appeared more like reticular vascular glands than actual cavities: many of these are extended into oblong or many-pointed figures of considerable length; and, besides these, larger (vascular) canals proceeded from within, pretty parallel but thinly scattered. The said gland-like cells were about $\frac{1}{2000}$th of an inch in long diameter, the vascular canals about $\frac{1}{1000}$th of an inch. It is most worthy of remark that the cemental cells entered into very large and numerous communications with the (minute opake) cells in the outer part of the dentine. The cement was very porous in the clefts of the tooth, and manifested still less regular tubes and cells than in the situations above described. The quantity of cement in the Ox is far greater than in the Sheep: the above-described coarse tubes (vascular canals), were here regularly branched and proceeded likewise in an almost horizontal direction on the sides of the teeth. But the cells were smaller and more regular than in the sheep: they were very closely aggregated, approaching the circular form and about $\frac{1}{2000}$th of an inch in diameter." In Pl. 109, fig. 4, is given Dr. Erdl's figure of a portion of the cement from the root of the molar of a Calf, as seen by reflected light: the opake calcigerous radiated cells are clustered together chiefly towards that side which was next the outer surface of the cement: and from these cells proceed the cemental tubes, which here and there dilate into smaller and more simple cells, as they approach the dentine.

194. *Succession.*—The deciduous series of teeth in the Ruminants consists of:—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{4-4}{4-4}: = 32.$$

The superior incisors and canines are represented in the cavicorn Ruminants and most *Cervidæ* by minute rudiments imbedded in the gum, and were first observed in the embryos of the Cow and Sheep by Mr. John Goodsir.(1) I have detected similar rudiments of a molar tooth, very near the canines, in the fœtus of a Fallow-deer. These rudiments present themselves in the form of minute papillæ sunk in depressions of the primitive groove, and, as Mr. Goodsir remarks, "after the closure of the latter, they remain for a short time as opake nodules imbedded in the gum, in the course of the line of adhesion." They do not attain to that stage of calcification which distinguishes the rudimental hidden teeth discovered by Geoffroy in the gums of the fœtal whales. In the Camel tribe, the third or outermost of the upper incisors together with the canine and first premolar, are completely calcified and have permanent successors: in the Musk-deer and the Muntjac the permanent canine attains, as we have seen, unusual size and becomes a formidable weapon; but the primitive rudiments of the upper incisors and of the first molars in both jaws, disappear without giving origin to the matrices of any successors. The functional and fully developed milk-teeth, commonly found in the Ruminants, are the six incisors and two canines of the lower jaw, and the second, third and fourth molars in both jaws, the first molar being rudimental and not calcified or manifested above the gum except in the Camel tribe. The interest attached to the change of dentition, as indicative of the age of the valuable domestic cattle derived from the Ruminant order has attracted more than usual attention to its successive phases in these. Bojanus(2) has given the most accurate account of these phenomena in the Sheep. The whole of the functional deciduous series, viz:

$$in.\ \frac{0-0}{3-3};\ c.\ \frac{0-0}{1-1};\ m.\ \frac{3-3}{3-3}:$$

(1) Report of the British Association, 1839.

(2) Nova Acta Nat. Curios. tom. xii, pt. ii, p. 702.

have cut the gum, in the Lamb, in the course of the first month after birth; the first true molar (*m* 1, fig. 4, Pl. 133) next appears, behind the third milk molar in both jaws at the sixth month: at the end of the first year the second true molar comes into place and there are five molar teeth on each side of both jaws. This transitional period may be detected and distinguished from an older stage, when the same number of molar teeth may have been produced by the loss or extraction of one of the six permanent molars, by the form of the third tooth in the lower jaw (fig. 4, *d* 3), which tooth in a Sheep between one and two years old, is divided into three lobes; the permanent tooth (*p* 3) which succeeds it consists of one principal lobe and a small posterior lobule.

In the course of the second year the first or internal deciduous incisors fall and are replaced by the broader permanent ones. The state of dentition in the lower jaw of a sheep of twenty months is shown in Pl. 133, fig. 4. The first permanent incisor (*i* 1) and the first and second true molars (*m* 1 & 2) coexist with the second and third deciduous incisors (*di* 2 & 3), the deciduous canine (*d c*) and the three deciduous molars (*d* 1, 2 & 3). Towards the end of the second year, the third true molar (*m* 3) appears above the gum, and at the same time the deciduous molars begin to give place to their vertical successors, falling with brief but irregular intervals, the third being sometimes pushed out a few days or a few weeks before the first and second. The variations in those phases of development of the molar series, which are dependent on individual constitution, food, season and time of birth, never prolong the process beyond the end of the second year. The change of the incisors and canines is not completed until a later period. The second permanent incisor (*i* 2) displaces its deciduous predecessor in the course of the third year; the third comes into place usually during the first half of the fourth year: the outer cutting teeth of the lower jaw manifest their essential nature as canines by the lateness of their development, not appearing above the gum and displacing the deciduous canines until the fifth year, the entire series of permanent teeth being in place and use before the end of the fifth year. At the fourth

year the roots begin to be developed from the base of the crown of the last molars, having previously been added to those of the precedent teeth.

In the Calf, according to M. Rousseau,(1) the first deciduous incisor and the first deciduous molar both cut the gum a few days after birth: the second incisor and the second and third molars between the fifth and tenth days: the third incisor between the fifteenth and twentieth days, and the deciduous canine, which, with Bojanus and Cuvier, he terms the fourth incisor, a few days later. The second dentition is commenced, as in the Sheep, by the eruption of the first true molar, between the fourth and sixth month after birth: the first or median permanent incisor and the second true molar appear between the fifteenth and twenty-second month: and about the latter period the first premolar pushes out the first deciduous molar. The second premolar and the second incisor appear between the twenty-eighth and thirty-second months. The third premolar and the third incisor appear between the thirty-eighth and the forty-eighth month. The last true molar cuts the gum between the forty-fourth and the fifty-second month. The permanent canines (fourth incisors of M. Rousseau) are the last to appear, as in the Sheep, but at an earlier period, according to that Author, viz., before the Ox has attained its fifth year.

The birth and growth of a young Giraffe at the Zoological Gardens of London have enabled me to make the following observations on the course of development and succession of the teeth in that rare Ruminant, which is the largest existing species of its Order. The four middle deciduous incisors began to cut the gum one week after birth, and their crowns were entirely extricated at the end of four weeks, at which time the summits of the crowns of both the first and second deciduous molars were visible. At two months the third incisor had cut the gum; at three months the third deciduous molar, and at four months a fourth molar, were in place; the latter being the first of the permanent series of true molars.

The progress of shedding the deciduous teeth was traced by

(1) Anatomie Comparée du Système Dentaire, 8vo. 1839, p. 229.

observation of the parent Giraffe. She arrived at the Zoological Gardens in May 1836, and was then about eighteen months old, and had all the deciduous series with the first permanent true molars. The two middle deciduous incisors were shed in the month of March 1838, the second incisor on each side in the following July, the first deciduous molars in October, and the second deciduous molars in November and December of the same year. At this time the second true molars come into place. The last true molars began to appear above the gum in August 1839, and the last deciduous molar was replaced by the third premolar before the end of that year: the shedding of the whole deciduous series was completed by the fall of the canines in the female Giraffe at the period of the birth of her second fawn in May 1841, when she must have been six years and a half old: the large bilobed crowns of the permanent canines were not completely in place until September 1841.

The middle incisors are relatively larger in the deciduous than in the permanent series as compared with the outer ones and the canine, in most ordinary Ruminants; the Giraffe deviates furthest from the typical proportions of these teeth in the superior expanse of the bilobed crown of the permanent canine, but it is interesting to find that the deciduous canine, though its crown is also bilobed, is relatively smaller in proportion to the incisors, and thus shows a less amount of deviation from the common type. The third lobe of the last inferior deciduous molar, in the Giraffe, as in the Sheep and Ox, is relatively larger and retains its central enamel-crescent longer than in the last inferior true molar. This tooth in the great extinct Sivatherium (Pl. 133, fig. 3) retained more of the form of its deciduous analogue the last milk-molar than is usually seen in existing species of Ruminantia.

195. *Suidæ*.—Of all the natural groups of *Ungulata* the Hog-tribe offers the greatest diversity of dentition, especially in the structure of the molar teeth: the African Wart-hogs (*Phacochœrus*) rival the Elephants in the relative size and complexity of the last molars, whilst these teeth in the South American Peccaris are simply tuberculate, without increase of size: so

likewise amongst the ancient extinct aberrant forms, the *Hippohyus*(1) presents almost a ruminant pattern of the grinding surface, whilst the *Chœropotamus* manifests in its whole dentition a close resemblance to the plantigrade *Carnivora*.

The folds of the dental capsule upon the coronal surface of the molar teeth of the typical Hogs are shorter than in other hoofed Mammals, but are very numerous, and produce a multicuspid or rather multituberculate grinding surface, especially in the last molar, which is commonly much larger than the rest. The canines form projecting tusks, and are remarkable in most *Suidæ* for their extraordinary size, shape, and direction, especially in the males. The incisors are less constant, varying in number in different genera. The progressive increase of size in the molar teeth as they are situated further back in the mouth, may also be noticed as a family characteristic, which, with the complication of the crown and the development of the tusks, reaches its maximum in the Phacocheres.

196. *Sus*.—The wild progenitor of our domestic breeds of Hog (*Sus scrofa, Linn.*) offers as the normal formula:—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ pm.\ \frac{4-4}{4-4};\ m.\ \frac{3-3}{3-3};\ = 44.$$ (Pl. 140, fig. 1.)

The upper incisors decrease in size from the first to the third: the first has a short, strong, obliquely bevelled crown, which inclines towards and touches that in the other intermaxillary by its produced inner part; the crown, before it is worn, presents a depression; it is implanted by a short, thick, curved fang; this incisor is relatively larger in the *Sus larvatus* than in the *Sus scrofa*. The second incisor, in the common Hog, has a crown as broad as the first, but shorter and thinner; its edge is trenchant and dentated, but is soon worn down: in this state the abraded surface of both incisors shows a dark mark in the centre. The third is a very small tooth, a little removed from the second. The form and position of the short vertical crowns of the upper incisors remind one of those of the Kangaroo; and the resemblance is carried out by the procumbent position of the

(1) An extinct genus so called by its Discoverers, Captain Cautley and Dr Falconer.

incisors of the lower jaw, whose crowns oppose their upper sides to the ends of those above, as in the herbivorous Marsupials. But the incisors in the Hog are six in number below, as well as above: they are long, sub-compressed, nearly straight; the second is rather larger than the first; the third is the smallest, as in the upper jaw. In the two larger procumbent incisors the crown is remarkably long, and the enamel continued far into the socket, especially upon the upper and under surfaces; the under surface is slightly convex and even; the upper one has a peculiar character in a strong median longitudinal rising, divided by a depression on each side from the two margins of the crown, of which the outer one forms a dentated ridge; these characters become obliterated by use, but the lateral flattening or compression of the long and straight fang may assist in the determination of one of these incisors. The lateral incisor curves towards the second.

The upper canines, in the Wild-boar, curve forwards, outwards, and upwards; their sockets inclining in the same direction, and being strengthened above by a ridge of bone which is extraordinarily developed in the Masked Boar of Africa. The enamel covering the convex inferior side of this tusk is longitudinally ribbed, but is not limited to that part; a narrow strip of the same hard substance is laid upon the anterior part, and another upon the posterior concave angle forming the point of the tusk, which is worn obliquely from before upwards and backwards to that point. I have never seen a permanent upper tusk of either sex of the *Sus scrofa* in which the enamel was limited to the outer surface as described by M. Rousseau(1): in the lower tusks it covers the anterior and inner as well as the outer sides. The longitudinal ridges on the lower plate of enamel are fewer and stronger in the Masked Boar (*Sus larvatus*) than in the common Wild Boar. In the Sow the canines are much smaller than in the Boar. In some domestic breeds the upper tusk has a short descending pointed crown, with an anterior and posterior margin, divided by indentations from a median convexity, something like

(1) 'Anatomie Comparée du Système Dentaire,' p. 206.

the canine of a horse. Castration arrests the development of the tusks in the male.

The teeth of the molar series progressively increase in size from the first to the last: the first premolar (Pl. 140, fig. 1, *p* 1) has a simple compressed conical crown, thickest behind, and has two fangs: it is further removed from the second in the *Sus larvatus* than in *Sus scrofa*. The second premolar (ib. *p* 2) has a broader crown, with a hind-lobe, having a depression on its inner surface; and each fang begins to be subdivided. The third premolar (ib. *p* 3) has a similar but broader crown implanted by four fangs. The fourth premolar (ib. *p* 4) has two principal tubercles and some irregular vertical pits on the inner half of the crown. In the masked Boar the third upper premolar is larger, thicker, and more pointed than in the common Boar. The first true molar, when the permanent dentition is completed, exhibits the effects of its early development in a more marked degree than in most other Mammalia, and, in the Wild Boar, has its tubercles worn down, and a smooth field of dentine exposed by the time the last molar has come into place (Pl. 141, fig. 3, *m* 1): it originally bears four primary cones, with smaller subdivisions formed by the wrinkled enamel, and an anterior and posterior ridge. The four cones produced by the crucial impression, of which the transverse part is the deepest, are repeated on the second true molar (ib. *m* 2) with more complex shallow subdivisions and a larger tuberculate posterior ridge. The greater extent of the last molar (ib. *m* 3) is chiefly produced by the development of the back ridge into a cluster of tubercles: the four primary cones being distinguishable on the anterior main body of the tooth. The hind lobe is more simple and smaller in the masked than in the common Boar. There is generally a small tubercle at the outer and inner interspace between the two principal lobes of the true molars. The number of fangs increases with the increasing size of the crown.

The crowns of the lower molars are very similar to those above, but are rather narrower, and the outer and inner basal tubercles are much smaller or are wanting. The transverse

depression on the first and second true molars is deeper in the lower than in the upper jaw; its borders of enamel are very sinuous; in the second true molar each anterior lobe is penetrated by a secondary fold at its posterior margin, and the posterior division is divided into three lobes, the enamel coats of which form three islands arranged in a triangle when the surface is worn down to a certain extent: the last molar is divided by two transverse depressions into three principal lobes, the last being the longest in the common Hog, and the shortest in the Masked Hog; the two anterior divisions are each subdivided by the longitudinal furrow into two tubercles, and these are broken by many secondary depressions into smaller tubercles. The inferior canines of the Wild Boar are longer, and curve upwards, outwards, and backwards, in a more normal direction than those above: they are three-sided; the broadest convex side is directed obliquely inwards and forwards; the outer and posterior sides are nearly flat; the latter surface has no enamel, and the tusk wears obliquely from behind, upwards and forwards to a point, with two sharp enamel edges. Both upper and lower canines have the characters of true tusks in the projection of their crown beyond the lips, and their insertion by a long undivided and undiminished base, widely excavated for a persistent matrix which ensures the uninterrupted growth of these formidable weapons. Each tusk in a lower jaw of one foot in length, from a German Wild Boar, measures eight inches along its curve: but tusks of twelve inches in length have been obtained from the Wild Boars of Assam.

The smaller species of Asiatic Hog, called Babiroussa, has obtained from the extraordinary development and direction of its tusks the name of 'horned Hog' (Pl. 140, fig. 3); and both molar and incisor teeth offer some varieties from those of the ordinary species of *Sus*. The incisors are reduced to four in number in the upper jaw by the early loss of the two small outer ones; the first and second, on each side, which remain, correspond in form with those of the common Hog. The six incisors are retained in the lower jaw. The upper canines are more slender than in the

Wild Boar, are compressed laterally with an elliptic transverse section, and a smooth unenamelled exterior. Their socket seems as if it had been pulled out or produced from the alveolar border of the upper maxillary bone, and then bent abruptly upwards, giving the tusk a direction upwards and backwards. The tooth pierces the integuments of the upper lip, like a horn, and its growth, being unchecked by any opposing tooth, sometimes forces the tip again through the integument and into the substance of the skull. The lower tusks have the ordinary direction, but rise rather more vertically and much higher than in the Wild Boar; they are subtrihedral with rounded angles, except the inner one towards the point, and sometimes show upon their inner side slight marks of abrasion against the outer side of the base of the upper tusks. These tusks are well adapted by their position to defend the eyes, and assist in the act of forcing the head through the dense entangled under-wood of a tropical forest, as suggested in Home's Comparative Anatomy (Vol. I, p. 221); but their use has not been determined by actual observation: speculation, however, has not been idle in assigning final purposes to these singularly developed teeth, which are too absurd for repetition. The molar series is speedily reduced in the Babiroussa to two premolars and three true molars on each side of both jaws: the great activity of the vascular matrix of the long tusks soon exhausts the conservative force of those of the adjoining small premolars. The upper molars much resemble those of the Hog, but are relatively narrower; the four principal tubercles are better marked on the penultimate and last true molars, and the accessory tubercular talon of the latter is relatively smaller. In the lower jaw, also, the third lobe of the last molar is smaller, and the four principal tubercles constitute a more conspicuous and important part of the crown.(1)

(1) A fossil under jaw has been described and figured in Silliman's American Journal of Science, Vol. xliii. 1842, Pl. 3. fig. 1, under the name of *Sus Americana*, by Dr. Harlan, who conceived that from "its general appearance and number of the teeth this fragment bore a close analogy with the same part in the *Sus babirussa*, Buff., although the Babiroussa was a much smaller animal." Having compared a cast of this fossil jaw, I find that, besides the difference of size, there is a difference in the proportions of the true molar teeth, the

197. *Phacochærus*.(1).—The rate of increase of size from the first to the third true molar (Pl. 141, fig. 2) is carried to its maximum in the Phacocheres or Wart Hogs of Africa, and the folds of the capsule producing the multicuspid grinding surface here attain a depth, number, cylindrical figure, and regularity of arrangement, which produce so peculiar a modification of the structure of the molar teeth, as, with other and minor differences, to justify the subgeneric separation of those large and formidable Hogs from the rest of the *Suidæ*.(2)

The Wart Hog of Nubia, Abyssinia and Kordofan (*Phacochærus Æliana*, Rüppell)(3) has the incisors reduced to two in the upper jaw, corresponding with the median pair in other Hogs; a single short, thick, and inwardly curved incisor being inserted near the end of each intermaxillary bone: the margin of the unworn crown of this incisor in the young animal is divided into three equal tubercles by two notches, which are soon obliterated: they are larger in the males than in the females, according to Rüppell, (loc. cit. p. 62). The upper tusks are longer and larger than the lower ones and curve outwards, upwards and backwards: they

first being two-thirds the size of the last, whilst in the Babiroussa it is less than half. The last molar in the fossil has the anterior transverse ridge proportionally larger and the posterior lobe proportionally smaller than in the Babiroussa, resembling the *Lophiodon* in the points in which it thus differs from the *Sus* cited. The form of the jaw differs at this part of the fossil from that in the Babiroussa, in which the socket of the last molar overhangs the inner surface of the ramus, whilst in the fossil the inner surface of the ramus beneath the last molar describes a gentle convexity from the tooth to the lower margin. The outer part of the ramus of the jaw of the Babiroussa begins to expand below the fourth and fifth molars, counting forwards from the last, to form the socket of the large tusk, but the fossil jaw does not offer the least indication of an enlargement for that purpose, and the fractured anterior end, as displayed in the cast, is very different in shape from the corresponding part of the jaw in the Babiroussa, and shows merely the dental canal and no socket for the tusk which would be here situated in the Babiroussa or Wild Boar. The nearest approximation which the fossil in question allows to be made to any known existing or extinct animal is to the great tapiroid Pachyderms.

(1) φάκος a Wart, χοῖρος a Hog.

(2) M. F. Cuvier says, "Nous voici arrivés à un système de dentition tout-à-fait différent de celui des sangliers." Dents de Mammifères, p. 213; but this is rather too strong an expression.

(3) 'Atlas zu der Reise im Nördlichen Afrika,' fol. 1826, Erste Abth. p. 61, fig. 25 & 26. The 'Sanglier du Cap Verd.' of 'Buffon,' (t. xiv., p. 409), is of this species.

are four-sided, with rounded angles, gradually diminishing to a point, and showing the action of the lower tusk upon the fore part of their basal half: both upper and under surfaces are traversed longitudinally by a broad and shallow groove; and the tip of the first formed end of the tusk is similarly impressed on its fore-part, but this is subsequently worn away; the enamel, also, with which the end of the tusk is at first covered, is soon rubbed off. The number of molar teeth present at one time on either side of the upper jaw appears not to exceed five, and is soon reduced to four, and finally to two or one.(1)

I have not been able to obtain evidence of more than two premolars in the upper jaw, which correspond with the third and fourth in the common Hog. The anterior premolar (Pl. 141, fig. 2, *p* 3) is implanted by one anterior and two posterior short and thick fangs, and has an oval crown, four lines by three lines across, and presenting, in a much worn specimen, a notch or enamel-fold on the inner side: the last premolar, (ib. and Pl. 140, fig. 4, *p* 4) with a grinding surface nearly circular, and five lines in diameter, presents four peripheral enamelled lobes or islands, surrounding a central lobe: when much worn these are reduced to an external and an internal lobe, with a central enamel fold or island. The first true molar, which cuts the gum and is in use long before the preceding teeth are developed, or their deciduous predecessors are shed, presents itself, in the mature Nubian Phacohere (Pl. 141, fig. 2, *m* 1), as a smooth almost worn-out stump; squeezed, as it were, between the last premolar and the second true molar: more commonly its place only is indicated by a short diastema separating these teeth, and showing a remnant of the socket of the displaced tooth; and this vestige soon disappears, the second true molar being pushed forward in contact with the last premolar, as shown

(1) This is the state of dentition in the old *Phacochærus Æliani*, figured in Home's 'Lectures on Comparative Anatomy, Vol. II, pl. 38, which M. F. Cuvier cites, in the Mémoires du Muséum, t. viii, p. 453, as "une jeune tête de phacochærus tout-à-fait dépourvue d'incisives." The single incisor of the upper jaw and the sockets of two incisors in the lower jaw are, however, plainly shown in the engraving: the original specimen demonstrates six incisive sockets below, and the incisor in each intermaxillary above, with other characters of the Nubian species of Wart Hog, as the cartilaginous 'septum narium.'

in Pl. 140, fig. 4, and in the figures given by Dr. Rüppell. In the young individual, the crown of the first true molar (Pl. 141, fig. 1, *m* 1) is divided into two principal lobes, each lobe resembling the entire crown of the last premolar, and having a central enamel-island surrounded by four or five similar peripheral ones: it is implanted by four long and strong fangs; the antero-posterior diameter of the grinding surface measures nine lines. The second true molar (Pl. 140, fig. 4, & Pl. 141, fig. 1 & 2, *m* 2), which does not cut the gum until the first is more than half worn down, presents a broader subquadrate crown, nine lines by seven lines across the grinding surface, which presents a central enamel island, surrounded by four principal and some smaller islands or lobes. The third and last true molar (ib. *m* 3) is the most characteristic tooth of the Phacocheres, and perhaps the most peculiar and complex tooth in the whole class of Mammalia: the surface of the crown in the specimen before me, measures two inches in antero-posterior extent and eight lines in transverse breadth, and presents three series of enamel-islands, in the direction of the long axis of the grinding surface: the middle row of eight islands are elliptic and simple; those of the other rows are in equal number, but are sometimes subdivided into smaller islands: these islands or lobes are the abraded ends of long and slender columns of dentine, encased by thick enamel, and the whole blended into a coherent crown by abundant cement, which fills up all the interspaces and forms a thick exterior investment of the entire complex tooth. In the closed alveolus of the third molar of a young Phacochere, I found a number of the hollow prisms of enamelled dentine detached (Pl. 141, fig. 1, *m* 3): the formative matrix continues for a long period to be reproduced, maintaining by its successive calcification the crown of the tooth entire to the bottom of the socket, where the orifices of the constituent cylinders and the vacant interspaces, which lodged the complex vascular matrix are seen in the dried tooth.

In the lower jaw of the Nubian Phacochere the four middle incisors are strong, subtetragonal, porrect, subequal, with the ridge and grooves upon the upper side of the crown as in the ordinary

Wild Boar, but less obliquely abraded. The two small lateral incisors are more incurved towards the intermediate ones. The incisors are disposed more nearly in a transverse line on the broad expanded symphysis of the Phacochere than in the narrower jaw of the Hog. The lower canines are more slender, more divergent, and sharper than in the Wild Boar; but otherwise resemble them in their trihedral shape and in the partial disposition of the enamel, and its continuation into the alveolus. I have seen but one premolar tooth on each side of this jaw, with a crown reduced by attrition to one anterior and two posterior lobes, five lines in long diameter. In one specimen the stump of the first true molar remained, wedged in between the last premolar and the second true molar; in another a short vacancy showed the place whence the first true molar had been expelled: the second and third molars resemble those above, but are rather narrower transversely. The crown of the first true molar, examined at a period before its characteristic structure is obliterated, as in the young Phacochere before the second true molar has cut the gum, has the same complex pattern as that above; and measures nine lines by three lines, on the grinding surface: it is supported by four fangs, the hind pair being very long and strong.(1) The last molar in this jaw has the same

(1) The first true molar tooth, in both jaws of the *Phacochærus Æliani* appears to have escaped the attention of MM. F. Cuvier and Rüppell. M. F. Cuvier in his Monograph on the two species of *Phacochere* in the 'Mémoires du Muséum' tom. VIII. 1822, p. 450, represents a skull of the Nubian species with the last upper molar only in place: and in the 'Dents de Mammifères, p. 213, he assigns but three molars to each side of the upper jaw in both species, which teeth appear from his description to be the two premolars and the last true molar. The figure of the teeth of the upper jaw, in Pl. 87 of the 'Dents de Mammifères, is taken from the South African Wart Hog (*Phacochærus Pallasii*, v. der Hoeven.) Dr. Rüppell's elaborate Monograph relates exclusively to the Nubian or North African Phacochere. He says, "In all our specimens of both young and adults, and of both sexes, the upper jaw has *four*, the under jaw *three* molars: the first and second are small, narrow, roundish, with simple crowns, and each implanted by two roots in two separate sockets: the third (in the upper jaw; second in the lower) is strong (stark) 'and as broad as the fourth; its grinding surface has five simple crowns' ('kronen-kerne', our enamel-islands) 'four at the angles and one in the middle: it has four roots wedged into four separate sockets.'" Then follows the description of the complex last molar tooth, the fourth in the upper, the third in the lower jaw. The smaller rooted teeth above described are the two premolars, and the second true molar in the upper jaw;

rootless condition as the one above, upon which its longer duration than the preceding rooted molars depends, as Dr. Rüppell well remarks. (loc. cit. p. 63.)

In the Wart Hog of South Africa, (*Phacochœrus Pallasii*, v. der Hoeven)(1) there are no incisive teeth in the upper jaw of the mature animal, and the traces of four small incisors are almost obliterated in the lower jaw of the skull before me.(2) The large upper tusks differ from those of the *Ph. Æliani* in the deeper and narrower groove along their front and back part, and they are inclined more forwards. One simple, single fanged premolar, remains in the place near the base of the tusk corresponding with that of the first of the three deciduous molars in the young animal. The analogues of the two premolars in the specimen of *Ph. Pallasii* described, are shed, together with the first and second true molars, and the work of mastication has been carried on by the last large complex molar exclusively. The three series of columns of which this tooth consists appear to be more regular in form than in the *Ph. Æliani;* but this may depend on the tooth having been worn lower in the specimen of *Ph. Pallasii* here described, in which the long diameter of the grinding surface is two inches one line, the short or transverse diameter half an inch. In the lower jaw the stumps of four small incisors may be seen razed to the level of the edge of the symphysis. The canines,

and the figures (loc. cit. tab. 26, figs, *c*, *d*,) well exemplify this stage of dentition, which is the most common in the adult *Phacochœrus Æliani*. How the first true molar, or the vestiges of its socket and the vacancy between the last premolar and second true molar should have escaped the observation of the accomplished Abyssinian traveller, in the younger specimens to which he alludes, I cannot explain: they are obvious in three out of five examples of this species in the Hunterian Museum. In the immature Nubian Phacochere five molars are present when the second true molar has risen into place; and it will be seen from the description of the deciduous dentition of the *Phacochœrus Æliani* in the text that it had escaped the notice of Dr. Rüppell. The skull of the *Phacochœrus Æliani* figured in Home's Comparative Anatomy, tom. II, Pl. xxxix, shows the two premolars and the second and third true molars.

