The figures in table 4 show that while in Denmark four-fifths of the annuals flower after the first of July, we have in the South-Russian steppe (Yekaterinoslaw) about one half, in Greece and Spain about one third, and in the Transcaspian lowlands about one fifth which are late-flowering.

In the series: Libyan desert, Transcaspian desert, Spain, South-Russian Steppe, Denmark, the number of summerannual plants thus steadily increases. And throughout the same series the summer becomes less warm and In Cairo there is no rain during 4-6 summer less drv. months and the mean temperature of July is 29° C.; in Merw 3-4 summer months are rainless, and the mean July temperature is 30,2° C., (Askhabad 29,7° C., Petro Alexandrowsk 28,7° C.; Table 1 p. 17). In Spain no month, is perfectly rainless though July and August are very dry, and the mean July temperature is, for instance, Murcia 29° C., Madrid 24.5° C. Yekaterinoslaw has as mean July temperature of 23,0° C. and the precipitation is greatest in July and smallest during winter.¹)

This leads us to the conclusion that the number of summer-annual plants is more especially dependent on the summer rainfall, as might be expected. From north towards, the south the conditions of life during summer become more and more unfavourable, so that fewer and fewer annual species are able to endure, namely only those adapted to withstand increasingly unfavourable conditions.

But the winter temperatures may also play a part in determining the relative number of annual summer-plants, since plants have a better chance of hibernating in countries with warmer winters than where the cold is severe. In this way annual summer-plants might become perennials. The statement by VOLKENS (l. c. p. 21), that facultative annual and perennial plants are characteristic for the Libyan desert, is perhaps not only correlated with the summer but also with the winter conditions.

The mean temperature at Cairo for Jan. is 11,9° C., and even if (according to HANN) a few degrees of frost are some-

¹⁾ The temperature records are cited from HANN 1897, III.

times recorded, this is nothing compared with Merw which has a mean temperature for January of -0.6° C. (Askhabad -0.2° C., Petro Alexandrowsk -5.5° , table 1) and Yekaterinoslaw which has -7.4° C., the minimum temperatures of both localities being nearly -20° C. or even less.

Spain, which as regards July-temperature takes third place, becomes second in this respect since the winter there is much warmer than in Transcaspia (Murcia $9,_{3}$ ° C., Zaragoza $5,_{2}$ ° C., Madrid $4,_{9}$ ° C. in January). The number of annual summer-plants in this case is thus in accordance with the July temperature, not that of January. This leads us to the conclusion that the January temperature may be a major factor only when it is high, while marked differences in the lower temperatures do not seem to be of any importance. The data are, however, too scanty to allow us to come to any decisive conclusion.

Table 5.

Distribution of the growth-forms of Transcaspian species amongst certain natural orders.

	Number of species	Percentage of species occurring as growth-forms					
		F	Ch.	Н	G	нн	Th.
Borraginaceae	42		4	29	10		57
Caryophyllaceae	25		36	20			44
Chenopodiaceae	94	13	11	4			72
Compositae	103	2	8	45	3		42
Cruciferae	51			10			90
Gramineae	44			25	18		57
Labiatae	20		5	55		10	- 30
Liliaceae	24			14.4	100		
Papilionaceae	85	27	10	42		- 10	21
Polygonaceae	26	80		8		4	8
Ranunculaceae	23		4	48	4	4	40
Umbelliferae	31			84			16
Tamaricaceae	18	95	5				
Zygophyllaceae	17	12		69		1	19

From table 5 it will be seen which natural orders are specially represented by annual species in the Transcaspian - 166 -

desert; as the distribution of the growth-forms of the species of larger families are here given as percentages. The orders which are especially represented by annual species are the *Cruciferae* and the *Chenopodiaceae*, the percentage of these being respectively 90 and 72. Of these the Cruciferae are all early flowering ephemerals, whereas about 82 per ct. of the annual Chenopodiaceae are summer-plants which flower after the beginning of July. A large proportion of the early flowering annual Chenopodiaceae also live far into the summer.

These two families, the *Cruciferae* and the *Chenopodiaceae* are thus typical representatives of two widely different series of adaptations to desert-life: the one shows itself in the quick development of plants of mesophytic structure during the favourable season; the other is characterised by slow development combined with the power to withstand the unfavourable conditions of the dry season. The former series include all the other families in table 5 with a large number of annual plants, e. g. *Borraginaceae*, *Gramineae* and *Ranunculaceae*. Outside the Chenopodiaceae there are very few annuai summer-plants.

That the adaptation of the ephemeral plants is advantageous is easily seen, the continuity of the race is ensured with a slight expenditure of material. Life with these plants seems a much simpler matter than in the case of the annual summer-plants which have to contend with a long hot summer before their seeds are ripened. The existence of the latter is far more expensive, because for one thing material must be produced for the development of mechanical, waterstoring, and other specialised tissues which the ephemerals do not require; moreover many of the annual summer-plants do not complete their natural span of life because they are buried by the sand, or the soil blows away, or they die of thirst.

In this connection attention is drawn to the outstanding difference between the mode of occurrence of the ephemerals and the annual summer-plants. As already described, the former often appear in masses during spring, while the latter almost always occur as single plants standing widely apart. This is of course largely due to the greater number of species of the ephemerals, but my opinion is that the number of individuals of most of the ephemeral species is much larger than that of the summer-annuals. This question ought to be more closely investigated.

Even though the adaptations of the summer-annual plants must be regarded as favourable, otherwise the plants would not be able to exist, they seem to be much less favourable than the adaptations of the ephemerals or those of the perennials. The latter remain alive year after year, capable of storing nutriment and of developing a strong root-system, while as regards propagation by seeds they have the same chance as the annual plants.

The annualness of the annual summer-plants inherent in their nature thus seems to be an unfavourable point in their adaptation to the conditions of the Transcaspian desert. That so few species of them occur there is perhaps a result of this.

Next to the Therophytes the Hemicryptophytes are the most abundant type in the Transcaspian desert. Their percentage (27) ranges between the figures from the North-African and North-American desert (19, 20, 18) and Samos (32) as shown in Table 3. They are far less numerous here than in the South-Russian steppe (Yekaterinoslaw) and Pamir.

Most of them flower early, about the month of May. After calculation, I find that only about 10 per ct. of the Hemicryptophytes flower after July 1, so that about 90 per ct. are early flowering. These figures are only approximate, as details on the flowering season of many species are lacking.

Actual numbers have less interest here than in the case of annual plants, because the latter usually die after they have produced flower and fruit, whereas perennial plants in many cases continue to be vegetative after that time. Statistics of the flowering season therefore give no information about the vegetative period of perennials.

Most Hemicryptophytes flower early and have completed flowering before the end of June. As previously stated (p. 59) many of them wither when the seeds are ripe. This is probably the case with the majority, some of them have already been referred to. They have also ephemeral shoots, mesophytic in structure and arising from perennial hypogeal parts. In other Hemicryptophytes the epigeal shoots live through the whole summer, e. g. in species of Zygophytlum, Anabasis, Statice, probably also in a few Cousinia and Astragalus; their shoots are xerophytic in structure and have this biological character in common with the annual summerplants that the shoots die when winter sets in.

No information is available on the few plants recorded as biennials, for instance *Tragopogon*. It is unlikely that the species of *Tragopogon* carry fresh leaves throughout the whole summer.

The *Chenopodiaceae* as a group are strikingly deficient in hemicryptophytes, they have only 4 per ct. The *Tamaricaceae* and the *Liliaceae* have none at all. The paucity of hemicryptophytes in the Chenopodiaceae, so many of which seem specially adapted to desert-life, may perhaps be explained in this way, that this type is not well adapted to the natural conditions prevailing during summer in the desert. Yet the correctness of this supposition may be questioned when we consider the *Zygophyllaceae*, likewise true summerplants and with 11 hemicryptophyte-species (69 per ct.).

Of the remaining orders the *Umbelliferae* in particular include a large number of hemicryptophytes all or most of which are spring-plants. (See table 5).

Next in order to the Hemicryptophytes (Table 3) follow the Fanerophytes, the trees and shrubs. These all belong to RAUNKLER'S Micro- and Nanofanerophytes.

In the Transcaspian desert there are 11 per ct. Fanerophytes, about the same proportion as in the North-African deserts (Libyan desert 12, Cyrenaica 9) and in Samos (9), but much less than in Death Valley with 23 p. ct. On the other hand, the South Russian Steppe shows only 5 per ct. and the Spanish Steppe about the same number¹). Denmark has 7, Stuttgart 9 per ct. (RAUNKLÆR).

Only 14 out of 87 Fanerophytes in the list may still be found flowering after July 1st and of these 8 are Cheno-

¹) WILLKOMM 1895 p. 280.

podiaceae. What was said of the Hemicryptophytes is still more the case here: that the early flowering species may be summer-plants; here every one is such, and not one is known to rest during the summer-periods, although some of the species of *Astragalus* may shed their leaflets.

The Transcaspian Fanerophytes occur in greatest numbers and attain their highest development in the Sand-desert. As already stated (p. 79), the Sand-desert has a rain-absorbing soil, but its capillary action is slight, hence there must be larger supply of water in the deeper layers than in the Claydeserts. This is naturally correlated with the occurrence of trees since these have long roots capable of extending down to the water; compare also p. 48.

