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THE HEPATICAE OF WEST GREENLAND
FROM CA. 66° N TO 72° N

BY

R. M. SCHUSTER AND K. DAMSHOLT

WITH 33 FIGURES AND 11 TABLES IN THE TEXT,
AND 80 MAPS

KØBENHAVN
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Abstract

This work, the result of two seasons intensive field work and of many months of microscopic study of the collected materials, represents an in-depth taxonomic and ecological study of the *Hepaticae* known to occur in West Greenland (from 66° to 72° N). It is based primarily on study of living plants and, as such, is the most comprehensive study of Arctic *Hepaticae* ever undertaken; in addition a large mass of herbarium material from the Botanical Museum of Copenhagen has been examined as well as various early collections (in part of BERGGREN, housed at Lund). The emphasis on study of living plants is unique and allows formation of taxonomic judgments which a study based on dead (herbarium) materials would not allow. Several new species are described and many taxa are here first reported for Greenland. Detailed study of phenotypic variation of various critical taxa has made possible a clearer understanding of these plants. In difficult groups keys are provided and illustrative matter provided (where it supplements or complements the illustrations found in the senior author's The *Hepaticae* and *Anthocerotae* of North America, Vols. I–III, Columbia University Press). Distribution maps showing the regional range are provided, and an introductory general section giving historical and environmental perimeters of the study.

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INTRODUCTION

The *Hepaticae*, or liverworts, form a conspicuous and important part of the Arctic vegetation. Although usually less common and less conspicuous than mosses, and indeed often present in small quantity among the mosses, they occur in striking diversity in the Arctic. Concurrent with their ability to undergo ecesis in various, difficult sites, many show a high level of malleability and somatic adaptability. Also their history in the Arctic is exceedingly complex; their capacity to tolerate low temperatures seems almost unlimited and the ability of some taxa to tolerate desiccation is scarcely less impressive. Therefore, it must be assumed that there was localized survival during the Pleistocene in high Arctic niches, which did not suffer total inundation by ice. Such populations, undoubtedly decimated as regards diversity of biotypes, in more recent times have probably been "fortified" with new genes from populations that had migrated south during the Pleistocene and migrated back north only in the last several millenia. To what extent this hypothetical history is in accord with the observable variability of many taxa is subject to discussion. In some cases the genetic history must be much simpler, as with *Ptilidium ciliare*, a taxon seemingly always sterile in the Arctic. In any event, the Arctic liverwort flora presents formidable difficulties, some of which remain intractible to the present. This memoir is an attempt at a resolution of some of these problems but is primarily an annotated inventory of the hepatic flora of a large and geologically complex portion of coastal Greenland. It represents an in-depth investigation of the liverwort flora of West Greenland from ca. 66°N. to 72°N. Our own collections are almost all from 68°30′N. to 72°N., with a more limited suite made in the area peripheral to the head of Søndre Strømfjord at ca. 67°N.; we have also taken in account a few of the collections made by T. W. Böcher (1959–1963) in the areas south and west of where we collected (Holsteinsborg Distr.). Although there have been scattered collections made in this region prior to our own, chiefly by Porsild, Harmsen, Holmen, Holmen & Steere, Jakobsen and others, those of Berggren (1870, publ. 1875) are very significant and are discussed in detail below (pp. 12–14). Our own collections were made in the periods July–August 1966 and July–Sept. 1970. A detailed account of the stations visited (and

the relevant dates), as well as the collection numbers from each site and a map showing these locations, are given on pp. 27–30.

The present study should be consulted in conjunction with a parallel study of the *Hepaticae* of North and Northwest Greenland (R. M. SCHUSTER, in prep.), based on collections from North Greenland made in 1947–50 by K. HOLMEN and in Northwest Greenland by R. M. SCHUSTER, in 1960. Taxonomic problems discussed at length in that paper, which was written principally in the years 1960–61, although completed only recently, are only peripherally treated in this work, and vice versa. There are also, at various points, discussions of the Greenland taxa herein treated in the senior author's The *Hepaticae* and *Anthocerotae* of North America, Vols. I–III. However, space restrictions in that work forbade the detailed approach which the highly technical nature of the Arctic populations demands; insofar as possible, we refer back to this work, especially to the illustrations. In the present memoir we have restricted ourselves to such illustrations as supplement those in SCHUSTER (1966–1974). We have also refrained from giving keys to the various taxa, when these are found in the aforementioned work. Particularly pertinent in that work are the specific keys to Arctic taxa—given in those cases where problems with Arctic populations are particularly acute.

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We are greatly indebted to Professors T. W. Böcher, M. Köie, and Dr. F. Salomonsen, directors of the Arctic Station, Godhavn, Greenland, where we were housed during two Arctic summers, for their courtesy in making its facilities available. Mr. Harry Christensen, station manager, was constantly helpful in expediting the field work and in providing adequate laboratory space.—We are also very grateful to Dr. Tyge Christensen, Univ. of Copenhagen, for having translated into Latin the descriptions of the 23 new taxa.

We should also like to acknowledge our indebtedness to Mrs. Olga M. Schuster, wife of the senior author, who aided in collecting the material during the 1966 and 1970 seasons and who was responsible for the preparation of the bulk of the material, and typing and editing initial versions of the manuscript.

During the summer of 1966 the senior author held a grant from the Arctic Institute of North America (AINA Grant 58) for field work in Greenland, as well as for a brief stay in Copenhagen, during which time critical material was studied. In 1970, part of the field expenses were subvented by a grant from the National Science Foundation, GB 3884; this grant also provided funds for an artist who prepared some of the illustrative material under the direction of the senior author. The majority of figures, including all cytological drawings, are the work of the senior author. The junior author wishes to thank the Danish Rask-Ørsted foundation and the Ministry of Greenland for the financial support received in 1966 and 1970–71, through the warmest recommendations of Prof. Th. Sørensen.

The 80 Maps are reproduced with permission of the Geodetic Institute, Copenhagen (A 270/73).

METHODOLOGY

With few exceptions, collected materials were studied fresh at the Danish Arctic Station at Godhavn; because of time limitations, however, some had to be examined at our respective institutions. In addition, much material was jointly restudied in February–May, 1971, while the junior author was in residence at Amherst, Massachusetts.

We are convinced that, whenever possible, Arctic populations must be studied from living materials. Arctic phenotypes often depart perceptibly from temperate-boreal phenotypes from which the species, in general, were described, and species criteria of a whole host of Arctic taxa are so subject to environmental modification, often of the grossest sort, that recourse must be had to cytological criteria. We agree with Buch (1924, p. 1) who points out what is today considered a truism, but what then was not: "although *Hepaticae* exhibit a more copious morphological differentiation than most algae, the number of available, taxonomically useful, external structures is much lower than in Pteridophytes and Phanerogams." Buch noted that henceforth it would be proper to employ criteria of the living cell in the systematics of *Hepaticae*, as had been customary in the systematics of the algae. We frankly admit that without use of criteria derived from the living cell one can make very little taxonomic progress in study of Arctic *Hepaticae*. For that reason, cell drawings of living plants are given herein for many West Greenland populations. Wherever new, salient data have come to hand that need illustrative documentation, figures are provided. For the most part, the student must turn to the cited literature for detailed drawings of plants as a whole and, often, of their morphological details.

Study of the mass of material here involved occupied two of us (RMS & KD) for two full summer seasons at Godhavn. One of us (RMS), in addition, has spent an equally large amount of time in detailed restudy of much of the material during the years 1966–70, coincidental with preparation of the treatments of pertinent groups in Vols. II and III of The *Hepaticae* and *Anthocerotae* of North America. In the laboratory, one of us (KD) generally made the initial determinations, the other (RMS) reworked and in some instances revised the determination. In the case of some critical collections, so marked in the field, one of us (RMS) was generally solely responsible for their determination. By and large KD made routine determinations, RMS concentrated on the more intractable "problems", and while engaged in this pursuit, made detailed notes and

necessary drawings; these constitute the backbone of much of the following taxonomic treatment. If, at times, we disagreed as to the disposition of a specific collection, the specimen was subjected to renewed study and (sometimes prolonged) discussion. In this way we trust we have achieved a high level of reliability in the taxonomic treatment.

The nature of the Arctic environment is such that inevitably some populations do not match temperate-climate "stereotypes"; even though we think we can mentally put aside these stereotypes in study of the Arctic taxa, one cannot ever be quite sure. Put in the baldest way possible, we are convinced that, unlike the majority of higher plants which have speciated to adapt themselves to the Arctic environment, the hepatics in many, if not most, cases have made relatively slight genetic adjustments, but with their much higher phenetic malleability, linked with high sterility (and hence, lack of the needed genetic mechanism), have maintained themselves as labile, in many instances, noncomitted populations. This malleability, of course, is the bête noire of Arctic bryophyte taxonomy; without prolonged cultivation experiments which are desperately needed, it will remain such. The malleability may, in part, be the result of growth under decreased competition, especially when plants grow on rock faces or peat as primary colonizers. This is analogous to the situation, e.g., on small, remote islands. Thus Wace & Dickson (1965, p. 281) postulate that "under the conditions of relaxed competition in ... species poor insular ecosystems, it is possible ... species have a higher ecological amplitude and are more polymorphic ..."

The seemingly boundless plasticity of many Arctic taxa is an intrinsic problem that, of necessity, casts an upper limit to the contribution that classical taxonomy can make. We have tried to pierce this limit, when at all possible, by extrapolation from ecological information: the phenotype of the organism reflects not only its genotype, but the shaping force of the environment of the moment. A second limiting factor, an essentially extrinsic one, is that often the material is so sparing, or so juvenile, that intelligent evaluation is almost impossible. Thus, to cite a single example, juvenile *Scapania paludicola* may mimic *Scapania irrigua*, and juvenile *Scapania irrigua* may mimic *Scapania obcordata*, while juvenile *Scapania obcordata* may mimic the genus *Lophozia* [and was actually described as *Jungermannia (Lophozia) globulifera*]. At each "interface" created by such mimicry, the possibility for erroneous identification occurs. Furthermore, relatively immature individuals may produce antheridia or perianths, so that fertility is no necessary guarantee of maturity; and, inversely, sterility is no guarantee whatsoever that the plant is immature! We have no formulae to cope with these problems, but, we trust, have acquired both the field experience and as a result of thousands of hours at the microscope the "Fingerspitzgefühl" without which work with Arctic bryophytes is hopeless.

We have also not hesitated to discard material from consideration if (a) it is so scrappy as to defy determination; (b) is so juvenile or atypical as to defy comprehension. At times we have trusted ourselves to name material that may seem exceedingly sparing to others; this has been chiefly in those cases where, with the living plant at hand, we have obtained a fuller comprehension of the organism than is possible from mere acquaintance with the remnant left in the herbarium packet.

Finally, we would plead most strongly that the field of Arctic bryology is not one in which one can make decisions dictated solely, or even principally, from a knowledge of only herbarium plants. In no other part of the world is field work more necessary, and the "feeling" acquired from long exposure to the living organism more necessary. We have never seen a higher percentage of misdeterminations, based solely on herbarium study, than in the Arctic hepatics. In this era of greatly simplified access to the Arctic there is, today, no excuse at all to attempt to derive taxonomic conclusions solely or even principally from the methodology of the closet taxonomist.

Since these lines were typeset we have seen (Feb. 1974) the paper by SCHLJAKOV (1973) on *Lophozia*, in which serious misconceptions of Arctic *Lophoziae* occur. This paper in part contradicts SCHLJAKOV (1969) —as, e.g., in the interpretation of that *nomen confusum L. murmanica* Kaal.—a plant SCHLJAKOV (1969) describes in terms that suggest it can only be a member of subg. *Massula;* yet SCHLJAKOV (1969) places *L. heteromorpha*, a species clearly of subg. *Lophozia*, into synonymy of his "*L. murmanica*"*!* In 1973 SCHLJAKOV admits his "*L. murmanica*" was "p. maj. p." misidentified and represents a supposed new species, *L. savicziae*, which, judging from the crude figures in SCHLJAKOV (1969) of oil-body form and number, stem anatomy, gemmae, and the polymorphous leaves, may be a synonym of *L. hyperarctica* (to which it keys on pp. 422–23 in SCHUSTER, 1969). This all suggests that the poor type material of *L. murmanica*, interpreted by MÜLLER (1905–16) as *L. wenzelii*, scarcely allows certain recognition. The SCHLJAKOV papers epitomize exactly the dangers cited in the preceding paragraph. We have been able to deal with the problems created in his papers only peripherally in matter inserted in galley (pp. 90, 99, 132–33). Similarly, the paper by LADYZHENSKAJA & ZHUKOVA (1971) was seen after manuscript went to press. In it *L. elongata* is erroneously reported from loci such as Denmark and the highlands of western Europe, East Greenland, Alexandra Land in USSR, and elsewhere. From the crude figures we cannot judge what species the authors had before them—surely not *L. elongata s. str.*, which bears no direct affinity to *L. excisa* (see SCHUSTER, 1969). These papers all emphasize the fact that all taxonomy of Arctic *Lophoziae*, without detailed knowledge of the comparatiev ecology and of living plants, is apt to merely add to an already embarrassingly large literature of inadequate papers.

HISTORICAL BACKGROUND

Disko and Disko Bugt are, botanically, one of the most thoroughly investigated areas in Greenland. Botanists taking part in various expeditions often casually collected bryophytes, but only in recent years have bryological expeditions been organized. As background to our own results, however, an outline of earlier field work and publications on the *Hepaticae* of the area is of interest.

In 1828–36 JENS VAHL visited Greenland and collected in the Disko Bugt area at Umanak, Niaqornat, Sarqaq, Pâkitsoq, Rodebay, and Sydostbugten. As he concentrated on collecting hepatics mainly in two other areas, Tasermiut in South Greenland and Ameralik at Godthåb, only about 28 collections are known from our area; a revised list of species from these collections follows:

Anastrophyllum minutum
Anthelia juratzkana
Asterella ludwigii
Athalamia hyalina
Calypogeia sphagnicola
Cephalozia bicuspidata
Cephaloziella byssacea
Chandonanthus setiformis
Gymnomitrion concinnatum
Jamesoniella undulifolia
(J. schraderi) +)
Lophozia alpestris
– *binsteadii (J. attenuata)* +)
– *kunzeana*
– *lycopodioides*
Pleuroclada albescens
(Cephalozia albescens) +)
Peltolepis grandis
Preissia quadrata
Ptilidium ciliare
Sauteria alpina +)

The above list includes 19 species, but only a few (4+) were published by LANGE & JENSEN (1887). The most interesting find is that of *Jamesoniella undulifolia*, which has been collected in the area only once since.

In the summer of 1867 ROBERT BROWN visited the Disko Bugt area; the following year he published *Florula Discoana*, which also contained a brief treatment of the *Hepaticae* collected, mainly from Jakobshavn, and which were determined by B. CARRINGTON. The list includes 11 species:

Anastrophyllum minutum (J. minuta)
Cephalozia leucantha ? *(J. catenulata)*
Cephaloziella byssacea (J. divaricata)
Chandonanthus setiformis (J. setiformis)
Lophozia alpestris (J. alpestris)
– *binsteadii (J. barbata* v. *attenuata)*
– *collaris (J. acuta)*
– *hatcheri (J. barbata* v. *floerkei)*
– *lycopodioides (J. barbata* v. *lycopodioides)*
Marchantia polymorpha
Ptilidium ciliare

SVEN BERGGREN, as a member of the Nordenskiöld Expedition to West Greenland in 1870, visited about 30 localities from Aulatsivik Fjord in the south to Qeqertaq and Nûgssuaq to the north. The expedition visited especially the long and narrow inlets in the eastern part of Disko Bugt which are often difficult to navigate and which extend close to the the Inland Ice. On the return Godhavn and Sukkertoppen were visited. BERGGREN collected a large number of specimens which were only partly determined after his return home and published in 1875. His work was for its time the chief publication on the *Hepaticae* of West Greenland and was freely quoted by LANGE & JENSEN (1887). It treats the bryophyte communities of each locality and gives a list of taxa with locality data. As BERGGREN published only a small part of his collections, various herbaria often contain unpublished specimens. Unfortunately many specimens published have not been seen (in herb. Lund, Stockholm, and Copenhagen). BERGGREN collected about 133 specimens (with hepatics) in the area dealt with (Sukkertoppen excluded). This estimate is based upon collections at hand (52) and published data. Thus, the number of collections from Aulatsivik Fjord is only 3, while at some of the localities of Disko Bugt BERGGREN collected 10–11 specimens (Ritenbenk, Tasiussaq). This corresponds with the herbarium, kept unintercallated in Lund, with collections poorly labeled but mainly from the Aulatsivik Fjord. A thorough revision of these collections may solve some of the problems left over from BERGGREN. Based upon the 52 known specimens a list of species is as follows (BERGGREN's names are given in parentheses):

Anastrophyllum assimile (J. plicata)
— *minutum (J. minuta)*
Aneura pinguis
Anthelia juratzkana (J. julacea)
Asterella ludwigii (Fimbriaria pilosa)
Athalamia hyalina (Clevea hyalina)
Blepharostoma trichophyllum (J. trichophylla)

Calypogeia muelleriana (Calypogeia trichomanis)
Cephalozia bicuspidata (J. bicuspidata)
Cephaloziella arctica (J. divaricata v. *incurva)*
— *byssacea (* — – — *)*
Chandonanthus setiformis (J. setiformis)
Diplophyllum albicans (J. albicans)
Gymnocolea inflata (J. inflata)
Gymnomitrion concinnatum (Gymnomitrium concinnatum)
— *corallioides (* — *corallioides)*
Lophozia alpestris (J. alpestris)
— *hatcheri (J. quinquedentata)*
— *heterocolpos (J. plicata* v. *gracilis)*
— *kunzeana (J. floerkei)*
— *lycopodioides (J. lycopodioides)*
— *quadriloba (J. attenuata)*
— *ventricosa longiflora (J. wenzelii)*
Marchantia polymorpha
Marsupella arctica (Sarcoscyphus emarginatus v. *arcticus)*
— *revoluta (* — *revolutus)*
— *ustulata* ? *(Sarcoscyphus adusta)*
Mylia anomala (J. anomala)
Odontoschisma ? *elongata (Sphagnocetis communis)*
— *macounii (* — *tessellata)*
Peltolepis grandis (Sauteria alpina p. p.*)*
Plagiochila asplenioides (Plagiochila interrupta)
Pleuroclada albescens (J. albescens)
v. *islandica (J. islandica)*
Ptilidium ciliare
Sauteria alpina
Scapania brevicaulis (Scapania bartlingii)
— *curta (* — *curta)*
— *hyperborea (Scapania undulata, Sc. nemorosa* and *Sc. bartlingii* p. p.*)*
— *mucronata (* — *curta* p. p.*)*
— *obcordata (Jungermannia plicata* v. *gracilis)*
— *spitzbergensis (Scapania nemorosa)*
— *subalpina (Scapania undulata* p. p.*)*
Solenostoma oblongifolium (Jungermannia cordifolia)
— *pumilum* ssp. *polaris (Jungermannia pumila* v. *polaris)*
Tritomaria quinquedentata (J. quinquedentata)

The most interesting finds are *Scapania brevicaulis* (published as *S. bartlingii*) from Claushavn, cited by Buch (1928) as the type of *S. arnellii*,

and *S. spitzbergensis* (BERGGREN's *S. nemorosa*), published by MÜLLER (1915) and BUCH (1928). BUCH also reports *S. kaurinii* (BERGGREN's *S. undulata*, *S. nemorosa*, and *S. bartlingii*, p. p.). These pertinent collections probably all belong to *S. hyperborea*. Lastly *Solenostoma oblongifolium* (BERGGREN's *Jungermannia cordifolia*) and *Anastrophyllum assimile* (BERGGREN's *J. plicata*) should be mentioned.

The publication of "*Grønlands Mosser*" by LANGE & JENSEN (1887) is another milestone in the bryological investigation of Greenland. Included in this paper, in addition to an enumeration of the collections made by VAHL, BERGGREN, and BROWN, are the collections of WARMING and HOLM ("Fylla" Expedition of 1884) and L. KOLDERUP ROSENVINGE ("Fylla" Expedition of 1886). At Manîtsoq, WARMING and HOLM found *Cephaloziella byssacea*, *Diplophyllum taxifolium*, *Gymnocolea inflata*, *Gymnomitrion concinnatum*, *Lophozia binsteadii (attenuata)*, *L. kunzeana*, and *Pleuroclada albescens*; *L. kunzeana* was reported from Christianshåb and Navdluarssuk at Jakobshavn.

The Drygalski Expedition (1892–93) visited the rather inaccessible area at the base of Nûgssuaq, on the northern side of the peninsula. From here VANHÖFFEN collected some 6 species of *Hepaticae*, later (1897) published by STEPHANI.

From the second "Fram" Expedition, BRYHN (1906) published 5 species of *Hepaticae* collected by H. G. SIMMONS at Egedesminde: *Chandonanthus setiformis*, *Lophozia hatcheri (L. baueriana)*, *L. kunzeana*, *Ptilidium ciliare*, and *Tritomaria quinquedentata*.

The University of Michigan Expedition visited Kronprinsens Ejland and Godhavn in 1927–28. Collections made by C. O. ERLANDSEN were published (1934) by FRANCIS J. THORPE. From Kronprinsens Ejland he records *Anastrophyllum minutum*, *Cephalozia bicuspidata*, and *Scapania lingulata*; from Godhavn, *Athalamia hyalina*, *Lophozia hatcheri*, *Marchantia polymorpha*, *Peltolepis grandis*, *Ptilidium ciliare*, *Scapania spitzbergensis*, and *Tritomaria quinquedentata*.

In 1934–38 J. LAGERKRANZ collected on the west coast of Greenland; his collections, together with a few made by others, were published in 1942 by PERSSON. From Godhavn *Cephaloziella alpina*, *Lophozia heterocolpos*, *L. porphyroleuca*, *L. quadriloba*, *Mannia pilosa*, *Scapania cuspiduligera*, *S. hyperborea*, and *S. mucronata* were reported; from Tartûssaq (PORSILD), *Athalamia hyalina*.

In 1949, H. DE LESSE, a member of the French expedition led by PAUL-ÉMILE VICTOR, collected a few bryophytes at Eqe, later (1952) published by JOVET-AST: *Lophozia kunzeana*, *L. lycopodioides*, *L. ventricosa* ?, and *Ptilidium ciliare*.

PHYTOGEOGRAPHICAL, CLIMATIC, AND GEOLOGICAL CONSIDERATIONS

Introduction

The region from Søndre Strømfjord to Svartenhuk, in which Disko and Disko Bugt occupy a median sector, represents one of the most critical areas, phytogeographically, in Greenland. We have here three notable variables: (a) striking variation from oceanic and hyperoceanic sites, e.g., Kronprinsens Ejland and Manîtsoq, to highly "continental" sites, as at the head of Søndre Strømfjord, of Pâkitsup ilordlia and of Kangerdluarssuk; (b) equally pronounced differences between a "southern" element, and a "northern" element, which is Arctic and in part high Arctic; (c) marked geological differences, owing to the intrusion of huge to small and local masses of basalt, basic rocks, especially in the western coastal sectors, into a region which is otherwise largly formed of acidic, igneous rocks.

These three variables, individually and jointly, are in large part responsible for making possible the existence of an extremely rich hepatic flora in West Greenland, consisting of some 136 species in 41 genera. The only other areas in the Arctic at similarly high latitudes with a comparably rich and diversified hepatic flora are the north slope and coast of Alaska and (possibly) oceanic Spitsbergen. These two areas have a very rich and diversified flora for reasons other than those lending such diversity to the West Greenland flora; in the case of Alaska, we have unquestioned survival of many pre-Pleistocene relicts in unglaciated areas (e.g., *Hygrolejeunea alaskana*, *Ascidiota blepharophylla ssp. alaskana*, *Radula prolifera*, *Lophochaete fryei*, etc.); in Spitsbergen there is the modifying but attenuated effect of the Gulf Stream.

Phytogeography: The early works of Porsild (1902, 1920) and others established the fact that in this general region there are remnants of a flora whose affinity is distinctly southern and not, strictly speaking, Arctic. Among such taxa, which attain their northern limits on Disko are *Equisetum scirpoides*, *Botrychium lanceolatum*, *Luzula parviflora*, *Platanthera hyperborea*, *Thymus praecox ssp. arcticus*, *Coptis trifolia*, etc. Similarly, in the inner, continental portions of Søndre Strømfjord

occur southern elements such as *Sisyrinchium groenlandicum* (BÖCHER, 1954, 1966), a species immediately allied to the temperate-boreal *S. montanum*.

Among the *Hepaticae* there is a considerable list of taxa, many of which are temperate-subarctic in range:

Asterella saccata
Blasia pusilla
Calypogeia integristipula
— *muelleriana*
— *neesiana*
Cephalozia leucantha
— *loitlesbergeri*
— *lunulifolia*
Cephaloziella hampeana
— *subdentata*
Diplophyllum albicans
— *obtusifolium*
(known again from Inglefield Bredning)
— *taxifolium*
Lophozia longidens ssp. *longidens*
— *lycopodioides*
Mannia fragrans
Marsupella boeckii
— *sparsifolia*
Mylia anomala
Nardia scalaris
Riccia beyrichiana
— *sorocarpa* (to Inglefield Bredning)
Scapania degenii
— *paludicola*
— *scandica*
Solenostoma pyriflorum s. l.
Tritomaria polita (incl. ssp. *polymorpha*)

There is a considerably less impressive list of taxa which are, basically, strictly Arctic or high Arctic and, to date at least, not known in Greenland south of the region discussed; among these are:

Anastrophyllum sphenoloboides
Arnellia fennica
Lophozia alboviridis
— *heteromorpha*
— *longidens ssp. arctica*
— *pellucida*
Lophozia polaris
— *rubrigemma*
Scapania crassiretis
— *serrulata*
Tritomaria exsectiformis ssp. *arctica*
— *heterophylla*

In addition to these taxa is a limited suite of species with a disjunct range, including the following:

1. *Anthelia juratzkana*, *Lophozia hatcheri*, *L. excisa*, *Ptilidium ciliare*, *Calypogeia sphagnicola*, *Marsupella sparsifolia*, and *M. ustulata*. These taxa are all bipolar in range, with (except for *L. hatcheri*) a very restricted range in the southern hemisphere.
2. *Metacalypogeia schusterana*, known from one Greenland station and then again from northern Alaska, Newfoundland, and Nova Scotia.
3. *Lophozia elongata*, known from Fennoscandia and doubtfully elsewhere in Europe, and again from one site on Disko.

4. *Marsupella condensata*, known from N. Europe, Spitsbergen, Scotland, and central Europe (Alps; Tatra Mts.) recurring in Iceland; known from one station on Disko, one in southwest Greenland.
5. *Marsupella revoluta*, known from Baffin Isl., E., NW., and W. Greenland, but not S. Greenland; also on the southern slopes of the Alps (Type), Fennoscandia, the Tatra Mts., Japan, Formosa, SW. China, and the Himalaya, southward again in Borneo and New Guinea.
6. *Anastrophyllum assimile*, known from NW., E., and W. Greenland, coastal Alaska, Queen Charlotte Isls., S. Norway, the central European Alps (where supposedly a pre-Pleistocene relict), Sikkim-Himalaya, Korea, Japan, and Borneo.

Numbers 3 and 4 (*L. elongata* and *M. condensata*) may represent European taxa which have established (or retained?) only scattered sites as far west as Greenland.

Numbers 5 and 6 (*M. revoluta* and *A. assimile*) have strikingly similar ranges. In Greenland they nearly always occur together.

The number of taxa with a highly disjunct range is rather small. The last two (*M. revoluta* and *A. assimile*), however, are species with so strikingly dissected and relict a range that we must assume it is an old, pre-Pleistocene one. These two taxa, much like the Sword moss, *Bryoxiphium norvegicum* (see STEERE, 1937), seem very largely restricted to regions which escaped Pleistocene glaciation. Their presence on the Greenland coast suggests that somewhere along that coast—perhaps in the far north—nunataks, on which they could have survived during the glacial periods, must have existed. *Marsupella revoluta* is known only sterile (or with unfertilized gynoecia) in Greenland, while we have seen only ♂ plants of *Anastrophyllum assimile* in northwest Greenland, although it produced capsules in West Greenland (Qôrorssuaq).

A seventh species, *Anastrophyllum sphenoloboides*, known from Greenland again only from the Inglefield Bredning area (SCHUSTER, 1969), is also known from northern Alaska and the Mackenzie Region—the last two areas which to a large extent escaped continental glaciation. The presence of this species in West and northwest Greenland suggests, also, that there may have been very localized survival of bryophytes on headlands or nunataks that escaped inundation by the ice. However, the actual number of "phytogeographically critical" species is so small that no profound phytogeographic conclusions can be drawn. [However, if we add to those "old" species the list of taxa apparently endemic to the eastern American Arctic (p. 37) a rather convincing case can be made that somewhere in the eastern American Arctic a refugium or refugia existed that allowed survival of some elements since before the start of the Pleistocene. This topic is further pursued on pp. 36–37.]

History of the flora: The history of the hepatic flora in West Greenland is probably a very complex one. The present admixture of high Arctic, Arctic and boreal elements, as regards the *Hepaticae*, is probably largely fairly recent. It seems almost impossible to visualize taxa, confined largely to the oceanic portions of our region (such as *Blasia pusilla*, *Calypogeia muelleriana*, *Cephalozia leucantha*, *C. lunulifolia*, *Diplophyllum albicans*, *D. taxifolium*, *Lophozia incisa*, *L. lycopodioides*, *Marsupella sparsifolia*), as having survived the Pleistocene on nunataks or hypothetical ice-free headlands. Thus much, if not most, of the hepatic flora must be regarded as of recent derivation, presumably from the south. Other elements (among them *Arnellia fennica*, *Lophozia pellucida*, *Tritomaria heterophylla*, *Lophozia polaris*, *Scapania serrulata*) very likely entered our area from the north—perhaps from Pearyland or other northern, locally ice-free, enclaves. Alternatively, one could postulate their survival since late-Tertiary times on local nunataks or ice-free headlands. Of the cited species the first four are among the most exposure-tolerant of our hepatics, and if any liverworts survived on windswept nunataks or isolated headlands, these could be regarded as logical "candidates". Weak evidence for survival, essentially *in situ*, of a few taxa with highly disjunct distribution is offered chiefly by: *Anastrophyllum sphenoloboides*, *A. assimile*, *Marsupella revoluta*, and one or two other taxa.

Whatever the late-Tertiary and Pleistocene history may have been, it is clear that earlier in the Tertiary and in Cretaceous times climatic conditions were such that probably few if any members of the present flora—aside from "tolerant" taxa such as *Diplophyllum albicans*, today found in essentially frost-free loci, as far south as Cornwall and Macaronesia—could then have grown at lower elevations in West Greenland. In early Cretaceous times the lowland flora consisted essentially of Gymnosperms accompanied by ferns, including those of the tropical and antipodal family *Gleicheniaceae*. The classical studies of HEER (1883) and SEWARD (1926) of the Kome, Atane and Pautût floras have shown that in Cretaceous times the coastal region as a whole must have had a warm temperate flora. As late as the Tertiary there existed a typically "Arcto-Tertiary" flora (KOCH, 1963, 1964). It seems likely that almost all hepatic components of this flora, like all the vascular plant components, were obliterated coincident with late-Tertiary and Pleistocene deterioration of the climate. However, a very few taxa, which today can be found within 0.2–0.5 miles of existing ice caps, such as *Anastrophyllum assimile*, possibly may be the last remnant of the old Arcto-Tertiary flora and may have survived the Pleistocene, *in situ*. There is, also, very weak evidence that taxa like *Diplophyllum obtusifolium*, found—like *A. assimile*— in Inglefield Bredning within 0.5–1 km of existing ice caps, may represent pre-

Pleistocene relicts. In any event, numerically, these components represent a very small proportion of the extant flora.

It is possible, and indeed likely, however, that many of the Arctic and high Arctic elements of the present flora existed in Greenland, and/or the adjoining portions of the Canadian Arctic Peninsula, as alpine elements in early Tertiary times. Thus, with removal of the continental ice sheet from Greenland, one must assume that, owing to isostasy, elevations much over the average maximal 3000 m heights which now exist probably were found somewhere in the region between Axel Heiberg Island and East Greenland. Even if we had a warm temperate flora at the latitude of Disko in early Tertiary times, at and near sea level, one almost must assume the existence of persistent snow fields and probably montane glaciers on mountains further in the interior. We would, therefore, assume that perhaps many of the elements that are today Arctic were then alpine—present in similar latitudes but at much higher altitudes. This altitudinal displacement is still seen today to some extent; thus *Prasanthus suecicus*, which is frequent at and near sea level at 68–77°30′ N. in West Greenland today, occurs in South Greenland (latitude 63°) at ca. 750 m and is lacking nearer sea level.

The point is that, in spite of the demonstrated occurrence at the latitude of Disko Bugt of warm-temperate coastal vegetation, alpine loci probably existed in which some of the extant components of the flora were already present. Thus *Marsupella revoluta* occurs today at ca. 4000 m near the equator in New Guinea (Schuster, 1968) and *Anastrophyllum assimile* occurs as an alpine species on the south slopes of the Alps, where it supposedly survived at least the last glacial period as a relict (Müller, 1951–58), as well as at high elevations on Mt. Kinabalu in Borneo (Kitagawa, 1967). Thus, even if most present-day components of the flora are (a) either recent immigrants; or (b) recent evolutionary units, we must assume that several of the critical taxa, cited above, represent relicts of the warmer Tertiary.

These historical facts are important for the taxonomist to keep in mind, since they indicate that, to a large extent, the regional hepatic flora is a "young" one, and one which is in a state of flux. It seems likely that none of the species which seem to be endemic to the area (e.g., *Scapania invisa*) will prove to be true endemics. A number of taxa (e.g., *Scapania ligulifolia*, *S. serrulata*, *Tritomaria heterophylla*, *Lophozia hyperborea*, *L. rubrigemma*, *L. heteromorpha*, *L. pellucida*) that are Arctic and high Arctic possibly if not probably survived north or west, or both, of the main center of Pleistocene glaciation. These taxa, except for *L. hyperborea*, do not occur in Greenland south of the Disko Bugt region. It is possible that these taxa did not migrate southward, south of the glacial borders,

during the Pleistocene, but represent part of the pre-Pleistocene Arctic flora of very high altitudes and/or latitudes. It seems more likely, however, that these are relatively "new" species, which are rather recent evolutionary units often specialized for survival under exceedingly difficult conditions—as the accounts on the following pages of the ecological perimeters of *L. rubrigemma* and *L. pellucida* make clear.

In summary, then, except for the rather few exceptions noted above, the bulk of our taxa seems to represent post-Pleistocene immigrants into the region. This is particularly true of thermophytes like *Riccia sorocarpa*, *R. beyrichiana*, and *Mannia fragrans*. In a few instances it is possible that immigration may have been from both north and south. Thus *Cryptocolea imbricata* and *Lophozia latifolia* are known from 2 and 1 stations, respectively, in the Great Lakes region—north of a "Driftless Area" (SCHUSTER, 1958a) and both recur in the high Arctic, from 82–83° N. lat. The possibility that regional populations of some taxa have had a dual, recent, origin may, in part, account for the evident polymorphism and the untidy perimeters some of the taxa have in our region.

