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The allotetraploid *Saxifraga nathorsti* **and its probable progenitors** *S. aizoides* **and** *S. oppositifolia*

Tyge W. Böcher

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Contents

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The allotetraploid *Saxifraga nathorsti* and its probable progenitors *S. aizoides* and *S. oppositifolia*

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Saxifraga nathorsti is an endemic Greenland species geographically restricted to Northeast Greenland. Morphologically it is intermediate between *Saxifraga oppositifolia* with purplish petals and *S. aizoides* with yellow petals. A hybrid between these two species is difficult to obtain and is not known from Greenland or anywhere else.

New material from Northeast Greenland has been cultivated and studied cytologically. One strain of typical *S. nathorsti* corresponded to the material studied previously. It also had 52 chromosomes and showed a high degree of pairing during meiosis. It was fertile, but exhibited several meiotic irregularities. Another strain seemed morphologically more closely related to *S. oppositifolia*. It was sterile and had the triploid number 2n = 39. It was assumed to have two genomes from *S. oppositifolia* and one from *S. aizoides*. It appears most probable that triploids of this kind after fertilization with pollen from *S. aizoides* can give rise to *S. nathorsti*.

Anatomical studies of the structure of epithem hydathodes in *S. nathorsti* and its two possible ancestors, *S. oppositifolia* and *S. aizoides*, show that *S. nathorsti* in several important hydathode characters occupies an intermediate position between *S. oppositifolia* and *S. aizoides*. Thus, all available facts support the theory of the origin and stabilization of *S. nathorsti* as an allotetraploid species.

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Introduction

Saxifraga nathorsti (Dusén) v. Hayeck was first described by Dusén (1901) as *S. oppositifolia* var. *nathorsti*. Its hybrid nature was questioned by v. Hayeck (1905) and Sørensen (1933), but chromosomal evidence strongly supported the view that *S. nathorsti* is an allotetraploid stabilized species with 2n = 52, originating from a hybrid between *S. aizoides* and *S. oppositifolia* which both have 2n = 26 (Böcher 1941). New material obtained from Mestersvig in Northeast Greenland (Cult. No. 6725) also had the tetraploid number, while another strain from Ella Ø, Northeast Greenland (Cult. No. 6319) had 2n = 39. The same deviating triploid number was ascertained by Jørgensen et al. (1958: 76) in material from Tyrolerfjord in Northeast Greenland.

S. nathorsti has a distribution which is restricted to Northeast Greenland. It is a striking fact that *S. aizoides* and *S. oppositifolia* are sympatric in extensive areas, e.g. in the Alps, Scandinavia, Iceland, Greenland and Northeast America. The primary hybrid does not seem to have been found anywhere, and it is difficult or perhaps impossible to produce it in culture. Artificial cross pollinations between the presumed parent species and back-crossings of them to *S. nathorsti* were tried in the Arctic Greenhouse in Copenhagen, but no viable seeds were obtained.

Taxonomically the two presumed parent species are placed in different sections of the genus, thus *S. aizoides* in Xanthizoon Griesebach and *S. oppositifolia* in Porphyrion Tausch. It is probably correct to place the two species in separate sections. However, they approach one another in certain morphological features. Warming (1909), dealing with the structure of the arctic species of *Saxifraga*, refers them to the same morphological type, viz., the creeping-herb-type. He points only to some minor differences, e.g. that *S. oppositifolia* has a tendency to develop into a sub-shrub, its stems becoming more woody than those of *S. aizoides*. At our present stage of knowledge, however, we must acknowledge the sectional allocation and therefore in our discussion include a theory assuming sudden rises of allotetraploid fertile populations. According to this possibility we would obviously have to imagine fertilizations of unreduced egg cells with unreduced pollen, and such unreduced sexual cells might result from meiotic inhibition due to climatic factors in a higharctic climatic regime. However, another possibility would be that a triploid hybrid was fertilized by normal haploid pollen. Tetraploid strains of *S. oppositifolia* have been ascertained from Spitzbergen, arctic North America and the

USSR (see Löve & Löve 1975: *S. pulvinata* Small), but so far no tetraploids have been found among Greenlandic populations of *S. aizoides* or *S. oppositifolia*. The triploid population related to *S. nathorsti* (No. 6319) shows reduced fertility and such a triploid might serve as an evolutionary stage in the building up of the fertile allotetraploid *S. nathorsti* (see further p. 21).

Special part

Morphology of *Saxifraga nathorsti*

Dusén (1901, plate 6) has a very accurate picture of the typical *S. nathorsti*, which deserves to be reproduced again here (Fig. 1). It shows the habit and the variation in phyllotaxis from alternate to opposite position. The leaves in *S. nathorsti* are ovate-lanceolate, acuminate and with marginal hairs. The new material from Mestersvig (Cult. No. 6725) resembles the type material, and the plants flower with red-yellow petals. The flowers are slightly larger and more open than in most cultivated strains of *S. oppositifolia*.

Fig. 2 shows the differences found between the typical tetraploid (No. 6725) and the deviating triploid (No. 6319). In culture the latter material has not yet produced any flower and it is hardly possible to point out clearly defined differences between this strain and strains belonging to *S. oppositifolia*. The leaves and branches are opposite. The upper leaves do not form rosettes of larger leaves. The marginal hairs are not so rigid as in *S. oppositifolia* and the terminal lime secreting pit (hydathode) is less distinct. However, the rosette formation and larger leaves in plants of No. 6725 are obvious. All facts indicate that No. 6319 represents a semisterile triploid hybrid between *S. aizoides* and *S. oppositifolia*. Taxonomically it approaches *S. oppositifolia* most, having probably two genomes from this species and only one genome from *S. aizoides*.

Meiotic behaviour in *Saxifraga nathorsti*

A comparison between *S. nathorsti*, *S. aizoides* and *S. oppositifolia* (Böcher 1941, figs 2–4) revealed a number of minor structural disturbances in *S. nathorsti*, while the course of meiosis was completely regular in the two diploid parent species. The material of *S. nathorsti* originating from Trail Island had dwarf pollen grains and showed signs of bridge-fragment configurations indicating inversion heterozygosity. The new material from the Mestersvig area unveiled several clear cases of meiotic disturbances resulting in constantly occurring eliminated segments of chromosomes including minute fragments (Figs 3–4) and dwarf pollen (Fig. 5C). Eliminated, and probably acentric parts of chromosomes

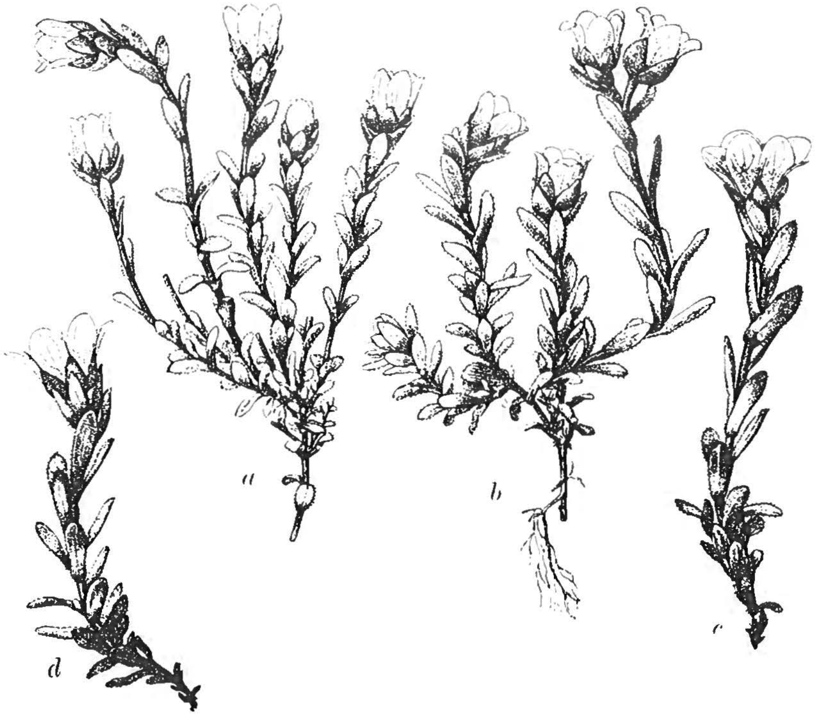

Fig. 1. Life sized drawings of flowering branches of *Saxifraga nathorsti*. Dusén 1901, plate 6, figs a-d.

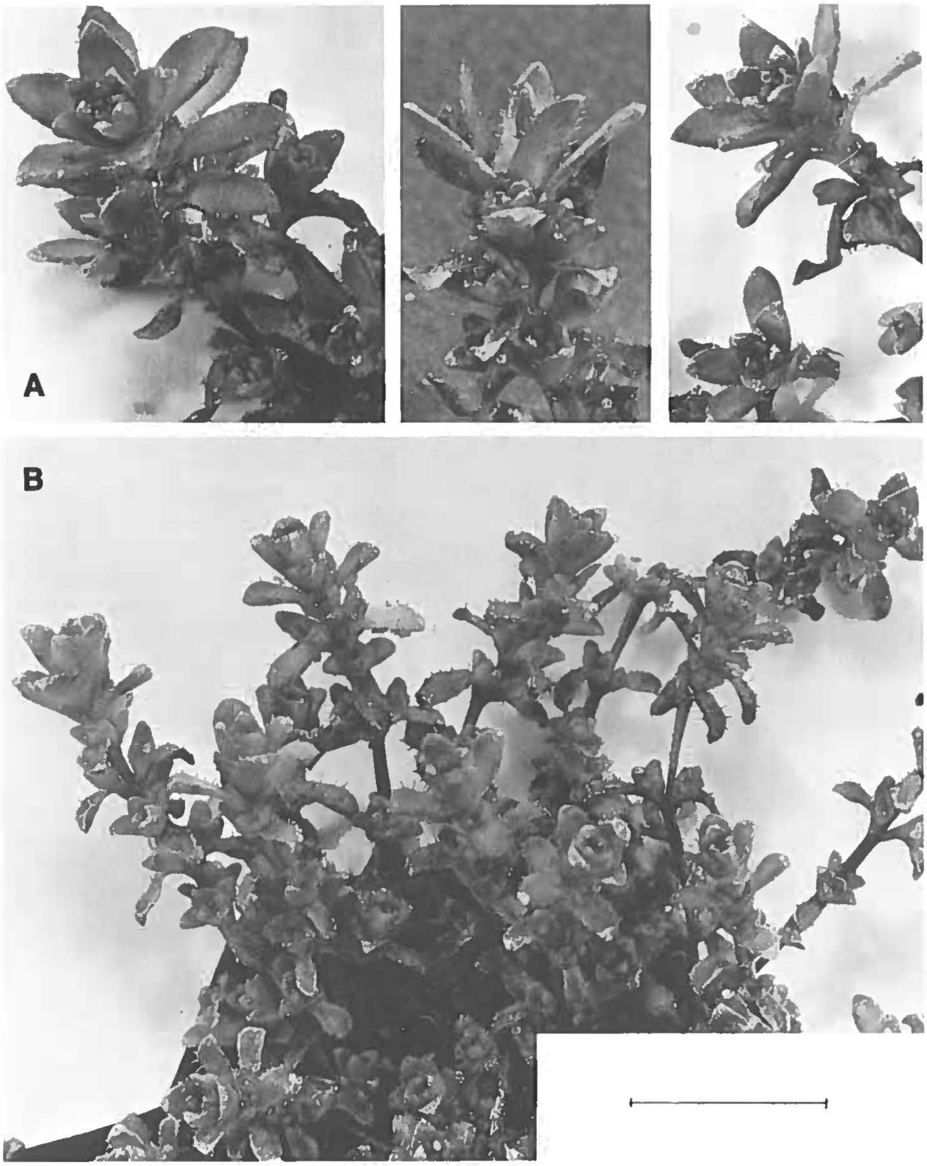

Fig. 2. Comparative cultivations in the Arctic Greenhouse in Copenhagen. A: Three terminal shoots of *Saxifraga nathorsti* showing terminal rosette formation of lanceolate flattened larger leaves (No. 6725 from Mestersvig, NE Greenland, 2n = 52). B: Shoots of a strain from Ella Ø, NE Greenland, with smaller, opposite leaves which do not form terminal rosettes. Probably a triploid hybrid (with 2n = 39) between unreduced *S. oppositifolia* and reduced *S. aizoides*. Scale: 1 cm.

were ascertained in all stages from diakinesis to the divisions in the pollen grains. In a few cases, deviating pollen grains with three nuclei were formed but without differentiation of generative cells (Fig. 5B). A common type of fragment occurrence is a small and a minute fragment in the same cell and often placed near one another (Figs 3–4). They probably result from one particular regularly recurrent anomaly. It can be concluded that although the doubling of the chromosomes involves meiotic stabilization in some populations, there are several irregularities during meiosis in other populations which thereby approach the behaviour of species hybrids with reduced fertility.