Another factor of importance for the ground-water and therefore for the Fanerophytes, is the density of the vegetation. Wherever in dry regions there is a rich vegetation of herbs or small shrubs, these will intercept and absorb the water, so that it is not allowed to sink into the soil. Kostyrtscheff points out that forests might grow on the South-Russian steppe if the surface were loosened, so that water might penetrate the soil. Why this does not take place is, he states, because the surface of loess is impervious to water, especially when covered by plants.

Without entering into the question why the Russian steppe is treeless, it is noteworthy that Transcaspia presents better conditions for growth of trees than South-Russia; this is a result of the absorptive capacity of the soil due to its structure and to the open plant-covering, aided also by climatic conditions. Reference may be made in this connection to SCHIMPER's statement (p. 527) that the South-Russian steppe has a dry as well as a cold winter, an element hostile to the growth of trees. For when dry winds blow at the same time as the ground is frozen, the trees with their branches and buds more exposed than smaller plants, will be unable to compensate for loss by transpiration.

Somewhat similar conditions prevail on the Spanish steppes; the winter is cold, dry and windy¹). May has the greatest amount of precipitation.

¹) Climatic tables for Zaragoza and Valladolid in Meteorol. Zeitschrift 9. 1874. p. 218. In Transcaspia the conditions are just the reverse. As may be seen from table 1 (p. 17), the precipitation is greatest in winter so that the coldest season is comparatively humid. In this respect the climate to a certain degree favours the growth of trees. But as a whole it is only to a slight degree favourable! The long dry period which occurs during the vegetative period for trees necessitates the utmost economy as regards water. Therefore only the more xerophytic trees are able to live; their external and internal structure will be described below (chap. 13).

Fanerophytes occur in comparatively few of the natural orders represented in Transcaspia (Table 5). For instance in Borraginaceae, Caryophyllaceae, Cruciferae, Labiatae, Ranunculaceae and Umbelliferae they are totally absent. On the other hand, the numerous species of Tamarix and Calligonum have this effect that the Tamaricaceae and Polygonaceae consist mainly of trees and bushes. The species of Calligonum are more especially true desert-plants. Many of the fanerophytic Papilionaceae (Astragalus, Ammodendron, Eremosparton) and Chenopodiaceae (Salsola, Haloxylon), are likewise true desert plants, xerophytic in structure. On the contrary the only two fanerophytic Compositae (Artemisia procera and Zollikoferia acanthodes) are unimportant species, rarely recorded.

The 10 per ct. of Geophytes in the Transcaspian desert is a rather high figure compared with the "Normal-Spectrum", but it is in agreement with Samos and Cyrenaica (Table 3). Of the 72 geophytes, 33 (46 per ct.) are rhizomeplants, 24 (33 per ct.) are bulbous plants, 9 tuberous plants (13 per ct.), and 6 parasites (8 per ct., *Orobancheaceae*).

As far as known only 5 geophytes may be found flowering after July 1. Only one of these *Eremurus Olgae* is a bulbous plant. The others (*Tournefortia sibirica*, *Pluchea caspica*, *Cressa crelica*, *Saccharum spontaneum*) have rhizomes. The term early flowering when applied to the rhizome-geophytes does not indicate that the epigeal shoots die after that time, for they continue to vegetate e. g. in *Heliotropium Radula* and *chorassanicum*, *Acroptilon*, *Dodartia*, *Aristida* and *Elymus*. Bulbous and tuberous plants, on the contrary, almost all finish the aerial period of their life before the end of June and thus belong to the mesophytic aspect of the vegetation, whereas many Rhizome-geophytes are very xerophytic e. g. *Heliotropium*, *Cressa*, *Aristida*, *Elymus*, *Dodartia*. The Irises and some others are mesophytic.

The natural order *Liliaceae* consists entirely of geophytes. (Table 5). The grasses include some very important and characteristic desert-forms of geophytes: *Aristida*, *Elymus*, *Aeluropus* and several species on the river-banks e. g. *Phragmites*, *Saccharum*, *Calamagrostis pseudophragmites*. The *Borraginaceae* include important species of *Heliotropium*. Most of the orders have no geophytes at all. (Table 5).

There are few Chamaephytes in the Transcaspian desert. Assuming that the classification of growth-forms is correct, 52 species belong to this type, all undershrubs with the exception of *Nanophytum erinaceum*, which is rather a cushion-plant. The aerial shoots of such chamaephytes die back until near the surface of the soil, and the buds for rejuvenation are situated at the base of the lignified and persistent stems. This is also the case with *Capparis spinosa* and *Hulthemia berberifolia*, but the shoots of these lie prostrate on the ground as in the more typical chamaephytes.

The species given in the list as Chamaephytes are generally desert-plants, with green shoots which live through the whole summer and contribute to the xerophytic aspect. More than half of them — at least 29 — flower after July 1. Some species play a rather prominent part in the desert, thus Anabasis salsa, Arthrophytum, Noaea spinosissima, Artemisia, Convolvulus erinaceus and fruticosus, Alhagi, Psoralea drupacea, Hulthemia berberifolia, Haplophyllum obtusifolium, Reaumuria squarrosa and Stellera Lessertii. These chamaephytes seem to have attained a high degree of adaptation to desert-life. The generally follow the clay-soil although some of them appear on the less fugitive sandy soils (Convolvulus erinaceus).

Although there are relatively few Chamaephytes in the Transcaspian desert (7 per ct.), they are far more numerous there than in temperate countries. Denmark for instance has only 3 per ct. But if we go southwards from Transcaspia we find in certain tropical or semi-tropical deserts a far greater percentage, thus in the Libyan desert 21 and at Aden 27 per ct. (RAUNKLÆR). This would seem to suggest that the cold winter of the Transcaspian desert is unfavourable to the chamaephytes.

It is known that aridity and heat favour lignification (WARMING 1909 p. 127), and this may sufficiently explain the occurrence of the chamaephytes — at any rate the undershrubs — in dry desert areas. That the Chamaephyte form is in itself a favourable adaptation for the plants is not directly obvious. Lignification and mechanical strength must be favourable (WARMING l. c.), and perhaps it may have this effect that the assimilating shoots are removed from the surface of the soil.

The *Caryophyllaceae*, *Chenopodiaceae* and *Papilionaceae* include proportionately the greater number of chamaephytes, while most of the other orders in Table 5 have few or none.

As to the 39 species of Aquatics and Marsh-plants I can add nothing of special interest for Transcaspia. Besides a number of *Cyperaceae* and *Potamogetonaceae*, the list includes plants like *Valisneria spiralis*, *Lycopus europaeus*, *Lemna*, *Najas*, *Epilobium hirsutum*, *Polygonum amphibium*, *Salvinia*, *Typha*. So far as the biological type is concerned, there is nothing about these plants to characterise them as especially Transcaspian. Something might be found by a closer study of their finer adaptations, such as anatomical structure, flowering, etc., an investigation I have not attempted.

The Aquatics and Marsh-plants are so far as known early flowering, only 5 species flowering entirely or partially after July 1.

Summarising what has been said about the growthforms and their vegetative season, we may divide the growthforms into those characteristic for the xerophytic aspect (the summer aspect), allowing at the same time that they may live and vegetate in spring; and those which vegetate only in spring and belong to the mesophytic aspect.

The Xerophytic Aspect includes:

All the Fanerophytes; All the Chamaephytes; A few Hemicryptophytes; Some Rhizome-Geophytes (but only a few); A few Therophytes.

The Mesophytic Aspect includes: Many Hemicryptophytes; Most of the bulbous Geophytes and some Rhizome-Geophytes;

Many Therophytes.

The percentages of early and late-flowering species already given show that by far the greater proportion of the plants of Transcaspia are early flowering. The number of lateflowering species in the list of plants is 123, which is 16 per ct. of all the species. The species whose flowering season is not stated, are as a rule taken as early flowering.

It holds good for most growth-forms that the majority of the species flower early. This also applies to the Therophytes, but for one group of these the summer-annuals, the opposite is the case; the same is seen in the Chamaephytes.

CHAPTER 13

Descriptions of the Growth-Forms.

In this chapter an attempt is made to give a description of some of the structural features of Transcaspian desertplants. Even a brief description of each of the desert-plants of our area would fill a large volume, hence the following is limited to species known from personal observation and collected by myself supplemented in some cases by other material. In this respect the "Herbarium florae Rossicae" has been of great service.

The plant-species are arranged according to their "biolo-

gical types" in the sense adopted by RAUNKLER, a method of arrangement which offers the best opportunities for comparison between morphological and biological characteristics, especially those of shoot-structure and branching in relation to the nature of the leaves. Amongst the various types I have given most attention to those contributing to the summeraspect, i. e. the true Xerophytes, more especially the Fanerophytes and Chamaephytes. This course was adopted because I had more material of these plants at my disposal, and partly because of the special interest attached to the structure of plants with persistent epigeal shoots.

In what follows, the occurrence, foliage and ramification of each species are described, flowering and fructification being also referred to. Some of the descriptions are accompanied by photographs of herbarium specimens, or by sketches some of which are taken from material preserved in alcohol. So far as material permitted, the anatomy of the assimilating organs has been examined. Axial organs which are not assimilatory I have not examined, first because the material was too limited for such an investigation so that any comparative conclusions would be rather doubtful, secondly in order to limit the work, and finally because thorough descriptions of the anatomy of the axial organs of a number of species are given in B. Jönsson's valuable memoir.

A. Fanerophytes.

The trees and shrubs have been included as far as possible. The descriptions begin with the "dry" plants and proceed towards the more succulent.

Eremosparton aphyllum F. & M.

