4.

Saxifragaceæ.

2. The Biological Leaf-anatomy of the Arctic species of Saxifraga.

By

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INTRODUCTION.

A biological-anatomical description of the Arctic species of *Saxifraga* must essentially have reference to the foliage-leaves, as they are the organs which most distinctly bear the impression of external factors in nature. The roots were less suitable for anatomical investigation in the material which has been within my reach. All the material which I have had for examination has been placed at my disposal by the director of the Botanical Museum in Copenhagen.

The literature of the subject does not contain much regarding the leaf-anatomy of the genus *Saxifraga*. ENGLER was the first to give a more exhaustive account of it in his monographic treatment of the whole genus (Breslau, 1872. See list of literature). He does not treat the individual species anatomically, but confines himself to a kind of comprehensive characterization, without entering more fully into the peculiarities of the different species. The genus is treated in very much the same way by THOUVENIN (1890) and LEIST (1890). (I have unfortunately been unable to have access to a paper by WALDNER (Graz, 1885) on the "lime-druses" of the *Saxifragas*).

The first three works mentioned above give, therefore, only very scattered data regarding the species we are here considering, and treat them according to systematic principles, without discussing the connection between structure and biological conditions.

More exhaustive descriptions are given by LEIST (1889), BONNIER (1894), BØRGESEN (1895), LAZNIEWSKI (1896). These works aim particularly at elucidating the relation between habitat and anatomical structure, — LEIST and LAZNIEWSKI with regard to the Alpine, BØRGESEN with regard to the Arctic plants. BONNIER compares Alpine with Arctic specimens of the same species; among the many examples he gives, he mentions only one *Saxifraga (S. Aizoon)*. FREIDENFELT (1904) occupies himself with the root-anatomy of a few species, considering them to a certain extent from a biological point of view. HOLM (1885) mentions the anatomy of several Arctic species,

and I shall have occasion to refer to his work in the following pages. LINDMARK (1902), also, has made a few anatomical observations on the subject.

It is beyond the scope of this paper to discuss more fully the contradictory conclusions which previous authors have considered might be drawn from their studies of Alpine plants; here it will suffice for me to give the names of the contending parties (BONNIER, LEIST, WAGNER and LAZNIEWSKI) in the list of literature, and also STENSTRØM who has, in a very comprehensive manner, studied and discussed the questions here under consideration. Quite recently SCHROETER (1904—08) has published some valuable observations upon Alpine *Saxifragas*. The investigations of these authors have been taken into consideration only in so far as they have touched upon Arctic species.

Here we are only concerned with those Arctic species which have been partially investigated by TH. HOLM and F. BØRGESEN. I shall not enter more closely into the general and comprehensive results which BØRGESEN gives in his paper.

The specimens investigated by me are the following: —

Saxifraga aizoides L. . . . . p. 266
— *Aizoon* Jacq. . . . . p. 280
— *cernua* L. . . . . p. 242
— *Cotyledon* L. . . . . p. 276
— *flagellaris* Willd. . . . . p. 269
— *groenlandica* L. . . . . p. 261
— *hieraciifolia* W. K. . . . . p. 253
— *hypnoides* L. . . . . p. 258
— *nivalis* L. . . . . p. 250
— *oppositifolia* L. . . . . p. 285
— *rivularis* L. . . . . p. 246
— *stellaris* L. . . . . p. 255
— *tricuspidata* Rottb. . . . . p. 273

These belong to six different sections. Common to all the species is a leaf-venation which is either palmate or appears to have been derived from the palmate type even in such divergent forms as S. *aizoides* and *oppositifolia*, the relatively serrate and entire leaves of which, with regard to venation and form, are connected by gradually transitional forms (especially *S. tricuspidata*) with the palmate leaf of, for instance, *S. cernua*. Moreover,

hydathodes are present in all the species. Consequently, the principal form (the type) had probably palmately-veined leaves with hydathodes. Nearest to this type-form are the mesophytic species with large leaf-blades, distinct leaf-stalks and marked differentiation between palisade-tissue and spongy parenchyma (the sections *Boraphila*, *Nephrophyllum*, and *Dactyloides* in part); less close to the type are the more decided xerophytes, with leaf-rosettes, narrow leaf-blades, etc. (the sections *Trachyphyllum*, *Euaizonia*, *Porphyrion*).

The following is a list of the chief literature upon the subject: —

Bonnier: Recherches expérimentales sur l'adaptations des plantes au climat alpin (Ann. des sc. nat., VII sér., T. XX) 1895.

— Les plantes arctiques comparées aux mêmes espèces des Alpes etc. (Révue gén. d. bot., T. VI) 1894.

Børgesen, F.: Bidrag til Kundskaben om arktiske Planters Bladbygning (Bot. Tidsskrift, Bd. 19) 1895.

Engler, A.: Monographie d. Gattung Saxifraga. Breslau, 1872.

Freidenfelt: Der anatomische Bau der Wurzel etc. (Bibliotheca botanica, Heft 61) 1904.

Holm, Th.: Novaja-Zemlia's Vegetation, særligt dens Phanerogamer. (Dijmphna-Togtets zool.-bot. Udbytte, København, 1885).

Lindmark: Bidrag til kännedomen om de svenska Saxifraga-artens yttre byggnad. (Bihang till k. svenska Vet.-Akad. handl., Bd. 28, Afd. III, Nr. 2) 1902.

Lazniewski, W. v.: Beitr. z. Biol. d. Alpenpflanzen (Flora) 1896.

Leist: Ueber den Einfluss des alpin. Standortes auf die Ausbildung d. Laubblätter (Separat-Abdruck aus Mittheil. d. Naturf. Gesellsch. von Bern) Bern, 1889.

— Beitr. z. vergleich. Anat. d. Saxifragen (Bot. Centralblatt XLIII) 1890.

Norman, J M.: Norges arktiske Flora, II, 1895.

Rosenvinge, L. Kolderup: Andet Tillæg til Grønlands Fanerogam- og Karsporeplanter. (Meddelelser om Grønland, III) (separate copy) 1892.

Schroeter: Das Pflanzenleben d. Alpen. Zürich, 1904—08.

Stenstrøm: Ueber das Verhalten derselben Arten in verschiedenen Klimaten etc. (Flora) 1895.

Thouvenin: Recherches sur la structure des Saxifragacées (Ann. d. sc. nat., sér. VII, T. II) 1890.

Wagner, A.: Zur Kenntniss des Blattbaues d. Alpenpflanzen etc. (Sitzungsber. d. Wiener-Akad., Bd. CI, Abth. I) 1892.

Warming, E.: Grønlands Vegetation. (Meddelelser om Grønland, Hefte XII) 1888.

1. *Nephrophyllum.*

The two species of this group which have been investigated agree in the following points: — (1) The leaves are stalked and palmately lobed, (2) the epidermis has undulating radial walls, (3) glandular hairs are present, (4) the cells of the spongy parenchyma are decidedly stellate (without a compact layer of tissue under the epidermis), (5) the hydathodes are exactly marginal, without a cavity and without secretion of lime.

The species differ most in regard to the thickness of the outer walls of the epidermis, and the more or less decidedly stellate form of the cells of the spongy parenchyma. The two species can easily be distinguished from each other by these features, while, however, their mutual relationship is very distinctly expressed in their anatomy. A key to their determination by their leaf-anatomy would be as follows: —

Outer walls of the epidermis: —

(a) thin (2—3 μ): *S. cernua.*

(b) irregularly thickened (as much as 8—10 μ): *S. rivularis.*

Glandular hairs: —

(a) long-stalked upon the upper, and short-stalked upon the lower surface: *S. cernua.*

(b) similar upon the upper and lower surface: *S. rivularis.*

Saxifraga cernua L. (Figs. 1 and 2).

This species according to Norman (l. c., pp. 303—04) is a decidedly Arctic plant which extends beyond the tree-limit 697 metres and upwards. Grows both upon flat and sloping ground, as commonly on the northern as on the southern side, more rarely on the eastern and western sides. It prefers cold and damp localities, among moss, along the banks of rivers, upon stones in rivers, etc., and must be characterized as decidedly hygrophilous.

The leaves are long-stalked, reniformly-palmately lobed

with 5—7 lobes. Each lobe terminates in a hydathode (Fig. 1 *A*). Along the margin and upon both surfaces glandular hairs occur, long upon the upper surface and short upon the lower (Fig. 2 *E.*)

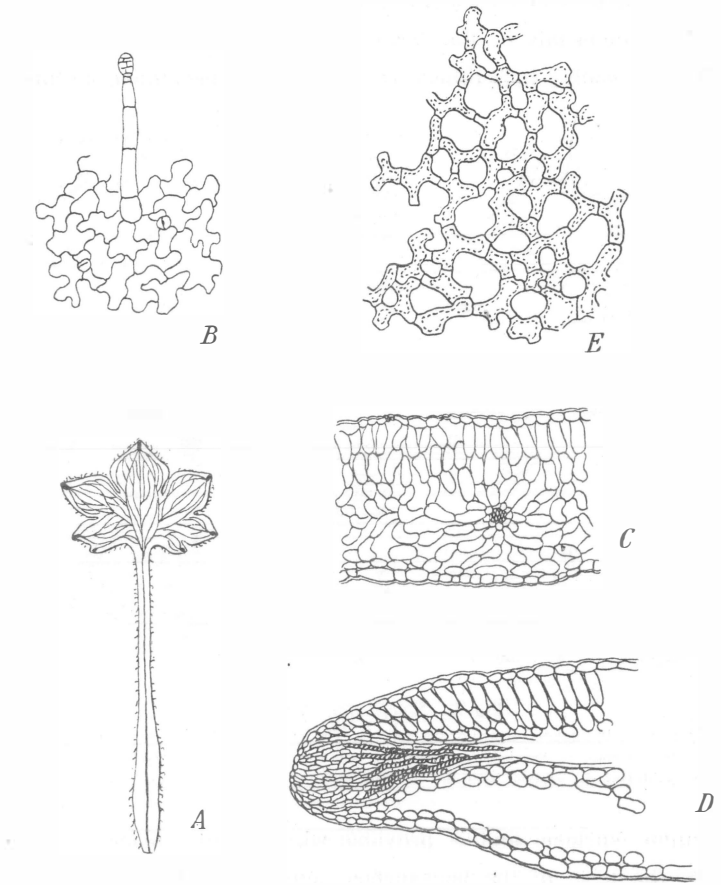

Fig. 1. *Saxifraga cernua.*
A (3/2), Leaf-form. *B*, Upper epidermis with a glandular hair. *C*, Transverse section of leaf. *D*, Longitudinal section of leaf-apex with hydathode. *E*, Spongy parenchyma. (*B*, *C*, *D* and *E* 50/1).

The epidermis of the upper surface consists of cells with undulating walls (Fig. 1 *B*), the lateral and outer walls of which are thin (2—3 μ). Cuticle is very slightly developed. The epidermis of the upper surface is provided with stomata which project above

the leaf-surface and also with scattered, long-stalked glandular hairs. Børgesen (l. c., pp. 225—26) states that the stomata are most numerous upon the upper surface, where there are 10 per unit of surface, while on the lower surface only 8.

The epidermis of the lower surface has even more strongly undulating walls; it is otherwise very slightly developed (as upon

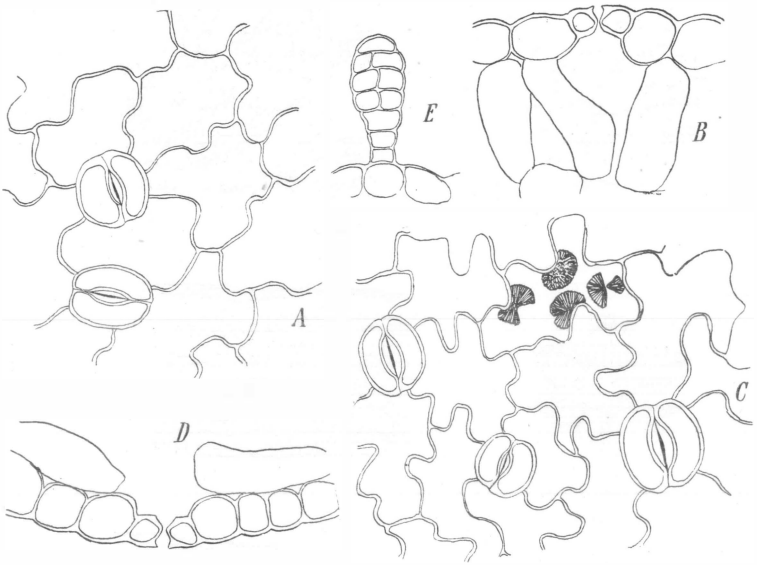

Fig. 2. *Saxifraga cernua.*
A, Epidermis of the upper surface of the leaf. *B*, The same in vertical section. *C*, Epidermis of the lower surface of the leaf (in a solitary cell several crystal-aggregates are seen). *D*, Lower epidermis in vertical section. *E*, Hair from the lower surface of the leaf ($^{282}/_{1}$).

the upper surface) and is provided with stomata, placed slightly above the level of the leaf-surface, and short-stalked glandular hairs exactly similar in appearance to those upon the margin of the leaves (Fig. 2 *E*).

The mesophyll is very loosely arranged, with large and numerous intercellular spaces (Fig. 1 *C*). The palisade-cells form indistinct rows and, in the greater part of the leaf, are placed almost vertically within the epidermis while towards the apex of the veins they are placed somewhat obliquely — a circumstance

which has been exhaustively discussed by Lazniewski (l. c.) in regard to rosette-plants and which we shall find again in the very decidedly rosette-forming species (*S. Cotyledon*, *Aizoon*, etc.). The 2—3 palisade-layers are differenced, but not very distinctly, from the cells of the spongy parenchyma, which are decidedly stellate (i. e. branched), long, and loosely arranged (Fig. 1, *E.*)

The veins are not accompanied by mechanical tissue, but are surrounded by a (usually one-layered) bundle-sheath of elongated cells devoid of chlorophyll (Fig. 1 *C*).

All the veins at the apices of the leaves terminate in a hydathode. The epithema is interwoven, and enveloped by the spirally thickened tracheids of afferent veins and is covered with a small-celled epidermis with water-pores. Lime-secretions were totally absent from the Arctic specimens examined by me. The surface of the epithema is convex and situated directly at the edge of the leaf-margin; a hydathode-cavity is absent (compare, *S. oppositifolia*, *S. Aizoon*, etc., the hydathodes of which open upon the upper side of the leaf-margin and have a cavity). Fig. 1 *D*.

The leaves of the bulbils are morphologically somewhat different; a gradual transition may be traced from entirely bladeless scale-leaves to bulb-scales with rudimentary leaf-blades which have entire margins, and ultimately to bulb-scales with a small three-lobed blade (the cells of which are devoid of starch-grains although the latter occur in quantities in the leaf-base).

