amount of chlorophyll. The inner cortex consists of large groups of sclerenchyma separated by narrow bands of translucent cells. The cortex of the youngest branches is green, but when the epidermis becomes filled with tannin the branch assumes a dark-brown surface which ultimately is ruptured by cork-formation.

## Alhagi Camelorum Fisch.

One of the most common plants in Trancaspia. It looks like a stumpy shrub with green branches. The aerial parts, however, are not persistent and in general *Alhagi* is doubtless a root-geophyte. But as short stems are occasionally found — probably rhizomes originally — from which new shoots rise 10—30 centimetres above the ground, and as the determination of RAUNKLER'S biological types is dependent on the position of the least protected buds, I propose to classify the species under the chamaephytes.

The light-shoot of *Alhagi* is green and spiny. The plant frequently assumes the globular form since the close-set expanded branches project equally in all directions. The leaves are small, at most a couple of centimetres long, oblong-ovate or spathulate, and the majority fall off during the early part of summer. This is especially the case with the leaves developed later, whereas many of the older, lower leaves persist for a long time. This is probably due to the great heat and dryness of the summer which prevents the perfect development of new leaves.

All the leaf-axils except the very uppermost bear thornbranches. These are leafless and green, about 4 centimetres long and with a yellow tip; only the upper thorn-branches bear flowers. These branches arise not in the middle of the leaf-axil but obliquely towards the cathodic side of the leaf (the phyllotaxy is a  $\frac{2}{5}$  spiral). Many of the leaf-axils of the main-shoot give rise to long-shoots beside the spine, on the anodic side; these long-shoots bear leaves which also subtend spines except sometimes the upper ones, more rarely they bear long-shoots.

Alhagi has horizontal roots which at intervals send out

light-shoots directed upwards. Normally these die during winter down to the surface of the soil and new shoots appear next year from the upper part of the subterranean perennial

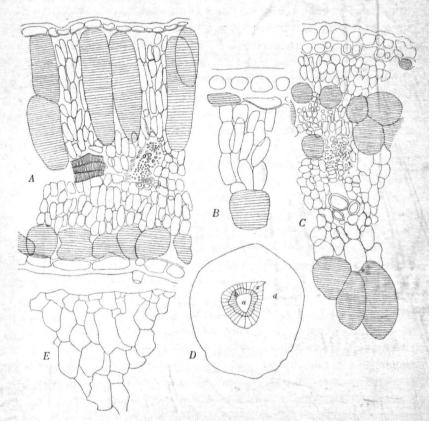


Fig. 50. Alhagi Camelorum. A, Leaf in transverse section. B, Part of a transverse section of the outer cortex of a thorn shoot. C, Part of transverse section of a young shoot. D, Transverse section of a sandshoot (rejuvenescence-shoot); a, pith; b, wood; c, inner cortex; d, outer cortex (cork). E, The outermost part of the outer cortex in D. D: slightly magnified; the others,  $\times$  203. Cells containing tannin are hatched.

rhizome. These as well as old roots (?) may become very thick; I have seen them  $4^{1/2}$  centimetres in diameter.

From what has been already said, it will be understood that the *Alhagi* are gregarious plants, and that their subterranean parts contain food-reserves which enable them to contend against very unfavourable conditions. *Alhagi* has been frequently mentioned in the preceeding pages (e. g. pp. 122, 128).

When buried by the sand axillary shoots encased in a thick corky coating (see below) grow upwards through the sand to the surface (comp. fig. 22 which shows a somewhat similar case in *Heliotropium*). Specimens of *Alhagi* were found where this had taken place twice: The first restoration shoot had after burial formed a new shoot. On the other hand rhizomes or roots laid bare by the sand being blown away from them may form new light-shoots.

The red flowers of *Alhagi* appear in isolated groups 2-7 together on the upper spines, they commence to expand in June. The fruit is an jointed crooked pod, (not a lomentum) with 5-8 joints and as many seeds; it is very light.

The anatomy of *Alhagi* has been examined among others by B. JÖNSSON who gives a number of somewhat diagrammatic figures.

The structure of the leaf in my Transcaspian specimens agrees with his description and figures. The hypoderm containing tannic acid on the lower surface, (see fig. 50, A) may, however, be wanting. When present it is seen in sections parallel to the surface to form a net-work below the epidermis. The stomata are slightly sunk, the epidermis is one-layered and there are 4-5 layers of short palisade cells on the upper and lower sides.

As most of the leaves fall off early, the branches are well provided with assimilating tissue (fig. 50 B and C). The epidermis consists of two layers, and many of the cells of the inner layer contain tannic acid; the palisades are nearly similar to those of the leaf and are apparently best developed in the thorn-branches (fig. 50 B).

Within the green tissue there lies a parenchyma with many large cells containing tannic acid. In older branches the leptome has bands of sclerenchyma on the outer side. The pith is large-celled, many of its cells containing tannin. The presence of tannin in fig. 50 is indicated by hatching. Reference should also be made to SCHUBE, B. JÖNSSON and VOLKENS; the latter (tab. III, fig. 10) gives a transverse section of an internode of *Alhagi manniferum*. A restoration-shoot grown up through the sand from a buried shrub of *Alhagi* had its subterranean part beset with scale-leaves and with a yellow coating which was thick and spongy to the touch. When cut through the coating proved to be a thick layer of cork (fig. 50, D, E), formed from a phellogen in the cortex; this was double the thickness of pith, wood and inner cortex together. All the cells had exceedingly thin corky walls, easily torn and all empty and dead. Inside such an air-filled case the growing shoot must be well protected.

## Heliotropium dasycarpum Ldb.

An undershrub occurring in the clay-desert. It has leaves 1 to 2 centimetres in length, coated with stiff hairs; the foliage is so open that the whole plant is transparent. The flowers appear in June and July and evidently only the lower flowers of the scorpioid cyme produce fruit. The achenes are long-haired and hard-shelled.

The leaf is almost isolateral in structure. The epidermis is one-layered with stomata on both surfaces and not sunk. Both surfaces are coated with hairs most of which are bent to one side while some are short and somewhat dome-shaped. The cuticle extends over all the epidermis as a warty covering. The hairs arise from large thin-walled epidermal cells which contain stratified cystoliths, the so-called haircystoliths (see SOLEREDER 1899, p. 632, fig. 127; the hairs mentioned here are similar to fig. B). The upper face of the leaf has one layer of long palisade cells, the lower face two layers of shorter ones. Grouped around the veins in the middle are some isodiametric or slightly oblong cells, translucent or containing a little chlorophyll.

## Frankenia hirsuta L. (= F hispida D. C).

This species occurs in comparatively moist localities and as a rule on a saline soil. It has decumbent, lignified branches. The leaves are about half a centimetre long, revolute, with scattered hairs and with grains of salt. The small red flowers may be found still open in July. The structure of the leaf is dorsiventral (fig. 51), but the stomata and salt-secreting glands are found on both surfaces, whereas the setaceous hairs are absent on the upper side. There are long palisade cells on the upper side, generally transversely divided, and short palisades on the lower side

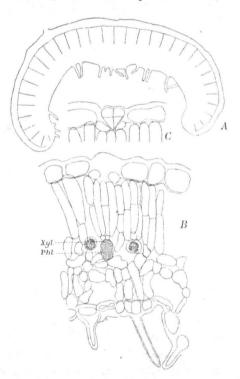


Fig. 51. Frankenia hirsuta. A, Outline of leaf in transverse section with epidermis, palisade cells and hairs indicated. B, Part of leaf in transverse section. Xyl., Xylem; Phl., Phloëm. C: Gland.  $A: \times 47$ ; B, C:  $\times 203$ .

and a loose spongy parenchyma with crystal-cells in the middle. The air-spaces in the interior of the leaf are generally fairly large. Sclerenchyma is wanting.

#### Convolvulus eremophilus Bois. & Buhse.

An undershrub growing on clay or stationary sand. The year-shoots arising from the perennial branches are branched two or three times. The tertiary series of branches and the upper ones of secondary order are apparently always short (up to about 4 centimetres) and rarely have more than 2 or 3 internodes. It seems as if growth were interrupted by the drying up of the terminal bud. Each of these small branches bears one or two flowers.

The lower leaves are lanceolate-linear and may attain a length of about 3 centimetres; the upper ones are small scales, so that the plant is thus practically leafless. All the green parts are covered with slanting bipartite hairs similar in form to those of *C. erinaceus* (see fig. 53).

The white flowers open in June. The capsule contains two large, long-haired and hard-shelled seeds.

I had no opportunity of examining the anatomy of the leaf. The primary cortex resembles that of the next species. The epidermis consists of one layer and contains tannic acid; the stomata are not sunk. There are three layers of palisade cells which towards the interior are supported by one or a few layers of tangentially extended cells, almost devoid of chlorophyll, and among these are a few bast cells opposite the groups of phloëm.

## Convolvulus divaricatus Rgl. & Schm.

An undershrub which grows on stationary sand. The year-shoots, about 30-40 centimetres in length, are sinuous, white-woolly and two or three times branched. The leaves are small, (5 to 15 mm. long) and with a broad cordate base.

The isolated white flowers open in May.

The structure of the leaf is isolateral. About five layers of palisade cells occur, the middle ones being the smaller. The epidermis is one-layered and contains tannic acid. Both surfaces are covered with long projecting hairs which are bipartite but one arm is much reduced. Alongside the veins there are secreting cells (laticiferous cells). The structure of the green cortex of the young branches is similar to that of the previous species, but the hairs are erect and the coating is much denser.