In the previous paper (Böcher op. cit.) the occurrence of one precociously separated pair in *S. oppositifolia* and *S. nathorsti* was mentioned. Furthermore, there were two particularly large pairs in *S. aizoides* and *S. nathorsti*. This very interesting situation appeared to give evidence of allopolyploid origin of *S. nathorsti*. Although the new material does not show the same differences in the precocity of a single pair or in the size of the pairs, there are no observations which refute the

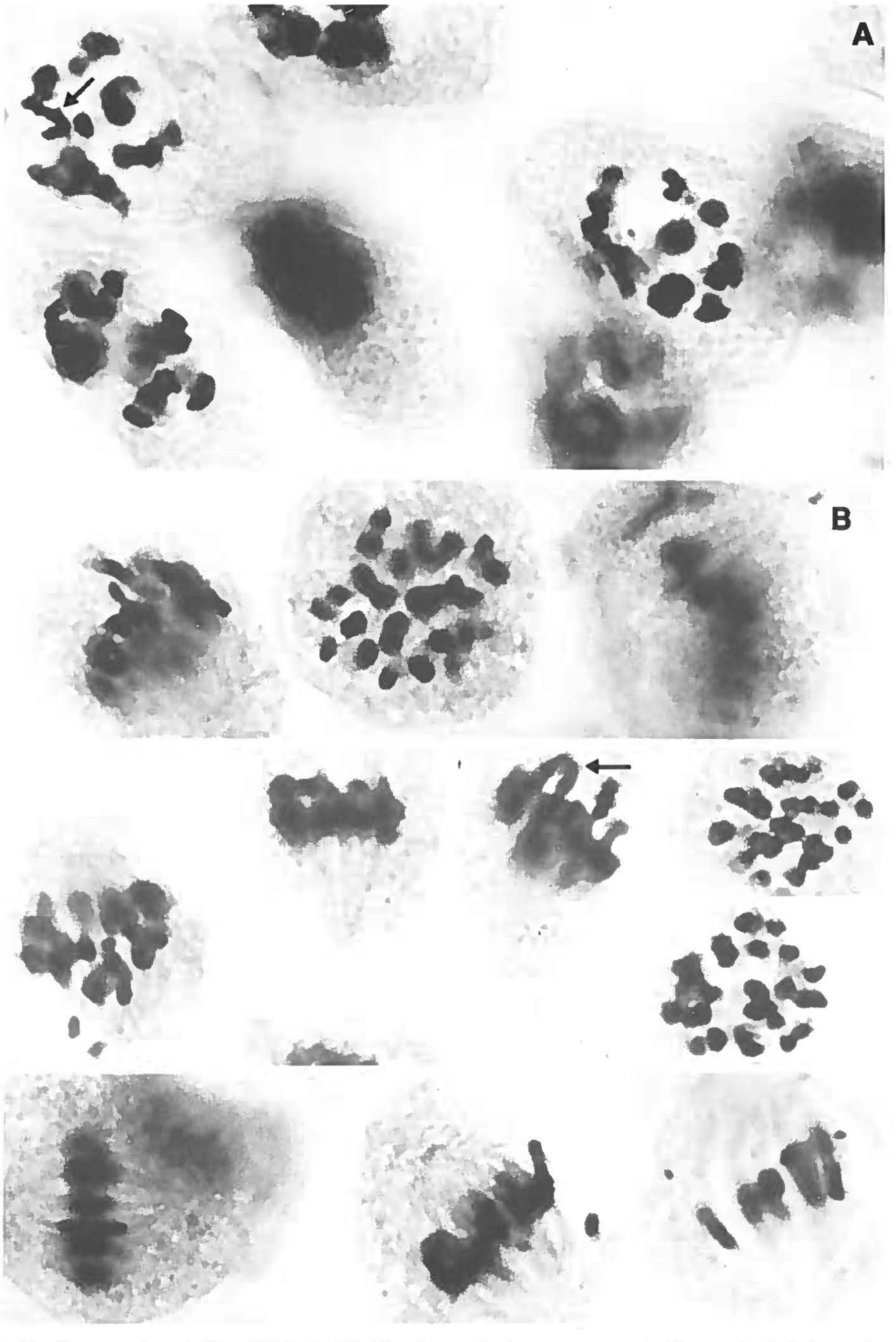

Fig. 3. Meiosis in *Saxifraga nathorsti,* No. 6725. A: Diakinesis, a trivalent occurs probably on the left (arrow), while small and larger fragments are seen in the cell to the right. B: Metaphase I with about 26 bivalents; frequent occurrence of a small and a larger fragment chromosome (possibly acentrics), and at the arrow a triploid configuration. × 2000.

older ascertainments. The differences in meiotic behaviour between the old and new material are believed to be due to environmental differences or more probably to minor differences in the chromosomal interaction. *Saxifraga nathorsti* is not cytologically uniform. It may have been established more than just one time in Northeast Greenland where vast areas were not covered by the Inland Ice for very considerable periods. On the other hand, it is perhaps more relevant to explain the meiotic heterogeneity by assuming segregations in the offspring due to a certain amount of chromosomal aberrations (inversions, deletions etc.).

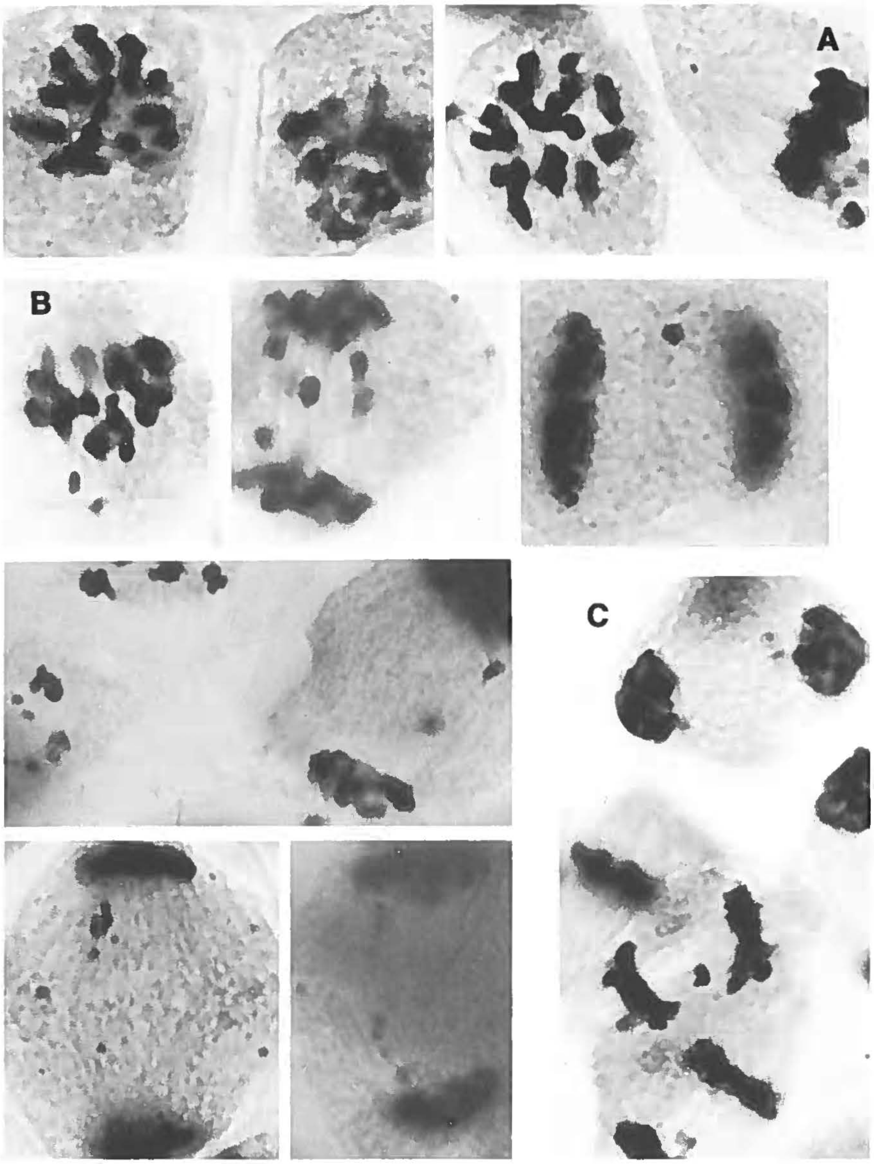

Fig. 4. Meiosis in *Saxifraga nathorsti*, No. 6725. A: Metaphase I showing tendency towards concatenation of bivalents as well as fragmentation. B: First and C: second anaphase with lagging univalents and many minute lagging acentric fragments. × 2000.