There is, thus, much less evidence for survival *in situ* of components of our flora than there is in, e.g., Alaska-Yukon, or in northern Ellesmere Island (see STEERE, 1953; SCHUSTER, in SCHUSTER *et al.*, 1959; BRASSARD, 1971). It is a striking fact that certain taxa that surely survived the Pleistocene in northern Alaska and/or the Yukon, such as *Lophochaete fryei*, *Mesoptychia sahlbergii*, and *Scapania simmonsii*, occur today far eastward of the region of their Pleistocene survival; the first is found east to Hudson Bay, the latter two to southern Ellesmere Island and eastern Devon Island—areas where survival during the Pleistocene is almost impossible to visualize. One can, therefore, postulate that there has been, in the last 5–10.000 years, radiation outward from the Alaska-Yukon "survival center" eastward. Some striking and isolated taxa—like the three mentioned—have migrated eastward to, in part, the eastern edge of the Canadian Arctic, but have not—at least yet—extended their ranges into West Greenland. The regional absence of such strikingly isolated and phytogeographically important taxa like the genera *Mesoptychia* and *Lophochaete* suggests that the Greenland flora has gained little if anything from the Alaskan-Yukon center. *Metacalypogeia schusterana*, known from one station in West Greenland, as well as from unglaciated northern Alaska, at first glance seems to represent such a taxon; its only close relative occurs in Japan to Korea. This plant, however, also occurs in single stations on Cape Breton and in western Newfoundland—areas which possibly may have escaped (at least on their now submerged coastal plains) total Pleistocene glaciation. FERNALD (1925) in a classical paper elaborated the thesis—to a large extent invalidated by subsequent work—that portions of western Newfoundland and of Nova Scotia

escaped glaciation during the Pleistocene. Although it has been shown that the highlands were all glaciated at least once, it has never been conclusively documented that (a) the upland regions were all simultaneously covered by ice sheets, so that all possible refugia were simultaneously obliterated; (b) the shallow and wide coastal plain, now inundated, was fully glaciated during the height of the Pleistocene. It is perhaps not co-incidental that Cape Breton and western Newfoundland, from which *Metacalypogeia schusterana* is known, both harbor a number of disjuncts (such as *Schizea pusilla*) which otherwise occur only south of the proven southernmost extension of the Pleistocene ice sheet.

Climate: The meteorological data are obtained from Leo Lysgaard *Grønlands Klima* and a single series of measurements are from *Danmarks Natur*, Vol. 10.

Winds: Records from the area are given only from a single station, Egedesminde. To determine variation of the dominating directions of wind during the year, the winds are classified as Northern (NW, NNW, N, NNE, NE), Western or Oceanic (WNW, W, WSW, SW, SSW) and Continental (S, SSE, SE, ESE, E, ENE). Oceanic and northern winds dominate in summer, May–September, while continental winds dominate in the winter. Calm days occur most frequently in late summer (August). The force of the wind varies during the year; in June, July, and August stronger winds (more than Beauf. 4) are less frequent than in any other month of the year.

Temperature and precipitation: A curve drawn on the basis of the mean monthly temperature (1961–65) for Godhavn, Jakobshavn, and Umanak shows that average temperatures above 0° C. prevail in the beginning of May at all stations and that killing frosts start in the middle of September. The lowest mean temperature is obtained at the northerly station Umanak (March) and the highest at Jakobshavn (July), probably due to its location deep in the bay. In Godhavn the winter is relatively mild; on the other hand, the mean summer temperature is somewhat lower than in Jakobshavn and Umanak. This indicates a more oceanic climate in Godhavn, substantiated by the record of yearly precipitation: 391 mm in Godhavn, 261 mm in Jakobshavn. The low (217 mm) precipitation in Umanak could be explained by its situation in the rain shadow of Nûgssuaq and the fact that the northern location is also generally correlated with a lower annual precipitation. In Greenland precipitation decreases towards the north.

We are of the opinion that precipitation (and incidence of fog) is a much more important factor than temperature per se. During most, if not nearly all, of the period when the lowest temperatures prevail, and

when the plants are dormant, they are snow covered. Areas apt to be freed of snow by strong winds are, usually, singularly barren of all but 1–2 species of *Hepaticae* (e.g., *Chandonanthus setiformis*).

During the months November–April, 90–100 % of the precipitation is in the form of snow. The change from snow to rain takes place in May–June, and the snow increases again in September–October (Jakobshavn).

The growing season, when there is no snow cover, is reduced to the period from mid-June until mid-September. (However, the actual growing season in the region is not solely determined by temperature. Persistent snow banks in many areas, which may melt only in July, or even as late as early August, result in the existence of microenvironments which are much harsher than mere temperature readings would suggest. Thus we observed at Marrait, Nûgssuaq, that *Salix glauca* on recently snow-free slopes had not started to flower by August 9, and still had not unfolded its leaves. Similarly, in late snow valleys above Godhavn, *Anthelia* and other *Hepaticae* remained snow-covered until well into July). During this period the soil covering the permafrost in level areas becomes very boggy and saturated. The depth of the saturated soil varies from $^1/_2$ to $1^1/_2$ m.

The period of the midnight sun is relatively long because of the location far north of the Arctic circle. The plants receive daylight for most of the 24 hours and ground frost is rare from mid-June until the beginning of August. The number of days with fluctuations from thaw to frost is very few and the transition from summer to winter is very sudden.

Geology: The area visited has a very complex geology which, to a great extent, influences the nature of the vegetation. In the paper by ROSENKRANTZ & PULVERTAFT (1969), from which the following summation is largely derived, the Cretaceous-Tertiary stratigraphy and tectonics of the area are dealt with in detail.

The Precambrian is exposed in the eastern sector, while in the western area it is covered by a series of sediments, mostly overlain by a basalt cover. This situation is apparently the result of a major downthrust of the western sector (Disko, west Nûgssuaq, and Svartenhuk Halvø) which began in the lower Cretaceous, west of a north-south running fault. A sequence of limnetic and marine sediments more than 2000 m thick was laid down. Later (from Danian and into the Tertiary) lava-producing dikes were created on the bottom of the sea, and the lava eventually covered both sediments and the Precambrian. Today these lava flows appear as thick basalt piles on the mountains in the western part of the area. The basalt cover has served to protect the underlying Mesozoic deposits, which otherwise are unknown on the west coast of Greenland.

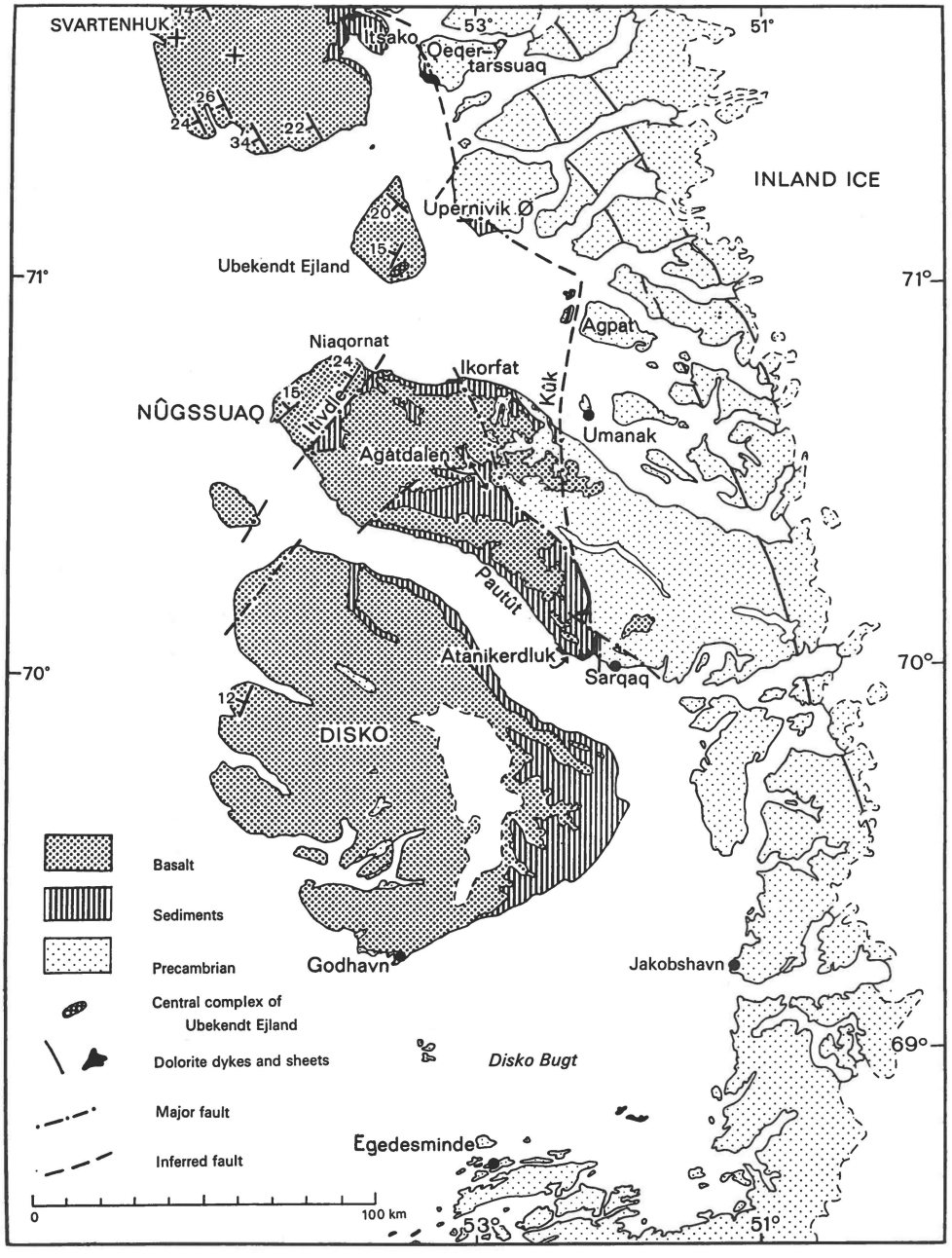


Fig. 1. Map showing the distribution of Cretaceous-Tertiary rocks in West Greenland. (From Rosenkrantz & Pulvertaft, 1969).

During the Pleistocene period Greenland at times was covered by the Inland Ice to a greater extent than it is today. The basalt was probably removed in the eastern sectors and lies only in smaller areas around the Cretaceous-Tertiary basin directly on the Precambrian. In the western part of the area the basalt was sheltered by the Precambrian because of the N–S running fault. Transgression of the ice gave the Precambrian landscape its more rounded character. Some mountains in the area, however, have sharp, serrated ridges, which indicate the height the ice may have reached in the last glaciation; these ridges probably projected through the ice as nunataks. The lower Precambrian area in the eastern part of Disko Bugt was probably invested by a thick ice cover and accordingly was subject to rough polishing, while the areas to the west were covered only by local ice sheets during the last glaciation. Glaciers from these local ice sheets have removed the basalt in several valleys on Disko and thus exposed the underlying Precambrian (Eqalúnguit, Stordal, Godhavn, etc.).

In the western, basalt-dominated area the soil is mostly formed by disintegrated basalt; in the eastern part of the area, however, it is composed of disintegrated Precambrian rocks, mostly granite and gneiss. This seems to be the chief factor governing the distribution of plants in the area. Species that prefer basic soil dominate in the west, while those preferring acid soils occur more frequently in the east.

In the otherwise acid-rock Precambrian region are numerous dikes of diabase, and a few sites where marble and phyllite occur. The geologists, indeed, distinguish a phyllite formation, extending along the inner part of the fjord system south of Svartenhuk Halvø. Disintegration of these rocks creates niches for species which otherwise would be found mostly in the basalt regions. This phenomenon affects the otherwise simple hepatic distribution patterns which are also affected by the occurrence of the earlier mentioned exposed Precambrian in the deep valleys of west Disko.

The species-richest collecting grounds have been found to be those areas in the Precambrian where basalt dikes occur; here we find transition from communities in which only Ca-avoiding taxa occur to communities in which the taxa are either Ca-dependent or -tolerant. Similar transitions occur also, as at Godhavn, where the overlying basalt has been removed near the shoreline. The ecologically anomalous situation may there exist where waters, which had percolated through the basic basaltic overlying rocks, run through the lower Precambrian rocks. In such loci one can find rock-pool or tarn communities where such Ca-avoiding taxa as *Odontoschisma elongatum* occur mixed with the seemingly Ca-dependent *Odontoschisma macounii*—two species which are normally mutually exclusive in their ecological requirements.

COLLECTING STATIONS AND MODE OF CITATION

All collections made jointly and determined in 1966 and 1970 are cited and, in addition, other collections made in the area which we regard as significant in either defining the taxonomy or distribution of the taxa in question. Of common taxa such as *Ptilidium ciliare* we mention, in addition to our own gatherings, only representative collections made by others, sufficient to adequately define the range of the species within our area; further collections made from closely juxtaposed localities are not all included—usually only single collections, from widely spaced localities. Additional collections that document the distribution established on the dot maps are in the herbarium of the Botanical Museum of the University of Copenhagen.

In the case of critical taxa, we have felt it necessary to cite all examined material, if the material was adequate for critical study. In the case of taxa such as *Lophozia ventricosa* s.l. we have not studied previously gathered herbarium specimens since varietal categories in that species are to a large extent based on cytological characters and almost impalpable color differences which, to be understood, necessitate examination of living material.

The materials we collected during the 1966 and 1970 seasons have been divided equally between the herbarium at Copenhagen, and that of the senior author (currently at Amherst, Mass.; place of permanent deposit undetermined at this time of writing). In some cases, when a rare species occurred only in minute admixture, the micropacket containing it has not been subdivided; the material is, then, generally to be found at the Copenhagen herbarium.

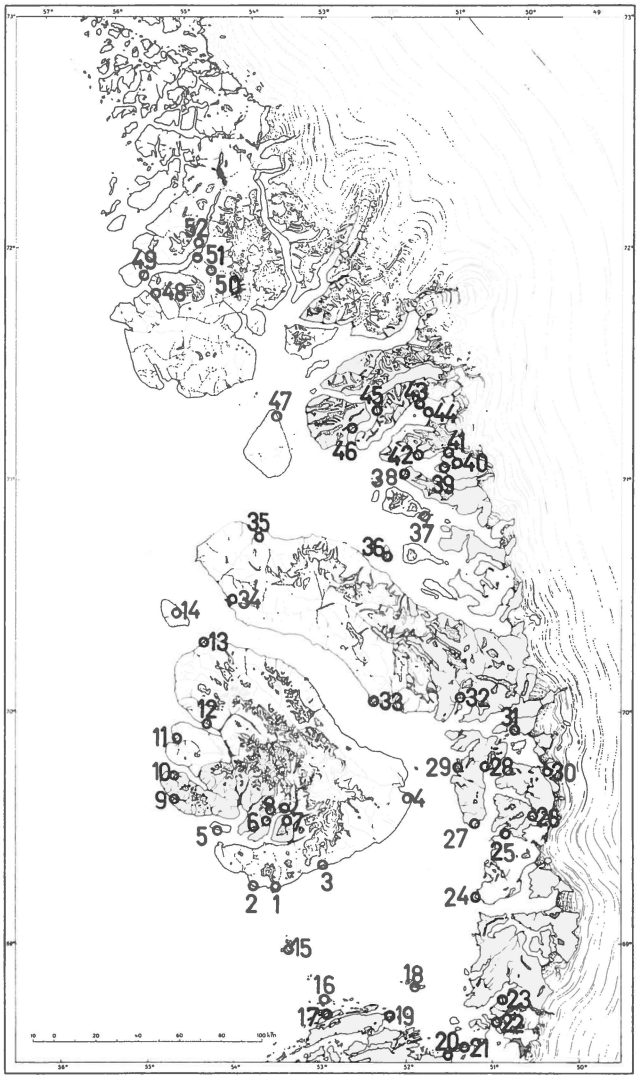


Fig. 2. Map of localities. (Reproduced with permission (A 270/73) of the Geodetic Institute, Copenhagen).

List of localities and collection-numbers.

1A:	Disko: Behind Arctic Station, Godhavn below Lyngmarksfjeld	
	(69°15′N, 53°30′W) July 6–8, 1966	66–0102
	July 5, 1970	66–0146
		66–0148—66–0197
		66–0271
		66–0274—66–0287
		70–2003—70–2022
		70–2024—70–2059
		70–2182—70–2184
1B:	Disko: Lyngmarken, Godhavn below Lyngmarksfjeld	
	(69°15′N, 53°30′ W) July 30–31, 1966	66–0342—66–0344
	July 5, 1970	66–0550—66–0569
		66–0690—66–0699
		70–2023
1C:	Disko: Blæsedalen, mouth of valley near Lyngmarksfjeld	
	(69°26′N, 54°12′W) July 23, 1966	66–0302—66–0305
		66–1570—66–1580
1D:	Disko: Skarvefjeld, slopes below the mountain	
	(69°16′N, 53°26′W) July 13, 1966	66–0231—66–0232
		66–0297—66–0299
		66–0306—66–0321
		66–0324
		66–0406—66–0441
2:	Disko: Fortunebay	
	(69°16′N, 53°50′W) June 27, 1966	66–0123—66–0145
		66–0147
		66–0198—66–0215
		66–0365—66–0386
3:	Disko: Sinigfik, south coast of Disko	
	(69°21′N, 52°55′W) July 11, 1966	66–0442—66–0469
4:	Disko: Flakkerhuk, near Mudderbugten	
	(69°39′N, 51°55′W), July 1, 1966	66–0120
		66–0173
		66–0350—66–0364
		66–0387—66–0405
		66–0470—66–0483
5:	Disko Fjord: Qeqertaq	
	(69°31′N, 54°18′W) Aug. 11, 1966	66–1525—66–1549
6:	Disko Fjord: Eqalúnguit	
	(69°33′N, 53°38′W) July 11, 1970	70–2191—70–2254
7:	Disko Fjord: Angûjârtûtit	
	(69°34′N, 53°27′W) July 10, 1970	70–2157—70–2181
8:	Disko Fjord: Kuánerssuit	
	(69°35′N, 53°22′W) July 10, 1970	70–2126—70–2156

9: Disko: Eqaluit, Nordre Laksebugt
(69°37′–38′N, 54°48′W) Aug. 8, 1970 70–2520—70–2561
70–2780—70–2807

10: Disko: Enoks Havn, south side of Mellemfjord
(69°44′N, 54°48′W) Aug. 7, 1970 70–2750—70–2778

11: Disko: Qasigíssat, mouth of Vesterdalen
(69°53′N, 54°49′W) Aug. 7, 1970 70–2720—70–2746

12: Disko: Perdlertut, north side of Nordfjord
(69°58′N, 54°25′W) Aug. 7, 1970 70–2670—70–2710

13: Disko: Jens Vahls Dal
(70°19′N, 54°30′W) Aug. 5, 1970 70–2630—70–2667

14: Hareøen: Umîvínguaq, east side of the island
(70°27′N, 54°51′W) Aug. 5, 1970 70–2570—70–2622

15: Disko Bugt: Kronprinsens Ejland, Nunarssuaq
(68°59′N, 53°20′W) July 6, 1970 70–2060—70–2125

16: Disko Bugt: Manîtsoq, north of Egedesminde
(68°46′N, 52°54′W) Aug. 21, 1970 70–3000—70–3024
70–3075—70–3098

17: Disko Bugt: Tupilak, west of Egedesminde
(68°42′N, 52°55′W) June 24, 1966 66–0001—66–0037
66–0104—66–0119
66–0121—66–0122

17a: Disko Bugt: Egedesminde, east of the village
(68°43′N, 52°50′W) Aug. 8, 1966 66–0942—66–0952

18: Disko Bugt: Grønne Ejland, Ivnarssuatsiâq, west of Basisø
(68°45′–46′N, 51°58′W) Aug. 24, 1970 70–2810—70–2830

19: Disko Bugt: Nûk, east end of Alángup nunâ
(68°42′N, 52°10′W) Aug. 22, 1970 70–2835—70–2885

20: Sydostbugten: Kûgssuaq, south of Qeqertasugssuk
(68°32′N, 51°28′W) Aug. 22, 1970 70–2890—70–2919

21: Sydostbugten: valley south of Umiasugssûp tunua
(68°33′N, 51°18′W) Aug. 22, 1970 70–2925—70–2951

22: Disko Bugt: Orpigsôq, jct. with Qarajaq
(68°40′N, 50°55′W) Aug. 23, 1970 70–3100—70–3119

23: Disko Bugt: Kangersuneq, valley east of Ivnarssuaq
(68°46′N, 50°52′W) Aug. 23, 1970 70–3120—70–3159

24: Disko Bugt: Jakobshavn
(69°12′N, 51°05′W) July 16, 1966 66–0216—66–0230
66–0233—66–0248

25: Disko Bugt: Sarfaq between Pâkitsoq and Pâkitsup ilordlia
(69°30′N, 50°45′W) July 20, 1970 70–2320—70–2377

26: Disko Bugt: Pâkitsup ilordlia, Qissugssalik
(69°32′–33′N, 50°20′W) July 20, 1970 70–2255—70–2319
70–2380—70–2395

27: Arveprinsens Ejland: Upernaviarssuk
(69°31′N, 51°08′W) July 21, 1966 66–0484—66–0498
66–0516—66–0527

28: Arveprinsens Ejland: Atâ
(69°46′N, 50°57′W) July 21, 1970 70–2485—70–2513

29:	Ritenbenk (Agpat) (69°46′N, 51°20′W) July 19, 1966	66–0252—66–0260 66–0262—66–0270 66–0272—66–0273 66–0500—66–0515 66–0520 66–0528—66–0549 66–0650--66–0665
30:	Atâ Sund: Eqe near Eqip sermia (69°46′N, 50°14′W) July 20, 1966	66–0249—66–0251 66–0261 66–0288—66–0296 66–0322—66–0323 66–0325—66–0341 66–0666—66–0689
31:	Anap nunâ, southwest corner (69°55′N, 50°33′W) July 21, 1970	70–2400—70–2436
32:	Nûgssuaq: Qôrorssuaq, north of Qeqertaq (70°04′N, 51°14′W) July 22, 1970	70–2438—70–2484
33:	Nûgssuaq: Atanikerdluk (70°04′N, 52°20′W) Aug. 2, 1966	66–0700—66–0725
34:	Nûgssuaq: Marrait kangigdlît (70°30′N, 54°10′W) Aug. 2.–3, 1966	66–0726—66–0769
35:	Nûgssuaq: Hollænderbugt (70°47′N, 53°48′W) Aug. 10, 1966	66–1500—66–1525
36:	Umanak Fjord: Umanak (70°41′N, 52°10′W) Aug. 9, 1966	66–1471—66–1499 66–1560—66–1570
37:	Umanak Fjord: Agpat, Iterdlak (70°52′N, 51°38′W) Aug. 9, 1966	66–1420—66–1470
38:	Umanak Fjord: Uvkusigssat (71°03′N, 51°53′W) Aug. 9, 1966	66–1380—66–1419
39:	Qaumarujuk: Tasiussaq (71°04′N, 51°16′W) Aug. 8, 1966	66–1221—66–1279
40:	Qaumarujuk: Mârmorilik, head of the Fjord (71°06′N, 51°12′W) Aug. 8, 1966	66–1171—66–1220
41:	Qaumarujuk: Mârmorilik, mouth of the Fjord (71°07′N, 51°18′W) Aug. 7, 1966	66–1160—66–1170
42:	Alfred Wegener Halvø: Magdlak (71°07′N, 51°40′W) Aug. 8, 1966	66–1350—66–1379
43:	Kangerdluarssuk: Kangerdlugssuakavsak (71°21′N, 51°40′W) Aug. 7, 1966	66–1280—66–1319
44:	Kangerdluarssuk: Akuliarusikavsak, Qaersukavsak (71°19′N, 51°35′W) Aug. 7, 1966	66–1320—66–1349
45:	Inukavsait: Sagdliaruseq (71°19′N, 52°16′W) Aug. 6, 1966	66–1051—66–1099
46:	Upernavik Ø: Inukavsait, Qalatôq (71°14′N, 52°35′W) Aug. 6, 1966	66–1100—66–1159
47:	Ubekendt Ejland (Igdlorssuit): Íngia (71°18′N, 53°35′W) Aug. 6, 1966	66–1031—66–1050

48: Svartenhuk Halvø: Amitsup suvdlua, small valley east of the fjord
(71°49′N, 55°15′W) Aug. 3, 1966 66–0770—66–0819
66–1550—66–1552

49: Umîarfik: Skalø (Tuperssússat)
(71°54′N, 55°28′–30′W) Aug. 5, 1966 66–1000—66–1030

50: Svartenhuk Halvø: Simiútap kûa, valley
(71°56′N, 54°30′W) Aug. 4, 1966 66–0861—66–0899

51: Svartenhuk Halvø: Umîarfik, Simiútap kûa, shore
(71°59′N, 54°50′W) Aug. 4, 1966 66–0820—66–0860
66–0900—66–0960
66–1642

52: Svartenhuk Halvø: Umîarfik, Ingnerit: Qôrnoq
(72°02′N, 54°40′W) Aug. 5, 1966 66–0961—66–0999

53: Søndre Strømfjord, head of the Fjord
(67°00′N, 50°40′W) June 23, 1966 66–0038—66–0101
July 3, 1970 and Sept. 2, 1970 70–2001—70–2002
70–3200—70–3216

List of localities in the area visited by earlier collectors.

Place names cited are those used by the collectors and may be inconsistent with present spellings. The initials of the collector are added in parenthesis.

54: Holsteinsborg: (66°56′N, 53°40′W) JENS VAHL, 1832–33 (J.V.)
WARMING & HOLM, 1884 (W. & H.)

55: — Ulkebugt (66°57′N, 53°41′W) T. W. BÖCHER, 1963 (T.W.B.)

56: Ujarasugssuliup qáqâ (66°59′N, 53°43′W) L. KOLDERUP ROSENVINGE, 1886 (L.K.R.)

57: Disko: Nipisat (69°26′N, 54°12′W) K. HOLMEN, 1956 (K.H.)

58: — : Itivneq kitdleq, along little lake, midway between Disko Bugt and Disko Fjord (69°23′N, 53°40′W) M. P. PORSILD, 1898 (M.P.P.)

59: — : Kvannit (69°15′N, 53°30′W) K. HOLMEN & W. C. STEERE, 1962 (K.H. & W.C.S.)

60: — : Kugssuaq, between Sinigfik and Igpik (69°21′N, 53°02′W) M. P. PORSILD, 1898 (M.P.P.)

61: — : Taserârsuk (69°21′N, 53°00′W) L. HARMSEN, 1932 (L.H.)

62: — : Skansen (69°26′N, 52°28′W) M. P. PORSILD, 1898 (M.P.P.)

63: — : Mudderbugten (69°40′N, 52°00′W) C. HOLMQUIST, 1956

64: — : Ingigigsoq (69°48′N, 52°10′W) M. P. PORSILD, 1898 (M.P.P.)

65: — : Ûnartuarssuk (69°58′N, 52°49′W) M. P. PORSILD, 1898 (M.P.P.)

66: — : Gamle Qutdligssat (70°02′N, 52°57′W) M. P. PORSILD, 1898 (M.P.P.)

67: — : Asuk (70°12′N, 53°20′W) M. P. PORSILD, 1898 (M.P.P.)

68: — : Hammers Dal (70°09′N, 54°45′W) M. P. PORSILD, 1902 (M.P.P.)

69: Nordfjord: Qamavit (69°56′N, 54°25′W) M. P. PORSILD, 1902 (M.P.P.)

70: Mellemfjord: Sarqardlît silardlît, Kûgssuaq (69°47′N, 54°40′W) M. P. PORSILD, 1902 (M.P.P.)

71: Disko Fjord: Nagerdloq (69°33′N, 54°25′W) M. P. PORSILD, 1902 (M.P.P.)

72: — — : Kuánit (69°34′N, 54°16′W) M. P. PORSILD, 1898 (M.P.P.), L. HARMSEN, 1932 (L.H.)

73: Disko Fjord: Igdlokasik (69°34′N, 54°00′W) K. Holmen, 1956 (K.H.)
74: — — : Kangerdluarssuk (Ekigsoq) (69°30′N, 53°33′W) M. P. Porsild, 1898 (M.P.P.), K. Holmen, 1956 (K.H.)
75: — — : Kuánerssuit suvdluat, Qârusuit (69°33′N, 53°36′W) L. Harmsen, 1932 (L.H.)
76: Disko Bugt: Kronprinsens Ejland: Ivnârssulik (69°01′N, 53°21′W) C. Kruuse, 1897 (C.K.)
77: — — : Kronprinsens Ejland: Oqaq (68°59′N, 53°27′W) C. Kruuse, 1897 (C.K.)
78: — — : Kitdlît (Vester Ejland) (68°38′N, 53°33′W) C. Kruuse, 1897 (C.K.)
79: — — : Agpalilik (Kullen) (68°46′N, 53°07′W) C. Kruuse, 1897 (C.K.)
80: — — : Egedesminde, Tørveø (68°43′N, 52°53′W) L. Harmsen, 1932 (L.H.)
81: — — : Sarqardlîp nunâ, Tasiussaq, warm spring (68°41′N, 52°45′W) A. Kornerup, 1879, Warming & Holm, 1884 (W. & H.)
82: — — : North coast of Sarqardlîp nunâ (68°42′N, 52°30′W) L. Harmsen, 1932 (L.H.)
83: Sydostbugten: Angnertussoq (68°34′N, 52°00′W) L. Harmsen, 1932 (L.H.)
84: — : The area south of Qeqertasugssuk (68°32′N, 51°32′W) L. Harmsen, 1932 (L.H.)
85: — : The area south of Sarpiussat (68°33′N, 51°20′W) L. Harmsen, 1932 (L.H.)
86: — : Orpigsoq, Seqíneqârajutoq (68°42′N, 50°56′W) L. Harmsen, 1932 (L.H.)
87: — : Kangersuneq, head of the Fjord (68°51′N, 50°45′W) J. Vahl, 1835? (J.V.), K. Hansen, 1956
88: Disko Bugt: Christianshåb (68°49′N, 51°10′W) K. Holmen, 1956 (K.H.)
89: — — : Marrait (Lerbugt) (68°59′N, 51°06′W) S. Berggren, 1870 (S.B.)
90: — — : Tasiussaq, inland coast (69°02′N, 51°01′W) S. Berggren, 1870 (S.B.)
91: — — : Itivdliup ilua (Sandbugt) (69°03′N, 51°05′W) S. Berggren, 1870 (S.B.)
92: — — : Claushavn (69°05′N, 51°07′W) S. Berggren, 1870 (S.B.)
93: — — : Jakobshavn, Navdluarssuk (69°13′N, 50°43′W) Warming & Holm, 1884 (W. & H.)
94: — — : Rodebay (Oqaitsut) (69°21′N, 51°01′W) J. Vahl, 1833 (J.V.)
95: — — : Pâkitsoq (69°31′N, 50°45′W) J. Vahl, 1833, 1835 (J.V.), K. Holmen & G. Mogensen, 1971 (K.H. & G.M.)
96: Nûgssuaq : Qeqertaq (70°00′N, 51°19′W) S. Berggren, 1870 (S.B.)
97: — : Qôrorssuaq (Majoriârssuatsiaq) (70°05′–08′N, 51°16′W) S. Berggren, 1870 (S.B.), K. Jakobsen, 1948 (K.J.)
98: — : Sarqaq (70°01′N, 51°56′W))J. Vahl, 1835 (J.V.), K. Holmen, 1956 (K.H.)
99: — : Sarqaq valley (70°03′–06′N, 52°06′W) K. Jakobsen, 1947 & 1948 (K.J.)
100: — : Ipeqarfiunge (Between Manik and Pautût) (70°13′N, 52°40′W) L. Harmsen, 1932 (L.H.)
101: — : Kugssinerssuaq (70°17′N, 52°55′W) L. Harmsen, 1932 (L.H.)
102: — : Atâ (70°19′N, 53°00′W) L. Harmsen, 1932 (L.H.)
103: — : Auvfarssuaq, Qapiortoq kitdleq (70°26′N, 53°25′W) Østlig Dyndvulkan, K. Jakobsen, 1948 (K.J.)

104: Nûgssuaq : Aufvarssuaq, Qapiortoq kangigdleq (70°27′N, 53°34′W) Vestlig Dyndvulkan KR. SKOU (Skou) 1958
105: — : Nûssaq (70°26′N, 54°04′W) KR. SKOU, 1958 (SKOU)
106: — : Nûgssuaq (70°41′N, 54°36′W) K. JAKOBSEN, 1948 (K.J.), K. HOLMEN, 1956 (K.H.)
107: — : Tunorssuaq (70°44′N, 53°40′W) K. JAKOBSEN, 1947 (K.J.)
108: — : Niaqornat (70°47′N, 53°40′W) J. VAHL, 1834 (J.V.)
109: — : Kangilia (70°45′N, 53°26′W) K. JAKOBSEN, 1947 (K.J.)
110: — : Ikorfat (70°46′N, 53°07′W) K. JAKOBSEN, 1947 (K.J.), K. HOLMEN, 1962 (K.H.)
111: — : Kûtsiaq (70°41′N, 52°27′W) K. JAKOBSEN, 1948 (K.J.)
112: — : Umiartorfik (70°31′N, 51°55′W) K. JAKOBSEN, 1947 & 1948 (K.J.)
113: — : Nugfiumaneq (70°26′N, 51°28′W) K. JAKOBSEN, 1947 (K.J.)
114: — : Eûaluit (70°24′N, 51°15′W) K. JAKOBSEN, 1947 & 1948 (K.J.), K. HOLMEN, 1956 (K.H.)
115: — : Kûgssuaq (70°21′N, 51°04′W) K. JAKOBSEN, 1947 (K.J.)
116: — : Puiagtukavsak (70°19′N, 50°44′W) K. JAKOBSEN, 1947 (K.J.)
117: — : Sêrsínerssuaq (70°18′N, 50°43′W) K. JAKOBSEN, 1947 (K.J.)
118: — : Itipilua (70°20′N, 50°33′W) K. JAKOBSEN, 1947 (K.J.)
119: — : Itipiluautâ (70°19′N, 50°27′W) R. E. BESCHEL, 1961 (BESCHEL)
120: — : Itipilua qáqâ (70°20′N, 50°40′W) K. JAKOBSEN, 1947 (K.J.)
121: — : Boyes Sø (70°10′N, 51°00′W) K. JAKOBSEN, 1948 (K.J.)
122: — : South of Eqaluit (70°17′N, 51°12′W) K. HOLMEN, 1956 (K.H.)
123: — : Uigordleq (70°17′N, 51°22′W) K. HOLMEN, 1956 (K.H.)
124: — : Tasíngortaq (70°20′N, 51°35′W) K. HOLMEN, 1956 (K.H.)
125: — : Sarqap taserssua (Taserssuaq)(70°20′N, 52°00′W) K. HOLMEN, 1956 (K.H.)
126: — : Auvfarssuaq, west of Sarqap taserssua (70°25′N, 52°26′W) K. HOLMEN, 1956 (K.H.)
127: — : Kangersôq (70°32′N, 53°07′W) K. JAKOBSEN, 1948 (K.J.)
128: — : Agatdalen (70°35′N, 53°05′W) K. HOLMEN, 1956
129: — : Avataussaligssuaq (70°36′N, 53°15′W) K. JAKOBSEN, 1948 (K.J.)
130: Umanak Fjord: Qarajaq, Qarássap imâ, Tasiussaq (Karajak Station) (70°27′N, 50°36′W) C. VANHÖFFEN, 1897 (C.V.)
131: — — : Storø (70°41′N, 51°30′W) A. ROSENKRANTZ, 1954 (A.R.)
131a: — — : Agpat, Qaqortuatsiaq (70°57′N, 51°55′W) K. HOLMEN & G. MOGENSEN, 1971 (K.H. & G. M.)
132: Qaumarujuk: Akuliarusikavsak (71°07′N, 51°23′W) K. HOLMEN, 1956 (K.H.)
133: Alfred Wegener Halvø: Tuperssuatsiait (71°05′N, 52°02′W) K. HOLMEN, 1956 (K.H.)
134: — — — : Umîvik (71°08′N, 52°14′W) K. HOLMEN, 1956 (K.H.)
135: — — — : Tornit (71°12′N, 52°04′W) K. HOLMEN, 1956 (K.H.)
136: Kangerdluarssuk: Kangerdluarssûp qeqertâ (71°18′N, 51°46′W) K. HOLMEN, 1956 (K.H.)
137: — : Esersiutilik (71°17′N, 51°32′W) K. HOLMEN, 1956 (K.H.)
138: — : Itivneq (71°24′N, 51°41′W) K. HOLMEN, 1956 (K.H.)
139: — : Qaqortukavsaq (71°12′N, 52°12′W) K. HOLMEN, 1956 (K.H.)
140: Inukavsait: Small Island (71°15′N, 52°24′W) K. HOLMEN, 1956 (K.H.)
141: — : Inukavsait qáqarssue, below the mountain (71°15′N, 52°16′W) K. HOLMEN, 1956 as Qîoqe (K.H.)