The bulb-scales are without hydathodes. The cell-walls of the lower epidermis are almost straight; no stomata were found by me although they were found by Th. Holm (l. c., p. 47). The hairs are similar to those upon the lower surface of the foliage-leaves.

The cell-walls of the upper epidermis are straight, and there are no stomata. The hairs are similar to those upon the upper surface of the foliage-leaves.

All the cells of the mesophyll are alike, isodiametric and closely filled with starch-grains.

There is a solitary vein with a one-layered bundle-sheath devoid of starch.

The structure of the foliage-leaf and bulb-scale here described I found to be identical with that of the specimens from Módruvellir in Iceland, and Egedesminde in Greenland.

As already mentioned, this species is hygrophytic in its choice of localities. Its anatomical structure is in distinct conformity therewith: Stomata (projecting above the level of the leaf-surface) on both sides; thin epidermis, — in short, no means of protection against excessive transpiration.

Saxifraga rivularis L. (Figs. 3 and 4).

Saxifraga rivularis L. is a decided mountain-plant which occurs most frequently on sloping ground, more numerously upon the shady than upon the sunny side. Probably grows usually in damp localities, and in the choice of its localities is almost exactly like *S. cernua* (Norman, l. c.).

The leaf is reniform and palmately-lobed, with usually 5 lobes, each provided with a hydathode at its apex (Fig. 3 *A*). Glandular hairs occur sparsely upon both surfaces.

The epidermis of the upper surface consists of large cells, which have slightly undulating walls and thin lateral and inner walls and irregularly thickened outer walls (Fig. 4). Cuticle thin. Stomata numerous and prominent. Glandular hairs are scattered over the whole surface, but are not abundant. Børgesen (l. c., p. 225) states that the stomata are most numerous upon the upper side, but yet he mentions (l. c., p. 226) having found 9 per unit of surface upon both the upper and lower surface.

The epidermis of the lower surface is almost exactly like that of the upper, but the cells are somewhat larger, and the walls more undulating (along the veins, however, to a less degree than outside them). (Fig. 4 *A, C.*)

The stomata here also are placed very slightly above the level of the leaf-surface; they are most numerous outside the veins (in the angles between the lobes), but are not entirely absent from along their length.

The mesophyll is exactly like that of *S. cernua*. What has been said above of the palisade-cells, spongy parenchyma and veins of the latter species will apply without any alteration to the

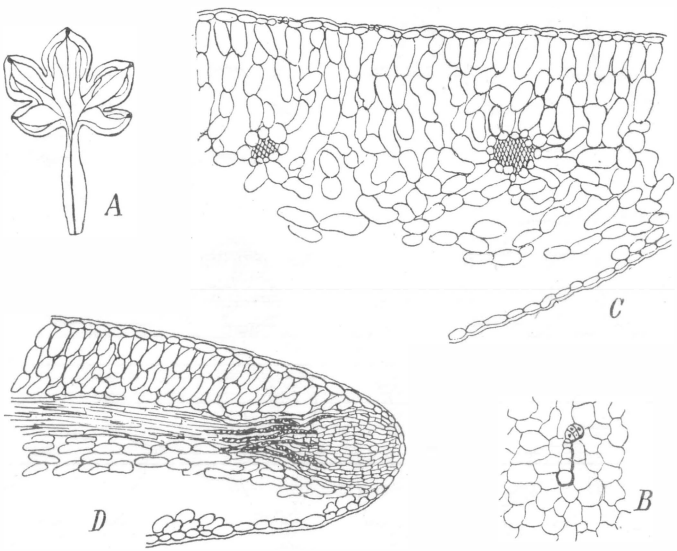

Fig. 3. *Saxifraga rivularis*.
A, (2/1) Leaf-form. *B*, Upper epidermis. *C*, Transverse section of leaf. *D*, Longitudinal section of tip of same with hydathode. (*B*, *C*, and *D* 50/1).

present species also. The palisade-cells in this plant also are oblique; BØRGESEN evidently did not observe this feature, neither does he describe the hydathodes; the latter are exactly like those of *S. cernua*. It is extremely interesting to note how the modes of life of these two closely-allied species are reflected, with such close correspondence, in the anatomical structure of their leaves.

The material upon which the description here given is based, comes from the following localities: — Jan Mayen (July 22,

1896), Mödruvellir (Iceland, May 19, 1889), Upernivik (July 18, 1886), Danmarks Ø (Aug. 1, 1892), Frederikshaab (June 8, 1888), Malersomiarfik (July 6), Nova Zembla and Tromsø (June 26,

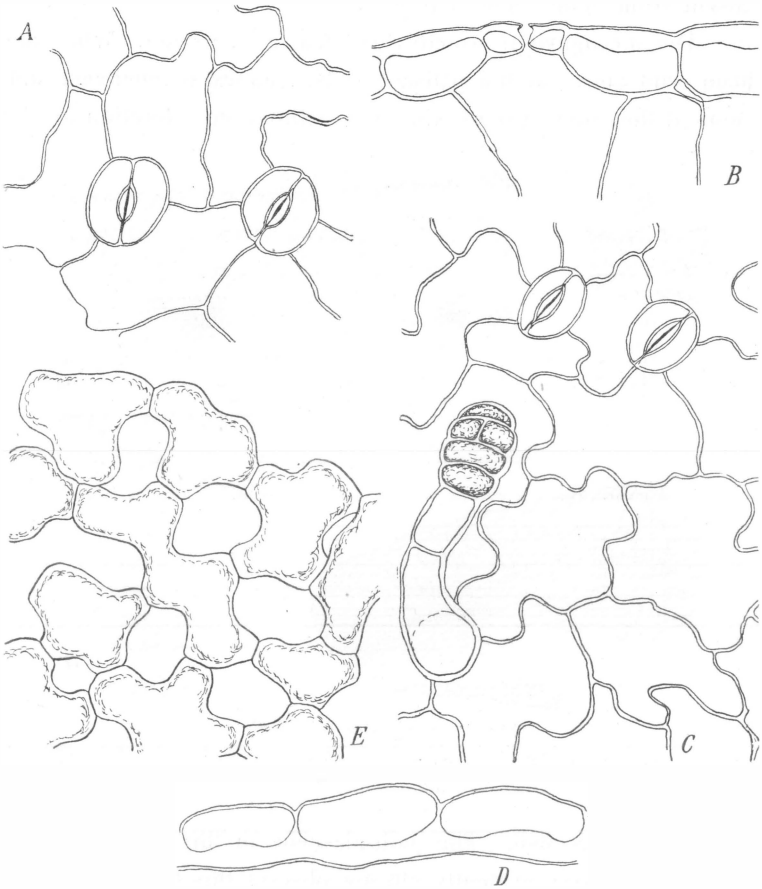

Fig. 4. *Saxifraga rivularis.*
A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same. *E*, Spongy parenchyma. (*A*, *B*, *C*, *D*, and *E* $^{282}/_{1}$).

1885); therefore from Norway, Iceland, Nova Zembla, Greenland and Jan Mayen. In spite of the widely separated localities of the individuals they were all absolutely identical in regard to leaf-anatomy. The specimens which have been investigated

give no insight into possible seasonal differences; they were all collected between the end of June and the beginning of August.

Lastly, I may add, that I have examined numerous roots of this plant, without finding any kind of mycorhiza; but this also, no doubt, could scarcely be expected to be found.

2. *Boraphila.*

The three species of this group agree closely in the following features: — (1) Epidermis with undulating walls, (2) glandular hairs, (3) marked difference between the palisade-tissue and the spongy parenchyma (the spongy parenchyma varying from cells which are slightly branched, but arranged in irregular meshes and rows, with larger intercellular spaces (*S. stellaris*) — to much branched ("stellate") cells in the species *S. nivalis* and *S. hieraciifolia*; compact spongy parenchyma immediately beneath the epidermis does not occur), (4) hydathodes exactly like those in the section *Nephrophyllum.* The differences are as follows: —

Hairs: —

Two kinds (i. e. both glandular hairs and marginal non-glandular hairs): *S. nivalis* and *S. stellaris.*

Glandular hairs only: *S. hieraciifolia.*

Spongy parenchyma: —

(1) very loosely arranged, consisting of unbranched and branched cells, in rows of irregular length, the main direction of which is parallel to the longitudinal axis of the leaf: *S. stellaris.*

(2) all the cells of the spongy parenchyma branched: *S. hieraciifolia* and *nivalis.*

It can therefore be seen that the leaf-anatomy of this section corresponds closely with that of the section *Nephrophyllum.* It is in reality impossible, on the basis of our knowledge

of the species of which the investigation is here recorded, to point out any anatomical difference which characterizes the whole of the one section in contradistinction to the whole of the other.

Saxifraga nivalis L. (Figs. 5 and 6).

Saxifraga nivalis L. occurs far above the tree-limit in Arctic regions, where (according to NORMAN) it usually grows on

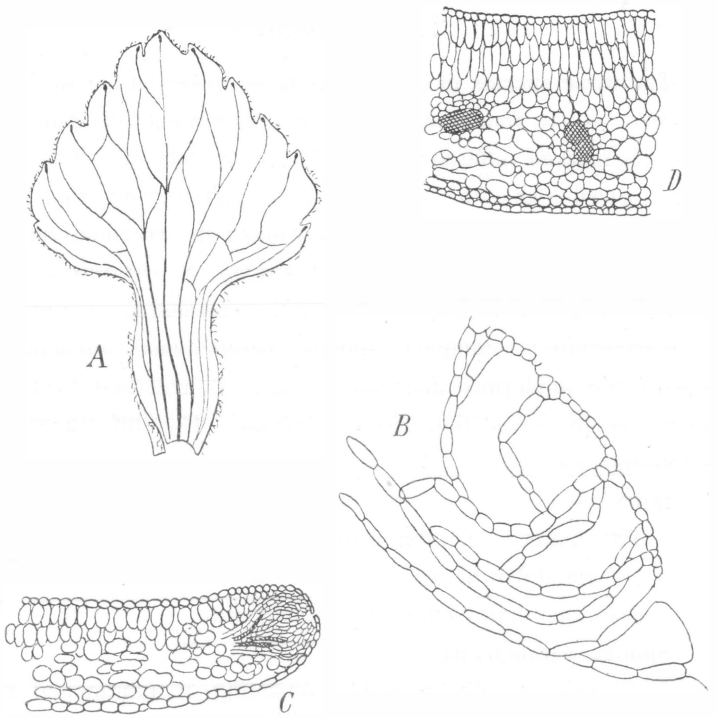

Fig. 5. *Saxifraga nivalis*.
A (2/1), Leaf-form. *B*, Hairs from leaf-margin. *C*, Longitudinal section of leaf with hydathode. *D*, Transverse section of leaf. (*B*, *C*, and *D* 50/1).

sloping ground, three times more commonly on the sunny side than on the shady side; it usually grows in dry localities, more rarely in damp. M. PORSILD informs me verbally that in Greenland it is found among damp moss and upon cliffs wetted by spray. The plant according to my judgement is fairly distinctly

mesophytic in its anatomical structure. The leaves are cordate, with a hydathode at the apex of each tooth. (Fig. 5 *A*.)

The epidermis of the upper surface consists of cells which have undulating walls and thin (about 2 μ) lateral, inner and

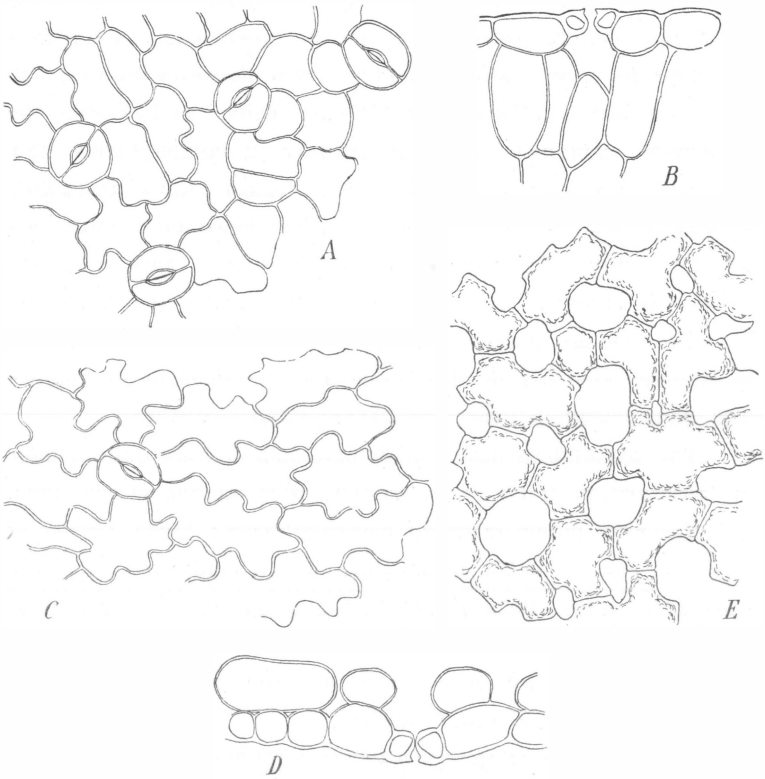

Fig. 6. *Saxifraga nivalis.*

A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same. *E*, Spongy parenchyma. (*A*, *B*, *C*, *D* and *E*, $^{262}/_{1}$).

outer walls. Cuticle very slightly developed. Stomata numerous, and prominent (Fig. 6, *A*, *B*).

The epidermis of the lower surface is almost similar to that of the upper; but the cells are a little larger, and the lateral walls are somewhat more undulating. The stomata are precisely similar to those of the upper surface (Fig. 6, *C*, *D*).

Dr. Børgesen states that the stomata are equally abundant on both sides (l. c., p. 225); he has however counted 17 upon the upper surface, and 20 upon the lower per unit of surface (l. c., p. 226).

The mesophyll is fairly distinctly differentiated into a palisade-layer and spongy parenchyma; in the specimens examined by me there are three distinct palisade-layers (Børgesen found 2—3). The presence of these three layers, which implies that the specimens examined had been growing in comparatively ligh localities, harmonizes excellently with Norman's above-mentioned statement that the species occurs three times more commonly on the sunny side than on the shady side (I have not seen "shade-specimens," but Børgesen has evidently found them).

The spongy parenchyma is loosely arranged and consists of stellate cells (Fig. 6). The veins are accompanied by colourless, long-celled, usually one-layered bundle-sheaths.

The hydathodes have convex epithema and are quite similar in structure to those of *S. cernua*; they do not secrete lime.