Comparative leaf anatomy with special reference to the epithem hydathodes

Saxifraga aizoides

Saxifraga aizoides has linear succulent amphistomatal leaves. The epithem hydathodes were described by Gallöe (1910), Kurt (1930) and Perrin (1972). My observations correspond with those of Kurt (l.c.), who mentions several marginal hydathodes. He counted 2–9 water pores in the epidermis covering the hydathodes. The epithem cells are recorded as relatively large with few intercellular spaces, located particularly at the vein endings. In my material 7–9 water pores occur densely spaced in a group (Fig. 7). The epithem has many elongate intercellular spaces which become filled with dark substances (Fig. 6). Some of the dark material is gathering as a plug in the water cave. Connections were found from the plug to several intercellular spaces filled with the dark substance. The latter exhibits a peculiar network structure (Fig. 8), which was assumed to be a result of a merging of intercellular fibrillar material or of some kind of bubbling during the exudation of the material. The glandular nature of the distal part of the

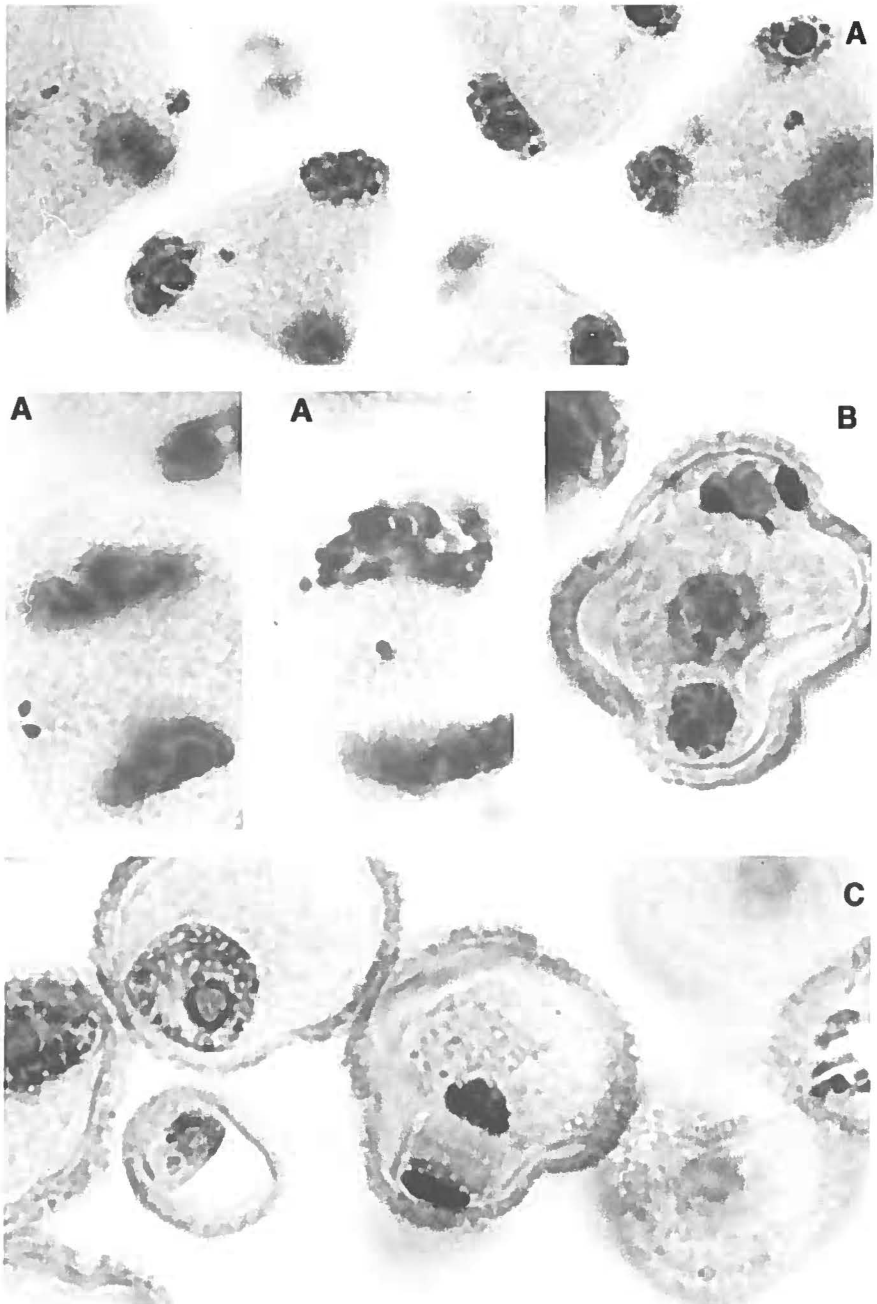

Fig. 5. Meiosis and pollen formation in *Saxifraga nathorsti*, No. 6725. A: Anaphases with laggards. B: Deviating three-nucleate pollen grain. C: Pollen grains with mitoses. One dwarf pollen grain. × 2000.

epithem is obvious and in accordance with the hydathode structure in *Saxifraga ligulata* studied by Häusermann & Frey-Wyssling (1962). Kurt (l.c.) did not find any exudation of calcium carbonate which is in agreement with my observations.

There is a 2–3-layered epidermis immediately at the pores and SEM pictures show circular openings in two layers (Fig. 7). The bundle sheath continues in an epithem sheath which in the drawing by Gallöe (l.c., fig. 17) has only one layer, while Kurt describes two layers.

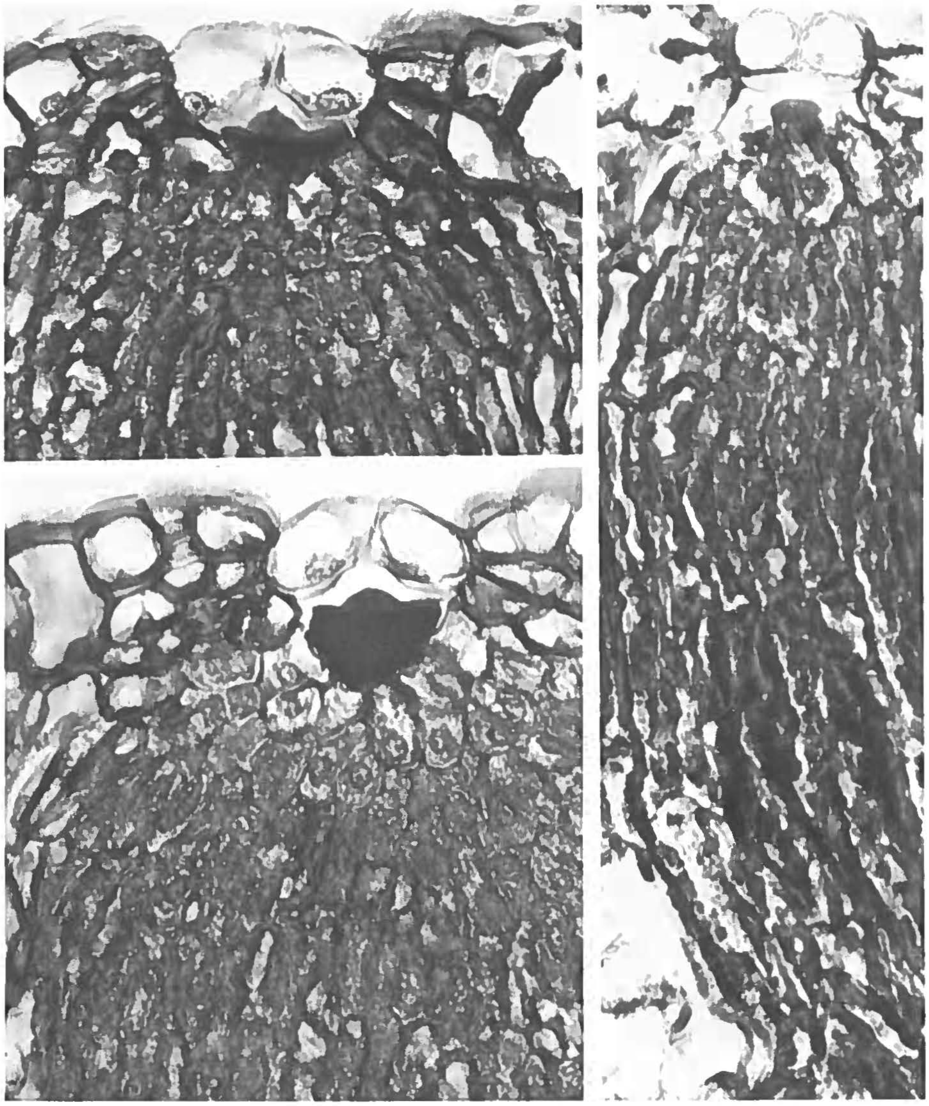

Fig. 6. Longitudinal sections of epithem hydathodes in *Saxifraga aizoides*. Intercellular spaces in epithem and water cave beneath water pore guard cells are blocked by dark material, see text. × 500.

In my material the epithem sheath borders the epidermis and becomes 2–3-layered at the point where the contact with the epidermis is established (Fig. 6). The epidermal cells have a high content of tannin.

It is remarkable that none of the previous workers have noticed dark substances in the epithem intercellular spaces nor plugs of the same substances in the water caves. *S. aizoides* is associated with wet soils, often with seeping water. In West Greenland it is abundant on banks of salt lakes, and in such places the surface of the alkaline soils usually dry up during summer (*Saxifraga aizoides-Juncus triglumis*-sociation in Böcher 1977: 47–51). At the time when the soil surface dries up, a plugging of the hydathodes might be advantageous by counteracting water losses. But it may be just a normally recurrent phenomenon or a stage in the hydathode development and activity. In aquatic plants (e.g. *Ranunculus fluitans*, Wilson 1947, Mortlock 1952) and in certain amphibious marsh plants such as *Caltha palustris* (Stevens 1956) the epithems in mature hydathodes become blocked by brown, gummy substances which are assumed to be secreted by the epithem cells. *Saxifraga aizoides* can stand water logged soils and it occurs in springs even in a semiaquatic environment. The dark substances which occur in the epithem intercellular spaces are therefore comparable to the plugs of brown

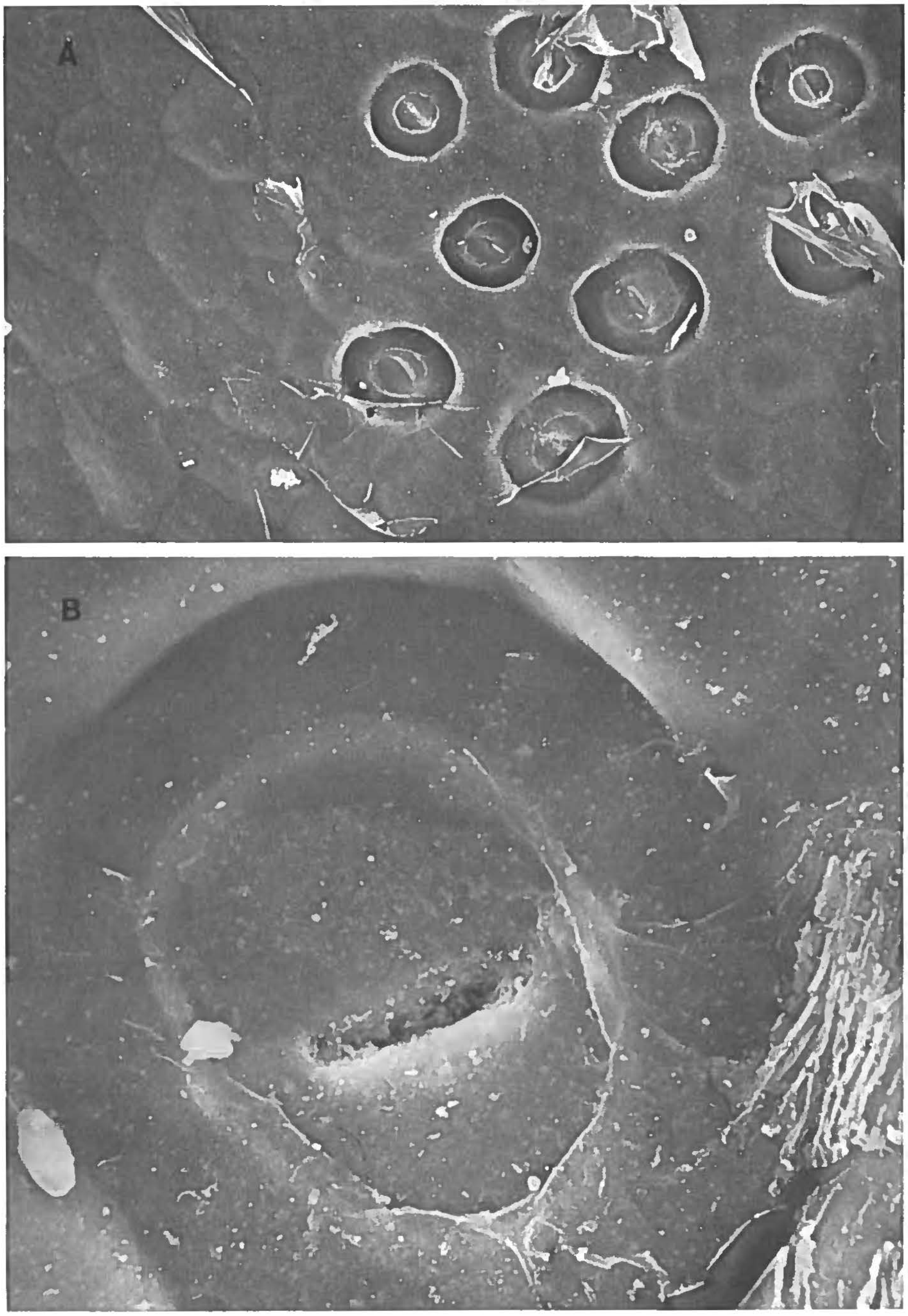

Fig. 7. Water pores in *Saxifraga aizoides.* A: Nine water pores in the epidermis covering the epithem. SEM × 180. B: Single water pore. SEM × 1200.