142: Inukavsait: Upernivik Ø, Niaqornánguaq (71°20′N, 52°24′W) K. Holmen, 1956 (K.H.)
143: Kangerdlugssuaq (71°22′N, 52°13′W) K. Holmen, 1956 (K.H.)
144: Ubekendt Ejland: Igdlorssuit (71°14′N, 53°35′W) K. Holmen & W. C. Steere, 1962 (K.H. & W. C. S.)
145: Svartenhuk: Uligssat (71°26′N, 54°03′W) K. Jakobsen, 1950 (K.J.)
146: — : Itsako: Itsakup igdloqarfia (71°39′N, 53°50′W) K. Jakobsen, 1950 (K.J.)
147: — : Amitsoq (71°49′N, 55°25′W) K. Holmen, 1956 (K.H.)

TAXONOMIC TREATMENT

Introduction

Before we treat in detail the various taxa, we feel that, on the basis of the intensive experience we have had with the Arctic *Hepaticae*, several generalizations should be made which may prove helpful in evaluating the following pages.

1) Most of the species herein treated were first described from Europe, from climatically very different areas (see pp. 50, 107, 246, for specific cases). We need only mention photoperiod: the continuous daylight during most if not all of the growing season in sectors of the Arctic—where steep slopes (and consequent shading) fail to occur—affords a strikingly different physiological environment from the growing season environment in lower latitudes. Also, the obvious matter of duration of snow cover (and hence, imposed dormancy) present other problems. We think that temperature, per se, is probably of relatively minor significance. In many instances we deal with populations genetically adapted to—and selected by—the difficult Arctic environment; these fail to correspond exactly to their European counterparts, and cannot be understood by use of European-derived species concepts. As a consequence, in many instances species perimeters have had to be visibly broadened to accommodate the Arctic phenotypes included here.

2) Because of the drastically different environmental extremes found, it is probable that selection pressure has caused different ecotypes to evolve—or survive, in taxa with frequent sexual reproduction. At the latitudes dealt with here, the majority of species produce sporophytes, even if a little less frequently so than in more temperate regions (for example, *Blepharostoma trichophyllum*, which often "fruits" in temperate regions, rarely has sporophytes as far north as 70°). At the same time, phenotypes adapted to less rigorous climates have been probably systematically weeded out, especially during periods when climatic conditions were even more severe than they now are. In many cases, no doubt, we have at hand populations whose genetic (hence taxonomic) perimeters are conspicuously different from those inhabiting lower latitudes.

3) The question is how, practically, to treat such populations. We feel that basically, as with all other taxonomically complex situations, no

a priori ground rules will hold; each species complex has to be evaluated on its own merits. In general, however, we have used the approach of adopting varieties (when no clear geographic pattern emerges) and subspecies (when the Arctic populations seem reasonably geographically segregated). Obviously, as more material accumulates and is subject to progressively more rigorous investigation, the relatively pragmatic approach we have been forced to adopt will need refinement. It is quite clear that for many previously unsuspected problems only culture work and/or reciprocal transplant experiments will provide meaningful answers. In the interim, the pre-existing taxonomic chaos can be cleared to some extent by the approach we have used. Our investigations have shown that, in many instances, the Greenland hepatics—such as *Lophozia excisa* and *Lophozia ventricosa*—are as diverse and complex as many of the phanerogams, as *Papaver radicatum* (KNABEN, 1959), *Stellaria longipes* (HULTÉN, 1943; BÖCHER, 1951), *Cerastium alpinum*, and *Carex bigelowii*.

As a matter of general practice, we have recognized as varieties or subspecies only those gatherings whose placement is quite unambigous. Thus plants whose varietal status is doubtful have been cited under the main species. In some instances we have discussed such problematic plants; there are too many, however, for all to be treated herein.

4) The problem of subspecies requires special mention. As is pointed out in SCHUSTER (1969) there is a tendency in several Arctic populations for leaves and bracts to become shorter (and hence correspondingly broader) vis à vis temperate-zone populations. (This is somewhat analogous to the gradual abbreviation of ears in mammals as one goes north). The analogy also holds for the mosses. Thus BRYHN (1906–07, p. 3) states; "In the Arctic the bryophytes change their habitus. The Arctic mosses have a strong tendency to produce threadformed shoots and all leaves are as a rule unusually short, especially the lamina is often strongly reduced". We have segregated as subspecies (e. g. *Solenostoma pumilum* ssp. *polaris*, *Tritomaria polita* ssp. *polymorpha*) the northern populations in which the distinctions are so marked as to possibly cause problems in interpretation. It is likely, however, that a broad spectrum of intergradation will be found and that these taxa may form clines with respect to the length-width ratio of leaves and bracts.

5) In addition to the variation in leaf dimension cited above, we also find in several taxa that the sexuality of the plants (or at least the phenotypic expression of the sexuality) undergoes changes that are taxonomically difficult to interpret. One of us (RMS) has already discussed this situation with regard to *Lophozia latifolia* (SCHUSTER *et al.*, 1959; SCHUSTER, 1969) and *Solenostoma pumilum* (SCHUSTER, 1969). Additional data dealing with sexuality of these two taxa are given below (p. 100). Similarly, in *Lophozia gillmani* (and sometimes also in *Lophozia rutheana*)

there is the problem of bisexual (paroecious) taxa which, under Arctic conditions show a tendency for antheridium suppression—so that seemingly unisexual individuals result. Also, in *Solenostoma pyriflorum* (see p. 175) and *Solenostoma oblongifolium* (p. 166) there are major problems with respect to the sexuality of the plants.

In brief, in bisexual taxa there is a tendency, in the Arctic, for evolution of phenotypes which show tendencies towards unisexuality. In some cases (*Lophozia excisa-latifolia-elegans* complex) this is accompanied by other differences, suggesting there has been at least imperfect speciation. In other cases (*Lophozia gillmani-bantriensis*), antheridium suppression on paroecious individuals may occur to the point where a paroecious taxon (*L. gillmani*) may "mimic" a unisexual taxon (*L. bantriensis*)—and thus raises the problem of whether species distinctions actually exist. In the *Solenostoma pumilum-polaris* complex the uniformly paroecious "temperate" taxon (ssp. *pumilum*) in the Arctic sometimes "throws off" plants which have purely gynoecial axes which bear androecial branches, so that autoecious plants may result (SCHUSTER *et al.*, 1959, p. 49).

We do not know, at this point, how to best treat such cases taxonomically, and are, arbitrarily, treating them conservatively. Only if there are other criteria, in addition to sexuality, are we maintaining species distinctions.

6) As is brought out on preceding pages (pp. 18–21), the situation with respect to the American Arctic populations may be appreciably more complex than that characterizing the limited Arctic populations found in Europe. It is well known that much of the north slope region of Alaska was unglaciated. According to some geologists, portions of Peary Land also escaped glaciation. It has also been postulated that, in other parts of Greenland, nunataks existed which remained ice-free during the height of the Pleistocene. On purely phytogeographic evidence —admittedly a weak reed to lean upon—STEERE (1937) and SCHUSTER (SCHUSTER *et al.*, 1959) have postulated that at least isolated "pockets" on the Greenland coast and on Ellesmere Island escaped continental glaciation during the Pleistocene.

If it can be shown that such refugia existed during the entire Pleistocene, then the genetic history of the American Arctic *Bryophyta* may be very complex indeed; probably there has been a dual post-Pleistocene history involving merging of northern, relict populations that survived in the far north since the Tertiary, with southern populations that have re-migrated northward more recently. If selection plus depletion of biotypes was severe in the Arctic, then the relict populations possibly consisted of genotypes differing drastically from the invaders. The post-Pleistocene history of at least some of these species may reflect such a

commingling of genetically long-isolated stocks; hence the history may be even more complex than has been previously assumed. As is well known, migratory routes from north to south, and vice versa, are "easier" in America than in Europe where the east-west oriented Alps form a major barrier. This may account for the more complex post-Pleistocene history of the American Arctic populations.

The probability of survival in the far north during the Pleistocene becomes stronger if we consider the fact that in the eastern American Arctic we today know a number of seemingly "endemic" *Hepaticae*, e.g.,

Anomomarsupella cephaloziellοides
Cephaloziella uncinata
Lophozia albo-viridis
— *heteromorpha*
— *rubrigemma*
— *subapiculata*
Scapania invisa
— *paradoxa*
— *perssonii*
— *pulcherrima*
— *serrulata*
Tritomaria heterophylla

There are also cases of endemic taxa, sometimes frequent in the far north but known as only isolated populations southward, as, e.g. *Cryptocolea imbricata* and *Metacalypogeia schusterana*, and several instances of species which are known from the eastern American Arctic and recur in the unglaciated portions of the Arctic in Yukon-Alaska. Finally, isolated species, rarities from the western Arctic, such as the monotypic Arctic genus *Mesoptychia* (with only *M. sahlbergii*), are known from as far east as Devon and Ellesmere Islands, and then recur in unglaciated Alaska and Siberia (see map in Persson, 1949, p. 511). It is noteworthy that none of these Arctic taxa found in Greenland or in adjoining Devon-Ellesmere, or both, are known from the European Arctic regions.

We thus assume that the Greenland hepatic flora includes an "old" element, among which we number *Anastrophyllum assimile*, *A. sphenoloboides* (see p. 18), *Cryptocolea imbricata*, *Marsupella revoluta*, etc.

These assumptions have been central to our thinking with respect to the complex intraspecific taxonomy of many of the taxa with which we deal on the following pages.

7) A special problem, which still eludes a satisfactory solution, is offered by the rather frequently occurring, so-called "large-celled varieties". These occur in a large number of cases. In essence, we find that for some species, usually non-Arctic (as regards the type locality), there exist both a phenotype with cells of normal size and plants which bear drastically larger cells. Associated with this we find that the gemmae (if any are produced) are larger-celled, and, since the cell volume is much larger, the oil-body number is larger. It has been assumed (as by Arnell, 1956, pp. 118, 148) that these larger-celled plants are "probably polyploid". This remains to be demonstrated, but seems a reasonable hypothesis.

While only a few such varieties (of *Tritomaria quinquedentata*, *Lophozia silvicola*, *L. heterocolpos*, and *L. wenzelii*) were known, they were described by BUCH & ARNELL (1950) as the "var. *grandiretis*" of the species proper. We have seen many more such large-celled forms; the following represents a partial list:

	Small-celled phenotypes	Large-celled phenotypes
1.	*Anastrophyllum minutum* v. *grandis*	*Lophozia cavifolia*
2.	*Cephalozia bicuspidata* ssp. *ambigua*	*Cephalozia bicuspidata* ssp. *bicuspidata*
3.	*Cephaloziella arctica*	*Cephaloziella grimsulana*
4.	*Lophozia grandiretis* v. *parviretis*	*Lophozia grandiretis*
5.	— *longidens*	— *longidens* ssp. *arctica*
6.	— *pellucida* v. *minor*	— *pellucida*
7.	— *ventricosa* v. *confusa*	— *ventricosa* v. *rigida*
8.	— — v. *silvicola*	— — v. *grandiretis*
9.	— *wenzelii* v. *wenzelii*	— *wenzelii* v. *lapponica*
10.	*Plagiochila asplenioides*	*Plagiochila arctica*
11.	*Scapania curta* v. *curta*	*Scapania curta* v. *grandiretis*
12.	— *degenii*	— *pulcherrima*
13.	— *hyperborea*	— *tundrae*
14.	— *mucronata* ssp. *praetervisa*	— *lingulata*
15.	*Tritomaria quinquedentata*	*Tritomaria quinquedentata* v. *grandiretis*

It is interesting that this phenomenon seems most widespread in the related families *Lophoziaceae* and *Scapaniaceae*. It is also to be noted that there is currently a lack of consistency in taxonomic approach. Thus pairs 2, 4–9, 11 and 15 are treated as constituting a single species each, while 1, 3, 10 and 12–14 are treated as species pairs. As is brought out on subsequent pages (pp. 332–33) each of these "species pairs" could also be interpreted as really forming a single species, with the larger-celled phenotype regarded as only a separate variety. In several cases this has not been done, principally because (as with *Scapania hyperborea* and *Cephaloziella arctica*) the small-celled populations already form such a complex *typus polymorphus* that adding the larger-celled phenotypes as mere varieties would overburden the taxonomic edifice to the point of overwhelming complexity; in other cases (the *Sc. degenii-pulcherrima* problem) it has not been done because there are additional morphological characters that seem to separate *Sc. pulcherrima* from *Sc. degenii*.

The *Plagiochila asplenioides-arctica* complex is particularly interesting; as SCHUSTER (1959–60, figs. 10A, 10B) has shown, high Arctic phases of these two taxa may be identical in aspect, but differ in cell size and oil-body number. Furthermore, it was shown that in *P. asplenioides* "chimeras" occurred, in which isolated leaves revealed patches of larger cells (l. c., fig. 10A:8; compare with the "normal" cells in fig. 10B:4 drawn to the same scale). It was assumed that "possibly" this was due to localized polyploidy, originating through some defect in mitosis in a single cell which, through subsequent mitotic division, gave rise to a a patch of diploid cells in an otherwise haploid individual. If such origin can be demonstrated, then the status of taxa such as *P. arctica* as species becomes indefensible. Furthermore, SCHUSTER (1966, p. 238) placed great emphasis on the observation made by TATUNO (1941) that Japanese plants of *Calypogeia neesiana*—with the haploid chromosome number n = 9—produce gemmae abundantly, which, although normally also haploid, may be diploid. Since gemmae form from dedifferentiated leaf cells, more than a mere analogy seems at hand. It is also noteworthy that of the 15 cases cited above, all but 4 are of taxa in which gemma production is almost always abundantly present. TATUNO's observation clearly gives us a model that could account for the frequent development of large-celled phenotypes. The problem, taxonomically, is, in part, how to equate the easy origin of such presumed polyploids with the obvious differences that ensue—and the fact that, as a breeding system, these polyploids seem effectively genetically isolated from their haploid ancestors. (This, we think, may account in part for the fact that the presumed polyploids often seem to show some, if minor, morphological or color distinctions vis à vis the presumed haploid ancestral type).

Order *Calobryales* (*Haplomitriales*)

Family *Haplomitriaceae* DĚDĚCEK

The most recent version of the International Code of Botanical Nomenclature published (1966) demands that the family name be derived from a currently recognized genus, although the rules prior to this allowed retention of family names derived from no-longer valid genera. For this reason, the older and more widely used family name *Calobryaceae* must now be replaced by the name *Haplomitriaceae*, *Calobryum* having been shown to be a synonym of *Haplomitrium* (SCHUSTER, 1963, 1967).

Haplomitrium NEES

Haplomitrium hookeri (SMITH) NEES

Distribution

55: Holsteinsborg, Ulkebugt (T.W.B. publ. 1963, p. 109).

Found a single time, in *Salix callicarpaea* scrub. The determination was made by E. CLAUSEN. This is the only report of the species, family, and order from West Greenland; the species is known at a higher latitude only in Spitsbergen (ARNELL & MÅRTENSSON, 1959) and from the Angmagssalik District (MOLENAAR, 1968).

H. hookeri appears to be imperfectly holarctic; it has been found, since the treatment of SCHUSTER (1966, 1967), in western North America, in S. Alaska, British Columbia, and Washington (WORLEY, 1969), and has recently been reported from Japan and the Himalaya. Its ecology is discussed in detail in WORLEY (l. c.). The nearest ally seems to be *H. ovalifolium* SCHUST., an alpine and sub-antarctic taxon known only from New Zealand and Campbell Island (SCHUSTER, 1971).

Order *Jungermanniales*

Family ***Blepharostomataceae*** K. MÜLL.

Blepharostoma (DUMORT.) DUMORT.

Blepharostoma trichophyllum (L.) DUMORT. (Table I).

A subcosmopolitan species in the northern hemisphere, extending as far north as there is land (82°40′ N. in Greenland; 82°32′ N. in Ellesmere Island; SCHUSTER, 1966, p. 751). Southward it occurs in North America to the Escarpment ravines of the Southern Appalachians in Georgia and South Carolina and then reappears as a disjunct in the mountains of Mexico, Costa Rica, and the Andean region in South America (ssp. *australis* SCHUST.). In Europe it extends to the Mediterranean region and reappears in the mountains of E. Africa. In Asia it extends into the Himalaya and reappears, as a disjunct, in Java and then at very high elevations (11.000 ft. and higher) in New Guinea (SCHUSTER, 1968; see distribution map in SCHUSTER, 1969a, map 14:1).

Associated with the wide range is the corresponding plasticity. In addition to the Andean race, ssp. *australis* (distinct in the larger cells of the rudimentary leaf disk), a ssp. *brevirete* is separated from ssp. *trichophyllum*. Ssp. *brevirete* is an exclusively Arctic taxon (ARNELL, 1951; SCHUSTER, 1966), supposedly distinct in, i. a., the abbreviated, often subquadrate cells of the leaf lobes. In actuality, the situation (as discussed below) is much more complex, with a broad zone of intergradation geographically and (in part) seasonally, between "*trichophyllum*" and "*brevirete*" characters. It is of interest that this zone of intergradation should fall in the Disko Bugt region, where there is a strong floristic break between low and high Arctic elements.

ssp. *trichophyllum* (L.) DUMORT.

Distribution (Map 1)

1A: Behind Arctic Station (70–2012c). 7: Angûjârtûtit (70–2161b, 70–2174a). 11: Qasigíssat (70–2734). 8: Kuánerssuit (70–2126). 16: Manîtsoq (70–3009b). 21: Umiasugssûp (70–2947). 23: Kangersuneq (70–3147a). 31: Anap nunâ (70–2422, trans. ad ssp. *brevirete*). 32: Qôrorssuaq (70–2440e, trans. ad ssp. *brevirete*).

Additional collections:

1B: Lyngmark (M.P.P. 344). 6: Eqalúnguit (M.P.P. 2644). 34: Marrait kangigdlît (K.H. Sept. 1956). 38: Uvkusigssat (K.H. 62–1580). 40: Mârmorilik, head of the Fjord (K.H. 14.628). 60: Kugssuaq (M.P.P. 736a). 64: Ingigigsoq (M.P.P. 3114c). 86: Seqíneqârajutoq (L.H. 15). 87: Kangersuneq (K. HANSEN, Aug. 1958). 88: Christianshåb (K.H. 12.079, 16.827). 98: Sarqaq (J.V. 247b). 99: Sarqaq valley (K.J. 241b). 106: Nûgssuaq (K.H. 15.636b). 114: Eqaluit (K.J. 792). 129: Avataussaligssuaq (K.J. 889).

Typical *B. trichophyllum* is frequent, at least as far north as Disko Bugt, where it is confined very largely to rich, mesic sites. Unlike in ssp. *brevirete*, gemmae are apparently frequent in Greenland populations of ssp. *trichophyllum*; they occur, i.a., in 70–2012c, 70–2947, 70–3009b and 70–3147a (see Table I).

This, the southern subspecies, has previously been reported only from South Greenland (SCHUSTER, 1966); ARNELL (1951) stated that all material from Greenland, which he examined, represented the "*brevirete*" extreme. As Table I shows, transitions between the two extremes are frequent. Admittedly southern ssp. *trichophyllum* "tends" to have narrower, more slender segments, with strongly elongated lobe cells, averaging 2–4 × as long as wide; the septa between cells are always conspicuously dilated. Transitions also occur in the Hudson Bay area, although ARNELL (1951) reports only ssp. *brevirete* from there. Furthermore, seasonal and/or age differences are occasionally found on single stems.

It is probable the *brevirete* extreme is induced, at least in part, by difficulties in water uptake and/or nutrition. Growth experiments are clearly necessary. As a matter of practicality, we refer all plants having elongated leaf lobes with elongated cells to ssp. *trichophyllum*. Such leaf lobes always show at least slightly dilated septa; by contrast, weaker leaves on the same stem may show nondilated or even constricted septa. On optimally developed leaves, the cells in the middle of the segments may be ca. 72 × 22–24 μ, thus average 3 × as long as wide (as in 70–2161b). In none of the populations here referred to ssp. *brevirete* have we seen leaf lobes with such strikingly elongated cells. There is also a marked tendency for ssp. *trichophyllum* phases to have slenderer lobes, with the cells only (14–15) 16–20 (24) μ wide, whereas in ssp. *brevirete* the lobes are often stouter, with blunter, hardly tapered apices and lobe cells (in the middle of the segments) average 24–31 μ broad.

Table I.

Blepharostoma trichophyllum ssp. *trichophyllum* and ssp. *brevirete*

	Gemmae	Average of basal 2 cells W × L	Terminal 3 cells W × L	Cortical cells W × L	Septum between cells Swollen or not	Longest lobe cells L × W	Perianth mouth cells	Perianth middle cells
70–2161b								
Blepharostoma trich.		31–39×	23–26×	18–26×	+	60–72×		
ssp. *trichophyl.*	–	52–57μ	55–56μ	21–104μ		20–24μ (3–3.2:1)		
70–2174a								
Blepharostoma trich.		39×	16×	26×	+	55–60×		
ssp. *trichophyl.*	–	42–44μ	42–46μ	52–99μ		14–18μ (3–4:1)		
70–2734								
Blepharostoma trich.		36×	16–21×	21–23×	(+ > –)	52–72×		
ssp. *trichophyl.*	–	36–49μ	37–49μ	73–83μ		22–24μ (2.5–3:1)		
70–3009b								
Blepharostoma trich.		21–36×	18×	18×	+	38–43×		
ssp. *trichophyl.*	+	36–42μ	43–54μ	39–62μ		17μ (2.2–2.5:1)		
70–2947								
Blepharostoma trich.		31–36×	16×	26×	+	50–60×		
ssp. *trichophyl.*	+	34–35μ	28–40μ	44–91μ	–	19–20μ (2.5–3:1)		
70–3147a								
Blepharostoma trich.		31×	16×	20–23×	+	46–58×		
ssp. *trichophyl.*	+	34–36μ	31–41μ	36–55μ		16–19μ (2.4–3.4:1)		
70–2012c								
Blepharostoma trich.		34×	16×	23×	+	36–50×	34–47×	13–18 ×
ssp. *trichophyl.*	+	39μ	28–30μ	55–65μ		14–23μ (2–3.2:1)	8–10μ	31–39μ spores 12–13μ
70–2126								
Blepharostoma trich.		42–49×	16–20×	18–21×	+	48–60×		
ssp. *trichophyl.*	–	42–52μ	30μ	42–49μ		16–19μ (2.7–3.1:1)		
70–2440e								
Blepharostoma trich.		34–36×	18×	16–18×	– > +	36–42×		
ssp. *brevirete*	–	36–42μ	22–29μ	26–62μ		22–24μ (1.6–1.8:1)		
70–2422								
Blepharostoma trich.		39×	13–18×	21–23×		31–42×		
ssp. *brevirete*	–	42–47μ	23–30μ	29–68μ	+ (> –)	24–26μ (1.3–1.7:1)		

(continued)

Table I (cont.)

	Gem-mae	Average of basal 2 cells W × L	Terminal 3 cells W × L	Cortical cells W × L	Septum between cells Swollen or not	Longest lobe cells L × W	Perianth mouth cells	Perianth middle cells
70–2810c								
Blepharostoma trich.	–	33–36×	18×	21–31×	+ > –	28–36×		
ssp. *brevirete*		36–39μ	25–26μ	49–57μ		20–24μ		
						(1.2–1.7:1)		
70–2597								
Blepharostoma trich.		31–47×	18×	23–31×		33–46×		
ssp. *brevirete*	–	42–44μ	28–33μ	52–86μ	– > +	24–25μ		
						(1.4–1.9:1)		
70–2611								
Blepharostoma trich.		29–31×	18–21×	23–26×	–	33–38×		
ssp. *brevirete*	–	36–42μ	22–33μ	34–60μ	(± moniliform)	28–31μ		
						(1.1–1.3:1)		
70–2775a								
Blepharostoma trich.		31×	18×	21–23×	–	24–26 (35)×		
ssp. *brevirete*	–	39μ	26–31μ	42–65μ		24–26μ		
						(1–1.4:1)		
70–2633								
Blepharostoma trich.		39×	23×	26×	– (> +)	28–36×	24–26×	
ssp. *brevirete*	–	36μ	27–28μ	52–70μ		24–27μ	28–31μ	
						(1.2–1.5:1)	(0.8:1)	
66–0163								
Blepharostoma trich.		49–52×	18–21×	26–34×	–	38–45×	31–52×	19–25×
ssp. *brevirete*		78–83μ	32–35μ	52–78		25–28μ	10–13μ	38–52 (80)μ
						(1.2–1.6:1)		
70–2315								
Blepharostoma trich.		36–39×	18–19×	18–26×	–	26–33×		
ssp. *brevirete*	–	42μ	20–23μ	52–101μ		24–29μ		
						(1.0–1.3:1)		

ssp. *brevirete* (Bryhn & Kaal.) Schust.

Distribution (Map 1)

1A: Behind Arctic Station (66–0152a, 66–0157, 66–0161c, 66–0162, 66–0163, 66–0166, 66–0173, 66–0183, 66–0278a, 70–2038). 1B: Lyngmarken (66–0342a). 1D: Skarvefjeld (66–0306, 66–0308a, 66–0309a, 66–0314a, 66–0321). 2: Fortunebay (66–0124, 66–0135a, 66–0137, 66–0142, 66–0202). 6: Eqalúnguit (70–2214a, 70–2219a, 70–2222a, 70–2227b, 70–2231a, 70–2238b). 8: Kuánerssuit (70–2148a). 9: Eqaluit (70–2550a). 10. Enoks Havn (70–2775a, 70–2778). 11: Qasigíssat (70–2726). 12: Perdlertut (70–2671, 70–2675a, 70–2683, 70–2688, 70–2693, 70–2696, 70–2703). 13:

Jens Vahls Dal (70–2633, 70–2637e, 70–2644, 70–2646). 14: Hareøen (70–2597a, 70–2591a, 70–2608, 70–2611). 15: Kronprinsens Ejland (70–2071, 70–2088b, 70–2102, 70–2105). 17: Tupilak (66–0020a, 66–0021, 66–0029b, 66–0036a, 66–0112, 66–0118a). 18: Grønne Ejland (70–2810c). 19: Nûk (70–2852, 70–2872a, 70–2877f). 21: Umiasugssûp (70–2935b). 25: Sarfaq (70–2357). 22: Orpigsôq (70–3119b). 26: Pâkitsup ilordlia (70–2259, 70–2246b, 70–2299, 70–2314, 70–2315, 70–2316a). 29: Ritenbenk (66–0258). 30: Eqe (66–0244, 66–0289c, 66–0292, 66–0296, 66–0325). 31: Anap nunâ (70–2431, 70–2436). 36: Umanak (66–1483). 39: Tasiussaq (66–1260, 66–1259). 40: Mârmorilik, head of the Fjord (66–1199, 66–1178, 66–1204, 66–1206). 42: Magdlak (66–1352, 66–1361, 66–1364a, 66–1372, 66–1376). 43: Kangerdlugssuakavsak (66–1288). 44: Akuliarusikavsak (66–1320). 45: Sagdliaruseq (66–1093). 48: Amitsup (66–0785, 66–0788, 66–0800, 66–0802, 66–0813). 49: Skalø (66–1010). 51: Simiútap kûa, shore (66–0915b, 66–0916, 66–0917). 53: Søndre Strømfjord (66–0076b, 66–0080a, 66–0097).

Additional collections:

2: Fortunebay (LÆGAARD, Aug. 1962). 17: Tupilak (K.H. 12.198, 13.016, 15.539). 28: Atâ (LÆGAARD, July 1962). 29: Ritenbenk (S.B. 1870). 34: Marrait kangigdlît (K.H. Sept. 1956, K.J. 1137). 40: Mârmorilik, head of the Fjord (K.H. 13.707). 41: Mârmorilik, mouth of the Fjord (K.H. 14.628). 42: Magdlak (K.H. 16.843). 44: Akuliarusikavsak (K.H. 16.107). 45: Sagdliaruseq (K.H. 13.157). 50: Simiutap kûa, valley (K.H. 12.966). 51: Simiutap kûa, shore (K.H. 12.892, 16.325). 57: Nipisat (K.H. 14.584). 67: Asuk (M.P.P. July 1898). 69: Qamavit (M.P.P. 447). 73: Igdlokasik (K.H. 14.497c). 83: Angnertussoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 15.711). 92: Claushavn (S.B. Aug. 1870). 98: Sarqaq (K.H. 15.811). 99: Sarqaq valley (K.J. 186b). 105: Nûssaq (SKOU, Aug. 1958). 106: Nûgssuaq (K.H. 15.637). 107: Tunorssuaq (K.J. 911). 110: Ikorfat (K.J. 281). 111: Kûtsiaq (K.J. 771). 114: Eqaluit (K.J. 792, 515). 116: Puiagtukavsak (K.J. 679a). 120: Itipilua qáqâ (K.J. 695c). 124: Tasíngortaq (K.H. 13.311a). 125: Sarqap taserssua (K.H. 17.114a). 126: west of Sarqap taserssua (K.H. 13.414b). 127: Kangersôq (K.J. 1087). 129: Agatdalen (K.H. 15.486). 143: Kangerdlugssuaq (K.H. 16.390). 144: Igdlorssuit (K.H. & W.C.S. July 1962). 145: Uligssat (K.J. 10.186h).

Although plants approaching this Arctic phenotype may be the product of difficult environmental conditions, in the far north only ssp. *brevirete* occurs, even in the moistest and most favorable sites. Hence we assume the existence of some genetic basis for ssp. *brevirete*. Furthermore gemmae apparently are not produced in the Arctic subspecies (SCHUSTER 1966, p. 753). Plants from favorable sites, even as far north as Inglefield Bredning, may show slight tendencies towards the facies of ssp. *trichophyllum*, as in, e.g., RMS 45523a; note the slightly elongated cells and distinctly dilated septa between leaf lobe cells. Under conditions usually found even in West Greenland, but especially in the high Arctic, leaves tend to have erect to incurved, short, rigid, slightly tapered leaf lobes formed of subquadrate cells.

Although *B. trichophyllum* (*s.l.*) supposedly has only terminal branches of the *Frullania* type, SCHUSTER (1966) showed that *Microlepidozia-*

type terminal branches are also readily found. We have seen them not only in ssp. *brevirete* but also in ssp. *trichophyllum* (e.g., in 70–2161b).

As Table I shows, distinctions in size of cortical cells [introduced by ARNELL (1951) to separate ssp. *brevirete*] seem unreliable. The form of the septa between leaf cells (whether dilated so that the setiform lobes appear dilated or ringed at the septa, as in ssp. *trichophyllum*, or not protruding externally, as in ssp. *brevirete*) is hardly more reliable. In "normal" ssp. *brevirete* some or many cells are inflated, so that the lobes may appear to be formed of submoniliform cells.

Ssp. *brevirete* is almost "weedy" in Greenland, being absent or rare only under very xeric conditions (e.g., in the *Lophozia hatcheri-Chandonanthus-Racomitrium* communities of fell fields or in the *Gymnomitrion-Andreaea* communities on exposed rocks).

Family ***Ptilidiaceae*** KLINGGRÄFF

Ptilidium NEES

Ptilidium ciliare (L.) NEES (Table II)

Distribution (Map 2)

1A: Behind Arctic Station (66–0149, 66–0192a). 2: Fortunebay (66–0206, 66–0212). 6: Eqalúnguit (70–2212, 70–2254). 9: Eqaluit (70–2561a). 10: Enoks Havn (70–2762). 12: Perdlertut (70–2702). 16: Manîtsoq (70–3000). 17: Tupilak (66–0015, 66–0004, 66–0114). 19: Nûk (70–2847). 24: Jakobshavn (66–0216, 66–0217, 66–0227, 66–0237). 25: Sarfaq (70–2343, 70–2349a, 70–2350). 26: Pâkitsup ilordlia (70–2318). 30: Eqe (66–0337). 32: Qôrorssuaq (70–2449, 70–2456c, 70–2460). 37: Agpat (66–1450). 39: Tasiussaq (66–1257). 44: Akuliarusikavsak (66–1335). 46: Qalatôq (66–1126a). 48: Amitsup (66–0783, 66–0776). 52: Umîarfik, Qôrnoq (66–0966). 53: Søndre Strømfjord (66–0064, 66–0094, 66–0099).