(1) *Sus Æthiopicus*, Pallas, Miscell. Zool., 16, tab. XI.

(2) M. F. Cuvier first pointed out the absence of incisors as a specific distinction of the South African species: but he had also observed on the margin of the symphysis of the lower jaw 'quatre dépressions à égale distance l'une de l'autre.' 'Mém. du Mus.' viii, p. 453. Similar depressions contain stumps of incisors in the specimen here described.

like those above, are larger than in the Ælian Wart Hog. The stump of a premolar is retained on one side, separated by an interval of an inch from the last molar, the rest having been shed, as in the upper jaw: the grinding surface of the molar is of the same length as that above, and is five lines in breadth: it presents a middle row of eight columns and two lateral rows of seven each, twenty-two in all.

198. *Succession.*—Before proceeding to the Peccari, which deviates still further in its dentition from the characteristics of the *Suidæ* and represents that of the extinct forms of the family, which lead on the one hand to the Plantigrades and on the other, by closer steps of affinity, to the Hippopotamus, I shall notice the succession and structure of the teeth in the more typical Hogs.

The first or deciduous dentition of the Hog consists of:—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{molars } \frac{3-3}{3-3}: \ = 28.$$

The first milk incisor, above, is large, oblique, trenchant, and with a depression on the inner surface of the crown: the second and third are small and pointed. The first and second incisors, below, are trenchant and oblique; and have the indentations and ridge slightly marked on the upper or inner side of the long and narrow crown; the third is pointed. The canines are feeble and have their normal direction in both jaws, the upper ones descending according to the general type, which is not departed from until at a later period of life. The first and second deciduous molars (Pl. 140, fig. 2, *d* 1, *d* 2) have simple compressed conical crowns crenate at the edge, and with an anterior and posterior basal tubercle; the second is a little larger than the first: the third manifests the characteristic increase of size and complexity, yet is kept within the bounds of the more common type: in the upper jaw it has four principal tubercles, and thicker ridges at the fore and back part of the base of the crown: when the enamel is worn from the middle of the subdividing valley, and the dentine of the two tubercles is united, the pattern closely resembles the characteristic trefoil of the grinders of the Hippopotamus. In the lower jaw, the last

deciduous molar (ib. *d* 3) has the crown divided into three lobes and a posterior tubercle; each lobe being subdivided into an outer and an inner cusp with irregular, subtuberculate surfaces: the lobes increase in thickness from the first to the third, the entire tooth bearing a strong resemblance in miniature to the corresponding deciduous molar of the Hippopotamus.

The second and third deciduous molars appear before the first, and the first and third incisors, with the canine, rise into place before the second incisor: the development of this tooth and of the first molar completes the caducous dentition. The first permanent true molar (ib. *m* 1) next comes into place behind the deciduous series, and the first premolar (ib. *p* 1) appears in front of that series, not displacing any predecessor: the second permanent true molar (ib. *m* 2) also cuts the gum before any of the deciduous teeth are shed.(1) The fall of the milk-teeth follows the order of their appearance: the *iter dentis* of each of the three replacing premolars ('dents de remplacement' of Cuvier) opens upon the inner side of the alveoli of the teeth which they displace. With respect to the anterior and smaller premolar (*p* 1) I am doubtful whether to regard it as belonging to the first or the second dentition: it maintains its place sometimes longer than the adjoining posterior premolars (*p* 2, *p* 3), and would, therefore, appear, like its analogue in the Bear and Dog, to be the first of the permanent series: but I have seen an instance in an Indian Wild Boar, in which, on the right side of the upper jaw, a premolar with a larger crown (Pl. 141, fig. 3, p. 1') had been developed between the small anterior premolar and the second normal premolar, and a little to the inner side of the anterior tooth, which it seemed, therefore, to have been destined to succeed, but had not displaced; there being five premolars and three true molars, or eight teeth on that side of the upper jaw.(2) The third large true molar

(1) The figure which Cuvier gives (Ossemens Fossiles, 4to. 1822, tom. II, Cochons, pl. I, fig. 4 & 6), as the dentition "d'un jeune animal qui n'a encore que des molaires de lait:" exhibits the first and second true molars which are certainly not milk-teeth, together with the small anterior premolar which, likewise, is not displaced by a successor as a true milk-tooth always is.

(2) Cuvier regards the anterior small molar (p 1) as the first of the deciduous series, and describes its displacement and succession by a 'dent de remplacement,' as constant, though

(Pl. 140, fig. 2, *m* 3) does not come into place until all the deciduous teeth have been shed; it is the last molar: the cavity in the lower jaw figured by Home, 'Lectures on Comparative Anatomy,' Vol. II, Pl. 27, fig. 3, as "a new cell formed for a succeeding tooth," is a medullary cell of the osseous tissue, not a closed alveolus with a tooth-germ.

In the Phacochere the first small and simple equivocal premolar is not developed in either jaw. The three deciduous molars are present in the upper jaw, but only two, the second and third, in the lower jaw, of a young *Phacochœrus Æliani* with the deciduous incisors still retained, and the second true molar not yet protruded: nor is there any trace of an alveolus of the first deciduous molar of the lower jaw, which may, therefore, be transitorily manifested, 'en germe' and never functionally developed. With this reduction in number, the deciduous dentition of the Phacochere, nevertheless, departs much less from the typical characters of the Suidæ than does the dentition of the adult. The three milk molars of the upper jaw present the same degree of increase of size, as do the three true molars of the Wild Boar. But the first is much more simple, has a compressed crown three lines long, supported by two fangs: the second milk-molar has a triangular crown broadest behind, and is supported by one anterior and two posterior fangs; the third is subtetragonal, with a grinding surface of six lines by four lines, with a central enamel island, surrounded by six somewhat larger islands; it is implanted by four fangs. The same cause, viz. the large matrix of the tusk, would seem to have drawn off the supply from the first and second premolars, and to have prevented their development; the third and fourth premolars, which have been above described in the Ælian Phacochere are more simple, especially the fourth, than the teeth which they displace. The last deciduous molar in the lower jaw (Pl. 141, fig. 1, *d* 3) very closely resembles in size and shape the corresponding tooth in the

late, in the upper jaw; but with regard to the lower jaw, he says 'peut-être même n'est-elle jamais remplacée en bas.' (Ossemens Fossiles, 4to. 1822, tom. II, pl. 1.) I have not, hitherto, found a successor to the small tooth in question, unless the above-cited Indian Wild Boar be regarded as an instance, but as this tooth p 1^{1} has not displaced p 1, it seems rather to be an anomalous or supernumerary premolar.

young *Sus scrofa*. I could find no germ of a successor to the small anterior deciduous molar (ib. *cl.* 2); and we have seen that the lower jaw of the nearly full-grown Phacochere presented only one premolar (Pl. 140, fig. 4, *p* 4). The germ of this tooth is shown in Pl. 141, fig. 1, *p* 4: the first true molar (ib. *m* 1 has already lost half its crown by the wear of mastication, and its early loss, with the obliteration of its alveolus, as in Pl. 140, fig. 4, accounts for its having hitherto escaped the notice of the Naturalists who have paid most attention to the remarkable dentition of the Phacocheres.

The single permanent incisor in each intermaxillary of the *Phacochærus Æliani* is preceded by a deciduous and more simple incisor.

199. *Microscopic structure.*—The dentine of the teeth of the common Hog is dense, unvascular, susceptible of a bright polish. In a vertical section of the second premolar the calcigerous tubes radiate from the pulp-cavity, passing from its summit into the crown in almost straight lines, and with a flexuous course from its sides: the strongest curve is at their commencement, but it is short, and they then proceed straight towards the enamel, with a few dichotomous acute-angled divisions, the terminal third part of the thus divided tubes bending gently from the grinding surface in curves which diverge slightly from the centre of each tubercle; the ultimate divisions at the outer surface of the dentine are extremely numerous, fine, and plexiform. The diameter of the tubes at the middle straight part of their course is $\frac{1}{8000}$th of an inch, and here they are separated by interspaces equal in diameter to the breadth of nearly two tubes: they gradually diminish as they approach the enamel. Fine ramuli are sent off from the sides of the main-tubes, which curve across the interspaces, and are mostly lost in the compartments of the basal substance.

The dusky yellow-coloured osteo-dentine, into which substance the pulp is finally converted, presents a much more flexuous arrangement of dentinal tubes, the ramuli of which not unfrequently dilate into angular calcigerous cells; these in the osteo-dentine of the base of the teeth are numerous, and present in some parts a concentric arrangement.

The enamel-fibres are smaller than those of the teeth of the *Carnivora*: and the cement is much thicker upon the roots of the teeth of the Hog, and can be more readily traced over the enamelled crown, especially in hollows of the irregular grinding surface, and upon those parts of the dentine of the tusks which are not covered by enamel. Here, and upon the roots of the teeth, the Purkingian cells were developed, and of a full oval figure, about $\frac{1}{2500}$th of an inch in long diameter: the cemental tubuli, communicating with these cells on the one hand, and with the terminal plexuses of the dentinal tubuli on the other, traverse the thicker layers of cement in horizontal and parallel directions, resembling in this respect the dentinal tubes.

The complex molar of the Phacochere yields a beautiful demonstration of the microscopic characters of the several tissues of a tooth.

The dentine, as we have seen, is broken up into detached, long, and slender prisms. In a longitudinal section of one of these denticles, the calcigerous tubes ascend vertically through the central third part of the prism, and in the lateral parts gently diverge or bend away towards the periphery; and when they are close to the enamel increase their outward curve and the width of their clear interspaces, bifurcating there once or twice: several of the terminal branches dilate into opake cells close to the enamel; the secondary undulations of the tubes are minute but well marked, especially in the ends of the tubes. One or two medullary canals, with a thin coat of osteo-dentine, extend along the centre of the prism. In transverse sections the ends of the tubes, cut across, occupy all but the marginal part: they rarely shew interspaces wider than the breadth of a tube, and are in some places even closer together. The peripheral terminations of the tubes, appear to be more strongly bent than when seen in longitudinal sections. The tubes are smaller, more numerous, and send off much fewer lateral ramuli than in the dentition of the Horse.

In the middle part of the transverse section the dentinal cells are sub-elliptic, with a clear outline, and include about twenty of the dentinal tubes; towards the periphery they are indicated by

slightly curved lines, with the feeble convexity turned towards the periphery.

In the middle of the transverse section of the dentinal prism, a narrow tract of osteo-dentine is seen surrounding the area of the central vascular canal: it is characterized by its more transparent texture; its fewer and more contorted tubuli, and the minute opake cellules dispersed through it. The clear substance is arranged in concentric layers around the canal, and the outer boundary of this small sub-circular patch of osteo-dentine is very well defined from the true dentine: the central ends of the tubes of this tissue are closely crowded round the clear boundary of the osteo-dentine, but a very few are traceable into that substance.

The enamel-fibres, as exposed by a vertical section of the complex tooth, extend obliquely upwards and outwards in a straight line, for the first half of their course, then bend outwards to the periphery of the enamel, which is very irregular. The transverse section of the cylinder of enamel displays a strong wavy, or crenate outline: the rounded lobes which project into the cement being of nearly equal breadth with the intervening notches. The contour-lines of the enamel are well shown in this section, and alter their course from the parallel of the even margin of the dentine to that of the crenate outer margin of the enamel.

A very small outer part of the exterior cement of the molar is nearly clear, with the fine cemental tubes penetrating the substance at right angles to the surface. A thick and densely aggregated stratum of Purkingian cells, mostly of a full oval figure, are next seen, these cells being rather less thickly arranged in the middle of the cement. The vascuar canals of the cement are chiefly present near the enamel; some were seen forming loops turned towards the outer surface of the cement.

200. *Chæropotamidæ*.—The dental formula of the Peccari (*Dicotyles*,) is:—

Incisors $\frac{2-2}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{3-3}{3-3}$: = 38.

The two middle upper incisors are the largest, and are thick, short, curved and convergent, as in the Hog. The external surface

of the crown has two lateral ridges; the internal surface presents a strong basal ridge. The margins of the crowns of the lateral incisors are notched. In the lower jaw the incisors are long, narrow, and procumbent; similar in form, as well as position, to those in the Hog.

The upper canines have moderately long, narrow, compressed, two-edged, straight, descending crowns, with an entire covering of enamel; the fang has a longitudinal groove on both the outer and inner surface; the socket is strengthened by an anterior semi-lunar ridge. The canine is separated from both incisors and molars by an interspace of nearly an inch, both before and behind it. The three premolars are contiguous, and gradually increase in size; their crowns are more or less triangular: each has two outer cusps and one inner cusp, with an accessory tubercle behind the inner one, which progressively increases in the second and third premolar. The true molars are quadricuspid, with an accessory tubercle at the fore part of the interspace of each transverse pair of cusps, and with an anterior and posterior crenate ridge. There is a slight increase in the size, and in the development of the accessory ridges of the grinding surface in the second and the last molars.

The lower canines have a long, slightly curved, and trihedral crown; the narrow posterior side having no enamel, and playing upon the anterior margin of the upper canine, which thus becomes blunted and deprived of enamel. The first premolar has one blunt tubercle, the second has two: both have also anterior and posterior ridges, the latter being developed in the third premolar into a second pair of tubercles. The true molars of the lower jaw are quadri-cuspid, with an accessory tubercle at the posterior interspace of each transverse pair of cusps, the second of which is developed into a small third lobe in the last molar tooth. Each true molar has also an anterior basal ridge.

This type of dentition was closely adhered to, or rather foreshowed, by some very interesting forms of ancient extinct Pachyderms, amongst which, remains of the following genera have been found in the oldest tertiary deposits in England and on the Continent.

201. *Hyracotherium.*(1)—In the *Hyracotherium leporinum*, an animal about half the size of the Peccari, the upper canines were compressed and directed downwards: the typical number of premolars, (which probably are transitorily represented in the Peccari) was here constant, the first of the four being situated near the middle of the diastema between the canine and the second premolar; like the latter it had a simple subcompressed short conical crown with an anterior and posterior basal talon and two fangs. The third and fourth premolars suddenly assume an increased size and complication of crown, resembling the two last premolars in the Peccari: they present one internal and two external cusps, with two intermediate smaller tubercles, and a cingulum or basal ridge almost surrounding the entire crown. Each true molar (Pl. 140, fig. 6) has the four principal and the two accessory cusps, as in the Peccari, but the anterior and posterior basal ridges are united by internal and external ones so as to form a cingulum, and the last molar is not longer, and is narrower posteriorly, than the penultimate one: no vestige now remaining of the characteristic predominance of size of the last molar in the typical *Suidæ*. Each principal cusp of the molars in the specimen described by me had its summit worn into a little pit. The dentition of the lower jaw and the incisive formula of the *Hyracotherium* are as yet unknown.

202. *Chæropotamus.*—The *Chæropotamus Cuvieri*(2) was about one third larger than the Peccari, and deviated further than the Hyracothere in a direction towards the Hippopotamus. All the premolars were more simple in comparison with the true molars; the last premolars had each an external large and an internal low and small tubercle, both inclosed by the cingulum. The true molars are each like two premolars combined, and with the inner tubercles developed to equality with the outer ones; they have also the two small intermediate tubercles and a well-developed cingulum (Pl. 140, fig. 5): the last upper molar resembles that of the Hyracothere in form and proportions. In the lower jaw the canine had much of the form and proportions of that of a Carnivore. There are three

(1) Geological Transactions, 2d Series, Vol. VI, p. 203, Pl. 21.

(2) Geological Transactions, 2d Series, Vol. VI. p. 41, Pl. 4.

premolars in this jaw, the first with a compressed pointed crown and a small posterior talon, like that above; the second and third increasing in breadth, but narrower and more simple than those above. The true molars below are also narrower than the upper ones, but are quadricuspid with accessory tubercles, and a largely developed hinder talon in the last molar. Nothing as yet is known of the incisors of the *Chœropotamus*; the rest of the dentition closely resembles that of the Peccari, but the premolars are more simple and the canines by their size, shape, and direction, and the lower jaw by the backward prolongation of its angle, alike manifest a marked approximation to the Ferine type. The occasional carnivorous propensities of the common Hog are well known, and they correspond with the minor degree of resemblance, which this existing Pachyderm presents to the same type. The extinct *Chœropotamus*, still better adapted by its dentition for predacious habits, presents an interesting example of one of those links, completing the chain of affinities, which the revolutions of the earth's surface have interrupted, as it were, and for a time concealed from our view.

203. *Hippohyus*.—In this extinct genus of quadrupeds from the Himalayan tertiary deposits, the dental formula shows incisors $\frac{3-3}{3-3}$, and corresponds with that of the *Chœropotamus* in the number of canines, premolars, and molars; but the true molars have a more complex crown, approaching nearer to those of the typical *Suidæ* in the depth and number of the secondary enamel-folds. Each upper true molar (Pl. 140, fig. 7) has its crown cleft by the common or primary crucial valleys, the transverse one passing somewhat obliquely from within forwards and outwards. Each of the four principal lobes is subdivided, not by a vertical central depression, but by a fold penetrating its anterior and posterior margins: the enamel at first shows additional minor plications; but is worn down progressively to the simpler pattern above described; the outer lobes are convex externally. The first premolar is very small and simple, separated by an interval of its own breadth from the second: both this and the third have transversely compressed crowns, the fourth has a sub-trihedral crown. The *Hippohyus* equalled in size the *Chœropo-*

tamus; but exhibits as strong a tendency towards the Hippopotamoid family as that does towards the plantigrade *Carnivora.*

HIPPOPOTAMIDÆ.

204. *Hippopotamus.*—The tendency to excessive and, as it may be termed, monstrous development, which characterises the canine teeth in the typical *Suidæ* affects both these and the incisors in the present remarkable family, of which the Hippopotamus of the great rivers of Africa is now the sole existing representative. Figure 4 in Pl. 141 gives an oblique view of the formidable apparatus of variously directed prominent incisive and canine tusks in this animal. The upper incisors, two in each intermaxillary bone, curve downwards and oppose their extremities to the sides or upper surface of the straight and porrect incisors, also four in number, in the lower jaw; and they thus repeat in their relative position the characters of the upper and lower incisors of the *Suidæ*. The mid-incisor above (*i* 1) is subcylindrical, slightly curved, with the apex obliquely abraded along the inner side: the outer incisors (*i* 2) are placed behind and to the outer side of the median pair, are more curved, and oppose themselves more directly to the outer pair below.

The two median inferior incisive tusks are cylindrical, of great size and length, obliquely abraded at the upper and outer part of their extremity: the basal portion which is lodged in the deep alveolus is longitudinally grooved: the two outer incisors are likewise cylindrical and straight, are much smaller and are worn towards the inner side of their point. The upper canines (*c*) curve downwards and outwards, their exposed part is very short and is worn obliquely at the fore part, from above downwards and backwards; they are three-sided, with a wide and deep longitudinal groove behind. The lower canines (*c*) are extremely massive and large, curved in the arc of a circle, subtrihedral, the angle rounded off between the two anterior sides, which are convex and thickly enamelled, the posterior side of the crown being almost wholly occupied by the oblique abraded surface opposed to that on the upper canine.

The implanted base of each of these incisive and canine teeth is simple and excavated for a large persistent matrix contributing to

their perennial growth by constantly reproducing the matter to replace the abraded extremities. The direction of the abraded surfaces is in part provided for by the partial disposition of the enamel: in the upper median incisor this is laid upon the fore and outer part of the tooth: in the lateral incisor there is a narrow strip of enamel along the convex side of the tooth. The enamel is soon entirely worn away from the crowns of the lower incisors; but it is persistent in the canines, where it extends to the end of the implanted base; in the upper canine being laid upon the posterior and outer, and not on the fore part, whilst its position is reversed upon the inferior canine. The grooves and ridges upon the enamel of this tusk are strongly developed: most of them are longitudinal, but the prominent anterior part of the outer surface is traversed by a series of oblique ridges; and strongly marked transverse grooves and ridges cross the tusk at irregular distances, apparently indicating epochs of the eruption of the tusk.

The molar series consists of $p.\ \frac{4-4}{4-4}$, $m.\ \frac{3-3}{3-3}$, $= 28$.(1) The first premolar has a simple subcompressed conical crown and a single root: it rises early, and at some distance in advance of the second premolar, and is soon shed, the other premolars form a continuous series with the true molars in the existing species; but in the extinct *Hippopotamus major*, whose remains are found in the superficial deposits of this island and on the continent, the second premolar is in advance of the third by an interval equal to its own breadth. This and the fourth premolar retain the simple conical form but with increased size, and are impressed by one or two longitudinal grooves on the outer surface, which when the crown is much worn give a lobate character to the grinding surface: there is a strong tuberculate ridge on the inner and hinder part of the base of the crown, and in the anterior premolars the ridge on the fore and back part of the cone, extending to the summit of the crown is notched or tuberculate near its base. In the premolars of apparently the *Hippopotamus minor* figured in the work of Scilla 'De Corporibus

(1) M. Fr. Cuvier assigns 'fausses molaires $\frac{3}{3}$, molaires $\frac{3}{3}$, to the genus *Hippopotamus* in the 'Dents des Mammifères' p. 206; but the first molar was shed and the last deciduous molar was not shed in the lower jaw of the specimen which he figures and describes, whence the mistake.

marinis,' tab. xii, fig. 1, (1747) the notches extend to the summits of these ridges. I have given an original figure (Pl. 142, fig. 3) of one of these problematical teeth, from the specimen which now forms part of the Woodwardian Collection at Cambridge, by the kind permission of the eloquent Professor of Geology in that University; the anterior border is not so regularly notched as in Scilla's figure; and the two fangs shew the moderate proportions of those of the premolars of the Hippopotamus, and by no means the ventricose character of the roots of the teeth of a seal, to which family of *Carnivora* this ancient fossil has been referred(2).

The true molars are primarily divided into two lobes or cones by a wide transverse valley, and each lobe is subdivided by a narrow antero-posterior cleft into two half cones, with their flat sides next each other; the convex side of each half cone is indented by two angular vertical notches, bounding a strong intermediate prominence, the analogue of that which rises out of the outer depression of the Ruminant's molar (Pl. 134, fig. 3, *o o*): a strong ridge bounds the fore and the back part of the base of the crown and extends completely round the last upper molar. A view of the unworn summits of the crown of a true molar of the Hippopotamus is given in Pl. 143, fig. 3. When these summits begin to be abraded each lobe or pair of demi-cones presents a double trefoil of enamel on the grinding surface: when attrition has proceeded to the base of the half cones, then the grinding surface of each lobe presents a quadrilobate figure, as shown in Pl. 143, fig. 4. The crown of the last molar tooth of the lower jaw is lengthened out by a fifth cone, developed behind the two normal pairs of half cones, and smaller in all its dimensions. The enamel on all the molars of the Hippopotamus is thick and has a wrinkled and punctate exterior. The three last persistent premolars have each two fangs in both jaws. The true molars have four fangs, except the last below, which has five.

Extinct Hippopotamidæ.—The fossil *Hippopotamus major* adheres closely to the type of the dentition of the existing species, the most marked distinction being the diastema between the second (first per-

(2) It is the *Phoca dubia melitensis* of M. de Blainville, 'Ostéographie de Phoca, 4to. p. 46; apparently on the authority of M. Agassiz, p. 44.

sistent) and third premolars. The smaller extinct species (*Hippopotamus minor*) has the same close resemblance in its dentition, and though much reduced in size, yet in both the number (four) and the cylindrical form of the procumbent lower incisors, it adheres to the typical dentition of the Hippopotamus.

205. *Hexaprotodon.*—The fossil Hippopotamus of the Sewalik tertiary beds, had the same number of incisors as the Hog, viz: six in both jaws, or $\frac{3-3}{3-3}$: those below are more equal in size than they are in the *Hippopotamus*, the median being rather less than the two outer incisors; they are all more oblique in position and the abraded surface is more confined to the extremity. The lower tusks are relatively shorter (Pl. 143, fig. 1, *c*). The first premolar (*p.* 1) is retained longer than in the Hippopotamus: the second (*p* 2) is removed from the third as in the European fossil Hippopotamus, but is relatively thicker; the second and third deciduous molars are retained in the specimen figured. The form of the true molars, and the pattern of their grinding surface resemble those in the true Hippopotamus.

206. *Merycopotamus*(1).—In the true molars of the *Merycopotamus* (Pl. 140, fig. 8) the inner demi-cones, *i i*, are simply convex, and the two grooves on the outer ones form a deep external depression, at the bottom of which is the convex ridge, *o o:* the antero-posterior cleft dividing the primary lobes, instead of being straight as in the Hippopotamus, forms two bends convex inwards, and thus the symmetrical pattern of the Hippopotamic molar is converted into the double-crescentic one of the Ruminant molar. The cement at the bottom of the valleys is thinner than in the Ruminants, the enamel is as rugose as in the Giraffe or Sivathere; but the strong rugged ridge along the inner half of the base of the crown forms the chief distinction between the molars of the *Merycopotamus* and those of the Ruminant. The teeth in the lower jaw make a similar approximation to the Ruminant type, but the anterior and posterior primary divisions are separated by a wider cleft; the last molar has a third hinder lobe, the lower molars are implanted by two roots. The forms,

(1) This genus, together with *Hexaprotodon*, was discovered in the sub-himalayan tertiary deposits and determined by Capt. Cautley and Dr. Falconer.

proportions, and relative position of the canines and incisors of the *Merycopotamus* closely accord with the Hippopotamic type of these teeth.

207. *Anthracotherium.*—In this genus although the molars, especially those of the lower jaw, depart from the Hippopotamic type less than the molars of the *Merycopotamus*, yet the canines and incisors retain more of the ordinary forms and proportions of those teeth in other Pachyderms: the canines, for example, though large are simply conical, the premolars have strong conical crowns with a basal ridge; the upper true molars have four principal cones, and a basal cingulum, the two outer cones encroach upon the two inner ones, and manifest, like those of *Merycopotamus*, an approximation to the Ruminant type.(1) In the lower jaw, the cones are more equal and symmetrical: the last molar, of which a reduced view is given in Pl. 135, fig. 10, has four distinct cones, and a large and slightly bifid posterior lobe: the surfaces of the four chief cones which are turned towards each other are somewhat angular and support projecting ridges, the opposite surfaces are simply convex. The entire dentition of the Anthracotherium is not yet known, but sufficiently so to prove that this extinct genus formed, with the closely allied *Merycopotamus*, links connecting the *Hippopotamidæ* with the *Ruminantia*.

208. *Microscopic Structure.*—The dentine is hard and unvascular in all the teeth of the Hippopotamus, and the sections of this compact substance take a fine polish: the dentinal cells are very conspicuous in the deciduous teeth, in an incisor of the first dentition they are subhexagonal, about $\frac{1}{4000}$th inch in diameter, arranged in layers parallel with the outer surface of the dentine and are pierced by the dentinal tubes which proceed at right angles to that surface; about twelve tubes are included in the area of a single cell. There is no peculiarity in the size, course, division, branching or termination of the dentinal tubes of the molars of the Hippopotamus. The calcigerous tubes of the dentine of the tusks are smaller, their diameter does not exceed $\frac{1}{12000}$th of an inch, and their intervals not more than $\frac{1}{8000}$th of an inch. They radiate from the pulp-cavity to the periphery of the tusk, inclined obliquely towards its extremity, and describe numerous subspiral curves, or waves succeeding each

(1) See Cuvier, Ossemens Fossiles, tom. iii, pl. lxxx. fig. 1.

other at equal distances of about $\frac{1}{300}$th of an inch, throughout their whole course, the waves of adjoining tubes being parallel along planes which are parallel with the outer conical surface of the exposed end of the tusk before it is worn. Each bend of the tube appears to equal the thickness of the layers into which the dentine of the tusk is resolved in decomposition, and which form the fine concentric lines upon the cut or broken transverse sections of the ivory. The tubes gradually diminish in size as they approach the periphery of the dentine; they give off minute branches; and in some places these dilate into very minute corpuscles, along the lines of the concentric rings of the transverse sections, and the contour lines of the longitudinal sections of the tusk.

The dentinal tubes at their commencement from the pulp-cavity of the molar teeth give a diameter of $\frac{1}{7000}$th of an inch; and their dichotomous bifurcations are more conspicuous than in the tusks.