"gumming-up" substance observed in hydrophytes (cf. Mortlock l.c., fig. 3E). In *Caltha* the blocking material is referred to as "granulae" (Stevens l.c.), The similarity in appearance of the dark substances in *Caltha* and *Saxifraga aizoides* is obvious but needs further elucidation.

Saxifraga oppositifolia

Leaf anatomical studies have been undertaken by Lazniewski (1896, figs 9–13), Gallöe (1910: 285–290), Belin-Depoux (1969) and Perrin (1972, plate 11, fig. 7). Anatomical deviations from *S. aizoides* concern the

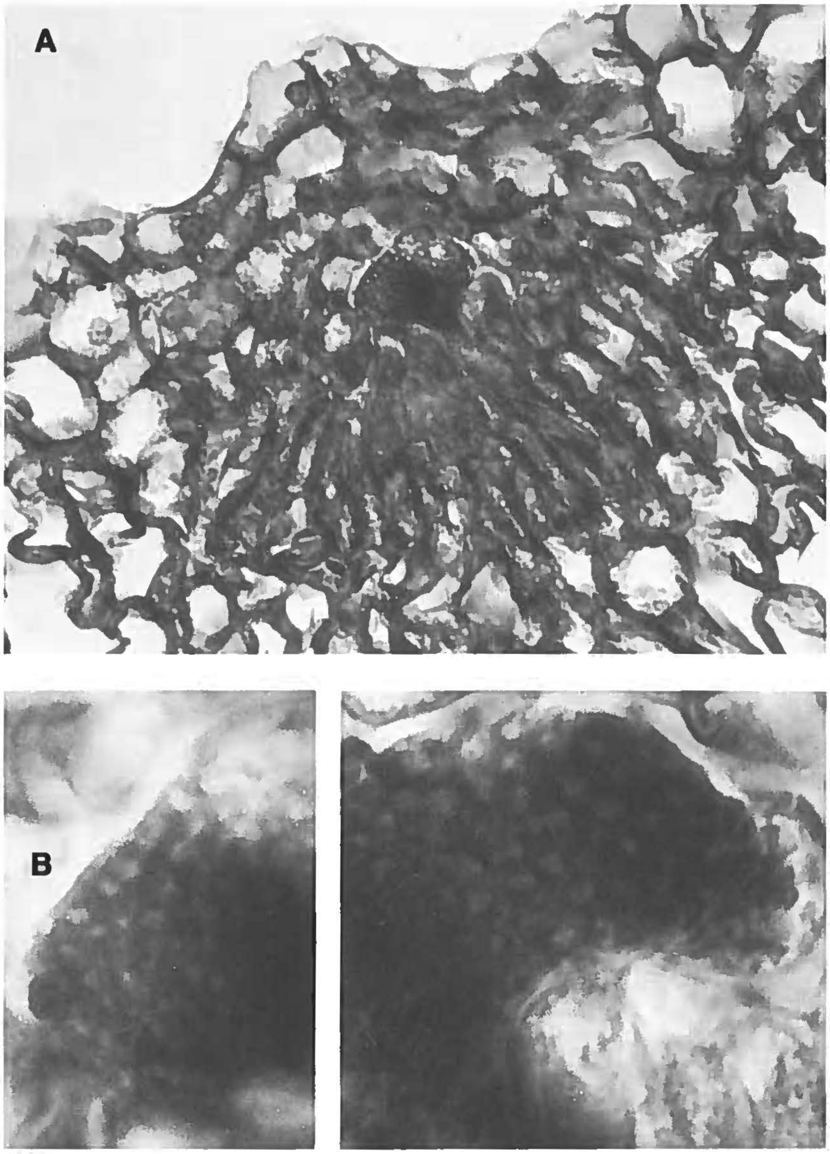

Fig. 8. *Saxifraga aizoides.* A: Oblique transection of upper (distal) part of epithem surrounding dark substance with a foamlike appearance which is gathered in the water cave. × 500. B: The same substance photographed at higher magnification. It continues in the epithemial intercellular spaces. × 2000 (interference contrast).

greater thickness of the cuticular layer of the leaf apices and the position and structure of the hydathodes. The leaves are not succulent. The outer epidermal walls increase in thickness towards the apex. Stomata are absent from the extreme part of the apex where a cavity (pit) is developed containing a hydathode. Stomata occur behind the apex in a band across the leaf, but the density of the stomata is greatest on the adaxial side (Lazniewski l.c., fig. 11A). The thick outer epidermal cell walls appear bright in polarized light. With Sudan IV the cuticle alone is stained, while the thick cellulosic stratified birefringent wall beneath remains unstained (Fig. 9A). The leaf is slightly dorsiventral and almost hyperstomatous.

The hydathode is located at the bottom of a narrow cavity in the oblique upper surface of the truncate leaf apices (Figs 9, 10, 11). The epithem is almost spherical and surrounded by a sheath of 2(–3) cell layers. There is usually a single water pore and occasionally an additional smaller pore (Fig. 12B). The epithem cells are roundish to slightly elongate and often with somewhat undulating walls making room for smaller transverse spaces. The intercellular space inside the water pore guard cells is wide and surrounded by two cell layers

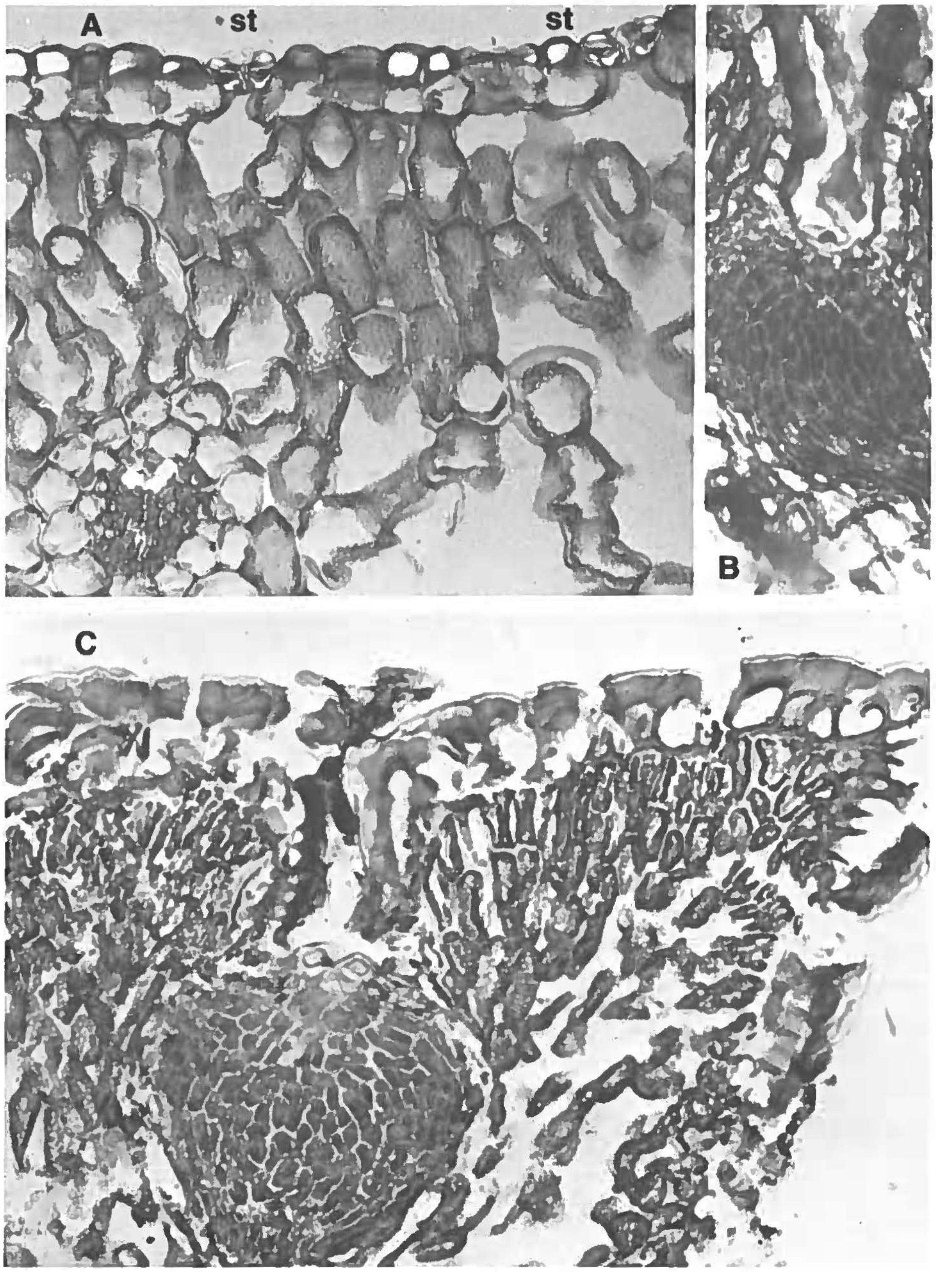

Fig. 9. *Saxifraga oppositifolia.* A: Transection of distal part of leaf in semipolarized light showing birefringence of very thick outer epidermal walls (st: stomatal apertures) and in the xylem in the vascular bundle. × 320. B: The pit leading down to the hydathode which has an almost spherical epithem. × 200. C: The thick outer epidermal wall distinct from cuticle. Single water pore at the bottom of the pit. Quadruple staining. × 200.

only. Beneath follows a smaller space which has connections to many narrow spaces in the central part of the epithem. The spaces do not contain dark substances, nor were crystals of calcium carbonate observed anywhere in the epithem. The epithem sheath is not particularly rich in tannin, but Perrin (l.c.) describes tanniferous cells, which accompany and surround the epithem and the veins and further occur in the epidermis near the water pore. He found small or no starch grains in tanniferous cells. In TEM, Perrin observed