Børgesen found scattered glandular hairs; these consist of a single row of cells, terminating in an undivided, obovate, one-celled head. Holm (l. c. Pl. X, Fig. 9) has figured a glandular hair with a two-celled head, — a feature which I have not met with. The hairs are more abundant upon the lower, and few in number upon the upper, surface.

The structure of the leaves is essentially the same in specimens from all the localities from which material has been examined; thus, I have more closely investigated specimens from Upernivik (July 10, 1887), Hold with Hope (July 10, 1891), Julianehaab (June 14, 1887), Dyrefjord (June 10, 1895), and Tromsø (June 28). The only deviation from the description given above was observed in the specimens from Hold with Hope and Dyrefjord, all of which contained a considerable quantity of oxalate of lime as crystal-aggregates in the cells of the spongy

parenchyma near to the bundle-sheaths of the veins at the base of the leaf.

As may thus be seen, the structure of the leaf is distinctly mesophytic or perhaps even hygrophytic; the prominent stomata upon both leaf-surfaces, the thin-walled epidermis, and the loose structure of the spongy parenchyma show this. The agreement between the structure of the leaf and the character of the habitat, as it has been described to me by M. Porsild, is unmistakable.

Saxifraga hieraciifolia W. K. (Figs. 7 and 8).

Saxifraga hieraciifolia W. K. occurs in precisely the same localities as *S. nivalis* (according to verbal information from M. Porsild), and it should be expected to have a structure similar to that of the latter; that it has it will be more clearly proved by what follows.

The leaf is long-stalked, oval, with distant teeth and a hydathode at the apex of each tooth (Fig. 7). The thickness is slight, less than in *S. nivalis*.

The cells of the epidermis of the upper surface (Fig. 8 *A* and *C*) have undulating walls, and rounded, wavy contours; all the walls are thin, with cuticle very slightly developed. The stomata are numerous, and prominent. Scattered glandular hairs occur which consist of a single row of cells with a one-celled head.

The epidermis of the lower surface (Fig. 8 *B* and *D*) is essentially like that of the upper; but the undulating outline of the lateral walls is more acutely angled. Stomata are numerous, and prominent. Børgesen writes that there are as many upon the upper as upon the lower surface, but yet, at the same time, records seven upon the upper and twelve upon the lower surface per unit of surface.

The mesophyll (Fig. 7 *B*, *C* and *D*) is distinctly differentiated into palisade-tissue and spongy parenchyma. Børgesen found 2—3 layers; my specimens showed two; nowhere in the leaf are they placed obliquely. The cells of the spongy parenchyma

are stellate, the whole of the tissue is highly lacunose. The veins are without mechanical tissue, but are accompanied by colourless, long-celled bundle-sheaths. The hydathodes are precisely similar in structure to those of *S. nivalis*, exactly marginal, with convex epithema; they secrete no lime (Fig. 7 *C*).

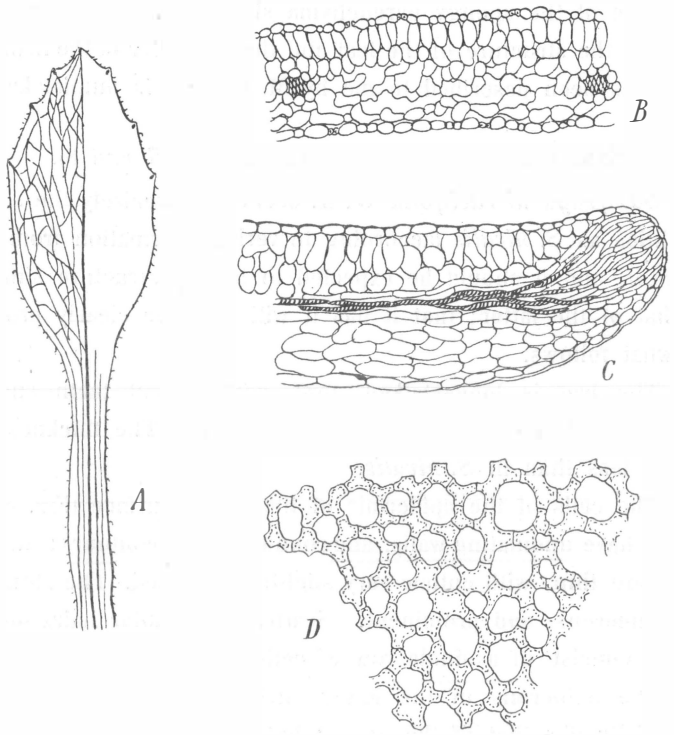

Fig. 7. *Saxifraga hieraciifolia.*
A (3/2), Leaf-form. *B*, Transverse section of leaf. *C*, The same in longitudinal section (with hydathode). *D*, Spongy parenchyma. (*B*, *C*, and *D* 50/1).

In its choice of localities this species probably nearly agrees with *S. nivalis*. In its structure (as may be seen from the above) it is more typically mesophytic than that species, the whole of its mesophyll being even more loosely arranged. Its means of protection against excessive transpiration are as slightly developed as those in *S. nivalis*; it can be distinctly seen that the palisade-tissue is less developed than in *S. nivalis*, —

from which it may perhaps be concluded that this species does not grow in quite as light localities as does *S. nivalis*.

Only specimens from Nova Zembla and Cape Tscheljuskin have been at my disposal; they were precisely similar in structure.

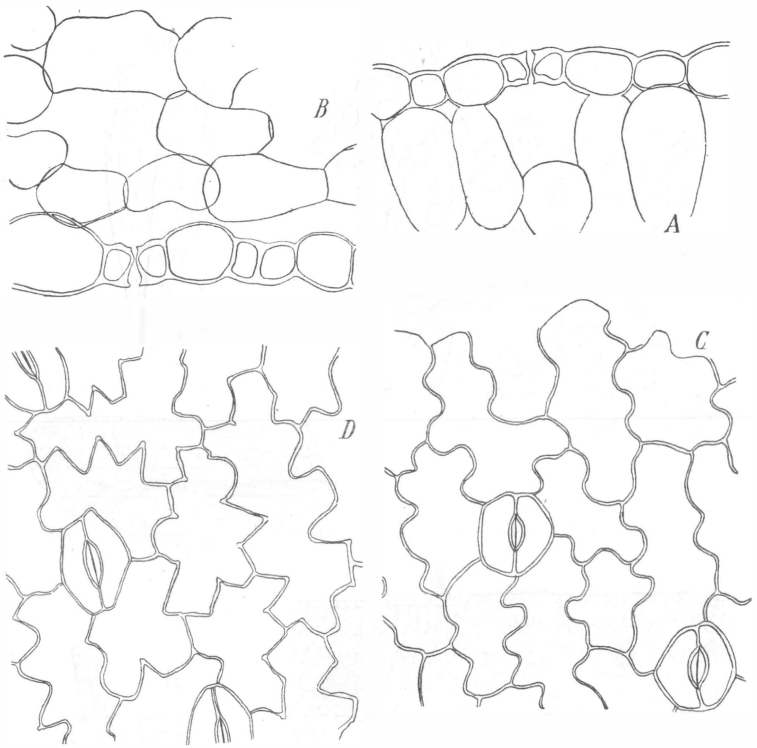

Fig. 8. *Saxifraga hieraciifolia.*
A, Upper epidermis. *B*, Lower epidermis. *C*, Upper surface. *D*, Lower surface ($^{282}/_{1}$).

Saxifraga stellaris L.

Saxifraga stellaris L. (Figs. 9 and 10) grows generally at very considerable heights on damp and cold ground, among moss, in clefts of rocks, along streams, in short it is a moisture-loving plant, as is also distinctly indicated by the anatomy of the leaf.

The leaf has slight and distant teeth and a hydathode at the apex of each tooth (Fig. 9). The epidermis of the upper surface

Fig. 10 *A* and *B*) has undulating walls which are thin everywhere. The outer walls are also thin, and have a distinct cuticle. Stomata are numerous, uniformly distributed, and prominent.

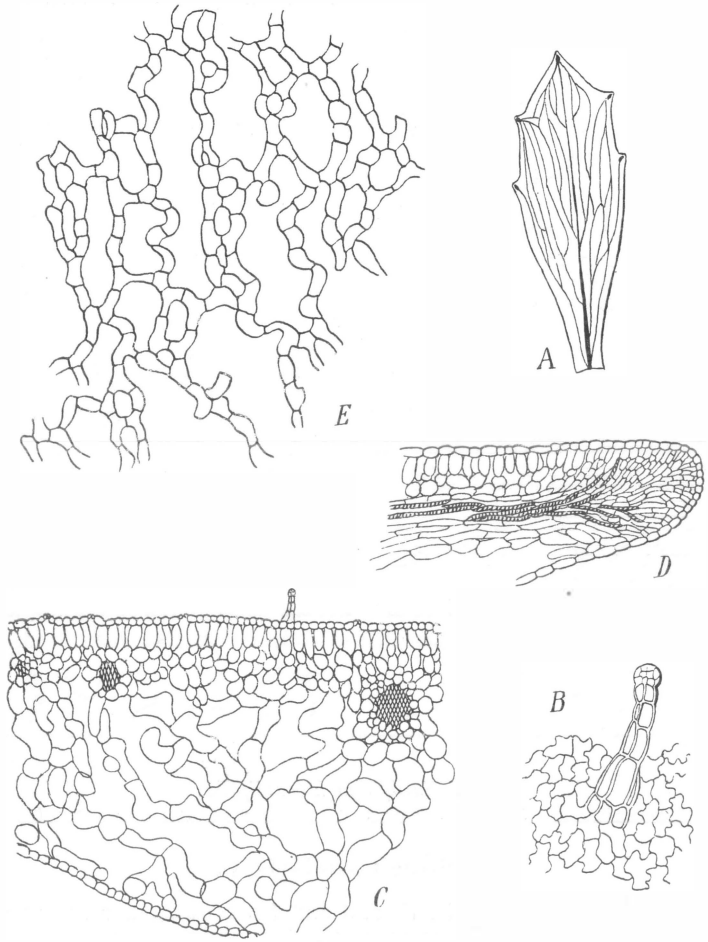

Fig. 9. *Saxifraga stellaris.*

A (2/1), Leaf-form. *B*, Epidermis of the upper surface of the leaf. *C*, Transverse section of leaf. *D*, Longitudinal section of leaf. *E*, Spongy parenchyma. (*B*, *C*, *D* and *E* 50/1).

Glandular hairs occur scattered over the whole leaf-blade; a definite head is wanting to some of the marginal hairs (Fig. 9).

The epidermis of the lower surface (Fig. 10 *C* and *D*) closely

resembles that of the upper, but the cells are greatly elongated just above the veins and at that place stomata are wanting. The stomata are placed both upon the upper and lower surface, with their apertures principally in the direction of the length of the leaf. Glandular hairs are absent.

The mesophyll (Fig. 9) is very loosely arranged. All the cells above the veins are cylindrical — either shorter or longer — with

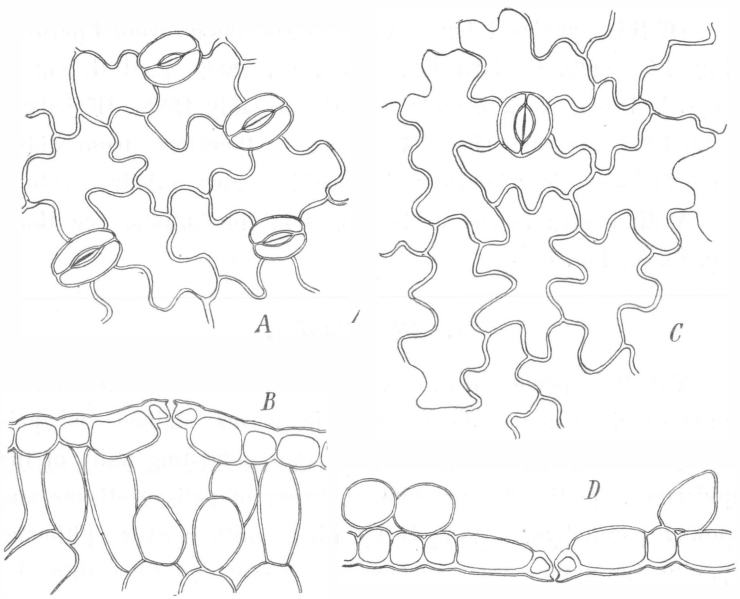

Fig. 10. *Saxifraga stellaris.*
A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same (transverse section). (*A*, *B*, *C* and *D* $^{282}/_{1}$).

their axes at right angles to the epidermis. They can be readily distinguished from the stellate cells of the spongy parenchyma which form a very large-celled lacunose tissue. How many of the 3—4 layers of cylindrical cells are to be called palisade-cells ("collecting-cells" of HABERLANDT) is quite arbitrary.

The veins are accompanied by colourless, one-layered (rarely many-layered) bundle-sheaths. Mechanical tissue is entirely

absent. The structure of the hydathode is exactly similar to that, for instance, of *S. nivalis*; it does not secrete lime.

The leaf is consequently very distinctly mesophytic (more particularly hygrophytic), and is presumably the most hygrophilous of the three species of the section *Boraphila* here dealt with, a fact which agrees excellently with its usually very damp habitat; Lazniewski also states that it is: "nicht selten im Wasser wurzelnd angetroffen" (l. c., p. 246).

Of this species I have examined specimens from Upernivik (July 18, 1886), Frederikshaab (Aug. 17, 1886), East Greenland (Sept. 4, 1885), Nova Zembla, the Færöe (July 1895), Härjedalen (Aug. 1884), Tromsø (July 21, 1885), — therefore, from widely separated localities; but they all agreed in regard to their structure.

With regard to the fleshy leaves of the bulbils, see Holm, l. c. Pl. X, Fig. 6.

3. *Dactyloides.*

The two species of this group which have been investigated agree precisely in (1) the form of the leaves (stalked and palmately lobed to palmately cleft), (2) the undulating walls of the epidermis, (3) the distinct differentiation of palisade-tissue and spongy parenchyma, and (4) hydathode with convex epithema, opening upon the upper surface of the leaf slightly within the margin. — The layers of the spongy parenchyma, from the epidermis of the lower surface to beneath the palisade-cells, differ in compactness; immediately within the epidermis the cells are polygonal, without intercellular spaces; higher up, intercellular spaces occur in considerable numbers. The difference between the two species is most apparent in the extent to which they are hairy.

Saxifraga hypnoides L. (Figs. 11 and 12).

Saxifraga hypnoides L. greatly resembles *S. groenlandica* (see below) in its anatomy.