A leafless shrub or small tree, generally about 1-2 metres high, rarely exceeding 4 metres. It is at home in the sand-desert where it is one of the most characteristic plants. The roots are long and some are horizontal. According to PALEZKIJ, the roots are capable of producing aerial shoots and although this species might for this reason be cultivated

in the plantations, this is not done, because the seeds are destroyed by insects and it does not grow well from cuttings. *Eremosparton* has slender, pliant branches (fig. 23). The

bark is yellow in older specimens, green in younger ones.



Fig. 23. Eremosparton aphyllum with fruits. The middle thicker branch is the year-shoot of the previous year, broken at the point. X, X: last year's assimilation-branches, now dead. Beyond these new branches have arisen. June. The year-shoots have small, scattered, scaly leaves, mere rudiments which can play no part in assimilation. In their axils lateral shoots occur which are smaller than the main shoot and bear scale-leaves. The year-shoots are therefore branched. The lateral shoots (year-shoot branches) bear flowers



Fig. 24. A year-old branch of *Eremo-sparton aphyllum*. A bunch of new assimilation-shoots arising from an old leaf-axil at the base of three dead (strongly shaded) assimilation-shoots.

in the upper leaf-axils.

Before the beginning of the next vegetative period, the ultimate parts of the yearshoot and all its smaller branches die, and only the primary axis (the main shoot in fig. 24) remains, after losing its green bark and assuming the vellow, smooth, hard bark instead. The branches of the. year-shoot thus live only through one vegetative period. they are biologically equivalent to leaves and may be termed assimilation-branches. (RINDOWSKY, see below p. 178).

The next year-shoot arises from the nodes of the primary year-shoot where the assimilation-branches formerly were or where their remains may still be seen, so that serially the new shoots arise below the old ones. During the first year, between the assimilationbranch and the scale-leaf subtending it, one may find the

little bud which develops into a new year-shoot (fig. 25). Sometimes not one but several shoots are formed from a node, some of these being vigorous and persistent, while others are short-lived assimilating shoots. It has not been possible to determine whether these serial shoots are lateral shoots on an assimilation-branch of the first year, or on each other, or whether they are lateral shoots on the main shoot of the first year. The new shoots of the third year

may again arise from the same nodes. Some of these may be plainly seen to be placed low down on the second year's shoot; others are situated further towards the end of it, at the nodes, in bunches or singly.

Eremosparton flowers in May or June. The flowers are red, short-stalked, and being arranged widely apart they form loose racemes. Even at the beginning of June fruits are found on the lower parts of the plant. The flowers developed last do not seem to yield



Fig. 25. Eremosparton aphyllum. Longitudinal section through part of a year-shoot (A). This bears a leaf (F), an assimilation-branch (B) and a bud (C), from which a new branch will arise next year. \times 11.



Fig. 26. Eremosparton aphyllum. A, Transverse section of year-shoot. Sclerenchyma shown black; palisade-tissue hatched in one direction; Vascular bundles cross-hatched. Dead hairs cover part of the surface. B. Detail of A:S, storage sheath; Phl., Phlœum; Camb., Cambium; Vas., Vessels. C & D, Hairs; D, shows a stoma (St), and K, inner limit of the cuticularised layer. A, \times 47. B-D, \times 230.

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fruit, probably they are burned by the heat of summer. The fruit is a crescent-shaped, one-seeded, woolly-haired pod about 1 centimetre in length and easily transported by the wind (see fig. 23).

The anatomical structure of the assimilation shoots and the year-shoots is very similar, but the former have no cambium; Fig. 26 shows the inner structure. There are 8 or 9 grooves within which the palisade tissue lies in V-shaped tracts bounded towards the interior by a row of storage-cells. At the apex of each ridge there is a mass of collenchyma and deeper-seated is a band of sclerenchyma of which another band is found outside each vascular bundle. Stomata only occur in the grooves, they are slightly sunk and hidden by scale-hairs.

Calligonum Caput Medusae Schrenk.

A shrub or small tree, 1 to about 3.5 metres high and leafless. Its home is the sand-desert and it is extensively utilised in the plantations along the railway; 90 p. cent. of the cuttings strike root, and year-old plants from the nurseries always transplant successfully. Comparatively speaking the plant is distinctly green, but in this respect it is far behind the *Salsola* species.

The year-shoots are long (about 40 centimetres), thin and jointed. The leaves are scale-like and membranous, and form a sheath round the stem (Polygonaceae). All or most of the leaves subtend branches, the upper ones often flowers, the lower ones annual assimilation - shoots. RINDOWSKY (1875 l. c.) drew attention to the difference in Calligonum between "rami assimilationis" and "rami lignosi", see also B. JÖNSSON (l. c. p. 18). There is, however, no very hard and fast limit between the two sorts of branches. The outer part of the year-shoot dies away after the cessation of the vegetative-period, generally together with the branches. New year-shoots arise singly or several together from the leaf-bases of the old shoots, sometimes on branches several years old (see figures 11 and 27). Where several are present together, some are generally more strongly developed

than the rest, and these become rejuvenescence-shoots; the others (secondary shoots) fall off at the end of the summer. They often bear flowers (fig. 28). The same leaf-bases may



Fig. 27. Calligonum Pallasia. Year-shoot from last year with bunches of new, flowering branches. May. 12*



Fig. 28. Calligonum Caput Medusae. June. A, The horizontal two-year-old branch bears two year-shoots of last year, with the upper parts dead (strongly shaded); at their bases bunches of new shoots arise, while others are borne on more distal still living parts. The shoots now bear fruits, most of which have fallen. B, a fruit with the setae cut away from the side in view. C, a fruit of Calligonum Pallasia.

produce annual assimilation-shoots several years in succession and by degrees a low cushion is formed from which others arise. Even nodes bearing year-old branching shoots, may again be seen to produce new shoots.

Calligonum Caput Medusae flowers in June. The flowers are small and reddish, the fruits (figures 11 and 28) are very characteristic (see above p. 88), they are easily transported by the wind and are found massed together in sheltered places in the desert.

As regards anatomical structure we refer to fig. 29; there are sclerenchyma bands below the epidermis 14 in number, two palisade layers of which the outer one is very loose, an



Fig. 29. Calligonum Caput Medasoe.
A, Part of transverse section of a young branch: Phl.,
Phloem, X 71. B, Detail of A: epidermis, two palisade layers, starch sheath and outer cells of the water-storage tissue of the cortex. X 250.

amyloid or starch sheath, and the inner bark formed of bands of sclerenchyma between which is aqueous tissue; this contains much tannin. Other bundles of mechanical tissue occur between the vascular bundles and between them and the pith. The pith is a large-celled, water-storage tissue containing tannic acid. The stomata are sunk. VOLKENS, who (p. 142) described the anatomy of *Calligonum comosum* found under the epidermis a layer of loose, thin-walled cells, but only one palisade layer. B. Jönsson, who examined an undetermined species from Turkestan, found on the contrary a thick-walled hypodermal layer, and only one palisade layer.

With Calligonum Caput Medusae are related the other species of this genus which grow in Transcaspia, see the plant-list p. 154. Borszczow has described many species; as to the systematic value of these I have no definite views. Variations are especially common in the fruits, but there is also considerable variety in height and in usefulness as sheltering plants. PALEZKIJ states that most of the species have a tendency to lose their branches in summer, a result of the heat of the sun. This shows itself first as rustcoloured spots which gradually make their way through the branches. Calligonum eriopodum is the species which suffers least from this injury, it is also of high stature and being hardy in several respects it is more extensively used in planting shelter-belts than the other species. Calligonum arborescens is also employed on account of its size, it is said to attain a height of 6 metres.

Calligonum plants are raised in the nursery; one-yearold specimens are about one metre high. They can only endure water as seedlings during the cotyledonary stage.

Under natural wild conditions *Calligonum Caput Medusae* and *C. Pallasii* (= *Pterococcus aphyllus*) seem to be the most common. The fruits of the latter have eight broad wings instead of tufts of setae (fig. 28 C). All the species have thin assimilation-branches.

Ephedra alata Dcne. (= E. strobilacea Bge.).

I have seen this plant in the sand-desert as a shrub one foot high, but it is said to become much higher. Part of a stem I saw was 14 centimetres in circumference.

The leaves are membranous and sit three and three together at the joints. The year-shoots may grow long, they are placed laterally on the previous year-shoot, and arise one, two or three together. Some nodes may for several successive years be the starting point of new branches which thus form bunches. My notes include no other observations on the shoot-structure.



Fig. 30. Ephedra alata. A, Transverse section of bark of a young branch. B, T. S. of a year-old branch. $\times 230$.

The anatomical structure of the green bark is briefly described by VOLKENS (p. 151), and Ross (p. 17) describes an undetermined *Ephedra* species. Fig. 30 shows the assimilating cortex of a young and of a somewhat older branch. The outer wall is very thick with a strong cuticularised layer. The palisade cells become more rounded towards the interior and at the same time contain less chorophyll. Below the epidermis and in the deeper layers there are numerous sclerenchyma-cells which traverse the stem longitudinally; in the older branch their lumen has almost disappeared.

Ammodendron Conollyi Bge, (The Sand-Acacia).

This species is found in the sand-desert and prefers deep sand. It attains a height of 2-4 (-8) metres and is a shrub (on the more stationary soils) or more frequently a slender and in most cases a one-stemmed tree. The hairiness of the leaves gives it a whitish grey appearance, the crown is very open and casts only a light shade. The ends of the branches are pendulous, long, thin, pliant and whip-like. Two branches are shown in Fig. 10. PALEZKIJ has measured roots 19 metres in length.