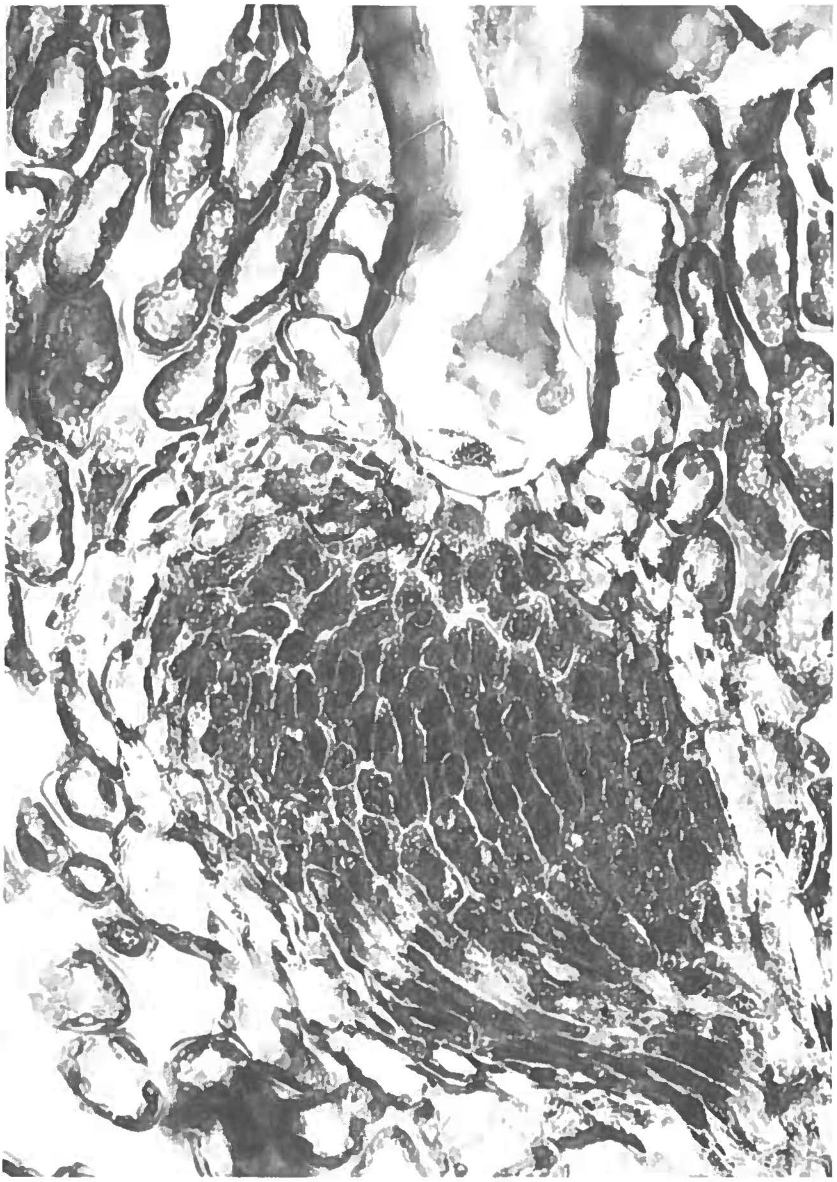

Fig. 10. *Saxifraga oppositifolia.* The guard cells in the water pore are elevated; one of them is seen at the bottom of the pit. Starch grains occur in the uppermost part of the epithem as well as in the photosynthesizing cells on both sides of the pit. × 500.

small intercellular spaces in the epithem and a sinuous structure of the plasmalemma in the cells.

The cavity above the water pore is deep. Lazniewski compared plants grown under normal (neutral) conditions with another plant which was placed in a chamber with water saturated air. The plants grown under neutral conditions had deep cavities filled with calcium carbonate crystals (l.c., fig. 11), while that grown in the chamber had less deep, but wider cavities and no crystals (l.c., fig. 13). The secretion of calcium carbonate in hydathodes of *S. oppositifolia* has been mentioned by all previous investigators. In the plants studied by me in the experimental field and in the Arctic Greenhouse, the lime exudation varied from strain to strain and even between plants within the same strain according to chronology. An extreme case of abundant lime secretion was observed during the first year of cultivation in plants originating from Jotunheimen in Norway. The

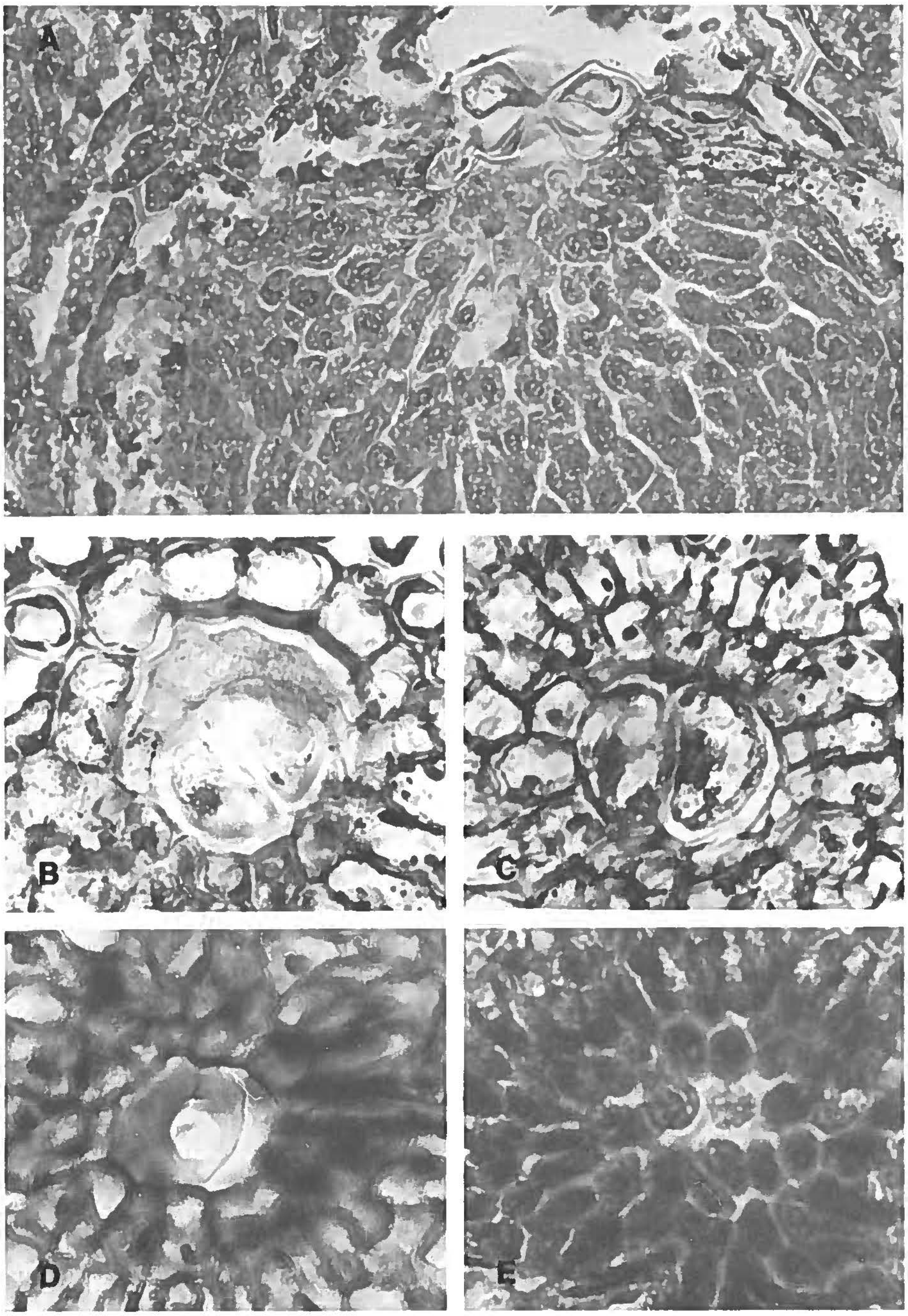

Fig. 11. *Saxifraga oppositifolia.* A: Top of epithem with elevated water pore. B: Bottom of pit with marginal cells of pit and guard cells surrounded by fine granular deposit. C: The guard cells. D: Rear cavity with hollow surrounded by the interior parts of the guard cells. E: Epithem just below rear cavity, starch grains in several cells. × 500.

plants were kept in pots in the experimental field. Later the same plants did not show any lime secretion. This agrees with observations in *Saxifraga aizoon* mentioned by Volkens (1883: 200). According to Belin-Depoux (1969: 653) *S. oppositifolia* and *S. aizoon* show a remarkable agreement in the hydathode structure and function, both having a cavity above the water pore and both being able to exude calcium carbonate which may gather at the bottom of the cavity (see Fig. 12).

The hydathodes in *S. oppositifolia* become differentiated at a very early stage. A spherical epithem initial could be ascertained in the third leaf pair below the

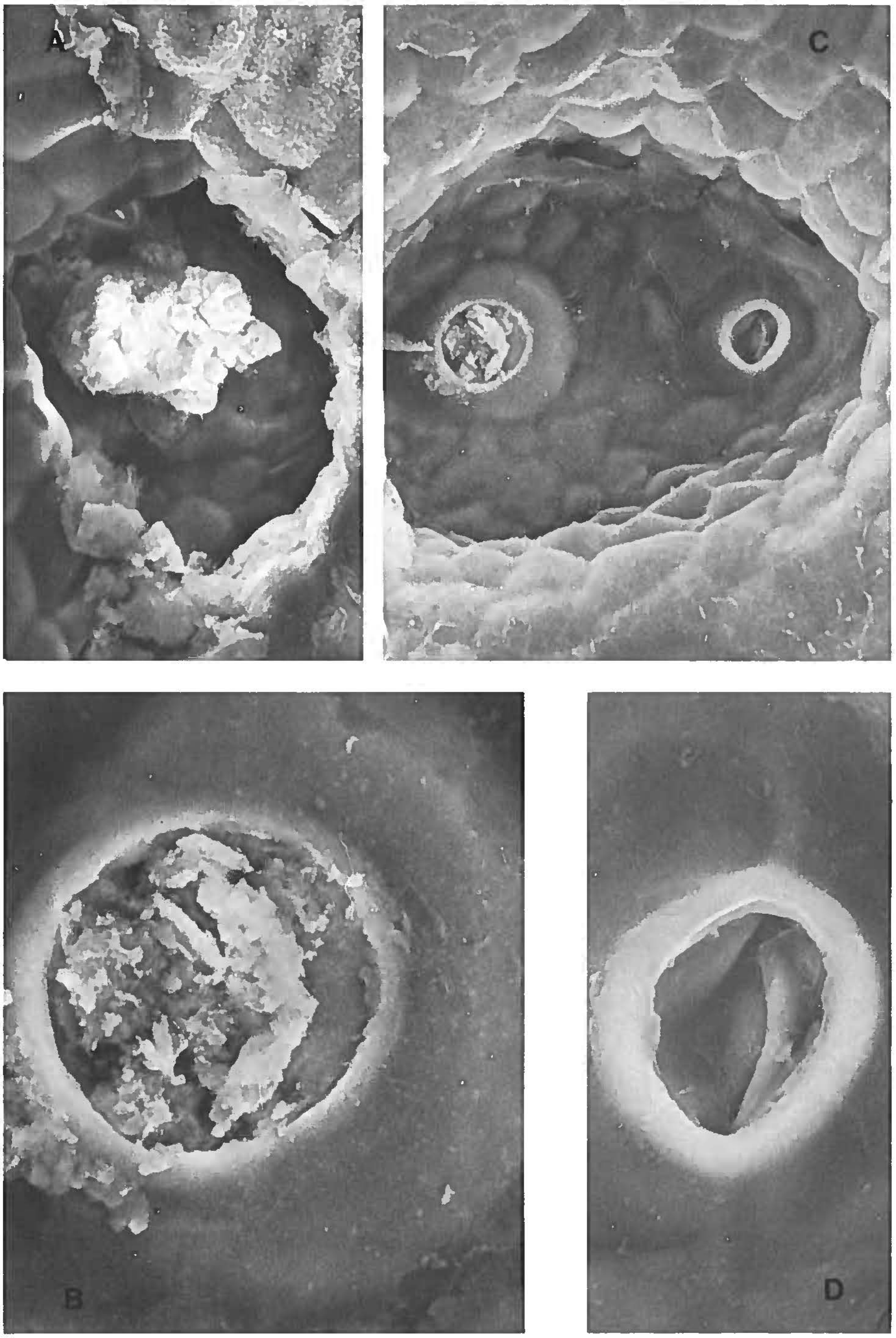

Fig. 12. *Saxifraga oppositifolia.* SEM. A-B: Two pits. A, with assemblance of CaCo$_3$ crystals. × 300. – C-D: The two water pores in B at higher magnification; C with many CaCo$_3$ crystals. × 1200.

shoot apex at a stage in which the leaf apices develop rapidly to form a helmet which protects the apical shoot meristem.