The epidermis of the upper surface (Fig. 11 *B* and *C*) consists of two kinds of cells, (1) large, somewhat straight-walled and elongated cells, (2) irregularly-shaped cells with undulating walls. The inner, lateral and outer walls are thin (the last about 2 μ in thickness). In the leaf-stalk the cells are greatly elongated, narrow

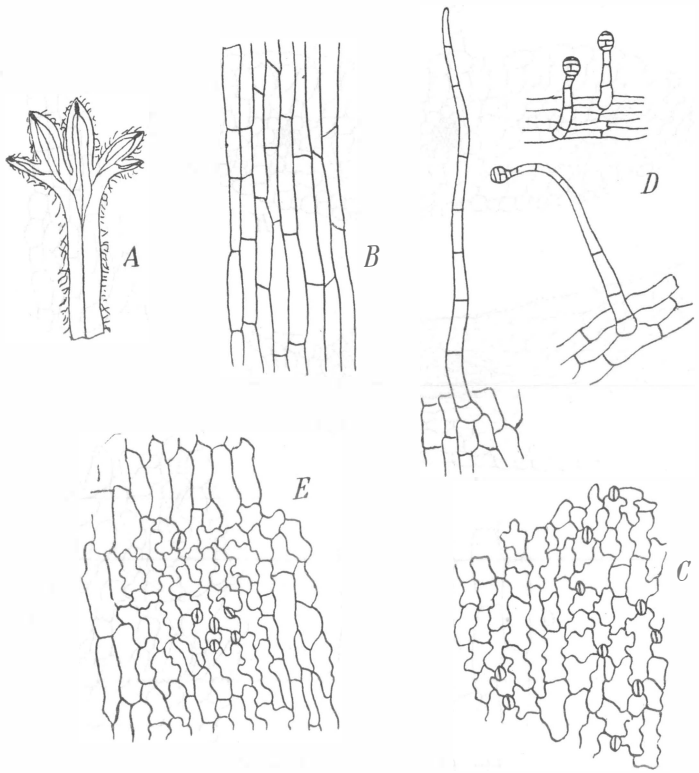

Fig. 11. *Saxifraga hypnoides.*
A (2/1), Leaf-form. B, Epidermis of the upper side of the leaf-stalk. *C*, Epidermis of the upper surface of the leaf. D, Hairs (see text). *E*, Epidermis of the lower surface of the leaf. (*B*, *C*, *D* and *E* 50/1).

and straight-walled. The stomata are placed on a level with the leaf-surface and are distributed in groups of very variable size; their apertures principally lie parallel with the longitudinal axis of the leaf. All the epidermal cells between and in immediate proximity to a group of stomata are smaller than the ordinary

epidermal cells, and their walls are far more undulating. The groups of stomata are continued as a long and very narrow stripe along — and slightly within — both the margins of the leaf-stalk, and are here also accompanied by the highly charac-

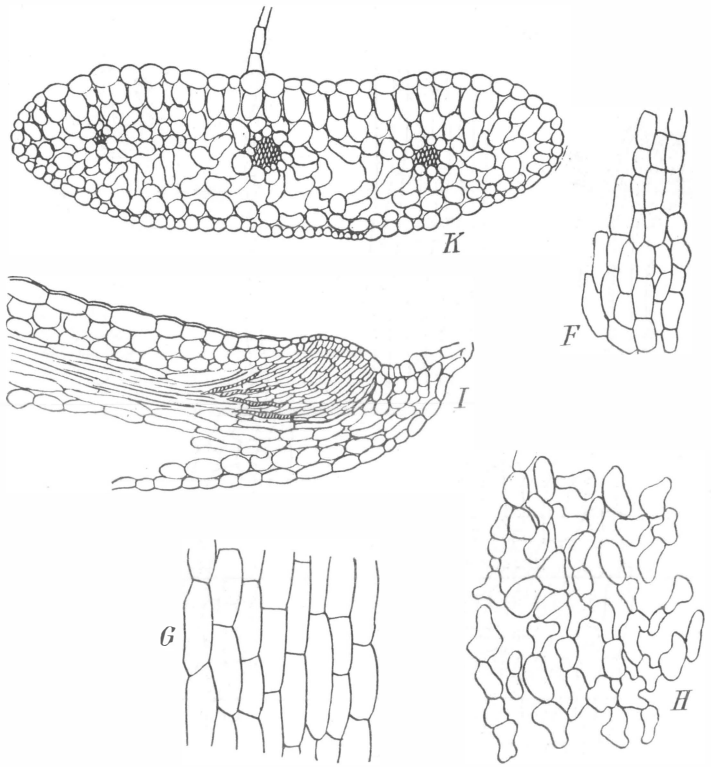

Fig. 12. *Saxifraga hypnoides.*
F, Spongy parenchyma from just below the epidermis of the leaf-blade. *G*, The same from just below the epidermis of the leaf-stalk. *H*, The same from midway between the epidermis and veins. *I*, Longitudinal section of leaf. *K*, Transverse section of leaf. (*F*, *G*, *H*, *I* and *K* 50/1).

teristic small epidermal cells with undulating walls. Almost all the hairs are without apical glands; they occur invariably in the spaces between the groups of stomata and arise from the straight-walled cells — never from those with undulating walls.

The structure of the epidermis of the lower surface (Fig. 11 *E*)

is like that of the upper, only the hairs of the former are glandular (upon the leaf-stalk, however, non-glandular hairs occur).

Along the margin of the leaf-stalk there are numerous hairs similar to those upon the upper surface of the leaf.

The mesophyll (Fig. 12) is differentiated to about the same degree as in *S. groenlandica*: the palisade-cells are short (in the specimens investigated very indistinctly, or not at all, obliquely placed) and the layer passes fairly gradually into the spongy parenchyma. The latter is loose and lacunose in the middle of the leaf, but immediately within the lower epidermis it becomes very compact and polygonal, and is almost without intercellular spaces.

The veins are without mechanical tissue, and are accompanied by a bundle-sheath of elongated cells one-layered on the whole.

The hydathode is well-developed, with convex epithema, and it opens upon the upper side of the leaf-margin and does not secrete lime (Fig. 12 *I*).

The description here given is based upon the investigation of specimens gathered by F. Børgesen at Velbestad (the Færøes), July 5, 1895; that is the only material I have had at my disposal.

Saxifraga groenlandica L. (Figs. 13, 14 and 15).

Saxifraga groenlandica L. is common everywhere on the heather moors and upon the rocky flats of Greenland, and ascends to the mountain heights there and also in Norway (Warming, Norman). Grows almost as commonly on the sunny side as on the shady side upon the mountains; and usually in dry localities.

The leaves are deeply palmately cleft, the leaf-stalk is broad and flat. A hydathode occurs at the apex of each segment. Glandular hairs occur fairly numerously upon both surfaces.

The epidermis of the upper surface (Figs. 13 *B* and 15 *A* and *B*) has everywhere thin-walled cells; the latter, upon the leaf-

segments, are short and have undulating walls (straight-walled, however, above the veins and at the base of each hair). Upon the rest of the leaf-blade the epidermal cells are large and straight-walled; this also applies to the leaf-stalk, only its

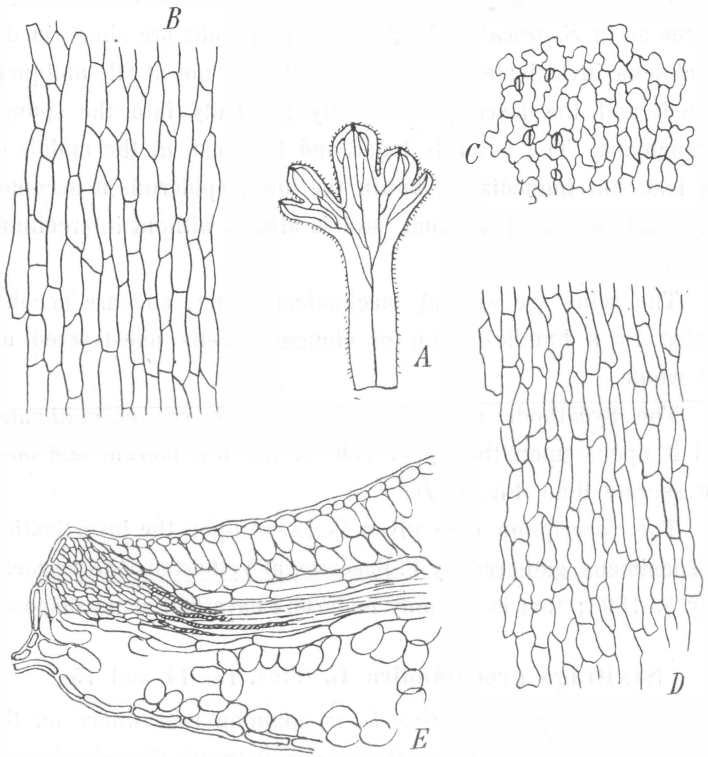

Fig. 13. *Saxifraga groenlandica.*
A (²/₁), Leaf-form. *B*, Epidermis of the upper side of the leaf-stalk. *C*, Epidermis of the lower surface of the leaf, near the midrib. *D*, Epidermis of the lower surface, just above the midrib. *E*, Longitudinal section of leaf. (*A*, *B*, *C*, *D* and *E* ⁵⁰/₁).

epidermal cells, above the veins, are somewhat narrower than those upon the leaf-blade. Glandular hairs are found in numbers upon the leaf-segments, and are fewer in number upon the rest of the leaf-blade and along the margin of the leaf-stalk. The upper side of the leaf-stalk is very slightly hairy. The stomata are numerous and evenly distributed upon the leaf-segments;

upon the rest of the leaf-blade they are arranged in groups or rows and are always accompanied by short cells with undulating walls. Stomata are also found (very sparsely) along the margins of the leaf-stalk, accompanied by cells with undulating walls.

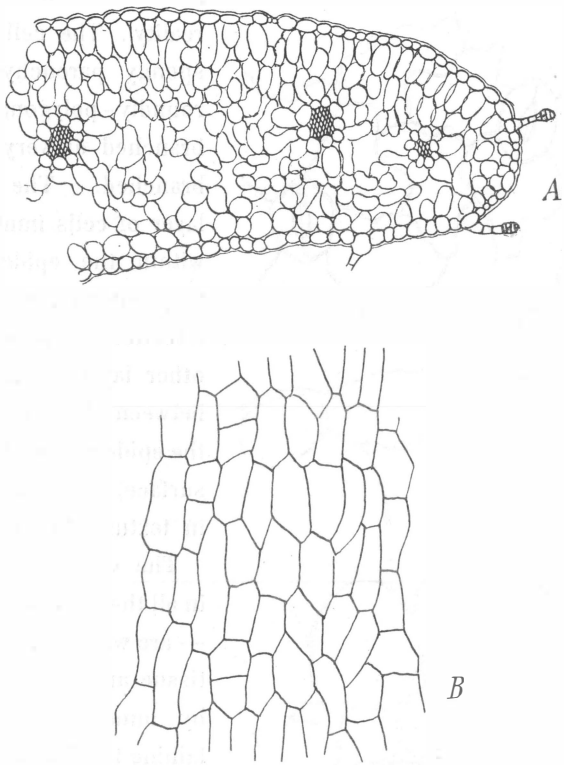

Fig. 14. *Saxifraga groenlandica.*
A, Transverse section of leaf. *B*, Spongy parenchyma from just below the epidermis (50/1).

All the stomata have their apertures parallel with the longitudinal axis of the leaf.

The epidermis of the lower surface (Fig. 13 *C* and *D*; Fig. 15 *C*) closely resembles that of the upper, only that the stomata, and the cells with undulating walls connected with them, are less numerous; the large-celled groups of hair-producing cells are more numerous than upon the upper side. Only glandular hairs occur.

The mesophyll is distinctly, but not markedly differentiated. The palisade-cells are oblique and short. The spongy parenchyma is fairly compact; (the section figured had been partly torn during preparation and has therefore been drawn as more lacunose than it was in reality). The cells of the spongy parenchyma are roundly-polygonal, unbranched or very shortly branched. The lowest layer of cells immediately within the epidermis is very compact, without intercellular spaces; the other layers (e. g. midway between the veins and the epidermis of the lower surface) are much looser in texture (Fig. 14).

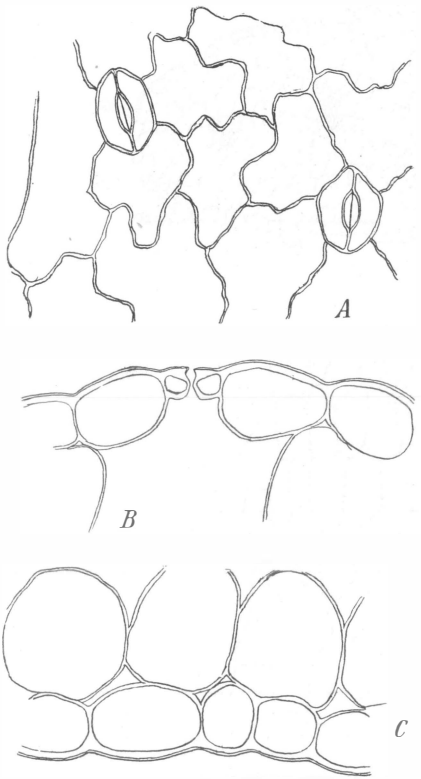

Fig. 15. *Saxifraga cæspitosa.*
Epidermis of the leaf. *A*, Upper surface. *B*, The same (transverse section). *C*, Lower surface. (*A*, *B*, *C* $^{282}/_{1}$).

The veins — like those in all the previous species — are without mechanical tissue and are surrounded by bundle-sheaths containing tannin. The hydathodes almost exactly resemble in structure those of *S. hypnoides*; they do not secrete lime.

The description here given refers to the specimens from Jan Mayen (July 22, 1896). Somewhat different from these (but otherwise resembling each other) were the specimens from Danmarks Ø (Aug. 6, 1892) and Disco (July 20, 1884), these

latter having fewer stomata upon the upper surface and none at all upon the lower surface.[1]

4. *Trachyphyllum.*

The three species which have been examined, agree in (1) the structure of the hydathode (it opens upon the upper surface of the leaf, with flattened or highly convex epithema; hydathode-cavity absent), (2) the structure of the hairs (they are everywhere irregularly-multicellular and retain this feature, either they have, or are without, an apical gland, — in contradistinction to the sections *Boraphila, Nephrophyllum, Dactyloides*), and (3) the cells of the spongy parenchyma are very little or not at all branched. — The three species differ most in the form of their leaves, but are separated also by other, smaller differences.