## Convolvulus erinaceus Ldb.

An undershrub with very long roots and preferring somewhat stationary sandy soil. It attains a height of about

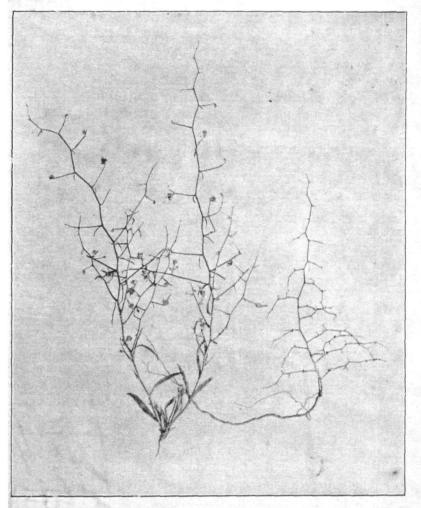


Fig. 52. Convolvulus erinaceus. To the left a leaf-bearing plant (June). To the right a specimen which has shed its leaves. (July).

40 centimetres, but according to AITCHISON it may reach the height of 1 metre (2-3 feet). The year-shoots are stiff, strongly branched, geniculate at the nodes and the branches

15

are spread out or reflexed. In spring and early summer the plant developes leaves (see fig. 52) which are linear-lanceolate, 2-3 centimetres long, and white-haired, but the leaves fall off later in the summer so that the branches become the only assimilating organs. In late summer the larger plants are leafless, globular and spiny shrubs. The spines are formed by the year-shoot branches of secondary and tertiary

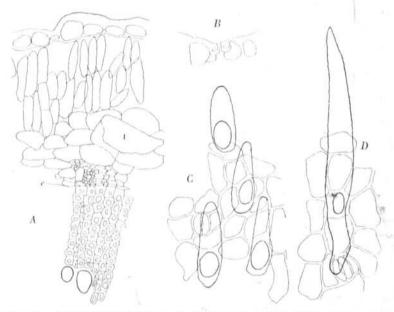


Fig. 53. Convolvulus erinaceus. A, Transverse section of the green cortex and part of the wood; two vessels are represented; c, Cambium; l, Secreting cell. B, Stoma. C, Epidermis with hairs, seen from above. D, A similar view of Convolvulus fruticosus. ( $\times$  203).

order, and also by the uppermost ones of primary order which as a rule have formed only one internode and the beginning of a second one when growth ceases, hence the branch remains as a spine, terminated by a dead, withered point.

The white flowers occur singly on these small branches, and open in June and July. AITCHISON says that they open at sunrise, but I have found them open in the middle of the day in a broiling sun. The capsule often (always?) contains only one seed with short woolly hairs and a hard shell.

I have not examined the anatomy of the leaf. The primary cortex of the branches is similar to that of the two species of *Convolvulus* described above, as will be seen from fig. 53. The inner cortex, as in these species, includes secreting cells

(fig. 53, A.1.), which as seen in longitudinal section stand in long rows like piles of barrels. (comp. HALLIER). Similar cells are found in the pith which also encloses leptome tissue (a generic character).

# Convolvulus fruticosus Pall.

Grows on clayey or stony ' soil. An undershrub with stiff, spiny branches. The yearshoots issuing from the low knotted perennial parts are branched once, twice or three times. The branches, more especially the ones of secondary order, are spread out or bent backwards; the branches of tertiary order and also the upper ones of secondary order are spines, of which the lower ones bear flowers. Each bears

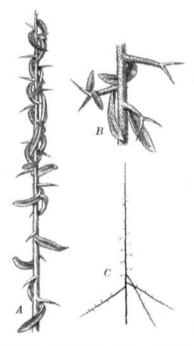


Fig. 54, Convolvulus fruticosus. Upper (A) and middle part (B) of a shoot. C: Scheme of branched year-shoot. August.

only one terminal flower with small foliage-like prophylls each subtending a branch-spine which is generally leafless. After the flower and the two leaves have fallen off, a forkshaped spine remains behind. (fig. 54 B, C). The upper thorns are unbranched.

The leaves are small and lanceolate; the lower ones are the larger and may attain a length of about  $2^{1/2}$  centimetres, while higher up they are shorter and narrower. In the

15\*

month of July they all become bent vertically downwards and curl up into something like a spout. (fig. 54).

The plant flowers in May, the corolla being comparatively large, pink and coated with woolly hairs.

The young branches and also the leaves are white with a coating of bifurcate convolvulaceous hairs, the arms of which are very unequal in length (fig. 53, D). The longer arm is directed towards the apex of the organ.

The leaf is isolateral in structure. The outer wall of the epidermis is very thick, as thick as the cell cavity which contains tannic acid. The stomata are sunk. There are two or three layers of palisade cells above and below; strong bundles of bast surround the veins.

The outer cortex of the young branches has the same structure as half a leaf.

#### Acanthophyllum elatius Bge.

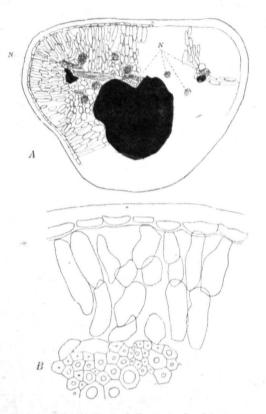
A plant of stony and clay soils. The woody base gives rise to numerous straight unbranched twigs about half a metre long, with white bark and bearing opposite stiff prickly leaves. Before the next vegetative period the branches have died off almost down to the ground. They bear small axillary leaf-rosettes, and the apex carries a cymose inflorescence.

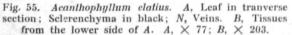
In the middle of the leaf is found a thick band of sclerenchyma, many times thicker than the midvein which extends along its upper side. Laterally there are a couple of smaller veins partly accompanied by narrow bands of sclerenchyma on the leptome side. From the median strand palisade cells radiate in all directions. The epidermis has very thick outer walls. The stomata are not sunk. The intercellular spaces in the interior of the leaf are of considerable size (fig. 55, B).

Acanthophyllum pungens closely resembles the above species. As for the other species recorded, I have not examined them.

## Noaea spinosissima L.

An undershrub which prefers stony soils (on mountains). It is much branched and forms a thick, spiny, globular shrub; the branches die down almost to the ground and arise from a lower, lignified long-lived part. The leaves are





long, triangular and pointed like a spine. They all subtend thorn-shoots which attain a length of 3-6 centimetres and these in their turn frequently bear lateral thorn-shoots.

Flowering season October, the flowers being closely surrounded by bracteoles. The fruit is a nut enclosed in a winged perianth. Nanophytum erinaceum Pall.

My knowledge of this species is derived solely from herbarium specimens. It is almost a cushion-plant as the



Fig. 56. Anabasis salsa. End of June.

shoots have short internodes and many small knotted lateral shoots with the leaves arranged in rosettes. The leaves stand close together and are ovate-lanceolate with a small spinose point.

### Anabasis salsa (C. A. M.) (Brachylepis).

This species occurs on clayey or stony and saline soil. Its habit is shown in fig. 56. It is an undershrub-chamaephyte, with slightly branched year-shoots which die off almost down to the surface of the ground. They are richly furnished with flowers which arise in the axils of the small opposite scale leaves. The flowers are out in July or August. The fruit is somewhat fleshy, it is surrounded by the nonwinged perianth.

The assimilating stem is constructed after the ordinary centric type of the Chenopodiaceae. The epidermal tissue consists of three layers, of which the inner layer is a thinwalled "crystal-layer". The stomata are slightly sunk. A ring of palisade cells surrounds the starch-sheath and within

this is an aqueous tissue with large crystal-cells and the veins.

Anabasis aphylla L.

This species is a saltplant like the previous one and relationship is also shown as regards shoot-structure. In its fruit *A. aphylla* is a true *Anabasis*, the leaves of the perianth being broadly winged and the fruit dry.

Arthrophytum subulifolium Schrenk.

An undershrub growing on firm soils. It probably does

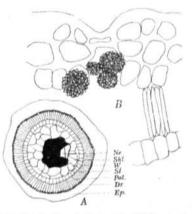


Fig. 57. Arthrophytum subulifolium. A, leaf in transverse section; Ne, vein; Skl., sclerenchyma (black); W, aqueous tissue; Sl, starch-sheath; Pal, palisade cells; Dr, crystal-layer; Ep, epidermis. B, Part of transverse section of a young branch showing epidermis, hypoderm with crystal-cells, palisade cells and starch-sheath. A,  $\times$  47; B,  $\times$  203.

not exceed a height of 30 centimetres. Sometimes it may be a hemicryptophyte, but in its least protected form it is a chamaephyte with a low thick perennial epigeal base, which bears rather short green branches. These bear opposite subulate leaves with the axils woolly-haired, and with the basal part persisting through the winter.

I have not seen the plant in flower. The fruit is said to be somewhat fleshy and wingless.

As regards the assimilating, epidermal, and aqueous tissues, the structure of the leaf and stem is similar, both belonging to the centric type. A thin-walled hypoderm contains crystal-groups. (Fig. 57).

The Chamaephytes described have the following characters in common: They are undershrubs with a perennial lignified and often thickened base, and with year-shoots the larger distal part of which dies before the next vegetative period. *Nanophytum* alone is a cushion-plant, or nearly so.