Additional collections:

1A: Behind Arctic Station (M.P.P. Aug. 1942). 2: Fortunebay (LÆGAARD Aug. 1962). 6: Eqalúnguit (M.P.P. 2078). 8: Kuánerssuit (L.H. 171). 17: Tupilak (K.H. 12.309, 16.422, K.J. 1344). 24: Jakobshavn (K.H. 12.125). 44: Akuliarusikavsak (K.H. 12.559, 12.796). 45: Sagdliaruseq (K.H. 15.738). 52: Umîarfik, Qôrnoq (K.H. 13.069). 57: Nipisat (K.H. 14.367). 60: Kugssuaq (M.P.P. 1726). 63: Mudderbugten (C. HOLMQUIST, June 1956). 73: Igdlokasik (K.H. 14.080). 74: Kangerdluarssuk (K.H. 14.105). 78: Kitdlît (C.K. July 1898). 83: Angnertussoq (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958, J.V. Sept. 1835?). 88: Christianshåb (K.H. 13.004). 90: Tasiussaq (S.B. July 1870). 95: Pâkitsoq (J.V. 170). 97: Qôrorssuaq (K.J. 418). 98: Sarqaq (J.V. 45, K.H. 13.569). 99: Sarqaq valley (K.J. 989). 106: Nûgssuaq (K.J. 80). 112: Umiartorfik (K.J. 633, 883). 113: Nugfiumaneq (K.J. 826, 827). 114: Eqaluit (K.J. 468, K.H. 13.239). 115: Kûgssuaq (K.J. 749). 116: Puiagtukavsak (K.J. 668). 117: Sêrsínerssuaq (K.J. 616, 633). 118: Itipilua (K.J. 721). 120: Itipilua qáqâ (K.J. 690). 122: South of Eqaluit (K.H. 13.332). 123: Uigordleq (K.H. 12.865). 125: Sarqap taserssua (K.H. 16.235). 126: west of Sarqap taserssua (K.H. 13.416). 130: Qarajaq, Tasiussaq (C.V. July 1893).

136: Kangerdluarssûp qeqertâ (K.H. 12.820). 140: Small Island (K.H. 16.729). 141: Inukavsait qáqarssue (K.H. 12.741). 145: Amitsoq (K.H. 12.003). 146: Itsako (K.J. 10.332).

P. ciliare is an abundant species with a bipolar distribution; it is cited from disjunct stations in Tierra del Fuego and New Zealand (SCHUSTER, 1966, 1968). In the northern hemisphere it is imperfectly holarctic, boreal-arctic, but becomes infrequent in high Arctic sites and although reported from a single site from Ellesmere Island, at 82°26′N. (SCHUSTER *et al.*, 1959), it is not known north of Inglefield Bredning area of northwest Greenland.

Regionally it is very common in areas with acidic rocks; it also occurs (in localized acidic sites) in basaltic areas but never directly over rocks. It tolerates considerable desiccation, hence often occurs with *Racomitrium lanuginosum*, *Dicranum*, *Lophozia hatcheri*, and *Chandonanthus setiformis*. All Greenland material seen has been uniformly sterile; in the absence of any mode of sexual reproduction, dispersal of the species remains a mystery.

In the arctic *P. ciliare* is very malleable, showing much variation in vigor and in the degree of ciliation and form of cells within the cilia. Two extremes occur, separable as follows:

1. Cilia along dorsal leaf margin from (7) 10–35 (39–42); cilia ± short, cells within uniseriate sectors of cilia abbreviated, length-width ratio ca. 1.4–2.9:1; cilia often 2–3 cells broad towards base. f. *ciliare*

2. Cilia along dorsal leaf margin mostly from (30–39) 40–57; cells within cilia strongly elongated, ca. 2.6–4.3:1; cilia strongly elongated, slender, usually simple (rarely 2–3-sympodial), uniseriate to base. f. *polaris*

f. *polaris* SCHUST.

This plant is illustrated in SCHUSTER (1966, fig. 79: 2–3). As Table II shows, the Disko Bugt region forms a transition zone between the "low" Arctic element and the high Arctic element; the first 8 specimens cited are clearly typical f. *ciliare* (although both 66–0004 and 66–0217 are transitional); the last 5 specimens cited from West Greenland are f. *polaris*. Both number of cilia and cell length within the cilia, however, show considerable transition in the Disko Bugt region.

The f. *polaris* described from Ellesmere Island (RMS 35318) appears to be the dominant form north of here. The several Inglefield Bredning area specimens we have checked (RMS 45730b and 45478 from Kânâk; RMS 46252, from Dundas) clearly represent f. *polaris*; only f. *polaris* is known from northern Ellesmere Island. Should there be a reasonably clear geographic restriction of this entity to the northern portions of the

Table II. Variation in *Ptilidium ciliare*

Specimen	Uniseriate cilia along dorsal leaf margin	W. and L. of longest cilium cells found.	L/W	Av. cell W. & L. in cilia from dorsal margin	av. L./ av. W.
70–2561a Eqaluit	10–15	23–26×44–52 μ	1.9–2.0:1	23×33 μ	1.4:1
70–3000 Manîtsoq	7–11	26–31×47–49 μ	1.6–1.8:1	23×40 μ	1.8:1
70–2460 Qororssuaq	10–16	16–23×42–47 μ	2.6–2.0:1	22×38 μ	1.8:1
70–2702 Perdlertut	25–39	16–18×47–52 μ	3.0–2.9:1	22×48 μ	2.2:1
66–0149 Godhavn	12–28	21–26×55–60 μ	2.6–2.3:1	21×51 μ	2.4:1
66–0337 Eqe	22–32	16–18×60–68 μ	3.7–3.8:1	17×44 μ	2.6:1
66–0004 Tupilak	25–42	26–29×68–73 μ	2.6–2.5:1	23×65 μ	2.8:1
66–0217 Jakobshavn	18–31	18×55–60 μ	3.0–3.3:1	20×57 μ	2.9:1
70–2343 Sarfaq	35–43	23–29×62–70 μ	2.7–2.4:1	21×55 μ	2.6:1
66–0064 Sdr. Strømfj.	22–39	16–23×49–52 μ	3.0–2.3:1	17×52 μ	3.0:1
66–0206 Fortunebay	48–55	16–21×62–75 μ	3.8–3.5:1	17×43 μ	2.5:1
70–2254 Eqalúnguit	36–57	18–23×55–65 μ	3.0–2.8:1	17×56 μ	3.3:1
70–2762 Enoks Havn	33–49	18–21×78 μ	3.7–4.3:1	16×69 μ	4.3:1
45–478 Kânâk, Thule	(28)32–41	21–23×77–80 μ	3.4–3.8:1	20×60–70 μ	3.0–3.5:1
46–252 Dundas	30–38	16–19×65–80 μ	4.2–4.0:1	16–17×48–55 μ	3.0–3.4:1
35–318 Alert (Type of f. *polaris*)	(29)36–55	17–21×75–88 μ	4.8–4.2:1	14–17×58–61	3.6–4.1:1

species range, elevation to subspecies would seem advisable. The problem will require study of a longer suite of specimens than now available; possibly a situation parallel to the *Blepharostoma trichophyllum-brevirete* problem may be at hand. There is one striking difference: in the *Blepharostoma*, as we go north, cell length within the ciliary leaf segment decreases while in the *Ptilidium* cell length increases drastically. As a consequence of the longer cell length (while cell number per cilium remains relatively invariable) and average larger number of cilia, the f. *polaris* looks marked-

ly more copiously "hairy" than f. *ciliare*. These distinctions hardly emerge from the accompanying table which clearly shows, however, that length-width ratio of the longest cilium cells and of the average cell length within longer cilia undergo drastic change.

Family ***Calypogeiaceae*** (K. MÜLL.) H. W. ARN.

Metacalypogeia (HATT.) INOUE

Metacalypogeia schusterana HATT. & MIZUT.

Distribution (Map 3)

34: Marrait kangigdlît (66–0726).

This rare species, known only from single stations in Nova Scotia, Newfoundland, Alaska, and Greenland (SCHUSTER, 1969) seems to be an Arctic and subarctic ally of *M. quelpartensis* HATT. & INOUE of Korea and Japan, which, however, differs in the obscurely dentate or repand-dentate antical leaf margin and more ovate leaf form. A detailed diagnosis and illustrations are found in SCHUSTER (1969). *Metacalypogeia*, with only 5 species, is principally Asiatic and North Pacific, with one species in Hawaii.

M. schusterana is a distinct calciphyte, occurring on damp, black humus over basic rocks (in Nova Scotia and Newfoundland), or, as in the case of the single Greenland station, on peaty soil in a calcareous wet fen traversed by small rills, associated with *Eriophorum*, *Lophozia gillmani*, *L. rutheana*, *Odontoschisma macounii*, *Scapania gymnostomophila*, and *Blepharostoma trichophyllum brevirete*. Of these taxa, *L. gillmani* is again associated with the *Metacalypogeia* in both Newfoundland and Nova Scotia.

It seems likely that the report of "*Bazzania tricrenata*" from southern Ellesmere Island (in BRYHN, 1906–07) represents an error in identification for *M. schusterana* (see SCHUSTER, 1969, p. 76); the two taxa are sometimes superficially similar, especially in the furcate, *Frullania*-type branching.

Calypogeia RADDI emend. NEES

Until recently only the sole species, "*Calypogeia trichomanis*" was reported from Greenland (LANGE & JENSEN, 1887, etc.); in SCHUSTER (1969) the following 4 species are all reported as new to Greenland and it is shown that all prior reports of *C. trichomanis* appear to represent *C. sphagnicola*. The subjoined data supplement the detailed treatment in Schuster (l. c.). A detailed discussion of branching modalities in *C. sphagnicola* and *C. integristipula*, based on the Greenland reports cited below, is given in SCHUSTER (1974a).

Regionally the species of *Calypogeia* principally inhabit peaty, organic soils or (*C. sphagnicola*, less often *C. integristipula*) occur over *Sphagnum* and other mosses in moors or along the edges of tarns. Only *C. muelleriana* appears to be rather frequent on soils low in organic materials.

Calypogeia sphagnicola (Arn. & Perss.) Warnst. & Loeske

Distribution (Map 4)

1B: Lyngmarken (66–0561a). 1C: Blæsedalen (66–1570). 6: Eqalúnguit (70–2214, 70–2230). 15: Kronprinsens Ejland (70–2060, 70–2117a, 70–2119a f. *paludosa*, 70–2115 f. *bidenticulata*). 16: Manîtsoq (70–3016a). 17: Tupilak (66–0104a, 66–0107). 17a: Egedesminde (66–0951, 66–0950). 18: Grønne Ejland (70–2814e, 70–2816). 19: Nûk (70–2841, 70–2870b, 70–2871, 70–2873a, 70–2877d, 70–2885). 21: Umiasugssûp (70–2949a). 22: Orpigsôq (70–3106a, 70–3109b). 23: Kangersuneq (70–3131, 70–3125b). 24: Jakobshavn (66–0224, 66–0225, 66–0228 f. *paludosa*). 26: Pâkitsup ilordlia (70–2290, 70–2294c, 70–2307, 70–2385). 29: Ritenbenk (66–0534). 37: Agpat (66–1422). 48: Amitsup (66–0798). 53: Søndre Strømfjord (66–0048a, 66–0049a, 66–0054a, 66–0055, 66–0056, 66–0058, 66–0061, 66–0062, 66–0081).

Additional collections:

2: Fortunebay (K.H. & W.C.S. 62.038b). 16: Manîtsoq (W. & H. July 1884). 17: Tupilak (K.H. 16.999). 87: Kangersuneq (J.V. 108c). 129: Avataussaligssuaq (K.J. 914c).

By far the most frequent species of the genus in Greenland and reported in Schuster (1969) from as far north as Inglefield Bredning. With few exceptions, it is a species of moors and peaty sites, very often found over *Sphagnum* hummocks at the edges of tarns and shallow lakes; it occurs almost exclusively in areas with acidic rocks, where it is probably present in almost all permanently moist moors. Capsules are frequent. Associates are usually *Cephalozia pleniceps*, *C. bicuspidata s.l.* (rarely *C. leucantha* and *C. lunulifolia*), *Riccardia sinuata*, *Mylia anomala*, *Lophozia binsteadii* and, less frequently, *Calypogeia neesiana*, *Anastrophyllum minutum*, *A. sphenoloboides*, *Scapania hyperborea*, *Lophozia excisa*, *L. opacifolia*, *L. latifolia*, *L. grandiretis* v. *parviretis*, *L. kunzeana*, *L. quadriloba*, *L. ventricosa* (especially vars. *confusa*, *silvicola*, *longiflora*), *Cephaloziella subdentata*, *C. uncinata*, *Blepharostoma trichophyllum brevirete.*

Plants from Manîtsoq (70–3016a) show very abundant terminal branching; indeed, postical-intercalary branches are almost impossible to find. Branches are nearly all of the *Frullania* type, with a narrowed, ovate-lanceolate "half-leaf" associated with the branch, with the following exceptions:

1. In a single case the anterior end of a lateral merophyte gave rise to two closely juxtaposed branches, arising one dorsal to the other. In this instance there clearly was development of both a *Frullania*-type

branch, from the postical half of the acroscopic end of the merophyte (replacing the ventral half of a leaf) and a *Microlepidozia*-type branch from the antical half of the acroscopic end of the merophyte (replacing the dorsal half of a leaf). As was to be expected, the merophyte in question did not produce any trace of a leaf. Branching of this type, in which two juxtaposed lateral-terminal branches occupy the entire anterior end of a merophyte, hence replace a whole lateral leaf, has been reported a single time, in *Temnoma quadripartitum* (SCHUSTER, 1966, p. 446). Strikingly enough, on the plant in question, a terminal, *Frullania*-type branch was also produced from the adjacent merophyte of the opposite side of the axis. Hence the plant fasciculately branched distally, appearing resolved into 4 daughter axes all of nearly identical vigor (the copious branch production seemingly having "sapped" the vigor of the plant so that the main axis could be recognized only with some difficulty).

2. On another plant of the same collection, a very weak individual, two undoubted *Acromastigum*-type branches were found on a single stem, replacing a "half-underleaf" in each case. The two branches developed from adjacent ventral merophytes; in one case the right-hand side of the underleaf was replaced, in the other instance the left-hand side. The residual "half-underleaves" showed exactly the form one would expect, judging from the form of the normal underleaves of the same stem (these were bifid, sometimes with a lateral tooth of one or both sides of the underleaf): one "half-underleaf" was lanceolate, without a lateral tooth, the other one was lanceolate with an angular tooth of one margin.

The demonstration that, admittedly exceptionally, *Microlepidozia*-type branching may occur in *C. sphagnicola*, together with evidence (SCHUSTER, 1969, p. 127) that *C. neesiana* may produce *Acromastigum*-type branching, thus indicates that branching modalities in *Calypogeia* are infinitely more complex than assumed by BISCHLER (1963). Indeed, all of the branching types found in *Lepidoziaceae*, except lateral-intercalary branching, have now been seen in the *Calypogeiaceae*.

Variation: The species shows a wide amplitude of variation. In most instances plants are relatively small and slender, and very freely produce terminal, *Frullania*-type branches; they commonly show at least an indication of trigones and have pointed to obtuse leaf apices. This, the most common phenotype, we have interpreted as "typical" *C. sphagnicola*. Occasional extremes are relatively large, with very leptodermous cells, as, e. g., 66–0228 and 70–2119a; these represent the f. *paludosa* (WARNST.) SCHUST.

Perhaps more sharply distinct is f. *bidenticulata* SCHUST. (l. c., p. 141) in which a majority of leaf tips is narrowly bidenticulate; 70–2115,

growing amidst *Scapania paludicola*, with 7–12 oil-bodies per cell, all very small and 0–3-segmented, represents this phenotype.

It has been shown that several of the species of *Calypogeia* exist in 9 and 18 chromosome states; possibly the large-celled phases, i.e., f. *paludosa*, may represent the 18-chromosome version. Counts are clearly necessary.

Calypogeia muelleriana (SCHIFFN.) K. MÜLL.

Distribution (Map 3)

1A: Behind Arctic Station (66–0161b, 66–0172, 66–0176, 70–2018a, 70–2047, 70–2184). 9: Eqaluit (70–2522, 70–2526). 14: Hareøen (70–2579). 16: Manîtsoq (70–3008a). 52: Umîarfik, Qôrnoq (66–0979).

Additional collection:

1A: Godhavn (S.B. 1870, recorded by BERGGREN 1875 as *C. trichomanis*).

Principally non-Arctic in range; *C. muelleriana* is not known from further north than the presently reported localities. It is stated to have 18 chromosomes, but the Appalachian ssp. *blomquistii* SCHUST. at least has n = 9 (SCHUSTER, 1969). Chromosome numbers of the Greenland collections should be counted but in general the plants agree with the typical European subspecies in the high incidence of terminal *Frullania*-type branches (see SCHUSTER, 1969, fig. 120, based on South Greenland material); terminal branches are frequent not only in 70–2526 but also in 66–0979, 70–2047, and 70–3008a.

The Greenland plants occur in both acidic and, less frequently, weakly basic areas, frequently along rills, on peaty, exposed, shaded soil, or on shaded soil in recesses between rocks on steep slopes. Associates are mostly *Cephalozia pleniceps*, *Nardia geoscyphus*, *Anthelia juratzkana*, less often *Diplophyllum taxifolium*, *Scapaniae* of the *Curta* group (*S. parvifolia*, *S. curta*, *S. lingulata s.l.*), *Calypogeia integristipula*, *Pleuroclada albescens*, *Lophozia grandiretis*, and *Plagiochila asplenioides*. In basic areas *Cephalozia pleniceps*, *L. grandiretis*, less often *L. heterocolpos s.l.*, *S. curta*, and *P. asplenioides* are typical associates (in 66–0172, 66–0161, 70–2579).

Plants of 70–2526 represent a highly nitid, convex, mod. *parvifolia-densifolia*, growing on peaty, permanently damp soil between rocks, along a broad river valley, associated with *Cephalozia pleniceps*, *Nardia geoscyphus*, *Anthelia juratzkana*, and *Pleuroclada albescens*. The plants, less than 2 mm wide, agree with other Greenland phenotypes seen in having frequent terminal branches—sometimes as many as 3 on a single plant. Colorless oil-bodies are 4–9 per cell, each only 1–2–3- up to 5–7-segmented, depending on the cell studied. The capsule wall thickenings

were in sinuous sheets (much as in SCHUSTER, 1969, fig. 123:4, 12), with sporadic walls devoid of thickened sheets. Except for the slightly smaller than average cell size, the plants seem quite typical. Plants of 70–2047 are essentially identical but have cells only 24–32 μ in the leaf tips and oil-bodies only 2–6-segmented and to 4.5×7 μ; spores are 12.5–14 μ in diam. Plants of 66–0979 seem basically identical to 70–2526 and 70–2047: nitid, rather small (as contrasted to phenotypes from temperate regions), with terminal branching present; median cells in these plants are 31–42×40–44 μ, and subapical cells are 27–34×26–34 μ.

The relatively high level of homogeneity of West Greenland plants is noteworthy: it is almost as if only a closely interrelated series of genotypes is present. The normal maximal width is 1.8–2 mm—much less than the "2.7–3.5 mm wide" found as the norm in temperate zone plants (SCHUSTER, 1969). Also, the apparently constant presence of terminal branches—as in *C. sphagnicola*—isolates these populations from plants of the Appalachian system in North America assigned to *C. muelleriana* (referred in part to ssp. *blomquistii* in SCHUSTER, 1969), in which only ventral-intercalary branches are found. Similar populations, with larger size linked with purely ventral-intercalary branches, occur in Europe (e.g., Glencoe region of Scotland; RMS 72–311). Obviously there are unresolved taxonomic problems in the delimitation of *C. muelleriana* and the Greenland populations are of interest in showing that in certain areas the species seems to have genetic perimeters visibly different than in other areas.

Calypogeia integristipula STEPH. (syn.: *C. meylanii* BUCH)

Distribution (Map 5)

1A: Behind Arctic Station (70–2047a). 16: Manîtsoq (70–3009). 31: Anap nunâ (70–2415, 70–2425). 45: Sagdliaruseq (66–1081).

Additional collection:

45: Sagdliaruseq (K.H. 14.590).

C. integristipula is usually confined to less strongly acidic sites than *C. neesiana* and *C. sphagnicola*; in this regard it agrees with the relatively tolerant *C. muelleriana* (with which it may occur admixed, as in 70–2047a). However, the species seems to avoid basaltic regions but at times occurs with *Sphagnum* and other mosses around shallow tarns or lakes where there is some basic seepage from dikes (as at Anap nunâ; there with *Lophozia excisa*, *L. hatcheri*, *Cephalozia bicuspidata*, and *L. ventricosa s.l.*). It may also occur on peaty soil fed by a basalt-draining rill; here *Cephalozia pleniceps*, *Pleuroclada albescens*, *Diplophyllum taxifolium*, *Solenostoma subellipticum*, and *Scapania curta* are associated.

Plants of 66–1081, 70–2425, 70–2415 and 70–3009 all epitomize the problems involved in recognition of this taxon at the species rank. *C. integristipula*, long known as *C. meylanii* Buch or *C. neesiana* var. *meylanii* (Buch) Schust., was, with many reservations, recognized as a valid species (Schuster, 1969) although earlier (Schuster, 1949, 1953) the plant was accepted as a variety of *C. neesiana*. Study of present plants suggests that the latter course might have been the wiser one; they exhibit a baffling mélange of characters: the large size (to 2.2–2.8 mm wide), the very large underleaves (3–4 × the stem width or more), the very extensive, often brownish rhizoid-initial regions, and the leaf shape are all reminiscent of *C. integristipula*. Also, in general, oil-bodies occur in all cells of the lateral leaves, a feature Buch (1936) emphasized as separating *C. integristipula* ("*C. meylanii*") from *C. neesiana*. This criterion is of ambiguous value; at least in the plants of *C. neesiana* from the eastern U.S. oil-bodies occur in all, or nearly all, leaf cells. Unlike *C. integristipula*, however, but as in *C. neesiana*, many leaves are quite distinctly, if locally, bordered with tangentially elongated cells at the leaf apices, and, in spite of the large underleaf size, these are almost always shallowly to moderately notched, exactly as is normal for *C. neesiana*. An additional (and so far unique) peculiarity exhibited by plants of both 70–2425 and 70–3009 is the rather frequent terminal-lateral, *Frullania*-type branching which is otherwise quite unknown in the *C. neesiana-integristipula* complex (Schuster, 1969). Ventral-terminal, *Acromastigum*-type branching, however, has been recorded (Schuster, 1974a) as a rarity in *C. neesiana*.

Plants of 70–3009 present additional problems; they are somewhat more nitid than normal for *C. integristipula* and were found with a single mature capsule, which had epidermal cells with sheetlike thickenings that were hardly nodularly produced. They quite fail to correspond with those of "typical" (non-Arctic) *C. integristipula*, as illustrated in Schuster (l. c., fig. 107:2).

Calypogeia neesiana (Mass. & Car.) K. Müll.

Distribution (Map 5)

18: Grønne Ejland (70–2814, 70–2816e). 37: Agpat (66–1421). 53: Søndre Strømfjord (66–0078).

Additional collection:

86: Seqineqârajutoq (L.H. 18).

Unlike the generally larger *C. integristipula*, this species is confined to acidic sites. On Grønne Ejland it occurs, amidst *Polytrichum*, *Sphagnum*, and *Aulacomnium*, as well as *Salix herbacea*, with a whole ensemble of species typical of acidic, peaty sites: *Lophozia ventricosa silvicola*, *Mylia anomala*, *Calypogeia sphagnicola*, *Cephalozia leucantha*, *C. lunulifolia*,

Anastrophyllum sphenoloboides, *A. minutum*, and *L. opacifolia*. Of these the first 5 represent a southern element in the Disko Bugt flora, as does *C. neesiana*.

Only a trace is present in 70-2816e, but the plants have the very typical underleaves, the dull, rather glaucous cast when dry, and the margined leaves normal to the species. An additional feature noted, stressed by BUCH as absolutely diagnostic of *C. neesiana* vis à vis all other European-American *Calypogeiae*, is the absence, even on young leaves, of oil-bodies from all but a small minority of laminar cells, away from the peripheral and basal sectors. (In the much larger Greenland plants here referred to *C. integristipula*, oil-bodies are always present in all leaf cells.) In the more copious collection of 70-2814, oil-bodies [which are often unsegmented or only 3-5-segmented, exactly as BUCH (1936) describes them for this species] are present only in 2-5 rows of marginal cells and in some basal cells, but are absent from all cells of the remainder of the lamina. These plants show the border of elongated leaf cells to an optimal extent; underleaves also are, in part, rather remote and small (exactly as shown in fig. 130:1 in SCHUSTER, 1969).

The northernmost collection, from Agpat (66-1421), is a rather small, mostly dense-leaved phenotype with many bidentulate leaves and all underleaves clearly notched. The dull, bluish white texture when dry; the (on maturer leaves) often strikingly distinct border, with some cells in the leaf tips 3-4:1; the purely intercalary branching; and the small rhizoid-initial fields all place these plants within *C. neesiana s. str.* As BUCH (l. c.) emphasized, a high proportion of the ovate leaves in this species are subtruncate at their tips. Associated are *Lophozia binsteadii*, *Cephalozia lunulifolia*.

Family ***Jungermanniaceae*** REICHENB.[1])

Subfamily *Chandonanthoideae* INOUE

Chandonanthus MITT.

Chandonanthus setiformis (EHRH.) LINDB.

Distribution (Map 6)

1A: Behind Arctic Station (66–0194, 70–2039). 2: Fortunebay (66–0202). 3: Sinigfik (66–0468). 6: Eqalúnguit (70–2210, 70–2253). 15: Kronprinsens Ejland (70–2076, 70–2100, 70–2111, 70–2120). 16: Manîtsoq (70–3000, 70–3023). 17: Tupilak (66–0001, 66–0003a, 66–0005, 66–0033a). 17A: Egedesminde (66–0948a). 22: Orpigsôq (70–3120). 24: Jakobshavn (66–0243). 25: Sarfaq (70–2341, 70–2350). 26: Pâkitsup ilordlia (70–2278). 29: Ritenbenk (66–0520). 31: Anap nunâ (70–2429). 32: Oôrorssuaq (70–2459, 70–2463). 37: Agpat (66–1437a). 46: Qalatôq (66–1126a).

[1]) A detailed discussion of the various taxa is included in SCHUSTER (1969). For this reason we have limited our discussion here to problems not treated or not resolved in that book, and to new problems uncovered during the 1970 field season.

Additional collections:

1: Godhavn (S.B. 1870, M.P.P. 2384). 3: Sinigfik (HOLMQUIST June 1956). 6: Eqalúnguit (M.P.P. 2058). 17: Tupilak (K.H. 17.002). 24: Jakobshavn (K.H. 12.110, 15.946). 45: Sagdliaruseq (K.H. 13.127). 57: Nipisat (K.H. 14.162). 74: Kangerdluarssuk (K.H. 14.153). 82: Sarqardlîp nunâ (L.H. Aug. 1932, GRØNTVED Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958). 88: Christianshâb (K.H. 12.080). 95: Pâkitsoq (J.V. 176). 120: Itipilua qáqâ (K.H. 690). 121: Boyes Sø (K.J. 369). 124: Tasíngortaq (K.H. 13.295). 125: Sarqap taserssua (K.H. 16.203, 16.241). 139: Qaqortukavsaq (K.H. 12.807). 140: Small Island (K.H. 16.731). 141: Inukavsait qáqarssue (K.H. 12.742, 16.277, 16.297). 142: Niaqornánguaq (K.H. 14.943). 147: Amitsoq (K.H. 12.004).

The ecology of this species is highly diagnostic: it is a drought-tolerant plant of highly acidic sites, typically forming large, often pure, tawny mats consisting of erect, almost unbranched stems, adjoining and sometimes intermingled with *Racomitrium lanuginosum*. The species is a typical one of denuded, often almost soilless gneissic hills, and of the fell-mark, occasionally associated with a limited suite of other drought-resistant, Ca-avoiding hepatics: *Lophozia hatcheri*, *L. rubrigemma*, *L. kunzeana* (in its most xeromorphic manifestation), *Anastrophyllum minutum*, *Cephaloziella byssacea*, and *Ptilidium ciliare*. As smaller modifications, the species at times spreads to nearby rock faces and then occurs admixed with *Gymnomitrion concinnatum* (as in 66-0003a) and *G. corallioides* (in 66-0948a). Admixtures with other *Hepaticae*, however, are almost the exception rather than the rule, *C. setiformis* being one of the few local hepatics that often forms extensive, pure patches. The wide dispersal in relatively dry sites is difficult to explain on the basis of the almost invariable sterility of the species, which has no gemmae.

In West Greenland the species is almost restricted to the Precambrian area; although known north to 80°40′N. in Spitsbergen, it is known in Greenland north to only 77°40′N. in Inglefield Bredning (SCHUSTER, 1969).

Except for the variation in degree of suppression of the basal teeth of the leaf lobes and in leaf lobe number, *C. setiformis* hardly undergoes any noteworthy variation in the region.

Subfamily *Lophozioideae* MACV.

Lophozia DUMORT.

Subg. ***Orthocaulis*** (BUCH) SCHUST.

Lophozia (Orthocaulis) binsteadii (KAAL.) EVANS

Distribution (Map 7)

1A: Behind Arctic Station (70–2031, 70–2041, 70–2042, 70–2056). 1B: Lyngmarken (66–0343, 66–0561b). 2: Fortunebay (66–0208). 6: Eqalúnguit (70–2225). 15: Kronprinsens Ejland (70–2064, 70–2067, 70–2099). 16: Manîtsoq (70–3022). 17:

Tupilak (66–0009b, 66–0012, 66–0024, 66–0112, 66–0117a, 66–0118). 17A: Egedesminde (66–0942, 66–0951). 19: Nûk (70–2877f, 70–2839). 22: Orpigsôq (70–3112, 70–3119a). 23: Kangersuneq (70–3125, 70–3155). 24: Jakobshavn (66–0235). 25: Sarfaq (70–2349, 70–2351). 26: Pâkitsup ilordlia (70–2271a, 70–2279c, 70–2294b, 70–2391). 37: Agpat (66–1421). 53: Søndre Strømfjord (66–0085, 66–0090, 66–0091).

Additional collections:

2: Fortunebay (K.H. & W.C.S. 62.038a). 16: Manîtsoq (W. &. H. July 1884). 17: Tupilak (K.H. 16.994, K.J. 1355, 1452). 74: Kangerdluarssuk (K.H. 14.470, M.P.P. 1766). 77: Oqaq (C.K. July 1897). 79: Agpalilik (C.K. July 1897). 80: Egedesminde, Tørveø (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958, J.V. 108b?). 88: Christianshåb (K.H. 16.654). 90: Tasiussaq (S.B. 1870). 95: Pâkitsoq (J.V. 168?). 99: Sarqaq valley (K.J. 989a). 140: Small Island (K.H. 16.741).

L. binsteadii is an essentially Arctic species known north to 77°40′N. (SCHUSTER, 1969) but in our area scarce only north of Nûgssuaq. A diagnostic species of acid, moory ground, often occurring in large quantity with *Sphagnum* on the margins of shallow, rocky tarns and lakes, almost exclusively in areas with igneous rocks and gneissic rocks, usually near standing water. Associated are very often *Anastrophyllum minutum* (often in the var. *grandis*), *Lophozia ventricosa* (in vars. *silvicola* and *longiflora*), *L. kunzeana*, *L. cavifolia*, *L. wenzelii*, *Calypogeia sphagnicola*, *Blepharostoma trichophyllum brevirete*, *Cephalozia bicuspidata*, and occasionally *Ptilidium ciliare*. On wet, mucky peat, under abnormally moist conditions, *Scapania paludicola rotundiloba* and/or *S. hyperborea* and *Gymnocolea inflata* may be associated (70-3119a; 66-0009b) or *Mylia anomala* (66-0561b), more rarely *Anastrophyllum sphenoloboides*, *Cephaloziella arctica*, and *Cephalozia pleniceps*, or *Lophozia grandiretis*, *L. opacifolia*, and *Riccardia sinuata*. Very rarely, on moist peat in shallow rock depressions of gneiss hills, *Gymnomitrion corallioides* may be admixed (70-3112); here the species has perianths—an exceptional situation in the local plants. By contrast, reddish purple gemmae are not infrequently produced.

L. binsteadii rarely causes any problems in identification. Its habitat, the almost uniformly trifid, subquadrate leaves with usually narrow, sharp and incurved lobes, and the often tawny to reddish brown color are diagnostic. The species is usually said to possess very coarse trigones and narrow leaves, with lobes longer than broad (see SCHUSTER, 1969, p. 266). Some bog phenotypes (66-0208 Fortunebay; HARMSEN, Aug. 13, 1932), however, may have "abnormally small trigones and leaves that are wider than normal (width ca. 860 μ × 650 μ long; thus ca. 1.33 × as wide as long)." Such extremes may occur mixed with more normal plants having leaves no wider than long and coarse trigones. The presence of such individuals, in effect, allows the separation of *L. binsteadii* from the otherwise similar *L. atlantica*, a species known from only the southwestern portion of Greenland. [*L. atlantica* has been actually reported from our area by

Böcher (1963, p. 204), from Holsteinsborg (as *Orthocaulis atlanticus*). We have not seen the specimen and assume that possibly a broad-leaved phenotype of *L. binsteadii* is involved].

Lophozia (Orthocaulis) kunzeana (Huebn.) Evans

Distribution (Map 8)

1A: Behind Arctic Station (66–0191, 70–2013, 70–2035c f. *acuta*, 70–2039, 70–2040, 70–2041). 1B: Lyngmarken (66–0343). 2: Fortunebay (66–0215). 6: Eqalúnguit (70–2212, 70–2216a, 70–2245, 70–2246). 7: Angûjârtûtit (70–2160). 9: Eqaluit (70–2533b, 70–2536). 10: Enoks Havn (70–2759, 70–2768). 15: Kronprinsens Ejland (70–2073, 70–2074, 70–2076a, 70–2087a, 70–2088a, 70–2091a f. *acuta*, 70–2097a, 70–2099, 70–2114). 16: Manîtsoq (70–3000, 70–3024b). 17: Tupilak (66–0007, 66–0014a, 66–0015, 66–0019, 66–0021a, 66–0022 f. *acuta*, 66–0024a, 66–0104, 66–0107, 66–0111a, 66–0112, 66–0114, 66–0115). 17a: Egedesminde (66–0944, 66–0942). 19: Nûk (70–2847a, 70–2842). 21: Umiasugssûp (70–2939, 70–2951). 22: Orpigsôq (70–3108c, 70–3113a, 70–3115a). 23: Kangersuneq (70–3131c, 70–3134a, 70–3135, 70–3139a, 70–3142, 70–3156a). 24: Jakobshavn (66–0218, 66–0220, 66–0221, 66–0222, 66–0227). 25: Sarfaq (70–2344c, 70–2349a, 70–2357, 70–2364). 26: Pâkitsup ilordlia (70–2282, 70–2289b, 70–2310, 70–2316a, 70–2319). 29: Ritenbenk (66–0254, 66–0270a, 66–0237b). 32: Qôrorssuaq (70–2449, 70–2456c, 70–2459b, 70–2470, 70–2473). 45: Sagdliaruseq (66–1057). 48: Amitsup (66–0781). 53: Søndre Strømfjord (66–0051a f. *wenzelioides*, 66–0057, 66–0068, 66–0090, 66–0093 f. *acuta*, 66–0099).