The leaves are scattered and pinnate with two linearlanceolate leaflets densely coated with silky hairs. The rachis sometimes ends in a slender thorn one centimetre long, which frequently persists till the next year. Stipules are absent or represented by two small spines.

The distal part of the year-shoot probably always dies away before the next vegetative period, also when it is not an inflorescence, which is, however, generally the case (see fig. 10). The succeeding year-shoot arises from the middle part of the first year-shoot. Vigorous year-shoots may be branched, but there is no indication that we have here assimilating branches lasting only one summer. The plant has likewise true leaves.

The flowers are purple and are arranged in terminal racemes. Only the lower flowers in a raceme set fruit; these are also the earliest to develope (April); the later flowers are dried up by the heat of summer. The fruit-bearing branches in fig. 10 show the inflorescence bare above the fruits, and it is seen how few fruits there are compared with flowers.

The fruit is a yellow, one-seeded, indehiscent, winged "pod" which ripens in May. When ripe it is spirally twisted and this with its lightness enables it to be easily carried off by the wind. The seeds are very hard. According to PALEZKIJ



Fig. 31. Ammodendron Conollyi. Epidermis with hairs.× 53.

only 2 per ct. of the fresh seeds germinate but they can all be made to do so by cutting the skin. The leaves are isolateral in structure. The epidermis is thick with sunk stomata on both surfaces. Its coating of unilateral bairs is shown in fig. 31. There are about three layers of palisade cells on each side and hardly any spongy mesophyll. The veins have sheaths of hard bast.

As to the other Ammodendron species, A. Karelini is closely related to the species just described. A. Siewersii, which can hardly be distinguished from A. Lehmanni, is more thorny, the petiolar rachis-thorn being longer, while the stipules are always present as thorns. A. Eichwaldii is a stunted, closely branched shrub with two pairs of leaflets. Biologically these species are closely related.

Ammothamnus Lehmanni Bge.

This I have not examined in its habitat, and only know from herbarium-specimens and descriptions. It is a shrub scarcely attaining the height of one metre. The leaves which have small linear stipules are long and pinnate with 7-13leaflets. These are obovate, cuneate at the base and broad, but small (less than one centimetre long). They are green, but like the year-shoots are provided with stiff hairs. The distal part of the year-shoot dies away (always?), and the new shoots arise from the apex of the surviving part. The white flowers are arranged in a raceme, they come out in April. The fruit is a long velvet-haired pod, spirally twisted, and containing many seeds.

The leaves are isolateral in structure with stomata on both sides, 3—4 layers of short palisade cells on each side and almost devoid of spongy mesophyll.

Smirnowia turkestana Bge.

A shrub attaining the height of about 1 metre. It is a true desert-plant and is most frequently found on clayey soil. The outer bark peels off the older branches in long shreds and then the branches turn yellowish. A coat of hairs makes all the younger parts look greyish. The leaves are simple and almost circular with a diameter not exceeding $1,_5$ centimetres. As a result of the petioles turning or bending, the leaves assume a vertical position.

The year-shoots are branched, many of the axils bearing rather short leafy branches which only live through one vegetative period; they are thus true assimilation-branches. The distal part of the year-shoot itself is also annual; sometimes only a very short piece at the base survives. The new year-shoots arise on the surviving part beyond and below the dead assimilation-shoots, their buds may as in *Eremosparton* be found the year before; several successive series of new year-shoots may arise from the same place, so that they are arranged in bunches.



Fig. 32. Smirnowia turkestana. A, Transverse section of leaf: N, vein. B, a stoma. C, epidermis with bipartite hairs. A and $B, \times 220$; C, $\times 53$,

The flowers are arranged in few-flowered racemes which are placed laterally on the year-shoots.

The fruit is an inflated hairy pod 2—3,5 centimetres long, it contains about 3 seeds which are hard-shelled, flat and reniform; as the pod is swept along by the wind, the seeds may be heard rattling inside.

The structure of the leaf is isolateral (fig. 32) with stomata on both sides, and 3-4 layers of palisade cells filled with starch on the upper side and about the same number

on the lower side. Round the veins, which are numerous, there are rings of large translucent cells between which there are very narrow hands of chlorophyllous tissue.

Astragalus unifoliatus Bge.

A shrub attaining a height of until 0,7 metre. It is strongly branched, the branches being spread out and crooked. The bark of older branches shows a network of fibres. The green parts are densely coated with grevish or whitish hairs. The leaves are small and pinnate with four leaflets at the beginning of the vegetative season, but later they are ternate or only single-leaved. Towards summer most of the leaflets fall off and the rachis remains like a wooden peg 0,5-2 centimetres long, later during the summer it likewise withers. The leaflets are elliptical or lanceolate and small, generally no more than a centimetre long, but occasionally they may be 2 centimetres. The stipules are connate, clasping the branch.

Part of a young year-shoot is shown in fig. 33 where the branching is seen. Sometimes the branches again produce lateral shoots. These branches are assimilating shoots which do not persist. In their place one or more new shoots will arise next year so that here again, sometimes in a very marked degree, we find branches arranged in bunches.



The small red flowers which appear in May or June are arranged in small terminal racemes. The fruit is a pod, 6 mm. in length, densely coated with white hairs and containing 1-2 seeds.

The leaf is isolateral in structure. The epidermis is covered with bipartite hairs on short bases, and has stomata on both sides, not sunk. There are 2—4 layers of palisade cells (filled with starch) on each side, and 1—3 layers of translucent cells surround the veins. The larger veins have sclerenchyma on the phloem side. Sometimes, though rarely, lignified bast-cells issue from this bast-sheath and traverse the palisade layers till they reach the epidermis (fig. 34). "Speichertracheïden" are found in great numbers in the mesophyll. Among the palisade cells are a few translucent, globular bodies which seem to consist of mucilage.



Fig. 34. Astragalus unifoliatus Part of transverse section of leaf with sclerenchyma and a "Speichertrachede". \times 71. The green bark of the young branches has about 4 layers of short palisade cells below a single-layered, hairy epidermis. Bast bundles are found outside the vascular bundles.

Closely related to Astragalus unifoliatus are a number of other shrubby species of Astragalus e. g. A. Ammodendron, paucijugus, hyrcanus, villosissimus, macrocladus, brachypus, squarrosus. All belong to the section Ammodendron which is characterised by connate, clasping stipules, by a small inflated hairy and few-seeded pod and by the frequency of persistent petioles. The section belongs to the sub-genus Cercido-

thrix, characterised by bipartite hairs. A. *brachylobus* with the same type of fruit, and A. *sleroxylon* with linear, curved pods also belong to this group.

All the species named are early flowering shrubs or dwarf shrubs with a few small and hairy leaflets. In some of them the petiole persists till next summer though dead, thus in *A. paucijugus*, *hyrcanus*, *villosissimus*, *squarrosus* and perhaps others; in the first-named it attains a length of about 30 centimetres. The shoots are often curved and the bark in older branches is fibrous. In some of them the branches are arranged in bunches (A. Ammodendron, hyrcanus and perhaps others).

My knowledge of these *Astragalus*-species is mainly derived from literature and herbarium material.

Halimodendron argenteum D. C.

A shrub attaining a height of about 2 metres, which prefers clayey soil. It is also common in the neighbourhood of rivers and is often met with in oases, by roadsides and such places. It has long, hori-

zontal roots from which aerial shoots issue at long intervals.

The year-shoot seems to become completely lignified and to remain alive throughout its whole length. The primary bark is green, the secondary brown. Within the bark and surrounding the branch there is a circle of six large bast-bundles (fig. 35), three larger ones on one side corresponding to the



Fig. 35. Halimodendron argenteum. Part of transverse section of a year-old branch: P, Pith; V, Wood; Phl., Phloeum; C. Cork. The black part is sclerenchyma. The largest sclerenchyma - band belongs to a leaf-rachis thorn, the next largest to a stipular thorn. \times 24.

nearest leaf above with its two stipules, and three smaller ones on the other side corresponding to the next but one set of leaves higher up. All the bundles disappear at a distance about $1^{1/2}$ nodes below the leaf from which they issue. The lower part of each node of the stem has therefore only three bast-bundles. The rachis of the leaf and the stipules form thorns, and the larger bundles of sclerenchyma in the bark are the downward prolongations of the thorns. The intervening spaces are not quite regular as the leaf-arrangement is a 2/5 spiral. The structure of the bark (and the pith) has been described by B. Jönsson (p. 31) who has found mucilage-cork and air-lacunæ; I have not examined these. Jönsson calls the persistent leaf-rachis a thorn-branch bearing leaves arranged in pairs and accompanied by secondary thorns. The real condition is that the leaves are pinnate with four cuneate leaflets. The rachis remains as a thorn which may attain a length of more than 4 centimetres, and this is accompanied by two smaller stipular thorns. The



Fig. 36. Branch of *Halimodendron argenteum*. A new year-shoot is seen at the top of the left-hand branch. Other flowering (now fruit-bearing) short-shoots arise from each leaf-axil on the shoot of the previous year. End of May.

leaflets are silvery haired and motile since by curvature of the petiole they can assume a vertical position.

On the year-old shoot (see fig. 36) short-shoots arise in the leaf-axils, they bear flowers two together on a slender, furcate stalk. These open in April or May, and by the end of May ripe fruits occur. The fruit is a hard, few-seeded, inflated pod, 1—2 centimetres long, placed on a short gynophore (fig. 36). Owing to its lightness, hardness and roundness the fruit may roll a long time before the wind without being injured.