With the exception of *Capparis*, they have all small leaves, and some of the Chenopodiaceae are practically leafless. In some species all or some of the leaves are shed during summer, and the stems assume the function of assimilating organs (*Alhagi, Convolvulus*).

The structure of the leaves is isolateral except in *Frankenia*. The leaves of many species are coated with hairs, some have tracheids, others aqueous tissue.

The year-shoots are almost always branched which is the rule for undershrubs (WARMING 1892).

As already stated all the chamaephytes are late flowering. The structure of the fruit so far as I have observed, presents no general characteristic common to all.

## C. Hemicryptophytes.

The majority of these (see chap. 12, p. 167) are springplants the aerial parts of which are dead during the warmest part of summer. So far as I know this is, for instance, the case with all the Umbelliferae belonging to this type; and

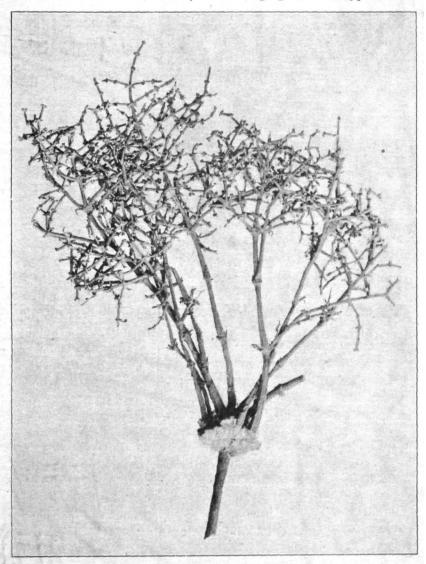


Fig. 58. Anabasis eriopoda. August.

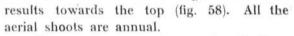
most species of Astragalus and Cousinia, amongst the larger genera, disappear during summer.

The more important hemicryptophytic summer-plants are some halophytes which will be dealt with below.

#### Anabasis eriopoda (C. A. M.).

This species is common in very dry clay- and stonedeserts. It has a very characteristic appearance as will be seen from figures 58 and 59. The year-shoots measure 30 cm. long or even more, and arise from a white woolly cushion which lies in the uppermost crust of soil. The leaves are reduced to small opposite scales, which on older branches terminate in rather long slender spines; in their axils many white woolly hairs occur.

The lower leaf-axils of the year-shoots are branchless. but the upper ones all bear branches. The more vigorous branches give rise to new ones so that a tangle of branches



The two lowermost leaves of each shoot are embedded in the cushion whence all the shoots issue, they are very short, but have long apical spines (fig. 59), and their leafaxils are very woolly. The woolly cushion must be formed by the hairs in the lower leaf-axils of successive shoots, and my observations indicate that the shoots arise in these very leaf-axils, though not conclusive enough to prove this positively.

The small inconspicuous flowers open in July, and the fruits which are fleshy and not covered by the perianth ripen during September or October.

The anatomy of the shoots is shown in fig. 60. The epidermis is very thick con-

sisting of three layers; inside it is a thin-walled "crystal layer" which is, however, interrupted in many places. The ordinary layers of palisades are present, likewise a starchsheath and an aqueous tissue.



Fig. 59. Anabasis eriopoda. Part of a cushion with two shoots. August. Natural size.

## Zygophyllum.

The species of this genus are to some extent at least summer-plants. Z. Eichwaldii C. A. M. may be taken as an example. It has long furcate shoots sparsely covered with leaves. These have long stalks and are pinnate with small flat leaflets. The older leaves die off and fall while the apex of the stem is still growing (Translocation of water, comp. above p. 71). The plant flowers in spring (also in summer?), but may still be found with living shoots well into summer.

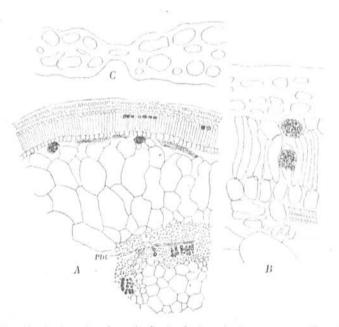


Fig. 60. Anabasis eriopoda. A, Part of stem in transverse section; Phl, phloëm within which lies wood with vessels. B, Details of A; C, Epidermal tissue with stoma.  $A, \times 47$ ; B & C,  $\times 203$ .

The leaf is isolateral and in contrast to the species described by WARMING 1897 (p. 41) and VOLKENS (p. 113) it consists of palisade cells throughout. These become larger and more translucent towards the interior, but they all contain chloroplasts, hence there is no aqueous tissue present. The epidermis consists of one layer and seems to be mucilaginous, the stomata are slightly sunk. In a young stem the pith is a water-storing tissue. The primary cortex includes bundles of bast at regular intervals. Outside is the green outer cortex with its cells slightly palisade-like.

Zygophyllum Fabago and miniatum both have broader leaves and shorter branches than Z. Eichwaldii.

The leaves of *Peganum Harmala* are repeatedly furcate with linear segments. The branches lie prostrate on the ground like those of *Zygophyllum*. It flowers in spring and the shoots wither during the summer. (comp. VOLKENS p. 114.)

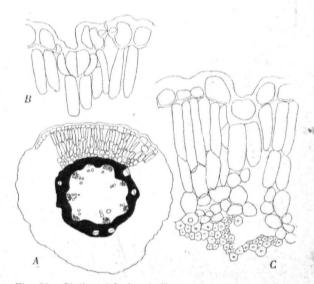


Fig. 61. Statice otolepis. A, Transverse section of inflorescence-axis. The wood is black, the white holes indicate vascular bundles which are also present within the ring. B and C, Details of A; B shows a gland and a stoma.  $A, \times 47$ ; B and C,  $\times 203$ .

## Statice otolepis Schrenk.

This species has large broad basal leaves which are dorsiventral with two layers of palisades on the upper side, and spongy tissue with stomata on the lower. These leaves die on the approach of summer. Meanwhile the plant has flowered in May or June and the richly branched floral axes remain green and persistent, and as in *S. cordifolia* (Ross p. 20) they are the assimilating organs for summer. Their structure may be seen in fig. 61: collateral vascular bundles occur in the pith (comp. SOLEREDER 1899 p. 564); the wood forms a solid cylinder of libriform cells; the cortex consists of green tissue, details of which are given in figures B & C.

Some Summer-Hemicryptophytes occur in the more favourable localities, in depressions near rivers and similar places. These are only slightly xerophytic and have distinct leaves, generally not very large and often hairy. These plants which I have not investigated very closely include, for instance, the following species: Convolvulus pilosellifolius and subhirsutus, Inula caspica, Jurinea derderioides, J. Pollichii,

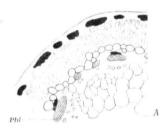
Cousinia triflora, platylepis and dissecta (spiny), Centaurea iberica, Echium italicum, Lindelofia anchusoides and Aster Tripolium.

#### D. Geophytes.

The majority of these are bulbous plants (comp. chap. 12, p. 170), and I have only investigated specimens of three important genera *Dodartia*, *Heliotropium* and *Aristida*.

#### Dodartia orientalis L.

This species is a Root-Geophyte which grows in the more favourable localities on clayey soil. Its leafless branched shoots bear purple flowers in May or June. The branches, as illustrated in fig. 62, have a thick epidermis and below



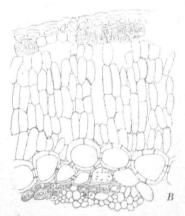


Fig. 62. Dodartia orientalis. A, Part of transverse section of stem; *Phl*, Phloëm. Sclerenchyma black. B, Detail of A. A,  $\times$  47; B,  $\times$  203).

that a hypoderm in which some cells become bast-cells while others remain thin and ultimately disappear leaving empty spaces between the bast-bundles. There are 4 or 5 layers of palisade cells of which the innermost are bounded by a storage-sheath of large thick-walled lignified cells with numerous pits. Internal to these are vascular bundles with the leptome sheathed by small bundles of bast, while between the vascular bundles is a small-celled tissue. The pith is a large-celled aqueous tissue.

### Heliotropium sogdianum Bge.

This species which has been referred to several times in the preceding chapters (e. g. p. 123, 124), forms long horizontal



Fig. 63. Heliotropium (Radula?). Part of a horizontal rhizome with aerial shoots.

subterranean shoots from which aerial shoots arise, sometimes widely apart. A creeping stem of this type is shown (fig. 63) densely covered with shoots. At the base of these shoots, roots are often formed. The aerial shoots are frequently rosette-like. The older light-shoots have a white, glossy cortex covered externally with long stiff protruding hairs. The ovate or ovate-elliptical leaves are also stiffhaired. The length of the leaves is 1-1,5 (- 2) centimetres, the veins are very prominent on the lower surface and the depressions between them appear on the upper surface as convexities, so that the leaf has an embossed appearance. The hairs on the upper surface are comparatively few, but thick and stiff; they are white and each one occupies a white circular base. On the lower surface these hairs are very numerous. The white flowers are out in May.

Heliotropium Radula, so far as it has been possible to determine the frequently sterile light-shoots, seems to have the same mode of growth and the same form of leaf and hair-coating as *H. sogdianum*. The hair-coating is, however, somewhat closer.

The leaf of H. sogdianum is isolateral. The epidermis is one-layered, densely hairy (with hair-cystoliths, see H. dasycarpum p. 222), and with slightly sunk stomata on both sides. There are about two layers of short, starch-filled palisade cells on each side. The veins are surrounded by translucent cells.