The fibres of the enamel of the tusk have the usual disposition vertical to the plane of the dentine, but are little curved, and have no transverse striæ; most of these fibres are hexagonal and extend through the entire thickness of the enamel: near the base of the tusk they may be detached singly or separately from the part where they had been last laid on. In the thicker enamel of the molars the fibres are more wavy in their course, and I could perceive none that extended through the entire thickness of the section; but new ones every where arise by small ends wedged into the intervals of those next the dentine, the larger ends of the fibres being always towards the periphery. The cement which covers thickly those parts of the incisive and canine tusks which are bare of enamel, also extends in a very thin layer upon that substance, from which it is soon worn in the teeth in use. The coronal cement of the molar teeth forms a thicker layer, especially in the angles of the folds, but it is by no means so abundant as in the teeth of the corresponding folds of the molar teeth of the Ruminants.

In the parts of the crown where the cement is thickest, and upon the fangs, a few vascular canals are present: the radiated cells are most numerous at the periphery of the cement, generally affecting an oval form, arranged in concentric layers, with the long axis in the direction of the layer, these layers being crossed

by sub-parallel cemental tubuli, about $\frac{1}{5000}$th of an inch in diameter, the branches of which anastomose freely with the tubes radiating from the cells.

The osteo-dentine forms a pretty thick layer in the centre of the lobes of the crown, and of the fangs of old molars. The tortuosity of the fine tubes in this substance is extreme and they are very irregular.

In the ordinary-sized tusks the fine-tubed dentine, which forms the concentric-lined ivory, continues with little or no alteration of texture from the periphery to the pulp-cavity: but in very large and old tusks the apex of that cavity contains osteo-dentine, and this tissue is abundantly developed when the normal function of the dentinal pulp is disturbed by injury or disease. I have been favoured by Dr. Malcolmson, with a very remarkable example, in the inferior canine tusk of the Hippopotamus (Pl. 142, figs. 1 & 2), of the subserviency of the osteo-dentine in the reparation of a complete fracture. The injury was indicated externally by a sudden transverse constriction of the tusk at xx, with an interruption in the enamel at that part, and irregular deposits of dentine both there and at the adjoining concavity of the tusk. A longitudinal section of the tusk showed the pulp-cavity obliterated at the fractured part and for some distance below it, towards the base of the tusk, by a mass of osteo-dentine, deposited principally in the form of nodules closely impacted together, their convex sides projecting into the re-established pulp-cavity next the base: the general disposition of the osteo-dentine being very like that in the centre of the tooth of the Cachalot. The remains of the pulp-cavity in the protruded part or crown of the tusk were unusually conspicuous in the form of a narrow canal near the concave side of the tusk, and opening, like a fistula, upon that surface just beyond the fracture, another irregular slender canal extended transversely through part of the uniting substance and opened upon the concave side of the tusk, just below the preceding. From these appearances it may be concluded that the tusk, either by the action of a shot, or other violence, had been snapped across its implanted and hollow base with probably also fracture and injury to the prominent socket; but that the broken portions being held together by their adhesion

to the surrounding parts, inflammation of the pulp and capsule had ensued, ending in an altered mode of action in the calcifying processes, which produced the substance, called from its nearer resemblance to bone 'osteo-dentine.' In this substance is seen the transition of the normal dentinal tubes into the radiating tubes of the calcigerous cell; and a well-marked stage in the transformation of dentine into bone. In ordinary teeth the change in the mode of conversion of the last part of the pulp is sometimes so gradual as to render the confluence of the dentine with the osteo-dentine complete; and the present instance demonstrates the same confluence of the osteo-dentine with the ivory of the upper part of the tusk formed before the fracture, and with that at the base formed after the fracture, when the ordinary processes in the development of the tusk had been resumed. In the complete resumption of these processes, after the entire conversion of the matrix at the fractured part of the tusk into the mass of osteo-dentine which constitutes the uniting medium, we have a striking example of the truth of the conversion-theory of dental development. It will scarcely be contended that the calcified substance which manifests, besides the complex tortuous tubuli, numerous concentric series of radiated purkingian cells, and the larger vascular or medullary canals, called 'Haversian,' in osteology, is the product of a disordered secretion of a pulp inflamed by injury; we see, on the contrary, evidence of the conversion of such altered pulp by a series of centripetal processes of calcification, resulting in the aggregate of subspherical nodules of the osteo-dentine. Now, if the pulp of a continually growing tusk were a persistent secreting organ, an accident occasioning such destruction of it as is manifested by the microscopic structure of the mass uniting the fractured parts of the Hippopotamus's tooth under consideration, must have put an end to the secreting actions of such matrix, and to the future formation of the tusk. But here, on the contrary, it is shown that the inflammatory effects of the injury terminated in the abnormal conversion of the affected pulp into a bone-like substance, and yet that the subsequent development of the tusk was effected by the reproduction of a vascular basis or pulp, undergoing the ordinary processes of calcification to which the formation of the dentine, enamel and cement is due.

209. *Succession.*—The true natural affinities of the Hippopotamus are clearly manifested by the character of its deciduous dentition; and, if this be compared with the same dentition in other *Ungulata*, it will be seen, by its close correspondence with that of the Hog-tribe, and more especially with the Phacochere, that the Hippopotamus is essentially a gigantic Hog. The formula of the teeth which are shed and replaced is:

$$i.\ \frac{2-2}{2-2};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{3-3}{3-3}:\ =\ 24.$$

If the simple premolar which is developed anterior to the deciduous molars, and which has no successor, be regarded from its early loss in the existing Hippopotamus, as the first of the deciduous series, we must then reckon, with Cuvier, four milk molars on each side of both jaws. The incisors in both jaws are simply conical and subequal, with an entire cap of enamel on the crown. The deciduous canines scarcely surpass them in size in the upper jaw, and not at all in the lower; projecting forwards here, from the angles of the broad and straight symphysis, they appear like an additional pair of incisors; and we have seen that the character of equality of development was retained, with the more typical number of incisors, by the ancient form of Hippopotamus which formerly inhabited India. The first true deciduous molar (*d* 1) has a conical crown and two fangs in both jaws: that above has also a conical crown with one strong posterior and two anterior ridges. The second deciduous molar has a large trilobate crown, the first lobe small with an anterior basal ridge; the second large, conical, with three longitudinal indentations; the third lobe still longer and cleft into two half cones by an antero-posterior fissure assuming the normal pattern of the true molars; the third deciduous molar above more closely resembles the ordinary upper true molar, but its second pair of demi-cones is relatively larger. In the lower jaw the last deciduous molar has a more complex crown than that of any other tooth, whether of the permanent or deciduous dentition(1); it has three pairs of demi-cones, progressively increasing in size, from before backwards, with an anterior and posterior basal ridge and tubercles:

(1) This tooth is described as the first of the four true molars by M. F. Cuvier, loc. cit. p. 207; but its true nature was recognised by Baron Cuvier, see 'Ossemens Fossiles,' 4to. i. p. 289

like the last trilobate deciduous lower molar of the Hog it increases in thickness posteriorly, instead of diminishing here like the last true molar of the lower jaw of the adult Hippopotamus.

ANISODACTYLE PACHYDERMS.

210. *Equidæ.*—The Horse will yield us the first example of the dentition of the hoofed quadrupeds with toes in uneven number, because it offers in this part of its organisation some transitional features between the dental characters of the typical members of the Isodactyle and of those of the Anisodactyle *Ungulata.*

All the kinds of teeth are retained and in almost normal numbers in both jaws, with as little unequal or excessive development as in the Anoplothere; but the prolongation of the slender jaws carries the canines and incisors to some distance from the molars, and creates a long diastema, as in the Ruminants and Tapirs. The first deciduous molar is very minute, and is not succeeded, as in the Anoplothere, by a permanent premolar; yet remaining longer in place than the larger deciduous molars behind, it represents the first premolar and completes the typical number of that division of the grinding series. If the dental formula of the genus *Equus* be restricted to the functionally developed permanent teeth, it will be:

Incisors $\frac{3-3}{3-3}$; canines $\frac{1-1}{1-1}$; premolars $\frac{3-3}{3-3}$; molars $\frac{3-3}{3-3}$: = 40.

The incisors are arranged close together in the arc of a circle at the extremity of both jaws; they are slightly curved, with long simple subtrihedral fangs, tapering to their extremity. The crowns are broad, thick and short, the contour of the biting surface, before it is much worn, approaches an ellipse. These teeth, if found detached, recent or fossil, are distinguishable from those of the Ruminants by their greater curvature, and from those of all other animals by the fold of enamel, (Pl. 136, fig. 11, *a*) which penetrates the body of the crown from its broad flat summit, like the inverted finger of a glove. When the tooth begins to be worn, the fold forms an island of enamel, inclosing a cavity (*a*, figs. 8 & 9) partly filled by cement, and partly by the discoloured substances of the food, and is called the 'mark.' In aged Horses the incisors are worn down below the extent of the fold, (fig. 11, *a*) and the 'mark' disappears. The cavity is usually

obliterated in the first or mid-incisors at the sixth year, in the second incisors at the seventh year, and in the third or outer incisors at the eighth year, in the lower jaw. It remains longer in those of the upper jaw, and in both the place of the mark continues for some years to be indicated by the dark coloured cement, as in the incisors (fig. 10) of a Horse about sixteen years old. At this period the worn summits of the incisors present a subtriangular form.

The canines (figs. 9 & 10 *c*) are small in the Horse and rudimental in the Mare; the unworn crown is remarkable for the folding in of the anterior and posterior margins of enamel, which here includes an extremely thin layer of dentine. The upper canine is situated in the middle of the long interspace between the incisors and molars; the lower canine is close to the outer incisor as in the Ruminants, but is better distinguished by its cuspidate form. The representative of the first premolar (figs. 1 & 6, *p*, 1) is a very small and simple rudiment, and is soon shed. The three normal premolars (*p* 2, 3 & 4) are as large and complex as the true molars; the anterior one, (*p* 2) is usually the largest of the series in the upper jaw, the anterior lobe extending forwards into an obtuse angle.

The upper molar teeth of the Horse present a modification of the complex structure intermediate between the Anoplotherian and Ruminant patterns. The crown is cubical, impressed on the outer surface by two wide and deep longitudinal channels, penetrated from within by a valley *b* entering obliquely from behind forwards and dividing into, or crossed by the two crescentic valleys *c* & *e*, which soon became insulated as in the Camel; but a large internal lobe (*p*), at the end of the valley *b*, presents more of the Anoplotherian proportions than is shown by any Ruminant; it is also at first distinct, as in *p* 4, and though it soon becomes confluent with the anterior lobe in the existing species of Horse, it continued distinct much longer, and with more of the conical or columnar form in the primigenial Horse (*Hippotherium*, fig. 3, *p*) of the miocene tertiary period.

The molar teeth of the Horse have also, Cuvier remarks, a closer analogy with those of the Rhinoceros than might at first be supposed. The anterior crescentic enamel island (*e*) represents the termination of the principal valley (*b*), which is cut off by a bridge

of dentine analogous to that in the leptorhine Rhinoceros (Pl. 138, fig. 7). The posterior crescentic enamel island (*c*) is a further development of the fold (*c*) in the Rhinoceros' molar, but is much earlier insulated in the Horse.

In the lower jaw the same analogies may be traced: the teeth here, as is usual in other quadrupeds, are narrower transversely than in the upper jaw; they are divided externally into two convex lobes (Pl. 136, fig. 2, *m* 1, *o o*) by a median longitudinal fissure, and on the inner side they present three principal unequal convex ridges, and an anterior and posterior narrower ridge; but the crown of the molar is penetrated from the inner side by deeper and more complex folds than in the Anoplothere and still more so than in the Rhinoceros or Palæothere. The anterior valley between the narrow ridge and first principal internal column expands into a sub-crescentic fold: the second is a short simple fold and terminates opposite that which penetrates the tooth from the outer side: the third inner fold expands in the posterior lobe of the tooth like the first; two short folds partially detach a small accessory lobe at the posterior part of the crown. All the valleys, fissures or folds in both upper and lower molar teeth, are lined by enamel, which also coats the whole exterior surface of the crown.

The character by which the Horse's molars may best be distinguished from the teeth of other Herbivora corresponding with them in size, is the great length of the tooth before it divides into fangs. This division, indeed, does not begin to take place until much of the crown has been worn away; and thus, except in old Horses, a considerable proportion of the whole of the molar is implanted in the socket by an undivided base. This is slightly curved in the upper molars, the outer side of the bases of which is shown in Pl. 136, fig. 5, the inner side in fig. 6. The deciduous molars have shorter bodies and sooner begin to develope roots, as in fig. 5, *d* 2, 3 & 4; but in these, or in an old permanent molar with roots, the pattern of the grinding surface, as it is shewn in figs. 1 & 2, though it be a little changed by partial obliteration of the enamel folds, yet generally retains as much of its character as to serve, with the form of the tooth, to distinguish such tooth from the rooted molar of a Ruminant.

Cuvier(1) was unable from the materials at his command to detect any characters in the bones or teeth of the different existing species of *Equus* or in the fossil remains of the same genus, by which he could distinguish them, save by their difference of size. Amongst the numerous teeth of a species of *Equus*, as large as a horse fourteen hands and a half high, collected from the Oreston cavernous fissures, I have found specimens clearly indicating two distinct species, so far as specific differences may be founded on well-marked modifications of the teeth.

One of these, like the ordinary *Equus fossilis* of the drift and pleistocene formations, differs from the existing *Equus caballus* by the minor transverse diameter of the molar teeth; the other, in the more complex and elegant plication of the enamel, and in the bilobed posterior termination of the grinding surface of the last upper molar more closely approximates to the extinct Horse of the miocene period, which H. v. Meyer has characterised under the name of the *Equus caballus primigenius*. The Oreston fossil teeth differ, however, from this in the form of the fifth or internal prism of dentine in the upper molars, and in its continuation with the anterior lobe of the tooth; the fifth prism *p* being oval and insulated in the *Equus primigenius* of v. Meyer, (*Hippotherium*, Kaup. Pl. 136, fig. 3).

The Oreston fossil molar teeth, which in their principal characters manifest so close a relationship with the miocene *Equus primigenius*, differ, like the later drift species (*Eq. fossilis*), from the recent Horse in a greater proportional antero-posterior diameter of the crown and also in a less produced anterior angle of the first molar. I have named this ancient British fossil Horse *Equus plicidens*(2). The fossil Horse (*Equus curvidens*) of South America which coexisted with the Megatherium and, like it, became extinct apparently before the introduction of the Human Race, differs from the existing Horse by the greater degree of curvature of the upper molars.(3).

(1) 'Ossemens Fossiles,' 4to. 1822, tom. II. pt. i, p. 111.

(2) 'History of Brit. Fossil Mammalia, 8vo. p. 392.

(3) See 'Catalogue of Fossil Mammalia in the Museum of the Royal College of Surgeons,' 4to. p. 235.

211. *Microscopic Structure.*—The body of the long molar teeth of the Horse consists of columns of fine-tubed unvascular dentine (Pl. 137, *a*), coated by enamel (*b*) which descends in deep folds into the substance of these teeth; the enamel is covered by cement (*c*), thickest in the interspaces of the inflected enamel-folds and upon the crowns of the molars, where it is permeated by vascular canals, thinnest on the crowns of the canines and incisors. At the roots of these teeth, and on those developed from the worn down molars, the dentine is immediately invested by cement.

In a vertical section of the incisor, as in Pl. 136, fig. 11, the pulp-cavity, contracting as it approaches the vertical enamel-fold, divides near the end of that fold, and extends a little way between it and the periphery of the incisor, or leaves a few medullary canals and a modified thin tract of irregularly formed dentine, between the reflected and the outer coat of enamel but rather nearer the former. Above this tract, near the summit of the crown, the dentinal tubes proceed in a nearly vertical direction, with a gentle sigmoid primary flexure, where they diverge from the perpendicular; lower down the dentinal tubes diverge in opposite directions, curving from the remains of the pulp-fissure towards the outer and the inner enamel; and are described by Retzius as being bent in the form of the Greek ε (1); but the course of two distinct series of dentinal tubes, and not that of a single tube is illustrated by this comparison; when the pulp-cavity becomes single and central, as at the lower half of the tooth, the tubes diverge to the periphery, with one principal primary curve, convex towards the crown. Each tube is bent in minute secondary gyrations to within a short distance of its peripheral termination, where it is much diminished in size, and is dichotomously branched. The tubes at their commencement from the upper calcified tracts of the pulp-cavity, which usually retain some remnants of that vascular receptacle in the form of medullary canals, are strongly and irregularly flexuous, before they fall into the ordinary primary curves. Those tubes proceeding towards the inner reflected fold of enamel, are more vertical than the tubes going to the periphery.

(1) Loc. cit. p. 27.

A transverse section of the incisor of a young Horse or Ass taken across the part marked *a* in fig. 11, shows a long oval island of vascular cement in the centre, bounded by a border of enamel, with an irregular crenate edge next the cement, and an even edge next the dentine; which is here clearly seen to be divided into an inner and an outer tract by an irregular series of the vascular canals continued from the summit of the pulp-cavity, and by the irregularly tortuous dentinal tubes which, with the canals, indicate the last converted remnant of the pulp in this part of the crown. The inner tract of dentine next the island of enamel is well defined, and a little broader than the section of the enamel itself, and shows the extremities of the tubes cut transversely across, which tubes, as before observed, were at this part directed chiefly in the axis of the incisor towards the working surface of the crown. The tubes in the outer tract of dentine, inclining more towards the sides of the tooth, are more obliquely divided and at the ends of the section they are seen lengthwise elegantly diverging towards the sides of the section. This tract of dentine is bounded externally by a layer of enamel, one sixth part thicker than that forming the central island; and the enamel is coated by an outer layer of cement, of its own thickness at the sides, but thinning off at the two ends of the section. The dentinal tubes proceeding from the residuary pulp-tract make strong and irregular curvatures, diverging to include the divided areæ of the vascular canals, and in the outer layer at one side of the section, they describe strong zig-zag curves at the middle of the outer division of the dentine.

The diameter of the dentinal tubes at their central and larger ends is pretty regularly, about $\frac{1}{6000}$th of an inch; at the middle of their course $\frac{1}{9000}$th of an inch; thence decreasing, and very rapidly after the terminal bifurcations commence.

The dentinal tubes are separated from one another by intervals varying between once and twice the thickness of the tubes; in some parts of the dentine of the incisor they are more closely crowded together, especially near their origin from the pulp-cavity. The secondary gyrations of the dentinal tubes describe a curve about $\frac{1}{1500}$th of an inch in length; these subside in the slender terminations

of the tubes, which bifurcate dichotomously once or twice, and send off small lateral branches near the enamel. The small lateral branches are chiefly visible in the peripheral third part of the tubes, and are sent off at very acute angles, except in the strongly and irregularly bent origins from the pulp-tract. I have never seen these small branches of the dentinal tubes terminating in radiated cells like those of cement and bone, as Retzius describes, (loc. cit. p. 27), and figures (Tab. V, fig. 3); but the peripheral smallest branches near the enamel occasionally dilate into corpuscles much more minute than the radiated cells, as they do in the teeth of most quadrupeds. The dentine, as seen in a longitudinal section of the crown of a molar, by a magnifying power of three hundred linear dimensions is figured at *a*, Pl. 137. The tubes are here separated by rather wider interspaces than those of the incisor, and do not decrease in size so rapidly: the convexity of the terminal bend of the tubes is turned towards the summit of the crown.

The clear dentinal cells are very small near the peripheral part of the dentine in the incisor, but increase in size as they approach the pulp-cavity: they are of a sub-circular figure, with bright transparent outlines.

The central cement in the crown of the incisor is permeated by vascular canals, separated by intervals of from two to three times their own diameter, directed in the middle of the substance in the axis of the tooth, but diverging like rays obliquely towards its periphery: the clear substance forming the walls of the canals is arranged in concentric layers; the thickness of the wall being about equal or rather less than the area of the canal. The radiated cells, generally of a full oval, sometimes of an angular form, are chiefly dispersed in the interspaces of the vascular canals, and with their long axis parallel with the plane of the layers of the coats. The finer system of tubes radiating from the cells, and corresponding by minute branches from the vascular canals, freely intercommunicate. In the peripheral cement of the incisors examined by me, I found no vascular canals, but only the radiated cells, and the fine tubuli which I have called 'cemental', and which traverse the cement at right angles to its plane, and communicate with the

tubes radiating from the cells. These are more usually elliptical than in the thicker central cement, their long axis being parallel with the borders of the cement; they are most abundant next the enamel and rarely encroach upon the clear peripheral border of the cement. The exterior coronal cement of the molars (Pl. 137, *c*,) is as richly permeated by vascular canals (*v*) as is the central cement of the incisor.

The enamel-fibres of the Horse's incisor are very slender, not exceeding twice the diameter of the dentinal tubes: they extend with a gentle sigmoid curve through the entire thickness of the layer; contiguous fibres curving in opposite directions. The peripheral border, or that next the cement, is everywhere indented with hemispherical pits from $\frac{1}{500}$th to $\frac{1}{2000}$th of an inch in diameter, four to six of the radiated cells of the cement being often clustered together in the larger depressions. The inner or dentinal border of enamel is nearly even and straight; here are seen the short cracks or fissures extending into the enamel. The fibres are rather more wavy in the thicker enamel of the molar teeth (Pl. 137, *b*)

If the enamel is viewed in sufficiently thin sections, it is free from those wavy dusky markings which are produced by the more tortuous fibres of the human enamel; and I have been unable to distinguish any transverse striæ in the fine fibres of that tissue in the Horse: the appearance of such is given by thicker sections of the enamel-fibres taken obliquely across them, and is produced by the cut ends of the fibres.

I may here briefly describe a very rare diseased state, which I have met with in a fossil molar tooth of a large-sized Horse, from the tertiary formations near Cromer. The tooth, which was from the lower jaw, with a grinding surface measuring one inch five lines in long (antero posterior) diameter, and eight lines in short (transverse) diameter, presented a swelling of one lobe, near the base of the implanted part of the tooth. To ascertain the nature and cause of this enlargement, I divided it transversely, and exposed a nearly spherical cavity, large enough to contain a pistol-ball, with a smooth inner surface. The parieties of this cavity, composed of dentine and enamel of the natural structure, were from one to

two lines and a half thick and were entire and imperforate. The water percolating the stratum in which this tooth had lain, had found access to the cavity through the porous texture of its walls, and had deposited on its interior a thin ferruginous crust, but the cavity had evidently been the result of some inflammatory and ulcerative process in the original formative pulp of the tooth, very analogous to the disease called 'spina ventosa' in bone. I have given two figures of this singular case of primæval disease in my "History of British Fossil Mammalia."

212. *Succession.*—The practical inducements to pay attention to the times of cutting and shedding the teeth have operated more strongly in the case of the Horse than in that of the domestic Ruminants, and have led to more numerous and persevering researches on the development and succession of the teeth. The deciduous formula of the genus *Equus* is:—

$$m.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ m.\ \frac{4-4}{4-4}:\quad 32.$$

The second molar ('first grinder' of Veterinary Authors, *d m*, fig. 4, Pl. 136) is the first to pierce the gum: the white summits of the ridges of the crown are usually apparent at birth, but sometimes the gums do not yield until from the second to the fifth day; the third molar ('second grinder', fig. 5, *d* 3) rises a day or two later, often simultaneously with the proceeding: their appearance is speedily followed by that of the first incisor ('centre nipper', fig. 4, *di* 1), which usually cuts the gum between the third and sixth days. The second incisor (*di* 2) appears between the twentieth and fortieth days, and about this time the first small deciduous premolar (fig. 4, *p.* 1) takes its place, and the fourth deciduous molar ('third grinder', fig. 5, *d* 4) also begins to cut the gum. About the sixth month the inferior lateral or third incisors, (fig. 4, *di* 3) make their appearance together with the small deciduous canine (fig. 4, *d c.*) This minute tooth is shed, in the lower jaw at least, almost as soon as the crown of the contiguous incisor is in full place, being carried out by the same movement; whence the small canine had almost escaped notice until Bojanus drew the attention of veterinary authors to it by his memoir, 'De dentibus caninis

caducis,' &c.(1) Bojanus never found the lower deciduous canine retained beyond the first year. The deciduous canine of the upper jaw, being developed at a short distance behind the incisors, in the maxillary bone, is less disturbed by the eruption of the outer incisor, but is neverthess shed in the course of the second year. The deciduous canines appear from Camper's observations, to retain their place longer in the Zebra than in the Horse.(2)

M. Rousseau, who describes the first dentition as being terminated by the appearance of the lateral incisors, assigns from the seventh to the tenth month as the period of its completion.(3) The deciduous incisors have thinner and more trenchant, normally-shaped crowns than those of their permanent successors. The first true permanent molar (fig. 5, *m* 1) appears between the eleventh and thirteenth months. The second true molar (ib. *m* 2) follows between the fourteenth and twentieth month. The crowns of the premolars and the last true molar are now advancing in the closed sockets of reserve, as shown in Pl. 136, fig. 5. The first premolar (*p* 2) (essentially answering, as in the Ruminants, to the second of the Anoplothere), displaces the second (*d* 2) and, usually at the same time, the first very small deciduous molar, at from two years to two years and a half old. The first permanent incisor (fig. 6, *i* 1) rises above the gum between two years and a half and three years. At the same period the second premolar (ib. & fig. 5, *p*. 3) pushes out the third deciduous molar (*d* 3). The last premolar (ib. *p*. 4) displaces the last deciduous molar (ib. *d* 4) about the completion of the fourth year, and the appearance above the gum of the last true molar (ib. *m* 3) is usually anterior to this. Figure 6 shows the state of the dentition about this period, and should the last deciduous molar (*d* 4) have been prematurely drawn, the position of the crown of its

(1) Nova Acta Nat. Cur., tom. XII, pt. ii, 1825. p. 697. The tooth which M. Rousseau figures in his 'Anatomie Comparée du Système Dentaire,' Pl. XXV, fig. 2, as the "crochet caduc de lait," in a Horse about three years old, appears rather to be the small canine of a Mare. Compare with fig. 8, Pl. 26, of the same work, where no trace of the 'crochets caducs,' appears in a Horse of two years old.

(2) Œuvres de Pierre Camper, Paris, 1805.

(3) The appearance of the third deciduous incisors, or 'corner nippers', completes the stage of dentition called the *'colt's mouth'* by Veterinary Authors.

successor below the level of the second and fourth of the large grinders, and especially the non-development of the last grinder will betray the fact that the young Horse has not passed his third year. The incisors give evidence with which it is still more difficult to tamper without detection. The first permanent incisor as above stated, takes its place before the end of the third year; and should its growth have been accelerated by extraction of its predecessor the strong 'mark' on the third deciduous incisor will indicate the deception. The second incisor (fig. 6, *i* 2) pushes out its predecessor between three and a half and four years. The small persistent canine, or 'tusk' contrary to the usual rule, next follows, its development having received no check by the retention of its rudimental predecessor: its appearance indicates the age of four years; but it sometimes makes its appearance earlier, rarely later. The third incisor pushes out the deciduous one about the fifth year, but is seldom completely in place before the Horse is five years and a half old.(1) The third premolar is then usually on a level with the other grinders.

213. *Toxodon.*—This extinct genus of large pachydermal Quadrupeds is represented by two species, both equalling the Hippopotamus in size, whose remains have been discovered by Mr. Darwin and M. de Angelis in the recent tertiary deposits of South America. In both, the teeth consist of molars and incisors, separated by a long diastema, or toothless space. In the upper jaw the molars are *fourteen* in number, there being *seven* on each side; the incisors *four*, which differ in their proportions in the two species. In the *Toxodon platensis* the outer or second incisor is very large, and the inner one small, in each intermaxillary bone. In the lower jaw there are *six* incisors and *twelve* molars.

The general form and nature of the teeth are indicated by the sockets, and the structure of the grinders is exhibited in a broken molar, the last in the series on the left side of the skull of the *Toxodon platensis*, discovered by Mr. Darwin; and by another perfect

(1) Upon the rising of the third permanent incisors or 'corner nippers' the 'colt' becomes a 'horse', and the 'filly' a 'mare', in the language of the dealers. For the subsequent changes in the character of the teeth, see the descriptions of the Plate 136.

molar, the last but one on the right side of the upper jaw. This tooth is curved, with the convexity turned outwards when lodged in the socket, contrary to the position of the superior curved molars in the Guinea-pig and Wombat. The outer surface of the tooth is traversed by two slight convex longitudinal risings: the inner side presents, anteriorly, a slightly concave surface, and posteriorly two prominent longitudinal convex ridges separated by a deep channel, which is flat at the bottom: a fold of enamel is continued from the anterior angle of this channel obliquely forwards half-way across the body of the tooth. The outer coat of enamel is interrupted at the anterior and posterior margins of the grinder. The form of the grinding surface of this molar is shewn in Pl. 86, fig. 4.