The anatomy of the leaves has been described by J. WEYLAND and B. JÖNSSON. I have found the same structure as these authors, but like WEYLAND I have not seen the hypoderm on the underside of the leaf which JÖNSSON figures. The leaf is isolateral, with about three layers of palisade cells containing starch on each side, a translucent tissue of rounded cells, and strong sclerenchyma bands along the veins. On each side the stomata are slightly sunk. The leaf, like the bark, contains numerous tannin cells lying almost exclusively amongst the palisade cells, but different in shape.

Ewersmannia subspinosa (Fisch.) Fedtsch.

A low shrub occurring at least in the northern part of the territory dealt with here, but which I have not seen growing. The bark of the branches is fibrous. The leaves are two-rowed, pinnate with 9—11 leaflets half a centimetre long; they have small membranous stipules each of them subtending two thorn-branches one of which is generally longer than the other. The flowers arise from the longer thorn-branch which attains a length of 3-4 centimetres, they appear in May. The fruit is a few-seeded, flat pod with one or more S curves; it is carried swiftly by the wind.

Prosopis Stephaniana Spr.

A small strongly branched shrub which attains the height of about half a metre. It seems to thrive best on sandy clay. The leaves are bipinnate with about 10 leaflets on each pinna, these are 3—9 mm. long, oblique, hairy and when the sun shines they are directed upwards. Older branches have white bark and are covered with prickles.

The year-shoot is branched. During the same year each axil gives off either an inflorescence or a branch, or two bran-



Fig. 37. Prosopis Stephaniana. Section through the leaf. \times 230. ches, or a branch and an inflorescence. The longest year-shoot branches are about 15 centimetres long at the beginning of June and only the outermost 2 centimetres are not fully lignified. The year-shoot branches bear many leaves which often subtend inflorescences, but apparently no new branches. The year-shoot branches cannot be termed assimilating shoots as they are persistent.

Prosopis flowers from May to July. The inflorescences are long racemes with small flowers. The fruit is a fleshy pod 3-4 centimetres long.

The leaf is isolateral in structure (fig. 37). The epidermis contains tannin and has stomata on both surfaces; 6-7 layers of palisade cells fill up the whole leaf.

The veins have bast sheaths on both sides. "Speichertracheïden" are present.

Zollikoferia acanthodes Bois.

is said to be a stunted thorny shrub with forked angular branches and with thorn-like short-shoots. A few ovate or oblong leaves occupy the base of the branches, they are thickly coated with white spines and soon fall off. (From BOISSIER fl. orientalis.)

Atraphaxis spinosa L.

A strongly branched shrub never exceeding a height of one metre. The leaves are shortly petiolate, circular-ovate, rather thick and about one centimetre long. The bark is white. The distal part of the year-shoot dies before the next vegetative period but persists as a point often thorny. The year-shoots may be branched and are often twice branched. The inflorescences are short racemes placed on branches of secondary order. Under unfavourable conditions, for instance

on rocky ground, no long-shoots are formed but only short-shoots. (A. compacta).

The white or reddish flowers appear in April or May. The fruit is a nut enclosed in the three-winged perianth.

Salsola Arbuscula Pall.

A characteristic and very variable plant. Its varied aspect was described and illustrated so long ago as 1833 by -EICHWALDT. On clay it is a stunled, twiggy, stiff shrub with short shoots and hard stiff leaves. But where it occurs on moving-sand it may become a small tree with long pliant shoots and leaves. In the sand-desert it varies in pliancy and hardness, in length of shoots, and in hairiness of shoots and leaves. It has very long roots which in the dune-valleys may be seen exposed and stretching from dune to dune, thus showing that some at least are horizontal.

The best developed form (*var. angustifolia* Fzl.) will be considered first (fig. 12.) As a tree it attains a height of 3-5 metres, with foliage greener and denser than that of any other desert-plant in these parts; the stem is light-coloured and elegant. It appears thus on the moving-sand, and here also may be found specimens with fasciated branches, a character which often accompanies luxuriant growth.

Salsola Arbuscula is one of the most important plants for sand-binding purposes along the Transcaspian railroads. Small pieces of the stem are stuck into the sand and of these 100 per ct. germinate, but many of them are injured by lepidopterous larvæ. In the course of two years the plants attain a height of about 3 metres. The hardihood of the plant in withstanding sand-drift has already been considered (p. 88).

In vigorous specimens from the sand-desert the leaves are 7 centimetres long or rather longer. They are cylindrical almost filiform, and pendulous. The year-shoots may attain the length of half a metre, they are always branched, often twice branched. The bark is green at first, but soon turns white and glossy.

The distal part of the year-shoot often dies away before the next vegetative period. The new year-shoots arise close up to the dead part, the lower part of the old year-shoot being branchless.

The year-shoot generally bears flowers towards its apex; a flower is placed in each axil and the length of the internodes decreases upwards. In less luxuriant plants the branches are formed high up, and arise in the axils below the lowest flowers. These branches have rather short nodes, bear flowers in every leaf-axil and die away after the ripening of the fruits. They are thus annual assimilating as well as flowering shoots. In more vigorous plants the branches of a year-shoot are long, drawn out and zigzag, they are also numerous as they arise from almost every leaf-axil on the year-shoot (fig. 12). In the most strongly developed specimens the branches of the year-shoot are lignified, and are then scarcely assimilating shoots but rejuvenescence shoots. They may bear flowers in each leaf-axil or only in the upper ones, and as a rule they have flowering branches towards the apex.

The year-shoot branches of secondary order are similar to the primary branches described above for the more feebly developed plants; they are flower-bearing, with short internodes, and quickly perish.

The year-shoot branches which bear flowers throughout their whole length — such as those in fig. 12 — live, to all appearances, only one vegetative period, and one often finds dead ones bearing the scars of fruits, they are thus assimilating and flowering shoots; on the other hand, the year-shoot branches, which bear leaves at the base, become so strong and thick that the lower part probably survives the winter. The tips of the branches, however, which in September are soft and still growing, probably die away like the tips of the main shoots.

The small form of Salsola Arbuscula which prefers a

clay soil is a dwarf shrub attaining a height of 30—50 centimetres; a branch of it is seen in fig. 38. The leaves are 1 or perhaps 2 centimetres long, thick and erect, fresh green and often coated with fine setaceous hairs (comp. pp. 70 &



Fig. 38. Salsola Arbuscula. Clay-desert form. June. (The upper branches are broken and bent to one side, and do not show the natural habit).

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88). The year-shoots are erect, stiff, 3 to 7 centimetres long and frequently bear flowers in the upper axils. The distal flower-bearing part of the year-shoot generally seems to die away, though it is lignified and remains as a dry and almost thorny point. The next series of year-shoots arise lower down on the older one, and as these in turn lignify and die away at the tip, a system of short stiff branches is produced spreading in all directions. New shoots may also arise on branches several years old.

The flowers in Salsola Arbuscula are inconspicuous as in other Chenopodiaceae. Some open in June and July, but the



Fig. 39. Salsola Arbuscula. A, Cross section of a leaf: N, vein; sclerenchyma shown black. B, Hair. C, Surface view of a leaf: beneath the epidermal layer the cells of the crystal-layer are shown, one of them with a group of crystals. $A, \times 47$; B and C, \times 202.

majority in August or September. The flower is surrounded by three leaves; in front a subtending foliage leaf with a spoonshaped base, and at each side a broad thick green prophyll or bract, sometimes scale-like, and sometimes with a short blade. The perianth-segments are thick-walled on both surfaces ; before and after anthesis they fold together forming a pyramid in which the stamens and carpels are enclosed. Such is the protection of these late-expanding flowers. The fruit (a nut) remains enclosed in the perianth the five parts of which form a broad horizontal wing. The fruit is not ripe till October. Being light and provided with wings it is easily carried along by the wind.

The leaves are centric in structure, of the type so often described, with a palisade layer and a starch sheath towards which the veins pass obliquely through the central aqueous tissue. (See VOLKENS p. 138). The vein is surrounded by sclerenchyma (fig. 39).

Between the epidermis and the palisade cells is a layer of cells with very thin walls and large intercellular spaces (fig. 39 A and C). Some of them contain clusters of crystals, also described and illustrated by VOLKENS (tab. XII, 3). This crystal-layer appears to be distinct from the epidermis but it may be compared with the corresponding one in *Haloxylon* (WARMING 1897 p. 218). where it is included amongst the epidermal tissues, and in both cases it may probably be regarded as a hypoderm; there must be air between its cells.

In *var. longifolia* the leaves are perfectly cylindrical; in the stunted form they are often slightly concave or flat on one side.

Salsola subaphylla C. A. M.

A shrub or small tree attaining a height of about 2 metres. It somewhat resembles the last species, but does not attain the same height, its foliage is less dense, and it sets fruit earlier. According to PALEZKIJ its life-period does not at the most exceed four years, hence it is not employed for sand-binding purposes. It is by preference a sand-plant and attains its highest development where the sand is moving. On clay or stony soil it appears as a small shrub of about 30 centimetres high.

The leaves (fig. 13) are thick, cylindrical or half-cylindrical and attain the length of about two centimetres.

The year-shoots are branched, sometimes twice. The distal parts of the year-shoots and branches are in the month of July covered with flowers (fig. 13) subtended by scale-like bracts; the fruit-bearing branches may be quite hidden under the broad wings of the numerous fruits.