The chief structural features useful in diagnosis are the following: —

Leaves: —

toothed at the apex, with three acute teeth: *S. tricuspidata.*

entire: —

margin hairy along the lower half of the leaf: *S. aizoides*,

margin hairy along its whole extent: *S. flagellaris.*

Hairs: —

irregularly-multicellular marginal hairs: *S. aizoides*,

glandular hairs with irregularly-multicellular stalks: *S. flagellaris*,

(1) with globular head: *S. flagellaris*,

(2) with club-shaped head: *S. tricuspidata.*

[1] Besides the principal form I also examined specimens of the variety *palmata* from Thingvellir in Iceland (June 13, 1895). The latter is very remarkable by reason of its agreeing in almost all points with *S. hypnoides* in regard to leaf-anatomy; the only difference being that a few of the marginal hairs of the leaf are glandular.

The other differences are not characteristic enough to be given as a key; they are best seen in the figures.

Saxifraga aizoides L. (Figs. 16, 17 and 18).

Saxifraga aizoides L. according to NORMAN is a decided mountain-plant which grows both upon very wet and very dry ground, and occurs most commonly on the sunny side.

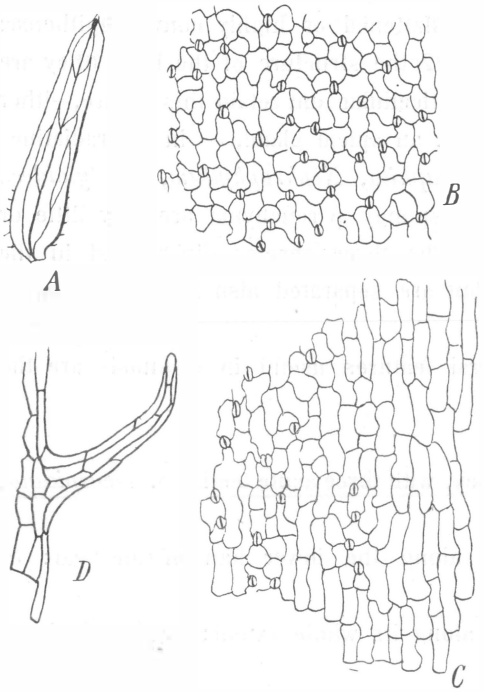

Fig. 16. *Saxifraga aizoides.*
The leaf: *A* (2/1), Leaf-form. *B*, Upper epidermis. *C*, Lower epidermis: the middle line of the leaf is to the right. *D*, Marginal hair. (*B*, *C*, *D* 50/1).

The leaf is linear, thick and succulent and terminates in a point at the base of which is found the only hydathode of the leaf. A few hairs occur along the margin towards the base; the leaf is otherwise glabrous.

The epidermis of the upper surface (Figs. 16 *B*; 18 *A* and *C*) consists of cells with slightly undulating, lateral walls and well-developed outer walls with distinct cuticle. At the base of the leaf, the lateral walls of the cells are straight and the cells are long and narrow. Stomata are absent at the base of the leaf upon its middle part, but in other places are evenly distributed. The stomata are parallel with the longitudinal axis of the leaf; they are placed on a level with the leaf-surface.

The epidermis of the lower surface (Fig. 16 *C*; Fig. 18 *B* and *D*), along the margin of the leaf, is almost exactly like that of the upper; the stomata are absent from a broad band along the middle, where the cells are elongated and narrow.

The differentiation of the mesophyll is fairly distinct. The palisade-cells, towards the apex of the leaf, are obliquely placed.

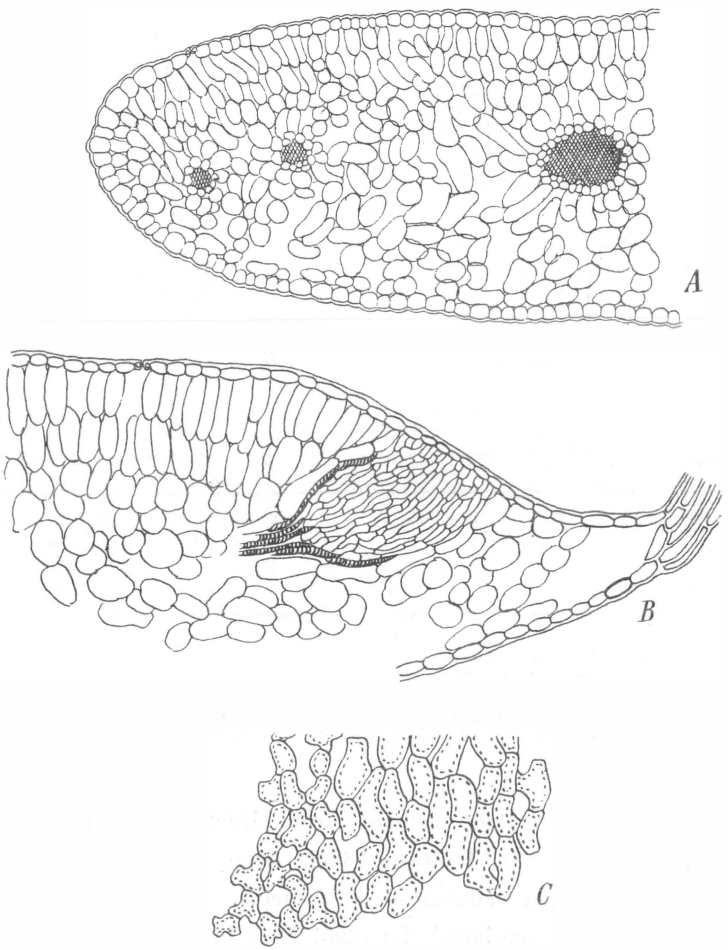

Fig. 17. *Saxifraga aizoides.*
The leaf: *A*, Transverse section. *B*, Longitudinal section. *C*, Spongy parenchyma. (*A*, *B*, *C* $^{50}/_{1}$).

The spongy parenchyma consists of roundish, shortly branched cells, which are placed more closely together, are elongated and are even more shortly branched in the middle band which is devoid of stomata.

The hydathode is situated at the apex of the leaf upon the upper surface; it does not secrete lime. The nerves are without stereom and are surrounded by a hyaline bundle-sheath.

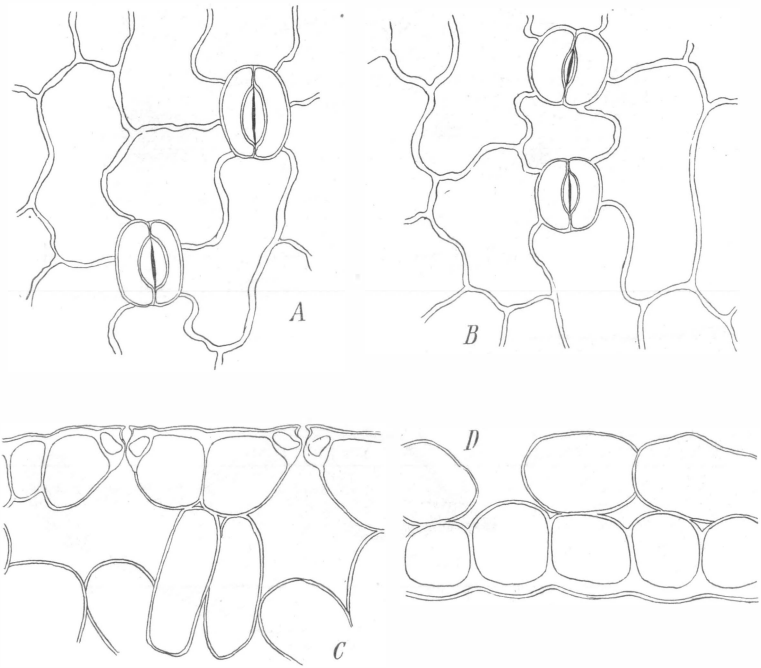

Fig. 18. *Saxifraga aizoides.*
The leaf: *A*, Upper epidermis. *B*, Lower epidermis. *C*, Upper surface. *D*, Lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

I have investigated specimens from Greenland (Ilua; Ivigtut, Aug. 20, 1883) and Tromsø (1885); from all three localities the specimens were similar in all respects.

As already mentioned the plant lives both in very wet and very dry localities. The specimens examined by me were not accompanied by notes containing further information regarding

their habitats. The fact of their occurring more commonly upon the sunny side appears to suggest a predominant xerophytic tendency. At any rate, the anatomy shows, although not very decidedly, several xerophytic features (succulency, fairly well-developed epidermis, narrow leaves, etc.). Bonnier (Ann. des sciences nat., VII ser., T. XX) has grown the species in Alpine regions (1600 metres) and found the specimens grown there to contain several palisade-layers more than are found in the individuals from the lowlands, — probably a natural result of the more intense light upon mountains. The Arctic specimens, in that respect, resemble rather the lowland than the mountain specimens.

Saxifraga flagellaris Willd. (Figs. 19 and 20.)

Saxifraga flagellaris Willd. There are too few data regarding the habitats of this species to enable me to form an opinion concerning the extent of its adaptation.

The lamina is almost oval and passes gradually into the leaf-stalk. Large glandular hairs occur — along the margin, one upon the leaf-apex itself, and a few scattered over the upper surface (Fig. 19).

The epidermis of the upper surface (Fig. 20) consists of cells which have undulating walls; above the veins the cells are larger and more straight-walled than outside them. The outer walls of the cells are only fairly strongly developed, with distinct cuticle. The stomata are placed slightly above the level of the leaf-surface, are evenly distributed, and have their apertures parallel with the longitudinal axis of the leaf.

The epidermis of the lower surface (Fig. 19 *B*), along a very broad longitudinal band down the middle, has less undulating walls than upon the upper surface, and consists of longer cells. The outer walls are somewhat thickened (Fig. 20 *D*). Along the margin the epidermis, like that of the upper surface, has undulating walls, with only few stomata.

The cells of the mesophyll (Fig. 19) are not markedly differentiated; the palisade-cells are obliquely placed. The cells of the spongy parenchyma are roundish. The whole leaf is somewhat suc-

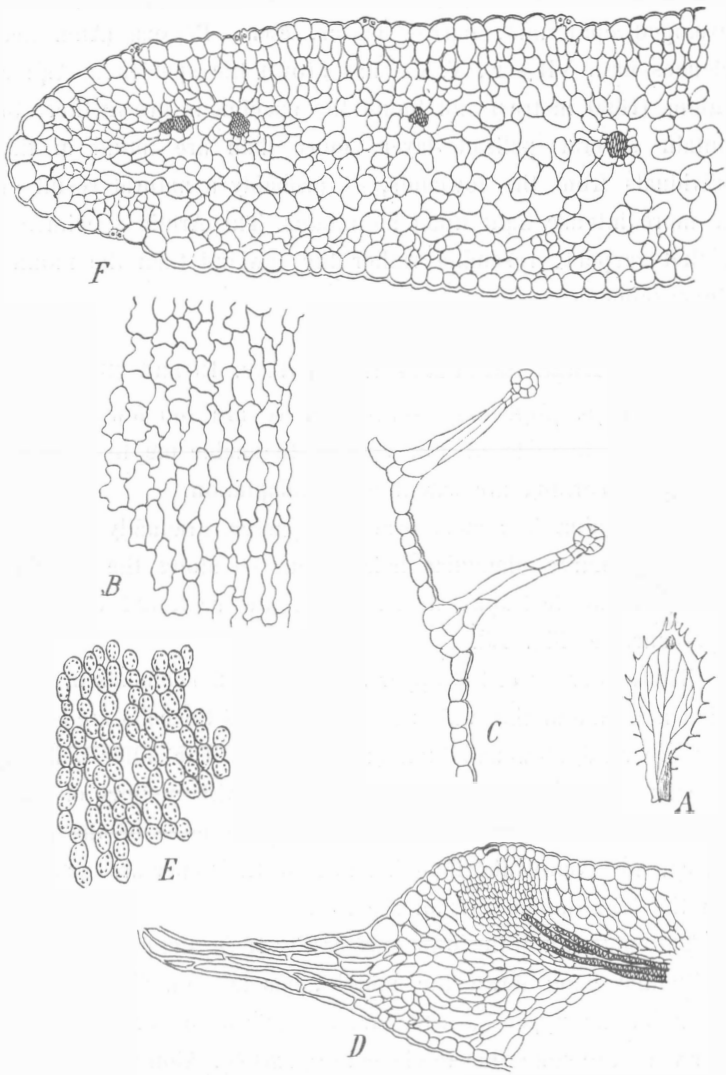

Fig. 19. *Saxifraga flagellaris.*
The leaf: *A* ($^2/_1$), Leaf-form. *B*, Lower epidermis. *C*, Marginal hairs. *D*, Longitudinal section. *E*, Spongy parenchyma. *F*, Transverse section. (*B*, *C*, *F* $^{56}/_1$), (*D*, *E* $^{50}/_1$).

culent, and appears, although not very decidedly so (e. g. on account of the numerous stomata upon the *upper* surface) to be somewhat xerophytic. The hydathode occurs at the apex of the leaf, upon the upper surface (Fig. 19); the epithema is

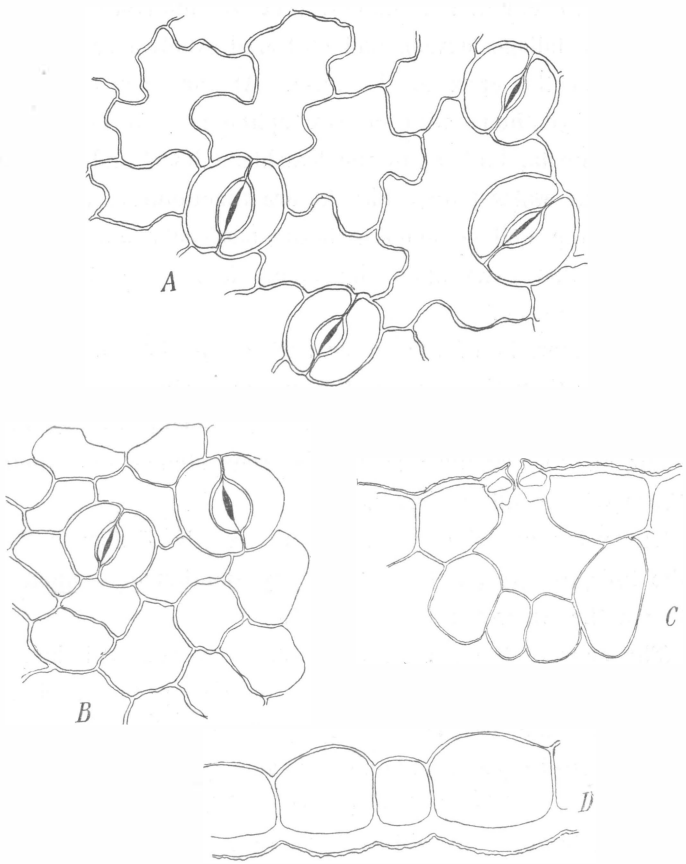

Fig. 20. *Saxifraga flagellaris.*
The epidermis of the leaf: *A*, Upper surface. *B*, The epidermis of the hydathode. *C*, Upper surface. *D*, Lower surface. ($^{282}/_{1}$).

convex. There is no secretion of lime. The veins are without stereom, and surrounded by a colourless sheath (Fig. 19).