The cells lining the cavity above the water pore have cuticular layers which increase their thickness towards the opening of the cavity. The walls of the guard cells in the water pore including the short outer ledges are cutinized and stain with Sudan IV. Only the dorsal walls towards the flanking cells remain unstained.

Saxifraga nathorsti

There are no previous records concerning the anatomy of this species. Its leaves are slightly succulent. As in the case of *S. oppositifolia* the apical meristem is protected by the first and the second pair of leaves which form an arched helmet (Fig. 13A). The leaves are not regularly opposite, but are often inserted in three ranks. They are not truncate, nor are the leaf apices thickened and flat-

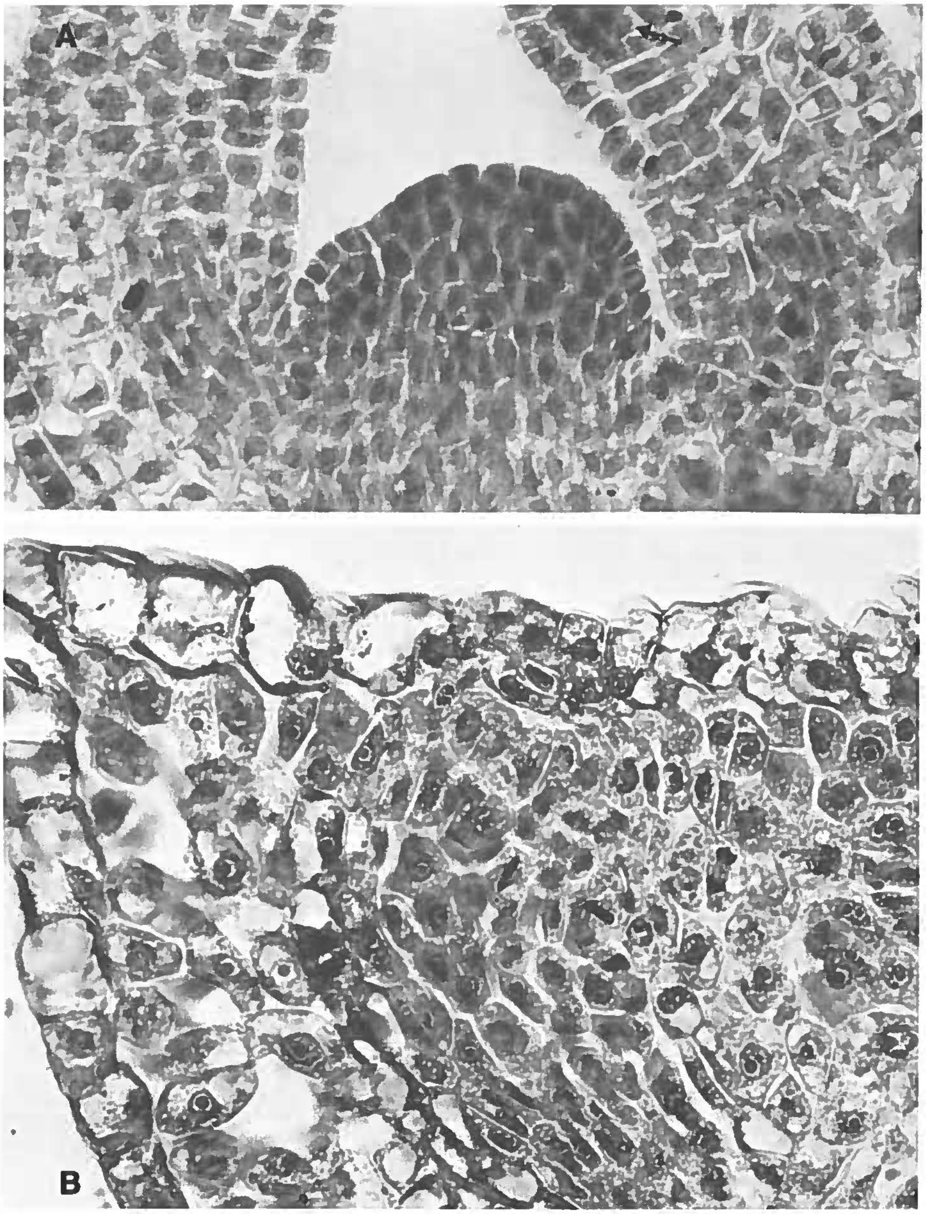

Fig. 13. *Saxifraga nathorsti.* A: Shoot apex between two opposite leaves, a third leaf premordium on the left of the apex does not belong to the same rank as the two first leaves which protect the meristematic parts. Arrow points to first initials of the epithem. × 200. B: Mitotic activity in young epithem. Interference contrast, × 500.

tened as in *S. oppositifolia.* The leaves are almost lanceolate and acuminate with scattered marginal tapering hairs composed of several thick-walled, finally empty cells. The youngest leaves appear dorsiventral with a differentiation between palisades and spongy parenchyma. The bundles have bundle sheaths which are poor in chloroplasts. The hydathodes are initiated early. In the next youngest leaf the epithem initials consist of densely packed cells with large nuclei (Fig. 13A, arrow). In the leaves formed next, the epithem sheath cells become conspicuous because of their content of tannin. A similar high tannin content occurs in the epidermal cells near the leaf apices.

In polarized light the walls of the apical cells surrounding the hydathode are bright as are similar cells in *S. oppositifolia,* but they have not attained a similar thickness in spite of the fact that they are generally wider (Fig. 14B).

As it appears from the preceding there are no cavities at the hydathodes in *S. aizoides* and a deep one in *S.*

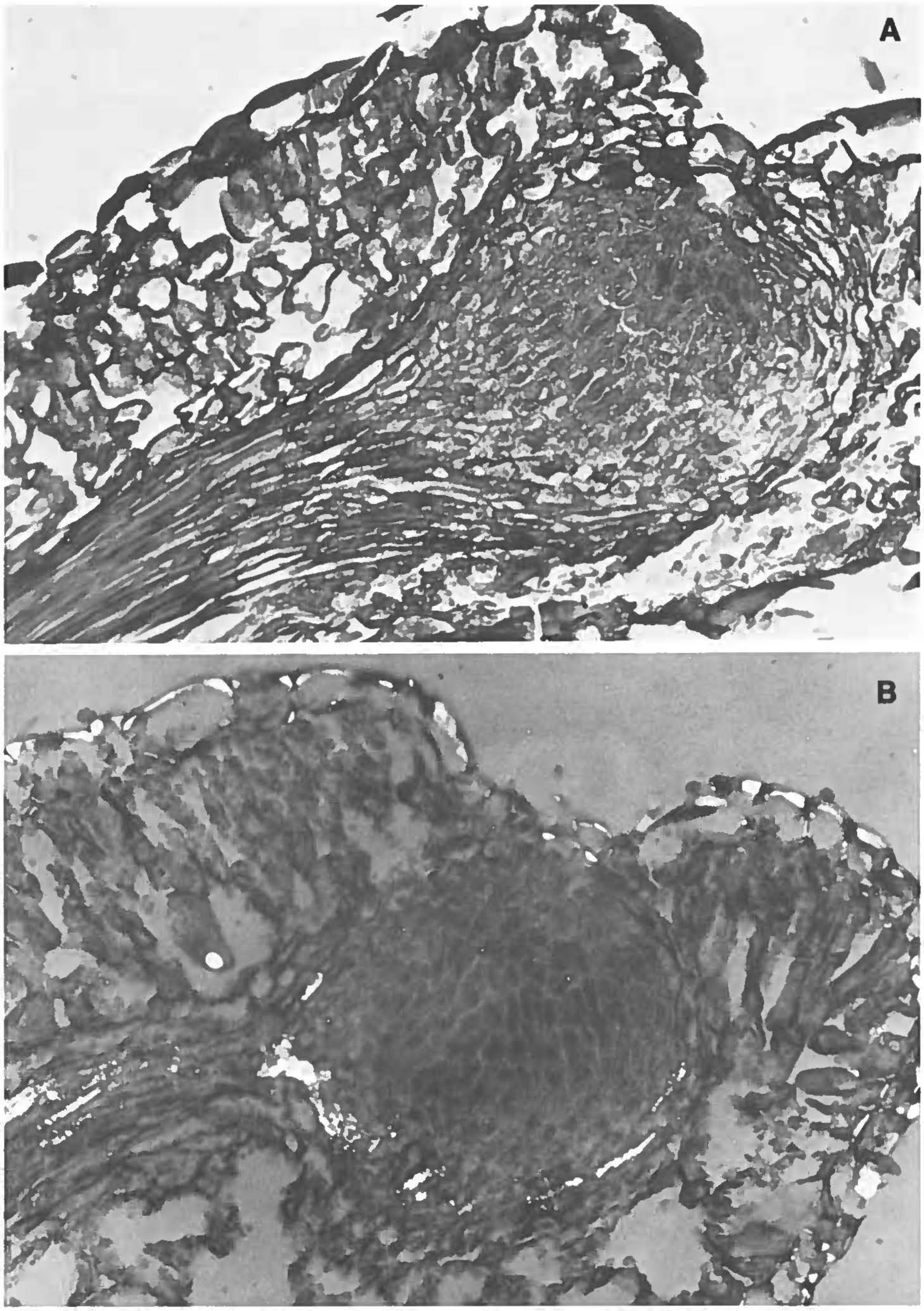

Fig. 14. *Saxifraga nathorsti.* A: Water cave, pore and shallow pit, epithem and tracheid endings at the epithem. B: As A, but observed in semipolarized light. The tracheid endings and rather thick epidermal outer walls show up. × 200.

oppositifolia. In this character *S. nathorsti* occupies an intermediate position by exhibiting a shallow cup-shaped cavity in connection with the hydathodes (Fig. 14). The guard cells in the water pores have a conspicuous size. The pores occur singly or two together of equal size (Figs 15, 16B, 17). The intercellular spaces in the epithem are elongate and distinct. The epithem cells have large vacuoles and nuclei and many small bodies, presumably mitochondria, often close to the nuclei (Fig. 16C, arrow; cf. figures in Belin-Depoux 1969: 642). A content of dark substances in the intercellular spaces is not clearly ascertainable as it was in *S. aizoides,* but in some cases it was possible to detect a greyish substance in the water chamber just inside the guard cells. No lime