After the cessation of the vegetative period the tips and

all the branches of the year-shoots generally die; the new year-shoots arise on the outermost living part of the old



Fig. 40. Salsola rigida. Branched and flowering year-shoots of the present year arising from the bases of older branches of which the dead tips are seen. June.

ones, beyond the year-shoot branches of last year, and from buds which may be seen the preceding year.

The flowers and fruits are very similar to those of the last species.

The anatomy of the leaf is also similar to that of *Salsola Arbuscula*, but the crystal-layer below the epidermis is absent.

Salsola hispidula Bge.,

which I have not seen, is according to descriptions very much like S. subaphylla.

Salsola rigida Pall.

A stumpy shrub attaining the height of 30 to 50 centimetres, and almost an undershrub. It is one of the characteristic plants of the clay-desert (p. 69). The leaves are cylindric, and although the lower ones disappear in July, foliage leaves are present through the whole summer. The whole plant is hairy and grey.

The year-shoots, which may be 30 centimetres long, bear flowers in all the axils at their extremities and here in this region there are generally a few curved, ascending branches (fig. 40). In the axils lower down, vegetative shortshoots are frequently present, which probably next year develope into rejuvenescence shoots. The distal parts of the year-shoot and the flowering branches die away before the next vegetative period.

The flowers are hidden between three bracteoles and open in June or July; the fruits are of the ordinary *Salsola* type and ripen in the autumn.

The anatomy of the leaf is the usual type. Central aqueous tissue, palisade cells with starch-sheath towards which veins pass from the midrib; the hypodermal crystallayer consists of scattered thin-walled cells.

Salsola laricina Pall.,

which I have not seen alive, resembles the preceding species as regards ramification.
Salsola verrucosa M. B.

A shrub attaining the height of about one metre, and most frequently found in the clay-desert. The cylindrical leaves soon fall off, and during summer the main assimilating organs of the plant are the subtending leaves and bracts of the flowers which as fleshy, spoon-shaped scales, three together enclose the flowers. The plant is thus what we have called (p. 71) a bracteole-succulent. Small globular shortshoots with 3 to 5 leaves are sometimes seen replacing the flowers.

The year-shoots are branched, sometimes twice branched.



Fig. 41. Salsola vertucosa. Transverse section from the underside of a bracteole. \times 202.

The branches, especially those of secondary (or tertiary) order bear flowers so close together that the branches are hidden. The tips of the year-shoots and all the secondary branches die away before the next vegetative period.

Salsola verrucosa flowers in summer. The fruit is of the ordinary Salsola type.

The anatomy of the foliage leaves was not examined. The bracteoles have green tissue of the usual type on the outer (under) side (fig. 41). On the inner (upper) side the aque-

ous tissue is bounded by a thin epidermis.

Haloxylon Ammodendron (C. A. M.) Bge. (Saxaul).

A shrub or tree thriving best on sand with a subsoil of clay or lime. It may become very old (see B. JÖNSSON p. 8) and may attain considerable dimensions, but large specimens are rarely found as they are cut down for firewood by the nomads (comp. above pp. 89 and 126). I have seen a thickstemmed tree which I estimated at 7 metres high. AITCHISON records a tree 14 feet high with a stem 12 feet in circumference. The wood is known to be hard and heavy, and old stems have deep irregular furrows. The roots are long, PALEZKIJ says about $10^{1/2}$ metres and more, and Jönsson states that Saxaul has both deep-seeking vertical and long horizontal roots. The latter, according to ANTONOW (p. 29), can form aerial shoots.

On account of its slow growth Saxaul is not much employed in sand-binding plantations. Yet, as stated above (p. 89), LIPSKY denies that the growth is very slow.

The leaves are reduced to small scales arranged in pairs opposite each other and united together. The young branches are long, slender and drooping (see for instance Bessey, pl. 10, LIPSKY 1911 pl. 4 and 5).

The year-shoot is green, its bark containing the only assimilating tissue of the plant. Most of the shoots are set together towards the apex of the previous year-shoot, the distal part of which frequently dies away. Sometimes two shoots of the same age are seen in the same leaf-axil, one outside the other, but the outer one is generally more feebly developed, and it is improbable that both of them ever persist. The year-shoots are branched and they bear flowering short-shoots (see fig. 14).

The flowers are inconspicuous and open in May. Each flower is protected by its subtending leaf-sheath and by two bracts. The perianth, on the contrary, is small before the anthesis but afterwards it grows larger. The fruit is a small nut loosely enveloped by the broad-winged perianth, and is ripe in October.

The anatomy of *Haloxylon* has been described by GERNET, GHEORGHIEFF, WARMING and B. JÖNSSON. The structure of the assimilating shoot I found to be quite in accordance with that described and illustrated by WARMING (1897, p. 217), it is of the ordinary centric type. The epidermal tissue is threelayered. Assimilating tissue is also said to be present in the secondary bark. (B. JÖNSSON p. 7). As regards the mucilaginous cerk in the bark mentioned by JÖNSSON, we refer to his memoir.

Halostachys caspica (Pall.) C. A. M.

A shrub which belongs to the clay- and salt-desert. Under specially favourable conditions it may attain a height of two metres, but in the desert it does not as a rule exceed half a metre. The shoot is of *Salicornia* type with reduced scale-like opposite leaves. The position of the branches is also regularly opposite (decussate or brachiate).

The year-shoot ends in a large paniculate inflorescence which is still present next year in a more or less dead condition. Underneath the inflorescence the year-shoot bears many branches; some of these are assimilating shoots which fall



Fig. 42. Halostachys caspica. A, Part of transverse section of an assimilating branch: N, vein: Phl., phloem; V, vessel; Ms, medullary rays. — B shows a vein leading from the central cylinder to the palisade tissue. \times 47. off before the next vegetative period, while others are persistent rejuvenescence shoots. New assimilating shoots arise both from the old and the new yearshoots in places where vegetative or inflorescence-branches were formerly present, and sometimes two branches issue from the same leaf-axil.

The flowers are small, and sit three together in the axils of peltate bracteoles; they open in July. The fruit is a nut ($^{3}/_{4}$ m. m. long) enclosed in the enlarged perianth; it may still be found on the plant in the following year.

The green assimilating bark is enclosed in a one-layered,

strongly papillose epidermis (fig. 42). There are about 5 layers of loose palisade cells of which the outermost contain the greatest, the innermost the smallest number of chlorophyll grains. Underneath the palisade cells there is no starch-sheath, but numerous veins are spread out there (fig. 42 B.) which lead to the central cylinder through the adjacent aqueous tissue.

The anatomy of the wood has been described by GERNET and GHEORGHIEFF.

Halocnemum strobilaceum (Pall.) M. B.

A stumpy, often decumbent shrub which grows on clayey soil rich in salts.

The year-shoot has a thick bark containing aqueous tissue and green tissue, and is covered with opposite, reduced leaves, united in pairs to form a sheath. Almost every axil on a year-shoot is occupied by a branch or short-shoot shaped like a more or less elongated bud or a short catkin. An illustration of a branch is given by VOLKENS in Nat. Pflanzenfamilien III (Chenopodiaceae) fig. 35. In fig. 43 is







Fig. 44. Halocnemum strobilaccum. Part of a transverse section of an internode. A vein from the central cylinder (C) branches out in the inner green tissue. In part of the green tissue the number of chlorophyll-grains is indicated. × 71. (Slightly diagrammatic).

represented a longitudinal section of part of such a shortshoot. As stated by WARMING (1897, p. 206), the leaves are somewhat peltate. Sometimes they support three buds (B. fig. 43), which are presumably flower-buds as the leaves on many short-shoots each subtend a triplet of flowers in the autumn. The flowering short-shoots die after the ripening of the fruits, and along with the distal part of the year-shoot drop off before the next vegetative period.

Beyond the dead short-shoots, new shoots are formed next year, often several together, either elongated year-shoots or new short-shoots.

The anatomy of the leaf has been described by WARMING

(1897, p. 206). Transcaspian specimens correspond with his description, but I have not found stone-cells in the basal part of the leaf, nor the layer of short subepidermal cells recorded by WARMING. In the leaf, as in the bark of young stem-internodes (fig. 44), there are three (or four) layers of small palisade cells which inwards are abruptly replaced by larger ones containing only a few chlorophyll grains. These adjoin a system of veins which branch out in great numbers through a certain zone of the bark or the mesophyll, and only within this zone is there a perfectly translucent aqueous tissue; this last is divided into two parts, an outer zone of large cells, and an inner zone of smaller cells.

The epidermis is thick and papillose, and the stomata are sunk.

Suæda microphylla Pall.

This species is known to me only from descriptions and herbarium material. Perhaps it should be considered as a chamacphyte as the stem is said to be decumbent. The stem may attain a thickness of 4 centimetres. The branches are long and widely spread out. The year-shoots are branched both in the inflorescence and in the vegetative portion, sometimes twice branched.

The leaves are typical $Su\alpha da$ -leaves, rather short. The plant flowers in July and the fruit is ripe in October.

Suæda physophora Pall.

This plant is said to be a shrub about one metre high, but I have not seen it.

Lycium ruthenicum Murr.

A shrub from 10 to about 60 centimetres high, spiny and with outspread branches. It is a salt-bush not generally found on sand.

Under specially favourable circumstances the year-shoots may attain a length of more than 60 centimetres, but as a rule they do not exceed 30 centimetres. They have a white bark, and are usually branched, branch-thorns arising in the leaf-axils; the leaf-base is thick and persistent. The branchthorns are generally short, about 1 centimetre long, and often bear only two leaves placed low down near the base. The branch-thorns may, however, become longer and bear several pairs of leaves. The flowers arise from the base of the branch-thorns either in the axils of the two low-set leaves, or next year they form part of the rosette-shoots which appear

in the axils of these leaves. On long branch-thorns the flowers may also arise higher up.