Additional collections:

1: Godhavn (Grøntved July 1932). 6: Eqalúnguit (M.P.P. 3322). 17: Tupilak (K.J. 1315, 1348, 1368, K.H. 13.011). 24: Jakobshavn (J.V. 1833, K.H. 15.972, 15.986). 28: Atâ (Lægaard July 1962). 53: Søndre Strømfjord (K.H. 3110b). 60: Kugssuaq (M.P.P. 1722). 62: Skansen (M.P.P. 3373). 72: Kuánit (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.825, W. & H. 1884). 90: Tasiussaq (S.B. 1870). 92: Claushavn (S.B. 1870). 95: Pâkitsoq (J.V. 163). 98: Sarqaq (J.V. 45). 99: Sarqaq valley (K.J. 989b). 106: Nûgssuaq (K.J. 40). 112: Umiartorfik (K.J. 876c). 114: Eqaluit (K.H. 13.228). 116: Puiagtukavsak (K.J. 663). 124: Tasíngortaq (K.H. 13.275, 13.293, 13.307, 13.311c). 140: Small Island (K.H. 13.603, 16.727).

L. kunzeana occurs high into the Arctic, north to Siorapaluk (77°48′ N.) on the west coast of Greenland (Schuster, 1969) and to 82°24′–26′ N. on Ellesmere Island (Schuster *et al.*, 1959; f. *rotundiloba*). [Although there have been earlier reports from Peary Land (Arnell, 1960), these represent *L. quadriloba* v. *glareosa*]. In West Greenland the species is abundant, usually in more or less helophytic sites, in acidic regions. In boggy sites it may grow amidst *Sphagnum* and *Aulacomnium*, associated with, i. a., *Scapania hyperborea*, *S. paludicola s. l.*, *Tritomaria quinquedentata*, *Cephalozia bicuspidata* (more rarely *C. pleniceps*), *Lophozia ventricosa confusa*, *Anastrophyllum minutum* (often v. *grandis*), *Cephaloziella uncinata*, *Calypogeia sphagnicola*, and *Riccardia sinuata*. Usually associated with the last two taxa found in peaty moss hummocks at the edges of

tarns and small lakes. Occurrences with Ca-tolerant taxa are few and sporadic. Occasionally found as a compact gemmiparous form with salmon-colored gemmae in moist, alluvial, sandy depressions (as at Eqaluit, 70-2533b), with pioneers such as *Anthelia juratzkana*, *Pleuroclada albescens*, and small forms of *S. hyperborea* and *Lophozia wenzelii*. Compact, often gemmiparous, forms may also grow on moist, dead peat, with *L. binsteadii*, *Gymnocolea inflata*, *Cephalozia bicuspidata*, and *S. hyperborea*.

Xeromorphic extremes of *L. kunzeana* may occur in the fellmark, in crevices between acid rocks, associated with *Chandonanthus setiformis*, *L. rubrigemma*, *L. hatcheri*, *Anastrophyllum minutum* (incl. var. *grandis*), occasionally *L. excisa infuscata*, *Ptilidium ciliare*, and *Cephaloziella rubella*.

L. kunzeana is a rather variable taxon, of which four distinct forms (including the typical) are recognized in SCHUSTER (1969, p. 296). Two of these, in addition to f. *kunzeana*, occur regionally:

f. *acuta* SCHUST.

This rather rare extreme is known from only the four West Greenland stations cited above. It is illustrated in SCHUSTER (1969, fig. 139:5–9); these figures show a plant with sharp leaf lobes, often ending in 2 superposed cells, giving one the impression of a "greenish *L. binsteadii*, which it approaches in the sharp leaf lobes and the cupped, hollowed, and usually rather dense leaves." (SCHUSTER, l.c., p. 299). Plants seem confined to rather difficult sites: 70-2035c grew with *Scapania lingulata*, *Lophozia ventricosa confusa*, and *Gymnomitrion;* 70-2091a, with *S. lingulata*. Collections are all from acidic regions.

f. *wenzelioides* SCHUST.

Distinct in the constantly shallowly bilobed leaves (sinus descending only 0.25–0.3 leaf length), whose incurved, broad lobes are blunt to narrowly rounded varying to subacute; underleaves are reduced, often a mere linear-lanceolate lamella, occasionally subobsolete.

Lophozia (Orthocaulis) quadriloba (LINDB.) EVANS

Distribution (Map 9)

1A: Behind Arctic Station (66–0157, 66–0165, 66–0170, 66–0173, 66–0281c). 1D: Skarvefjeld (66–0232, 66–0306, 66–0320). 2: Fortunebay (66–0135a, 66–0141, 66–0143). 6: Eqalúnguit (70–2214b, 70–2222, 70–2239a). 7: Angûjârtûtit (70–2169b). 8: Kuánerssuit (70–2126, 70–2127, 70–2131, 70–2139, 70–2140, 70–2149). 9: Eqaluit (70–2528a, 70–2558a). 10: Enoks Havn (70–2775b). 12: Perdlertut (70–2670c, 70–2677). 13: Jens Vahls Dal (70–2630, 70–2632, 70–2633, 70–2634, 70–2635, 70–2637d, 70–2640, 70–2642, 70–2643, 70–2645, 70–2647, 70–2648, 70–2650, 70–2651a, 70–2654, 70–2655, 70–2656, 70–2658, 70–2660, 70–2661, 70–2663, 70–2664a, 70–2665, 70–2667). 14: Hareøen (70–2570, 70–2571, 70–2573, 70–2576, 70–2582, 70–2583, 70–2585, 70–2587, 70–2589, 70–2590, 70–2591, 70–2593a, 70–2594, 70–2596, 70–2598, 70–2600,

70–2603, 70–2606, 70–2610, 70–2615, 70–2621, 70–2622). 26: Pâkitsup ilordlia (70–2262, 70–2297a, 70–2313, 70–2380). 30: Eqe (66–0288b, 66–0289, 66–0291, 66–0292, 66–0296, 66–0323, 66–0330a, 66–0333, 66–0340). 31: Anap nunâ (70–2420, 70–2428, 70–2432). 35: Hollænderbugt (66–1521). 38: Uvkusigssat (66–1396). 40: Mârmorilik, head of the Fjord (66–1206, 66–1207). 42: Magdlak (66–1377). 43: Kangerdlugssuakavsak (66–1288). 47: Íngia (66–1031, 66–1033, 66–1035, 66–1036, 66–1038). 48: Amitsup (66–0781, 66–0774, 66–0785, 66–0788, 66–0789, 66–0790a, 66–0791, 66–0800, 66–1551). 49: Skalø (66–1010, 66–1017, 66–1020, 66–1022). 50: Simiútap kûa, valley (66–0866). 51: Simiútap kûa, shore (66–0914h, 66–0916b, 66–0917a, 66–0937). 53: Søndre Strømfjord (66–0063, 66–0072).

Additional collections:

17: Tupilak (K.H. June 1956). 24: Jakobshavn (S.B. 1870). 34: Marrait kangigdlît (K.H. Sept. 1956, A.R. Sept. 1954). 44: Akuliarusikavsak (K.H. 16.782). 45: Sagdliaruseq (K.H. 16.956b, 17.192). 65: Ûnartuarssuk (M.P.P. 652b). 73: Igdlokasik (K.H. 14.497a). 84: Qeqertasugssuk (L.H. Aug. 1932). 99: Sarqaq valley (K.J. 186d). 101: Kugssinerssuaq (L.H. July 1932). 103: Qapiortoq kitdleq (K.J. 1052c). 106: Nûgssuaq (K.H. 15.634, 15.644, K.J. 76). 109: Kangilia (K.J. 453). 110: Ikorfat (K.J. 336, 339, 284, 379, K.H. 62.1574). 125: Sarqap taserssua (K.H. 16.218). 127: Kangersôq (K.J. 1091a). 128: Agatdalen (K.H. 13.902, A.R. 1954, I. Marcussen 1958). 129: Avataussaligssuaq (K.J. 894). 143: Kangerdlugssuaq (K.H. 16.385b). 144: Igdlorssuit (K.H. & W.C.S. July 1962). 145: Uligssat (K.J. 10.177, 10.186d). 147: Amitsoq (K. H. 14.630, 14.642a, 14.647).

L. quadriloba is a baffling and complex *typus polymorphus* in the Arctic. It occurs north as far as land, at least to Low Point in North Greenland (83°06′N.) and to Alert (82°30′N.) on Ellesmere Island (Schuster *et al.*, 1959); southward reaching only to northern Newfoundland (Schuster, 1969), Ontario (Bruce Pen.; also Pt. Mamainse, Lake Superior, Algona Distr., leg. Williams) and known in the United States only from the north tip of Michigan (Schuster, 1953, 1969). Very largely confined to basic regions and common only in the western, basaltic areas of West Greenland but also found in acidic loci (as at Eqe) if basalt dikes are present. It is particularly frequent in more or less permanently irrigated slopes in Ca-rich sites, often along permanent rills; associated here are *Blepharostoma trichophyllum brevirete*, *Odontoschisma macounii*, *Scapania cuspiduligera*, *S. curta*, *Lophozia polaris*, *L. heterocolpos*, *L. gillmani*, *Tritomaria quinquedentata*, *T. polita polymorpha*, less often *L. opacifolia* and *Cephalozia pleniceps*, occasionally *L. excisa*. On somewhat basic, compact soils occasionally found with *Nardia geoscyphus* and *Cryptocolea imbricata* (as in 70–2313), also in low, rich irrigated moss tundra with *S. cuspiduligera* (66–0143). The species also occurs on moist or irrigated clayey soils, associated with *Tritomaria scitula*, *T. quinquedentata*, *L. heterocolpos*, and *S. cuspiduligera*. Such sites, if rocky and better drained, may also be colonized by *L. quadriloba; S. gymnostomophila*, *S. ligulifolia*, *Arnellia fennica*, *T. scitula*, and *L. heterocolpos harpanthoides* are then associated.

L. quadriloba is only very exceptionally found in acidic areas (as at Pâkitsup ilordlia, 70–2297 a), growing with *Riccardia sinuata*, *C. bicuspidata*, and *O. macounii* in shallow, sandy-peaty depressions near a lake shore. Here a calcareous pocket must have been present as *Pinguicula vulgaris* and *Lophozia rutheana* occurred nearby. A similarly ecologically "mixed" site is that at Eqalúnguit (70–2214b), where acid and basic rocks are juxtaposed. Here the species occurs in an improbable combination with the oxylophytic *Calypogeia sphagnicola!* Perianths are very rarely present (e.g., in 70–2262).

Variation: *L. quadriloba* shows possibly the greatest degree of variability of any species of subg. *Orthocaulis;* this is documented in SCHUSTER (1969) in detail. Under the species proper are placed many small forms which could be regarded as representing var. *glareosa* (JOERG.) JOERG. and several which verge on v. *collenchymatica*. The following collections, however, represent these extremes, and f. *cephaloziellοides*, to the optimal extent:

v. *glareosa* (JOERG.) JOERG.

Distribution (Map 9)

2: Fortunebay (66–0207 trans. ad f. *collenchymatica*). 13: Jens Vahls Dal (70–2646). 14: Hareøen (70–2608b). 29: Ritenbenk (66–0260, 66–0264a). 35: Hollænderbugt (66–1505c).

Additional collections:

111: Kûtsiaq (K.J. 701a).

We interpret this phenotype to include also *L. quadriloba* var. *heterophylla* BRYHN & KAAL. Included are populations with mostly 2–3-lobed leaves whose lobe bases are unarmed or almost so; underleaves are usually simply bifid, usually without or with a single basal tooth. Plants are often fuscous to blackish and 500–600 μ wide. This phenotype may merely represent a plant developed in a difficult site; occasional plants, instead of producing only the feeble trigones usually seen in *L. quadriloba*, have rather coarse trigones and then show transition to var. *collenchymatica* (e.g., 66–0207). At the furthest perimeter of the species (and of this variant) lies the:

f. *cephaloziellοides* SCHUST.

Distribution (Map 9)

30: Eqe (66–0325b, 66–0339b).

Known only from the type locality (see fig. 144 in SCHUSTER, 1969). Initially inspected, the plant, with its small, subulate underleaves resembles an olive-green to dull brown *Cephaloziella*. It is only 280–380 μ wide

with remote, 0.55–0.75 bifid *Cephaloziella*-like leaves, and grew in thin soil over a basalt dike, associated with *Peltolepis grandis*, *Cephalozia pleniceps*, *Blepharostoma trichophyllum brevirete*, *Lophozia heterocolpos*, and *Tritomaria quinquedentata*—all Ca-tolerant or–demanding taxa.

v. *collenchymatica* SCHUST.

Distribution (Map 9)

2: Fortunebay (66–0139). 53: Søndre Strømfjord (66–0075). 42: Magdlak (66–1350a).

The var. *collenchymatica* differs from other phenotypes of *L. quadriloba* in (a) coarse, often bulging trigones, with thin intervening cell walls; (b) generally blunt to narrowly rounded tips of leaf lobes; (c) rather larger leaf cells, those of the lobe margins mostly 16–20 μ, of the leaf middle ca. 20–24 μ wide. Occasional plants (e.g., 66–0207, Fortunebay) are transitional between var. *glareosa* and var. *collenchymatica*.

At times var. *collenchymatica* gives the impression that it might have arisen by hybridization with *L. kunzeana;* the leaves are often almost devoid of cilia, postical base aside (see fig. 139:1 in SCHUSTER, 1969); weaker shoots have many (2)3-lobed leaves; sinuses often descend only 0.3–0.45 the leaf length; leaf sinuses are often only feebly reflexed.

Lophozia cavifolia (BUCH & S. ARN.) SCHUST. (Fig. 9: 4–6, p. 153).

Distribution (Map 30)

9: Eqaluit (70–2529, 70–2538a, 70–2540, 70–2541a, 70–2546a). 16: Manîtsoq (70–3020a, 70–3021a). 17: Tupilak (66–0032b, 66–0037). 17A: Egedesminde (66–0942). 23: Kangersuneq (70–3132). 26: Pâkitsup ilordlia (70–2257b, 70–2266, 70–2274, 70–2301a). 28: Atâ (70–2512c). 30: Eqe (66–0293b). 32: Qôrorssuaq (70–2450a). 48: Amitsup (66–0781).

Additional collections:

124: Tasíngortaq (K.H. 13.305, 13.311e).

A relatively rare plant, known from Sweden and Norway, with two reports (SCHUSTER, 1969, p. 331) from northwest and West Greenland [ARNELL, 1960, reports the species from Low Point, Peary Land; these plants represent *Anastrophyllum minutum grandis* (SCHUSTER, 1969)]. The northwest Greenland station at Dundas appears to be the northernmost one known.

In West Greenland the species seems sporadic in distribution, but is apparently not rare in the eastern acidic region. It can easily be overlooked for the ubiquitous *A. minutum grandis* (which may occur admixed, as in 70–2274). The species is Ca-tolerant but apparently not a calciphyte; it may occur on damp sand in weakly calcareous pockets in tundra along lake shores (as at Qissugssalik), there associated with *Cryptocolea imbricata*, *Tritomaria heterophylla*, *Nardia geoscyphus*, *Anthelia*, and *Ana-*

strophyllum minutum grandis. In similar sandy-peaty but acidic sites (as at Eqaluit), *Pleuroclada*, *Anthelia*, *Tritomaria quinquedentata*, *Lophozia ventricosa rigida*, *L. v. silvicola*, *L. v. confusa*, *L. wenzelii*, *Cephalozia pleniceps*, and *Gymnomitrion concinnatum* may be associated; in wet, peaty pockets, as at Manîtsoq, *Diplophyllum taxifolium* occurs admixed. Also occasional on acidic, irrigated, thin peaty soil over exposed rocks in temporary rills, associated with *Odontoschisma elongatum*, and, less often, *Scapania degenii dubia* (70–3020a, 70–3132).

The taxonomic position of this plant remains doubtful. BUCH (1951) placed it in *Orthocaulis* and SCHUSTER (1969, p. 330), following him, placed it into *Lophozia* subg. *Orthocaulis*. MÜLLER (1951–58), however, placed it next to "*Sphenolobus*" *minutus* (= *Anastrophyllum minutum*) and we are now almost convinced that we are dealing with a large-celled polyploid derivative of this last species and not with a fully autonomous species. In all of the plants referred here, however, we find a combination of (a) distinct collenchyma of the leaf cells; (b) more numerous oil-bodies, usually 4–9(10) per lobe cell and 7–9 per basal cell, ranging to (6) 7–11 per basal cell; (c) larger leaf cells, averaging 20–25 μ on the lobe margins, rarely down to 19–24 μ (in 70–2266) or up to 23–27 μ (in 70–2529; HOLMEN 13–311e). Where a stem section has been cut it corresponds to the figures given in BUCH (1951) and SCHUSTER (1969, fig. 156:10). Very rarely (and not nearly as frequently as shown in fig. 156:5, 8–9, l.c.) there are sporadic trifid leaves; we have seen quadrifid leaves in West Greenland plants only once (in HOLMEN 13–311e). These last plants, a rather lax phenotype, show highly plastic leaves: some are equally trifid, some have the median lobe of the 3 lobes shorter and narrower; in rare cases leaves are almost symmetrically quadrifid—as shown in SCHUSTER (l.c.). It is the sporadic occurrence of 3- or 3–4-lobed leaves that makes it difficult to reconcile these plants with *A. minutum*—or even with *Anastrophyllum.*

Reddish gemmae are occasionally present (e.g., in 70–3132, 70–2512c, 70–2538a, 66–0037, 70–2266).

In a single instance (in 70–2274) when *L. cavifolia* was mixed with the deceptively similar *A. minutum grandis*, the oil-body number (5–9 per lobe cell in the former; 2–5 per lobe cell in the latter) and the differences in cell size readily separated the two taxa. No androecia or perianths have been seen in regional plants; in *A. minutum* they are often frequent.

Subg. ***Barbilophozia*** LOESKE

Lophozia (Barbilophozia) lycopodioides (WALLR.) COGN.

Distribution (Map 10)

1A: Behind Arctic Station (66–0181). 1B: Lyngmarken (66–0553, 66–0566). 16: Manîtsoq (70–3002).

Additional collections:

1B: Lyngmarken, Engelskmandens Havn (M.P.P. 3304b, L.H. Aug. 1932). 17: Tupilak (K.J. 1447).

L. lycopodioides is a distinctly rare plant in West Greenland and occurs locally at its northernmost known stations; it is more common in South Greenland. It is cited (SCHUSTER, 1969) from only three Greenland localities, two from Disko and one from Ameralik. Older reports from East Greenland (as in JENSEN, 1897) all need verification.

Much doubt has been expressed about the distinctness of this plant from the much more ubiquitous *L. hatcheri* and a detailed discussion of the differences between them is found in SCHUSTER (1969, pp. 341–45). The above, without doubt, represent typical *L. lycopodioides*. The ecology of this species in Greenland seems distinct: it is rather sharply limited to rich, mesophytic moss tundra, often to late snow areas (then with *Salix herbacea*), sometimes with *L. wenzelii*. In the field it can be distinguished at a glance because, typically, it lacks all trace of gemmae and has much more crispate and undulate leaves of much greater width, with broader, convex-sided, shallower lobes, whose tips are often diagnostically abruptly long-mucronate. In 70–3002 the mucros may be 200–220 μ long and formed of 2–3 superposed cells. Terminal cells may even exceed the measurements given in SCHUSTER (l.c., p. 337), ranging to 22–24×110–120 μ. Such spinous teeth terminating the lobes never occur in *L. hatcheri*.

We have a single collection of what clearly seems to be a mixture of *L. lycopodioides* and *L. hatcheri* (66–0566); the former has (2)4–9(11) oil-bodies per cell, the latter 4–7(9) oil-bodies per median cell. Whether these differences are significant is doubtful. The two plants, in any event, are drastically different (compare fig. 159:2–8, in SCHUSTER, 1969, drawn from these plants). SCHLJAKOV (1973) places *L. hatcheri* as a variety of *L. lycopodioides*. This seems untenable.

Occasional collections of *L. hatcheri* (e.g., 70–2852) are gemma-free and may show slight gradation towards *L. lycopodioides*, especially in the strongly elongated cells of the often tortuous cilia of the ventral leaf margins. These cells, however, are at most 10×70 to 19×85 μ, and average under 5–6 × as long as wide. On that basis these plants readily key to *L. hatcheri* (see key on p. 336 in SCHUSTER, 1969). Also, although such gemma-free plants tend to have relatively broadly triangular leaf lobes on some leaves, others have those of the typical "*hatcheri* shape": nearly straight-sided and almost as long as wide.

Study of the Arctic collections of the *L. lycopodioides-hatcheri* complex tends to confirm the validity of the species distinctions here upheld between these two taxa. Thus *L. hatcheri* is reported (SCHUSTER, l.c.) from as far north as Inglefield Bredning (77°30′N.) in northwest Greenland, and to 78°45′N. in Ellesmere Island, far north of where the sub-

arctic to low-Arctic *L. lycopodioides* occurs. Similarly, *L. hatcheri* occurs in southernmost South America, and in Antarctica south to 65°38′S. (SCHUSTER, l.c., p. 347), yet none of the Antarctic collections show any tendency towards intergradation with *L. lycopodioides*. Indeed, their pattern of variation is quite distinct from that of the holarctic populations.

Lophozia (Barbilophozia) hatcheri (EVANS) STEPH.

Distribution (Map 10)

1A: Behind Arctic Station (66–0192, 70–2017a, 70–2043, 70–2048, 70–2052a). 1B: Lyngmarken (66–0558, 66–0566, 66–0567). 2: Fortunebay (66–0127a, 66–0132, 66–0203, 66–0204, 66–0205, 66–0206). 4: Flakkerhuk (66–0173a). 6: Eqalúnguit (70–2215, 70–2251a). 7: Angûjârtûtit (70–2160, 70–2162, 70–2165, 70–2168, 70–2171). 9: Eqaluit (70–2521b, 70–2522, 70–2555, 70–2558b, 70–2560). 10: Enoks Havn (70–2764). 11: Qasigíssat (70–2723, 70–2731). 12: Perdlertut (70–2678a, 70–2690, 70–2691, 70–2696a). 13: Jens Vahls Dal (70–2649, 70–2653). 14: Hareøen (70–2575, 70–2576, 70–2598, 70–2617). 15: Kronprinsens Ejland (70–2088, 70–2106, 70–2108, 70–2121). 16: Manîtsoq (70–3003a, 70–3006, 70–3023). 17: Tupilak (66–0004a, 66–0007, 66–0008, 66–0015, 66–0018). 19: Nûk (70–2837, 70–2845, 70–2852 intergrade to *lycopodioides*). 24: Jakobshavn (66–0216, 66–0236, 66–0238, 66–0239, 66–0241, 66–0243). 25: Sarfaq (70–2339a, 70–2345, 70–2352, 70–2357, 70–2360, 70–2372, 70–2373). 26: Pâkitsup ilordlia (70–2278a, 70–2298, 70–2317, 70–2318, 70–2395). 29: Ritenbenk (66–0255, 66–0266). 31: Anap nunâ (70–2414a, 70–2425, 70–2434). 32: Qôrorssuaq (70–2454, 70–2459c, 70–2475, 70–2477, 70–2483, 70–2521b). 37: Agpat (66–1450, 66–1469b). 39: Tasiussaq (66–1257). 46: Qalatoq (66–1110). 48: Amitsup (66–0799). 49: Skalø (66–1025). 53: Søndre Strømfjord (66–0057, 66–0065, 66–0068, 66–0086, 66–0092).

Additional collections:

1: Godhavn (M.P.P. Aug. 1942, S.B. Sept. 1870). 1B: Lyngmarken (W. & H. 1884, C.K. July 1897). 12: Perdlertut (K.H. & W.C.S. 62.841, 62.1432). 17: Tupilak (K.J. 1347, 1400, 1411, K.H. 13.014). 24: Jakobshavn (K.H. 15.971, 15.974, 15.983, 16.908). 28: Atâ (LÆGAARD July 1962). 29: Ritenbenk (S.B. 1870). 39: Tasiussaq (K.H. 16.858). 44: Akuliarusikavsak (K.H. 15.824). 45: Sagdliaruseq (K.H. 13.173). 51: Simiútap kûa, shore (K.J. 17.219). 57: Nipisat (K.H. 14.572, 14.578). 59: Kugssuaq (M.P.P. 737b). 63: Mudderbugten (C. HOLMQUIST June 1956). 65: Ûnartuarssuk (M.P.P. 652d). 66: Gamle Qutdligssat (M.P.P. July 1898). 69: Qamavit (M.P.P. Aug. 1902). 70: Sarqardlît (M.P.P. Aug. 1902). 72: Kuánit (M.P.P. 848). 76: Ivnârssulik (C.K. 399). 80: Egedesminde, Tørveø (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958). 88: Christianshåb (K.H. 15.716, 15.720, 15.722, 16.826, 16.828). 95: Pâkitsoq (J.V. 168). 97: Qôrorssuaq (K.J. 426). 98: Sarqaq (K.H. 15.813). 99: Sarqaq valley (K.J. 1000). 106: Nûgssuaq (K.J. 18, 20, K.H. 15.642). 113: Nugfiumaneq (K.J. 822, 826, 852). 114: Eqaluit (K.H. 13.236, 13.237). 115: Kûgssuaq (K.J. 749). 117: Sêrsínerssuaq (K.J. 640). 120: Itipilua qáqâ (K.J. 687). 122: South of Eqaluit (K.H. 13.328). 123: Uigordleq (K.H. 12.886). 124: Tasíngortaq (K.H. 13.301). 125: Sarqap taserssua (K.H. 16.202, 16.244). 128: Agatdalen (K.H. 13.857). 131: Storø (A.R. July 1954). 133: Tuperssuatsiait (K.H. 14.881). 134: Umivik (K.H. 13.869). 136: Kangerdluarssûp qeqertâ (K.H. 16.161, 16.163, 16.164). 137: Esersiutilik (K.H. 13.845). 139: Qaqortukavsaq (K.H. 16.077). 140: Small Island (K.H. 16.734, 16.735). 141: Inukavsait qáqarssue (K.H. 16.286c, 16.287, 16.289, 16.290). 142: Niaqornánguaq (K.J. 14.411, 14.997).

This bipolar, imperfectly circumboreal-circumarctic species recurs in southern South America and in Antarctica (SCHUSTER, 1969); in eastern North America it occurs from 77°30′ N. (West Greenland) and 78°45′ N. (Ellesmere Island) south to New England, with a strikingly isolated disjunct station far south in North Carolina.

L. hatcheri is one of the most abundant regional hepatics, with a correspondingly wide amplitude of variability and an ability to invade a wide range of sites. Generally, however, it is most common in "difficult" sites, as in the fell fields, where it may occur amidst rocks and boulders, associated with xerophytes like *Chandonanthus setiformis*, *Ptilidium ciliare*, occasionally *Lophozia kunzeana*, and *Racomitrium*. It may then occur as "normal" forms or as a mod. *parvifolia-colorata* (66–0216, Jakobshavn; see SCHUSTER l.c., p. 354) which may be "less than 1 mm wide, concave-leaved with incurved and often blunt lobes that ... almost never possess basal cilia of the leaves. Such plants freely develop gemmae, have almost constantly trifid leaves, and may have greatly reduced underleaves...". At the opposite pole are large, green, shade phenotypes, with limited or no gemma development; some of these phenotypes may also show only 1–2 basal cilia and often ± vestigial underleaves (66–0238, Jakobshavn), approaching certain of the Antarctic populations which also have lanceolate, reduced underleaves and few or no cilia of the leaves (SCHUSTER, l.c., p. 355). Normally, however, the ventral leaf bases are clearly ciliate, the underleaves bifid and ciliate, and numerous gemmae are developed. Such "normal" forms occur in a wider diversity of sites, both highly acid and more or less basic. Thus the species may occur with calciphytes such as *Tritomaria scitula*, *Lophozia quadriloba*, *L. polaris*, and *Odontoschisma macounii* (Jens Vahls Dal, Nordfjord, Eqaluit, Eqalúnguit, Fortunebay, all from Disko) in moss tundra over at least weakly basic rocky slopes, or, more normally on more acid sites, in moist to dry moss tundra, where common associates are *Lophozia excisa*, *L. ventricosa confusa*, *L. kunzeana*, *Cephaloziella arctica*, *Scapania mucronata praetervisa*, *S. lingulata*, *S. curta*, *Tritomaria quinquedentata*, *Anastrophyllum minutum grandis*. It is rarer in moss tundra on low, wet, sandy-peaty flat plains (as at Flakkerhuk, 66–0173a) under apparently circumneutral or basic conditions, judging from the associates: *L. opacifolia*, *L. polaris* (and the tolerant *L. excisa*). In our experience, *L. hatcheri* is almost ubiquitous except under very arid, sandy conditions, and in very moist or helophytic sites, where it would tend to be periodically submerged; it has not been found in our area in the sedimentary region.

The species also occurs, although rather rarely, as small forms, under exposed conditions, associated with *Gymnomitrion concinnatum* (as in 70–2251a, 70–2575); gemmae may be very abundant in such phenotypes. Gemmae, however, are also often present in large, vigorous phenotypes

(e.g., 70–2475) which may approach *L. lycopodioides* in robustness and leaf form. In at least one case (66–0566) we have collected these two closely allied taxa intermingled; they then remain clearly distinct (see fig. 159: 2–8 in SCHUSTER, l.c.).

Unlike *L. lycopodioides*, which is rare and always sterile in West Greenland, *L. hatcheri* is both abundant and often fertile. Perianths occur in, i.a., 70–2696a, 70–2165, 66–0266, and 66–0241. The last two collections also had mature capsules (July 16–19).

Lophozia barbata (SCHMID.) DUMORT.

Distribution (Map 10)

38: Uvkusigssat (K.H. 15.828). 53: Søndre Strømfjord (K.H. 4320). 141: Inukavsait qáqarssue (K.H. 16.288).

This species has a scattered and very sporadic range in Greenland; only three stations are cited in SCHUSTER (1969), the one from Søndre Strømfjord, one from Dundas, North Star Bay (RMS 46251) and another from South Greenland, where it must surely be more frequent. [The prior reports from northwest Greenland (HARMSEN & SEIDENFADEN, 1932) are referred to *L. hatcheri* and *L. heteromorpha* by SCHUSTER l.c.].

L. barbata is basically not Arctic at all; in eastern north America it extends south to Virginia and North Carolina along the Appalachian Mts. and is rare even so far north as Newfoundland (a single collection, RMS 68–1894). The scattered range in West Greenland and seeming absence in East Greenland are hard to explain, especially the station from North Star Bay, which is of typical, but rather brownish and xeromorphic plants. The plants of HOLMEN 4320 are quite typical.

Subg. ***Leiocolea*** K. MÜLL.

Lophozia (Leiocolea) rutheana (LIMPR.) HOWE

Distribution (Map 11)

19: Nûk (70–2879). 26: Pâkitsup ilordlia (70–2264a, 70–2383). 34: Marrait kangigdlît (66–0727), 51: Simiútap kûa, shore (66–0908, 66–0914a, 66–0916b, 66–0917a, 66–0937).

Additional collections:

2: Fortunebay (K.H. & W.C.S. 62.030). 17: Tupilak (K.H. 13.012). 34: Marrait kangigdlît (K.H. Sept. 1956). 36: Umanak (K.H. 13.618). 42: Magdlak (K.H. 16.841). 51: Simiútap kûa, shore (K.H. 13.688). 74: Kangerdluarssuk (K.H. 14.469). 104: Qapiortoq kangigdleq (SKOU July 1958). 106: Nûgssuaq (K.H. 15.636a). 126: west of Sarqap taserssua (K.H. 13.429). 137: Esersiutilik (K.H. 13.834).

L. rutheana, although primarily subarctic and low Arctic in range (reported from New York and Minnesota northward to 74°28′N. in East

Greenland), occurs northward in West Greenland to only ca. 72°N., although BRASSARD (1968) reports it from 81°07′N. in Ellesmere Island.

This, the most vigorous of the *Leiocolea* species, is rather rare and localized in occurrence, almost wholly confined to rich, fenlike sites where it may occur semisubmerged or over permanently moist peaty-sandy loci at the edges of tarns and ponds. In moors and fens it is sometimes found in acidic regions with localized basic seepage; thus at Qissugssalik (70–2383, 70–2264a) it is associated with *Tritomaria polita polymorpha*, *Cephalozia pleniceps*, and other taxa tolerating calcareous seepage, e.g., *Blepharostoma trichophyllum brevirete*, *Anastrophyllum minutum grandis*, *Riccardia sinuata*, and *C. bicuspidata;* on Nûk (70–2879) with *Aneura pinguis*, *R. sinuata*, *Odontoschisma macounii*, *Gymnocolea inflata*, and *C. pleniceps*. In such areas there may be a mere trace of calcareous seepage, judging from the presence of such usually oxylophytic helophytes as *Gymnocolea* and *C. bicuspidata*.

Usually, however, the species occurs in Ca-rich fens, then with *Cryptocolea imbricata*, *O. macounii*, *Lophozia heterocolpos*, *L. grandiretis*, *L. quadriloba*, *L. gillmani*, *A. pinguis*, and *R. sinuata* (66–0914a, Simiútap kûa). At Marrait it occurs with the Ca-demanding taxa *Metacalypogeia schusterana*, *L. gillmani*, and *Scapania cuspiduligera* in a rich, fenlike meadow traversed by small rills.

Arctic phenotypes are usually scorched (e.g., 70–2383) and may also bear some intense purplish pigmentation. Although perianths are not rare (in, e.g., 66–0908, 66–0914a), capsules are never developed in any Arctic phenotypes seen.

Greenland plants show some taxonomic peculiarities (e.g., suppression of antheridium formation so that the plants seem dioecious; see SCHUSTER 1969, p. 372). Also, perianths may become rigid and 4–5-stratose from the middle down (as in HOLMEN & STEERE 62.030), the walls then being 120–140 μ thick.

Lophozia (Leiocolea) gillmani (AUST.) SCHUST.

Distribution (Map 12)

2: Fortunebay (66–0142a). 7: Angûjârtûtit (70–2163). 12: Perdlertut (70–2690, 70–2710a). 13: Jens Vahls Dal (70–2633, 70–2635, 70–2638b, 70–2642, 70–2645, 70–2646, 70–2646a f. *orbiculata*, 70–2648, 70–2654, 70–2655, 70–2656, 70–2664). 14: Hareøen (70–2571, 70–2592c, 70–2594). 31: Anap nunâ (70–2400, 70–2401, 70–2402, 70–2403, 70–2436). 34: Marrait kangigdlît (66–0726a). 35: Hollænderbugt (66–1508a f. *orbiculata*). 39: Tasiussaq (66–1260). 40: Mârmorilik, head of the Fjord (66-1178, 66–1198). 42: Magdlak (66–1350, 66–1352a, 66–1356c, 66–1358, 66–1364, 66–1361, 66–1367, 66–1376). 45: Sagdliaruseq (66–1062). 48: Amitsup (66–0801). 51: Simiútap kûa, shore (66–0903, 66–0914f, 66–0916a).