#### Aristida pennata Trin.

This sand-binding grass has been already dealt with (p. 81-83). The thick, shrubby growth of the plant and its power of forming lateral shoots, which add to the tufts and when buried by the sand form new ones, makes this plant the "Conqueror of the Sand desert" (ANTONOW) and the most valuable of all sand-binders.

It has been already recorded and illustrated (fig. 9) that the roots are encased by a sand-stocking. Within this stocking the root lies loose, "wie das Bein in der Hose oder, besser und ästhetischer ausgedrückt, wie eine Phryganeenlarve in dem selbst gebauten Gehäuse" (VOLKENS p. 26). VOLKENS points out that this sand-stocking is formed by the roots-hairs cementing the sand-grains together, and he is of opinion that its function is to protect the roots against evaporation. This is confirmed by the fact that in grasses provided with a sand-stocking, there is no cork or other corresponding means of protection.

My observations show that the root, which sits loose in the sand-stocking, is devoid of cortex. It is enclosed in a thick-walled pericycle consisting of several layers of prosenchymatous cells with numerous pores and containing starch; outside this is a thin-walled endodermis which on its outward side bears shreds of the cortex.

The stocking itself was originally formed by mucilage secreted by the young root; later on the root-hairs penetrate the sand (R. PRICE), and long after they are dead, they keep the sand-grains bound together. Root-hairs are found on the epidermis which is still entire and forms the inner wall of the sand-tube. The internal diameter of the stocking

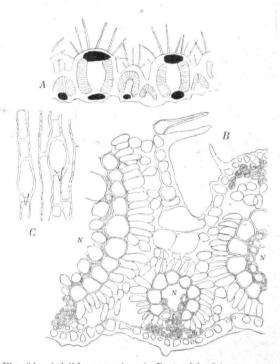


Fig. 64. Aristida pennata. A, Part of leaf in transverse section, slightly diagrammatic. Sclerenchyma black, green tissue shaded. B, Detail of A. N, Veins; C, Epidermis of the lower face with hairs. A,  $\times$  53; B and C,  $\times$  203).

thus indicates the original thickness of the root, but from the disappearance of the primary cortex the root becomes so thin that is lies loosely in the tube.

The straw or haulm is solid and the vascular bundles lie scattered in a somewhat thick-celled tissue; each of them has 3-4 vessels and a leptome group, while down both sides there is a strand of sclerenchyma.

The anatomy of the leaf has been described in the closely related, perhaps identical species, Aristida pungens, by DUVAL JOUVE (tab. 17, fig. 7) and TSCHIRCH (tab. 6, fig. 3). The Transcaspian specimens examined by me agree in their chief features with what has been found by these authors, yet it seems to me that the single cell-layer of the green tissue has a more pronounced palisade-form, and that the whole leaf has larger internal air-cavities than in the figures cited. Some figures of the structure of the leaf are given in fig. 64. The leaf can roll up towards the inner (upper) surface which has long hairs, and the epidermis includes hinge-cells. Like all Paniceae, the plant has the veins surrounded by a starchsheath which is open on the leptome side in the larger veins, while round the smaller ones it is interrupted on both sides; this again is surrounded by a palisade layer. In my specimens the lower surface is also furrowed, though faintly, and in the furrows opposite the air-spaces amongst the green tissue of the "prisms" there are stomata which are slightly sunk; other parts of the epidermis are covered with short, pointed hairs (fig. 64, B, C).

#### E. Therophytes.

It has been repeatedly stated in previous pages that some of the Therophytes are ephemeral spring-plants, while others — the smaller number — are summer-plants which persist through the dry, warm summer. The following includes observations on some of the species belonging to the latter group. The ephemeral species might likewise repay a careful investigation, for instance their variability as to xerophilous structure, depending on the soil and time of development, would be well worth examining. The material available did not, however, permit of such an investigation, particularly as regards anatomy. But the summer-plants seem to me more interesting, and during the journey my attention was chiefly directed towards them and towards collecting material of them.

## Cousinia.

Many Transcaspian species belong to this genus, most of them perennials. They are all rather broad-leaved, thorny, and frequently "cobweb-haired". *C. annua* and *C. dichotoma* were examined as examples of annual species. The former I found flowering in the sand-desert during the hottest time of summer. It was about half a metre high and had broad spiny leaves the axils of which bore rich dense inflorescences. The plant is glabrous, the stem snow-white and glossy.

The leaf is somewhat dorsiventral with two layers of palisade cells on the upper side and one on the lower, and a rather loose spongy paranchyma. The veins have baststrands, the larger ones projecting as ridges on the lower face.

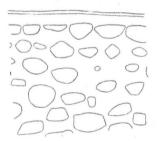


Fig. 65. Cousinia annua, Epidermis and collenchyma of stem.  $(\times 203)$ .

They lie several together, quite separate or connected by a translucent aqueous tissue which merges outwards into a collenchymatous tissue.

The epidermis is rather thinwalled and has stomata on both sides, slightly sunk.

The stem is without green tissue, and has a thick epidermis over a deep thick-walled collenchyma (fig. 65) all the way round.

Cousinia dichotoma is a smaller plant which may still be found flowering at the beginning of July, but it begins to wither about this time. The broad, spiny leaves still preserve their form and position because well-provided with sclerenchyma; they are somewhat dorsiventral and have stomata (not sunk) on both faces as in *C. annua*.

## Frankenia pulverulenta L.

A slender plant with decumbent branches. Like *F. hirsuta* (see p. 222) it occurs most frequently on somewhat moist soil. The leaves are small and flat with salt-crystals on both faces; the glands which are figured by SOLEREDER

(p. 121), thus occur on both surfaces, and the same is the case with the stomata (in contrast to the statement made by VOLKENS l. c. p. 109). On the other hand, the long hairs are only found on the lower side. The leaf otherwise is dorsiventral with two layers of palisade cells on the upper side and a rather loose spongy parenchyma.

## Crozophora gracilis F. & M.

An herbaceous plant with outspread branches and longstalked ovate-cordate leaves which are covered on both surfaces with a thick felt of stellate hairs. The plant occurs in places where the soil is not too dry, and it is still in flower in the month of July. The leaf is dorsiventral with one layer of long palisade cells on the upper surface, and one layer of short ones on the lower; there is no aqueous tissue. Crystalcells are present in considerable number. The epidermis consists of one layer and has slightly sunk stomata on both leaf-surfaces.

## Euphorbia Turczaninowii Kar. Kir. (E. carnosa Pauls.).

A thick-leaved, green, glabrous plant, attaining the height of about 10 centimetres. Like the previous species it occurs in more favourable localities. It is rarely found in flower in July although it frequently has fruits at that time of the year. The sessile, broad leaves are directed obliquely upwards, and are isolateral in structure. There is a thin epidermis with slightly sunk stomata on both surfaces.

#### Euphorbia cheirolepis F. & M.

An erect plant with rather long internodes; habitat the sand-desert. The leaves are about one centimetre long, petiolate, obovate, spinose-toothed; the upper surface is shining and cobweb-haired, the lower is almost woolly-haired. They are dorsiventral, yet with stomata (slightly sunk) both above and below. The epidermis is thin. The dorsal side has a layer

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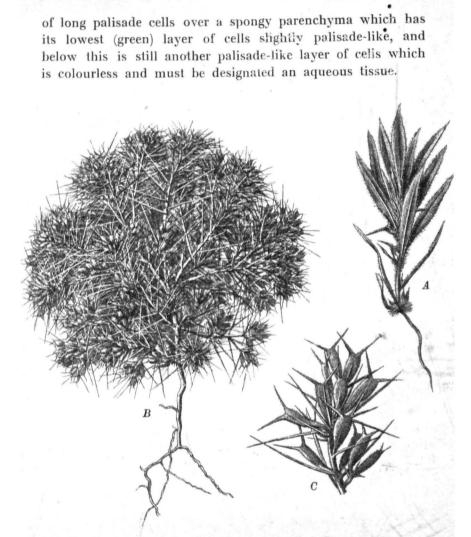


Fig. 66. Ceratocarpus arenarius. A, A young plant with green leaves and a few fruits in the axils. May. (natural size). B, An older plant, (reduced one-half), C, A branch of B,  $(\times 2)$ . The parenchyma has disappeared and the midribs remain as spines. August.

## Ceratocarpus arenarius L.

This very common plant occurs both on sandy and clayey soil; Fig. 66 shows its appearance. In spring the leaves are distinctly linear-lanceolate and bear single flowers in their axils (fig. 66, A). The plant is coated with stellate hairs. The leaves are isolateral with about two layers of palisade cells on each side and a number of crystal-cells. The midrib is surrounded by a thick sclerenchyma extending often from epidermis to epidermis. The small veins are surrounded by translucent storage cells. The epidermis consists of one layer, not very thick-walled, and has stomata (not sunk) on both sides.