The year-shoots generally terminate in a thorn; their distal part always seems to die away.

They flower during summer.

The leaf is isolateral in structure. There are stomata on both sides, generally flush with the surface but some of them are slightly raised and below them is a group of cells, 2-4 on each side, which are round and devoid of chlorophyll; throughout the rest of the leaf these cells are wanting (fig. 45). The palisade tissue is 2-3 cells



Fig. 45. Lycium rathenicum. Part of leaf in transverse section. \times 203.

thick, and towards the interior it merges gradually into a large-celled aqueous tissue containing a slight amount of chlorophyll. The veins which lie a little nearer the upper side than the lower, have bundles of bast on both sides and here are found a few perfectly translucent cells.

Nitraria Schoberi L.

A shrub, barely one metre high which prefers the claydesert. The bark is white, the leaves are thick and spathulate with short hairs, and are placed 2-4 together on a small cushion, with small scales between them. The leaves and the scales surround a bud. According to VELENOWSKY (1907 p. 501) this has the following significance:

Nitraria has a pinnate leaf (or bipinnate) the petioles of which are reduced so that the leaflets are placed beside each other, and the scales between them are then partly stipular scales partly rudiments of leaflets. The bud between these leaflets is thus in reality the axillary bud of the leaf. This may during the same year give rise to a short-shoot which forms several of these whorls of leaflets one above another so that a leaf-rosette is developed — this is thick at the base and may have as many as 20 leaves (leaflets). Besides these year-shoot branches, shorter thorn-branches may occur. The year-shoot itself terminates in a branched inflorescence which of course dies after the fruit is ripe, or it ends as a thorn.

Normal buds which have not formed a rosette during the first year, seem next year only to be able to form either rosettes or vegetative long-shoots, whereas the rosettes developed during the first year may give rise to both vegetative and floral long-shoots.

The plant flowers in May or June. The fruit is a black berry which is eaten by the natives.

The anatomy of the leaf has been described by B. Jönsson (p. 26, tab. III), whose observations are confirmed by my own. The leaf is isolateral with sunk stomata on both sides, and 2—3 layers of palisade cells the inner ones being larger and less green. Amongst the palisade are large mucilage-cells. Like Jönsson I have found no tannic acid. — Compare also VOLKENS (table XI) illustrations of the structure of *Nitraria retusa*.

JÖNSSON also describes the anatomy of the stem and the bark, the latter with mucilaginous cork.

Reaumuria oxiana (Ldb.) Bois.

A much-branched dwarf shrub about 30 centimetres high, which prefers a firm soil, clay or stone. The stem is crooked and bent. The non-branching year-shoots may attain a length of about 15 centimetres, but only a portion of this survives till the next vegetative period. The bark of the persistent part is brown.

The leaves are 2-4 centimetres long, linear-lanceolate. They are grey with salt-excretions which take the form of small white spots over depressions at the bottom of which the secreting glands are found. The structure of these (fig. 46 B) is very similar to that of the glands figured by VOLKENS (tab. V) from *R. hirtella*. VOLKENS was of opinion that during the night the excreted salts absorbed water from the atmosphere (dew), which might then be absorbed by the



Fig. 46. Reaumuria oxiana. A and B parts of leaf in transverse section; in A sclerenchyma-cells are seen; B, a salt-gland. $\times 202$. C, Surface section of palisade tissue, showing palisade-cells and sclerenchyma-cells intermingled.

gland and thus be utilised by the plant. MARLOTH (1887 p. 321) denies this and states that it is impossible for the glands of the leaf to absorb water from the surface without at the same time absorbing the salts. On the contrary the salt solution on the surface must absorb water from the gland, and according to FITTING this is what takes place (1. c. p. 267 note). And still more important, FITTING has arrived at the result that plants in the desert store salt internally up to a certain specific maximum varying for different species, and that in this physiologically determined limitation of salt storage they have a sufficient means for securing the high osmotic pressure which FITTING has pointed out in the desert-plants and which enables them to obtain water from the soil. In addition to sodium chloride, there is also excretion of carbonate of lime often in great quantities, so it is not at all certain that the excretion of sodium chloride is of any special importance. And finally FITTING points out that dew is exceedingly rare in the Sahara.

The flowers of *Reaumuria* are large and terminal on the branches, they appear in July. Below the calyx there are several bracteoles forming an involucre. The fruit is a capsule with about a score of white woolly seeds.

The leaf anatomy of *Reaumuria oxiana* has been briefly described by VESQUE. The thick epidermis consists of one layer, and the stomata and salt-glands are depressed. The leaf is isolateral with about two layers of palisade cells and a central water-storing tissue. Between the green tissue and the water-storing tissue, or amongst the palisade, are numerous bands of sclerenchyma running longitudinally within the leaf, and from these issue long, thin sclerenchyma-cells which as idioblasts stretch through the palisade to the epidermis as if to support it from the inside (fig. 46 A C; also VESQUE tab. 8, fig. 7).

Reaumuria fruticosa Bge.

On moderately stable sandy soil I have found shrubs of this species scarcely attaining the height of one metre.

It is strongly branched, the branches being strikingly thick and light in colour. The year-shoots may attain a length of 5 centimetres, and apparently always die back at the apex, which remains as a dry stick. Branches of two different kinds occur on the year-shoot, some are short but quite evidently branches with elongated internodes, others are rosette-like short-shoots. The former may be wanting, but when present they are generally placed towards the apex of the year-shoot. They are rarely 2 centimetres long, generally less than 1 cm., and bear leaves like the year-shoot. The leaves are small about 2 mm. long, but comparatively broad and flat and besprinkled with salt-grains. The rosette short-shoots are found in every axil except occasionally the ones which bear the branches with extended internodes. They carry about 12 leaves, shorter, thicker and more persistent than the subtending leaves. Rosette-shoots are also formed on old year-shoots, and altogether they are the most important assimilating organs of the plant.

I have not seen the flower.

The anatomy of the leaves is similar to that of R. oxiana and R. hirtella (VOLKENS), and also discussed by VESQUE, but his statements do not quite agree with what I have found; for instance he finds no mechanical tissue. — The epidermis is very thick and the epidermal cells are almost filled with mucilage from the outer wall. Sunk stomata and salt-glands occur, the latter being similar in structure to those of the preceeding species. There are two or more layers of palisade cells extending all the way round, and starch-sheaths enclose the veins. Large bands of sclerenchyma are present, irregularly arranged, but I have not found idioblasts between the palisade cells.

Tamarix.

Fifteen species of this genus have been recorded for Turkestan. They only thrive as a rule in places which are not too dry. On river-banks they are very abundant and ANTONOW says (see above p. 33) that Tamarisk in the desert is a sign of water not far off. In the sand-desert they are able to some extent to hold their own against the sand (comp. above p. 127—128) and where they are present water is presumably not very far down. They have long, vertical and obliquely descending roots. Under favourable conditions they are trees with thick foliage, but are only small shrubs under unfavourable conditions.

The leaves of Tamarisks, as is well known, are small green scales. The plant does not shed its leaves but the branches which bear the leaves, except in the case of per-

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sistent branches where only the leaves are cast. They thus have assimilating shoots which biologically play the part of leaves. In many (perhaps all) species the leaves are coated



Fig. 47. Tamarix laxa. Last year's year-shoot with floral (fruit-bearing) shoots at the base, vegetative shoots at the top. May.

with salt-concretions; especially is this the case with *T*. *hispida* and *T*. *Karelini*, where these are very numerous.

As regards the development of vegetative and floral branches, the species of Tamarix may be divided into two groups. In the first group the floral shoots appear on the year-shoot of last year while the present year-shoot is purely vegetative. This group includes Tamarix laxa, Meyeri, Androssowii, florida, elongata, polystachya. This characteristic is shown in T, laxa (fig. 47). The vegetative and floral shoots are, however, not always separated as in this case, but may be intermingled. A single one or several of the vegetative shoots seen in fig. 47 will become rejuvenescence shoots, the remainder are short-lived assimilating shoots. All the vegetative shoots, as will be noticed, are many times branched. The species of this group flower early, during April and May, and according to BUNGE (1852 p. 8) they have as a rule tetramerous flowers.

The species of the second group bear the flowers at the apex of the present year-shoot which has vegetative branches at its base. To this group belong *T. Pallasii, hispida, Karelini, arceuthoides, Ewersmannii, karakalensis, Korolkowii, leptostachya* and *pycnocarpa.*

The branch of *T. hispida* illustrated in fig. 48 is the shoot of this year. All the lower branches of primary order bear much-branched vegetative shoots at the base and inflorescences at the top, or they are purely vegetative. The upper year-shoot branches are entirely floral.

The species included here are said by BUNGE (l. c.) to have as a rule pentamerous flowers which open late, from July to September. As the flowers arise on the outmost part of the year-shoot and its branches, they cannot appear until these axes have attained a certain stage of development.

In this group as in the first, the flower axes and the greater part of the vegetative branches fall off, and only a single one or a few become rejuvenating shoots.

Short-lived vegetative branches may appear in all the species on old year-shoots in the axils of leaves which have fallen off. They may bear inflorescences as in the species of the second group.

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All the Tamarisks have small red or white flowers arranged in racemes. The fruit is a small capsule with woolly seeds easily transported by the wind.