Additional collections:

40: Mârmorilik, head of the Fjord (K.H. 16.098). 42: Magdlak (K.H. 15.756).

51: Simiútap kûa, shore (K.H. 16.311). 67: Asuk (M.P.P. July 1898). 128: Agatdalen (K.H. 13.968b).

Until recently this calciphilous species was known from only a very few stations in the Arctic, although restudy of much material has shown that a number of collections cited as "*Lophozia muelleri*" (= *L. collaris*) and "*L. bantriensis*" actually represents *L. gillmani*. Together with *L. heterocolpos*, it accounts for most collections of *Leiocolea* from Greenland. It has a very wide, imperfectly circumarctic-circumsubarctic range and reaches as far north as 82°30′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and 82°12′N. in North Greenland (SCHUSTER, 1969), while it extends south, as a relict of late Pleistocene times, to ravines in the Catskill Mts. of New York State and the east slope of the Berkshire Mts. in Massachusetts (SCHUSTER, l.c.). In West Greenland the species is widespread in the western basaltic regions, but eastward occurs wherever there are diabase dikes.

L. gillmani has a wide ecological range but usually occurs in moist to wet sites, sometimes in and near rich fens, at other times along cascading rills and streams. Associated then are *Aneura pinguis*, *Lophozia heterocolpos*, *L. rutheana*, *Cryptocolea imbricata*, *Blepharostoma trichophyllum brevirete*, *Scapania gymnostomophila* (occasionally *S. cuspiduligera*), and, rarely, *Metacalypogeia schusterana* (as at Marrait). In locally calcareous, wet, tundra meadows around tarns (as at Anap nunâ) or along small streams (Fortunebay), *L. grandiretis*, *Tritomaria polita polymorpha*, and *Odontoschisma macounii* may be associated. Occasionally on steep slopes, along drainage rills, where subject to minimal desiccation, it may occur with *Arnellia fennica*, *L. pellucida*, *L. polaris*, *L. quadriloba glareosa*, *L. heterocolpos harpanthoides*, and *Preissia quadrata*, mostly as a mod. *parvifolia*, often represented by the plant distinguished below as f. *orbiculata*.

L. gillmani, because of its relatively wide ecological tolerances, is found in several extremes which, on initial inspection, give the impression of representing distinct species. Particularly apt to cause difficulties are very small phenotypes, the size of *L. collaris*, which, however, are clearly paroecious. (See SCHUSTER l.c., pp. 379–84, and figs. 166–67, for a more detailed discussion). The following several extremes, however, represent taxonomic problems posed by more recent collections.

(1) The plants of 70–2401, growing in rich, fenlike depressions in an irrigated, low tundra slope, amidst *Cyrtomnium*, *Drepanocladus revolvens*, and other mosses, are critical. They are variable as to sexuality; some are paroecious, with ♂ bracts juxtaposed to ♀ bracts; others bear ♂ bracts some distance below the ♀ ones, several pairs of sterile leaves separating the two (a condition already noted in SCHUSTER, l.c., p. 379). A single shoot, however, was found with an intercalary androecium, succeeded

by many pairs of sterile leaves, with no evidence of a gynoecium distally. It is, of course, possible that after a considerable period of vegetative activity this shoot might have eventually developed a gynoecium. In practice, however, such seemingly purely androecial shoots (which SCHUSTER specifically noted, l.c., pp. 378–79, to be lacking in *L. gillmani*) cannot be separated from *L. bantriensis*. Furthermore, some plants of this collection, rather than having the concave leaves typical of *L. gillmani*, tend to have them convex (at least the dorsal half is so), typical of *L. bantriensis*. Also, the several paroecious individuals seen showed no evidence of fertilization—the perianths remaining juvenile and bearing 1–2 innovations beneath them. [Somewhat analogous plants occur along the "warm spring" in Disko Fjord (70–2163); these are clearly paroecious but there is no evidence of fertilization ever having taken place. The plants represent a warm brown "*bantriensis*-like" phenotype and occur with *Marchantia alpestris*].

The question naturally ensues: is the distinction between *L. bantriensis* and *L. gillmani*, which, in the final analysis, is between uni- vs. bisexual plants, actually valid? Accumulating evidence suggests that the distinction cannot be relied on, at least not in the Arctic. The cell distinctions usually cited are so "slight as to be unreliable" (SCHUSTER l.c., p. 391).

(2) By contrast, 70–2402 is a small, dense-leaved phase, mod. *densifolia-parvifolia-colorata-pachyderma*, with abundant fertilized gynoecia. Here ♂ bracts are usually juxtaposed to the ♀ ones. In such plants, associated with growth in a more exposed site, on soil in crevices along an exposed rivulet, we find a strong brownish pigmentation, the dry plants appearing fuscous except for the decolorate, blunt to rounded leaf lobes; cells in decolorate regions may have very coarse, nodose trigones.

v. *gillmani*, f. *orbiculata* SCHUST.

This represents the xeromorphic extreme of the species: small plants which have the aspect of a vigorous *L. badensis* "with which they share the broadly orbicular leaf form and sharp lobes" (SCHUSTER, 1969, p. 385). Subfloral leaves may lack antheridia, but the subfloral innovations are antheridial (and, at least in part, eventually gynoecial). The plants occur under more exposed conditions on steep, well-drained slopes formed by weathered, clayey soil mixed with rock fragments, usually along small drainage channels, mixed with *Distichium*, *Preissia*, *L. pellucida*, *Arnellia*, *Tritomaria scitula*, and *Solenostoma pumilum s.l.*

The f. *orbiculata* possibly should have been given a higher rank. As noted in the original discussion (SCHUSTER, l.c., p. 385) these "small, compact, warmly brown pigmented plants ... seem hardly reconcilable

with the *L. gillmani* complex but resemble, rather, a vigorous *L. badensis* ... or a small *L. collaris*." One of the smaller micropackets of the type, indeed, was originally sequestered as possibly *L. collaris* because of the frequent occurrence of unfertilized gynoecial plants without ♂ bracts below. We have also seen two axes with intercalary androecia. These are exceptional, however, and on one gynoecial shoot, which lacked a subtending androecium, the subfloral innovation was androecial (and, ultimately, terminally, gynoecial). Most of the better-developed plants were demonstrably paroecious, with 1–2-androus ♂ bracts that were quite ventricose at the base.

We have repeatedly seen lateral-terminal branches in f. *orbiculata* which were clearly of the *Radula* type, issuing smoothly posterior to a normal leaf. Branching in *Leiocolea* is most frequently lateral-intercalary (see SCHUSTER, l.c.), with *Frullania*-type branches present in *L. heterocolpos*. It is evident that three branch types therefore occur in *Leiocolea*.

Occasional extremes of f. *orbiculata* are virtually impossible to place without careful dissection of fertile shoot tips. Thus, on steep, well-drained calcareous slopes, highly reduced plants, which are so small as to almost defy recognition, may occur mixed with (as e.g., in 70–2646, 70–2646a) *Arnellia fennica*, *Lophozia heterocolpos harpanthoides*, *Lophozia quadriloba glareosa*, and *Tritomaria scitula*. Their leaves may be a maximum of 1000×1085 μ wide×long (if the decurrent bases are included, somewhat longer, then clearly longer than broad), but often only half that size, antically assurgent and quite concave and imbricate, or else almost flat; exposed shoot tips may be dull brownish or purplish brown. Recognition of such plants depends on finding paroecious inflorescences (fortunately almost always easily possible, the species being almost always fertile), and on the leaf cells. Even in the highly reduced plants cited, marginal lobe cells may average 33–37 μ and median cells 28–33×35–45 μ. Such small phases usually have sharp or even apiculate leaf lobes, sometimes with 2, rarely 3, cells at the lobe tips. In juxtaposed patches even more extremely reduced, almost julaceous, fleshy, brittle phenotypes occur which correspond to the ultimate degree of reduction achieved. Here leaves may be broadly ovate-rotundate, 850 μ wide×620 μ long or smaller, with a lunate sinus and sharp lobes. Leaf margins, especially of upper leaves and of the bracts, may be narrowly to broadly purplish tinted. Unless the paroecious inflorescences can be determined, such extremes are hardly certainly identifiable.

Lophozia gillmani v. *ciliolata* SCHUST.

Distribution (Map 12)

51: Simiútap kûa, shore (66–0918).

This plant represents the ultimate extreme of *L. gillmani:* it has

unusually large cells with many (to 7–10) oil-bodies per cell and a distinctly ciliolate perianth mouth (see fig. 166:1–6 in SCHUSTER, 1969); the leaf and bract lobes are usually diagnostically rounded to blunt.

The type material occurred with *L. heterocolpos* in a rich calcareous fen surrounding a shallow lake; intermingled were sterile plants approaching *L. bantriensis*.

Lophozia bantriensis (HOOK.) STEPH.

Distribution

50: Simiútap kûa, valley (66–0918 p.p.; questionable). 110: Ikorfat (K.H. 62–1574; questionable).

All reports of this species from the American Arctic must be regarded as questionable, including the above two reports (from SCHUSTER, 1969). The species differs from *L. gillmani* essentially only in the dioecious inflorescences. We have commented elsewhere (pp. 35–36) about the tendency, in Arctic populations of several taxa (e.g., *Solenostoma pumilum*, *L. latifolia*), for anomalous variations in sexuality due usually to partial or whole suppression of antheridium formation in some Arctic populations of paroecious species. No evidence of paroecious inflorescences could be found in the two collections cited, although 66–0918 occurs mixed with the paroecious *L. gillmani ciliolata*.

It should be noted that in typical European *L. bantriensis* (e.g., RMS 72–401, Honnister Pass, Cumberland, England) the androecia are always intercalary and the ♂ bracts never bear a tooth of the antical base. Although *L. gillmani* tends to be variable with respect to the ♂ bracts, one normally finds an antical tooth. This distinction is apparently not an absolute one since MÜLLER (1951–58) states that *L. bantriensis* may have a large tooth of the antical base of the ♂ bracts.

Lophozia collaris (NEES) DUMORT.

L. muelleri (NEES) DUMORT. of the older literature; in SCHUSTER (1969, p. 393) it is shown that this name cannot be retained and the combination *L. collaris* (NEES) SCHUST. is used; it was overlooked, however, that DUMORTIER (1835) had already made this combination.

Distribution (Map 13)

31: Anap nunâ (70–2403, 70–2422). 40: Mârmorilik, head of the Fjord (66–1178, 66–1198). 51: Simiútap kûa, shore (66–0901).

Additional collections:

41: Mârmorilik, mouth of the Fjord (K.H. 13.729). 42: Magdlak (K.H. 15.756). 138: Itivneq (K.H. 14.864).

The two collections from Anap nunâ are critical; they are clearly dioecious and androecial shoots similar to those figured in SCHUSTER

(1969, fig. 169:5) could be found, with the bracts only slightly laxer. The leaves are often narrowly bilobed, with a shallow sinus and the lobes not widely spaced—a feature often found in *L. badensis*. As in the latter, the plants are small (sterile shoots to 1 mm wide), but the following constellation of features, however, indicates *L. collaris:* conspicuous trigones, exactly as in fig. 169:1,3 in SCHUSTER (l.c.); cells in the lobes averaging no more than 24–30 μ and in leaf middle 24–30 μ wide; cuticle of leaves delicately verrucose distally and striolate below; small lanceolate underleaves, often only a filiform, 1–2-seriate appendage with slime papillae, are distinct at the shoot tips of sterile plants.

The same constellation of features recurs in 66–1178, 66–1198 (Mârmorilik); the plants have exactly the size and aspect of *L. badensis:* the subrotund leaves of that taxon, with arched margins and the dull purplish color of the perianth apices often seen in Arctic forms of *L. badensis*. But here and there, small underleaves occur; the cells are only 27–30 × 22–25 μ in the lobes and 23–28 × 23–26 μ in the leaf middle; trigones are coarse and often bulging; the cuticle is weakly striolate in at least the leaf bases. It is possible that plants with this constellation of features should be segregated as an Arctic variant of *L. collaris*, but study of longer series of specimens is needed. All collections from our area referred here have very rotund leaves with triangular, shallow and approximated lobes (sinus width rather consistently 0.2–0.25 the leaf width, usually rectangulate, descending to 0.25 the leaf length only).

The problems in distinguishing Arctic phases of *L. collaris* and *L. badensis* have already been touched upon in SCHUSTER (l.c., p. 397, footnote 70). The present plants clearly illustrate these problems.

L. collaris, although rather frequently reported from the American Arctic, seems to be actually a rare species there. It is known from as far north as 82°31′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and 82°14′ N. in North Greenland (SCHUSTER, 1969), but becomes very rare in eastern North America south of the Canadian border (reported only from Minnesota and Vermont). American plants often fail to correspond closely to the "typical" temperate-zone, European phenotypes. As with many other Arctic populations, deviant traits (e.g., fuscous to blackish pigmentation of the leaf lobes) frequently occur.

In the Arctic *L. collaris* is at times very difficult to separate from gemma-free, shade extremes of *L. heterocolpos*. Indeed, in our opinion there is no single reliable character that will separate the mod. *viridis* of these two taxa when gemmae are absent. On the other hand, forms of *L. badensis*, at least in the Arctic, may develop vestigial underleaves (see SCHUSTER, l.c.) and are then almost inseparable from *L. collaris*.

The species, like other *Leiocoleae*, occurs in basic sites, sometimes on rich basic humus, with *L. gillmani*, *L. heterocolpos*, *L. grandiretis*, *Pelto-*

lepis, *Sauteria*, *Tritomaria polita polymorpha*, and *Arnellia fennica*, but has not been collected in the basalt region. In relatively mesic niches, on humus over basic sites, the plants may be mixed with *Mnium*, *L. gillmani*, *Blepharostoma trichophyllum brevirete*, and other taxa. Here it is at once distinct from *L. gillmani* in the inferior size, the dioecious inflorescences, and the smaller, often remote, subrotund leaves. The *L. collaris* in such sites (e.g., 66–1178) may develop some deep purple pigmentation of the perianth apices; in admixed *L. gillmani* secondary pigments are lacking, or, rarely, pale fuscous.

Lophozia (Leiocolea) heterocolpos (THED.) HOWE

Distribution (Map 14)

1A: Behind Arctic Station (66–0146, 66–0150b, 66–0155, 66–0162b, 66–0163a, 66–0165, 66–0166, 66–0176, 66–0287, 70–2021, 70–2026, 70–2028, 70–2038). 1B: Lyngmarken (66–0342, 66–0562, 70–2023). 1D: Skarvefjeld (66–0231, 66–0306, 66–0309a, 66–0314a, 66–0320b). 2: Fortunebay (66–0135, 66–0141, 66–0143b, 66–0147, 66–0213). 6: Eqalúnguit (70–2213, 70–2223 mod. *rufescens*, 70–2238a, 70–2239, 70–2242b, 70–2247a). 7: Angûjârtûtit (70–2157b, 70–2160, 70–2161, 70–2174, 70–2176a, 70–2181). 8: Kuánerssuit (70–2126, 70–2127, 70–2130, 70–2131, 70–2136, 70–2139, 70–2140, 70–2148, 70–2151, 70–2154, 70–2155, 70–2156). 9: Eqaluit (70–2524, 70–2527, 70–2528a). 10: Enoks Havn (70–2771). 11: Qasigíssat (70–2726, 70–2730, 70–2736). 12: Perdlertut (70–2671, 70–2674, 70–2680, 70–2681, 70–2683, 70–2685, 70–2690, 70–2695, 70–2703). 13: Jens Vahls Dal (70–2635, 70–2636, 70–2639, 70–2640, 70–2649, 70–2650, 70–2654, 70–2655, 70–2656, 70–2658, 70–2659, 70–2660, 70–2665, 70–2667). 14: Hareøen (70–2576, 70–2583, 70–2589, 70–2590, 70–2591, 70–2593a, 70–2594, 70–2596, 70–2598, 70–2605, 70–2609, 70–2610, 70–2621, 70–2622). 17: Tupilak (66–0034). 18: Grønne Ejland (70–2811a). 21: Umiasugssûp (70–2945). 25: Sarfaq (70–2359). 26: Pâkitsup ilordlia (70–2258b, 70–2299, 70–2302, 70–2304, 70–2308, 70–2384). 30: Eqe (66–0295a, 66–0339). 31: Anap nunâ (70–2407a, 70–2408a, 70–2412a, 70–2424, 70–2427, 70–2431, 70–2435). 38: Uvkusigssat (66–1391, 66–1390, 66–1385). 39: Tasiussaq, (66–1260, 66–1262). 40: Mârmorilik, head of the Fjord (66–1206b, 66–1204, 66–1205, 66–1207). 42: Magdlak (66–1356 66–1358a). 45: Sagdliaruseq (66–1076). 48: Amitsup (66–0788, 66–0801). 49: Skalø (66–1006, 66–1007, 66–1010, 66–1013, 66–1015, 66–1016, 66–1018, 66–1020). 51: Simiútap kûa, shore (66–0914b, 66–0915a, 66–0918, 66–1642).

Additional collections:

1: Godhavn (S.B. Sept. 1870, J. LAGERKRANZ 1934–36). 7: Angûjârtûtit (L.H. Aug. 1932). 8: Kuánerssuit (M.P.P. 2520). 12: Perdlertut (K.H. & W.C.S. 62.1439). 24: Jakobshavn (S.B. 1870). 40: Mârmorilik, head of the Fjord (K.H. 16.009). 43: Kangerdlugssuakavsak (K.H. 14.850). 65: Ûnartuarssuk (M.P.P. 114). 71: Nagerdloq (M.P.P. 782). 88: Christianshåb (K.H. 16.675a). 92: Claushavn (S.B. Aug. 1870). 96: Qeqertaq (S.B. 1870). 98: Sarqaq (J.V. 247c). 100: Ipeqarfiunge (L.H. July 1932). 106: Nûgssuaq (K.H. 15.635). 110: Ikorfat (K.H. 62.1574d). 133: Tupersuatsiait (K.H. 14.882). 142: Niaqornánguaq (K.H. 16.755). 143: Kangerdlugssuaq (K.H 16-385c). 144: Igdlorssuit (K.H. & W.C.S. July 1962).

L. heterocolpos is perhaps the most frequent and tolerant of the "*Leiocolea* species" in Greenland and the one most often found in only

feebly basic sites. It occurs from 83°06′ N. in Greenland and from 82°26′ N. in Ellesmere Island southward to New England and New York, in eastern North America.

With a wide ecological range, it may occur in crevices of basalt, with *Tritomaria scitula*, *Scapania gymnostomophila* (and sometimes *S. ligulifolia*), or on peaty soil in rich, calcareous fens (then with *Cryptocolea imbricata*, *Lophozia quadriloba*, *L. rutheana*, *L. grandiretis*, *T. scitula*, *S. cuspiduligera*, *Odontoschisma macounii*, and *Aneura pinguis*), or on rather well-drained, weathered calcareous, clay-stone fragment slopes (with *L. quadriloba*, *Arnellia fennica*, *Anthelia*, *S. ligulifolia*, *S. cuspiduligera*, *Solenostoma pumilum polaris;* then often as var. *harpanthoides*). It is often frequent along rills [as, e.g., along the "warm spring" in Disko Fjord (70–2157b), or at Lyngmarksfjeld, along a small rill, with *S. curta*, *Cephalozia pleniceps*, and *N. geoscyphus*]. Other frequent associates are *Cryptocolea imbricata*, *Pleuroclada albescens*, *Solenostoma pumilum*, *L. polaris*, *L. grandiretis*, *L. gillmani*, and *Plagiochila asplenioides*—all taxa that are at least Ca-tolerant. *L. heterocolpos* frequently produces sex organs and perianths and capsules are not rare (as early as July 5, in 70–2026; as late as July 27, in 66–0311). It is the only regional species of the subgenus that freely produces spores.

L. heterocolpos usually develops gemmae and is then readily separated from all other *Leiocoleae*, which are uniformly devoid of them. In rare instances, when no gemmae are present, confusion with *L. collaris* is possible. Associated with its abundance and ability to invade a rather wide range of sites in the Arctic is its variability; some of the variation is dealt with in SCHUSTER (l.c., p. 404).

Particularly confusing are extremes with strong reddish to purplish pigmentation of the distal portions of shoots; such mod. *rufescens* (of which 70–2223c is a good example) may have served as the basis for "*Leiocolea arctica* S. Arn." which ARNELL (1950) stated had cells larger than in ordinary *L. heterocolpos*. In the latter, median cells are ca. 22–25 × (21)25–30(32) μ, while in the reddish plants of 70–2223c they are 23–29 × 23–35 μ. In 66–0789, in which the plants are intensely purplish red to reddish not only above but often far down the shoots, median cells are 29–34 μ wide × 30–33 μ long. This corresponds well with the cell size attributed to *L. heterocolpos* var. *harpanthoides* (sensu ARNELL, 1956 = *Leiocolea arctica* ARN. = *L. heterocolpos* var. *arctica* MÅRTENSSON). Such plants not only have somewhat larger cells, but appear to be polyploid [ARNELL (l.c.) states they possess 16 chromosomes]; they also tend to have occasional trilobate leaves. A distinct genotype seems to be at hand, as follows:

v. *arctica* (ARN.) SCHUST. & DAMSHOLT, comb. n.
Leiocolea arctica S. Arn., Sv. Bot. Tidskr. 44: 374, 1950.

Leiocolea heterocolpos v. *arctica* O. MÅRTENSSON, Bryophytes of the Torneträsk Area I:43, 1956.

Leiocolea heterocolpos v. *harpanthoides* SCHUST. ex ARN., Illus. Moss. Fl. Fennosc. 1:112, 1956 (not *L. harpanthoides* BRYHN & KAAL.).

Leiocolea heterocolpos v. *savicziae* SCHLJAKOV, Variet. duae Nov. Mag. Hepat. Akad. Sci. URSS, (Nov. Syst. Plant. Non. Vasc. 1971 vol. 8, pp. 327–32).

Distribution (Map 14)

48: Amitsup (66–0789, 66–0815).

Plants similar to this variant are illustrated in SCHLJAKOV (1971) as var. *savicziae*, supposedly differing from var. *arctica* in even larger cells [median cells (26)28–38(40)×26–44 μ]; his plant is also described as with sporadic trilobed leaves—but such also occur in 66–0789. However, the larger-celled Greenland plants, as is noted above, have median cells only 29–34×30–33 μ; they are also ± reddish, often strongly so—without conspicuous brownish pigments. By contrast, the Schljakov material is described as "viridis vel saepius plus minusve fusca"—a coloration more typical of var. *heterocolpos*. Clearly, in the Arctic *L. heterocolpos s.l.* becomes exceedingly plastic. It is probable that all the Arctic, large-celled types should be recognized as a single variety, as we have done above.

It is not impossible that the var. *arctica* may eventually need re-evaluation to a higher status than now given it—possibly to an Arctic subspecies of *L. heterocolpos*. In one of our collections (66–0815) both var. *heterocolpos* and var. *arctica* occur admixed and are at once distinct under the dissecting microscope, as follows:

	v. *heterocolpos*	v. *arctica*
Leaf color	Pale tawny brown	Intensely vinaceous distally
Gemmae	Abundant on slender shoot tips	Lacking
Oil-bodies per cell	2–4(5) per median cell	Variable: (4)5–9, rarely to 10–16 per median cell
Marginal cells in lobes	16–24μ	25–32μ
Median cells	21–26×18–23μ long	(26)29–33×22–33μ long
Cuticle	Distinctly roughened	Virtually smooth

If the distinctions prove as impressive and as constant as the above table implies, the var. *arctica* probably should be "elevated" to at least subspecies status. Complicating the taxonomic situation is the fact that the type material of *L. arctica* S. ARN. is figured by ARNELL (1950, fig.

2:d) as with 3–7 oil-bodies per cell and described as with 3–5 oil-bodies per cell. This is clearly less than in the plants of 66–0815.

At the opposite pole fall plants which are much less certainly genotypically distinct; they have somewhat smaller cells than var. *heterocolpos*, tend to bear deep castaneous pigmentation, often have rounded-lobed leaves. These constitute:

v. *harpanthoides* (BRYHN & KAAL.) SCHUST.

Distribution (Map 14)

1A: Behind Arctic Station (66–0161, 66–0170, 66–0173, 66–0179a, 66–0182, 66–0271). 1B: Lyngmarken (66–0568). 1D: Skarvefjeld (66–0311). 11: Qasigíssat (70–2744a). 12: Perdlertut (70–2670, 70–2693a). 13: Jens Vahls Dal (70–2637a, 70–2644a, 70–2645, 70–2646e, 70–2663). 14: Hareøen (70–2608b). 30: Eqe (66–0289). 42: Magdlak (66–1352). 51: Simiútap kûa, shore (66–0916b), 66–0919).

Additional collections:

99: Sarqaq valley (K.J. 241c).

The var. *harpanthoides* is confined to the most exposed sites, most subject to desiccation. A frequent habitat is over steep, exposed, Ca-rich clay-stone slopes where intermittent desiccation takes place. Associated then, regionally, are *L. pellucida*, *L. gillmani*, *L. grandiretis*, *L. quadriloba*, *Arnellia fennica*, *Scapania ligulifolia* (less often *S. gymnostomophila* or *S. cuspiduligera*), and *Solenostoma pumilum polaris*. It is not impossible that a mere extreme ecotype is at hand, which (associated with the exposed site) has more collenchymatous and appreciably smaller cells [those of the leaf tips are (13)14–19 μ; those of the leaf middle may average as small as 17–22×19–22 μ]. Leaves are usually only 0.15–0.2 bilobed, with more obtuse to crescentic sinuses than in var. *heterocolpos* and often with rounded to blunt leaf lobes. None of these distinctions is absolute. Also associated with the exposed sites, deep chestnut-brown pigmentation and, distally at least, some red pigments are usually present. Intermediate (in having reddish pigments with usually some strong brownish pigments) are plants from Tupilak (66–0034) and Disko (70–2744a).

Lophozia (Leiocolea) badensis (GOTT. ex GOTT. & RABENH.) SCHIFFN.

Distribution (Map 13)

12: Perdlertut (70–2682). 35: Hollænderbugt (66–1512, 66–1519, 66–1520). 42: Magdlak (66–1357c). 50: Simiútap kûa, shore (66–0826).

Found from the high Arctic, at 82°40′ N. in Peary Land and 82°26′ N. in Ellesmere Island (SCHUSTER, 1969), south to 36° N. in eastern United States. It is the dominant *Leiocolea* in the deciduous forest formation of eastern North America, often found in calcareous shale and sandstone

ravines, in damp rock crevices, with *Gymnostomum*, *Rhabdoweisia*, and other calciphilous mosses. By contrast, it is distinctly rare in Greenland, where it seems confined (in West Greenland) to basalt regions; it occurs over creviced, moist rocks near cascades, associated with *Mannia pilosa*, *Preissia quadrata*, *Sauteria alpina*, *Tritomaria scitula*, *Scapania cuspiduligera*, *S. gymnostomophila*, *L. quadriloba*, and *Solenostoma pumilum polaris* (66–1357c) and also in damp, run-off crevices of fast-drying, clay-shale slopes, associated with *L. pellucida* and *Cephaloziella* (cf. *grimsulana* in 66–1512, 66–1520).

Plants of 70–2682—like all collections from the Arctic—are critical insofar as they tend to show a mixture of "*badensis*" and "*collaris*" characters. Size (sterile shoots are only 369–920 μ wide; perianths are ca. 550 μ in diam. × 1000 μ long) is that of the smallest phenotypes of *L. badensis*. As in that species, the cuticle is smooth or virtually so and trigones are usually very small or minute. Underleaves may be represented by a single cell terminated by a slime papilla, or by two such juxtaposed structures—a situation not infrequent in typical *L. badensis*. Occasionally, however, a small, lanceolate rudimentary underleaf, formed of 4 cells (2 basal, side by side, with 2 single cells superposed) occurs, suggesting weak forms of *L. collaris*. Cell size, too, is ambiguous: marginal and subapical cells range from 24–30 to 28–35 μ, depending on the plant studied. The smaller than normal cell size may reflect the difficult habitats: steep, exposed slopes subject to intermittent desiccation where the plants may grow as scattered stems amidst tufts of *Distichium capillaceum* and other mosses.

Typical *L. badensis*, which has smaller leaf and stem cells and fewer oil-bodies [(2)3–6 per median cell, in 66–1520], occurs with a larger-celled form, as follows:

v. *apiculata* Schust.

Distribution (Map 13)

14: Hareøen (70–2580). 35: Hollænderbugt (66–1518).

Found on well-drained, fast-drying calcareous, clayey soils derived from sedimentary rocks, where it is limited to sheltered sites, such as run-off crevices. Associated are *Arnellia fennica*, *L. pellucida*, and *Distichium capillaceum*. The type material (66–1518) has mostly apiculate leaf lobes, with the large, pellucid marginal cells often rather projecting (hence the leaf margins may be noticeably crenulate). In plants of 70–2580, although cells are almost similarly large [cortical cells average 31–36 μ wide; cells in leaf lobes 28–39×35–38(40) μ; median cells 32–43×31–39 μ] and the trigones are small, the cuticle smooth—much as in the type—the leaf lobes are typically blunt to rounded. It is possible that this is a polyploid

phenotype, of difficult sites; the presence of mostly 6–10 oil-bodies per median leaf cells (see fig. 172:7, in SCHUSTER, 1969) is suggestive.

Subg. ***Protolophozia*** SCHUST.

Lophozia elongata (LINDB.) STEPH. (Fig. 3: 13–15)

Distribution (Map 11)

6: Eqalúnguit (70–2227).

This extraordinarily rare species has been collected but a single time, almost a century ago, in Norway by LINDBERG, although reported from Sweden and Yugoslavia (these reports need verification). A single Greenland report (JENSEN, 1906) is *L. quadriloba* (SCHUSTER, 1969).[1])

The present plants, from a gently north-sloping, irrigated, rich peaty slope below basalt cliffs, occurred admixed with *Pleuroclada albescens*, *Blepharostoma trichophyllum brevirete*, *L. heterocolpos*, *L. ventricosa confusa*, *L. grandiretis* v. *parviretis*, *L. latifolia*, *Riccardia* cf. *sinuata*, *Anastrophyllum minutum*, and other species. The plants, erect in growth (probably owing to crowding) stood out because of the clear, rather deep green color and somewhat shiny texture. Perianths (and androecia below them) were readily evident. Stem anatomy and the polymorphous leaf form, with deeply bifid leaves, all clearly match the type, as illustrated in SCHUSTER (l.c.). In particular, the rather soft stem, without a well-defined cortex but with a homogeneous medulla devoid of the brownish fungal infection normal to subg. *Lophozia* is notable; stem anatomy exactly matches that portrayed in Fig. 175:7 in SCHUSTER (1969). In the abundant material at hand, only one distinctive feature, vis à vis the type, stood out: somewhat more polymorphous leaves, occasionally trifid—and even one quadrifid leaf was seen; the sinuses were frequently rather deeper, extending to 0.35–0.45 the leaf length.

L. elongata has had a checkered taxonomic history. STEPHANI considered it as hardly distinct from *L. ventricosa;* EVANS (in BUCH, EVANS & VERDOORN, 1938) placed it into the genus *Orthocaulis;* MÜLLER (1951–58) placed it as a synonym of *L. excisa.* Thus it has been placed either in what here corresponds to *Lophozia* subg. *Orthocaulis*, or in subg. *Lophozia.*

It was finally assigned to *Lophozia* subg. *Massula* K. MÜLL. (SCHUSTER, 1969), because of the homogeneous stem medulla, the hardly collenchymatous and rather large and pellucid cells with a smooth cuticle, the rather polymorphous leaves, and other features, SCHUSTER (l.c.) stating that "unless the oil-bodies demonstrate a lack of logic in this disposition" the species fitted best into *Massula.* In living plants the oil-bodies are

[1]) Many recent reports by LADYZHENSKAJA & ZHUKOVA (1971) appear based on erroneous determinations, judging from both text and figures of gemmiparous plants.

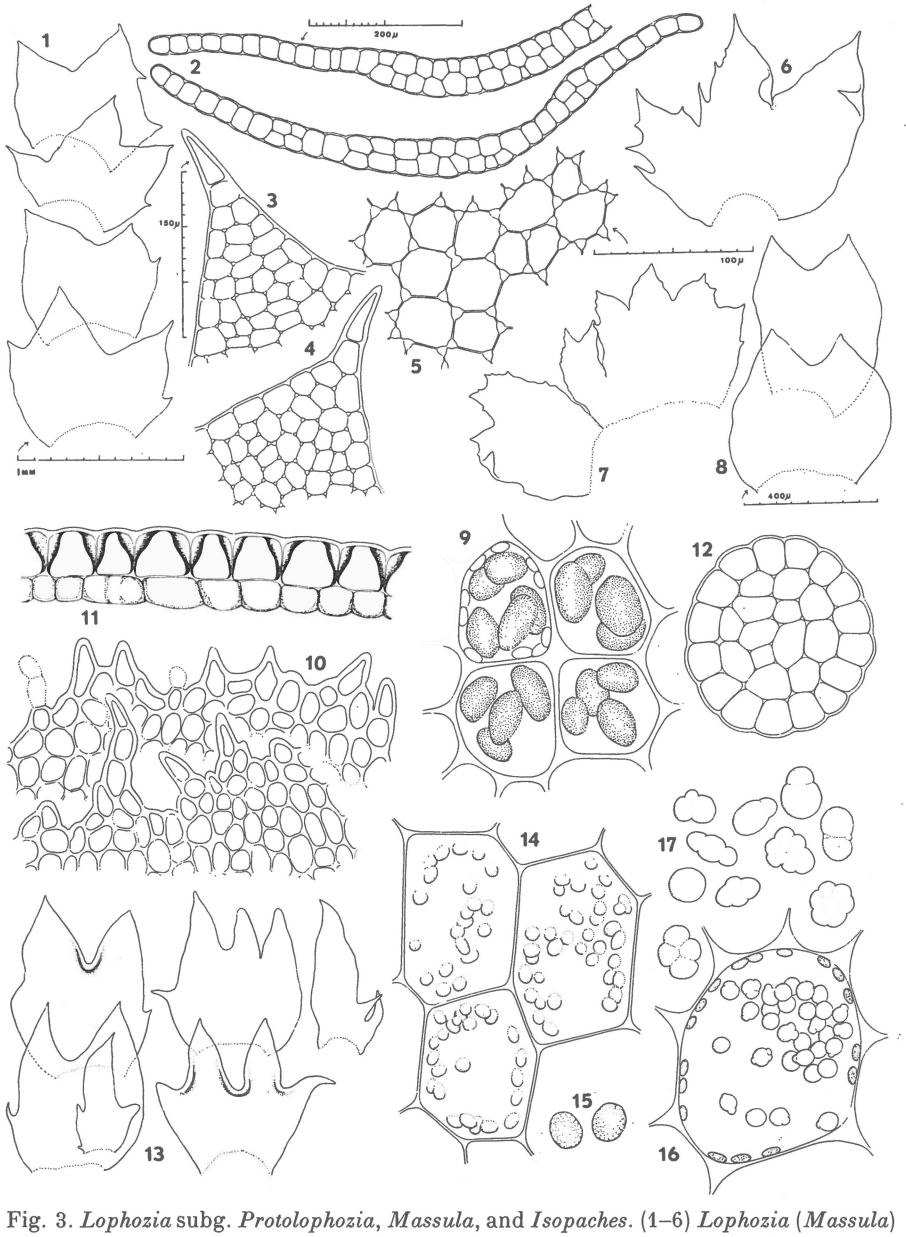


Fig. 3. *Lophozia* subg. *Protolophozia*, *Massula*, and *Isopaches*. (1–6) *Lophozia* (*Massula*) *incisa*. (1) Leaves (×22). (2) Cross sections of leaf bases (×100). (3,4) Leaf lobe apices (×145). (5) Median cells (×210). (6) Gynoecial bract (×22). (7–12) *Lophozia* (*Isopaches*) *alboviridis*. (7) Bracts and, between them, bracteole (×22). (8) Leaves (×44.5). (9) Cells with oil-bodies and, upper left, chloroplasts (×650). (10) Two sectors of perianth mouth (×210). (11) Capsule wall cross section (×362). (12) Seta cross section (×96). (13–15) *Lophozia* (*Protolophozia*) *elongata*. (13) Leaves and two underleaves from sterile shoot (×22). (14) Cells, leaf middle, with oil-bodies (×605). (15) Individual oil-bodies (×1000). (16–17) *Lophozia* (*Massula*) *grandiretis*. (16) Median cell with oil-bodies and chloroplasts (×500). (17) Oil-bodies (×800). [All from West Greenland material; 1–6, 70–3118d; 7–12, 70–2448a; 13–15, 70–2227; 16–17, 70–2877; 1, 6, 7, 13, drawn to 1 mm scale; 2, drawn to 200 μ scale; 3, 4, drawn to 150 μ scale; 5, 10, drawn to 100 μ scale; 8, drawn to 400 μ scale].

minute (2.8×3.5 μ to 3×3–4 μ up to 4×4.5 μ, thus hardly larger than the chloroplasts), appear homogeneous (although under oil immersion they are seen to be obscurely and finely granular botryoidal, with a smooth surface), are colorless and many per cell, usually 20–38, occasionally 40–42. These oil-body features are typical of *Massula*, hence demonstrate that the species more fittingly belongs there than in *Orthocaulis* or *Lophozia s.str.* The monoecious inflorescences, the polymorphous leaves, their deep sinuses, and distinct underleaves, at least towards larger shoot tips, however, suggest an even closer affinity to subg. *Protolophozia* SCHUST. of the Antipodes (see SCHUSTER, 1968).