In August *Ceralocarpus* resembles a spiny ball (fig. 66, B, C). The leaves are reduced so that only the midrib remains, and even if some still seem to retain their lamina, an anatomical examination shows that all the cells are collapsed and dead. At this season of the year all the leaves are thus

reduced to thorns, and the assimilating functions are carried on by the two connate prophylls which form the two-thorned fruitspathes (see fig. 66 *C*). A section of the wall of the fruit-spathe shows (fig. 67) that the inner surface is formed of two lignified thick-walled layers, the second of which shows

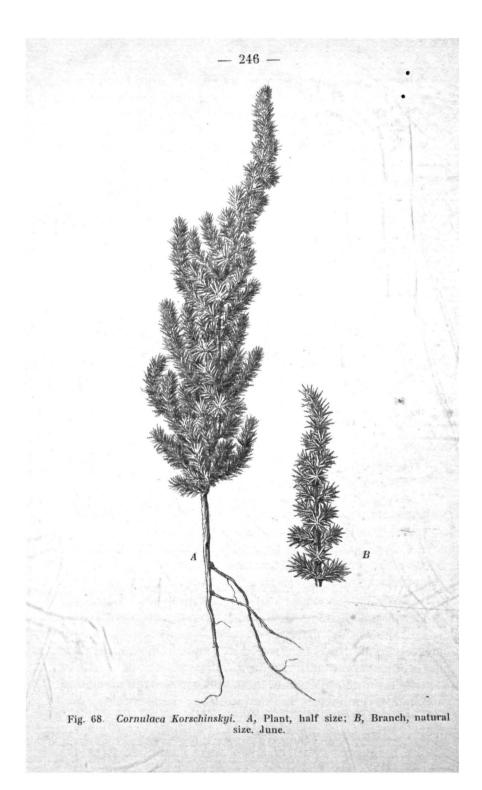


Fig. 67. Ceralocarpus arenarius. Transverse section of part of the fruit-spathe (Prophyll). (× 203.)

no cell-cavities; beyond these skeleton-cell-layers there lies an assimilating parenchyma made up of one layer of short palisade cells and 1 or 2 layers of transverse cells loosely arranged. All the cells are filled with starch. The veins (N)are enclosed in bundles of bast above and below, especially the two veins situated near the two margins of the spathe.

### Cornulaca Korschinskyi Litw.

An erect sand-desert plant thickly covered with short acicular leaves (fig. 68). Each leaf-axil gives rise to a rosetteshoot bearing many leaf-thorns, and in every leaf-axil, (i. e. on the lower parts of the leaves) there are a great number



of white, woolly hairs. These are slightly over 1 mm. long and are arranged in bunches. Each hair consists of one, two or three rows of cells, the thickness decreasing from below upwards (fig. 69).

The leaf is constructed after the ordinary centric type and resembles that of *Horaninowia ulicina* (fig. 71): There is an epidermis of one layer with large papillæ, a crystal-layer, one layer of palisade cells with a starch-sheath, a thin zone of aqueous tissue, and a thick sclerenchyma enclosing the vein.



Fig. 69. Cornulaca Korschinskyi. Parts of axillary hairs.  $(\times 302)$ .

The small flowers do not open till autumn. The perianth remains round the fruit and bears a spine 4 mm. in length.

#### Horaninowia ulicina F. & M.

A sand-desert plant with decumbent branches and acicular leaves. The branches may attain a length of 20-30 centimetres (see fig. 70), with long internodes between the pairs of opposite leaves. In the woolly-haired axils of the more or less cylindrical thornlike leaves, there are either rosette-shoots, or more or less elongated long-shoots, or flowers. The leaves on the main branch die rather early but the axillary shoots remain green.

In favourable localities the leaves may attain a length of a couple of centimetres, and the shoots are erect (*var longifolia*.) With regard to the structure of the leaf and stem, reference to fig. 71 renders any description unnecessary.• The

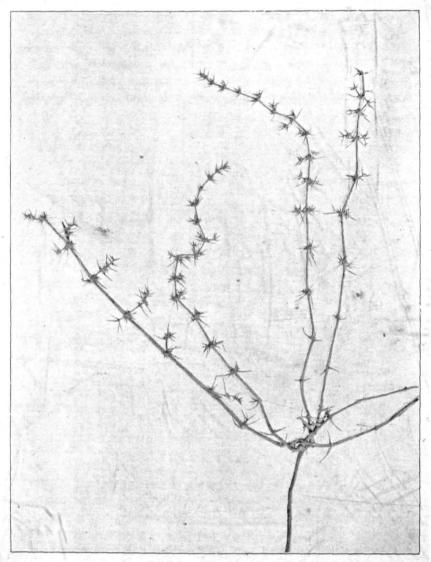


Fig. 70. Horaninowia ulicina. Part of a plant. July.

stem has bands of green tissue alternating with bands of collenchyma (fig. 71 C).

## Agriophyllum minus F. & M.

A<sup>•</sup> strongly branched, thorny-leaved sand-desert plant which may attain a height of about 30 centimetres: fig. 72 illustrates a small specimen. The leaves are up to 3 cm. long, flat with stellate hairs, hard in texture, parallel-veined and traversed by parallel ribs and furrows, and terminate in a spine. The lower ones are lanceolate, but higher up they become narrower. The leaf-axils bear short-shoots with

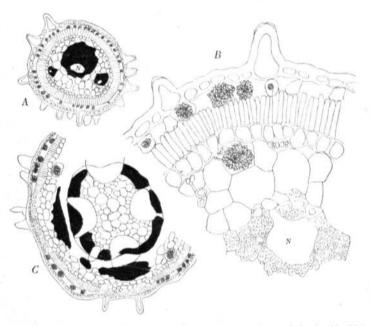


Fig. 71. Horaninowia ulicina. A, Transverse section of leaf; N, Vein. B, Detail of A. C, Part of transverse section of stem. Sclerenchyma black, collenchyma dotted, palisade tissue shaded.  $(B, \times 203; A \text{ and } C, \times 53)$ .

leaves which are quite narrow, acicular and ending in a straw-coloured spine. The flat leaves die away in the course of summer, while the short-shoots remain green.

The structure of the isolateral leaf will be seen from fig. 73. The superficial ribs consist of bands of sclerenchyma. There are one or two layers of palisade cells on each side, and translucent cells with numerous crystal cells in the middle.

The stem shows bands of collenchyma alternating with

bands of green tissue which have about two layers of low palisade cells supported by transverse storage-cells. Where root and stalk merge into one another, the axis is thickened and succulent. No green tissue occurs here but the collenchyma extends all round.

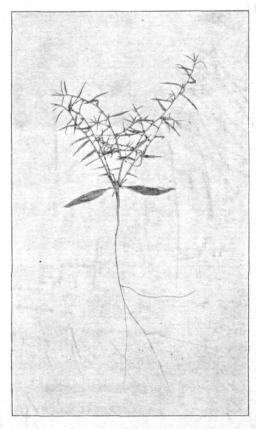


Fig. 72. Agriophyllum minus. June.

# Agriophyllum latifolium F. & M.

This resembles the previous species, but the lower leaves, which gradually disappear, are ovate-elliptical to broadly cordate with pinnate venation (fig. 74). They are covered with scattered stellate hairs and end in a spine. Higher up the plant the leaves become narrower with the spine longer; the uppermost leaves as well as the leaves of the rosettes are sessile and acicular as in the previous species. The leaf is not ribbed as in *A. minus* but the structure of the green tissue is almost the same. The veins have a thick bast-

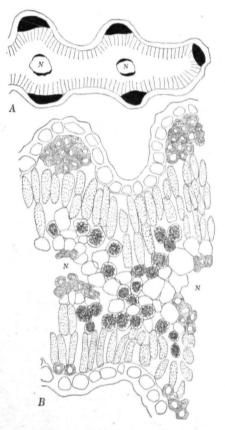


Fig. 73. Agriophyllum minus. A, Transverse section of leaf, showing the distribution of sclerenchyma (black), palisades (striped) and veins (N). B, Detail of A; N, Veins  $(A, \times 53; B, \times 203)$ .

sheath and a strand of bast runs along the margin. The stem (fig. 75) has thick hypodermal ribs of sclerenchyma and is better provided with green tissue than the previous species. Lying within the palisade tissue there is a layer of storage cells interrupted by the bast-bundles of the leptome. This genus includes a number of leaf-succulents some of which are thorny (S. Kali, aperta, sogdiana, Androssowii) while others (S. crassa, lanata, clavifolia) are thornless: also some

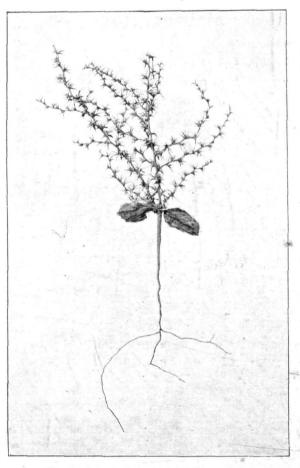


Fig. 74. Agriophyllum latifolium. June.

bracteole-succulents (comp. above p. 71), namely, Salsola spissa (fig. 8), incanescens and sclerantha.

I have examined S. sogdiana (fig. 76) and S. aperta both of which have thorny-pointed, semicircular leaves, and found them to have the ordinary centric structure like S. Kali (see WARMING 1897 p. 216). The bracteoles in *S. spissa* and *S. sclerantha* are similar in structure. The latter species is white-haired.

## Halocharis hispida C. A. M.

A clay- and salt-plant with stiff hairs which give it a greyish colour. The leaves are more or less cylindrical and long-

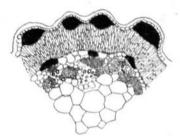


Fig 75. Agriophyllum latifolium. Part of a transverse section of stem. Bast in black, leptome crosshatched. (× 53).

haired, especially at the apex; they are very closely arranged on short-shoots arising in the leaf-axils. These short-shoots



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may stand so close at the tips of the branches that the plant becomes almost globular.