The fleshy leaves of the bulbils contain much starch. The form of their blade is nearly like that of the foliage-leaves, but

the leaf is more short-stalked than that of the latter. The epidermis of the upper surface consists in part of very distinctly transversely elongated cells with slightly undulating lateral walls. The outer walls are 6—8 μ thick, with distinct cuticle. The stomata occur in fair numbers (not so abundantly, however, as upon the foliage-leaves), and scattered evenly over the whole surface from the apex to the base. At the apex of the leaf there is a hydathode with convex epithema. So far I could see, the stomata, both upon the leaf-blade itself and upon the epithema (the water-pores), Fig. 20, are functionless, the middle lamella in the wall common to both guard-cells not appearing to part, so that even upon the oldest leaves the stomata are permanently closed.

The epidermis of the lower surface consists of elongated cells, longer than those upon the upper surface. Outer walls 6—8 μ in thickness; cuticle present and stomata absent. Along the margin are glandular hairs, precisely similar in structure to those of the foliage-leaves.

The veins and the hydathode are exactly similar to those of the foliage-leaves, but -- as already mentioned — upon the epithema the water-pores are closed.

The cells of the mesophyll are all more rounded than are those in the foliage-leaves; the cells of the layer answering to the palisade are set obliquely to the epidermis as in the foliage-leaves, although they are filled with starch-grains and are without chlorophyll; so this oblique position has absolutely no connection with any light-orientation which may have reference to assimilation. The cells of the spongy parenchyma are rounded and filled with starch.

Consequently, in these fleshy leaves are found three structural features which, for the existing functions of the leaves, appear to be useless rudiments inherited from parent-plants with foliage-leaves similar in structure to those of the present-day *S. flagellaris.*

These structural features are: —

(1) Functionless (permanently closed) stomata.
(2) Functionless hydathodes (the water-pores being closed).
(3) Light-orientated (obliquely placed) palisade-cells.

I have investigated specimens of this species from two localities, viz. Siberia (July 24, 1878, KJELLMAN) and Nova Zembla (Th. Holm). They were all alike.

Saxifraga tricuspidata Retz. (Figs. 21 and 22.)

Saxifraga tricuspidata Retz. a is usually found upon heaths and is xerophytic in the choice of its habitat, and this xerophytism is distinctly impressed upon the structure.

The leaf is narrow (Fig. 21 *A*), fairly thick, and, at the apex, is trifid and bears three hydathodes. The epidermis of the upper surface (Fig. 22) consists of fairly straight-walled cells, which at the base of the leaf are nearly isodiametric, but become more and more transversely elongated towards the apex of the leaf. The cells are not elongated along the midrib. Pits are present in the lateral walls. The outer walls are thick, with distinct cuticle (Fig. 22 *B*). Stomata are evenly distributed over the greater part of the leaf-blade, they are most numerous on the more exposed parts of the leaf, but are few in number at the base. They are somewhat prominent. Along the margin of the leaf are numerous irregularly-multicellular hairs. Glandular hairs occur, with long, club-shaped apical glands (Fig. 21 *B*).

The epidermis of the lower surface (Fig. 22) along the margin is, in structure, precisely similar to that of the upper surface — also in regard to its stomata. Along the middle of the leaf the cells are more elongated and the stomata few in number (more abundant, however, towards the apex of the leaf); BØRGESEN states that there are two per unit of surface, while the

upper side has twelve per unit. At the base of the leaf they are almost completely absent.

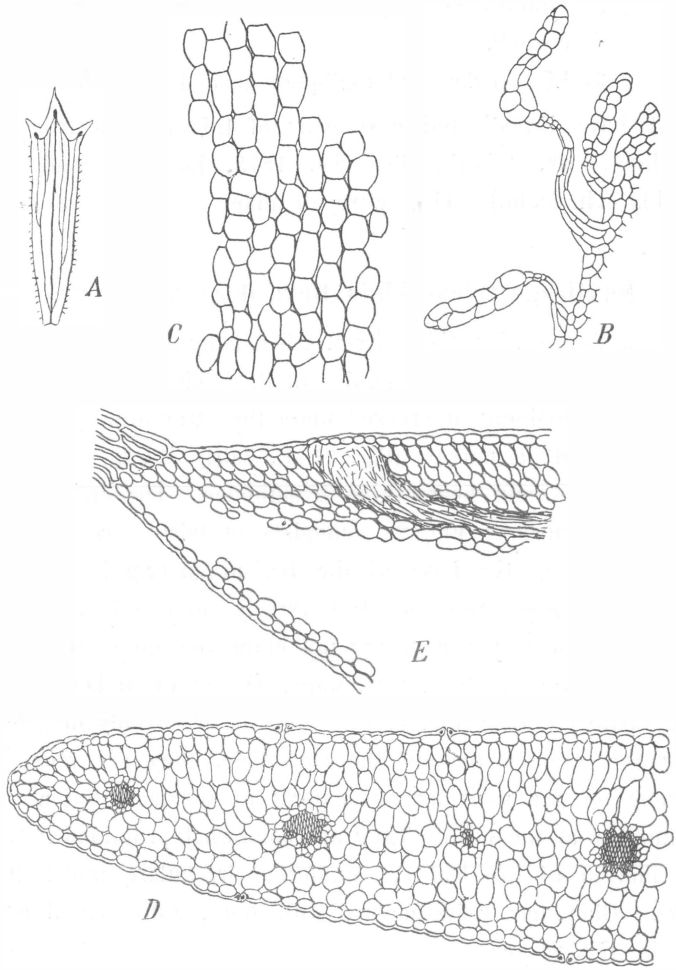

Fig. 21. *Saxifraga tricuspidata.*
The leaf: *A* (2/1), Leaf-form. *B*, Marginal hairs. *C*, Spongy parenchyma. *D*, Transverse section. *E*, Longitudinal section. (*B*, *D*, *E* 56/1), (*C* 50/1).

The mesophyll is slightly and indistinctly differentiated, and strongly recalls the condition in the section *Euaizonia* (see below). The palisade-cells are short and rounded, and

some are placed in rows which are decidedly oblique to the long axis of the leaf (Fig. 21 *D*, *E*).

The cells of the spongy parenchyma are rounded, unbranched, and most compact immediately beneath the lower epidermis (Fig. 21, *C*).

The veins are without stereom and have hyaline bundle-sheaths (Fig. 21 *D*).

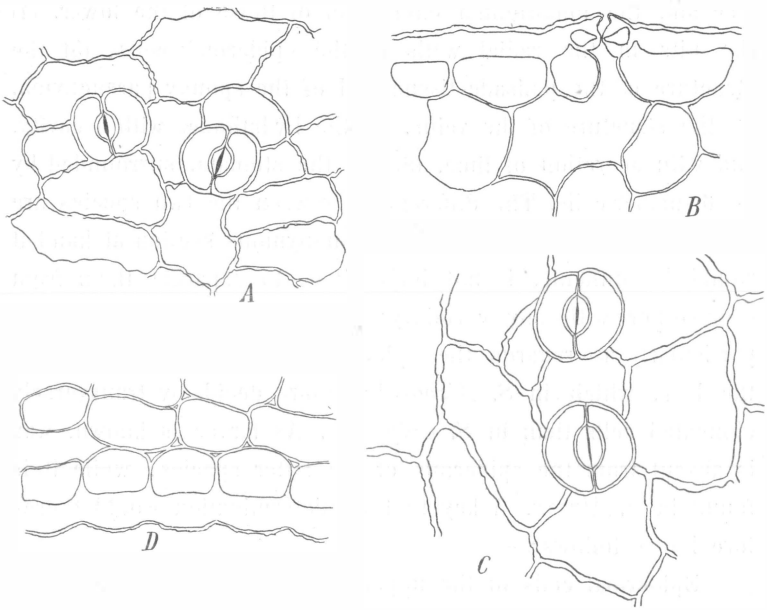

Fig. 22. *Saxifraga tricuspidata.*
The epidermis of the leaf: *A* and *B*, Upper surface. *C* and *D*, Lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

The hydathode opens upon the upper side of the leaf-margin (Fig. 21); it does not secrete lime. In one solitary specimen the water-pores were gathered very closely together, six being directly in contact with each other.

I have investigated specimens of this species from Disco (July 20, 1884), Amerdlok (July 11, 1884), Upernivik (May 10, 1887). They were all alike.

5. *Euaizonia.*

The two species of this group which have been investigated show their close relationship in (1) the form of the leaves (both are spathulate, and serrate, with a hydathode at each tooth), (2) the distribution and structure of the hairs, (3) the transverse elongation of the epidermal cells of the upper surface and the longitudinal elongation of those of the lower, (4) the pits in the radial walls of the epidermal cells, (5) the structure of the palisade-tissue and of the spongy parenchyma, (6) the structure of the veins, (7) the hydathodes with a cavity, and with secretion of lime, (8) and the stomata, surrounded by 4—6 smaller cells. The differences between the two species are so slight, that on the basis of the anonymous section at hand it would be difficult, if not impossible, to separate them from each other with any certainty; presumably they differ more particularly as regards the epidermis of the upper surface of the leaf, which in *S. Aizoon* has more decidedly transversely elongated cells than in *S. Cotyledon.* As far as is known, wax is absent from the epidermis of the latter species, while it is found in *S. Aizoon.* A key to their determination would therefore be as follows: —

Epidermal cells of the upper surface
very distinctly transversely elongated: *S. Aizoon*,
somewhat indistinctly, or more rarely not at all transversely elongated: *S. Cotyledon.*

Saxifraga Cotyledon L. (Figs. 23 and 24.)

Saxifraga Cotyledon L. This species is a Sub-alpine lowland plant which here and there extends almost down to the sea-level and scarcely ever extends higher into the mountains than about 500 feet; found most commonly at elevations of 200—300 feet above the sea. It grows partly upon level, partly (and most commonly) upon sloping ground, where it is

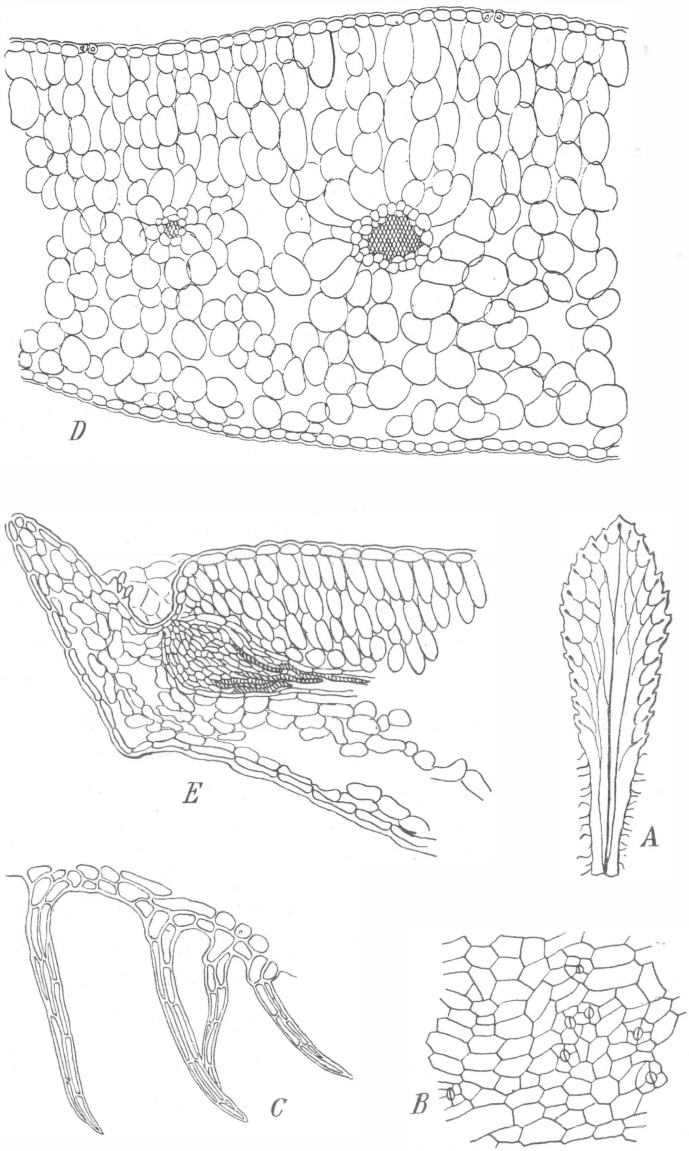

Fig. 23. *Saxifraga Cotyledon.*
The leaf: *A* (2/1), Leaf-form. *B*, Epidermis of the middle of the upper surface. *C*, Marginal hairs. *D*, Transverse section. *E*, Longitudinal section. (*B*, *C*, *D*, *E* 50/1).

about five times as common upon the southern side as upon the northern, while it scarcely ever occurs on the eastern and western sides (Norman, l. c., pp. 294—95).

The leaves are in a dense rosette, which somewhat recalls *Sempervivum*. Each of the teeth upon the leaves is provided with a hydathode (Fig. 23 *A*). The leaves are fairly thick.

The epidermis of the upper surface (Fig. 23 *B* and Fig. 24) consists of polygonal, straight-walled, usually transversely elongated cells; the lateral walls are rather thick (3—4 μ), with numerous thin-walled parts (pits). The outer wall is thick (8—10 μ), with a strong cuticle; stomata occur abundantly, but are absent towards the base, are more numerous upon the exposed parts of the leaves, and are all surrounded by 4—6 small cells; they project above the leaf-surface (Fig. 23 *B*).

The epidermis of the lower surface (Fig. 24) consists of elongated cells which are similar in structure to those upon the upper surface. The stomata are absent from along the whole of the middle band and from the base of the leaf, exactly as in *S. Aizoon* (a specimen from Kobbefjord — which see); but they are numerous along the margin, where the epidermal cells are less elongated, and are decidedly most abundant upon the lower side. Along the margin of the leaf-base there are some thick, irregularly-multicellular hairs (Fig. 23 *C*).

The mesophyll consists of remarkably homogeneous cells; the palisade-cells are somewhat longer than the cells of the spongy parenchyma, and approximately barrel-shaped (Fig. 23). They are placed, especially towards the apex, obliquely to the epidermis, and there are numerous, rather large intercellular spaces between them. Below, the palisade merges imperceptibly into the more isodiametric, unbranched cells of the spongy parenchyma, between which the intercellular spaces are still larger. The vascular bundles are without stereom, but are surrounded by a (usually one-layered) bundle-sheath which contains tannin. Sphaerocrystals, the nature of which has not been more

closely investigated, are found (in spirit-material) precipitated in some of the cells of the mesophyll which differ in no other respect from the rest of the mesophyll.