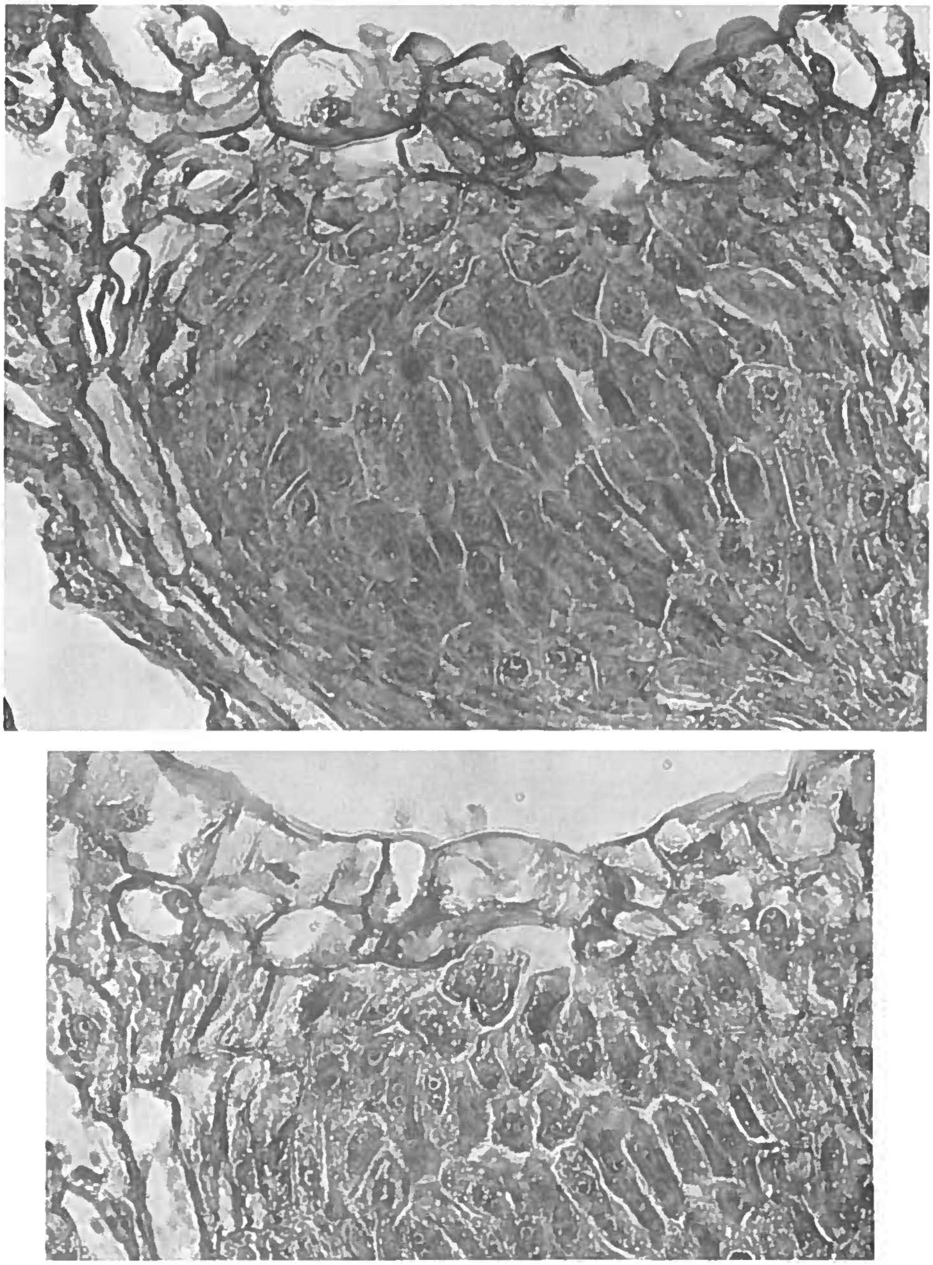

Fig. 15. *Saxifraga nathorsti.* Bottom of shallow pits with water pores, water caves, epithem and tracheid endings. Epithem cells large and slightly stretched. Epithem sheath. In the upper picture with two water pores of equal size. × 500.

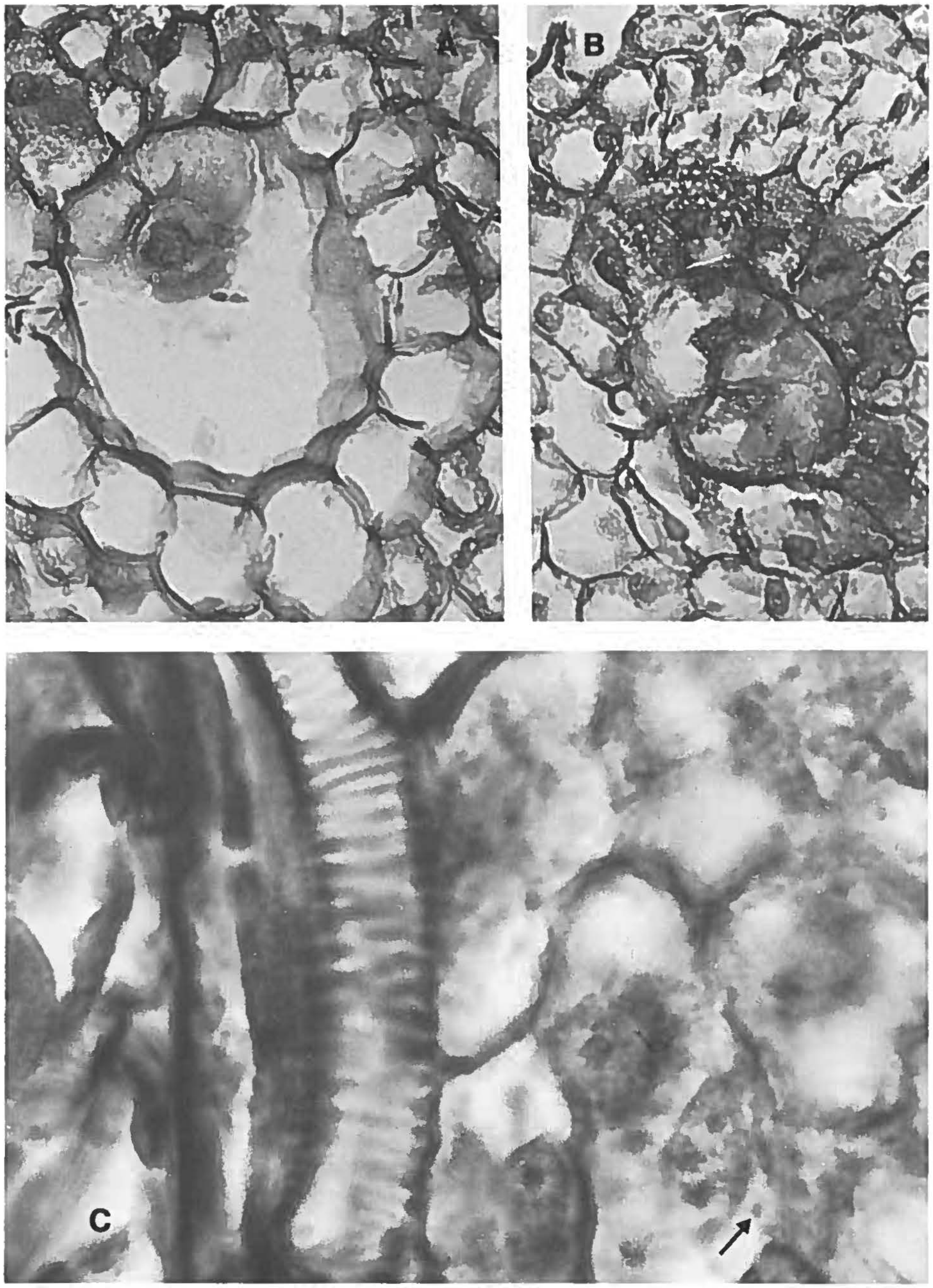

Fig. 16. *Saxifraga nathorsti.* A: Cells surrounding bottom of shallow pit with part of one of the water pores. B: Two water pore guard cells at the bottom of pit. × 500. C: Tracheid ending on the border between chloroplast containing photosynthesizing tissue (on the left) and epithem tissue. Transitional cells with large nuclei and presumed mitochondria (arrow) bordering tracheids. Mitochondria abound in epithem cells (dark irregular spots). × 2000.

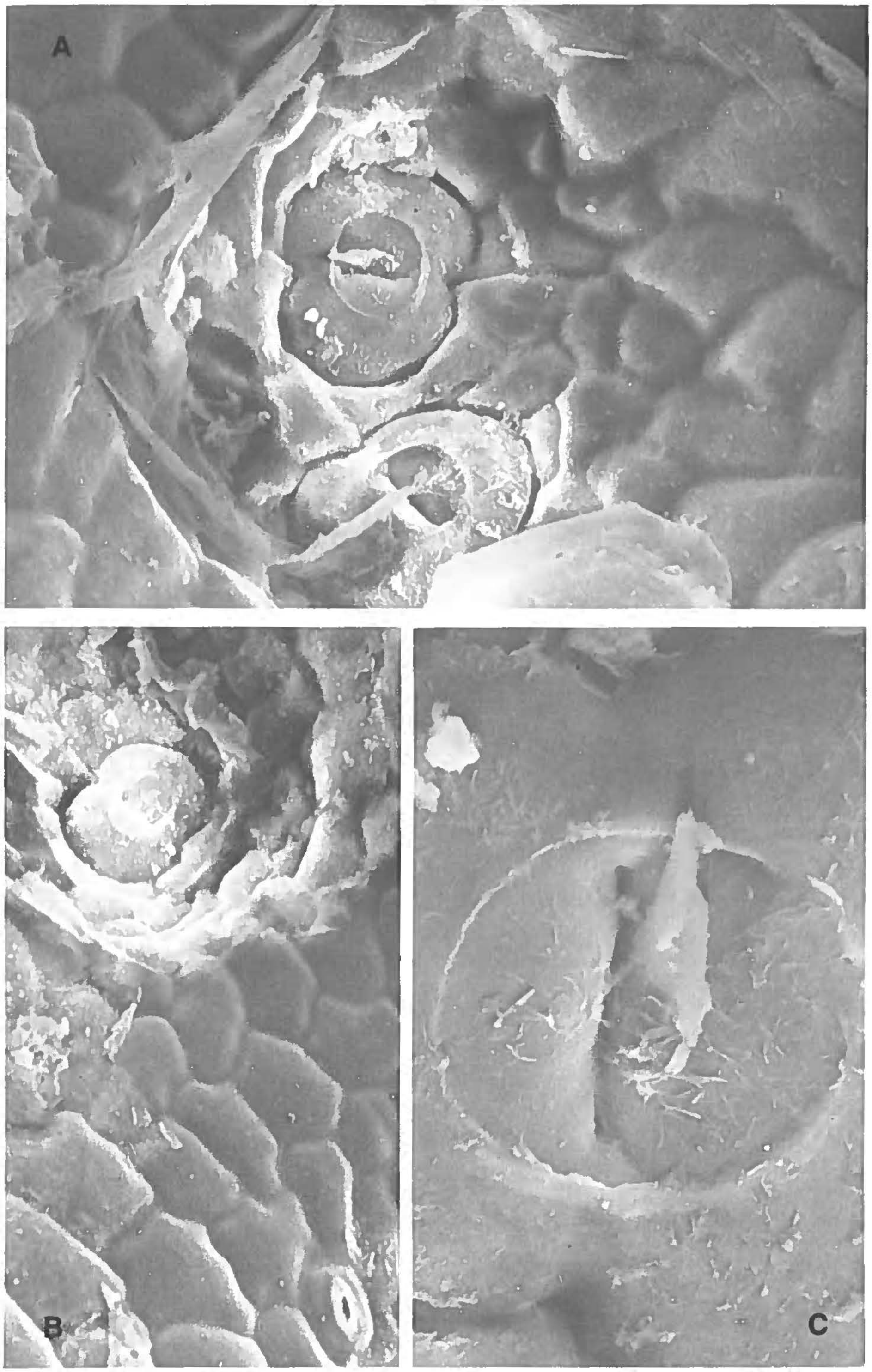

Fig. 17. *Saxifraga nathorsti*, SEM. A: Bottom of shallow pit with two water pores. × 300. B: Single water pore in another pit, and below stomatal aperture. × 180. C: Water pore. × 1200.