All the molar teeth are long and curved, and without fangs, as in the Wombat and most of the herbivorous species of the Rodent order: in those, however, with curved grinders, as the *Aperea*, or Guinea-pig, the concavity of the upper grinders is directed outward, the fangs of the teeth of the opposite sides diverging as they ascend in the sockets; but in the *Toxodon* the convexity of the upper grinders is outward, as in the Horse, but with so much greater curvature that the fangs converge and almost meet at the middle line of the palate, forming a series of arches, capable of resisting great pressure. It is this structure which suggested to me the generic term proposed for this most remarkable extinct Mammal.(1)

Of the upper incisors, the two small ones are situated in the middle of the front of the intermaxillaries, and the two large ones in close contiguity with the small incisors, which they greatly exceed in size. The sockets of the two large incisors extend backwards, in an arched form, preserving a uniform diameter, as far as the commencement of the alveoli of the molar teeth; the curve which they describe is the segment of a circle; the position, form, and extent of the sockets are such as are only found in those of the corresponding teeth of the Rodentia among existing Mammalia. The matrix, or formative pulp of the large incisors was lodged, as in the Rodentia, in close contiguity with the sockets of the anterior molars; and we are enabled to infer, from the form of the socket, notwithstanding the absence of

(1) Τόξον, *arcus*; ὀδούς, *dens*. 'Zoology of the Beagle, Fossil Mammalia,' 4to. 1839, p 16.

the teeth themselves, that the pulp was persistent, and that the growth of these incisors, like those of the Rodentia, continued throughout life. This condition, joined with the curvature of the socket, necessarily implies a constant wearing away of the crown of the tooth, by attrition against opposing incisors of a corresponding structure in the lower jaw: and as a corollary, we infer that the teeth in question had a partial coating of enamel, to produce a cutting edge, and were in fact, true *dentes scalprarii*. The number of incisors in the upper jaw of *Toxodon*,—four, instead of two—is not without its parallel in the Rodent order, the genus *Lepus* being characterized by a similar number of incisors, and of a similar relative size, but with a different relative position, the small incisors in the Hare and Rabbit being so placed immediately behind the large pair, as to receive the appulse of the single pair of incisors in the lower jaw. Since the sockets of the small mesial incisors of *Toxodon* gradually diminish in size as they penetrate the intermaxillary bones, we may infer that, like ordinary incisors, their growth was of limited duration, and their lodgment in the jaw effected by a single conical fang. The lower jaw of the *Toxodon platensis*, which was discovered at Bahia Blanca, in latitude 39°, on the east coast of South America, was remarkably compressed or narrow from side to side; while the rami were of considerable depth, in order to give lodgment to the matrices and bases of grinders enjoying uninterrupted growth. The pulps of the six incisors of the lower jaw are arranged in a pretty regular semicircle, whose convexity is downwards; the teeth themselves are directed forwards and curved upwards like the inferior incisors of the *Rodentia*. These incisors are nearly equal in size: they are all hollow at their base, and the indurated mineral substance impacted in their basal cavities well exhibits the form of the vascular pulps which originally occupied them: they have, likewise, a partial investment of enamel; but though, in this respect, as well as in the curvature and perpetual growth, they resemble the 'dentes scalprarii,' of the *Rodentia*, they differ in having a prismatic figure, like the inferior incisors of the Sumatran Rhinoceros or the tusks of the Boar. Two of the sides, viz., those forming the anterior convex and mesial surfaces of the incisor, have a coating of

enamel about half a line in thickness, which terminates at the angles between these and the posterior or concave surface. From the relative position of the bases or roots, we may infer that they diverged from each other, like the incisors of the Horse, as they advanced forwards in order to bring their broadest cutting surface into line. That they were opposed to teeth of a corresponding structure in the upper jaw, is proved by their oblique chisel-like cutting edge.

The molar teeth in this mutilated lower jaw, like those in the upper jaw of the *Toxodon platensis*, had persistent pulps, as is proved by the conical cavity at their base: they consequently required a deep socket and a corresponding extent of jaw to form the sockets and protect the pulps. In order to economize space and to increase the power of resistance in the tooth, and perhaps also to diminish the effects of direct pressure on the highly vascular and sensible matrix, the molars and their sockets are curved, but in a less degree than those of the upper jaw. They correspond with the superior molars in the long antero-posterior diameter, in being small and simple at the anterior part of the jaw, and by increasing in magnitude and complexity as they are situated more posteriorly. They are, however, narrower from side to side, the Toxodon agreeing in this respect with most other large herbivorous Mammalia, the fixed surface for attrition in the upper jaw being from obvious principles more extensive than the opposed moveable surface in the lower jaw. In the first three teeth, which are premolars, the enamel is confined to the outer surface: in the last three or true molars a plate of enamel is also laid upon the middle of the inner surface, and sends one or two simple folds obliquely forwards into the substance of the tooth. (Pl. 145, fig. 3).

The first grinder in the lower jaw is of small size and simple structure. It is more curved than any of the other molars, and appears to have differed from the external incisor only in its more compressed form and vertical direction of growth: it is interesting, indeed, to find so gradual a transition, in structure, from molar to incisive teeth as this jaw presents; for the robust incisors may here be regarded as representing molars simplified by the greater deficiency of enamel,

and with a change in their direction. The second molar presents an increase in antero-posterior diameter and in length, and the enamel of the middle of the outer side makes a fold which penetrates a little way into the tooth; the cement covering the inner side is slightly concave and unbroken. The third molar presents an increase of dimensions in the same directions as the second; the enamel on the outer side of the tooth presents a similar fold. In the fourth, or first molar, besides a further increase of size and a corresponding but deeper fold of enamel on the external side and nearer the anterior part of the tooth, the grinding surface is rendered more complicated by the two folds of enamel entering the substance of the tooth from the distinct plate on the middle of the inner side: these folds divide the antero-posterior extent of the tooth into three nearly equal parts; they are both directed obliquely forwards, the hinder one goes half-way across the substance of the dentine. The fifth molar presents the same structure as the fourth, which it exceeds only slightly in size. The sixth molar has a much longer antero-posterior diameter, which measures two inches; but the lateral diameter is but slightly augmented; its structure resembles that of the fifth. The outer coat of enamel extends over half the anterior and posterior ends of the tooth.

The partial disposition of the enamel upon the molars of the Toxodon is peculiar to that genus; but the enamel is continued, as in other rootless teeth, to the open end of the implanted base; it is thinner than in the Rhinoceros. The unenamelled parts of the tooth are coated by a thin layer of cement. The entire body of the tooth is composed of compact dentine, the pulp-fissure which penetrates the middle of the lobes defined by the inflected folds of the enamel, extends from the apex of the open basal pulp-cavity to the grinding surface. The dentinal tubes are $\frac{1}{500}$th of a line at their origin, and radiate in directions vertical to the superficies of the tooth, and of the inflected enamel-folds, and are but little inclined upwards from the horizontal plane. They maintain their original diameter, and their relative distance from each other, viz. $\frac{1}{2000}$th of a line, to near their peripheral ends. The dentinal cells are sub-hexagonal, and about $\frac{1}{4000}$th of an inch in diameter in the peripheral part of the substance.

In the discontinuity of the enamel covering the molars, the Toxodon differs from all known Pachyderms, and manifests a slight approach to the *Bruta*.

214. *Elasmotherium*(1).—This name has been given to an extinct Pachyderm with rootless molars, surpassing the *Toxodon* in size, and of which only the lower jaw and its dentition are as yet known; but the characters of the teeth are sufficiently remarkable to call for notice here. The molar teeth of the Elasmotherium are five in number in each ramus of the jaw, the anterior one being very small; the penultimate one is the largest, measuring three inches in the antero-posterior diameter, and two inches in the transverse diameter of the crown. The enamel is remarkable for its beautiful undulating folds; but its general disposition most resembles that in the inferior molars of the Rhinoceros(2). The teeth of the Elasmotherium differ from those of the Rhinoceros, and resemble those of the Horse in the great depth to which they are implanted in the jaw, before being divided into roots: the socket of the penultimate grinder extends, in fact, to the lower margin of the jaw without any indication of partitions for the lodgment of fangs: there is no trace of incisive teeth in the portion of symphysis which is preserved, and which extends a little more than three inches in advance of the first small molar. The above account is taken from a cast and the description by Cuvier, in the 'Ossemens Fossiles', 4to. tom. II. pt. i, p. 96. The original is preserved in the Museum of Moscow, and is unique; it was discovered in the frozen drift or diluvium of Siberia.

215. *Rhinocerotidæ*.—The present family of anisodactyle Pachyderms includes the typical *Rhinoceros*, the extinct *Acerotherium* which had no horn, and the equally hornless small existing genus *Hyrax*. The essential characteristics of the dentition of the genus *Rhinoceros* are to be found in the form and structure of the molar teeth. In the first place, they differ essentially from those of the Horse or Elasmothere by being implanted by distinct roots. In the upper jaw the crown is

(1) ἔλασμα *a plate*, θηρίον *beast*: in allusion to the plicated plates of enamel in the substance of the molar teeth.

(2) Compare figure 12 in Plate 136, with p. 3, fig. 11 in Plate 138.

subcubical, and the grinding surface, when moderately worn, subquadrate, and penetrated by two folds or valleys of enamel: the principal valley (Pl. 138, fig. 5, *b*) commences at the middle of the inner side, and extends obliquely outwards and forwards towards the antero-external angle of the crown about two-thirds across, where it terminates, according to the species, in a more or less expanded, sometimes bilobed, cul de sac, (*e*): the second and shorter valley (*ib. c*) is usually of a triangular form, and indents more or less deeply the posterior border of the crown: in most Rhinoceroses this is wanting in the last molar, which has a trihedral conical crown: both valleys are usually deepest at their blind terminations: the outer surface of the crown is gently undulated by one of the convexities (ib. *o*) being sometimes produced into a longitudinal ridge. In the lower jaw the molars (ib. fig. 9) have an oblong, laterally compressed crown, divided into two crescentic lobes, placed obliquely, with their convexities (*o o*) outwards and a little backwards; the anterior horn of the hinder crescent, before it is worn down, abuts against the middle of the convexity and below the upper margin of the crescent in front.

The normal formula of the molar series is:—*p.* $\frac{4-4}{4-4}$, *m.* $\frac{3-3}{3-3}$: = 28. There are no canines. As to the incisors, the species vary not only in regard to their form and proportions but also their existence; and in the varieties of these teeth we may discern the same inverse relation to the development of the horns which is manifested by the canines of the Ruminants. Thus, the two-horned Rhinoceroses of Africa, which are remarkable for the great length of one(1) or both(2) of the nasal weapons, have no incisors in their adult dentition (Pl. 138, fig. 2); neither had that great extinct two-horned species (*Rh. tichorhinus*), the prodigious development of whose horns is indicated by the singular modifications of the vomerine, nasal, and intermaxillary bones in relation to the firm support of those weapons.(3)

The Sumatran bicorn Rhinoceros, combines with comparatively

(1) *Rhinoceros bicornis, Rh. simus.*

(2) *Rh. Keitloa,* Smith.

(3) These bones in the fossil skull of the species cited are confluent with each other, forming a solid obtuse termination to the upper jaw, and are anchylosed to a strong bony partition wall extending from the vomer to the anterior outlet of the nasal passages, and thus

small horns, moderately developed incisors in both jaws; and the same teeth are present in the nearly allied extinct two-horned *Rhinoceros* called after its discoverer Schleiermacher. The incisors are well developed in both the existing unicorn Rhinoceroses, *Rh. indicus* and *Rh. sondaicus;* but they attain their largest dimensions in the singular extinct hornless species, the *Rhinoceros incisivus* of Cuvier, which makes the transition to the extinct genus *Palæotherium*, and forms the type of the aberrant subgenus *Acerotherium* of Dr. Kaup: (Pl. 138, fig. 1). The normal incisive formula is: $\frac{2-2}{2-2} = 8$: the median pair being the largest above and the smallest below: in the existing species the smaller incisors are disproportionally minute, and usually have no permanent successors, or are soon shed: the larger incisors are preceded by deciduous teeth which they succeed and replace. In the under jaw of a Sumatran *Rhinoceros*, now before me, the extremity of which is figured in Plate 138, fig. 15, the tips of the large permanent outer pair of incisors (*i* 2) are visible, but have not pushed out their deciduous predecessors (*d* 2); and the sockets (*d* 1) of those of the two small median incisors (*i* 1) are also retained. In one of the extinct species of *Rhinoceros* from the Himalayan tertiary beds Dr. Falconer informs me that there are six incisors in both jaws: the typical number was, therefore, retained in this ancient species, as in the contemporary Hippopotamus of the same formations. Cuvier believed that the ex-incisive character of the two-horned Rhinoceros of Africa was absolute. "Not only," he observes, "is its hide without folds, not only has it constantly two horns, but it has never more than twenty-eight teeth, all molars; and never possesses incisors, nor even a place for them at the anterior extremity of its jaws."(1)

affording extra support to the horn-bearing bones of the face whence the name *tichorhinus* given by Cuvier to this most common of the extinct Rhinoceroses of our Northern Hemisphere.

(1) "Non-seulement sa peau n'a point de plis; non-seulement il a constamment deux cornes, mais il n'a jamais que vingt-huit dents, toutes molaires; il manque toujours d'incisives, et n'a même point de place pour elles à l'extremité antérieure de ses machoires." 'Ossemens Fossiles,' 4to. 1822, tom. ii. pt. 1, p. 27. The otherwise excellent zoological descriptions of the two-horned Rhinoceroses in Dr. Smith's 'Illustrations of the Zoology of South Africa, do not

I have shown in many parts of this Treatise how strikingly the duly defined law of Unity of Organization is exemplified by the dental system; and, anticipating that this system would adhere to the typical formula by transitory representatives of the defective teeth in the adult, I made search for the germs of incisors in the dried jaws of a fœtal *Rhinoceros bicornis* of South Africa. The alveolar border of the short symphysis of the lower jaw was apparently edentulous, and thickly coated with the dried gum; after soaking this for some hours in warm water, and cutting down into its substance, I detected the germs of the four lower incisors, which are figured, of half the natural size, in Pl. 138, fig. 14, *i* 1, *i* 2. Although these teeth are destined to be absorbed and never to make their appearance above the gum in the living animal, they manifest the typical relative proportions to one another, the outer pair (*i* 2) being more than double the size of the inner pair (*i* 1). The outer incisor is six lines in length, and in great part lodged in the socket; the crown is one line and a half in breadth, convex anteriorly, flattened behind; it protrudes from the jaw about five lines in advance of the alveolus of the first molar, and close to the anterior border of the jaw. At the same border, about one line nearer the symphysis, the first or inner incisor is situated; it is about two lines in length, and half a line across the crown, which just peeps above the bone. There were no sockets of reserve beneath or behind these deciduous germs of incisors. The anterior end of the thin and small intermaxillary lamella of the same skull is expanded, and was covered by a thick, dried gum, but I could find no calcified rudiments of upper incisors; it is highly probable, however, that germs of these teeth or their matrices, may be manifested at an earlier period.

The permanent median incisors of the upper jaw have a peculiar and easily recognizable generic form in all the species possessing them; they are short, broad, much compressed, rhomboidal, or sub-triangular, the crown forming the base of the triangle and the

contain any reference to the teeth: Mr. Macleay, in the Entomological number of the same work, exaggerates in affirming of the genus *Rhinoceros*, "that the dentition varies extensively in almost every species." No. III, p. 6.

end of the fang the truncated apex: the crown, which is very short and thin in proportion to its breadth, usually commences by a sudden expansion, and terminates before it has suffered much abrasion, by an oblique trenchant edge, directed vertically downwards; they are less parallel in position, and are thicker in the Indian than in the Javanese one-horned Rhinoceros; they are a little smaller in the Sumatran two-horned species (Pl. 138, fig. 12, *i* 1). The external incisors are very small in all the above-cited species; and are lost before the animals attain maturity. They are each seven lines in length and two in breadth in the skull of a nearly full-grown Sumatran Rhinoceros (ib. *i* 2), and are situated close to the suture with the maxillary bone. In the nearly allied extinct *Rhinoceros Schleiermacheri* Dr. Kaup found them with an enamelled crown of four lines extent, which is longer than in the *Rh. Sumatranus:* the large mid-incisors of the *Rh. Schleiermacheri* are about two inches long, with a crown one inch and a quarter broad. In the *Rh. incisivus* (Pl. 138, fig. 1) these incisors have been found of nearly four inches in length, and with a short, oblique crown measuring upwards of two inches in breadth, but are relatively thinner.

The large external inferior incisors are procumbent, or project almost horizontally from the angles of the symphysial end of the lower jaw; in the Sumatran Rhinoceros the crown is an inch and a half in length, almost flat above and on the outer side, and convex below. The enamel is only laid upon the under and outer sides, terminating by a sharp edge along the inner part of the crown, and at its rounded termination. In the Javanese Rhinoceros they have a more definite trihedral form, and terminate anteriorly in a sharp-point: they are relatively thicker than in the Indian species in which Cuvier(1) has figured them as worn down to a thick truncated base. The small mid-incisors of the lower jaw are relatively larger and longer retained in the *Rhinoceros Schleiermacheri*(2), the outer incisors resemble those of the *Rh. Sumatranus.* In the *Rh. incisivus* (Pl. 138, fig. 1) these teeth acquire their greatest

(1) Loc. cit. Pl. II, fig. 4.

(2) Kaup, loc cit., tab. XI.

size, are more divergent, and directed more upwards; they have been found of the length of from eight to ten inches, of which the implanted base measured three-fifths of the entire length of the tooth, and the crown was one inch and a quarter in breadth; this is worn obliquely inwards at its upper enamelled part.

Not a trace of a canine tooth or its alveolus has been observed in the skull of a mature individual of any existing or extinct species of *Rhinoceros*, but such we must consider the small and simple tooth (Pl. 138, fig. 13, *c*) developed at the fore part of the superior maxillary bone in the fœtal *Rhinoceros indicus*, two lines in advance of the alveolus of the first small deciduous molar (*p* 1) and one line behind the suture which unites the maxillary with the intermaxillary bone. The specimen in which I detected this tooth, the crown of which had pushed through the jaw, but not through the gum, appeared to be at the full-time, or newly born. The tooth and its socket must soon disappear, for in the specimen of the upper jaw of a young Indian *Rhinoceros* figured by Cuvier in the 'Ossemens Fossiles,' tom. cit. Pl. v, fig. 3, there is no trace of the alveolus of the rudimental canine in the tract of bone between the first deciduous molar and the intermaxillary suture; anterior to this the intermaxillary bone shows the sockets of the two comparatively large incisive teeth. This discovery of vestiges of canines in the genus *Rhinoceros* shows an additional character, although a transitory one, linking that genus with the nearly allied extinct Palæotherium.

The first of the permanent series of seven molar teeth is very small in both jaws, and is soon shed. The first upper premolar is notched on the inner side in the one-horned Rhinoceros (Pl. 138, fig. 3, *p* 1); the notch sinks deeper and expands in the African two-horned species; and in the Sumatran bicorn Rhinoceros it presents a detached lobe on the inner side: the second upper premolar is more suddenly enlarged in the one-horned than in the two-horned Rhinoceros. Before the crowns of these large and complex premolars and molars begin to be abraded, the eminences bounding the valleys terminate in sharp enamelled ridges, the principal extending along the outer border of the grinding

surface, and two others continued from this obliquely backwards to the inner border, one from the antero-external angle, the other from near the middle of the outer wall; the inner terminations of these two parallel oblique ridges form the summits of the two cones which constitute the inner half of the crown.(1) Small or secondary ridges project from the sides of the principal ridges into the intervening valleys, in extent and number varying according to the species, the most constant being the one, marked *f* in fig. 5, from the posterior oblique ridge. The first effect of mastication is to wear away the enamel from the summits of the ridges, and to expose a tract of dentine which widens as attrition proceeds, varying the pattern of the grinding surface as the valleys are thus progressively obliterated. These changes are illustrated by the figure of the molar series of the upper jaw of the *Rhinoceros indicus* (Pl. 138, fig. 3). The chief valley, marked *b* in fig. 5, is expanded and bilobed at its termination, and is deepest at each terminal division, and at the middle of its course; in the second true molar (*m* 2) its entire extent is shown; in the last molar (*m* 3) the posterior terminal division is insulated by the wearing away of the enamel from the shallower part of the valley between the two divisions: the same insulation has taken place in *m* 1, and the shallow entry of the valley is almost worn away; in *p* 4 it is obliterated, and the peninsular fold of enamel is converted into an island. The same change is effected in the short posterior fold *c*, it deepens as it penetrates the crown, and in *m* 4 its beginning has been worn down to the dentine, and its end converted into an island of enamel. The same three islands are shown in *p* 3 and *p* 2, with the addition of linear tracts formed by the wearing down of the crown to the basal ridge at the antero-internal lobe. The grinding surface is sometimes reduced to a plain tract of dentine before the molar is shed. There is no posterior fold *c* in the last molar.(2)

The modifications in the form of the valleys and secondary

(1) See the germ of the upper molar, Pl. 138, fig. 8.

(2) These, and similar details in other chapters of this work, may be deemed tediously, perhaps unnecessarily, minute: they are, however, indispensable to whoever would make successfully the noble application of anatomy to the restitution of lost species and the past history of the globe.

ridges of the upper molars are constant and characteristic of the species, and materially aid in the determination of fossil remains.

Even in existing species so nearly allied as the unicorn Rhinoceroses of India and Java, each might be determined by a single detached molar tooth. The principal valley is bent back at its termination in the Java species, but being shallower than the rest of the valley, it is obliterated and the valley simplified in form as in fig. 4. The posterior fold (*e*) is soon converted into an island; the chief fold is next insulated by the wearing down of the dentine to its beginning, and is the last to disappear.

The African *Rhinoceros bicornis* has a relatively larger molar, especially in its antero-posterior extent; the beginnings of the two folds (ib. fig. 5, *b* & *c*), being deeper than their terminations, no islands are formed in the progress of abrasion. In the Sumatran Rhinoceros the valley (*b*) is relatively wider at its commencement, and contracts to its termination, which is pointed, in little-worn molars; a simple secondary process projects from the posterior ridge into the valley, and partially detaches the narrow and at first triangular termination; when attrition has reached the shallow part of the valley at the end of the process, answering to *f* in fig. 5, the entire termination of the valley is insulated: a second and posterior island is formed when abrasion has removed the enamel from the wide and shallow beginning of the posterior valley *c*. Thus with regard to the first formed island *c*, which characterises the abraded molars of the Indian one-horned and Sumatran two-horned Rhinoceros, this results from the insulation of part of the blind termination of the principal valley in the one-horned species, and from the cutting off of the whole termination of the valley in the two-horned species. Cuvier, not having attended to this difference, failed to perceive that the fossil molar teeth which he figures, loc. cit. Pl. VI, fig. 5, and Pl. XIII, fig. 4, and which are copied in Pl. 138, figs. 6 & 7, belonged to two distinct species of Rhinoceros.(1) Figure 6 is the second true upper molar tooth

(1) He describes the tooth (Pl. 138, fig. 6) figured in his 'Ossem, Foss. Rhinoceros,' Pl. VI, fig. 5, as follows:—"Fig. 5, est la cinquième du côté gauche peu usée. On y voit aussi très-bien la fossette, résultant de l'union du crochet postérieur avec la colline antérieure et l'échancrure

of the *Rhinoceros tichorhinus*. It most nearly resembles the one-horned Indian Rhinoceros in the pattern of the grinding surface of the molars, the valley (*b*) has at first the same contracted beginning and expanded bilobed termination, and the island (*e*) is formed by the cutting off of the hinder lobe. Fig. 7 is a corresponding molar of the *Rhinoceros leptorhinus*, which in the structure of its upper molars, most nearly resembled the Sumatran Rhinoceros; the valley (*b*) has the same wide beginning and contracted end, which is wholly insulated at *c* by the obliteration of the enamel covering the shallow part of the valley between the end of the secondary process *f*, and the anterior lobe or ridge of the grinding surface: the upper molars of the *Rh. leptorhinus* are further distinguished from those of the *Rh. tichorhinus* by the longer ridge (*n*) along the base of the anterior side, and by the narrow prominent longitudinal ridge *o'* on the outer side of the crown. Both the above-named extinct species of Rhinoceros have left their remains in England as well as on the continent. The *Rh. incisivus*, which has not hitherto been found in British strata, is readily distinguished by the more simple form and almost uniform width of the valley *b*; and still better by the basal ridge which is continued from the anterior side along the whole of the inner to the posterior side of the crown of the molar, at some distance above the basal termination of the enamel; in these modifications it offers the nearest approach to the configuration of the upper molars in the *Palæotherium*. This basal ridge is also well developed in the molars of the *Hyrax*.

There are corresponding, but less marked differences in the molar teeth of the lower jaw of the different species of Rhinoceros; on which, however, I shall not here dwell. The first premolar is the smallest and simplest; the bilobed structure is at best feebly indicated by the undulations of the outer surface: and on the inner surface, by a simple depression or a notch: in the Sumatran Rhinoceros the notch is near the front margin of the tooth; it affords

postérieure commence à être cernée," p. 57. And the tooth (Pl. 138, fig. 7) figured in his Pl. XIII, fig. 4, as follows: "Fig. 4, Pl. XIII, est un sixième du côté gauche, peu usée, des Crozes, Département du Gard. Le trou antérieur y est déjà distinct par l'union du crochet de la colline postérieure avec la colline antérieure, mais l'échancrure postérieure n'y est point encore cernée."

a more marked difference by its position in relation to the symphisial termination of the jaw; in the Rhinoceroses with persistent incisive teeth the symphysis is prolonged beyond the first premolar; but in the African species this tooth is situated close to the anterior end of the jaw. In the extinct tichorhine Rhinoceros in which the germs of the lower incisors endured longer and attained a greater relative size than they do in the living *Rh. bicornis*, the depressed spatulate symphysis is prolonged, as in the Indian and Sumatran Rhinoceroses, beyond the molar series, which begins opposite the posterior border of the symphysis, as shown in Pl. 138, fig. 10. In the leptorhine Rhinoceros (ib. fig. 11) the molar series extends closer to the anterior end of the symphysis, which both in form and relation to the molar teeth, more resembles that of the two-horned African Rhinoceroses. The first premolar (*p* 1) is soon shed, and all traces of its socket soon obliterated; this has led to the supposition that some of the fossil Rhinoceroses had only six molars on each side of the lower jaw; but specimens of young individuals have demonstrated the normal number in species where it has been most formally denied.(1) The second lower molar (*p* 2) has its lobes distinctly defined by the vertical furrow on the outer surface, but the variations of the form of its inner surface in different species are such as to make it, perhaps, the most characteristic tooth of the lower jaw; the anterior lobe is always the smallest and thinnest; and its internal indentation is shallow. The two lobes assume a more equal size and crescentic figure in the third (*p* 3) and fourth (*p* 4) premolars, which progressively increase in size: the three true molars resemble the fourth premolar, the last tooth not being distinguised by an accessory lobe.

216. *Microscopic Structure.*—Retzius(2) describes the dentinal tubes as he saw them in longitudinal sections of the root of a molar tooth of a Rhinoceros, to proceed transversely from the pulp-cavity

(1) The specimen in Dr. Buckland's Museum, from Lawford near Rugby, Pl. 138, fig. 10, shows the first of the four premolars *in situ*, in the lower jaw of the *Rhinoceros tichorhinus*. M. Christol, who has figured a very perfect lower jaw of an older individual of the same species, in which the first premolar has been shed, describes it as 'munie de toutes ses molaires.' Annales des Sciences, 1835, p. 46, Pl. 2, fig. 1.