Only lateral-intercalary branches were seen in *L. elongata*, whereas terminal, *Frullania*-type branching is common in *Massula*. This strongly suggests that *L. elongata* is perhaps closer to *Protolophozia*, a subgenus stated to have "mostly lateral-intercalary branches" (SCHUSTER, 1969, p. 258). The numerous small, spherical or subspherical oil-bodies in *L. elongata* can be matched with those found in several species of *Protolophozia*. As a consequence we are convinced that a good case can be made for placing this species in *Protolophozia* rather than in *Massula*.

The Greenland collection was abundantly supplied with (mostly yet immature) capsules; the 3–4-stratose capsule wall, with an epidermal layer 14–19 μ high, is 45–50 μ thick. Epidermal cells are short-oblong and bear, mostly on longitudinal walls, few and strong brown "nodular" (I-shaped, vertical) thickenings. Inner cells are much narrower and strongly elongated, ca. 12–13.5 μ wide, with numerous, rather close, almost always tangentially complete and well-defined semiannular bands. Spores are brownish and 12.5–14.5 μ, twice the diameter of the closely bispiral elaters, which are 6–7 μ in diameter. The seta is formed of ca. 18 rows of epidermal cells, similar or rather larger in diameter to the internal cells, which are in two concentric circles of 4 and 12 rows (but suppression of 1 or 2 divisions, or development of 1 or 2 accessory divisions, often occurred, so that these figures represent an approximation).

Greenland material, like the type material, is devoid of gemmae, a notable feature for a species of the *Massula-Protolophozia* complex, which normally develops gemmae. However, within *Protolophozia* several taxa are gemma-free, e.g., *L. crispata* SCHUST. of Fuegia and *L. nivicola* SCHUST. of New Zealand, whereas all known species of *Massula* bear gemmae.

Subg. ***Massula*** K. MÜLL. emend. SCHUST.

Lophozia incisa (SCHRAD.) DUMORT. (Fig. 3: 1–6)

Distribution (Map 15)

22: Orpigsôq (70–3118d).

Additional collections:

53: Søndre Strømfjord (K.H. 3113c). 85: Sarpiussat (L.H. Aug. 1932).

L. incisa is a species of acidic areas (very rarely over peaty ground on basalt; see SCHUSTER, 1969), which seems quite intolerant of Ca-rich sites. The plants of 70–3118d are from exposed, windswept, cliff faces, thinly soil-covered, on high, NE. facing gneiss hills; associated were *Prasanthus suecicus*, *Gymnomitrion corallioides*, *Anthelia*, *Tritomaria quinquedentata*, and *Anastrophyllum minutum;* the site is probably rarely snow covered for any length of time, even in winter.

♀ Bracts in 70–3118d are simpler than in some "normal" *L. incisa* and are no more complex than the subinvolucral bracts figured for *L. incisa* by SCHUSTER (l.c., fig. 178:3–4); leaves are not or little broader and hardly more complex than shown in fig. 178:9, and leaf lobe apices may be as cuspidate as shown in fig. 178:7–8, although usually less so. Leaves towards the base are bistratose (Fig. 3:2); they are more deeply 2–3-fid than is normal in *L. opacifolia*, with triangular lobes, usually longer than broad, and often ending in 1–2-celled cusps (Fig. 3:3–4). Cells are quite conspicuously collenchymatous, corresponding to var. *inermis* K. MÜLL., a plant perhaps better reduced to the status of a mere *forma.*

Size, ecology, and morphology all place these plants in *L. incisa* rather than in *L. opacifolia*—an abundant taxon in the basaltic region of West Greenland but absent, or nearly so, from the igneous zone.

Lophozia opacifolia CULMANN

Distribution (Map 15)

1A: Behind Arctic Station (66–0176, 66–0271). 1B: Lyngmarken (66–0567). 1D: Skarvefjeld (66–0314, 66–0567). 4: Flakkerhuk (66–0173). 7: Angûjârtûtit (70–2167, 70–2169). 8: Kuánerssuit (70–2137). 9: Eqaluit (70–2527). 11: Qasigíssat (70–2737). 12: Perdlertut (70–2690). 13: Jens Vahls Dal (70–2636, 70–2644c, 70–2649, 70–2652, 70–2654). 14: Hareøen (70–2576, 70–2578, 70–2583, 70–2601, 70–2614). 18: Grønne Ejland (70–2816d). 19: Nûk (70–2836a, 70–2877c, 70–2885). 26: Pâkitsup ilordlia (70–2308). 31: Anap nunâ (70–2412, 70–2434). 32: Qôrorssuaq (70–2476a, 70–2453a, 70–2484c). 46: Qalatôq (66–1140). 48: Amitsup (66–0788). 53: Søndre Strømfjord (66–0076a, 66–0097).

Additional collections:

8: Kuánerssuit (M.P.P. 1407). 16: Manîtsoq (W. & H. July 1884). 58: Itivneq kitdleq (M.P.P. 2398). 65: Ûnartuarssuk (M.P.P. 667). 90: Tasiussaq (S.B. 1870). 103: Qapiortoq kitdleq (K.J. 1043a). 129: Agatdalen (K.H. 13.968).

L. opacifolia is a very close ally of *L. incisa* and an excellent case could be made for treating it as an Arctic-alpine subspecies of the latter. Impoverished sterile plants of *L. opacifolia* "mimic" *L. incisa.* The species was unknown from the western hemisphere until reported from 82° 25′N. in Ellesmere Island (SCHUSTER *et al.*, 1959)—the northernmost report; southward it extends to Labrador, where it exhibits transitions to *L. incisa* (SCHUSTER, 1969). In Greenland it is known north to 77° 30–40′N. in Inglefield Bredning (SCHUSTER l.c.).

Although very close to *L. incisa*, *L. opacifolia* appears to have a slightly more distinct toleration for subbasic conditions, often occurring with *L. heterocolpos* (and its var. *harpanthoides*) and *L. grandiretis*, two taxa typical of peaty ground over basic rocks. Other common associates, on organic soils over Ca-rich, irrigated slopes, are *L. polaris*, *L. quadriloba*, *L. gillmani*, *Cephalozia pleniceps*, *Tritomaria scitula*, *Blepharostoma trichophyllum brevirete*, occasionally *Scapania cuspiduligera*, *S. curta*, *Tritomaria quinquedentata*, *T. polita polymorpha* and—occasionally—*L. hatcheri*. On low, wet, peaty ground over apparently nonbasic rocks as on the Grønne Ejland, (70–2816 d), associated with *Cephalozia lunulifolia*, *C. leucantha*, *Calypogeia neesiana*, *C. sphagnicola*, *Anastrophyllum minutum*, *A. sphenoloboides*, and *Mylia anomala*. The species also occurs in helophytic sites, around tarns and small lakes, in rich moss-tundra, as at Flakkerhuk (66–0173) on low, wet sandy-peaty flats, associated with *L. polaris*, *L. hatcheri*, *L. excisa*, and over locally feebly Ca-enriched, wet tarn margins, as at Nûk (70–2885, –2877 c), associated with *Calypogeia sphagnicola*, *L. polaris sphagnorum*, *L. ventricosa silvicola*, *Cephaloziella subdentata*, *L. binsteadii*, *Cephalozia pleniceps*, *C. bicuspidata*, *Mylia*, and *Riccardia sinuata*—all taxa of helophytic sites. It is rare on peaty soil over rocks along acid rills (as at Qôrorssuaq), with *Marsupella boeckii*, *L. alpestris*, *Anthelia*, and *Gymnomitrion concinnatum*.

Although unisexual, the species often develops capsules (July 10, 23, and Aug. 9), and usually has perianths.

The problems associated with recognition of this taxon as a separate species from *L. incisa* are outlined on p. 455 in SCHUSTER (l. c.). When "well developed" and fertile, *L. opacifolia* is usually quite distinct in the very broad leaves, with lobes broadly triangular and wider than long, their apices lacking cusps, in the short teeth of the perianth mouth (see fig. 181:4 in SCHUSTER, l. c.), and in the very broad gynoecial bracts. Weak and sterile individuals are often hardly separable from *L. incisa*, a species reported from as far north as 79° N. in Spitsbergen (ARNELL & MÅRTENSSON, 1959). Ultimately we must recognize *L. opacifolia* as a separate, if "weak", species as much on the basis of the differences in ecology as on the quantitative differences in morphology.

Among seeming transitions between *L. incisa* and *L. opacifolia* are weak—and probably indeterminable—plants such as those of HARMSEN (Aug. 15, 1932, 84: Qeqertasugssuk). Here the small plants bear leaves that, although bilobed, are clearly wider than long; lobes are only occasionally cuspidate. Leaf dimensions suggest a weak *L. opacifolia*, although leaves are apparently unistratose to the base. The existence of such plants casts doubts upon the validity of *L. opacifolia* as a species. Other plants (which we have kept as *L. incisa* because of the toothed leaves and cuspidate lobes) such as HOLMEN 3113 c, from Søndre Strømfjord,

may have leaves 3–4-stratose at base and locally 2-stratose even in the leaf middle.

Lophozia grandiretis (LINDB. ex KAAL.) SCHIFFN. (Fig. 3:16–17)

Distribution (Map 16)

1A: Behind Arctic Station (66–0161b, 66–0162a, 66–0163, 66–0172, 66–0176, 70–2184). 2: Fortunebay (66–0142a). 4: Flakkerhuk (66–0120). 6: Eqalúnguit (70–2239). 7: Angûjârtûtit (70–2176). 12: Perdlertut (70–2693, 70–2703). 13: Jens Vahls Dal (70–2644a, 70–2645, 70–2651a, 70–2654, 70–2659, 70–2663). 14: Hareøen (70–2579, 70–2588, 70–2592d). 19: Nûk (70–2877). 26: Pâkitsup ilordlia (70–2258). 28: Atâ (70–2512). 31: Anap nunâ (70–2400a, 70–2407, 70–2427). 42: Magdlak (66–1352, 66–1359, 66–1364b). 45: Sagdliaruseq (66–1062, 66–1065, 66–1069). 46: Qalatôq (66–1123). 48: Amitsup (66–0800). 51: Simiútap kûa, shore (66–0914c, 66–0916c, 66–0917a, 66–0919).

Additional collections:

106: Nûgssuaq (K.H. 15.632). 124: Tasíngortaq (K.H. 13.300, 13.311f). 129: Avataussaligssuaq (K.J. 914b).

L. grandiretis is a sporadically distributed taxon nearly confined to regions with basic rocks. It occurs north to at least 77°30′ N. in northwest Greenland (SCHUSTER, 1969) and to 79° N. in Spitsbergen (ARNELL & MÅRTENSSON, 1959), and south to Vermont and Minnesota (EVANS, 1914; SCHUSTER, 1953). It seems to be amphiatlantic in range, although found west to Manitoba.

This species is scattered throughout the basaltic districts of West Greenland, but not confined to them. It usually occurs as isolated plants or small, gregarious colonies—never in extensive patches—over rich, moist, peaty soil lying over basic rocks, often on irrigated slopes or along rills below basalt cliffs, there often associated with *L. heterocolpos*, *Cephalozia pleniceps*, *Solenostoma sphaerocarpum*, *Anthelia juratzkana*, *Tritomaria scitula*, *T. polita polymorpha*, *L. quadriloba*, *L. polaris*, *L. opacifolia*, *Cryptocolea imbricata*, *Scapania cuspiduligera*, *Calypogeia muelleriana*, and *Odontoschisma macounii*. It is also found, although rarely so, in the gneiss districts, perhaps associated with dikes or basic drifts. For example, the plants from Nûk (70–2877) occurred over peaty ground, on the sloping sides of hummocks at the edges of tarns, associated with calciphytes such as *L. rutheana*.

At such sites a large ensemble of species may occur admixed: in 70–2877, i.a., *Lophozia opacifolia*, *L. binsteadii*, *Calypogeia sphagnicola*, *Cephalozia bicuspidata*, *C. pleniceps*, *Mylia anomala*, *Blepharostoma trichophyllum brevirete*, and *Riccardia sinuata*.

The taxon is readily distinguishable in the field by the large size, the fleshy, brittle texture, the intensive purplish color (of at least older sectors of the plants), and the intense green of shoot apices lacking cell

wall pigments. The cells are diagnostically large; median cells may average 45–55 × 50–60 μ (Fig. 3:16) and bear 30–40 or more oil-bodies of diverse form. In some cells the oil-bodies are mostly spherical and glistening, homogeneous, or with a terminal discoid appendage; others are twinned, consisting of two glistening hemispheres; some cells have a high incidence of coarsely few-segmented oil-bodies. Some of the diversity as seen in neighboring cells of one leaf is shown in Fig. 3:16–17. For a species of *Massula* the oil-bodies are relatively large: spherical, simple ones are 4.5–5.5 μ, the few-segmented ones to 5–7 × 8 μ to 8 × 9 μ in extreme cases.

v. *parviretis* SCHUST.

Distribution (Map 16)

6: Eqalúnquit (70–2227c). 13: Jens Vahls Dal (70–2630). 14: Hareøen (70–2574, 70–2590, 70–2591). 38: Uvkusigssat (66–1390). 40: Mârmorilik, head of the Fjord (66–1198).

Additional collection:

110: Ikorfat (K.H. 62.1575).

The ecology of this small-celled variant sometimes resembles that of the parent species: isolated plants or small, gregarious individuals forming brittle, fleshy patches, over peaty soil, associated at Eqalúnguit, (70–2227 c) with, i. a., *Pleuroclada albescens*, *L. elongata*, *L. latifolia*, *L. ventricosa confusa*, *Anastrophyllum minutum*, *Blepharostoma trichophyllum brevirete*, etc. The plant seems to be more frequent, however, on irrigated but steep basic slopes where more exposed, as on the E. side of Hareøen and in Jens Vahls Dal, on clayey, damp soil with a high organic content, associated with *L. quadriloba*, *L. polaris*, *L. heterocolpos*, *Odontoschisma macounii*, *Tritomaria scitula*, *Anthelia juratzkana*, *Cephalozia pleniceps*, and *Blepharostoma trichophyllum brevirete*.

Previously known only from the type region in Inglefield Bredning (SCHUSTER, l. c.), this taxon, in all its parts, represents a much slighter plant than var. *grandiretis*. It is not impossible that a haploid phase is involved (*L. grandiretis s. str.* supposedly has 14 gametophytic chromosomes—possibly an inaccurate count for, more likely, 18 chromosomes). The stems are more slender, leaves are smaller, and the cells considerably smaller (marginal cells in the lobes, where not tangentially elongated, average 24–30 μ; median cells average 25–30 × 33–45 μ). As in the species proper, intense vinaceous-red to purplish pigmentation is developed, especially of older stem sectors.

Subg. ***Isopaches*** (Buch) Schust.

Lophozia (Isopaches) alboviridis Schust. (Fig. 3:7–12)

Distribution (Map 17)

32: Qôrorssuaq (70–2448b, 70–2457c). 42: Magdlak (66–1375).

A rare or at least local species, to date known from the type from Magdlak (gynoecial), the plants from Qôrorssuaq, and a fragment from Inglefield Bredning (Schuster, 1969, p. 488). The Qôrorssuaq plants occurred on bare, clayey, heaved soil, where there was partial polygon formation, on an acidic, partially vegetated, gently sloping plateau, associated with *Scapania parvifolia*, *Marsupella ustulata*, *Diplophyllum obtusifolium*, *Nardia geoscyphus*, *L. excisa*, *Prasanthus suecicus*, *Gymnomitrion corallioides*, *Anastrophyllum minutum grandis*, and *Cephalozia bicuspidata* (the *ambigua* extreme). The last four taxa were again consociated with the Inglefield Bredning collection. The plants from Kangerlugssuaq (Inglefield Bredning) are minute, strongly gemmiparous (then often with diagnostically lacerate-erose, grossly malformed-appearing leaves), mostly sterile, compact, fleshy but in a somewhat brittle sort of way. In this state they are hardly absolutely separable from the ubiquitous temperate-boreal *L. bicrenata*, but in the Qôrorssuaq plants the leaves are oblong-ovate, asymmetric, with little-arched dorsal sides, and (sterile shoots) average 330–450 μ wide × 370–475 μ long, thus clearly longer than wide. Also, the firm, thick-walled cells each have (2–3)4–8(10) large oil-bodies in all cells—including the marginal—which occlude the cell lumen. These features are as in the type of *L. alboviridis*. Several discrepancies, however, exist:

(a) Two fertilized plants were found, and on one a single, decayed antheridium could be identified, hence the plants may be sporadically paroecious; (b) the plants were deeper pigmented, aside from the lobes and margins, which were often bleached, and the leaf bases, which were green; (c) the ♀ bracts were often sharply triangular and edentate or feebly provided with denticulate teeth; (d) the perianth mouth was mostly even more feebly denticulate than in the type, the shallow lobes with remote, 1(2)-celled teeth. The subgynoecial leaves, which were all edentate and asymmetrically bilobed, with the base obliquely asymmetric (as in fig. 190:4 in Schuster, l.c.), could not in any case be identified as ♂ bracts—unlike in *L. bicrenata* (compare with fig. 188:1 in Schuster, l.c.). The single sporophyte seen had a seta 210 μ in diam., with 16 epidermal cell rows, ca. 9 lying immediately within and 4 occupying the center. The capsule wall was bistratose and, in anatomy, closely matched that figured for *L. bicrenata* in Schuster (l.c., fig. 189:10–11). On balance, the oblique, narrower leaves, angularly bilobed, the more feebly dentate ♀ bracts and perianth mouth, the fewer oil-bodies per cell, and

the—at least in general—dioecious inflorescence separate *L. alboviridis* from *L. bicrenata.* It is possible, however, that it should be regarded as a preponderantly dioecious Arctic subspecies, as is postulated by SCHUSTER (l.c., p. 490).

The association with small and compact soil forms of *L. excisa* is apt to prove a source of confusion. These, however, even though brittle and compact, are (as usual, and as is usual in *L. bicrenata!*) freely fertile; they are separable from *L. alboviridis* by the thin-walled cells, each with 15–20 or more small oil-bodies that do not begin to obscure the cell lumen. Sterile, gemmiparous plants, however, are likely to remain inseparable until cytologically examined.

Subg. ***Lophozia*** DUMORT.

Lophozia heteromorpha SCHUST. & DAMSH. (Fig. 4:1–3)

Distribution (Map 17)

11: Qasigíssat (70–2720). 45: Sagdliaruseq (66–1055, 66–1057).

Additional collection:

128: Agatdalen (K.H. 13.965).

This evidently very rare species has been known only through the type (Hackluyt Ø, Smith Sound, northwest Greenland), which was originally reported as *L. barbata* by HARMSEN & SEIDENFADEN (1932). The type is a lax and poorly developed plant, with leaves "soft, often wavy and undulate, extremely polymorphous" (SCHUSTER, 1969, p. 507). It is evident from the abundant plants of 70–2720 that the type collection hardly gives a clear idea of the species.

The Qasigíssat plants agree with the type in all essentials: (1) facies, which involves a clear green plant developing bright purplish secondary pigmentation of the margins and upper portions of the upper leaves (followed, somewhat later, thus on leaves further removed from the shoot tip, by brownish pigmentation, so that eventually the bright purple zone is succeeded by a brownish purple zone; with age the purple pigment disappears, so that old shoot sectors, from the previous year, may be brownish only); (2) an aspect somewhat reminiscent of *Massula*—on a small to high percentage of plants isolated, polymorphous, often lanceolate, lamellate underleaves occur; (3) frequent terminal, furcate branching, exactly as found in *Massula;* (4) masses of greenish polygonal to quadrate gemmae at the shoot tips, the bulk of gemmae ca. 16–17 × 17–18 up to 20 × 24 μ (but a few larger, to 25 × 26 and 19 × 31 μ).

The combination of abundant greenish gemmae and purplish color of the distal portions of the upper leaves (with lack of any pigmentation in the basal sectors of the leaves, specifically at the postical bases) is distinctive and separates the plants from others in subg. *Lophozia.*

The plants from Disko allow us a much clearer concept of this species. They have much denser leaves, more or less pectinate, distichous, often almost subvertical and loosely complicate, occasionally slightly folded or gibbous in the sinus. Leaves range from orbicular-quadrate and ca. 980–1050 μ wide × 840–900 μ long, and are almost always bilobed, a few trilobed (width-length ratio ca. 1.16–1.17:1) to broadly rotund-quadrate, 1050–1125 μ wide × 800–820 μ long (width-length ratio 1.31–1.37:1), which agrees rather closely with the type (width-length ratio 1.1–1.28:1). As in the type, the lobes are usually acute and (associated with former gemma formation) may bear a few accessory teeth. Aside from occasional trilobed ones, however, the leaves are less polymorphous; they are almost all bilobed by a shallow, usually crescentic sinus descending 0.2–0.25 the leaf length; occasional leaves have angular sinuses descending 0.3–0.4 the leaf length, but this is exceptional. Leaf cells average 23–26 (28) μ on the margins, away from former gemmiparous zones, and 24–29 × 25–35 μ medially, hence are somewhat larger than in the type. As in the type, the trigones are moderately large, never bulging. Oil-bodies are reminiscent of those of *L. ventricosa* var. *confusa:* there are (3–5)7–14 (15–16) rather hyaline, colorless, feebly granular-botryoidal, almost smooth-appearing oil-bodies per median cell and they range from 3.5–5 μ and spherical, to ovoid or ellipsoidal and 4.5×6 to 5×7–8, rarely to 7.5×9 μ; they are nonbiconcentric and usually obscure less than 0.5 of the surface area of the cells. If anything, underleaves are even more sporadically present than in the type; their production seems correlated with an abrupt and inexplicable broadening of the ventral merophytes, since in "normal" shoot sectors ventral merophytes seem only 2–3 cells broad. The underleaves are variable, but most closely match figs. 191:9–10 in Schuster (l.c.): lanceolate and averaging 320×730 to 280–450×780–1050 μ. A minority are symmetrically or asymmetrically bifid for 0.15–0.3, and then average obcuneate in shape and 430 μ wide × 700–820 μ long. They are thus similar in shape to those of the type, but average larger in size.

In the abundantly gemmiparous material from Qasigíssat, the dense pale green mealy masses of gemmae stand in obvious contrast to the purplish upper leaves, exactly as in the type. Gemma production, however, although largely a function of the greenish, yet wall pigment-free uppermost juvenile leaves, continues sporadically until after purple pigments are laid down; gemmae produced after this point develop the same dull purplish pigmentation as the juxtaposed leaf cells. Hence, gemma color in *L. heteromorpha* ranges from light green to purplish [as, e.g., in *L. (Massula) capitata*]; in this respect it is unique in subg. *Lophozia.*

In the sparing, poorly preserved type most gemmae were gone—with each soaking-up of the type plants more were lost—and the remaining few were all greenish. Variation from green to pigmented gemmae

occurs very rarely in subg. *Lophozia:* in *L. pellucida* from greenish to rusty or orange; in *L. ventricosa confusa* (or possibly a variant wholly distinct from this and undescribed), with very intense illumination, fuscous pigmentation of leaf lobes is initiated that "goes over" to the gemmae; in *L. wenzelii* plants from intensely illuminated sites may develop salmon colored gemmae.

A few well-developed gynoecia occur in the Qasigíssat material (only two decayed gynoecia were found in the type). They demonstrate that the initial assumption of a dioecious inflorescence is correct. Bracts are much as in *L. ventricosa:* one bract is subquadrate 0.25–0.30, and averages ca. 1270 μ wide × 1100 μ long, with an angulate sinus; the other bract is ca. 1125 μ wide × 1050–1100 μ long, trilobed for 0.25–0.35, with sharp, angular, sometimes gibbous or reflexed sinuses; the lobes are all acute, often a little ragged as a consequence of former gemma formation. The bracteole is united for ca. 0.20–0.25 its length with both bracts, irregularly lanceolate, and ca. 500–540 μ wide × 900–980 μ long. Perianths (only juvenile, unfertilized ones known) have a ciliate, often lightly purplish-tinted mouth, with the cilia or teeth variable, numerous but not densely crowded; these range from 1–4(5–6) cells long; the shorter are uniseriate, the longest approach laciniiform proportions and are 2–3 cells broad at base; cells in the distal parts are elongated, thick-walled, rigid, and terminal cells are longly acute, 14–16 μ wide × 36–45(50) μ long.

The other collection referred here, from Sagdliaruseq (66–1057), must be placed here only provisionally: it is a straggly, lax-leaved phenotype with oblong to subquadrate leaves, more than 95 % bilobed (a few only are trifid), lacking any accessory teeth of the antical margin. The plants grew in competition with the much larger *Drepanocladus* cf. *uncinatus* and *Kiaeria glacialis* and are hardly typical. They show the frequent furcate terminal branches, light green color with some leaf margins and lobes intensely purplish pigmented, which we regard as typical of *L. heteromorpha.* Underleaves are very exceptionally lanceolate and present away from branches. Gemmae are in pale green masses (the largest are 20–23×26–29 to 28×28 or 19×39 μ), but—and this is critical—some distance back from the shoot apices, older leaves, with purple lobes, still sparingly produce dull to intensely purplish gemmae. Ultimately then, it is this last feature which seems critical in placing 66–1057. Admittedly the affinities of this plant remain problematical. Occasional phases of *L. ventricosa* var. *confusa* may show some "reddish purple, with dull purplish older leaves" (SCHUSTER, 1969, p. 585), although brown to brown-fuscous pigmentation is normal. The var. *confusa*, however, never has mature gemmae with vinaceous pigmentation and never shows lanceolate underleaves.

There are also problematical affinities to the almost unknown *L.*

murmanica KAAL., a plant placed by both MÜLLER (1951–58) and by SCHUSTER (1969) as a synonym of *L. wenzelii*. This plant, according to SCHLJAKOV (1969), has a stem without a small-celled mycorrhizal ventral band and is illustrated as having (6)8–20 small, spherical oil-bodies only 2–4 μ in diam. If SCHLJAKOV's interpretation is correct—he illustrates a dense-leaved plant with subvertical, concave leaves—then *L. murmanica* must belong to subg. *Massula* and not subg. *Lophozia*. H. W. ARNELL (1928, p. 97) describes *L. murmanica* as wholly different than the figures of SCHLJAKOV suggest: the plants are described as soft, pale green to brown, remote-leaved, with leaves nearly longitudinally attached to the stem, some longly decurrent, with a small tooth along the decurrency; leaves are supposedly broadly ovate and mostly 2-, but sometimes 3-, rarely unequally 4-lobed, only rarely for more than 0.25 their length. Leaf margins, near the base, supposedly often bear 1–2 teeth. Underleaves, mostly at shoot apices, are described as numerous, subulate to lanceolate. ARNELL states the species differs from *L. wenzelii*, to which he believed it is most immediately allied, mainly in the often 3-lobed and dentate leaves, and in the presence of underleaves. In contrast, S. ARNELL (1956) states that, judging from the perianth description in JØRGENSEN (1934), "this species is possibly identical with *Lophozia silvicola* var. *grandiretis*," and that "most authors seem to be agreed that *L. murmanica* is not a good species." MÜLLER (1951–58), as noted, simply placed *L. murmanica* in synonymy of *L. wenzelii*, although he had stated earlier (1916, in 1905–16, p. 762) that his study of the type confirmed his assumption that *L. murmanica* was identical with *L. groenlandica* ("*Sphenolobus groenlandicus* (NEES) STEPH."), which he stated must be placed under *L. wenzelii*. [Both STEPHANI and MÜLLER were led astray as regards their concepts of *L. groenlandica* by JENSEN (1900, p. 800), who figured as "*Jungermannia groenlandica*" gemma-free plants with mostly 3-lobed leaves. The plant illustrated by JENSEN as 1-androus has 1–2-androus ♂ bracts and is clearly a mod. *parvifolia* of *Tritomaria polita*.

It is thus obvious that previous workers have confused under the name *Lophozia* (or *Jungermannia*) *groenlandica* plants which represent the "mysterious" *L. murmanica*—which SCHLJAKOV claims belongs to *Lophozia* subg. *Massula*, rather than to subg. *Lophozia*—as well as plants belonging to *Tritomaria* subg. *Saccobasis*. The moral seems to be, at least in part, that conclusions regarding Arctic taxa, based on herbarium study remain subject to an embarrassingly large incidence of wild errors].

These comments—all of which contradict the recent paper by SCHLJAKOV—suggest that "*L. murmanica*" is very much a *nomen confusum*. Since species limits in subg. *Lophozia* almost must involve study of the living plant, we have not tried to further evaluate *L. murmanica*, although the H. W. ARNELL (1928) and JØRGENSEN (1934) diagnoses suggest that

L. heteromorpha may fall very close to that plant. Critical are not only the *L. ventricosa*- and *L. wenzelii*-like oil-bodies of living plants of *L. heteromorpha*, but also the purplish color of the leaves, distally, and the at least sporadic violet to purple color of the mature gemmae. The last criterion, in our opinion, wholly prohibits placing *L. heteromorpha* either within *L. wenzelii* or *L. groenlandica*, however broadly one wishes to interpret these taxa. Stem anatomy and oil-bodies, equally, prohibit placing *L. heteromorpha* within *L. murmanica sensu* SCHLJAKOV (1969).[1])

Lophozia excisa (DICKS.) DUMORT. (Fig. 4:4–17)

This protean and malleable paroecious species appears to be genetically highly complex; its distribution is dealt with under the several varieties here recognized. *L. excisa s.l.* has a wider range than any other species of *Lophozia* and shows corresponding malleability. It is bipolar in range (SCHUSTER, 1968, 1969, 1969a), with isolated stations in Fuegia-Magallanes, South Georgia, West Antarctica, where one of us (RMS) collected it as far south as Hook I., and in New Zealand; apparently holarctic in the northern hemisphere, although known from few stations in Siberia and Japan (Honshu). In the Arctic it is known north to northern Ellesmere Island (82°25′N.; SCHUSTER *et al.*, 1959) and to northern Greenland, at Centrum Ø (82°44′N.; SCHUSTER, 1969); southward in North America it extends to North Carolina and Tennessee. As here broadly conceived, the species includes *L. cylindrica* DUMORT. [*L. socia* (NEES) BOULAY], as the lax end of the adaptive spectrum; *L. limprichti* (LINDB.) STEPH., as the small, compact end of the spectrum; and ordinary *L. excisa*, usually 5–10 mm long, occupying the "normal" or median range in the spectrum of variation. *L. jurensis* MEYL. ex K. MÜLLER (1916, p. 767, in 1905–16) appears to be a lax bog phase of the *L. cylindrica* extreme. In it we can find plants with ♂ bracts immediately below the ♀ ones, or ♂ bracts separated by several sterile leaf pairs from the ♀ ones. KITAGAWA (1965, p. 287) notes this last phenomenon in Japanese plants. We have observed the same, as a rarity, in Greenland material of *L. excisa*. In the following account, therefore, we regard *L. cylindrica*, *L. socia*, *L. limprichti*, and *L. jurensis* all as simple phenetic expressions of "normal" *L. excisa* var. *excisa*. Arctic species, when studied from abundant, living examples, show a bewildering degree of additional variability, far in

[1]) SCHLAJAKOV (1973), after (1969) erroneously placing *L. heteromorpha* under *L. murmanica* states that *L. murmanica* SCHLJAKOV (nec KAAL.) "p. maj. p." = *L. savicziae* SCHLJAKOV; to *L. murmanica* he continues to place *L. heteromorpha*. The confusion is now so great there is no room [in this footnote, added, Feb. 1974 in proof] to disentangle it. *L. savicziae* may be a dense-leaved form of *L. hyperarctica* SCHUST. *L. murmanica*, more than ever, is demonstrably a *nomen confusum*.