The anatomy of the leaf is of the ordinary centric type. There are two sorts of hairs: some are long stiff multicellular hairs, but more abundant are the short, stiff unicellular ones. No hypodermal layer of crystal-cells is present, but these cells are numerous in the green tissue and in the aqueous tissue. The epidermis is one-layered, with stomata slightly sunk.

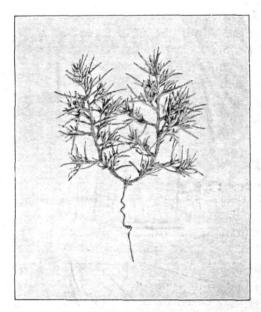


Fig. 77. Halimocnemis pilosa. July.

### Halimocnemis.

This genus is characterised by the ripening fruit, the perianth of which developes no wings or other protuberances, whereas the leaves harden and coalesce thus forming a protective cupule in which the fruit is placed. The species are true summer-plants growing on clayey and saline soil.

The habit of *H. pilosa* is illustrated (fig. 77), and related to this we have *H. macranthera* and *H. villosa*. These species

have long triangular and hairy leaves, the upper ones subtending the solitary flowers.

*H. villosa* and *macranthera*, probably also *H. pilosa*, have leaves constructed after the ordinary centric type. Since the leaf is thick the aqueous tissue in the middle is large; the midrib has a bast-sheath; the hairs consist of a basal cell and a long filamentous cell; the stomata are not sunk.

The leaves of *H. Karelini* (fig. 78), a bracteole-succulent, are similar in structure; they have very short hairs and the stomata are slightly sunk.

Closely related to the long-leaved species of *Halimocnemis* both in appearance and inner structure we have *Halanthium gamocarpum*, and probably also *Piptoptera turkestana*, the anatomy of which I have not examined.



Fig. 78. Branch of Halimocnemis Karelini, July. (Nat. size).

#### Suaeda.

The leaves of a number of species of this genus have been examined. As regards leaf-structure these may be divided into three groups.

The leaf-structure of the species of the first group is similar to that already described for *S. maritima* (see for instance WARMING 1897, p. 207, 1890, p. 221). Below the thin-walled epidermis there is a green mesophyll of palisadelike cells which become larger and contain less chlorophyll towards the interior; the veins lie in a curve in the middle of the leaf. Other species belonging to this group are: *S. setigera* and *S. Olufsenii* (from Pamir), also *S. linifolia* which differs in having flat leaves with ordinary isolateral greentissue.

The second group of Suaeda has underneath the epidermis a single layer of palisade cells all round and a starchsheath below this (fig. 79, B). Thus far these leaves follow the ordinary centric type of the Chenopodiaceae. But those veins, which in other organs of this type run obliquely through the central aqueous tissue and arrange themselves beside the starch-sheath, are here wanting. The aqueous tissue must therefore be capable of translocation and we also find that all its cells contain chlorophyll, though very little.

The veins, like those in the first group, lie in a curve with the concave side upwards (fig. 79, B). In longitudinal section they are seen to branch reticulately within the curved plane, the transverse section of which is the curve mentioned, but not outside it. To this second group belong S. pterantha, allissima, Lipskii, arcuata and dendroides.

S. microsperma is the only one of the species examined by me which belongs to the third group. As shown in

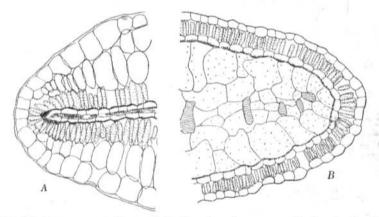


Fig. 79. Transverse sections of: A, Suaeda microsperma; B, Suaeda Lipskii. In  $\hat{B}$  the veins are indicated by horizontal hatching. ( $\times$  203).

fig. 79, A, the palisades and the starch-sheath of this species lie internal to the aqueous tissue which is quite translucent. The starch-sheath immediately adjoins the arc in which the veins run and branch.

#### Halopeplis pygmaea (Pall.) Bge.

A halophyte with sheathing and almost globular leaves. The epidermis is not very thick and the stomata are not sunk. About three layers of rather loosely arranged palisade cells are present, abutting internally on the network of finer veins which in turn are linked up with the primary vein by larger branches. Internal to this network of finer veins there is a translucent aqueous tissue. The structure of the leaf thus resembles that of *Halostachys caspica* (see above p. 201).

Some of the herbaceous plants described under C, D and E, are Halophytes e. g. Halopeplis, Suaeda, Halimocnemis, Salsola, Halocharis, Anabasis, Statice and Zugophyllum. With the exception of the two last-named they are Chenopodiaceae and have thick assimilating organs of the centric type, which is also the case with the vicarious branches of Statice. Linked with Zygophyllum we have Euphorbia Turzaninowii, both being thick-leaved and isolateral. Other representatives of the Chenopodiaceae are xerophytic plants (Cornulaca, Horaninovia, Agriophyllum, Ceratocarpus). They are spiny, with the assimilating organs thin and not succulent, but in the two first-named the same centric structure is observed. although on the whole they are better provided with sclerenchyma; to the same category belongs Dodartia. - Heliotropium and Cousinia are more nearly related to the hemicryptophytes with a more pronounced mesophytic structure (see p. 237) since they have flat leaves not much modified. Such leaves are as a rule isolateral, but dorsiventral also occur (Frankenia, Euphorbia, Crozophora).

The fruits exhibit a variety of types.

The material of herbaceous plants available is however insufficient to furnish a reliable general summary of the conditions of structure. The foregoing must therefore be regarded as a series of examples illustrating the different modes of adaptation to the conditions of life in Transcaspia.

If we endeavour, in conclusion, to summarise the features of all the plants described in this chapter, — keeping, however, in mente the Spring-plants — it is possible to formulate under three heads some of the specially characteristic features of Transcaspian desert-plants.

1. The difficulty attending the development of longlived aerial shoots. In this connection one must consider the large number of spring-plants with light-shoots which only live a short time, and also the chamaephytes and fanerophytes on which annual shoots are common, but where the persistent shoots of most species lose their distal parts.

2. Reduction of the leaves. It is a well-known feature of deserts that the leaves become small or disappear entirely. As a rule the stem assumes the part of vicar, it may be in some cases where leaves are still present, as assistant vicar, or in other cases, where leaves are entirely wanting, as deputy-vicar (B. JÖNSSON 1910). BOIRIVANT has proved by experiments a correlation between absence of leaves and formation of assimilating tissue in the stem.

The frequency of the centric type of assimilating 3. organs (in and outwith the Chenopodiaceae) and of isolateral leaves. Isolateral structure seems to be specially dependent on strong light (HEINRICHER), and it must promote the process of assimilation. The xerophytic structure of the assimilating organs is likewise a well-known feature in desert plants as recorded in the various text-books on plant-geography; see also HENSLOW 1893, with whose interpretation, however, I do not agree.

# SECTION IV. THE FLORA OF THE TRANSCASPIAN LOWLANDS.

#### CHAPTER 14

### The Elements of the Flora.

When at the beginning of the Quaternary period Transcaspia emerged from the sea which retreated towards, the West and North, a change in climatic conditions took place simultaneously in the various parts of Western Asia previously

washed by this sea. In this earlier period the climate, which was probably rather moist, had been favourable to the growth of plants and had resulted in a luxuriant and fairly homogenous flora developing over the immense area between the Himalava and the Pyrenees. When the sea disappeared the climate became dry. The plants came under the influence of a very different environment so that they were compelled to change. Only in the northern part of the Elburs and the western part of the Caucasus, near two great inland seas, are luxuriant forests still found which are regarded as the last, though perhaps somewhat altered, remnants of the old tertiary vegetation of Western Asia. The rest of the plants must either die or adapt themselves to the new conditions. At the same time the Aralocaspian lowlands, left by the sea, were open to immigration from the neighbouring countries. The result of the changes which took place was a new flora, xerophytic and especially adapted to a climate with a short vegetative period, but which was - and is - otherwise closely related to the elements of the flora of the Mediterranean lands with which they have a common origin<sup>1</sup>).

If the development took place as indicated here according to ENGLER, it is evident that the flora of Transcaspia must for the most part have originated from that of Western Asia, and that the plants must have descended from the mountainous parts towards the South and East (comp. Borsczow, above p. 30). Southern Russia cannot come under consideration as a starting point for the species which populated Transcaspia, because large tracts of it at the beginning of the guaternary period (SJÖGREN, see also KARPINSKI) were covered by water (the Aralocaspian Sea) and this "Caspian Transgression" probably originated in ice-water from the margins of the great European ice-sheet, so that the climate must have been cold. With regard to the climate of Western Siberia at that period there is no information, but it must also have been cold, colder than now, therefore the possibility of immigration from there need not be considered.

<sup>1</sup>) ENGLER 1879, pp. 57 and following, 184 and following.

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If the flora of Transcaspia originated thus from species which at the end of the tertiary period or the beginning of the quaternary period immigrated from the neighbouring mountains, it is natural to expect that many endemic species have developed. For all the factors of the lowlands, cosmic as well as terrestrial, differ from those of the highlands; besides, for many plants Transcaspia has been a closed basin enclosed towards the South and East almost everywhere by mountains — the Balchash basin being included — and barred towards the West by the Caspian, and towards the North by the cold.

A third condition favourable for the evolution of endemic species is the dryness of the climate, and consequently a very scattered plant-covering. There is no internecine struggle among the plants themselves, but always sufficient open ground available; they have only the conditions of the environment to contend with (comp. ENGLER 1882, pp. 48, 324; VAHL p. 154).