(2) Loc. cit., p. 32

with an irregular and, in some parts, slightly curved course, but he could not consider them as being undulated: they were $\frac{1}{5000}$th of an inch in diameter at their beginning, soon bifurcated, and gave off very numerous branches; the interspaces between the origins of the tubes, equalled the breadth of two tubes. The peripheral part of the dentine, close to the investing layer of cement contained a dense stratum of opake cells, in which many of the branches of the calcigerous tubes terminated; the extremities of the tubes meander through the interspaces of the cells, some terminating in the cells, other anastomosing with adjoining tubes in beautiful curves.

I have examined the microscopic structure of the molar of the Indian Rhinoceros, in vertical and horizontal sections of the crown. The pulp-cavity is continued in the form of fissures, into the middle of the eminences bounding the valleys of the uneven-grinding surface, and a few short vascular canals are continued into the dentine from the summits of the pulp-fissures, especially at their terminal angles. In horizontal sections dividing the vascular canals, their areæ appear like large opake cells, with a clear border, and the adjoining dentinal tubes diverge, as it were, to give place for them: the ends of a few tubes, which were given off from those canals being seen in the clear border. Retzius makes mention of larger groups of opake cells in the middle of the dentine of the root of the molar, which seemed to have forced aside the main-tubes, which bent round these groups of cells, and sent off some branches which there terminated.

The major part of the coronal dentine of the Rhinoceros's molar, is fine-tubed and unvascular: I found the dentinal tubes, at their origin from the pulp-fissure, to have a diameter of $\frac{1}{6000}$th of an inch, with interspaces averaging $\frac{1}{3000}$th of an inch. They ascend (in the lower molar), inclining at first very slightly from the pulp-fissure, and gradually bending more outwards with the convexity of the curve upwards, until near their termination, when they gently curve in the opposite direction. Throughout their course they are undulated, the secondary waves being pretty regular and stronger than in the Human dentinal tubes. Transparent tracts,

wider than the interspaces of the tubes, extend here and there from the pulp-cavity, in the directions of the tubes and of the short vascular canals; the tubes next these tracts make a sudden bend obliquely across them with wider clear intervals. The tubes divide sparingly in the first half of their course; and, not decreasing much in diameter, appear closer packed as they approach the enamel. In the outer third of their course they make here and there abrupt secondary bends, and send off the minute lateral branches from both sides. Here and there the tubes present slight partial enlargements; they very gradually decrease in size, until close to the peripheral stratum of minute opake cellules, (Pl. 139, d^{II} d^{II}) where they chiefly end by a bifurcation, the forks diverging at an angle of 45°, and bending in opposite directions, sometimes anastomosing, sometimes irregularly dilating into, or communicating with, the opake cellules. The traces of the compartments of the basal substance, or dentinal cells, are very faint; they are best seen in transverse sections, as in Pl. 139, d^{I} d^{I}; especially that part of their contour next the enamel which curves across from four to five of the dentinal tubes; the compartments or cells increase in size as they approach the pulp-cavity, but soon become fainter and disappear from view.

The contour lines (ib. *l l*) are unusually conspicuous and numerous, with interspaces of $\frac{1}{500}$th of an inch; they are not due to abrupt parallel bends of the tubes, nor to branches or opake cells, but to a slight increase of opacity of the basal substance which seemed to be due to oblique cracks along the lines in question. The enamel fibres (ib. *e e*), in a transverse or horizontal section of the crown, proceeded from the surface of the dentine across the thickness of the layer, with a gentle degree of flexuosity; their diameter is $\frac{1}{4000}$th of an inch. I could discern only a faint granular appearance in the fibre, certainly no transverse segmentation. The whole thickness of the layer of enamel is traversed by contour lines at varying intervals, running parallel to the border of the dentine. Here and there the fissures occur at the dentinal surface of the enamel, with irregular or stronger bends of the adjoining fibres. In a vertical section of the enamel the fibres were seen to run more obliquely

across the section, and those of one layer in an opposite direction to that of the subjacent layer of fibres.

Retzius notices the existence of radiate cells in both the radical and the coronal cement of the Rhinoceros's grinder: they were of various shapes, some round and $\frac{1}{2500}$th of an inch in diameter, some angular, and others prolonged in the form of tubes; all receive numerous fine tubuli which are clustered around them.

217. *Succession.*—The deciduous dentition of the genus Rhinoceros, is:—

$$\text{incisors } \frac{2-2}{2-2}; \text{ molars } \frac{4-4}{4-4} : = 24.$$

In the Sumatran Rhinoceros the small mid-incisors of the lower jaw (Pl. 138, fig. 15, *d* 1) are first shed and replaced by a larger pair (*i* 1), which protrude beneath them; these are small in comparison with the lateral pair, and are also shed before the last true molar cuts the gum. The first true molar appears before any of the deciduous set are shed, but the first milk-molar soon yields place to the first premolar; the second milk-molar gives way to the second premolar, and about the same time the second true molar advances into place. Next the deciduous outer incisors (ib. *d* 2) their fang deeply excavated by the absorbent process excited by the pressure of their large successors (*i* 2), are pushed or broken out; the last deciduous molar is displaced, and the last premolar rises above the gum about the same time that the last true molar comes into place. Thus, notwithstanding the close similarity of form and structure between the premolars and molars, each division of the permanent masticatory series has its own order and progression of development, and thereby manifests its essential distinction. The last milk-molar is not more complex than the last premolar which takes its place.

218. *Palæotherium.*—The vast hiatus, which, in the series of existing Mammals, divides the Rhinoceros from the Tapir and this from the Elephant, was once filled up by interesting transitional species of anisodactyle Pachyderms which have long become extinct. I shall briefly notice the leading features of the dentition of some of those ancient forms of Mammalia, as indeed, this enduring part

of their frame best exemplifies the progress of the affinities which the lapse of ages has interrupted.

The species of Palæotherium which appear to have accompanied the Anoplotheres in the first introduction of hoofed Quadrupeds upon this planet, were characterised by the same complete dental formula, viz :—

$$\text{Incisors } \frac{3-3}{3-3};\ \text{canines } \frac{1-1}{1-1};\ \text{premolars } \frac{4-4}{4-4};\ \text{molars } \frac{3-3}{3-3}: = 44.$$

(Pl. 135, fig. 4.) But the canines are developed to the proportions which these teeth usually bear as weapons of offence and defence, proportions such as are still manifested by the canines of the Tapir: there is consequently, in the Palæothere, a vacancy in the series of teeth between the incisors and canine in the upper jaw to receive the crown of the lower canine when the mouth was closed; and there is a longer vacancy between the canines and the premolars in both jaws.

The crown of the upper molars is bounded by four unequal sides, the outer side (*o o* fig. 5) being the longest; in the new-formed and unworn crown this side inclines inwards as it descends; it is divided by three longitudinal ridges into two concavities, rounded towards the root and terminating in a point at the grinding surface of the tooth: the angles of the base of each projecting triangle rest on the extremities of the salient longitudinal ridges. In the growing molar two vertical sinuous folds of the capsule penetrated the substance of the crown, one (*b*) entering from within outwards, the other (*c, e*) crossing it from before backwards. The antero-posterior fold described two curves, parallel with the exterior concavities; and, entering at the posterior margin, where the valley is widest and deepest, it terminated in a cul-de-sac close to the anterior and outer angle of the tooth, or at a little distance from the anterior margin: the transverse fold commencing at the inner side of the tooth terminated close to the middle longitudinal ridge on the opposite side, expanding and deepening where it crossed the preceding ridge. Of the salient ridges of enamel left by these folds, and defined by the corresponding valleys, the principal is the zig-zag one which forms the outer boundary of the grinding surface; from the

posterior angle of this a second is continued, first downwards, and then along the posterior border of the tooth to the posterior and internal angle where it forms a small eminence or lobe; a third ridge is continued along the anterior border of the crown to the internal and anterior angle, where it is continued into the summit of a trihedral crucial eminence, forming the anterior half of the inner side of the tooth. A strong conical eminence is developed between the anterior and posterior angles of the inner border of the tooth, and the whole base of the crown is belted by a ridge. As soon as the surface of the crown becomes worn by mastication, and part of the dentine is exposed, it is bounded by two parallel salient lines of enamel, and those upon the outer zigzag ridge form a double crescent, as in *m* 3: if the two inner lobes were equally developed and the intermediate one reduced in size, they would also present their double crescents of enamel, separated by the antero posterior depression from the anterior crescents, and the Ruminant type of molar would be manifested. By the rudimental state of the posterior angular lobes and the varying depth of the crucial fissures, the progress of attrition blends together different eminences and produces a pattern which is very like that of the molars of the Rhinoceros (Pl. 135, fig. 5, *m* 1). The antero-posterior depression, which is the shallowest, is first obliterated, and, with it, the chief resemblance to the Ruminant molar. The transverse fissure is arrested at the point (*c*) in the hind lobe: a portion of this fissure is sometimes insulated as at *e*, *p* 4. As attrition proceeds, both folds are converted into islands of enamel, and, first, the antero-posterior fold *c*: the islands are finally obliterated before the crown is quite exhausted.

The first premolar (fig. 5, *p* 1) is the smallest of the series and has a simple compressed pointed crown, with a strong basal ridge, broadest on the inner side, and a small posterior cusp. The other premolars increase in size until they equal the true molars, from which they scarcely differ in structure. The last true molar has its crown more extended from before backwards, but is contracted posteriorly, that side being the shortest. The first premolar is implanted by three roots: all the others have four roots.

The crowns of the lower molars are narrower and simpler than those above. The first of the series of seven molars in the lower

jaw (fig. 6, *p* 1) is the smallest and has a more simple crown than that above; the crowns of the succeeding teeth to the sixth inclusive are formed externally by two upright half cylinders (*m* 1, *o o*), and differ from the same teeth in the Rhinoceros chiefly by the equal height of the demi-cylinders. The seventh tooth, or third true molar (*m* 3), has a third similar but smaller lobe. On the inner side of the crown a longitudinal impression sinks, as it were, into each of the external convexities, and a corresponding internal convexity receives the entering angle between the two half-cylinders: the anterior of the inner depressions is the shallowest, especially in the second premolar, and both internal depressions contract as they descend. The base of the crown is usually surrounded by a ridge, which is continued at each end obliquely upwards to the angle formed by the backward folding of the half-cylinders. When the summits of those teeth begin to be abraded, two, and in the last molar, three, crescentic tracts of dentine, bordered by enamel, are exposed.

All the species of Palæotherium became extinct before the close of the middle (miocene) tertiary period. The largest surpassed the Tapir in size, and must have resembled it in external appearance.

219. *Macrauchenia.*—An extinct Pachyderm equalling the largest Camel in size, with very long and slender cervical vertebræ, as in the *Auchenia*, and having imperforate transverse processes, as in all the Camel-tribe, but with three toes on each foot, and an astragalus closely resembling that of the Palæothere, has been in great part restored(1) from fossil remains discovered in the tertiary deposits of South America, of much more recent date than any of those which in Europe have furnished evidences of tridactyle Ungulates. The parts most required to establish the affinity of the *Macrauchenia* to *Palæotherium* were undiscovered when the first account of it was published. A single tooth obtained by Mr. Darwin from a locality near Patagonia (Bahia Blanca) remote from that, (Port St. Julien') where the bones were discovered, bore sufficiently close resemblance to the inferior molars of the Palæothere to lead me to suspect that it might belong to the three-toed Pachyderm of Patagonia.(2) Subse-

(1) Fossil Mammalia of the Voyage of the Beagle, 4to. 1839, p. 35.

(2) See the 'Catalogue of Fossil Mammalia in the Royal College of Surgeons,' 4to. p. 229, No. 952.

quently, the left ramus of a lower jaw, found in tertiary deposits of Buenos Ayres, has been received at the British Museum, containing six molar teeth, three true and three false, most of which manifest the same pattern as the single fossil tooth above adverted to, and more decidedly and fully determining the resemblance to the lower molar series of the Palæothere, as will be obvious by comparing the figure of the grinding surface of the Buenos Ayrian fossil teeth (Pl. 135, fig. 7,) with those of the Palæothere (ib. fig. 6). The chief generic distinction is the absence of the third lobe in the last molar of the South American Pachyderm, by which it more closely resembles the Rhinoceros; but it differs, like the Palæothere, from the Rhinoceros in the greater exterior convexity and the equal height of the two demi-cylindrical lobes of which the last premolar and the three true molars are composed: and it differs from both Palæothere and Rhinoceros in the more simple form of the second and third premolars: the first small premolar of the South American Pachyderm may have existed in the part of the fossil jaw which is mutilated, anterior to the second premolar in the British Museum specimen: it is hypothetically added to the series, in Pl. 135, fig. 7, at p. 1. If, however, it was not functionally developed in the *Macrauchenia*, this genus would again differ from the Palæothere and resemble the Lophiodon and Tapir, in the number of the grinding teeth of the lower jaw. In the figure above cited, the teeth are given of half their natural size: the enamel is smooth, the dentine compact, and the coronal cement forms a very thin layer, as in both Rhinoceros and Palæothere. In the more simple form of the second and third molars we may trace a slight approximation to the Anoplotherian and Ruminant types; and, since no other Pachyderm of the size required to correspond with that indicated by the jaw and teeth here described, and, at the same time, with close affinities to the Palæothere and the Cameloid Ruminants, has, hitherto, been discovered in South America, excepting the *Macrauchenia*, I deem it to be highly probable that the teeth in question belong to that interesting annectant genus of Anisodactyle Pachyderms.

220. *Tapirus.*—The dental formula of the Tapir is :—

$$in.\ \frac{3-3}{3-3};\ c.\ \frac{1-1}{1-1};\ p.\ \frac{4-4}{3-3};\ m.\ \frac{3-3}{3-3}: = 42.$$ (Pl. 96. figs. 4 & 5.)

The median incisors above have a broad trenchant crown, separated by a transverse channel from a large basal ridge; the wedge-shaped crowns of the opposite pair below fit into the channel, and have no basal ridge: the outer incisors above are very large and like canines; those below are unusually small. The canines have crowns much shorter than their roots, and not projecting, like tusks, beyond the lips: they are pointed, with an outer convex, separated by sharp edges from an inner, less convex, surface: the lower canines form part of the same semi-circular series with the incisors: the upper ones project close to the intermaxillary suture, separated from the incisors by a short space for the reception of the crown of the lower canine: this first shows the effects of abrasion at the fore-part of the crown occasioned by the action of the upper laniariform incisors. A long edentulous ridge of the jaw-bone separates the canines from the molar series.

The first three premolars above have the outer part of the crown composed of two half-cones, the posterior one having a basal ridge: the rest of the crown is impressed by two grooves at right angles in the shape of a T, one dividing it from the two outer demi-cones, the other and deeper groove dividing the rest of the crown into two transverse wedge-shaped eminences; there are, also, anterior and posterior basal ridges: the anterior eminence is almost obsolete in the first premolar, which is the smallest and triangular: they are nearly equal in the rest, and their summits extend obliquely to the anterior part of the opposite demi-cones, which have a small tubercle at the inner angle of their interspace; when much worn these teeth present two peninsular folds of enamel one extending from the inner to near the outer part of the crown; the other, shorter and wider, continued a little way from the posterior margin of the crown. The type of the molars of the Palæothere and Rhinoceros is, here, feebly repeated. The anterior basal ridge rises into a small cusp in the second premolar, which increases in size in the third and fourth: in this tooth the transverse

depression divides at the base of the anterior and outer demi-cone and the posterior division is continued into the interspace of the two demi-cones; these, therefore, now become the outer ends of the two transverse wedge-shaped eminences, giving their summits a curve whose concavity is turned backwards: the last molar may be known by the shorter and more curved posterior eminence.

In the lower jaw the double transverse-ridged type of tooth, which has been before described in the Kangaroo, Diprotodon and Manatee, prevails throughout the molar series (Pl. 96, fig. 5): the teeth are narrower in proportion to their antero-posterior extent than in the upper jaw, especially the first premolar, in which the anterior basal talon is developed in a conical lobe, connected by a longitudinal ridge with the outer part of the first transverse eminence. This ridge is narrower than the posterior one, which has both its angles bent forwards, and the outer one produced as far as the anterior eminence. The two transverse eminences become more equal in the succeeding teeth; the angles of each are, as it were, slightly folded forwards and inwards, making the fore-part of each eminence concave: the anterior basal ridge decreases in breadth, and the posterior one, which is obsolete in the first and second premolars, gradually increases in the others, but is not developed into a third lobe or eminence in the last molar, nor is relatively so large in any of the molars as in the corresponding teeth of the Manatee. There is a small eminence at the outer part of the valley between the two transverse ridges, but no connecting ridge crossing the middle of the valley as in the Kangaroos; the transverse eminences are thicker and less elevated than in the Diprotodon and Notothere, but are higher than in the Manatee. From the relative position of the teeth in fig. 4, it will be seen that the corresponding tooth of the first premolar above is wanting in the lower jaw, and that the first there answers to the second lower premolar in the Palæothere. The upper molar teeth, with the exception of the first, are implanted by four fangs; the lower molars by two, which are more divergent than in the Manatee.

221. *Succession.*—The number of deciduous molars is $\frac{4-4}{3-3}$: the first above is relatively broader anteriorly than the premolar which succeeds it: the rest resemble the true molars of the permanent

series, their crowns being quite crossed by the transverse valley, which divides the grinding surface into two principal ridges. Cuvier well observes that, as the last true molar is not more complex than the others, so neither is the last of the deciduous series more complex than the premolar which displaces it. In the lower jaw two of the deciduous molars present the narrow elongated subtriangular crown, which is repeated by the first only of the permanent series; the third deciduous molar had the typical square double ridged crown.

222. *Lophiodon.*—Although the analogous instances(1) are so numerous as almost to establish a law, yet it was with unabated interest that I found in the Lophiodon another example of the retention throughout life, by an ancient extinct species, of a character which is transient and limited to the immature period of existence in its modern representative. The Lophiodons which rank amongst the most ancient of Pachyderms(2), had the same numerical dental formula as the Tapirs; but the compressed and more simple form of the crown was retained in the three premolars of the lower jaw, the square-shape and double transverse-ridged structure being established only in the three true molars.

In the upper jaw both the first and second premolars resemble the first premolar of the Tapir, having the outer wall of the crown divided into two demi-cones, and the inner part traversed by an oblique ridge continued from the cone which rises from the inner angle of the crown, and the anterior angle of the outer wall: this ridge is higher and more simple than in the Tapir; the valley on each side is bounded by a basal ridge. In the remaining molars the outer wall of the crown presents three demi-cones, in consequence of the great size of the angle of the anterior ridge: the inner side developes two cones which are continued by parallel oblique ridges, one to the anterior outer cone, the other to the interspace between the middle and posterior cone. The intervening valley stops at the base of the middle outer cone which is the highest, and does not cut quite across the crown in any of the true molars:

(1) *Dorcatherium*, p. 530, *Anoplotherium*, p. 523, *Machairodus*, p. 494, &c.

(2) The *Tapirus priscus* of the older pliocene or the miocene formations of Germany and France, had the same essential dental characters as the existing Tapirs; but the extinct species first appears at a more recent period than the Lophiodonts of the eocene marls and clays.

they, therefore, retain the structure of the second and third premolars in the Tapir, with slight modifications which make a nearer approach to the structure of the molars of the Rhinoceros. The first and second are implanted by three roots; the rest by four, the two inner ones being connate for some extent.

In the lower jaw the first premolar is relatively smaller and simpler than in the Tapir: the crown supports a subcompressed conical obtuse cusp, with a small anterior and larger posterior talon, and is girt by a basal ridge: in the second the anterior and especially the posterior basal lobes increase in size: in the third the posterior lobe almost equals the principal eminence, and is connected to it by a longitudinal ridge crossing the intervening valley: there is a basal ridge on each side the posterior lobe: in the three true molars of the lower jaw the crown is broader, quadrate, and supports two transverse anteriorly-curved eminences, with an anterior and posterior basal ridge, and they very closely resemble those of the Tapir: but the last molar differs by the development of the posterior talon into a wedge-shaped eminence half the height of the two that precede it. (Pl. 135, fig. 8.)

223. *Coryphodon.*(1)—This extinct Pachyderm, which was as large as a Horse, and of equal antiquity with the true Lophiodons, differed from them in having the second and third eminences of the last lower molar (Pl. 135, fig. 9) blended together into an obtuse-angled ridge, with each angle developed into a point; the anterior eminence is straight and is higher than the posterior one; it has each extremity prolonged into a point.

From the outer extremity of each of the two principal transverse eminences a ridge is continued obliquely forwards, inwards and downwards: the anterior one extends to the inner and anterior angle of the base of the crown: the posterior one terminates at the middle of the interspace between the two ridges. From the back part of the posterior transverse eminence a ridge, or talon, extends downwards and outwards.

Thus the crown of the last molar of the present species has the two transverse eminences of a Lophiodon's molar so modified

(1) History of British Fossil Mammalia, 8vo. p. 299.

that it supports two pairs of points and one single point, like the last lower molar tooth of the fossil jaw from Lot-et-Garonne, described by Cuvier in the 'Ossemens Fossiles,' 1822, tom III. p. 404; and like that from the Puy en Velay, described in the posthumous 8vo. edition of the same work, vol. v. p. 480, both of which are referred by Cuvier to the genus *Anthracotherium*. The last molar in the present fossil differs, however, from the teeth above cited, in the height of the connecting ridge of the anterior pair of points, and in the development of the fifth or posterior point from the apex of the angular ridge connecting the posterior pair of points.

From the closer resemblance which the fossil presents to the true Lophiodons, it must be regarded as a member of the same family of Tapiroid Pachyderms; indicating therein a distinct subgenus, characterised by the want of parallelism of the two principal transverse ridges, and the rudimental state of the posterior talon in the last molar tooth of the lower jaw. The name *Coryphodon*, which I have proposed for this subgenus, is derived from κορυφή a point and ὀδούς a tooth, and is significative of the development of the angles of the ridges into points.

A right canine tooth, obtained from the same eocene formation as the foregoing molar, but from a different locality in England, either belongs to the same extinct genus of Pachyderm or indicates another. The general proportions of this tooth, its degree of curvature, and the relative length of the crown and the fang, accord pretty closely with those of the canines of different species of *Lophiodon* figured by Cuvier in the 'Ossemens Fossiles,' 1822, tom. II. pt. 1. pl. 10, figs. 312. & pl. 9, fig. 11. The crown must have projected but a small distance beyond that of the adjoining teeth, and have been quite concealed by the lips, as in the Tapir, not forming a projecting tusk, and being shorter and thicker than the canine of a carnivorous quadruped. Cuvier does not give a figure of the transverse section of the crown of the canine in any of his Lophiodons: that of the present tooth is very characteristic, and resembles the transverse section of the crown of the teeth of the great extinct reptile called

Pliosaurus; the outer surface being nearly flat, and the rest of the crown so convex as to describe a semi-circle: a ridge of enamel along each border of the flattened side separates it from the convex side of the crown. This fossil tooth presents a peculiarity which I have not before observed, or found described, in having the crown defended by two layers of enamel: the outer and thicker layer has a minutely wrinkled surface and terminates near the base of the crown by a finely plicated border, extending lower upon the posterior and outer than upon the anterior and inner sides of the crown: the thin and smooth layer of the enamel extends to and defines the base of the crown, the outer layer being co-extensive with the inner one only at the two boundary ridges, and the inner layer being extended further upon the tooth at its anterior and inner sides. The length of this tooth must have been three inches when entire; the circumference of the base of the crown is two inches, nine lines.(1)

224. *Dinotherium.*—The most extraordinary of extinct Pachyderms is that which Cuvier regarded as a gigantic Tapir, on account of the character of the molar teeth, and which subsequent discovery of the cranium and the enormous tusks of the lower jaw (Pl. 99, fig. 6) has proved to be a genus connecting the Tapiroid with the proboscidian families of Pachyderms.

The permanent dentition of the genus *Dinotherium* is :—

$$\text{Incisors } \frac{0-0}{1-1};\ \text{canines } \frac{0-0}{0-0};\ \text{premolars } \frac{2-2}{2-2};\ \text{molars } \frac{3-3}{3-3}: = 22.$$

the deciduous dentition was most probably :—

$$\text{Incisors } \frac{1-1}{1-1};\ \text{canines } \frac{0-0}{0-0};\ \text{molars } \frac{3-3}{3-3}: = 16.$$

The first deciduous molar of the upper jaw has not yet been detected; it is highly probable that such a tooth existed, and I concur with Professor Kaup in regarding the two deciduous molars *in situ*, on each side of the fragment of the upper jaw of the young Dinotherium which he has figured in Tab. 1, of his 'Ossemens Fossiles de Darmstadt', as the second and third.

The crown of the second milk-molar supports two transverse

(1) History of British Fossil Mammalia, Pl. 306, fig. 105.

ridges with an anterior and posterior basal ridge; its contour is almost square. The third milk molar has a greater antero-posterior extent, and supports three transverse eminences with an anterior and posterior basal ridge, the anterior ridge being developed into a pointed tubercle at its outer end. The crowns of the first two permanent molars, or the premolars, were discovered by Dr. Kaup in their closed alveoli above the second and third deciduous molars, in a portion of the upper jaw.(1) These two premolars were in place, fully developed, with the crowns a little abraded, in the entire cranium subsequently discovered.(2) They conform to the general rule in being more simple than the teeth which they displace and succeed. The first upper premolar supports a longitudinal ridge on the outer side of the crown, and two mamilloid tubercles with confluent bases along the inner side of the crown, which is surrounded, except at its outer part, by a basal ridge. The unworn summits of both the ridge and tubercles are divided into smaller tubercles by a series of notches. The crown of the second premolar supports four tubercles, the outer ridge being deeply cleft, and the two anterior tubercles are united by a continuous ridge, which converts them into a transverse eminence, like those which characterise the true molar teeth. The transverse diameter of the second premolar exceeds the antero-posterior one, the proportions being the reverse of those of the deciduous molar which it displaces. The first true molar repeats the structure of the hindmost deciduous molar, its crown having a disproportionate antero-posterior extent and supporting three transverse eminences, with an anterior, posterior, and internal basal ridge. The Dinothere resumes the Tapiroid character and differs essentially from the Mastodon inasmuch as the posterior molars, instead of having an increased antero-posterior extent and more complex crowns, increase only in thickness and support two instead of three transverse eminences: they have also an anterior and a posterior basal ridge.

In the lower as in the upper jaw it is uncertain whether the

(1) Akten der Urwelt, 8vo. 1841, tab. VIII, fig. 1.

(2) Ibid. tab. VII.

two permanent premolars succeed two or three deciduous ones, nor has any specimen with the deciduous molars *in situ*, analogous to the fragment of the upper jaw above cited, been yet found. The last deciduous inferior molar has been found separate; it supports, like that above, three transverse eminences, but the first is narrower and the third is broader than in its analogue of the upper jaw. The first lower premolar is implanted like that above by two fangs; but it has a smaller and simpler crown, which is narrower in proportion to its antero-posterior extent, and is almost entirely occupied by the antero-posterior ridge: only the posterior of the two inner tubercles being developed: thus the crown presents more of a trenchant than a grinding character. The second premolar supports two transverse ridges. The third of the permanent series, which is the first true molar, has three transverse ridges like the one above, but is relatively narrower. The second and third true molars, the penultimate and last of the series, have each large square crowns, with two transverse ridges and an anterior and posterior talon, the latter being more developed than in the corresponding molars of the upper jaw (Pl. 96, fig. 7).

As the three-ridged or first true molar tooth is the first of the permanent series which comes into place, its crown, conformably with the general law, exhibits most abrasion; this character is well shown in Cuvier's Plate 5, 'Animaux voisins de Tapirs, Ossemens Fossiles,' tom. II., in the portion of jaw discovered in 1783 at Comminge, near the River Louze. The beautifully entire crown of Cuvier's gigantic Tapir, figured at Pl. 4, fig. 3, of the same volume is the penultimate molar of the lower jaw of the *Dinotherium giganteum*. Dr. Kaup was led, by the inspection of a drawing of a fossil tooth made in 1785, of which he has given a lithograph in his excellent Work 'Ossemens Fossiles de Darmstadt', Pl. 5, fig. 2, to conceive that the Dinotherium had three premolars, and that the tooth above cited was the first: there is no trace, however, of the alveolus of such a molar in the magnificent cranium discovered at Epplesheim in 1836, which from the unworn state of the last two molars cannot have belonged to an old animal. The same cranium also negatives the suppo-

sition that the Dinotherium had a seventh molar or fourth true molar, to which Kaup originally referred the comparatively small and simple tooth which he has figured in his 'Ossemens Fossiles de Darmstadt', Pl. II, figs. 7, *a*, *b* & *c*, and which I regard as being more probably the first deciduous molar of the lower jaw.