Table 1. Hydathode characters

Saxifraga aizoides	*Saxifraga nathorsti*	*Saxifraga oppositifolia*
No cave above water pores	Shallow cave above water pores	Deep cave above water pores
5–9 water pores	1–2 water pores	1(2) water pores
Epithem ovoid, elongate cells	Epithem pear-shaped, larger cells	Epithem spherical, short cells
Dark substances in intercellular spaces and in water cave below pores	Greyish substances in intercellular spaces demonstrable	No dark or greyish substances in intercellular spaces
No crystals of calcium carbonate	No crystals of calcium carbonate	Calcium carbonate crystals abound in cave

secretion was observed and accordingly no calcium carbonate crystals were present in the cavities.

The cell sizes in corresponding tissues or cell types in the three species decrease more than 10% from *S. nathorsti* to the two other species. This was already evident by comparing PMCs or pollen grains (see Böcher 1941, figs 2–4).

Discussion and conclusions

Saxifraga nathorsti is an endemic species restricted to Northeast Greenland. According to Sørensen (1933) it grows in river beds and desiccated ponds and shows the greatest ecological agreement with *S. aizoides.* With regard to the most important taxonomic key characters, e.g. colour and shape of petals, it occupies an intermediate position between *S. aizoides* and *S. oppositifolia.* Also the characters concerning the structure and function of the hydathodes are intermediate (Table 1). *Saxifraga nathorsti* is not uniform morphologically, but comprises some populations which approach *S. oppositifolia* with regard to, e.g., leaf position and shape. One such population has been studied in more detail and appeared to be semisterile and triploid, possessing probably two *oppositifolia*-genomes and one *aizoides*-genome. The behaviour, during meiosis, of tetraploid *S. oppositifolia* (see p.3–4) is not known, but it is most likely an autotetraploid.

Tetraploid *S. nathorsti* was studied cytologically from two different stations in Northeast Greenland (Böcher 1941, and the present paper). The two populations exhibit a number of differences during meiosis, but the degree of pairing is at the same level and both are very probably able to yield fertile offspring.

Böcher (1941) advanced the opinion that *S. nathorsti* was an allotetraploid species which had arisen after a doubling of the chromosomes in a diploid hybrid *S. oppositifolia* × *S. aizoides.* At that time nobody had found triploid specimens approaching *S. oppositifolia.*

It is now clear that such triploid specimens and populations do occur and they contribute to bridge the gap between the two presumed ancestral species of *S. nathorsti.* Such triploids are assumed, by pollination with haploid pollen, to produce tetraploid offspring, in other words be links in the origin of the fertile stabilized allotetraploid species which we recognize as *S. nathorsti.*

This species is perhaps one of the most well documented cases of an allopolyploid species which has established itself in nature. The fact that triploid hybrids have been ascertained twice while there are no records of diploid hybrids supports the view that the doubling of the chromosomes took place in one of the parent species, e.g. *S. oppositifolia,* in which tetraploid arctic populations have already been recorded. Tetraploids will probably be able to endure fertilization by alien pollen grains (e.g. from *S. aizoides*) and produce semisterile triploids which then finally, by another fertilization, will produce the allotetraploids. Thus, a theory of chromosome doubling in a sterile diploid hybrid in the case of *S. nathorsti* is not necessary and should probably be abandoned.

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1981

7. J. de Korte, C. A. W. Bosman & H. Meltofte:
»Observations on waders (Charadriidae) at Scoresby Sund, East Greenland«. 21 pp.

Populations of waders in three census areas at Scoresby Sund, central East Greenland, were studied during the three breeding seasons of 1973, 1974 and 1975. Ringed Plover (*Charadrius hiaticula*), Golden Plover (*Pluvialis apricaria*), Turnstone (*Arenaria interpres*), Knot (*Calidris canutus*), Dunlin (*Calidris alpina*) and Sanderling (*Calidris alba*) bred in the census areas, while Purple Sandpiper (*Calidris maritima*) and Red-necked Phalarope (*Phalaropus lobatus*) bred elsewhere in the region. Population densities were very low, compared to other areas further north in high arctic Greenland. Extensive, deep and late-thawing snow cover prevents waders from utilizing large areas in June. Time of breeding showed a high correlation with the snow melting conditions in the respective areas and years. Breeding success was generally low; only Ringed Plover had more than 50% nest and egg survival. Nest failures were probably mostly due to predation by Arctic Foxes (*Alopex lagopus*). Observation and examination of individuals from post-breeding flocks in the second half of July indicated that these flocks contained mainly non-breeders, but failed and successful breeders were also present. Measurements on eggs, pulli and adults are presented.

1982

8. Helge Abildhauge Thomsen:
»Planktonic choanoflagellates from Disko Bugt, West Greenland, with a survey of the marine nanoplankton of the area«. 35 pp.

Light and electron microscopy of whole mounts prepared from water samples collected in July and August 1977 at thirteen stations in the vicinity of Godhavn (Disko Bugt, West Greenland), has led to the enumeration of approximately 100 nanoplanktonic taxa. A full account is given of field and laboratory methods. The most conspicuous algal class was the Prymnesiophyceae with more than 38 species. Among the heterotrophic organisms listed the Choanoflagellida was the most important single group, comprising 28 species. Two new choanoflagellate taxa are described on the basis of West Greenland material: *Conion groenlandicum* gen. et sp.nov. and *Diaphanoeca undulata* sp.nov.

In order to facilitate immediate comparison of closely related taxa *Diaphanoeca sphaerica* sp.nov. is described on the basis of Danish material.

Thirteen of the loricate choanoflagellate species listed are new recordings for West Greenland. A summary of previous findings of the choanoflagellate species encountered in the Disko Bugt samples show that three species *(Conion groenlandicum, Pleurasiga caudata* and *Parvicorbicula serratula)* are so far known from arctic and subarctic localities only. A pronounced vertical distribution pattern of choanoflagellate species was observed at one station southeast of Godhavn. Three distinct species associations occurred in this particular water column (0–300 m).

1982

9. Eric Steen Hansen:
»Lichens from Central East Greenland«, 33 pp.

A total of 600 samples of 167 species of macro- and microlichens were collected mainly by Pauline Topham and Geoffrey Halliday on botanical expeditions to Central East Greenland in the years 1961, 1962, 1968, 1971, 1974 and 1980. Three of the species, viz., *Caloplaca tornoensis* Magnusson, *Rhizocarpon pusillum* Runem, and *Verrucaria thalassina* (Zahlbr.) Zsch. are additions to the known lichen flora of Greenland. The following eleven species have not previously been reported from East Greenland: *Catillaria philippea* (Mont.) Massal., *Cladonia luteoalba* A. Wilson & Wheldon, *C. macroceras* (Delise) Ahti, *Coelocaulon divergens* (Ach.) R. H. Howe, *Diploschistes muscorum* (Scop.) R. Sant., *Leprocaulon subalbicans* (Lamb) Lamb & Ward, *Peltigera kristinssonii* Vitik., *Pertusaria octomela* (Norman) Erichsen, *Rhizocarpon intermediellum* Räsänen, *Solorina saccata* (L.) Ach. and *Thelidium papulare* (Fr.) Arnold.

Information is provided on climatic conditions at two meteorological stations situated in the area investigated. Thirtyeight collecting localities are listed, together with brief notes on their geology. The localities are situated between the southernmost part of Liverpool Land and Jameson Land, c. 70°N, and the middle of Lyell Land and Traill Ø, c. 73°N.

A survey is given of some important ecological, phytosociological and distributional characteristics for the lichen species, together with information on the presence of perithecia or apothecia.

Lichens of particular interest are discussed in the special part of the paper.

A number of commonly used synonyms are listed in the Appendix.

1982

10. F. J. A. Daniëls:
»Vegetation of the Angmagssalik District, Southeast Greenland, IV. Shrub, dwarf shrub terricolous lichens«, 78 pp.

This paper deals with part of the results of the Dutch phytosociological expeditions in 1968 and 1969 to the Angmagssalik District, Southeast Greenland.

Shrub, dwarf shrub and terricolous lichen vegetation is treated here. The general part contains a description of the Angmagssalik District with emphasis on the applied methods.

The vegetation has been studied according to concepts of the French–Swiss School. The typology is based on about 250 records. The procedure of differentiation and classification of the plant communities is discussed. The term "decisive" differential taxon is introduced and defined. The association concept is considered from a regional point of view. The plant communities are arranged in a floristic hierarchic system.

Concerning habitat factors, the altitude a.s.l., slope and wind direction were measured. Other factors were roughly estimated. The soil types are indicated.

The following part contains a discussion of the vegetation units, with their floristic composition and physiognomy, habitat and distribution, and syntaxonomic position. This includes 24 vegetation units, 1 complex of communities, 11 communities and 12 associations. These are designed to the classes Oxycocco–Sphagnetea, Scheuchzerio–Caricetea, Betulo–Adenostyletea, Loiseleurio–Vaccinietea, Carici–Kobresietea, Salicetea herbaceae and Juncetea trifidi. Eight new associations and 1 new alliance are presented. Some syntaxa have been revised or validated.

The classification by Molenaar (1976) of mire vegetation and chionophytic herb communities is discussed and a new classification is proposed. Dwarf shrub vegetation with *Empetrum hermaphroditum* and/or *Vaccinium microphyllum* on acid, mainly mineral soil is extremely varied in composition and physiognomy and is considered a zonal formation, which largely determines the aspect of the region. The *Empetrum–Vaccinium* community is the climax vegetation of the district.

The greater part of the communities and associations can be assigned to alliances described from Scandinavia, and the phytosociological relationship with that region is emphasized. Only the Dryadion integrifoliae and the Cladonio–Viscarion all. nov. are not known from Scandinavia. The vegetation of the Angmagssalik District has its own character, as shown on the association level by the Sphagno–Salicetum, the Rhododendro–Vaccinietum, the Gymnomitrio–Loiseleurietum, the Carici–Dryadetum and the Cladonio–Viscarietum (all new), which are actually restricted to the area. The other 7 associations are also found at the southern and western coasts of Greenland. Most vegetation types (associations and communities) have a lowarctic-oceanic distribution. A few types are also found in Iceland and Scandinavia.

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