All the veins terminate in a hydathode (Fig. 23). The latter opens into a cavity upon the surface of the leaf and secretes

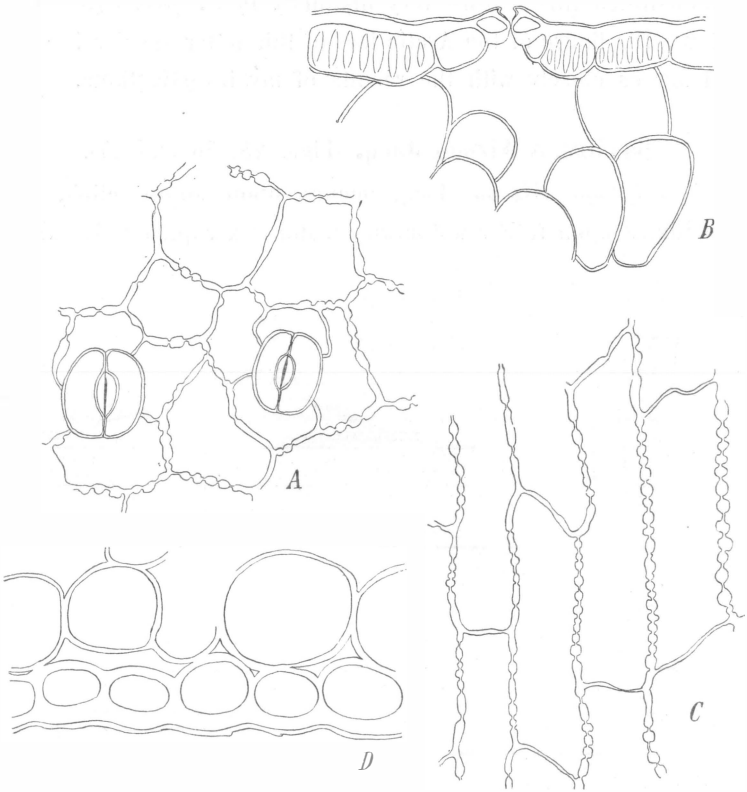

Fig. 24. *Saxifraga Cotyledon.*
The epidermis of the leaf: *A* and *B*, Upper surface. *C* and *D*, Lower surface. (*A*, *B*, *C*, *D* 282/1).

lime abundantly which in many cases entirely fills the cavity and spreads outside it (this is omitted in the figure).

Bonnier has proved that different specimens of this species, collected partly in the Arctic and partly in the Alpine regions of Central Europe, can be distinguished from each other by

the former having less markedly differentiated palisade-tissue than the latter. This somewhat indistinct differentiation also found by me in the Arctic specimens of *S. Cotyledon* at my disposal agrees closely with characters found by Bonnier in Arctic specimens; the same investigator (Rev. gén. d. bot., Tome VI, p. 514) has demonstrated this feature very distinctly in *S. oppositifolia* (see below). His figure of the Arctic leaf of this latter species is good and agrees closely with the results of my investigations.

Saxifraga Aizoon Jacq. (Figs. 25, 26 and 27).

Saxifraga Aizoon Jacq. occurs upon sunny cliffs, and sometimes upon rather wet moraine, and is xerophytic. Its whole

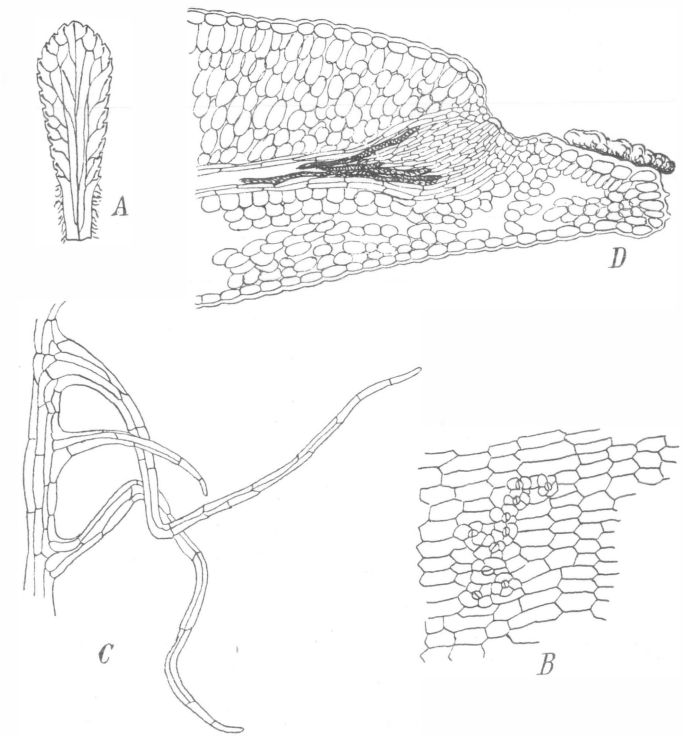

Fig. 25. *Saxifraga Aizoon*.
The leaf: *A* (2/1), Leaf-form. *B*, Epidermis of the upper surface. *C*, Marginal hairs. *D*, Longitudinal section (50/1).

morphological and anatomical structure has a great many points in common with that of *S. Cotyledon* (e. g. the succulent leaf-rosettes, the external form of the leaf, etc.).

The epidermal cells of the upper surface (Figs. 25 *B* and 27) of the leaf are elongated longitudinally at the base, but higher up in the leaf they become transversely elongated. The outer walls are thick, with distinct cuticle. The stomata are absent from the leaf-bases, they do not appear until above the

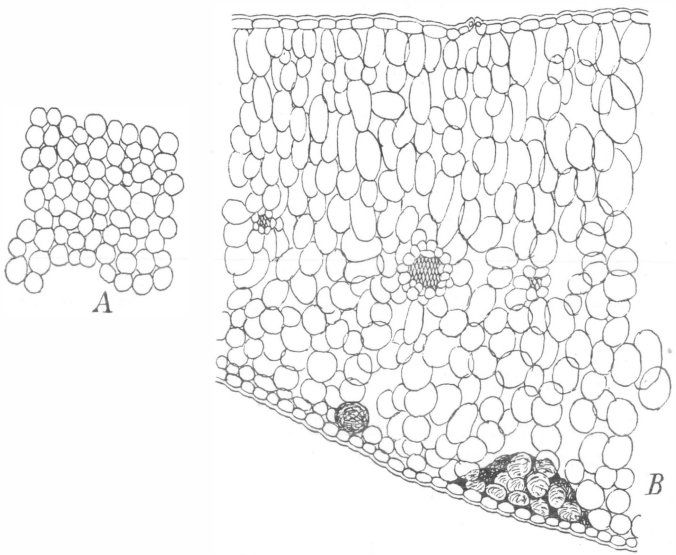

Fig. 26. *Saxifraga Aizoon.*
The leaf: *A*, Spongy parenchyma. *B*, Transverse section (below to the left, a tannin-cell, to the right a sphaerocrystal). (*A*, *B*, $^{50}/_{1}$).

marginal hairs. They are surrounded by, usually, four smaller cells (cf. Thouvenin l. c.) and are not definitely orientated (e. g. not parallel with the midrib).

The lower epidermis (Fig. 27) is of elongated cells at the base of the leaf and is continued as a median band of similar elongated cells without stomata, which gradually narrows towards the apex of the leaf. To the right and left of this band occur areas which are of smaller cells, and there all the stomata are placed in

groups. These two marginal bands commence above the marginal hairs of the leaf and widen continuously towards the apex to the sacrifice of the middle band. Therefore stomata are quite absent from the leaf-blade below the point at which the marginal hairs begin, they all occur towards the apex of the leaf.

Børgesen states (l. c., p. 225) that the stomata are more abundant upon the upper surface, but yet, at the same time, records that it has eight, while the lower surface has twelve, per unit of surface. The latter statement unquestionably corresponds better with my observations. Lazniewski's statement that the stomata are entirely absent from the exposed leaf-apices of many rosette-plants does not at all agree with the conditions found by me in this species, which has all its stomata especially placed in the most exposed parts of the leaf.

A wax-covering is present in the form of small grains of irregular form upon the apical, exposed parts of the upper side of the leaf.

The description given above of the mesophyll of *S. Cotyledon* exactly suits that of the present species. The palisade-cells are very slightly differentiated, are barrel-shaped, and the tissue merges below imperceptibly into the spongy parenchyma with its more isodiametric, unbranched cells (Fig. 26).

The palisade-cells are more or less obliquely placed towards the apex of the leaves. Lazniewski (l. c.) has found this to be the case in many rosette-plants, and connects it with the peculiar way in which light falls upon such a rosette with its obliquely erect leaves (this feature was first pointed out by Pick).

At the base of the leaf the difference between the palisade-tissue and the spongy parenchyma is even further obliterated, nor does any obliquity occur there; the whole mesophyll is homogeneous, exactly like that found by Lazniewski in many Alpine rosette-plants.

In many of the cells of the mesophyll there are quantities of tannin, which gives the usual reaction with iron. Besides these scattered tannin-idioblasts there are found, precipitated

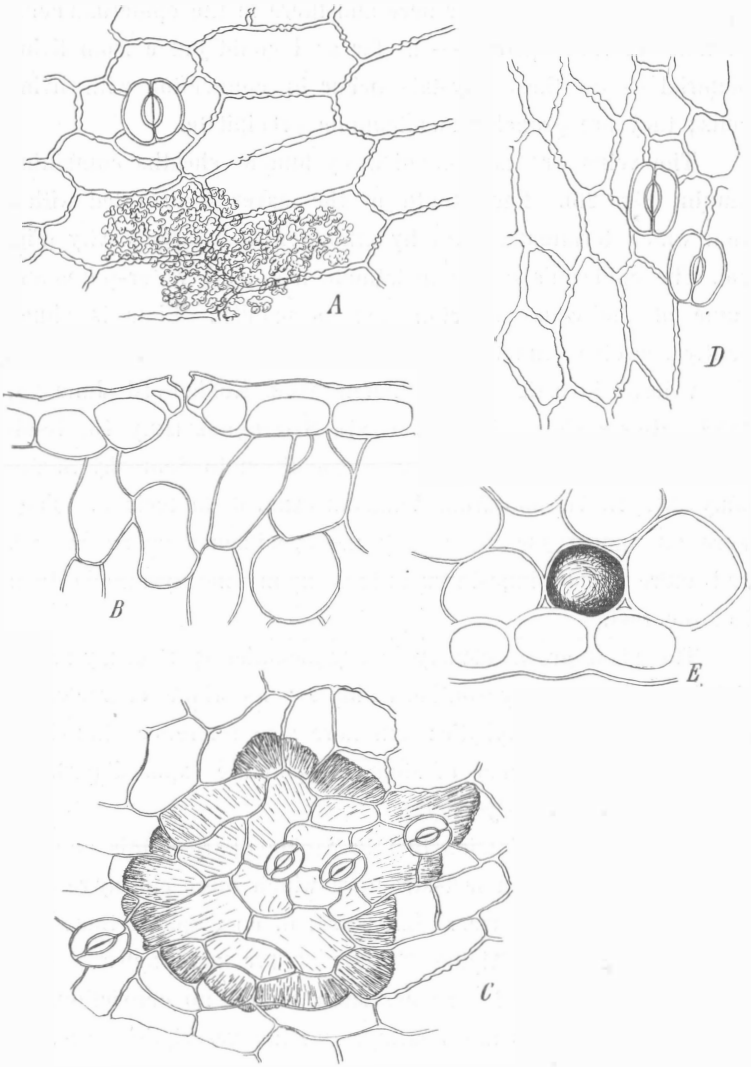

Fig. 27. *Saxifraga Aizoon.*
The epidermis of the leaf: *A* and *B*, Upper surface. *C*, Lower surface (a large sphaero-crystal is seen immediately beneath the epidermis, probably precipitated by alcohol. *D* and *E*, Lower surface (C $^{175}/_{1}$), (*A*, *B*, *D*, *E* $^{282}/_{1}$).

in many places (in spirit-material), large sphaerocrystals (the composition of which has not been more closely investigated) among the cells immediately beneath the epidermis (Fig. 27). Sphaerocrystals also occur here and there in the epidermal cells. In none of these places — as far as I could judge from living material — do these crystals occur in connection with living cells; they are probably an alcoholic precipitate.

The veins are accompanied by bundle-sheaths containing tannin (Fig. 26). Each tooth of the leaves is provided with a vein which terminates in a hydathode with a large cavity (Fig. 25). The epidermis of the hydathode has 1—2 water-pores and some of the cells are elongated as papillæ. Lime is abundantly secreted—much more abundantly than in *S. Cotyledon*.

I have investigated specimens from Kobbefjord (June 29, 1884), Holstensborg (July 17, 1884), Sarfanguak (July 15, 1884) in West Greenland, from Ryder's expedition to Scoresby Sound (July 28, 1887), and from Vatnsdal (Aug. 6) in Iceland. They were all almost identical; only the specimen from Sarfanguak had more ample lime-incrustations upon the hydathode than had the rest.

The plant grows usually in dry localities (part of my material came from sunny southern slopes); its whole character is rather decidedly xerophytic; but here also reference should be made to the occurrence of stomata upon the exposed parts of the leaf, as in *S. Cotyledon*.

Leist (1889) maintains that in Alpine districts this and the former species have a leaf-structure which more closely resembles that of shade-leaves. Lazniewski (l. c.) disputes this, and maintains that the Alpine *Saxifraga* are xerophytes. — It must be owned that Leist's assertion carries no conviction, as the necessary figures are wanting, and the descriptions are, by themselves, unsatisfactory.

6. *Porphyrion.*

Saxifraga oppositifolia L. (Figs. 28 and 29).

Saxifraga oppositifolia L. extends to the highest summits of the mountains into the snow-flora (Norman, Warming). Grows on dry, stony ground, upon the rock itself or among large boulders. Consequently it is a xerophyte, and shows this very distinctly in its internal structure. The leaf has only one hydathode at the apex. The marginal hairs are irregularly multicellular.

The upper epidermis (Fig. 29) has fairly straight lateral walls, with numerous pits. The outer walls differ in thickness in the different parts of the leaf; towards the apex they are very thick, and from thence become gradually thinner towards the leaf-base. The cuticle is distinct and very finely wrinkled. The stomata, with fair regularity, are placed parallel to the length of the leaf, only a few depart somewhat from this position. Their distribution upon the leaf-blade is very remarkable. They are entirely absent from the extreme tip of the apex, upon which is the hydathode. Immediately behind the apex they occur in a broad band across the leaf and are partially continued along the under-side of the leaf-margin.