As the Tapir recedes from the Palæothere by the non-development of the tooth answering to the first lower premolar, so the Dinothere recedes from the Tapir in the non-development of the teeth answering to the first and second premolars in both jaws. And as the Lophiodon manifested a more simple form of the posterior premolars than in the existing Tapir, so also, the Dinothere manifested a still more simple form of the tooth corresponding to the second lower premolar in Lophiodon, and to the third in the Palæothere. By the third ridge of the last deciduous molar, the Dinothere manifested in this transitional dentition a character which is retained in the permanent dentition of the Lophiodon.

The generic peculiarity of the Dinotherium is most strongly manifested in its tusks. These tusks (Pl. 96, fig. 6) are two in number, implanted in the prolonged and deflected symphysis of the lower jaw, in close contiguity with each other, and having their exserted crown directed downwards and bent backwards, gradually decreasing to the pointed extremity: each tusk has a slight longitudinal depression on its outer side: the long implanted base is excavated by a wide and deep conical pulp-cavity, like the tusks of the Mastodon and Elephant. In jaws with molar teeth of equal size the symphysis and its tusks offer two sizes: the larger ones, which have been found four feet in length with tusks of two feet, may be attributed to the male Dinotheres, the smaller specimens with tusks of half the size, to the females. The ivory of these tusks presents the fine concentric structure of those of the Hippopotamus, not the decussating curvilinear character which characterises the ivory of the Elephant and Mastodon. No corresponding tusks, nor the germs of such, have yet been discovered in the upper jaw of the Dinotherium.

It is highly probable from the shape of the skull of the

Dinotherium that this gigantic extinct Pachyderm was of aquatic habits like the Hippopotamus, and that the inferior tusks served to detach and tear up by the roots the aquatic plants on which it fed. From the apparently superior size of those remarkable teeth in the male, it may be concluded that they also served as weapons of defence and sexual combat.(1)

PROBOSCIDIANS.

225. *Mastodon.*—No family of Mammalian Quadrupeds has suffered more from the destructive operations of time than that which is characterised by the gigantic size of the individuals composing it and their peculiar endowment of a long and prehensile proboscis. Two species alone, the Indian and the African Elephants, continue to represent the Proboscidian type in the Mammalian series of the present day; whilst those that manifested the modifications of the dental system, which gradually reduce the complexity of the Elephantine dentition to the comparative simplicity of that of the Dinothere and Tapir, have long since been blotted out of the series of living beings. The name *Mastodon* was applied by Cuvier to certain species which, being at the Tapiroid or Dinotherian extremity of the Proboscidian series, manifested modifications of the teeth most meriting to be held generically distinct from those of the existing Elephants: the grinding surface of the molars, instead of being cleft into numerous thin plates, was divided into wedge-shaped transverse ridges, and the summits of these were subdivided into smaller cones more or less resembling the teats of a cow, whence the generic name.(2) A more important modification appeared to distinguish the extinct genus, in respect of the structure of the molar teeth: the dentine, or principal substance of the crown of the tooth, is covered by a very thick coat of dense and brittle enamel; a thin coat of cement is continued from the fangs upon the crown of the tooth, but this third substance does not fill up the interspaces of the divisions of the crown, as in the Elephants. Such, at least, is the character of the molar teeth of the typical,

(1) For other conjectural uses of the tusks of the Dinothere see the interesting Chapter xiv. in Dr. Buckland's 'Bridgewater Treatise.'

(2) μαστος a nipple, οδους a tooth.

and first discovered species of Mastodon, which Cuvier has termed *Mastodon giganteus* and *Mastodon angustidens*. Fossil remains of Proboscidians have subsequently been found, principally in the tertiary deposits of tropical Asia, in which the number and depth of the clefts of the crown of the molar teeth, and the thickness of the intervening cement, are so much increased as to establish transitional characters between the lamello-tuberculate teeth of the Elephants, and the mammillated molars of the typical Mastodons;(1) showing that the characters deducible from the molar teeth are rather the distinguishing marks of species than of genera, in the gigantic proboscidian family of Mammalian quadrupeds.

All Mastodons differ from the Dinotheres and resemble the Elephants in the presence of two large tusks in the intermaxillary bones. But those Mastodons with the more simple and typical molar teeth likewise manifest the Dinotherian character in having tusks in the lower jaw in the male: these are largest in the European species (*M. angustidens*, Pl. 90, fig. 6, *i*): they appear to have been present in the young of both sexes, and are shown in the immature jaw of the North American species (*Mastodon giganteus*) in Pl. 144, fig. 13, *d i*;(2) but it would appear from the examples

(1) Mr. Clift had foreseen the possibility of the discovery of such a link, since supplied by the praiseworthy exertions of Captain Cautley and Dr. Falconer, in his description of the Fossil Remains from Ava, in the Geological Transactions, second series, vol. II. "It is not impossible," he says, "that there may yet be a link wanting, which might be supplied by an animal having a tooth composed of a greater number of denticles, increasing in depth, and having the rudiments of *crusta petrosa*, that necessary ingredient in the tooth of the Elephant: the entire absence of which distinguishes the tooth of the *Mastodon*." Cuvier had previously enunciated the same supposed distinctive character between the structure of the teeth of the Elephant and Mastodon. "Dans l'éléphant ces vallons sont entièrement comblés par *le cortical*, tandis que dans le Mastodonte ils ne sont remplis de rien." Ossemens Fossiles, tom. I., 4to. 1821, p. 225. The truth is, that the exterior of the fangs in all Mastodons is covered by a moderately thick coat of cement (*cortical* of Cuvier, *crusta petrosa* of Clift); and that this substance extends upon the enamel of the crown, in a very thin layer, requiring microscopical sections and examination in the typical Mastodons; but augmenting in thickness in the Elephantoid and other species, with thinner and more numerous transverse divisions of the crown of the grinders.

(2) First described and figured by Dr. Godman, as indicative of a new genus, under the name of *Tetracaulodon*, in the "Transactions of the American Philosophical Society," New Series, Vol. III, 1830, pp. 478—485, Pls. 17 and 18.

in the British Museum, that only one of the lower tusks, usually the right, was retained or succeeded by a permanent tusk in the adult male (ib. fig. 14, *i*).(1) I first pointed out the inferior tusks, whether transitory or persistent, as a well-marked generic character of *Mastodon*, as contradistinguished from *Elephas*, in my "History of British Fossil Mammalia" (p. 275); and also defined a second character, in the displacement of the first and second molars, in the vertical direction, by a tooth of simpler form than the second, a true 'dent de remplacement', developed above the deciduous teeth in the upper, and below them in the under jaw. Both these dental characters, which are of greater importance than many accepted by modern Zoologists as sufficient demarcations of existing generic groups of Mammalia, have been recognised in the *Mastodon giganteus*, of North America, and in the *Mastodon angustidens* which is the prevailing species of Europe.

The molar formula of the genus *Mastodon*, according to the total number of grinders developed, is:—$\frac{7-7}{7-7} = 28$.(2) But in this number are combined both the deciduous and permanent teeth, contrary to the dental formulæ of most other Mammalia. The two series may, however, be distinguished in the Mastodon, notwithstanding the successive fall of the true theoretically permanent molar teeth. The first two molars in the upper jaw, for example, are unequivocally proved to be the analogues of the deciduous teeth in ordinary Pachyderms by their relation to a vertical successor, premolar, or 'dent de remplacement.' There are good grounds also, for regarding the third molar in the order of development, as the last of the theoretically deciduous series, although it has no vertical successor. According to these views of the teeth analogous to the permanent series in ordinary Pachyderms, the formula of *Mastodon* is:—

$$in.\ \frac{1-1}{1-0}\ \text{or}\ \frac{1-1}{1-1}\ (mas),\ \frac{1-1}{0-0}\ (fæm.;)\quad c.\ \frac{0-0}{0-0};\ p.\ \frac{1-1}{1-1};\ m.\ \frac{3-3}{3-3}:\ =\ 20.$$

(1) See my Memoir on the so-called *Missourium* and *Tetracaulodon*, Proceedings of the Geological Society, 1842, No. 87, p. 689.

(2) The presence of the small premolar in the lower jaw has not yet been determined; neither has its absence. An excavation in the jaw of the young *Mastodon* described by Dr. Godman, at the place where the germ of the premolar is hypothetically sketched in Pl. 144, fig. 7, *p* 1, would determine this point in regard to the *M. giganteus*.

The deciduous formula, is :—

$$\text{incisors } \frac{1-1}{1-1}; \text{ molars } \frac{3-3}{3-3}: = 16.$$

226. *Mastodon giganteus.*—I shall first describe the molar teeth in the *Mastodon giganteus*, as these best exhibit the tapiroid character of the grinding surface. This character is most strongly manifested, agreeably with the law which has been so frequently illustrated in the present work, by the molars which are first developed in the young animal, at the period of dentition when it has receded least from the common type. The crown of the first deciduous molar in the lower jaw (Pl. 144, fig. 1, *d* 1) is subquadrate, one inch four and a half lines in antero-posterior diameter, one inch three lines across its broadest part; it supports two transverse ridges, the anterior one most deeply cleft into two mastoid eminences, the posterior and broader ridge having one angle produced forwards: the front, back and outer part of the bases are girt by a tuberculate ridge; the whole is supported by two long subcompressed divergent fangs.(1)

The second deciduous molar (Pl. 144, fig. 2, *d* 2) has a crown, like the first in shape, but measuring one inch eleven lines, by one inch eight lines, and having both transverse ridges subdivided into two mastoid eminences, and a larger posterior basal ridge; it is supported by two fangs.(2) It is displaced and succeeded vertically by a tooth (ib. fig. 3, *p* 1) of a more simple form, having a crown broader in proportion to its length, supporting two bifid transverse ridges, and girt by a basal cingulum; it measures one inch five lines by one inch four lines. This tooth may be regarded as the first of the theoretically permanent or adult series of teeth: it answers to the penultimate premolar in the Dinothere and Tapir, but is very soon shed.

The tooth (ib. figs. 4 & 5, *d* 3) which answers to the last milk molar in the above cited Pachyderms, rises into place and use, as in these and other Quadrupeds, before the premolar is developed: its crown supports three bifid transverse eminences,

(1) On this tooth is founded the nominal species *Mastodon tapiroides* of Koch and Grant. Geol. Proceedings, vol. III, p. 771. It is figured on the left side of the lower jaw of the young *Mastodon* referred by Godman to the *Tetracaulodon*, loc. cit. Pl. 18.

(2) This tooth is also figured in the Plate above cited of Dr. Godman's Memoir.

and a tuberculate ridge along the front, back and outer part of its base: specimens vary in antero-posterior diameter from two inches ten lines, to three inches three lines in length; the tooth here figured was two inches four lines across the broadest posterior lobe. The crown is supported by two small anterior fangs and one large posterior root. This tooth ought, theoretically, to be succeeded and displaced vertically by a premolar, answering to the last in the Tapir; but the rapidity of the horizontal progress of the true molars, and their progressive increase of size and complexity, appear to be the conditions of the interrupted development of the premolar series, and which operate to their entire suppression in the genus *Elephas*.

The antepenultimate or first true molar, the fifth of the series developed in succession, (Pl. 144, fig. 6 & 7, *m* 1) resembles the preceding in conformation, but is larger, and the basal ridge is commonly less distinct on the outer side: its antero-posterior diameter is four inches one or two lines, its breadth which is more equable than in *d* 3, is three inches.(2) In the young tooth figured, the marks of the subdivision of the eminences of the primary mastoid lobes are not obliterated.

The penultimate, or second true molar, the sixth of the series in succession, (ib. fig. 8 & 9, *m* 2) has also the crown divided into three transverse eminences, each cleft down the middle, but the posterior basal ridge is usually more developed. The antero-posterior diameter of the crown is from five inches to five and two thirds; its transverse diameter three inches and a half to three and two-thirds. The first transverse eminence is supported by a single fang, the remainder of the tooth by a broad thick base, subdivided into three or more roots.(3)

(1) The lower jaw of the *Mastodon giganteus* figured by Dr. Hays, Transactions of the American Philosophical Society, Vol. iv, 1831, Pl. 20, shows the stage of dentition when the two true deciduous molars have been shed, the first true molar (c) in place, and before the first premolar (if this tooth be developed in the lower as in the upper jaw) had risen. The fractured state of the symphysis prevented the recognition of the remains of the alveoli of the deciduous tusks; the specimen being most probably of a young female *Mastodon*.

(2) A portion of this tooth is figured by Dr. Hays, loc. cit. Pl. 20, fig. 1, *d*.

(3) This tooth is figured by Dr. Hays, loc. cit. Pl. 21, *e*., and by Cuvier, 'Ossemens Fossiles' tom. i. Grand Mastodonte, Pl. 1, fig. 5.

The last, or third true molar, (ib. fig. 10 & 11, *m* 3) is subject to some variety of configuration, as well as size; it supports four bifid transverse eminences and a posterior talon;(1) but this is often developed into a fifth bifid transverse eminence, smaller than the others, and is sometimes followed by a sixth tuberculate lobe or talon. The antero-posterior diameter of the crown ranges from seven and a half inches to eight and a half inches, its transverse diameter at its thickest (anterior) part, from four inches to four and a half inches. The remains of the lateral basal ridges are usually present in this and the two preceding molars as tubercles at the outer and inner ends of the transverse valleys. The first and second transverse ridges are usually supported by a single root, the rest of the molar by a large conical mass subdivided into four or more roots.

The successive molars have here been described as they appear in the lower jaw; those above scarcely differ save in a slight increase of transverse diameter and more subdivided roots.

The superior tusks of *Mastodon giganteus* project more forwards than in the Elephant, and are slightly curved upwards and outwards. The length of the exserted part of those in the skeleton of the adult male Mastodon in the British Museum surpasses seven feet, along the curve. Some smaller and straighter specimens, which, from the contraction of their open basal end, would seem to have belonged to aged individuals, indicate a sexual inferiority in the length of the upper tusks in the female of this species.

The inferior persistent tusk in the lower jaw is commonly about three inches in diameter and one foot in length; it is nearly straight. Cuvier has apparently figured the end of one of these tusks in the first Edition of the 'Ossemens Fossiles, Grand Mastodonte' Pl. 3, fig. 4 & 5. In the same plate he has well represented a lower jaw of an old male Mastodon showing the persistent alveolus of the single tusk, in fig. 2. The original of this figure

(1) This variety is figured by Dr. Hays in the lower jaw of an old female Mastodon, loc. cit. Pl. 23, & Pl. 24, and in that of an old male Mastodon, with one tusk, in Pl. 29. Also by Cuvier, loc. cit. 'Grand Mastodonte,' Pl. 1, figs. 3 & 4.

(2) This variety is figured by Dr. Hays, loc. cit. Pl. 21, f, and by Cuvier, loc. cit. fig. 2.

is now in the Cabinet of the American Philosophical Society at Philadelphia. Dr. Hays has refigured the specimen, as a lower jaw of the *Tetracaulodon*, in his Memoir in the Transactions of the Society for 1831. Why Cuvier should have suppressed the instructive plate of this lower jaw in his 2nd Edition of the 'Ossemens Fossiles' I know not. The Plate 26 in Dr. Hay's Memoir would indicate that both lower tusks were occasionally retained in the male *Mastodon giganteus* as they commonly are in the male *Mastodon angustidens*.

227. *M. angustidens*.—The molar teeth of this extinct Europæan Mastodon are narrower in proportion to their antero-posterior extent, and their grinding surface is more mammillated and less transversely ridged than in the *Mastodon giganteus*. As in this species the molar series, on each side of the upper jaw and probably also of the lower, includes two deciduous teeth which are succeeded by one tooth in a vertical direction, and this by four other molars progressively increasing in size, and pushing out their predecessors as they advance: the total number of molars developed on each side of the upper jaw being seven; the greatest observed number in use, or exposed at the same time is three on each side; which is reduced in the old animals to one on each side.

The *first* milk-molar Pl. 144, fig. 12, *d* 1,(1) has an oblong subquadrilateral transverse section, rounded anteriorly: it is obscurely quadricuspid; the two anterior cusps are first blended together by attrition, then the posterior external cusp is worn down into the same surface; the posterior internal cusp remaining longest distinct. It has two fangs.

The *second* milk-molar (ib. *d* 2)(2) is at least three times as large as the first and supports three pair of cusps, the posterior ones being the largest: and the outer one of the middle pair indicates by its lateral projection the outer side of the tooth: a narrower tuberculate ridge is developed at the anterior and posterior margins of the crown. Each pair of cusps is reduced by progressive attrition to a transverse oval depression, the two exterior and posterior cusps being the last to yield. It has two

(1) Kaup, 'Ossemens Fossiles de Darmstadt," Pl. 16, fig. 1, & 1a, Pl. 20, fig. 2.

(2) Ibid. Pl. 16, fig. 1, & 1a, Pl. 17, fig. 12, Pl. 21, fig. 1.

fangs, the anterior and smaller one supporting the anterior pair of cusps, the posterior the remainder of the crown.

The vertically succeeding tooth of the second molar (ib. *p* 1) follows the usual law in having a less complicated crown than the tooth which it replaces: it has only two pairs of principal cusps, and is a sort of magnified representative of the first small deciduous molar, which has no successional tooth.(1) The external and anterior cusp is the longest, the base of the crown is partially surrounded by a tuberculate ridge. This tooth, when fully developed, has three roots, of which the outer and anterior one supports the corresponding cusp; the other two supporting the rest of the crown. Specimens have been found in which all the four cusps have been worn down to their base; but the insular patches of dentine have been distinct and severally surrounded by their thick enamel.

The fourth molar,(2) in the order of size, is anterior to the preceding in the order of development, and is the third in the order of position (ib. fig. 12, *d* 3) before the fall of the two deciduous teeth, and the second after the acquisition of the vertically succeeding molar. I regard it as being essentially the last of the true deciduous series, but which has no vertical successor. The grinding surface presents four pairs of cusps and a small posterior ridge or talon:(3) the first pair of cusps is the smallest and is most complicated with accessory tubercles: the bases of the cusps encroach reciprocally upon each other's interspaces across the middle longitudinal valley,

(1) If the premolar (*p* 1) succeeded the first small molar, as described by Dr. Kaup, (Sur le *Mastodon longirostris*, 4to. 1835, p. 70.) it would form an exception to the rule; but the specimen of the upper jaw of *Mastodon angustidens* from Dax figured by Cuvier, Ossem. Fossiles, Divers Mastodontes, Pl. III, fig. 2, shows the unworn cusps of the quadri-cuspid successional molar projecting into the socket, whence the sex-cuspid deciduous tooth has been extruded. Cuvier figures one of these teeth, from Dax, loc. cit., Pl. 1, fig. 2, in which the two anterior cusps are blended into a single irregular surface; behind which are the worn tips of the posterior pair of cusps.

2) Kaup, ib. Pl. XVI, fig. 1 & 1 *a*; Pl. XX, fig. 2; Pl. XVII, fig. 13 & 14.

(3) This tooth is described in my 'History of British Fossil Mammalia,' p. 286, as having three pairs of mastoid tubercles and 'a large posterior tuberculate talon', two of the tubercles in that talon (fig. 100, p. 284) corresponding with the fourth pair, here described. The two extremes in the varieties of the talon in this tooth may be seen in Cuvier's 'Divers Mastodons' Pl. iii, fig. 2, and Kaup's Pl. xvi, fig. 1 & 1a, and I have, as yet, no evidence that they characterize distinct species. The English fossil (fig. 100, 'Br. Foss. Mam.') is an intermediate variety.

and thus appear to alternate, when worn down. The anterior talon is continued from the internal cusp; the posterior talon consists of three tubercles.

The antepenultimate tooth would seem to be the analogue of the first of the three true molars in the Tapir and ordinary Pachyderms, since it presents, as in the *M. giganteus*, a marked increase of size, and consists of four pair of cusps and two talons, one anterior the other posterior; but these accessory elevations are relatively larger and more complicated. Dr. Kaup figures one molar in which the hinder talon is divided into nine tubercles; in another it was divided into three unequal tubercles. The large pairs of cusps are accompanied by small accessory tubercles which are worn away in the course of mastication.

The penultimate molar (Pl. 90, fig. 6, *m* 6)(1) differs in little else than size, from the preceding; the number of accessory tubercles to the normal cusps, which is always irregular, appears to be greater; and the terminal talons to be more sub-divided.

The last molar of the upper jaw, the seventh in the order of development, (ib. *m* 7)(2) has five pairs of cusps, the anterior talon of the antecedent teeth being here developed into a normal pair, which is also the largest: the posterior talon sometimes consists of a group of tubercles, the posterior of which represents an accessory talon: sometimes the anterior tubercles of the talon are so developed as to resemble a sixth pair of cusps; at other times the talon presents only two or three tubercles in the same transverse row; and is thus subject to great variety, as is also the entire tooth in respect of size. The tooth is supported by two principal roots, of which the anterior and smaller supports the two anterior pairs of cusps; the posterior mass the rest of the tooth: this broad fang becomes sub-divided into two or more, in the progress of age. Not any of the preceding molars have remained long enough in their sockets to exhibit the effects of such extensive abrasion as has been observed in specimens of the last molar: this, therefore, becomes itself a character of the tooth which is longest retained, when the distinguishing tubercles have thereby been destroyed.

(1) Kaup, Pl. xx, fig. 3. (2) Ib. Pl. xviii.

Cuvier has given a very interesting figure of a last molar in this stage, (loc. cit. Pl. III, fig. 5) which has its grinding surface reduced to an uniform disc of smooth dentine.

The first molar(1) of the lower jaw of the *Mast. angustidens*, was as small and apparently more simple in the crown, than that above. M. M. Croizet and Jobert consider that it had but one pair of cusps ; Dr. Kaup states that it is succeeded by a ' dent de remplacement,' a figure of which he cites from Meyer's ' Fossiles de Georgensmund,' Pl. 1, fig. 2.

The second molar of Kaup, which, if the first be so succeeded vertically, should be the third, has three pairs of cusps, and an anterior talon. The first pair of cusps or tubercles, are so much smaller than the second, as to appear like a large bi-tuberculate talon : the second pair is the largest, and forms the broadest part of the grinding surface ; in the middle of the valley between this and the third pair, there is ordinarily a small tubercle, which Dr. Kaup found to be, in one instance, eaten away by caries. The posterior talon is sometimes tuberculate, sometimes flat. Dr. Kaup indicates the resemblance between these teeth, and that of the *Mastodon augustidens*, from Simorre, figured by Cuvier, loc. cit. Pl. I, fig. 4.

The lower molar, corresponding to the last of the deciduous series (*d* 3) in the upper jaw, has three pairs of cusps and a posterior, often large, talon ; the anterior pair is rather larger than the second ; the posterior has a slight increase of breadth. Dr. Kaup figures one of these teeth in which each pair of cusps has been worn down to a single transversely oval cavity surrounded by enamel.

The ante-penultimate lower molar has four pairs of cusps and a posterior talon which consists of a small and single tubercle. The anterior pair of cusps is complicated, with some small tubercles, which are soon worn down. In a fully developed tooth, figured by Dr. Kaup, Pl. XIX, fig. 5, the two anterior pairs of cusps are abraded to a single quadrilobate surface, and this is followed by five subcircular depressions, formed by the abraded summits of the two posterior pairs of cusps, and the talon. The anterior pair of cusps and part of the second pair are supported by a vertical and slender

(1) Meyer, ' Fossiles de Georgensmund,' Pl. I, fig. 3.

fang; the rest of the crown by a thicker fang, which inclines obliquely backwards: these roots have sometimes a longitudinal channel on each side.

The penultimate molar (Pl. 90, fig. 6, *m* 6)(1) has four pairs of cusps, and a posterior bituberculate talon, which represents a fifth smaller pair of cusps: in the corresponding upper molar the posterior talon is divided into a greater number of tubercles, and the whole tooth is broader. Cuvier has likewise figured (loc. cit. Pl. III, fig. 14) a quadricuspid tooth of the *Mastodon angustidens*, from the collection of M. Hammer, which he compares with that of the upper jaw from Dax.

The last molar (Pl. 90, fig. 6, *m* 7) varies in size in different individuals, even more than the last molar of the upper jaw: it has usually five pairs of cusps, and a posterior talon. The cusps are slightly inclined outwards, and it is further distinguished from the last molar of the upper jaw by its narrower figure and the more conical shape of the talon. Its two roots are simple, but of very unequal size, and inclined backwards: the first, which is very long and slender in old teeth, supports only the anterior pair of cusps; the rest of the molar being supported by the large conical compressed posterior fang: a third small and short fang is sometimes developed from the interspace of the two longer ones.

I have been induced to characterise the different molars of the *Mastodon angustidens*, because the most common remains of the Mastodon in this country are detached grinding teeth of this species, which may thus be determined. Portions of the large upper tusks are occasionally found in the older pliocene crag of Norfolk and Suffolk, and I have recently received a large portion of the straight tusk of the lower jaw. It was about sixteen inches long, and part of the tusk which protruded from the jaw, the base of the fragment being as solid as the apex, and the whole being traversed by a sub-central canal, of nearly the same diameter, about two lines from one end of the fragment to the other. The outer layers of the ivory had been detached, excepting a very small portion near the apex, which retained its thin coating of cement. The transverse section of this tusk gave an irregular oval disk, one side being less convex than

(1) Kaup, loc. cit, Pl. XIX, figs. 1 & 2.

the other; and on the lower half of the more convex (outer) side of the tusk, faint traces were distinguished of longitudinal grooves, about a line in breadth. In all these characters, the fragment in question agreed with a similar fragment of a tusk, ten inches in length, obtained from the miocene, or older pliocene tertiary deposits at Eppelsheim, in Germany, which specimen Dr. Kaup had ascertained to belong to the lower jaw of the same species of Mastodon.

The division of the transverse eminences of the surface of the molar teeth into large rounded mammillæ, often placed sub-alternately, is common, with slight modifications, to the European *Mastodon angustidens*, with allied species in South America, Australia, and Southern Asia.

228. *Transitional Mastodons.*—Mr. Clift(1) has described and beautifully illustrated the dentition of one of the Asiatic Mastodons with molar teeth, which differ chiefly from those of the *Mast. angustidens* in their greater relative breadth: he has, therefore, termed the species *Mast. latidens.*(2) The last lower molar tooth is figured in Pl. 38, fig. 1, of the volume cited: it presents a grinding surface nine inches in length, and nearly four inches in breadth; divided into six transverse eminences and a posterior talon; each eminence is divided into two principal mammillæ, and these are again sub-divided into two smaller rounded mammillæ, except in the fifth eminence, which consists only of the two principal mammillæ, whilst the sixth division or talon, is formed by a single large obtuse eminence.(3)

In the same plate Mr. Clift figures part of the lower jaw with the last molar tooth of another more remarkable species of Proboscidian, which he has termed *Mastodon elephantoïdes.*(4) This tooth (Pl. 145, fig. 2) is twelve inches in antero-posterior extent, and three inches in breadth: its grinding surface is divided into ten nearly equal low transverse ridges, the summits of which are sub-divided into five or six small and equal obtuse mammillæ. The interspaces of the ridges are not filled with cement, as in the true Elephants;

(1) Geological Transactions, Second Series, vol. II, 1829, p. 369.

(2) This appropriate name was suggested to Mr. Clift by Mr. Broderip, the learned Secretary of the Geological Society.

(3) Pl. 145, fig. 1. This and other characteristic remains of the *M. latidens* were discovered in newer tertiary deposits on the banks of the Irawadi, in Ava.

(4) This name was likewise suggested by Mr. Broderip, the species was found in Ava.

only a thin layer of that substance is continued upon the unworn enamel, as in the true Mastodons.

With reference to the molar teeth of the *M. latidens*, Mr. Clift remarks that, in comparison with those of the *M. giganteus*, the ridges are more numerous, less distant, and the interstices less deep: they are also more sub-divided, and the teeth begin to assume the appearance of those of the Elephant:—"On advancing to *Mastodon elephantoides*, we shall find all these features of similarity more strongly developed:—the points and ridges are still more numerous, and the structure, were it not for the absence of 'crusta petrosa', becomes almost that of the tooth of the Elephant."