The anatomical structure of the leaf I have examined



Fig. 48. Tamarix hispida. Year-shoot with flowering branches at the top, vegetative at the base. August.

in *T. hispida*. All the cells of the single-layered epidermis are distinctly convex and papilla-like. The stomata on the upper and lower surfaces, and the salt-glands are sunk. One layer of palisade cells all round is present both in the leaves and the assimilating branches. The leaf also has rather open spongy parenchyma and veins with a bast-sheath besides storage-tracheids ("Speichertracheïden").

I have not investigated in detail the more mesophytic fanerophytes (*Elaeagnus*, *Ulmus*, *Morus*, *Populus*, *Salix*). *Elaeagnus hortensis* was observed in August with two series of branches on the year-shoot, but this does not appear to be the rule. The same holds good with regard to *Salix angustifolia*. The species of all the genera just mentioned flower in spring.

The above Fanerophytes have the following characteristics common to all or some of them.

The leaves are greatly reduced. In one set of species they take no part as assimilating organs (Eremosparton, Calligonum, Ephedra, Haloxylon, Halostachys, Halocnemum), while in others they are scale-like, but green (Tamarix, Reaumuria fruticosa). Astragalus has leaves which are wholly or partly shed during summer, but whether as in the case of Spartium junceum (according to BERGEN), there is no assimilation or at any rate very little after the leaves are shed, I cannot say, and one can scarcely draw a conclusion from a single case. Ammodendron, Halimodendron and Smirnowia have persistent, small, hairy leaves, while Prosopis, Atraphaxis, Lycium, Nitraria and Reaumuria oxiana have persistent small and glabrous leaves. The Salsola species have cylindrical persistent leaves.

The leaves in Salsola and the assimilating shoots in the leafless species are all centric in structure, the latter in most cases have abundant mechanical tissue.

In the flat-leaved species the leaves are without exception isolateral in structure.

The branches in most sand-desert species are slender,

pliant and more or less pendulous; in clay-desert species on the contrary they are generally stiff and short.

The year-shoots are branched except in a very few cases (*Halimodendron*, *Reaumuria oxiana*). Branched year-shoots are thus the rule, and non-branching the exception. A similar case has, to my knowledge, never been pointed out for any community of Fanerophytes.

WARMING (1892, pp. 408, 252) and after him MALME have drawn attention to a number of South American species with branched year-shoots. RACIBORSKI also gives illustrations of several species of this kind, but without recording this characteristic. These species are mostly forest-plants, but some belong to the Savannas (MALME). MALME regards the branched year-shoot as a primitive character in dicotyledonous trees, non-branching on the contrary being a secondary feature acquired in the course of time. However this condition in the case of the broad-leaved South American plants is of less interest to us than the branch system in other Fanerophytes poor in leaves or leafless. This condition is certainly worthy of special study although in the literature I have only found occasional references to it.

In many cases the year-shoot branches are annual assimilating shoots, more rarely they are continuation shoots which take part in the extension of branches. No definite limit can be drawn however between the two. The assimilating branches have been described in many of the species mentioned (e. g. *Eremosparton, Calligonum, Tamarix, Astra*galus, Salsola etc.); biologically they play the part of leaves.

Assimilating branches in many species are not confined to the last year-shoot, but also occur on older branches. In such cases they arise on the exterior side of lateral branches, or where such ones have previously been, and often several together. Thus the characteristic tufts of branches originate, which likewise distinguish so many of the trees and shrubs of the desert; they have been described and illustrated in the case of several species (e. g. Eremosparton, Calligonum, Smirnowia). Similar conditions are also found in Spartium, Carmichaelia, and others.

A further characteristic of the year-shoots is, that they do not as a rule persist throughout their whole length, but the outer part dies, (probably killed by the heat and drought during the height of summer) and it remains next year as a dead stick, frequently as a thorn. One of the few exceptions to this rule is *Halimodendron*.

As regards the majority of the fanerophytic Chenopodiaceae and Lycium, flowering takes place in summer; Haloxylon and probably all the rest flower during spring, at the latest in June. All the late-flowering species with the exception of Lycium have small flowers which are completely enclosed up to the time of anthesis. The early flowering species include a large proportion of Leguminosae, and it seems to be the rule, or at any rate is frequently the case, that only the early flowers fructify while the later ones become dried up.

The fruits (or the seeds) are in most cases such as may be easily transported by the wind; they are light and furnished with some kind of parachute, and as a rule they contain only one or a few seeds¹). The open network on the fruit (fig. 28) of *Calligonum*, the large bladdery pod of *Smirnowia* and *Halimodendron*, the winged fruits of *Salsola*, *Haloxylon*, *Ammodendron* and *Atraphaxis*, the small light pods of *Astragalus* and *Eremosparlon*, and the white woolly seeds of *Reanmuria* illustrate the different adaptations by which wind-transport is achieved.

Fruits with no special adaptation for flight are seen in the berries of *Nitraria* and the small nuts of *Halostachys* and *Halimocnemis*.

B. Chamaephytes.

As explained in chap. 12 (p. 173) these all belong to the xerophytic aspect, they are summer-plants and a great number of them are late flowering.

Capparis spinosa L.

A decumbent undershrub found on clay soils and more especially on stony soil. The branches are long and bear

¹) Comp. E. GAIN 1894: Moist soil produces many but small seeds, dry soils few seeds but large.

broad, large leaves, bright green in colour and with two spinous stipules at the base. According to VOLKENS (p. 97), the leaves during summer acquire a coating of wax so that they lose the bright green colour. I have not observed this, but it may also take place in Transcaspia since my opportunities for observing *Capparis spinosa* in summer were few. The year-shoots are branched. The lower part only is persistent and lignified, and it gradually increases in thickness. The beautiful large white flowers are placed singly in the leaf-axils; flowering begins in May and continues well into July, perhaps longer. The fruit is a stout berry.

The anatomy of the leaf has been illustrated by VOLKENS (tab. IX, figures 1-2), and my Transcaspian material shows the same structure. Some of the epidermal cells, however, have a thickened inner wall (mucilage?) and I have not observed that the palisade cells are arranged in groups round the large thick-walled tracheids ("Speichertracheïden"). The leaf is isolateral, with mesophyll consisting almost exclusively of palisade cells. The stomata are slightly sunk.

Hulthemia (Rosa) berberifolia Dum.

This species is likewise a clay soil plant with decumbent shoots and broad leaves. The latter are dentate, hairy, elliptical or spathulate, about 1 centimetre or rather more in length, and closely set because the internodes are shorter than the leaves, sometimes so short as to produce rosettes on short-shoots. The stem bears many strong curved white prickles as well as others which are thin and subulate. I have only seen the plant in May when it carries large, handsome, yellow flowers. The distal parts of the yearshoots may die away, but whether this occurs always I cannot say. No material was available for anatomical investigation.

Haplophyllum obtusifolium Ldb.

This is a typical undershrub which occurs especially on stationary sand. It is strongly branched but according to BUNGE (Rel. Lehm. p. 62) other forms occur in which the branching is only slight. The year-shoots arising from the persistent parts may be branched, but generally this does not seem to be the case. They are numerous and slender, and bear small, lanceolate leaves which attain a length of 1-2 centimetres, bright green in colour and containing many lysigenous oil-reservoirs.

The yellow flowers appear in July or August. The fruit has few loculi and a few seeds in each loculus.

The leaf is isolateral in structure. The epidermis consists of one layer with a thick outer wall and the stomata slightly sunk. There are about three layers of palisade cells on each side and a narrow middle zone of rounded cells. This zone includes many tracheids ("Speichertracheïden") besides the veins which both above and below have a sheath of rather thin-walled, non-lignified bast. There are many lysigenous oil-reservoirs measuring in diameter more than half the thickness of the leaf.

The green cortex has a thick-walled epidermis of two layers overlying 3 or 4 layers of short palisade cells limited towards the interior by a layer of thin-walled, tangentially extended cells which may be regarded as collecting sheath. Many bundles of bast occur in the inner cortex.

Stellera Lessertii (Wickstr.) C. A. M.

An undershrub 20—50 centimetres in height and occurring in the clay-desert. It is much branched and numerous dead branches are found; whole branch-systems may die off leaving short dry sticks projecting in all directions. New branches are formed from branches of the previous shootgeneration and also from old branches. The year-shoots bear branches the same year, often 2-3; these are unbranched, with long internodes, and they all terminate — if sufficiently long lived — in an inflorescence. This is a short, simple spike, and the small yellow flowers appear in July. The fruit is a pear-shaped nut about 4 mm. long, it is surrounded by the lower strongly woolly-haired part of the perianth.

The leaf is hairy, narrow and small, almost elliptical-

lanceolate and directed obliquely or vertically upwards. Its structure is isolateral (fig. 49). The epidermis is thick and most of its cells on both surfaces have a thick mucilaginous inner wall which in transverse section presents a characteristic appearance, two light stripes showing between the green tissue and the cell cavities of the epidermis. These cavities are filled with tannic acid and the contents are therefore dark.



Fig. 49. Stellera Lessertii. A, Leaf in transverse section. B, a hair. \times 203.

There are stomata on both surfaces. The palisade cells occur in 2 or 3 layers above and below; the centre is occupied by the veins which take up most of the space; between them there are 2 or 3 layers of rounded cells less rich in chlorophyli, and many "Speichertracheïden" (shaded in fig. 49).

A young stem shows a thick but non-mucilaginous epidermis with stomata which are not sunk; below this are 3 layers of rounded green-cells of which the outer ones are slightly palisade-like. These are followed by about two layers of round or tangentially extended cells containing a small