Moreover it is natural that there should be a close floristic relationship between Transcaspia and the surrounding mountainous parts. This relationship must be closest towards the South, since the country towards the East rises to a far greater height than towards the South where the natural conditions must resemble those of Transcaspia more closely.

Utilising the records of distribution given in the plantlist in chap. 12, we shall endeavour to formulate some conclusions which may be of interest with regard to these questions.

The 768 Transcaspian species enumerated in the plantlist (chap. 12) may be assigned with respect to their distribution outside Transcaspia to the following eight groups (comp. p. 138):

1. Endemic species, 169 or 22 p. cent.

2. Species distributed only towards the South (Western Asia), denoted in the list by V: 142 or 18 p. cent.

3. Species distributed only towards the North (Russia) denoted in the list by R: 29 or 4 p. cent.

4. Species distributed towards the East (High-Asia) denoted in the list by H: 83 or 11 p. cent.

5. Species distributed towards the North and South, but not towards the East, denoted in the list by RV: 56 or 7 p. cent.

6. Species distributed towards the East and South, but not towards the North, denoted in the list by HV: 68 or 9 p. cent.

7. Species distributed towards the East and North, but not towards the South, denoted in the list by HR: 52 or 7 p. cent.

8. Species distributed equally towards the East, North and South, denoted in the list by HRV: 169 or 22 p. cent.

From these statistics it follows by addition that 372 species (48 p. cent.) are distributed towards the East, 306 species (40 p. cent.) towards the North, 435 species (57 p. cent.) towards the South, while 169 species (22 p. cent) are endemic.

These figures form the basis of the following conclusions, but their accuracy must only be regarded as more or less comparative. As previously stated, the flora of Transcaspia is insufficiently investigated, and to a still greater extent is this the case with several of the neighbouring countries, especially Persia and Afghanistan. This will naturally involve mistakes in the figures given above. Another source of error is that the species are differently interpreted by the various authors who have described the plants of these countries, and no descriptive floras have been compiled for the countries in question. I have in several cases been obliged to decide according to my own judgment. Of course I believe that I am right in general, but future investigations on the flora of these countries may prove that many species which in this memoir are recorded as common to several territories ought to be divided into more species, each one endemic to its own territory, or that species which are here regarded as endemic to Transcaspia are identical with species in other countries.

The figures given above must therefore be treated with caution, and conclusions drawn from them can only be regarded as rough estimates.

As endemic species I have reckoned not only those

occurring within the territory defined in chap. 1, but also species which likewise occur in the Balchash-basin, with natural conditions which to my knowledge are almost identical with those of Transcaspia and without transition. Dsungaria, on the contrary, is left out, and species which are also found there are classed under those with an eastern distribution (denoted H). In my opinion this was necessary, firstly in order to fix a boundary between the eastern and the endemic species; secondly because Dsungaria, though much the same in character as the Balchash-basin, yet for the greater part lies higher and according to BUNGE (1880, No. 26) it also differs to some extent in phytogeographical respects from the countries lying to the west.

Nor are plants occurring in the areas north of the Aral Sea regarded as endemic. It is impossible to fix any natural well-defined boundary between Transcaspia in the south and the Kirghiz-steppe in the north, but the boundary I have selected, the  $46^{th 0}$  northern parallel of latitude, cannot be far wrong as it is confirmed in the recently published work by SAWITCH. This memoir shows that several plants which are common in Central Europe also occur in the desert north of the Aral Sea (see p. 5).

The census shows that there are 169 endemic species in the Transcaspian lowlands, that is 22 p. cent. of the total number of species. If the area had been differently defined so as to be wider in extent and to include for instance the the whole of West-Turkestan inclusive of the mountains, it is possible that the endemic percentage might be increased, but then it could not be regarded as an expression of, or to be connected with, the homogeneous natural conditions which pervade and have pervaded the Transcaspian lowlands. Since the area has been confined within such narrow limits, we must have a certain right to see such a connection, remembering, however, that the endemism is dependent not only on the number of species formed, but also on the faculty of migration and adaptation of these species. The endemism would have been still greater if the northern boundary of our territory had been moved farther north. If the Kirghizsteppe and the eastern part of Ciscaucasia to the Jergeni

mountains had been included, a number of Chenopodiaceae (e. g. Nanophylum, Alexandra, Ofaiston), Calligonum spp. and Ammodendron would be regarded as endemic. But as already indicated the natural conditions and the vegetation are rather different in these more northern areas.

The distribution of the endemic species amongst the various growth-forms will be seen from the following table 6:

	F.	Ch.	н	6	нн	Th
Endemic species p ct	17	6	32	11	0	34
Transcaspian " "	11	7	27	10	5	40

Table 6.

The endemic species are thus distributed over the growthforms in about the same proportion as the aggregate flora of the desert. The following variations may be of some interest: 1) There are no endemic aquatics and marsh-plants whatever; 2) The endemic species include comparatively greater numbers of fanerophytes and hemicryptophytes than the aggregate species; 3) The endemic species include comparatively fewer annuals than the aggregate.

The first variation is not surprising since it is well known that aquatics and marsh-plants have a wide distribution (see e. g. DRUDE p. 317).

The last point, that there are comparatively few endemic therophytes, may be explained thus: the therophytes are as a rule spring-plants, and many of these have a wide distribution because over considerable tracts of regions with winter-rains they find almost the same conditions during the short vegetative period. In accordance with this at least 28 p. cent. of the endemic therophytes are late-flowering, in comparison with 21 p. cent. of the total therophytes of the whole flora (comp. table 4, p. 162). The second point of variation suggests that the natural conditions of Transcaspia have been favourable to the development of fanerophytes and hemicryptophytes. This does not seem unnatural since the fanerophytes are one of the most prominent and apparently one of the best adapted types in the deserts. As regards the hemicryptophytes, about 30 out of 55 endemic species are spring-plants and about 25 are xerophytes (most of which, however, shed their blossoms before July 1. comp. p. 162). Unfortunately I have not been able to draw up sufficiently reliable comparative figures for the whole flora. If what has been stated about the annuals be taken as a starting point, it might be expected that the xerophytic hemicryptophytes were comparatively better represented among the endemic species than the mesophytic ones; but I am unable to decide this question.

The 169 endemic species belong to 83 different genera. Only 7 of these genera are endemic namely:

> Borszcowia Bunge. (Chenopodiaceae). Piptoptera Bunge. (Chenopodiaceae). Chartoloma Bunge. (Cruciferae). Cithareloma Bunge. (Cruciferae). Smirnowia Bunge. (Papilionaceae). Holopleura Rgl. & Schm. (Umbelliferae). Miltianthus Bunge. (Zygophyllaceae).

These genera are monotypic except *Cithareloma*, which has two species.

Of the two Chenopodiaceae, Borszcowia is closely allied to Suaeda and Bienertia, while Piptoptera is related to Halanthium and other Anabaseae. Thus both belong to groups of plants which are widely distributed in Transcaspia and surrounding countries.

The two Cruciferae are doubtless well-established genera, but both have some near relatives: Chartoloma is closely allied to Isatis, Tauscheria and Sameraria, of which Tauscheria is indigenous in the interior of Asia while the other two occur in western Asia and the eastern Mediterranean countries. Cithareloma is related to a number of oriental Hesperideae, such genera as Farsetia, Eremobium (N. Africa) and Malcolmia.

The validity of the genus *Smirnowia* likewise seems to be well-founded, in fact it stands amongst the endemic genera as one of the most isolated. It is allied to *Sphaerophysa* which likewise belongs to the interior of Asia, and to *Colutea* which is distributed from the south of Europe to the western Himalaya.

Holopleura, so far as I can learn, is insufficiently known and there may be some doubt as regards its right to generic rank. REGEL says that it is related to *Carum* and *Rumia*. Miltianthus is related to Zygophyllum.

Among the endemic species scarcely any one stands isolated. Whichever one be named, it is possible to indicate closely related species in the surrounding countries, more especially those towards the South and South-west. Through more intensive systematic studies one could probably enumerate a series of pairs of vicarious species. Studies of this kind have not been undertaken here, as I have restricted myself to the investigation of the distribution of the genera which contain endemic species in the lowlands of Transcaspia. The following genera have their main distribution in the Mediterranean countries, especially in the eastern ones, and in Nearer Asia whence some of them extend right into Central Asia.

Heliotropium	Pterotheca	Allium
Lappula	Scorzonera	Limodorum
Rochelia	Convolvulus	Cistanche
Gypsophila	Isatis	Hypecoum
Herniaria	Malcolmia	Trigonella
Saponaria	Peltaria	Crucianella
Silene	Sisymbrium	Haplophyllum
Centaurea	Crypsis	Scrophularia
Echinops	Lepturus	Tamarix
Jurinea	Lagochilus	Cachrys
Rhaponticum	Phlomis	Ferula
Matricaria	Tulipa	Valerianella

The following genera seem to have their main distribution more to the East, in the interior of Nearer Asia and in Central Asia:

Eminium	Salsola	Ammothamnuts
Acanthophyllum	Cousinia	Oxytropis •
Agriophyllum	Lachnophylium	Calligenum
Anabasis	Eremostachys	Aphanopleura
Cornulaca	Hypogomphia	Cryptodiscus
Girgensohnia	Eremurus	Hyalolaena
Halanthium	Rhinopetalum	Psammogeton
Halimocnemis	Ammodendron	Zygophyllum

The following genera have a wide distribution mainly in warm-temperate countries (or tropical):

Cleome	Aristida	Lactuca
Cuscula	Iris	
Euphorbia	Astragalus	

There still remain some large widely distributed genera:

Artemisia	Plantago	Ranunculu	S
Elymus	Delphinium	Carum	

These genera are distributed over so large an area that only a closer study could elucidate where the Transcaspian endemic species of these genera have their nearest relatives.