The difference, in regard to the coronal cement, or 'crusta petrosa,' between *Mastodon* and *Elephas*, is not absolute, but proportional; although the quantity in the more deeply cleft crowns of the Elephants' molars is considerably greater, the cement there fulfilling its office of binding together the plates of the crown, whose interspaces it completely fills.

Whether the more essential characters of the genus *Mastodon*, viz: the premolars, are present in the *M. elephantoides* of Clift, has not yet been determined. Dr. Falconer informs me that he has satisfied himself of the absence of the tusks in the lower jaw of very young individuals, which forms another striking feature of the transitional character of this extinct species. The same distinguished Palæontologist, in conjunction with his accomplished and scientific coadjutor, Captain Cautley, has brought to light the remains of extinct species of Proboscidians with more deeply cleft molars, occupied by the abundant cement which characterises the structure of the grinding teeth of the Elephantine genus. The difference in the thickness and height of the divisions of the crown of these teeth in the *Elephas planifrons* and *Elephas Hysudricus*, F. & C., establishes two intermediate links between the Elephantoid Mastodon and the Indian Elephant, in which latter species, amongst existing animals, the teeth present the greatest complexity of structure.

229. *Elephas*.—The dentition of the sole surviving genus of the great Proboscidian Family includes two long tusks (Pl. 146, fig. 1, *i*) one in each of the intermaxillary bones, and large and

complex molars (ib. *m* 3, 4 & 5) in both jaws: of the latter there is never more than one wholly, or two partially, in place and use, on each side at any given time; for, like the molars of the Mastodons, the series is continually in progress of formation and destruction, of shedding and replacement; and in the Elephants all the grinders succeed one another, like true molars, horizontally, from behind forwards; none being displaced and replaced by vertical successors or premolars.

The total number of teeth developed in the Elephant appears to be:—*in.* $\frac{2-2}{0-0}$: *m.* $\frac{6-6}{6-6} = 28$. The two large permanent tusks being preceded by two small deciduous ones, and the number of molar teeth which follow one another on each side of both jaws being at least six.

The deciduous tusk (ib. fig. 3, *d i*) makes its appearance beyond the gum between the fifth and seventh month: it rarely exceeds two inches in length, and is about a third of an inch in diameter at its thickest part, where it protrudes from the socket; the fang is solidified, and contracts to its termination, which is commonly a little bent, and is considerably absorbed by the time the tooth is shed, which takes place between the first and second year.(1)

The socket of the permanent tusk, (ib. fig. 3, *i*) in a new-born Elephant, is a round cell about three lines in diameter, situated on the inner and posterior side of the aperture of the temporary socket. The permanent tusks cut the gum, when about an inch in length, a month or two usually after the milk-tusks are shed. At this period, according to Mr. Corse,(2) the permanent tusks are "black and ragged at the ends. When they become longer, and project beyond the lip, they soon are worn smooth by the motion and friction of the trunk." The widely open base of the tusk is fixed upon a conical pulp, which, with the capsule surrounding the base, progressively increases in size, stimulates a concomitant increase in the capacity and depth of the socket, which cavity soon obliterates that of the deciduous tusk, and finally extends

(1) 'Memoir on the Teeth of the Elephant,' in the Philosophical Transactions, 1799, p. 211: in which a good figure of the deciduous tusk is given in Plate 5.

(2) Loc. cit., p. 212.

its base close to the nasal aperture (Pl. 146, fig. 1). The tusk, conical at its first-formed part, afterwards sub-cylindrical, being subject to no habitual attrition from an opposed tooth, and worn only by the occasional uses to which it is applied, arrives at an extraordinary length, following the curve originally impressed upon it by the form of the socket, and gradually widening from the projecting apex, to that part which was formed when the matrix and the socket had attained their full size.

These incisive teeth of the Elephant not only surpass other teeth in size, as belonging to a quadruped so enormous, but they are the largest of all teeth in proportion to the size of the body; representing in a natural state those monstrous incisors of the Rodents which are the result of accidental suppression of the wearing force of the opposite teeth.

The tusks of the Elephant, like those of the Mastodon, consist chiefly of that modification of dentine which is called 'ivory,' and which shows, on transverse fractures or sections, striæ proceeding in the arc of a circle from the centre to the circumference, in opposite directions, and forming by their decussations curvilinear lozenges (Pl. 146, fig. 8, *i*) This character is peculiar to the tusks of the Proboscidian Pachyderms.

In the Indian Elephant the tusks are always short and straight in the female, and less deeply implanted than in the male: she thus retaining, as usual, more of the characters of the immature state. In the male they have been known to acquire a length of nine feet, with a basal diameter of eight inches, and to weigh one hundred and fifty pounds; but these dimensions are rare in the Asiatic species.

Mr. Corse, speaking of the variety of Indian Elephant, called 'Dauntelah' from its large tusks, which project almost horizontally with a slight curve upwards and outwards, says, "The largest I have known in Bengal, did not exceed seventy two pounds avoirdupois; at Tiperah they seldom exceed fifty pounds."(1) There are varieties of the Dauntelah in which the large tusks of the male are nearly

(1) Loc. cit., p. 212.

or quite straight; and in a more marked breed called 'Mooknah' the tusks are much smaller, are straight, and point directly downwards. These ascertained varieties in an existing species ought to weigh with the observers of analogous varieties in the teeth of fossil Proboscidians, before they pronounce definitely on their value as characters of distinct species. More anomalous varieties occasionally present themselves in the Indian Elephant, as when one tusk is horizontal, the other vertical; or when, from some distortion of the alveolus, a spiral direction is impressed upon the growth of the tusk, as in that specimen figured by Grew in the 'Rarities of Gresham College,' Tab. 4, and which is now in the Museum of the English College of Surgeons. The tusk of the Elephant is slightly moveable in its socket, and readily receives a new direction of growth from habitual pressure: this often causes distorted tusks in captive Elephants, and Cuvier(1) relates the mode in which advantage was taken of the same impressibility, in order to rectify the growth of such tusks in an Elephant kept at the Garden of Plants.

The tusks of the extinct *Elephas primigenius*, or Mammoth, have a bolder and more extensive curvature than those of the *Elephas indicus:* some have been found which describe a circle but, the curve being oblique, they thus clear the head, and point outwards, downwards, and backwards. The numerous fossil tusks of the Mammoth which have been discovered and recorded, may be ranged under two averages of size:—the larger ones at nine feet and a half, the smaller at five feet and a half in length. I have elsewhere(2) assigned reasons for the probability of the latter belonging to the female Mammoth, which must accordingly have differed from the existing Elephant of India, and more resembled that of Africa in the development of her tusks; yet manifesting an intermediate character by their smaller size. Of the tusks which are referable to the male Mammoth, one from the newer tertiary deposits in Essex, measured nine feet ten inches along the outer curve, and

(1) 'Ossemens Fossiles,' 4to. 1821, tom. i, p. 47.

(2) 'History of British Fossil Mammalia,' 8vo. 1844, p. 244.

two feet five inches in circumference at its thickest part: another from Eschscholtz Bay, was nine feet two inches in length, and two feet one and a half inches in circumference, and weighed one hundred and sixty pounds. A Mammoth's tusk has been dredged up off Dungeness which measured eleven feet in length. In several of the instances of Mammoth's tusks from British strata, the ivory has been so little altered as to be fit for the purposes of manufacture; and the tusks of the Mammoth, which are still better preserved in the frozen drift of Siberia, have long been collected in great numbers as articles of commerce.(1)

Cuvier(2) states that the Elephant of Africa, at least in certain localities, has large tusks in both sexes, and that the female of this species, which lived seventeen years in the Menagerie of Louis XIV, had larger tusks than those in any Indian Elephant, male or female, of the same size which he had seen. The ivory of the tusks of the African Elephant is most esteemed by the manufacturer for its density and whiteness.

The molar teeth of the Elephant are remarkable for their great size, even in relation to the bulk of the animal, and for the extreme complexity of their structure. The crown, of which a great proportion is buried in the socket, and very little more than the grinding surface appears above the gum, is deeply divided into a number of transverse perpendicular plates, consisting each of a body of dentine, (Pl. 146, figs. 6 & 7, *d*) coated by a layer of enamel (*e*), and this by the less dense bone-like substance (*c*) which fills the interspaces of the enamelled plates, and here more especially merits the name of 'cement,' since it binds together the several divisions of the crown, before they are fully formed and united by the confluence of their bases into a common body of dentine. As the growth of each plate begins at the summit, they remain detached

(1) In the account of the Mammoth's bones and teeth of Siberia, published in the 'Philosophical Transactions' for 1737, (No. 446), tusks are cited which weighed two hundred pounds each, and "are used as ivory, to make combs, boxes, and such other things; being but little more brittle, and easily turning yellow by weather and heat." From that time to the present there has been no intermission in the supply of ivory, furnished by the tusks of the extinct Elephants of a former world.

(2) Loc. cit., p. 55.

and like so many separate teeth or denticles, until their base is completed, when it becomes blended with the bases of contiguous plates to form the common body of the crown of the complex tooth, from which the roots (ib. *r r*) are next developed.

But the growth of each constituent plate is analogous to, and almost as complex as that of the entire tooth; for each plate consists at the beginning of a series of separate slender conical columns or digital processes (Pl. 146, fig. 4), arranged transversely across the tooth. The formation of these columns likewise begins at their summit, and descends, their bases gradually expanding until they are blended together to form a continuous transverse plate (ib. fig. 5.)(1); just as the plates are subsequently blended together to form a continuous longitudinal crown of the grinder. After the digital processes have coalesced to form the transverse plate, the sides of this plate, which in the Asiatic Elephant are parallel, become wrinkled or undulated: giving a similar character to the line of enamel, when the surface of the tooth has been worn down to this point. The lateral margins of the plates are rounded and, though covered by a thick cement, still project so as to give a vertically ribbed surface to the sides of the complex molar (Pl. 148, fig. 5); when the cement is detached the margin of the plate is seen to be undulated by a number of small transverse risings: this structure is beautifully shown in some of the molars of the Mammoth, a portion of one of these is figured in Pl. 148, fig. 7.(2)

The plates of the molar of the *Elephas primigenius* are thinner in proportion to their breadth, and are generally a little expanded at the middle: the enamelled border is often undulated, as in the *Elephas asiaticus*, and sometimes with a greater degree of regularity. The coronal plates are in general more numerous in proportion to the size of the crown in the Mammoth, than in the *El. asiaticus*. (Compare fig. 6, molar of Mammoth, with fig. 3, molar of Indian Elephant in Plate 148). In the *El. africanus*

(1) Such detached plates of the large molars of the Mammoth offer a rude resemblance to a hand, and may be found figured in the works of the older collectors of petrifactions, under the name of 'Cheirolites,' as the fossilized hand of a monkey or a child.

(2) See 'History of British Fossil Mammalia,' 8vo. p. 337, fig. 91.

fig. 4), on the other hand, the lamellar divisions of the crown are fewer and thicker, and they expand more uniformly from the margins to the centre, yielding a lozenge-form when cut or worn transversely.

The horizontal as well as vertical course of development of the Elephant's grinder is well illustrated by the Mammoth's molar, the last of the lower jaw, in Pl. 148, fig. 5. The separate digital processes (*f f*) of the posterior plates are still distinct, and adhere only by the remaining cement; a little in advance we see them united to form the transverse plate; and, at the opposite extremity of the tooth, the common base of dentine (d^1) is exposed by which the plates are finally blended into one individual complex grinder(1): this never takes place simultaneously along the whole course of the tooth in the larger molars of the existing Indian Elephant, or its extinct congener, the Mammoth. The African Elephant, and some of the extinct Indian species, as the *El. planifrons*, (Pl. 147, fig. 1), manifest their affinity to the Mastodon by the basal confluence of the hindmost plates before the foremost ones are worn out. The grinders of the *El. planifrons* are also distinguished from the existing species by the number of roots (ib. *d d*), and the extent of the base (*a a*) from which they are simultaneously developed.

The formation of each grinder begins with the summits of the anterior plate, and the rest are completed in succession; the tooth is gradually advanced in position as its growth proceeds, and, in the existing Indian Elephant, the anterior plates are brought into use before the posterior ones are formed. When the complex molar cuts the gum the cement is first rubbed off the digital summits: then their enamel cap is worn away, and the central dentine comes into play with a prominent enamel ring: the digital processes are next ground down to their common uniting base, and a transverse tract

(1) Some anatomists describe the divisions of the crown of the Elephant's grinder as entire teeth; and Mr. Corse, (loc. cit. p. 213) who first propounded this view, calls each complex grinder 'a case of teeth,' and states "that these teeth are merely joined to each other by an intermediate softer substance, acting like a cement." But this description applies only to the incompletely formed tooth; and the detached eminences of the crown of any complex tooth, at that stage of growth when they are held together only by the still uncalcified supporting matrix, might with equal justice be regarded as so many distinct teeth.

of dentine with its wavy border of enamel is exposed; finally the transverse plates themselves are abraded to their common base of dentine, and a smooth and polished tract of that substance is produced.(1) From this basis the roots of the molar are developed, and increase in length, to keep the worn crown on the grinding level, until the reproductive force is exhausted. When the whole extent of a grinder has thus successively come into play, its last part is reduced to a long fang supporting a smooth and polished field of dentine, with sometimes a few remnants of the bottom of the enamel folds at its hinder part, as shown in Pl. 148, fig. 8. When the complex molar has been reduced to an uniform surface it becomes useless as an instrument for grinding the coarse vegetable substances on which the Elephant subsists: it is then attacked by the absorbent action, by which and the pressure of the succeeding tooth it is finally shed.

The grinding teeth of the Elephant progressively increase in size, and in the number of lamellar divisions, from the first to the last; and, as the rate of increase in both respects is nearly identical in both jaws, I shall describe them chiefly as they appear in the lower one.

The *first molar* which cuts the gum in the course of the second week after birth, has a sub-compressed crown, nine lines in antero-posterior diameter, divided by three transverse clefts into four plates, the third being the broadest and the tooth here measuring six lines across(2): the first and second plates have two mammilloid summits; the third and fourth have three or four such; there is a single, and sometimes a double mammilloid summit, at the fore and back part of the crown: the base slightly contracts, and forms a neck as long as the enamelled crown, but of less breadth, and this divides into an anterior and posterior, long, sub-cylindrical, diverging, but mutually incurved fangs: the total length of this tooth is one inch and a half. The corresponding upper molar (Pl. 148, fig. 1 & 2),

(1) In the fossil specimen, figured in Pl. 147, the left molar fig. 2, *l*, exhibits all the above described gradations of use; but the right molar *r*, through some accident to the opposing tooth in the lower jaw, has not been so worn, but projects beyond the level of the left molar, with the mammillated margins of the plates entire.

(2) These are also the dimensions of the first lower molar figured by Mr. Corse, loc. cit., Pl. VI, fig. 1, D, and fig. 3; but I have seen the first lower molar of smaller dimensions.

which Mr. Corse describes as cutting the gum a little earlier than the lower one, has the anterior single digital process or mammilla, and the posterior talon developed into a fifth plate smaller than the fourth with which its middle part is confluent: the neck of this tooth is shorter, and the two fangs are shorter, larger, and more compressed than those of the lower first molar.(1) This tooth is the analogue of the first deciduous molar in other Ungulates: it is not a mere miniature of the great molars of the mature animal, but retains, agreeably with the period of life at which it is developed, a character much more nearly approaching that of the ordinary Pachydermal molar, manifesting the adherence to the more general type by the minor complexity of the crown, and by the form and relative size of the fangs. In the transverse divisions of the crown is indicated the affinity to the Tapiroid type, the different links connecting which with the typical Elephants are supplied by the extinct Lophiodons, Dinotheriums, and Mastodons. The sub-division of the summits of the primary plates recalls the character of the molars, especially the smaller ones, of the Phacochere in the Hog-tribe. As the Elephant advances in age the molars rapidly acquire their more special and complex character.

The *first molar* is completely in place and in full use at three months, and is shed when the Elephant is about two years old.

The sudden increase and rapid development of the *second molar*, (Pl. 146, fig. 3, *m* 2), may account for the non-existence of any vertical successor or 'premolar', in the Elephant. The eight or nine plates of the crown are formed in the closed alveolus, behind the first molar by the time this cuts the gum, and they are united with the body of the tooth, and most of them in use, when the first molar is shed. The average length of the second molar is two inches and a half; ranging from two inches to two inches and nine lines. The greatest breadth, which is behind the middle of the tooth, is from

(1) This molar is represented, one third the natural size, by M. de Blainville in his 'Ostéographie des Eléphans,' Pl. VII, as being divided into four plates, with anterior or posterior tubercles.

one inch to one inch three lines. There are two roots, the cavity of the small anterior one expands in the crown, and is continued into that of the three anterior plates. The thicker root supports the rest of the tooth. The second molar is worn out and shed, before the beginning of the sixth year.

The *third molar* has the crown divided into from eleven to thirteen plates; it averages four inches in length, and two inches in breadth, and has a small anterior, and a very large posterior root; it begins to appear above the gum about the end of the second year, is in its most complete state and extensive use during the fifth year, and is worn out and shed in the ninth year. The last remnant of the third molar is shown at *m* 3, fig. 1. It is probable that the three preceding teeth are analogous to the true deciduous molars of ordinary Pachyderms.

The *fourth molar* presents, as M. de Blainville well observes, a marked superiority of size over the third, and a somewhat different form: the anterior angle is more obliquely abraded, giving a pentagonal figure to the tooth in the upper jaw (ib. fig. 1 *m* 4). The number of plates in the crown of this tooth is fifteen or sixteen: its length between seven and eight inches; its breadth three inches. It has an anterior simple and slender root supporting the first three plates; a second of larger size and bifid, supporting the next four plates; and a large contracting base for the remainder. The fore part of the grinding surface of this tooth begins to protrude through the gum at the sixth year: the tooth is worn away and its last remnant shed about the twentieth or twenty-fifth year. It may be regarded as the analogue of the first true molar of ordinary Pachyderms.

The *fifth molar* with a crown of from seventeen to twenty plates, measures between nine and ten inches in length and about three inches and a half in breadth. The second root is more distinctly separated from the first simple root than from the large mass behind. It begins to appear above the gum about the twentieth year: its duration has not been ascertained by observation; but it probably is not shed before the sixtieth year.

The *sixth molar*, which from the analogy of the Mammoth(1), I regard, with M. de Blainville, as the last, has from twenty-two to twenty-seven plates; its length or antero-posterior extent, following the curvature, is from twelve to fifteen inches: the breadth of the grinding surface rarely exceeds three inches and a half.

The reproductive power of the matrix in some cases surpasses that of the formative development of the cavity for lodging the tooth and the last lamellæ are obliged to be folded from behind forwards upon the side of the tooth. I have described and figured this condition in the last lower molar of the Mammoth in my 'History of British Fossil Mammalia.'(2) M. de Blainville has represented the same structure of the last molar tooth of both the upper and lower jaw of the *Elephas indicus*, in the Fasciculus of the 'Ostéographie des Eléphans.'

One may reasonably conjecture that the sixth molar, if it make its appearance about the fiftieth year, would, from its superior depth and length, continue to do the work of mastication until the ponderous Pachyderm had past the century of its existence.

Mr. Corse has figured the sixth molar (which he calls the seventh or eighth) with twenty-three plates, in tab. x of his Memoir, and a small cavity c is marked as an incipient alveolus for a succeeding grinder. Had it actually been such it might have been expected to contain some calcified portions of the anterior plates of such succeeding grinder. If, however, better evidence should subsequently establish the existence of a seventh grinder, it will at the same time add to the probability of the longevity ascribed by the ancients to the Elephant.

(1) I was not able to trace the series of molars of the upper jaw of this extinct Elephant, out of several hundreds which I have compared, beyond the sixth, 'with twenty-two coronal plates, and an antero-posterior extent of fifteen inches.' See 'British Fossil Mammalia, Part V, 2nd September, 1844, p. 225. The number of molars successively developed in the Indian Elephant is stated at seven or eight, on the authority of Mr. Corse; but I fully participate in M. de Blainville's doubts as to the adequacy of the grounds for such a conclusion.—See the 'Ostéographie des Eléphans,' 4to. My earliest knowledge of this valuable Part of M. de Blainville's great Work was from a copy transmitted by the Author, which I received from the hands of Professor Matteucci at the Meeting of the British Association at York, September 30th, 1844: it bears no date of issue.

(2) Part v, fig. 90, p. 233

The phenomena of the course and changes of the dentition of the extinct *Elephas primigenius* are closely analogous to those of the existing species of India. The first small molar having the same comparatively simple, four-plated, crown, with two long fangs,(1) was interpreted as evidence of a new genus of Pachyderms, when first discovered in a mutilated state.(2) The second molar, eight-plated, is three inches in length and one inch and a half in breadth :(3) and already indicates the specific difference of the *Elephas primigenius*, in the superior breadth of the molars. The third upper molar has from twelve to fourteen plates, measures three inches and a half in length, and one inch two-thirds in breadth. The fourth molar is subject to more variety, and presents, as in the existing Elephant, a sudden increase of size, but seems to have been subject to a greater range of variation in regard to the number and proportions of its coronal lamellæ : these I have estimated at from twelve to sixteen ; the greater number being usually in the lower molar ; its length at from six and a half to nine inches, and its breadth at three and a half inches in the upper and three inches in the lower jaw. The fifth molar, with an antero-posterior diameter of from eight to eleven inches, has from sixteen to twenty-four plates.(4)

The largest upper molar of the Mammoth which I have yet seen, measured fifteen inches in length and had twenty-two coronal plates : it was discovered in the drift at Wellsborne in Warwickshire. Mammoths' molars of less dimensions have had the crown divided into twenty-five and twenty-six transverse plates.

The largest lower molar of a Mammoth that has come under my observation, is the one figured in Pl. 148, fig. 5, its length,

(1) Hist. of British Fossil Mammalia, Part. V, p. 223.

(2) Kaup, Akten der Urwelt, 8vo. 1841, p. 11, tab. iv, *Cymatotherium antiquum*. M. de Blainville hints a suspicion of its true nature, loc. cit. p. 190. The Mammoth's molar from the drift at Fouvent, figured by Cuvier in the 'Ossemens Fossiles,' vol. i. pl. vi. fig. 2, as "une vraie molaire de lait," is a much worn and naturally shed second molar : the figure is half the natural size.

(3) Hist. Brit. Foss. Mam. p. 224. fig. 87.

(4) See the fifth upper molar of a Mammoth, with twenty-four plates in 'Hist. Brit. Foss. Mamm.' p. 336. figs. 91 & 92.

or antero-posterior diameter, following the curve on the convex side is one foot seven inches: the number of the lamelliform divisions of the crown is twenty-eight: this remarkably fine molar exhibits the most complete state in which the actions of mastication permit so large a grinder to be seen: the anterior portion of the crown having been worn down to the common base of dentine, from which the fang is continued, and the digital divisions, which form, by their basal confluence, the last or hindmost plates, are calcified. These terminal portions of the last molar, always in the Proboscidians the most subject to variation, manifest the same anomalous position which has been noticed in the corresponding tooth of the Asiatic Elephant, and are folded upwards and laterally upon the concave part of the tooth; the sides of the digitated plates being parallel with the grinding surface of the tooth.

The above generalisations have been derived from a comparison of some hundreds of the molar teeth of the *Elephas primigenius*, which have been disinterred from the superficial deposits of this Island, and are published with further details and observations on the varieties of race, age, and sex, in my 'History of British Fossil Mammalia.' They prove that the development, progressive complication, and succession of the molar teeth, obeyed the same laws in the ancient Mammoth, as in the existing Elephant; it may, indeed, be affirmed that these most remarkable phenomena in the comparative anatomy and physiology of teeth, are more fully and perfectly illustrated by the fossils which the primigenial Elephants have left in the superficial deposits of England, than by any collection of the molars of the Indian or African Elephants now existing in our metropolitan museums. John Hunter owed most of his illustrations of the succession and shedding of the teeth in the Elephant, to the fossil molars of the Mammoth, which, with similar remains, he had been silently collecting at a time when they attracted little, if any attention.

Cuvier first pointed out that the molars of the fossil Elephant were broader than those of the existing species, and that the

transverse plates were thinner and more numerous; they are also deeper, and more subdivided into digitated summits: and we may infer from the resulting increase of the dense enamel which enters into the formation of the broad grinding surface, that the extinct species had to subsist on a coarser and more ligneous vegetable diet, in conformity with the colder regions of the ancient world in which its peculiar warm clothing of wool and hair adapted it to exist.

The phenomena of the course and changes of the dentition of the *Elephas Africanus* have a close analogy with those of the preceding species with more complex teeth. The first molar has a four-ridged crown, with two long diverging fangs; the specific characters are least manifested in this early-developed tooth: they become more marked in the subsequent molars. The second has seven plates, five of normal size and already manifesting the characteristic median expansion; the first and last plates are much smaller: the length of this tooth is two inches and a quarter. The third molar manifests an increase in the size and thickness of the coronal plates, and of the width of their cement-filled interspaces, but not any in the number of the divisions; the first, however, presents more of the normal proportions. The fourth molar manifests a marked increase of size and especially of breadth, but its crown is not divided into more than seven plates. The fifth molar, (Pl. 148, fig. 4) which is about seven inches in length, has eight or nine coronal plates. The sixth molar, eight or nine inches in length has from ten to twelve plates in the lower jaw.

The molar teeth in all the species of Elephant succeed each other from behind forwards, moving, not in a right line, but in the arc of a circle (Pl. 146, fig. 1): the position of the growing tooth in the closed alveolus (*m* 5) is almost at right angles with that of the molar in use, the grinding surface being at first directed backwards in the upper jaw, and forwards in the lower jaw, and brought by the revolving course into a horizontal line in both jaws, so that they oppose each other, when developed for use. The imaginary pivot on which the grinders turn is next their root in the upper jaw, and is next the grinding surface in the lower jaw; in both towards the

frontal region of the skull: viewing the upper and lower molars as one complex whole, subject to the same revolving movement, the section dividing such whole into upper and lower portions runs parallel to the curve described by that movement, the upper being the central portion or that nearest the pivot, the lower the peripheral portion: the grinding surface of the upper molars is consequently convex from behind forwards, and that of the lower molars concave: the upper molars are always broader than the lower ones. The bony plate (ib. fig. 2, *a*) forming the sockets of the growing teeth is more than usually distinct from the body of the maxillary, and participates in this revolving course, advancing forwards with the teeth. The partition between the tooth in use and its successor is perforated near the middle; and in its progress forwards that part next the grinding surface is first absorbed; the rest disappearing with the absorption of the roots of the preceding grinder.

There are few examples of organs that manifest more strikingly the adaptation of a highly complex and beautiful structure to the exigencies of the animal endowed with it, than the grinding teeth of the Elephant. We perceive, for example, that the jaw is not encumbered with the whole weight of the massive tooth at once, but that it is formed by degrees as it is required; the subdivision of the crown into a number of successive plates, and of these into subcylindrical processes, presenting the conditions most favourable to progressive formation. But a more important advantage is gained by this subdivision of the tooth: each part is formed like a perfect simple tooth, having a body of dentine, a coat of enamel, and an outer investment of cement: a single digital process may be compared to the simple canine of a Carnivore; a transverse row of these, therefore, when the work of mastication has commenced, presents, by virtue of the different densities of their constituent substances, a series of cylindrical ridges of enamel, with as many depressions of dentine, and deeper external valleys of cement: the more advanced and more abraded part of the crown is traversed by the transverse ridges of the enamel inclosing the depressed tracts of the dentine, and separated by the

deeper channels of the cement: the fore-part of the tooth exhibits its least efficient condition for mastication; the inequalities of the grinding surface being reduced in proportion as the enamel and cement which invested the dentinal plates have been worn away. This part of the tooth is, however, still fitted for the first coarse crushing of the branches of a tree: the transverse enamel ridges of the succeeding part of the tooth divide the vegetable food into smaller fragments, and the posterior islands and tubercles of enamel pound it to the pulp fit for deglutition. The structure and progressive development of the tooth not only give to the Elephant's grinder the advantage of the uneven surface which adapts the millstone for its office, but, at the same time, secure the constant presence of the most efficient arrangement for the finer comminution of the food, at the part of the mouth which is nearest the fauces.