The epidermis of the lower surface (Fig. 29) closely resembles that of the upper; its cells, however, are somewhat more elongated longitudinally. The distribution of the stomata is like that upon the upper side.

The palisade-cells of the leaves (Fig. 28), at the exposed apex, are very distinct and occur both upon the upper and lower surface, the leaf being directed sharply upwards. Further down towards the base the differentiation between palisade-tissue and spongy parenchyma disappears entirely. The spongy parenchyma consists of rounded, unbranched cells, fairly compact; within the epidermis towards the leaf-base there is a single layer of cells which is quite without intercellular spaces. As already men-

tioned, the parts of the leaf which are exposed to the light possess a spongy parenchyma developed in the form of palisade.

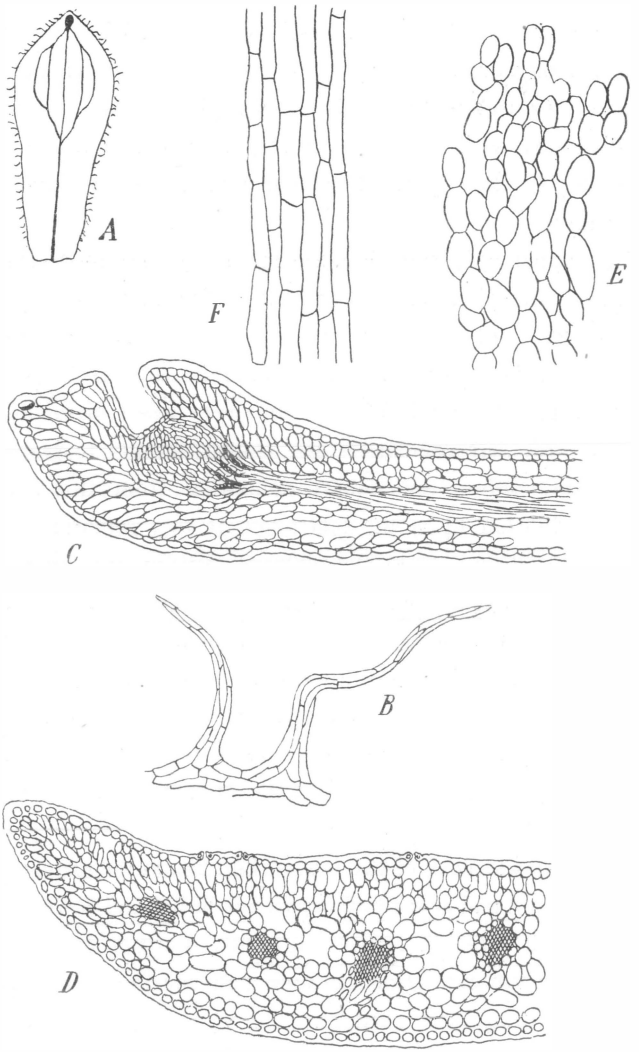

Fig. 28. *Saxifraga oppositifolia.*

The leaf: *A* (7/1), Leaf-form. *B*, Marginal hairs. *C*, Longitudinal section. *D*, Transverse section. *E*, Spongy parenchyma. *F*, Spongy parenchyma from the leaf-stalk. (*B*, *C*, *D*, *E*, *F* 50/1).

Lazniewski (Flora, 1896) has described the leaf-anatomy of this species very accurately and has given figures of it. He points out that the leaves are seated so closely together that, for the greater part, they overlap each other, and he then emphazises the fact that only that part of the leaf which is covered by neighbouring leaves bears stomata abundantly, while

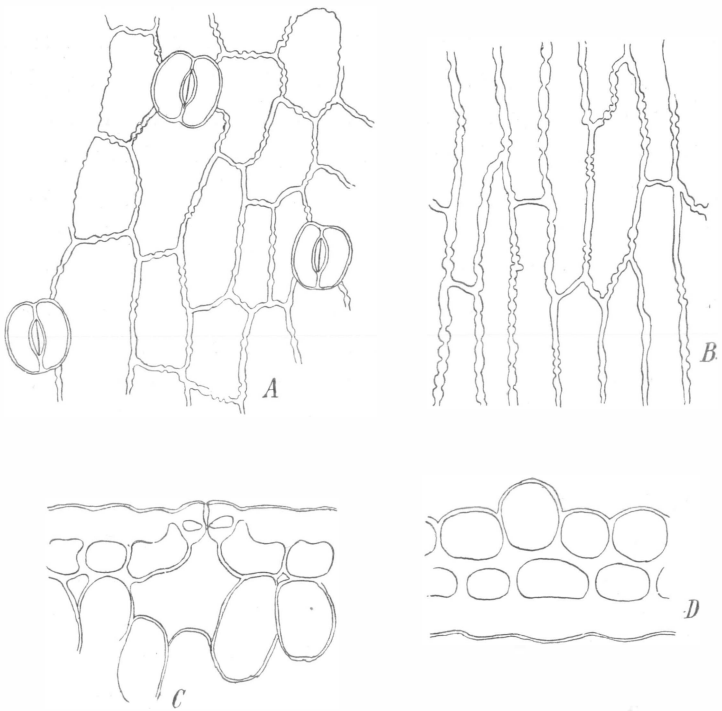

Fig. 29. *Saxifraga oppositifolia.*
The epidermis of the leaf: *A* and *C*, of the upper surface; *B* and *D*, of the lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

the light-exposed leaf-apex is almost without them, and has a very thick outer epidermal-wall and true palisade-cells (which, on the other hand, are absent from the shaded part). Lazniewski maintains that this distribution of the stomata is also found in rosette-plants and regards it as a protection against excessive transpiration.

In all the specimens examined by me I found the distribution of the stomata to differ somewhat from that mentioned by Lazniewski. His Fig. 11 (l. c., p. 239) shows the stomata to be below the line *A—B*. But in all the Arctic specimens the stomata-bearing band begins still higher up and only the oblique surface upon which the hydathode is situated is devoid of them. In the fully expanded specimens that part of the leaf which bears the stomata, is not at all shielded from exposure to light, in fact, the stomata occur especially upon the strongly exposed parts of the leaf which possess palisade-cells, with the exception only of the oblique surface bearing the hydathode. Hence we must resort to quite a different explanation of the distribution of the stomata: — They are absent from the oblique surface bearing the hydathode, which is the only part of the leaf that in the bud-condition of the shoot is exposed to light and air; we have here an instance of a primitive bud-protection which comprises only the very young leaves, while already the oldest leaves of the bud, which are exposed to the elements, are somewhat expanded before winter sets in.

Besides, the stomata are absent from the base of the leaf, — where I think they might be expected to occur in large numbers if Lazniewski's hypothesis should also apply to the Arctic species. The absence of stomata from the base of the leaf is to be connected with the fact that the "leaf-base" is in reality the morphological leaf-stalk (below the common starting point of the veins), where neither palisade-cells nor stomata occur (compare *S. groenlandica* and *S. hypnoides*); consequently the other *Saxifraga*-species have no stomata upon their leaf-stalks. Lazniewski's assertion that the stomata are hidden in "interfoliar spaces free from air-currents" does not apply at all to the Arctic specimens, as (1) the stomata are situated chiefly in the parts of the leaf possessing

palisade-cells and (2) they are entirely absent from the "interfoliar-spaces" (i. e. the morphological leaf-stalks).

As regards the seasonal biology of the leaves it may be observed that at the base of the buds which live over the winter partially expanded leaves usually occur, which probably assimilate for some length of time before beginning their winter-rest; but of course this has not been proved. The buds, moreover, are sharply limited below by dead leaves, which persist upon the stems for several years. Bud-scales are absent, and the only protection the younger leaves have is due to the circumstance already mentioned, that they are without stomata exactly upon the small space containing the hydathode which, in the bud-condition, is the most visible and most exposed part of the leaf.

A specimen from East Greenland (Danmarks Ø), collected February 28, 1892, was remarkable with regard to the arrangement of its chlorophyll-grains, the latter (in the two upper palisade-layers) having sunk down to the bottom of the cells, of which the upper part was occupied by a large vacuole. The other cells of the mesophyll showed no such feature. Whether this circumstance (which was not observed in any leaf gathered during the period of growth) is really a common winter-phenomenon in *S. oppositifolia* in Arctic regions, or is due to the imperfect way in which ordinary spirit-material on the whole is fixed when collected, I am not prepared to state with any certainty.

I investigated plants of *S. oppositifolia* from the following places: — Upernivik (May 17, 1887), Danmarks Ø (Febr. 18, 1892) and Julianehaab (May 22, 1887) in Greenland, Jan Mayen (July 22, 1896), Nova Zembla, Vallanæs (Iceland; Dec. 21, 1893) and from the Botanic Garden in Copenhagen (April 18, 1907). The leaves of all these species agreed very closely in all anatomical details. Any difference which could be attributed to the influence of the different geographical conditions could not be

demonstrated in spite of much investigation; the leaves all agreed with the description given.

The cultivated specimen from the Botanic Garden alone had very long internodes, but the structure of the leaf was exactly like that of, for example, the specimens from either Upernivik or Jan Mayen.

We have now seen what is the leaf-anatomy of the different species. It appears that the species belonging to any systematic section show greater anatomical relationship mutually, than they show with species of other sections. The structural features which vary least are here also of the most value as a supplement to the microscopical section-diagnosis. The structure of the hydathode and the appearance of the radial walls of the epidermis appear to be generally the characters which are least influenced by external conditions and which with a certain degree of constancy, remain uniform within the same section.

There are three different types of hydathodes: —

(1) Hydathode marginal, situated actually at the edge of the leaf; no secretion of lime: *Boraphila*, *Nephrophyllum*.

(2) Hydathode upon the upper surface of the leaf-margin; no cavity; no lime: *Dactyloides*, *Trachyphyllum*.

(3) Hydathode upon the upper surface of the leaf-margin; cavity present; lime secreted: *Euaizonia*, *Porphyrion*.

The other structural features, such as the thickness of the epidermis and the structure of the mesophyll, which are more easily influenced by external conditions, also are similar within each section, as may be seen from what has been written above. To this must be added, that Bonnier's investigations are greatly in favour of the idea that the structure of the mesophyll

in the species here investigated would be different if they were cultivated in Alpine regions. When nevertheless they agree within each section in Arctic regions, this proves that although the structure of the mesophyll varies according to climate, yet it varies correspondingly in the species belonging to the same section. LEIST found that *S. Aizoon* and *S. Cotyledon* (from the Alps) had exactly the same structural features; I, also, in my Arctic specimens, found that these two species, belonging to the same section, had quite similar leaf-structure, — but it must be admitted it was a structure which was entirely different from that found by LEIST in his Alpine specimens — a good example, therefore, of corresponding variation in closely related species.

If we wish to define how the Arctic species of *Saxifraga* are adapted in their leaf-anatomy to their natural surroundings, emphasis must be laid upon the fact that the same characteristic tests cannot be applied to all the species investigated, taken as a whole. They cannot as a matter of fact be termed either xerophytic or hygrophytic, these words having on the whole only a relative value, as they do not state anything about the plant's absolute relation to water-absorption and transpiration. If, on the other hand, we can show that the Arctic *Saxifragas* are either more, or else less, xerophytic than their Alpine colleagues, that would be a positive result of great significance, as it would bring about a comparison from which, to a certain extent, we might be justified in deciding how Alpine plants must adapt themselves in order to be able to live under the external conditions of Arctic regions, and vice versa. My endeavour has been to give as accurate a description of Arctic species as possible; future investigations must prove wherein such species differ from Alpine species. BONNIER has already attempted something of this kind, but more exhaustive investigations are highly desirable. The variations occasioned by external conditions are, in the greater number

of cases, so small that mere descriptions cannot indicate them, or can do so only with great difficulty and with little precision; detailed figures elucidate the variations better. It is my opinion, that much of the constant dispute as to how far Alpine plants are xerophytic or non-xerophytic in character is a merely verbal difference which might have been avoided if the several authors had given sufficient figures (for instance, as many as BONNIER or even more, by preference), — instead of the many verbal renderings, of very little characteristic importance or significance, of shades of difference.

Between the two extremes — submerged aquatic plants and leafless, xerophytic stem-succulents with abundant water-tissue — there is a long graduated series of life-types. It may be stated at once that no *Saxifraga* approaches these two extremes. The habitats of the species differ however fairly widely and therefore the degrees of adaptation are also somewhat variable. The subject may be best viewed by arranging the sections under investigation in a graduated series according to their greater or less xerophytism. Here we may note the very interesting circumstance that species belonging to the same section are fairly uniform in their degree of protection against excessive transpiration: the purely systematic divisions may be extended to include also anatomical and physiological characters. A careful study of the figures shows this fact more completely. The section *Porphyrion* (in casu *S. oppositifolia*) is the most xerophytic, then come the others in the following order: — *Trachyphyllum*, *Euaizonia*, *Dactyloides*, *Nephrophyllum* and *Boraphila*, the two last being almost similar in regard to this feature.

Lastly, if we wish to formulate the results thus obtained (the fact should, however, be particularly emphasized that they are of less importance than the information which may be gathered from the figures), it may be done as follows: —

(1) Each section has its own complex of structural

features in its leaf-anatomy which characterizes the whole group of species; this complex differs in the different sections (as regards its more minute details, see above).

(2) The species cannot, without a certain amount of arbitrariness, all be characterized in common. They show differing degrees of protection against excessive transpiration, from the highly protected species (*S. oppositifolia*, *Aizoon*, *Cotyledon, tricuspidata*) to the very slightly protected (e. g. the sections *Nephrophyllum* and *Boraphila*), in exact correspondence with the external conditions of their habitats.

(3) In the few cases in which we know the same species, as regards its leaf-anatomy, both from the Alpine regions of Central Europe and from Arctic regions, the specimens from the Arctic regions show less protection against excessive transpiration than the Alpine (for instance they have not their stomata hidden in "calm" interfoliar spaces, free from air-currents, as Lazniewski found to be the case in Alpine rosette-plants.

(4) Whether there are any differences between the Arctic and the Alpine specimens (besides those pertaining to transpiration) is as yet not known with any certainty, in this paper Arctic specimens, only, having been investigated; Alpine specimens have, it is true, also been investigated, but generally they have been described (and figured) so unsatisfactorily that a comparison would not be entirely reliable. — From the little we know (best from Bonnier and Lazniewski) it appears, however, that in the Arctic leaf there is generally a less decided difference between the spongy parenchyma and the palisade-tissue than in the Alpine, and that the former is

more abundantly provided with intercellular spaces than the latter.

(5) Individuals of the same species appear to vary very slightly in regard to leaf-anatomy, although they may have come from widely separated districts within the Arctic regions.

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