Leaving out of account the 6 genera last-named which are represented by 9 endemic species, all the rest of the plant genera containing endemic species in Transcaspia have their main distribution towards the South, most of them in the Mediterranean countries and in Western Asia. This is an indication that the flora of Transcaspia is closely allied to the flora of these countries.

The natural orders which contain endemic species can be ascertained by reference to the list of plants (pp. 138-158). More than one example of endemism is to be found in the following families:

• Numb • of ender specie	Percentage of total species		
Papilionaceae 31	(24 Astragalus)	36 p.	ct.
Compositae 28	(9 Cousinia, 8 Scorzonera).		
Chenopodiaceae 17	(5 Salsola)		
Polygonaceae 14	(Calligonum)	54 ,	
Umbelliferae 10		29	
Liliaceae		97	
Caryophyllaceae 8		32 ,	
Cruciferae 8		16	
Labiatae 6		30	
Zygophyllaceae 6		4.4	
Gramineae 5		11	•
Orobancheaceae 4		00	
Convolvulaceae 4		26	,
Borraginaceae 3		7	,
Ranunculaceae 3	· · · · · · · · · · · · · · · · · · ·	13 ,	
Rutaceae 3		50 ,	

Only a few orders contain no endemic species at all, for instance *Cyperaceae*, *Geraniaceae*, *Plumbaginaceae* and none of these orders are rich in species in Transcaspia.

The *Papilionaceae* take first place as regards endemism, and this is especially due to the numerous species of *Astragalus* the majority of which belong to the sub-genus *Cercidothrix* which has bifurcate hairs.

It is characteristic that several of the smaller families are comparatively rich in endemic species, thus half of the *Rutaceae* and two-thirds of the *Orobancheaceae* are endemic likewise one-thrird of the *Convolvulaceae*, *Liliaceae* etc. The one species of *Araceae* and the only Orchid are both endemic.

Endemism in Transcaspia may according to the preceding be denoted as recent, i. e. it has arisen from the development of species within a period not very remote in the geological sense. There are no forms at all standing quite isolated and showing indications of being relicts, but there are endemic species in almost all the natural orders and in several of the larger genera. The result we have arrived at does not, therefore, conflict with the theory of the migration of the flora into Transcaspia at the beginning of the quaternary period (see above p. 259). The great number of endemics moreover confirms ENGLER's assertion that dry areas (he also mentions "the Asiatic Steppes") whence a great number of plant types are excluded give rise to endemic species<sup>1</sup>).

Among the non-endemic species of Transcaspia we distinguish between those which have a northerly, those which have an easterly and those which have a southerly distribution (see above p. 260).

Northerly distribution is seen in such species as are distributed from Transcaspia over western Siberia and South Russia. The limit is fixed at about 46° N. Lat. (see above p. 262). Of such plants there are 306 or 40 p. cent. of all the species of Transcaspia; in the plant-list they are the species with the letter R included in the distribution-index. This is no small number, but the importance of the figure is lessened when we remember; (1) that with the exception of 29 of the 306 (9 p. cent.), they are equally distributed towards the east and south; (2) that only 96 species (12 p. cent. of the total number of species) are common to both Transcaspia and the government of Yekaterinoslaw, (these are indicated in the list by R\*). The first of the above points emphasises that the species occurring towards the North are on the whole widely distributed. The 29 species referred to (those indicated in the list merely by R) do not even extend far northwards, only one of them (Erodium Hoefftianum) is found as far north as Yekaterinoslaw. Most of them occur on the Kirghiz steppe which as already stated is very similar to Transcaspia. Nor do many of the remaining plants with a northern distribution reach the true steppe or forest areas.

As regards the second point (2), the number of species common to Transcaspia and Yekaterinoslaw, it may be remarked that, with the exception a few *Chenopodiaceae* and *Lycium* and *Statice*, the species common to both countries

<sup>1</sup>) 1879 p. 10, 1882 p. 50.

belong to the mesophytic aspect, and that all except *Erodium Hoefftianam* are species with a wide distribution; only a small number of them have not also an easterly and a southerly distribution in relation to Transcaspia.

Easterly distribution is seen in the plants occurring in the mountainous countries towards the East, i. e. from Hindukush, Badakshan, Hissar, Pamir to Tibet, Tianshan and Dsungaria (comp. p. 262). This category includes 372 plantspecies or 48 p. cent. of the total species of Transcaspia (in the list the letter H occurs in their distribution-index). Of these 372 species, 83 or 22 p. cent. are not distributed towards the North and South (indicated in the list by H alone). Many of the 372 species occur only in Dsungaria, (as to the similarity and dissimilarity between this country and the Balchash-basin see p. 262). As a test of the distribution of Transcaspian lowland plants over really high mountains, I have summed up the species this country has in common with the Pamirs (according to the boundaries given by OLGA FEDTSCHENKO). Such species are denoted in the list by H\*, and there are 41 (5 p. cent. of the total number of species). Only a few of these (Nitraria and a few Chenopodiaceae) belong to the xerophytic aspect. They are all species of wide distribution, and most of them also occur both towards the North and South.

Southerly distribution is seen in plants which beyond Transcaspia are distributed over larger or smaller parts of Afghanistan (Badakshan, however, being reckoned as part of High-Asia), Persia, Asia Minor, Syria and onwards to the Mediterranean countries, including North Africa.

There are.435 plants or 57 p. cent. with a southerly distribution — their distribution-index in the list contains the letter V — against 46 p. cent. with a northerly and 48 p. cent. with an easterly distribution. Thus more than half the plants of the Transcaspian lowlands have a southerly distribution. Of the 435 species, 142 or 33 p. cent. (18 p. cent. of the total number of species) have no distribution towards the North or East, they are thus Western-Asiatic species which avoid the higher mountains and the higher degrees of latitude. (In the list they are indicated by V alone). Recapitulating the above, we have that the "northerly" plants include only 9 p. cent. which are exclusively northern, the "easterly" ones 22 p. cent. exclusively eastern, while the "southerly" plants include 33 p. cent. exclusively distributed towards the South.

These figures as in the case of the percentage for the total distribution, show that the Transcaspian lowlands are most closely related to the countries lying towards the South and South-West, and most distantly related to the countries lying towards the North. This is the case though the Transcaspian lowlands towards the North are open and without any natural boundary, while in every direction towards the South they are hemmed in by mountains.

This result is further confirmed if we take into consideration the species which the Transcaspian lowlands have in common with Syria and Palestine (166 species, Post, indicated in the list by V\*), or with Egypt (91 species, ASCHERSON & SCHWEINFURTH); that is respectively 22 and 12 p. cent. of the total number of species. About one-third of these (Syria 30, Egypt 29 p. cent.) do not occur either east or north of Transcaspia, and less than half of them (Syria 39, Egypt 41 p. cent.) are widely distributed species which are also found north and east of Transcaspia.

Compare with this what has been stated about species common to Yekaterinoslaw and to Pamir. Here almost all the species in common have a wide distribution; this community therefore indicates a more distant relationship than that between areas with species in common which show a more limited distribution.

Though derived from imperfect and somewhat scanty materials, our figures point in the right direction, as they have shewn us that the Transcaspian lowlands in their floristic as well as their biological aspects (comp. above p. 160) are more closely related to the countries towards the South. This result will probably be further confirmed by future systematic investigations within the individual genera or families. Such investigations are already being carried on, and we may illustrate them by a short summary of Professor KUSNEZOW's interesting investigations on *Rindera* Pall., a genus of *Borraginaceae*. As the result of careful morphological and anatomical studies of the species of *Rindera*, it appears that the subgenus *Mattia* is the "central-type" of the genus, from which the sub-genera *Cyphomattia* and *Eurindera* have developed each in its own way.

KUSNEZOW presumes that the ancestors of *Rindera* (and *Paracaryum*) at the beginning of the tertiary period were widely distributed over the earth; the last remnants of them are the two existing monotypes: *Tysonia* in south-eastern Africa and *Myositidium* in New Zealand.

During the latter half of the tertiary period *Rindera* must have been widely distributed in the Mediterranean countries (from Spain to Central Asia), and the genus at that period had two sub-genera: *Mattiaria* (now one species) and *Mattia* (now 6 species). These seven species are constant with no intervening transitions, and they have small and well-defined areas of distribution from Algeria to Persia, — they must be regarded as relict forms.

At the end of the tertiary period when the lowlands were drying up, KUSNEZOW considers that the five species of the sub-genus *Eurindera* were evolved in the mountains of Turkestan; these species are harder to distinguish than those of *Mattia*. One of them, *Rindera tetraspis*, had the faculty of migration so that after the drying-up of the Transcaspian lowlands it was able to propagate here as well as in Western Siberia, South Russia and Ciscaucasia.

Simultaneously with *Eurindera*, there came into existence in Nearer Asia from *Mattia* the two species of the sub-genus *Cyphomattia* of which one, *Rindera lanala*, is very polymorphic and widely distributed.

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