230. *Microscopic Structure.*—The peculiar condition of the dentinal tubes in the tusks of the Elephant, upon which the texture of ivory depends, has been well described by Retzius; it consists in the minute size of the tubes, which at their origin from the pulp-cavity do not exceed $\frac{1}{15000}$th of an inch in diameter, in their close arrangement at intervals scarcely exceeding the breadth of a single tube, and above all on their strong and almost angular gyrations, which are so considerable that Retzius does not recognize them as analogous to the secondary curvatures in the dentinal tubes of ordinary teeth. (Pl. 149).

The dentinal tubes of ivory, as they radiate from the pulp-cavity, incline obliquely towards the pointed end of the tusk, and describe two slight primary curves, the first convex towards that end, the second and shorter one concave: these curves in narrow sections from near the open base of the tusk are almost obscured by the strong angular parallel secondary gyrations. The tubes divide dichotomously, at acute angles, and gradually decrease in size as they approach the periphery of the ivory, where they sub-divide, send off many minute branches, and terminate in a thin layer of the basal substance of a yellowish colour by transmitted light, which divides the ivory from the cement. In sections from

the extremity of the tusk, the ivory itself presents a modification of the exterior layer which is analogous to cement.

The characteristic appearance of decussating curved striæ, with oblique rhomboidal spaces, so conspicuous on transverse sections or fractures of ivory, is due to the refraction of light caused by the parallel secondary gyrations of the tubes above described. The strong contour lines observed in longitudinal sections of ivory, parallel with the cone of the pulp-cavity, and which are circular and concentric when viewed in transverse slices of the tusk, are commonly caused by strata of extremely minute opake cellules, which are unusually numerous in the interspaces of the tubes throughout the substance of the ivory, and, by their very great abundance and larger size in the peripheral layers of the ivory at the extremity of large tusks give them the character of cement. The close-set lateral branches of the calcigerous tubes unite with the tubuli of these minute cells. The decomposition of the fossil tusks into superimposed conical layers takes place along the strata of the opake cellules, and directly across the course of the calcigerous gyrating tubes.

The radiated cells of the true cement are larger and more uniform in size and shape; many of them approach nearer the circular figure, than in ordinary teeth; the long axis of the more elliptical ones is parallel with the plane of the stratum of cement: their average diameter is $\frac{1}{2500}$th of an inch, and their interspaces sometimes do not exceed that dimension. The cemental tubuli appear from their course, and sometimes from the overlapping of the substances in the sections examined, to be directly continued from the tubuli of the ivory; but Retzius expressly denies the continuation, and states that the cemental tubes at both the outer and the inner surface of the cement have terminations of less diameter than their middle part. This is exact with respect to the major part of the cement. In that near the base of the tusk I have seen a few vascular canals. The contour lines of the cement are usually wavy, and not parallel with the line of the outer surface of the ivory.

In the tusks of the *Mastodon giganteus* the outer layer of

cement is relatively thicker than in the tusks of the Mammoth or Indian Elephant, and in the section from the worn end of a Mastodon's tusk, of which a magnified view is given in Plate 103, figure 1, the minute terminations of the calcigerous tubes of the ivory are seen to be directly continued into the system of fine parallel tubes of the cement. The minuteness of the tubes of the ivory is illustrated by contrast with those of the tooth of the small Marsupial quadruped figured in the same plate. Some of the forms of the radiated cells which are so thickly distributed through the cement of the Mastodon's tusk are shown at *c*. The irregular disposition of the calcareous salts of these cells give them the appearance of being subdivided, like the granular cell-nuclei of which they are the remains: but their cavity, though irregular, is single, and has generally been filled by the crystalline matter of the fluids percolating the stratum in which such tusks have become fossilized. The general character of the microscopic structure of the ivory of the Mastodon's tusk is the same as that of the Elephant. The peripheral extremities of the dentinal tubes are, in some parts of the tusk, straighter than in the rest of their course; the straighter extremities were those which were first formed in the calcification of the peripheral part of the pulp, and this first-formed ivory is accordingly, in such parts, more like the ordinary dentine, and is analogous to the thin peripheral cap of such substance in the teeth of the Sloth and of some Fishes. The pulp soon, however, becomes subject to that modification of the calcifying processes by which the more tortuous disposition of the tubuli and the more frequent interposition of opake cellules are produced; modifications which, in establishing the characters of ivory, present a step in the transition from true dentine to osteo-dentine.

By the minuteness and close arrangement of the tubes, and especially by their strongly undulating secondary curves, a tougher and more elastic tissue is produced than results from their disposition in ordinary dentine; and the modification which distinguishes 'ivory' is doubtless essential to the due degree of coherence of so large a mass as the Elephant's tusk, projecting so far from the

supporting socket, and destined to be frequently applied in dealing blows and thrusts.

The central part of the tusk, especially near the base of such as have reached their full size, is occupied by a slender cylindrical tract of modified ivory, perforated by a few vascular canals, which is continued to the apex of the tusk. It is not uncommon to find processes of osteo-dentine, or imperfect bone-like ivory, projecting in a stalactitic form(1) into the interior of the pulp-cavity, apparently the consequence of partial inflammation or malformation of the vascular pulp. The musket-balls and other foreign bodies which are occasionally found in ivory, are immediately surrounded by osteo-dentine in greater or less quantity. It has long ceased to be a matter of wonder how such bodies should become completely imbedded in the substance of the tusk, sometimes without any visible aperture, or how a leaden bullet may have become lodged in the solid centre of a very large tusk without having been flattened. Such a ball, aimed at the head of an Elephant, may penetrate the thin bony socket and the thinner ivory parieties of the wide conical pulp-cavity occupying the inserted base of the tusk; if the projectile force be then spent the ball gravitates to the opposite and lower side of the pulp-cavity, as is indicated in Pl. 146, fig. 1.(2) The presence of the foreign body exciting inflammation of the pulp, an irregular course of calcification ensues, which results in the deposition around the ball of a certain thickness of osteo-dentine. The pulp then resuming its healthy state and functions, coats the surface of the inclosing mass of osteo-dentine, together with the rest of the conical cavity into which that mass projects, with layers of normal ivory.(3) The ivory,

(1) Haller seems to have been the first to notice these irregular internal deposits in the pulp-cavity of the Elephant's tusk. 'Elementa Physiologiæ, tom. viii, p. 519.

(2) Camper, 'Description Anatomique d'un Eléphant Male' fol. p. 54. Cuvier, 'Annales du Muséum, tom. viii, 1806, p. 115.

(3) Cuvier, 'Annales du Muséum,' tom. viii. p. 115, 1806. "Sur les défenses des Eléphans, la structure, l'accroissement les caractères distinctifs de l'ivoire et sur les maladies," first clearly stated that the ball or foreign body in the tusk of the Elephant was immediately surrounded by a substance different from the regular ivory. The great Anatomist observes, "Toute la portion d'ivoire en dehors de la balle est semblable au reste; il n'y a que ce qui l'entoure immédiatement qui soit irrégulier." Mr. Goodsir has confirmed this statement by

as it approaches the osteo-dentine, becomes modified by the presence of vascular canals, and assumes the character of vaso-dentine; and the canals frequently form loops directed towards the osteo-dentine. In this substance the medullary canals diverge, leaving clear interspaces into which numerous irregular branches proceed from the canals, partially uniting to form a net-work, and finally breaking up into distinct cells, of larger size than the purkingian cells of the external cement. In the small detached fusiform nodules of osteo-dentine, one or more vascular canals are present with concentric coats of the clear basal substance, studded by purkingian cells of the size of those in the cement, but with richer radiating systems of tortuous calcigerous tubes. Some of the larger-sized cells are likewise frequently here present. From both the medullary canals, their sub-divisions and the cells, minute calcigerous tubes diverge,

numerous interesting examples given in his Memoir in the 'Edinburgh Philosophical Transactions for 1841, where he states "One circumstance was at once detected in all these specimens, and its importance was evident, as affording a clue to the explanation of the mode of inclosure. The circumstance to which I allude is, that in none of the specimens are the bullets of foreign bodies surrounded by regular ivory. They are in every instance inclosed in masses, more or less bulky, of a substance which, although abnormal in the tusk of the Elephant is nevertheless well known to the Comparative Anatomist, as occupying the interior of the teeth of some of the other Mammals, and usually considered to be the ossified pulp." p. 93. Mr. Goodsir cites (p. 97) a paper read by his countryman Dr. Knox to the Royal Society of Edinburgh, five years before the date of his own Memoir (January 1841) in which the osteo-dentine (tissue like puddingstone of Cuvier) which fills the pulp-cavities of the tusks of the Walrus and the teeth of the Cetacea, was "first announced as a distinct species of dental tissue." I have not found any distinctive characters, microscopic or otherwise, of such tissue, pointed out in the publications of the Society referred to by Mr. Goodsir. The first clear definition of substances entering into the composition of teeth and presenting microscopic characters equally distinct from ivory, enamel and cement, and from true bone, is that which I communicated to the British Association in 1838. (See the Volume of Reports, 1838, p. 137). Of the two kinds there defined, "The first, or 'vaso-dentine', characterized by being traversed throughout by numerous coarse canals, filled with a highly vascular medulla or pulp," but 'differing from true osseous substance, and from the cœmentum in the absence of the purkingian corpuscles,' (loc. cit. p. 137), is not abnormal in the Elephant's tusk, but is a constant constituent of its central part; this fact I demonstrated by microscopic sections exhibited in my Hunterian Lectures on the Comparative Anatomy of the Digestive System, in the Theatre of the College of Surgeons in 1838, and at the same time showed the identity of the irregular ivory of Cuvier which surrounds the foreign bodies, with "the second distinct component substance of tooth, which more closely resembles true bone and cement, inasmuch as the purkingian cells are abundantly scattered through it," loc. cit.

with wider intervals and a more wavy and irregular course than the normal tubes of the ivory.

The portion of the cement-forming capsule surrounding the base of the tusk, and the part of the pulp, which were perforated by the ball in its passage, are soon replaced by the active reparative power of these highly vascular bodies. The hole formed by the ball in the base of the tusk is then more or less completely filled up by a thick coat of cement from without and of osteo-dentine from within. Traces of such a cicatrix closing the entrance have been more than once noticed: and Blumenbach deduced, therefrom, a property in the Elephant's tusk to pour out bony matter in order to heal such wounds. The reparation is, however, effected by the calcification of the reproduced parts of the capsule and pulp.

By the continued progress of growth, the ball so inclosed is carried forwards, in the course indicated by the arrow in Pl. 146, fig. 1, to the middle of the solidified exserted part of the tusk, as in the example in Blumenbach's collection which he considered so curious. Should the ball have penetrated the base of the tusk of a young Elephant it may be carried forwards by the uninterrupted growth of the tusk until that base has become the apex, and be finally exposed and discharged by the continual abrasion to which the apex of the tusk is subjected. Yet none of these phenomena prove the absolute non-vascularity of the tusk, but only the low degree of its vascularity. Blood circulates, slowly no doubt, through the minute vascular canals which are continued through the centre of the ivory to the very apex of the tusk: and it is from this source that the fine tubular structure of the ivory obtains the essential plasmatic colourless fluid by which its low vitality is maintained.

In order to obtain a complete and connected view of the microscopic structure of the molar teeth of the Elephant, I made vertical and transverse sections of the first molar, which, from its small size permits the entire course of the dentinal tubes to be traced.

The tooth examined was from the lower jaw, and was completely formed; the two fangs being of their full length. The pulp-

cavity was divided at its upper part into two conical prolongations, one for each of the principal lobes of the crown. A few vascular canals were continued from the apex of each cone into the two sub-divisions or plates of each lobe.

The dentinal tubes which radiate from the pulp-cavity and its prolongations, are as remarkable as those of the tusk for their minuteness and closeness of arrangement; but, in the tooth examined, they presented at only a few points secondary undulations approaching in extent to those which characterise the tubes of ivory. A few tubes from the end of the vascular canal in the centre of the cone of dentine go straight to the summit of that cone; the rest diverge from the vascular canals and apex of the pulp-cavity to the sides of the cone of dentine, with one general primary curve, whose convexity is turned towards the centre and summit of the cone, the terminations of the tubes being slightly bent in the opposite direction: in the roots the dentinal tubes pass, as usual, almost transversely.

The places where the tubuli exhibited the strong secondary undulations were along a contour line at the middle of the dentine. At their commencement the tubuli are straight, they then fall into slight waves, and after forming three or four stronger ones at the middle of their course, again resume the more feeble and irregular undulations: their close arrangement renders it difficult to distinguish bifurcation from decussation; yet in some parts I had clear evidence of division of the main tubes, which left little doubt that the usual dichotomy prevailed, to produce the same dense arrangement of tubuli at the broad peripheral as at the narrower central part from which the tubes diverge.

The number of minute lateral branches is extreme; especially in the peripheral third part of the tube. Those from near the usually bifurcated terminations of the tubes are lost in the stratum of minute opake cellules near the outer surface of the dentine. Many of the terminal bifurcations of the tubuli here bend back, and form loops by anastomosing with adjoining branches.

The fibres of the enamel present a minutely jagged, or crenate outline, but are not crossed, by transverse lines. Their

diameter is $\frac{1}{3000}$th of an inch: they are much less wavy than in the human teeth. The enamel fibres cross the plane of the layer on a less transverse direction than that of the ends of the tubes of the dentine directed towards the enamel: the outer surface to which the cement is attached, shows more pits and irregularities than that attached to the dentine.

A well-defined layer of cement covers the bottom of the crown at the interspaces of the two fangs, and extends over these to their extremity. The sub-circular or full-elliptic radiated cells are closely arranged, with their long axes parallel with the surface of the cement; numerous minute cemental tubuli run parallel to that surface, and communicate with the radiated tubes of the cells and with the terminal ramifications of the dentinal tubuli. The larger vascular canals are present only in the thicker deposit of cement at the bottom of the interspaces of the coronal plates.

Dr. Falconer having kindly permitted me to take a longitudinal section from a rare specimen of the first upper molar of the *Elephas planifrons*, one of the extinct species whose remains he has discovered in the Himalayan tertiary beds, I am able to give the following comparison of the microscopic structure of this tooth, and that of the nearly allied existing Indian Elephant.

The dentinal tubuli are as minute and as closely aggregated; they have the same general direction and primary curve; in parts of the dentine, as at the summits of the conical sections of the lamellar divisions of the crown, their secondary undulations are as minute and irregular; but the number of the strong undulations along the contour lines at the middle of the dentinal cone is greater. The strongest contour lines are accompanied by the strong undulations, but there are many other lines which appear to be formed by a slight opacity of the basal substance as in the Rhinoceros.

The stratum of opake cellules near the peripheral ends of the tubes is thicker; the terminal bifurcations and occasional anastomotic loops are the same as in the Indian Elephant. The enamel is thicker, and the component fibres are more flexuous in the *El. planifrons*, but in their size and other characters they agree with those of the recent species. The cells of the cement which covers the crown and

fills part of the interspaces of the coronal plates are sub-circular, with often a slightly angular outline; they are densely aggregated. There are no vascular canals in the thinner layer of cement which covers the fang, but these are always present in the thicker cement of the crown.

In portions of larger molars of the Indian Elephant which I have examined, the dentinal tubes have the same minuteness and close arrangement, and the same general primary curve, as in the small first molar; but the extent to which they manifest the strong undulations characteristic of ivory is greater(1). In old molars the pulp-cavity becomes in part obliterated by the modified ivory called osteo-dentine, and the tubes in the dentine of the roots describe numerous considerable undulations. The enamel does not extend upon the roots but terminates, as in other teeth, at the base of the crown; the cement is continued in a thin layer to the end of the roots (Pl. 150, fig. 2, *c c*), and there becomes continuous with the osteo-dentine which fills the central part of the pulp-cavity. The disposition of the calcigerous tubes in a longitudinal section of one of the fangs, with the central osteo-dentine, and the peripheral cement is shown in Pl. 150. The dentinal tubes come off from the clear part of the osteo-dentine by fasciculi, in certain parts of the pulp-tract; they are minutely and irregularly undulated throughout the course of the stronger undulations which here assume the character of primary curvatures. The terminations of the tubes at the semi-opake peripheral tract, along which the minute opake cellules are dispersed, seem to dilate slightly, and to be less sharply defined (ib. fig. 1, d^{11}.) Many of the terminal branches of these tubes pass into the cement, and anastomose with the fine tubes of that tissue; the cemental tubes are largest at its peripheral part (ib. c^{11}).

231. *Development.*—The matrix of the tusk consists of a large conical pulp, which is renewed quicker than it is calcified, and thus is not only preserved, but grows, up to a certain period of the animal's life: it is lodged in the cavity at the base of the tusk; this base is surrounded by the remains of the capsule, a soft

(1) These undulations produce on the fractured surfaces of the dentine of the molars in which they occur, the engine-turned character of true ivory.

vascular membrane of moderate thickness, which is confluent with the border of the base of the pulp, where it receives its principal vessels.

The account which Cuvier(1) has given of the formation of the complex molars of the Elephant is remarkably clear and comprehensive, but is vitiated by the terms of the 'excretion-theory' in which the different processes are explained: it is otherwise so minute and accurate that it needs little more than the substitution of the language of the 'conversion-theory' to convey all the requisite knowledge of the process.

Each molar of the Elephant is formed in the interior of a membranous sac—the capsule, the form of which partakes of that of the future tooth, being cubical in the first molar, oblong in the last, and rhomboidal in most of the intermediate teeth; but always decreasing in vertical extent towards its posterior end, and closed at all points, save where it is penetrated by vessels and nerves. It is lodged in an osseous chamber of the same form as itself, and usually in part suspended freely (as at *a*, fig. 2, Pl. 146) in a large cavity excavated in the maxillary bone; the bony case being destined to form part of the socket of the tooth. The exterior of the membranous capsule is simple and vascular, as shown at *m* 5, fig. 1, Pl. 146; its internal surface gives attachment to numerous folds or processes, as in most other Ungulate animals.

The dentinal pulp rises from the bottom of the capsule, or that part which lines the deepest part of the alveolus, in the form of transverse parallel plates extending towards that part of the capsule ready to escape from the socket. These plates adhere only to the bottom of the capsule; their opposite extremity or summit is free from all adhesion. This summit is thinner than the base; it might be termed the edge of the plate, but it is notched, or divided into many digital processes. The tissue of these digitated plates is identical with that of the dentinal pulp of simple Mammalian teeth; it becomes also highly vascular at the parts where the formation of the dentine is in active progress.

(1) 'Annales du Muséum,' tom. VIII, (1806) p. 94. The account is repeated verbatim in the posthumous edition of the 'Ossemens Fossiles,' 1834.

Processes of the capsule descend from its summit into the interspaces of the dentinal pulp-plates, and consequently resemble them in form; but they adhere not only by their base to the surface of the capsule next the mouth, but also by their lateral margins to the sides of the capsule, and thus resemble partition-walls, confining each plate of the dentinal pulp to its proper chamber; the margin of the partition opposite its attached base is free in the interspace of the origins of the dentinal pulp-plates. The enamel-pulp, which Cuvier appears to have recognized under the name of the internal layer of the capsule, is distinguishable by its light blue sub-transparent colour and usual miscroscopic texture, adhering to the free surface of the partitions formed by the true inner layer of the capsule. Although the enamel-pulp be in close contact with the dentinal pulp prior to the commencement of the formation of the tooth, one may readily conceive a vacuity between them, which is continued uninterruptedly, in many foldings, between all the gelatinous plates of the dentinal pulp, and the partitions formed by the combined enamel-pulp and the folds of the capsule. According to the excretion-hypothesis this delicate apparatus must have been subjected to compression in the unyielding bony box by the deposition of the dense matters of the tooth in the hypothetical vacuity between the enamel and dentinal pulps; a process of absorption must have been conceived to be set on foot immediately upon such altered condition of the gelatinous secreting organs; and the secreting function must be supposed to have proceeded, without any irregularity or interruption, while the process of absorption was superinduced in the same part to relieve it from the effects of pressure produced by its own secretion.

The formation of the dentine commences immediately beneath the *membrana propria* of the pulp: a part which Cuvier distinctly recognised, and which he accurately traced as preserving its relative situation between the dentine and enamel, throughout the whole formation of the dentine, and discernible in the completed tooth 'as a very fine greyish line, which separates the enamel from the internal substance' or dentine.

The calcification and conversion of the cells of the dentinal pulp

commence as usual at the peripheral parts of the lamelliform processes furthest from the attached base. It may readily be conceived, therefore, that, at the commencement, there is formed a little cap upon each of the processes into which the edges of the pulp-plates are divided. As the centripetal calcification proceeds the caps are converted into horn-shaped cones (Pl. 146, fig. 4); when it has reached the bottom of the notches of the edge of the pulp-plate all the cones become united together into a single transverse plate (ib. 5); and, the process of conversion having reached the base of the pulp-plate, these plates coalesce to form a common base to the crown of the tooth, which would then present the same eminences and notches that characterized the gelatinous pulp, if, during the period of conversion, other substances had not been formed upon the surface and in the interspaces of the pulp-plates.

Coincident, however, with the formation of the dentine, is the deposition of the hardening salts of the enamel in the extremely slender prismatic cells, which are for the most part vertical to the plane of the inner surface of the folds of the capsule to which they are attached; these cells or moulds give a sub-transparent bluish tint to the enamel-pulp, which Cuvier distinguishes as the internal layer of the capsule. The true inner part of the capsule forms those thick transverse folds or partitions which support the enamel-organ, and with it fill the interspaces of the dentinal pulps. With regard to the formation of the cement, Cuvier, after citing the opinion of Tenon—that it was the result of ossification of the internal layer of the capsule, and that of Blake—that it was a deposition from the opposite surface of the capsule to that which had deposited the enamel, states his own conviction to be—that the cement is produced by the same layer and by the same surface as that which has produced the enamel. The proof alleged is, that so long as any space remains between the cement and the external capsule, that space is found to contain a soft internal layer of the capsule with a free surface next the cement. The phenomena could not, in fact, be otherwise explained according to the excretion-theory of dental development. To the obvious objection that the same part is made, by this explanation, to secrete two different products, Cuvier replies,

that it undergoes a change of tissue: "Whilst it yielded enamel only it was thin and transparent, to give cement it becomes thick, spongy, and of a reddish colour."(1) The obvious characters of the enamel organ and cement-forming capsule, are here correctly defined; but the one instead of being converted into the other, is, in fact, changed into its supposed transudation: the enamel fibres being formed, and properly disposed in the direction in which their chief strength is to lie, by the assimilative properties of the pre-arranged elongated prismatic non-nucleated cells of the enamel pulp, which take from the surrounding plasma the required salts and compact them in their interior.

Whilst this process is on foot, and before the enamel-fibres are firm in their position, the capsule begins to undergo that change which results in the formation of the thick cement: the calcifying process commences from several points, and proceeds centrifugally, radiating therefrom, and differing from the ossification of bone chiefly in the number of these centres, which, though close to the new-formed enamel, are actually in the substance of the inner vascular surface of the capsular folds. The cells arrange themselves in concentric layers around the vessels, and act like those of the enamel pulp in receiving into their interior the bone-salts in a clear and compact state; during this process they become confluent with each other, their primitive distinctness being indicated only by their persistent granular nuclei, which now form the radiated Purkingian corpuscles. The interspaces of the concentric series of confluent cells become filled with the calcareous salts in a rather more opake state, and the conversion of the capsule into cement proceeds according to the processes more particularly described in the Introduction, until a continuous stratum is formed in close connection with the layer of enamel.

The uncalcified part of the capsule, always much softer than cartilage, is very readily detached from the calcified part, and to

(1) "Seulement elle change de tissu: tant qu'elle ne donnait que de l'émail, elle était mince et transparente; pour donner du cortical elle devient épaisse, spongieuse, opaque et rougeâtre."—Annales du Muséum, tom. VIII, p. 99. 'Ossemens Fossiles,' Ed. 1834, 8vo. tom. I, p. 514

the naked eye the separated surface seems entire, and might readily pass, as with Cuvier, for a secreting surface. The fine vascular processes which have been torn from the medullary canals of the calcified part are, however, conspicuous, and resemble villi, when the detached surface is examined, even with a moderate magnifying power, under water.

Calcification extending from the numerous centres, the different portions coalesce and progressively add to the thickness of the cement until all the interspaces of the coronal plates and the whole exterior of the crown is covered with the bone-like substance. The enamel-pulp ceases to be developed at the base of the crown; but the capsule continues to be formed, *pari passu* with the growth of the pulp, as this continues, progressively contracting, from the base of the crown, to form by its calcification the roots. The calcification of the capsule going on at the same time, a layer of cement is formed in immediate connection with the dentine. The circumscribed spaces at the bottom of the socket to which the capsule and dentinal pulp adhere, where they receive their vessels and nerves, and which are the seat of the progressive formation of these respective moulds of the two dental tissues, become gradually contracted, and subdivided by the further localization of the reproductive forces to particular spots, whence the subdivision of the base into roots. The surrounding bone undergoes corresponding modifications, growing and filling up the interspaces left by the dividing and contracting points of attachment of the residuary matrix. All is subordinated to one harmonious law of growth by vascular and cell-formations, and of modified form by absorption: mechanical squeezing and drawing out have no share in these changes of the pulp or capsule: pressure at most exercises only a healthy stimulus to the vital processes.

Cuvier believed that there were places where the dentinal pulp and the capsule were separate from each other: I have never found such except where the enamel-pulp was interposed between them in the crown of the tooth, or where both pulp and capsule adhered to the periosteum of the socket, below the crown. Cuvier affirms that the number of fangs of an Elephant's molar depends

upon the number of points at which the base of the gelatinous (dentinal) pulp is attached to the bottom of the capsule; and that the interspaces of these attachments constitute the under part of the crown or body of the tooth, the attachments themselves forming the first beginnings of the fangs. True to his hypothesis of the formation of the dental tissues by excretion he says(1) that the elongation of the fangs is produced by two circumstances: first, the progressive elongation of the layers of osseous substance (dentine) which force the tooth to rise and emerge from its socket: secondly, the thickening of the body of the tooth by the addition of successive layers to its inner surface, which, filling up the interior cavity, leaves scarcely room for the gelatinous pulp and forces it down into the interior of the roots.

This pulling up of the fang on the one hand and squeezing down of the pulp on the other, are forces too gross and mechanical to be admitted for a moment in a physiological explanation of the growth of the root of a tooth or of any other organized product; such modes of explanation were nevertheless inevitable consequences of the adoption of the excretion-theory of dental development; and their proposition by the great Anatomist recalls the analogous attempts of the great Master of Physical Science to explain some of the phenomena of polarized light in the terms of the 'emission-theory.'

But Newton, whatever difficulties of explanation his theory entailed upon him, is accurate as to the facts or phenomena: Cuvier, however, is compelled by his hypothesis to deny a matter of fact.(2) The cement (cortical), being, according to him, an excretion from the internal layer of the capsule, could only be

(1) "Ces racines et les pédicules qui leur servent de noyaux s'alongent ensuite par deux raisons: d'abord les progrès des lames de substance osseuse qui, s'alongeant toujours, forcent la dent à s'élever et à sortir de l'alvéole; ensuite l'épaississement du corps de la dent par la formation des couches successives qui, en remplissant le vide intérieur, n'y laissent presque plus de place pour le noyau gelatineux, et le refoulent vers l'intérieur des tubes des racines." Annales du Muséum, viii, 1807, p. 108, Ossem. Fossiles, 1834, p. 527.

(2) "Il ne se produit point d'émail ni de cortical sur les racines, parce que la lame interne de la capsule, qui a seule le pouvoir de sécréter ces deux substances, ne s'étend pas jusque là." loc. cit. (1807) p. 109; 1834, p. 527.

present on that part of the tooth over which such layer extended: but the enamel-pulp, which passed with Cuvier for the internal layer, unquestionably ceased to exist at the base of the crown or body of the tooth; therefore Cuvier denies that the fang has any covering of cement. That substance, nevertheless, does cover the whole exterior of the fang, though it forms a much thinner layer than upon the crown: its characteristic tissue is shown in Pl. 150, fig. 2, *c*, in a magnified section of the end of a root of an Elephant's molar, and it is often thickest at this part, where, in the Cuvierian hypothesis, it would be furthest from its formative organ, the inner layer of the capsule.

The conversion-theory of dental development as propounded and established in the present Work leads to no such difficulties: its truth is manifested in the same way as that of the undulation-theory of light and of every other right theory: viz. by its concordance with facts which are denied or misinterpreted on the wrong theory, and by its more rational explanation of all the phenomena.

THE END.

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