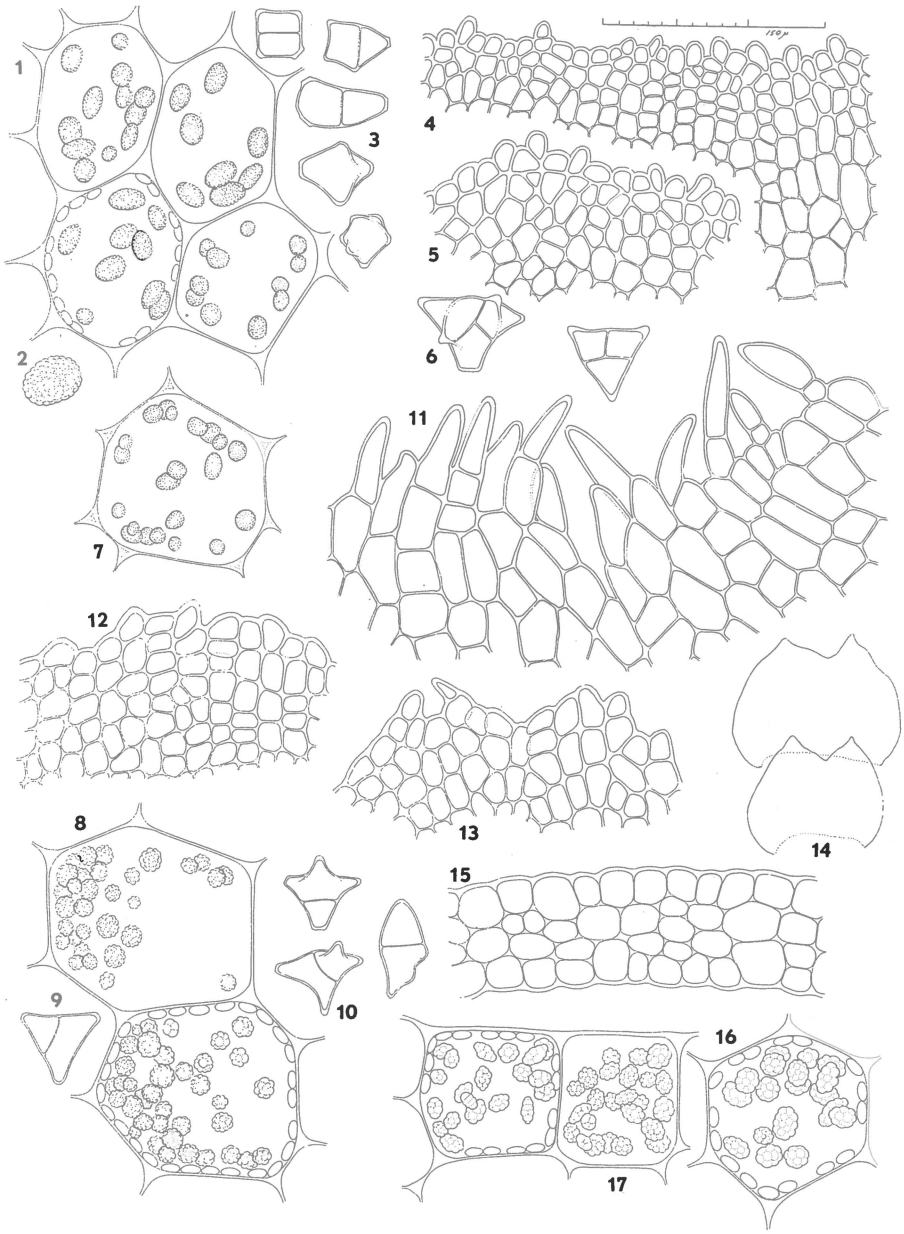


Fig. 4. *Lophozia heteromorpha* (1–3) and *L. excisa* (4–17). (1) Cells with oil-bodies and, lower left, chloroplasts (×580). (2) Oil-body (×1325). (3) Gemmae (×379). *L. excisa v. elegans* (4–6). (4, 5) Perianth mouth cells (×195). (6) Gemmae (×340). *L. excisa v. infuscata* (7–11). (7) Cell with oil-bodies (×660). (8) Cells with oil-bodies, ± fuscous-purple to fuscous on leaf margins and perianths (×500). (9–10) Gemmae (×245). (11) Cells of perianth mouth (×195). *L. excisa v. succulenta* (12–17). (12, 13) Cells of perianth mouth (×195). (14) Leaves (×14.5). (15) Cross section, one-sixth from base of perianth (×180). (16, 17) Median cell and two cells from lobe margins, respectively (×635, 590 respectively). [1–3, from 70–2720, Disko; 4–6, 70–2585; 7, 70–2347, Sarfaq; 8–11, 70–2479, Qôrorssuaq; 12–17, 70–3007b, Manîtsoq; 4, 5, 11–13, drawn to 150 μ scale].

excess of that attributed to it by workers dealing only with plants from temperate to boreal climates.

We recognize four distinct varieties in the Arctic populations, separable as follows:

1. Cells of leaf margins, in lobes, 24–30 μ (tangentially measured); median cells ca. 24–33 × 25–38 μ; oil-bodies normally 7–24 per cell.... 2.
   2. Firm, rigid, fleshy, dense-leaved, small, compact plants; perianths (2)3–4-stratose at base, at mouth clearly, shallowly lobulate-repand and denticulate with 1–2(3)-celled, rigid, firm teeth. Gemmae absent; clearly paroecious. v. *succulenta*
   2. Plants remote to dense-leaved, but usually larger; perianth 1(2)-stratose at base, mouth truncate or almost so, edentate or crenulate or sometimes with scattered, 1-celled teeth. Gemmae usually present..... 3.
      3. Gemmae 1–2-celled, usually ± dull purplish, to 25–27(30) × 28–32(40) μ; slightly branched, with stem almost terete. Paroecious; perianth mouth cells ± thin-walled, finger-like, strongly elongated. v. *excisa*
      3. Gemmae 2–3(4)-celled, bright red to 33–36 × 35–38(43) μ, in large masses; freely terminally branched, with axis strongly flattened. Dioecious (at least normally so); perianth mouth cells subisodiametric, very small, thick-walled. v. *elegans*

1. Cells of leaf margins, in lobes, (26–29)30–38(40) μ; median cells (32–35)36–45(48) × (36)40–55(60) μ; oil-bodies (12–18)20–36(40–45) per cell. Gemmae 1–2(3–4)-celled, bright red, (28)30–37 × 33–38(48) μ; with (sun forms) perianth fuscous and leaf margins ± fuscous (locally with some purplish). Perianth mouth dentate, with free teeth 0.5–2(3–4) cells long; terminal cells (where free) ca. 56–68(75–80) × 16.5–22 μ. v. *infuscata*

Lophozia excisa (DICKS.) DUMORT. v. *excisa*

Distribution (Map 18)

1A: Behind Arctic Station (66–0166a, 66–0281a, 70–2022, 70–2025, 70–2027, 70–2039a, 70–2054). 2: Fortunebay (66–0201a). 4: Flakkerhuk (66–0173c). 6: Eqalúnguit (70–2229a). 7: Angûjârtûtit (70–2158a, 70–2160, 70–2162). 8: Kuánerssuit (70–2141, 70–2151). 9: Eqaluit (70–2521). 10: Enoks Havn (70–2770, 70–2758). 11: Qasigíssat (70–2730). 12: Perdlertut (70–2686, 70–2694). 13: Jens Vahls Dal (70–2639). 14: Hareøen (70–2587, 70–2604). 15: Kronprinsens Ejland (70–2074). 19: Nûk (70–2836, 70–2839, 70–2870a). 21: Umiasugssûp (70–2948e). 23: Kangersuneq (70–3139, 70–3159). 24: Jakobshavn (66–0224, 66–0225). 25: Sarfaq (70–2362, 70–2363). 26: Pâkitsup ilordlia (70–2388, 70–2393). 29: Ritenbenk (66–0534). 30: Eqe (66–0293c, 66–0336b). 31: Anap nunâ (70–2425, 70–2435). 32: Qôrorssuaq (70–2443, 70–2448i,

70–2468, 70–2471). 36: Umanak (66–1563). 37: Agpat (66–1469c, 66–1429). 48: Amitsup (66–0797, 66–0817). 50: Simiútap kûa, valley (66–0862). 51: Simiútap kûa, shore (66–0836). 53: Søndre Strømfjord (66–0046, 66–0052).

Additional collections:

1: Godhavn (J.V. Sept. 1834). 17: Tupilak (K.J. 1404). 28: Atâ (LÆGAARD July 1962). 45: Sagdliaruseq (K.H. 16.933a). 72: Kuánit (L.H. Aug. 1932). 87: Kangersuneq (J.V. 109a). 88: Christianshåb (K.H. 15.717b). 97: Qôrorssuaq (K.J. 335). 112: Umiartorfik (K.J. 604a). 123: Uigordleq (K.H. 12.884). 124: Tasíngortaq (K.H. 13.311d). 129: Agatdalen (K.H. 13.968a). 135: Tornit (K.H. 13.487). 139: Qaqortukavsaq (K.H. 16.121b). 142: Niaqornánguaq (K.H. 14.949a). 143: Kangerdlugssuaq (K.H. 16.386a).

This abundant plant is so polymorphous in the Arctic that its perimeters are very difficult to define. Paroecious inflorescences are almost always easily demonstrated—yet the related var. *elegans*—is apparently uniformly (or preponderantly) unisexual (p. 97). Until now the paroecious inflorescence has been adequate to separate the species, s.l., from all others of subg. *Lophozia;* now even this perimeter is breached.

L. excisa v. *excisa* extends to at least 82°44′N. in North Greenland (SCHUSTER, 1969) and to 82°25′N. in Ellesmere Island (SCHUSTER *et al.*, 1959); in eastern North America it extends southward to the mountains of North Carolina and Tennessee, where it is very rare.

The extraordinary variability of this plant in the Arctic is matched by the wide range of microhabitats it invades. Perhaps most typical, for optimally developed plants, is the occurrence over hummocks in not too wet and not too acidic fens or peaty areas adjoining tarns and small lakes, and there often over *Aulacomnium* and *Sphagnum*, associated with *Scapania hyperborea*, *Calypogeia sphagnicola*, *L. polaris* and/or *L. polaris sphagnorum*, *Cephalozia pleniceps*, *C. bicuspidata*, occasionally *L. opacifolia*, *Riccardia sinuata*, and *L. hatcheri*, rarely (in 70–3139) *L. kunzeana*. Here the var. *excisa* occurs in large, freely fertile, vigorous, largely green phases usually showing some purplish pigmentation. In moss-tundra, in drier sites, it may be found between rocks, with *Chandonanthus setiformis*, *Anastrophyllum minutum grandis* (70–2039a) or with *Cephaloziella byssacea* (70–2686, 66–1469c, 70–2758) or less often *L. hatcheri*.

Much smaller, more compact phases (= "*L. limprichti*") occur over windblown sand (as at Eqe, 66–0336b), associated with crust-forming *Prasanthus*, *Gymnomitrion corallioides*, and *G. concinnatum*. The compact mod. *parvifolia* is also found over exposed compact soil in stone polygons (70–2448i, 70–2948e), with *Prasanthus*, *G. concinnatum*, *G. corallioides*, *S. parvifolia* generally associated, less often *Solenostoma sphaerocarpum*, *Nardia geoscyphus*, *Anastrophyllum sphenoloboides*, *L. ventricosa silvicola*, *L. alboviridis*, *Diplophyllum obtusifolium*, and *Cephalozia bicuspidata*.

In addition, *L. excisa* is often frequent in basaltic regions. It may be found on irrigated, south-facing basalt slopes (70–2141), on broken basaltic slopes mixed with *Distichium capillaceum*, *Tritomaria scitula*, *Blepharostoma trichophyllum brevirete* (66–0166a), or on basic clay-stone, steep slopes, with *L. polaris* and *L. heterocolpos* (70–2639). Occasionally, in small ravines over basalt, *L. polaris*, *L. quadriloba*, and *Scapania cuspiduligera* (66–0281a) or *S. gymnostomophila* (66–0862) may be associated.

The preceding account represents a mere scattering—although a fairly representative one—of the sites in which typical *L. excisa* may be encountered. Other sites may be invaded by the varieties treated below.

On p. 100 we deal with the problems posed by deviations in sexuality exhibited by *L. latifolia* in its common phase, growing amidst *Sphagnum* and mosses in rich fens. We have concluded that, in spite of the occasional occurrence of bisexual plants, this species could not be construed to be merely an extreme of *L. excisa*. Pertinent in dealing with this assumption are plants of 70–2836; these are sparing plants growing amidst *Sphagnum* and *Paludella squarrosa*, associated with *Riccardia sinuata*, having the same straggly growth pattern as *L. latifolia* and showing on a few leaves traces of brownish pigmentation mixed with reddish coloration. The predominant pigmentation of these plants, however, is vinaceous and purplish. Leaves may be margined with intense purplish pigmentation and in some instances the entire leaf is intensely purplish colored. Furthermore, there is a tendency for ventral leaf bases to have some reddish coloration. Finally, the few fertile plants seen were clearly paroecious and none of the ♂ bracts exhibited the diagnostical ventricose form found in *L. latifolia*. One can only conclude that these two taxa, when occurring in similar environments, retain striking differences in pigmentation.

Associated with the paroecious inflorescence is abundant production of capsules; we have seen them as early as June 27 (66–0201a) and as late as Aug. 8 (70–2521) and Aug. 23 (70–3139). The plant of 70–2521 is notable in that it bore one *Radula*-type branch—a branching mode not again encountered so far in subg. *Lophozia*.

Lophozia excisa v. *infuscata var. nov.* (Fig. 4:7–11)

A var. *excisa* ostio perianthii dentibus 1–2 cellulis manifesto armato, planta (praecipue perianthiis) valde fusca, cellulis majoribus plura corpuscula oleifera continentibus diversa.

Distribution (Map 18)

10: Enoks Havn (70–2757a). 22: Orpigsôq (70–3115). 25: Sarfaq (70–2341). 26: Pâkitsup ilordlia (70–2290a, 70–2311). 31: Anap nunâ (70–2414). 32: Qôrorssuaq (70–2479).

Plants green, with leaf and bract margins from fuscous dull-purple to fuscous; perianth strongly infuscated. Cells very large: marginal

mostly (26)30–38 μ, tangentially measured, median mostly 36–45(48) $\times$40–55 μ. Oil-bodies numerous, usually 20–36(40–45) per cell, spherical or subspherical, variable (some finely botryoidal, others rather coarsely so, the component spherules little or not bulging), usually 4.5–6 μ in diam., a few to 6$\times$7 μ. Perianth mouth typically denticulate-ciliolate with teeth 0.5–2(3–4) cells long, terminal cells long, to 56–68(75–80)$\times$ 16.5–22 μ. Spores 16–18(19) μ in diam., finely, closely spinulose. Elaters ca. 7.5 μ in diam. Gemmae bright red, 1–2(3)-celled, (28)30–37$\times$33–38 (48) μ. Paroecious. ♂ Bracts 2–3-androus.

Type. 26: Pâkitsup ilordlia, Qissugssalik (70–2311; a trace also in 70-2290a). The type grew along the shore of a lake, with *Dicranum* and *Aulacomnium;* 70–2290a was growing over *Sphagnum*, together with *Calypogeia sphagnicola* and *Cephalozia pleniceps.*

This extreme represents the large-celled, possibly polyploid, phase of *L. excisa.* Perianths show considerable variation with respect to pigmentation and armature of the mouth. Some perianths are quite brownish-pigmented and hyaline at the mouth; others are green, but have the cells at the very mouth purple, at least while still immature. The mouth may be crenulate, as in var. *excisa* (e.g., in 70–2757a), but usually some or many 1–2(3)-celled, lax teeth, formed of rather swollen, thin-walled, elongated cells may occur (Fig. 4:11). Although var. *excisa* usually has a merely crenulate mouth, extremes of this may show some 1-celled teeth (fig. 192 in Schuster, 1969).

Owing to the cell size, gemmae, and oil-bodies, the more or less dentate, crispate ♀ bracts, and the short-dentate perianth mouth, it is subject to confusion with the dioecious, more collenchymatous-celled *L. rubrigemma* Schust.

We also place here, with some hesitation, a sterile plant from Sarfaq (70–2341), which grew on windswept, sand-covered, narrow ledges on a cliff face, associated with *Chandonanthus*, *Racomitrium lanuginosum*, *Andreaea*, lichens, *Gymnomitrion corallioides*, and other xerophytes. These plants, in part strongly fuscous (and black when dry), ranged to deep purplish, or (when hidden among larger bryophytes) clear green, with purplish edges. The more xeromorphic plants had narrower, more deeply bifid leaves, the mesomorphic ones broader leaves, often with the lunate "*excisa*-type" sinus. Cells were as in the diagnosis, and oil-bodies ranged from 18–35 per cell. The somewhat smaller cells, relatively moderate trigones, and form of some leaves would place these plants here rather than with the dioecious *L. rubrigemma.*

A green form, with limited purplish pigmentation, from Qôrorssuaq, (70–2479), also belongs here. These plants, clearly paroecious, may have somewhat smaller cells on smaller-leaved, weak shoots [marginal cells (25)26–33(35) μ], but have the tetrahedral to polygonal, sharp-angled,

large, bright red gemmae typical of this variety. Gemmae range from ca. (28)30–36×33–38(48) μ and are usually 2-celled; a few show a weak septum of one cell. The perianth mouth teeth are optimally developed: always free for at least 0.5 cell, and not infrequently for 1–1.5 cells, occasionally 2- or even 3–4 celled teeth are present.

Perhaps the largest collection seen (but with few fertilized perianths) is that from Enoks Havn (70–2757 a), growing in a rich fen on a broad river terrace, among *Sphagnum* and *Paludella squarrosa*, together with *Scapania hyperborea*, *Cephalozia bicuspidata* and *Cephaloziella byssacea*. Perianths show the same variation from crenulate-denticulate to, locally, lobulate-ciliate, with a few teeth 2–3 cells long. Bracts show the same gross variation found in *L. excisa* var. *cylindrica*, from narrow and oblong, simply bifid, to broad, undulate, 2–3-lobed and with sinuous, repand margins. This collection is noteworthy in that a few basiscopic, terminal, *Radula*-type branches were found.

ARNELL (1954 and 1956, p. 124) describes a large-celled form of *L. excisa*, as "var. *grandiretis*", which has "orange-colourless gemmae" that are 30–40×40–50 μ. This plant, unisexual, represents *L. pellucida*.

Lophozia excisa v. *succulenta var. nov.* (Fig. 4:12–17)

A var. *excisa* perianthio crasso polystromatico carnoso, gemmis deficientibus diversa.

Distribution (Map 18)

16: Manîtsoq (70–3007b). 37: Agpat (66–1465).

Similar to small, compact soil forms of *L. excisa* var. *excisa* and similar in the unistratose, subrotund leaves, ca. 850 μ wide × 675 μ long and divided by a lunate sinus for $^1/_4$ their length; similar also in cell size (marginal cells ca. 23–27 μ) and in the oil-bodies (small, distinctly botryoidal, ca. 9–14, occasionally 18–20 per cell). Plants very fleshy, compact, with leaves at most 1.2 mm wide, green, with lobes and leaf margins bright red, perianths distally bright red. Stems fleshy, thick, succulent; leaves dense, imbricate, subvertical, unistratose, broader than long, the upper bright red distally, with age acquiring some brownish pigmentation and sometimes decolorate leaf margins. Clearly paroecious, ♂ bracts leaflike but with a somewhat gibbous base; antical base of bract transversely inserted, edentate, 1–2 androus. ♀ Bracts 2–3-fid, the lobes edentate, or with a few small teeth; a lanceolate to bifid, small bracteole usually present. Perianth 2–3–4-stratose at base, at mouth lobulate, often formed of rather thick-walled collenchymatous cells, denticulate with rigid, remote, 1–2(3)-celled teeth. Gemmae lacking.

Type. 16: Disko Bugt: Manîtsoq, north of Egedesminde (70–3007 b).

The sparing type material occurred among *Prasanthus suecicus*, *Gym-*

nocolea inflata, *Cephalozia bicuspidata*, *Anthelia juratzkana*, *Solenostoma sphaerocarpum nana*, *Pleuroclada*, and *Nardia geoscyphus*.

Until more copious collections come to light this plant will remain a puzzle; on the basis of the small, compact form and paroecious inflorescence apt to be mistaken only for *L. bicrenata* and small, compact forms of *L. excisa*. It differs at once from *L. bicrenata* (and the allied *L. alboviridis*) in that the cells remain thin-walled, except for the rather pronounced trigones; stems are at least 13 cells high, of leptodermous cells throughout, and are conspicuously mycorrhizal throughout much of the medulla; dentition of the perianth mouth is not coarse enough; leaf cells, unless bleached, all have many oil-bodies per cell; ♂ bracts are usually edentate. The inability to form thick-walled cells and the stem anatomy speak indubitably for *L. excisa s.l.* Plants from the type collection are distinct from the v. *excisa* in the firm, collenchymatous cells at and near the perianth mouth, the mouth itself being remotely denticulate with rigid, short, 1– to occasionally 2–3-celled teeth. Trigones at and near the perianth mouth may sometimes be weakly bulging. Also, unlike any other form of *L. excisa* known to us, the perianth base is (2)3–4-stratose and quite fleshy. The ♂ bracts, which are very broad, and much wider than long, never seem to have the antical tooth, normally found in *L. excisa*. The combination of denticulate, firm-celled perianth mouth, the polystratose perianth base, and edentate bases of the ♂ bracts isolate these plants from any other variety of *L. excisa*.

Lophozia excisa v. *elegans* Schust. (Fig. 4:4–6)

Distribution (Map 18)

13: Jens Vahls Dal (70–2651). 14: Hareøen (70–2585a). 43: Kangerdlugssuakavsak (66–1287). 47: Íngia (66–1036).

Additional collection:

110: Ikorfat (K.J. 334a).

The plants from Hareøen (70–2585a, with *L. quadriloba*, *Scapania cuspiduligera* and *S. curta*) agree exactly with the very sparing, sterile type plants (66–1287) which are described and figured in Schuster (1969), except that they are rather denser-leaved and, if anything, even more compactly fleshy and brittle. The var. *elegans* occupies an analogous position vis à vis var. *excisa*, as does *L. opacifolia* to *L. incisa*, and might, equally, be regarded as an autonomous species. Typical are the fleshy, brittle stems; the stiff, basally polystratose leaves (see fig. 194 in Schuster, l.c.; in the Hareøen plants the leaves may be polystratose to the middle or higher); the close, terminal branching; the abundant, very sharply stellate gemmae that are, at maturity, to a large extent 3–4-celled. All these features are evident in both type and Hareøen plants.

On the more adequate material from Hareøen three unfertilized gynoecial plants were found; these were definitely unisexual, no trace of antheridia being present either below the ♀ bracts or in the leaf axils of any of the copious subfloral innovations produced. ♀ Bracts, which are almost impossible to dissect free without breaking (they are short, very broad—ca. 2–2.8× as wide as long—polystratose to the middle or almost so, and have broad, rather bluntly acute, entire to sparingly, bluntly denticulate lobes), form a stiff, wide cup around the immature perianth. The latter is ovoid, rather wide at the mouth, bright red except at the base, and has a diagnostic mouth which, as in var. *excisa*, is truncate and crenulate to crenulate-denticulate (the majority of cells project merely by their ± rounded, gibbous, strikingly thick-walled ends; occasional, usually remote cells are somewhat longer and project for much of their length, or are superposed above the remaining cells to form short, rounded, 1-celled teeth). Cells of the mouth, however, are short and may be isodiametric or less than twice as long as wide—averaging 13–18×16–24(28) μ. Since the distal portions of the cells are prominently thick-walled (a feature rarely found in *L. excisa*, never in its near ally, *L. latifolia*), one must conclude that these cells have attained mature dimensions.

On these bases, it is clear that elevation of var. *elegans* to species status may be unavoidable. In addition to the criteria cited in the original diagnosis (stellate, sharply angled and often 3–4-celled gemmae; flattened, brittle, rigid, fleshy stems; dense, pectinate-distichous and rigid leaves, polystratose at least basally; copious, juxtaposed, terminal branching) there are now reproductive criteria of greater import (unisexuality vs. easily determined bisexuality; the small, mostly almost isodiametric cells of the perianth mouth, and their thick distal walls). These, collectively, possibly suffice to separate var. *elegans* as a well-defined species. On the basis of the similarities in perianth mouth (compare SCHUSTER, 1969, figs. 192:1, 193:1, 197:1), we remain of the opinion that var. *elegans*, in spite of the *Massula*-like aspect, must remain in sect. *Excisae* of subg. *Lophozia*.

The very small collection (split into two microcollections) of 70–2651 consists of sterile, minute, but very strongly fleshy-stemmed plants, the leaves reduced to almost ridgelike lamellae on the stems. The gemmae here show the usual strongly stellate to tetrahedral-spinous form typical of var. *elegans* and the bulk of gemmae are 3–4-celled; some, with gibbous cells cut off, have begun to germinate.

Occasional, very minute, compact, fleshy forms of *L. excisa* occur that to some extent seem to bridge the distinctions between var. *excisa* and var. *elegans*, i. a., 70–2770 (a trace, amidst *Scapania perssonii*, *Nardia geoscyphus*, *Cryptocolea*, *Cephalozia bicuspidata*, *Anthelia juratzkana*, on fine silty soil of a river margin, in mats with *Salix herbacea*). Plants here have strong reddish pigmentation of apices of the unistratose leaves.

The reddish gemmae are occasionally 3-celled and almost match those of var. *elegans*. Also, perianth mouth cells are rather thick-walled distally. These cells, however, are much larger (15–22[24]×31–48 μ). Furthermore, on these plants, a paroecious inflorescence is clearly present. Thus it seems likely that var. *elegans* is a unisexual, highly fleshy derivative of *L. excisa*, in which similar, but bisexual and unistratose-leaved phenocopies occur. If the ensemble of characters here regarded as typical of var. *elegans* proves to be constantly linked, its segregation as an autonomous species will prove unavoidable. Since it is still known only on the basis of few and sparse collections, we retain it here as a variety of *L. excisa*. The plant clearly needs further investigation and culture studies.

Lophozia latifolia SCHUST.[1])

Distribution (Map 19)

6: Eqalúnguit (70-2227e). 17: Tupilak (66–0107a). 23: Kangersuneq (70–3151). 26: Pâkitsup ilordlia (70–2298). 32: Qôrorssuaq (70–2444). 48: Amitsup (66–0798, 66–0816). 53: Søndre Strømfjord (66–0048, 66–0050a, 66–0055, 66–0077, 66–0081, 66–0082).

Additional collections:

44: Akuliarusikavsak (K.H. 15.824a). 45: Sagdliaruseq (K.H. 13.123). 53: Søndre Strømfjord (K.H. 4424b). 87: Kangersuneq (K. HANSEN Aug. 1958). 116: Puiagtukavsak (K.J. 679).

This predominantly Arctic species is known from several stations in the North American Arctic, from 81°52′N. in Peary Land (SCHUSTER, 1969) and 82°26′N. in Ellesmere Island (SCHUSTER *et al.*, 1959). The type, however, is from the "microclimatic tundra zone" along Lake Superior, in Minnesota, the southernmost station. GROLLE (1967) reports one station from Spitsbergen and states that reports from Scandinavia are in error.

L. latifolia has been discussed in three different papers (SCHUSTER, 1953a, 1959, 1969)—but it still represents a critical taxon. It is usually helophytic, often growing among *Sphagnum* and/or *Aulacomnium*, rather often with *L. kunzeana* (with which it grew at the type station), *Calypogeia sphagnicola*, *L. binsteadii*, *L. hatcheri*, *Anastrophyllum minutum*, etc., occasionally in irrigated moss-tundra (as in 70–2227e), associated with *L. elongata*, *L. grandiretis*, *L. ventricosa confusa*, *Pleuroclada*, *A. minutum*, and *Riccardia sinuata*. *L. latifolia* is apparently restricted to the Precambrian eastern part of our area.

[1]) SCHLJAKOV (1973) places this as a synonym of *L. jurensis* MEYL. We agree with K. MÜLLER (1951–58, p. 664) that *jurensis* is a helophytic phase of *L. excisa*. We have seen a type fragment of *jurensis* (ex herb. K. MÜLLER) with two fertile plants, both paroecious. See further p. 90 of this paper. It is admittedly possible that *L. latifolia* should be placed as an Arctic subspecies of *L. excisa*: but this seems unreasonable, since the last extends north to at least 82°44′. MÜLLER (1916, in 1905–16, p. 768, fig. 205:a, h) clearly shows that *L. jurensis* is paroecious.

Almost exclusively androecial plants of 70–2444, growing along a rill amidst *Sphagnum*, represent the most typical development of this species. They agree with the type (and with almost all other collections seen) in being straggly, very lax, and remote-leaved, and in showing a large amount of brownish-fuscous pigmentation, particularly of the androecia. They depart from the type, however, in the total lack of gemmae and in the occasional presence of some bluish purple or purplish pigmentation of ventral leaf bases, and, occasionally, rhizoid bases; such pigments are, locally, also mixed with the fuscous ones, especially on ♂ bracts (which, as a consequence, may be very deeply pigmented). Unlike in *L. excisa*, to which this species is most nearly allied, gemmae are never copiously developed; their seeming total lack, as in the present phenotype, is unusual, and serves to separate the plants from all phases of the often superficially similar *L. polaris*.

Androecia in *L. latifolia* have bracts that bear an inflexed antical tooth, usually not visible without dissection; in this feature *L. latifolia* is quite distinct from *L. polaris*, of which we have studied several ♂ collections, in all of which ♂ bracts lacked any trace of an antical basal tooth. Instead, the bract base, antically, was inserted somewhat up the stem, cutting off a distinct antical pouch.

The abundant collection from Kangersuneq (70–3151) is critical in the elucidation of this taxon. The plants have all of the usual *L. latifolia* features, i.a., numerous, long, spicate androecia, exactly matching those portrayed in SCHUSTER (l.c., fig. 195); gemmae rare, purplish red; lack of any reddish pigmentation except occasionally a small amount on ♂ bracts; fulvous warm brown secondary pigments present; straggly growth amidst mosses. A detailed examination, however, shows numerous deviations: on gynoecial plants the upper leaves approaching the bracts may have rounded lobes and strongly gibbous sinuses. In addition to the normal, unisexual plants, which are in a very large majority, a small minority exhibits deviations in sexuality, as follows: (a) One plant with a conspicuous gynoecium bore a vigorous subfloral innovation, which itself ramified, bearing two *Frullania*-type branches; the branches in turn produced spicate, slender, intercalary androecia, in one case as many as 8 or 9 pairs of bracts. Furthermore, the ♂ bracts were not infrequently diandrous rather than monandrous. (b) A gynoecial plant with several sterile leaves below the bracts bore one pair of ♂ bracts below these leaves; these bracts were monandrous. (c) A gynoecial plant without trace of ♂ bracts on the main axis bore a subfloral innovation which was swiftly androecial, with monandrous ♂ bracts. (d) A ♂ *Lophozia latifolia*-type androecium, with 4–5 pairs of ♂ bracts was succeeded by several pairs of sterile leaves subsequent to which a gynoecium was produced. (e) A vigorous, purely

gynoecial shoot bore an innovation which developed one or two pairs of ♂ bracts, several sterile leaves, and then a gynoecium. (f) The same situation as with (d), except that the leading gynoecial axis, several leaves below the ♀ bracts, bore one ordinary looking vegetative leaf with a single axial antheridium. (g) A long, unbranched leafy shoot bore two pairs of ♂ bracts, several sterile leaves, two more pairs of ♂ bracts, several sterile leaves, a third androecium, 7–8 pairs of sterile leaves, and then a gynoecium. (h) A leading gynoecial axis bore two or three leaf pairs below the gynoecium, a lateral-intercalary branch from near the ventral angle of the leaf, which was androecial. (i) A long, slender, sterile branch with damaged shoot apex bore three intercalary branches, two of which, after producing a number of pairs of sterile leaves, produced gynoecia; the third branch produced a long, slenderly spicate androecium. (j) A richly ramified sterile stem bore lateral-intercalary branches, one of which, after producing some pairs of sterile leaves, produced an androecium, then several sterile leaves, and then an aborted gynoecium. (k) A vigorous sterile axis, damaged at the tip, produced two lateral-intercalary branches, both with numerous pairs of leaves. One axis, after some 6–8 leaf pairs, produced one pair of monandrous ♂ bracts, then 6 or 7 pairs of sterile leaves, produced an androecium, then several sterile pairs of leaves, again three or four pairs of ♂ bracts, followed by several pairs of sterile leaves and another androecium.

In spite of these deviations, the more normal condition is unisexuality; for example, plants have been seen with the main axis gynoecial, bearing *Frullania*-type branches, and then subfloral innovations, which were also both gynoecial. Very richly ramified ♀ plants, all of which showed no trace of androecia, occur and, in other cases, ♂ plants with spicate androecia ramify, with each branch becoming again androecial. It is common to find gynoecial axes developing subfloral innovations which are again gynoecial, and equally common is a vigorous, gynoecial stem which shortly before producing the gynoecium develops a *Frullania*-type branch that is swiftly gynoecial.

These observations, which involved the dissection of hundreds of plants, clearly prove that the supposed unisexuality of *L. latifolia* is inconstant. The genetics and physiology of sex organ production in this species, vis à vis *L. excisa* (which is nearly always clearly paroecious), need careful study; it would be a rewarding problem to investigate.

Exactly analogous is the condition—also involving heteroecious inflorescences—in *Solenostoma oblongifolium* ssp. *heteroicum* (p. 167). The question raised is: why, in the Arctic, has there been selection for populations with such deviant sexuality? If all accounts of temperate-boreal populations are accurate, such deviations never appear to occur in non-

Arctic plants. The present observations are also of major importance in that they cast very serious doubt on the universal practice among hepaticologists of automatically using differences in sexuality (uni- vs. bisexual) as adequate bases for species recognition. One must then ask if *Solenostoma pumilum* should be re-interpreted to include the dioecious *S. atrovirens*, and whether *Lophozia gillmani* should be re-interpreted to include the dioecious *L. bantriensis* (see pp. 35–36).

Of particular importance is the fact that in *L. latifolia*, in contrast to the paroecious *L. excisa*, even though large numbers of androecia and gynoecia can be found, fertilized gynoecia (and sporophytes) are very rarely produced. Occasional gynoecia seen were clearly abnormal and aborted, but the antheridia all seemed quite normal. Striking also is the fact that, in spite of the free occurrence of bisexual plants (estimated at at least 20 %; with death of older shoot sectors it is possible that it may be much higher, former contacts between ♂ and ♀ axes having been destroyed), paroecious inflorescences with the ♂ bracts situated immediately below the ♀ ones are very rare and the androecia essentially all conform to the "*latifolia* type": slender, spicate, with ventricose bracts and suberect to weakly patent lobes. It has been assumed (SCHUSTER, l.c., p. 527) that *L. latifolia* always has monandrous bracts—all collections to date show only such bracts; in the present collection clearly a small minority of ♂ bracts are diandrous.

In spite of these observations we continue to regard *L. latifolia* as a good species; its ecology is quite distinct (growth usually amidst coarse mosses like *Aulacomnium*, or amidst *Sphagnum*, never on soil); the inability of vegetative sectors to develop reddish pigments—even the gemmiparous shoot tips lack them—is notable, the pigmentation being wholly brownish. The prevalence of slender, spicate, branches and—even when a single intercalary pair of ♂ bracts occurs on a leafy axis that becomes eventually gynoecial—♂ bracts with ventricose bases are diagnostic. It is, perhaps, symptomatic that the present plants were identified in the field as *L. latifolia* and that, in practice, confusion is more likely to occur in the field between *L. latifolia* and the unrelated *L. polaris*.

Lophozia longidens (LINDB.) MACOUN

This species, *s.l.*, is very largely boreal, rather than Arctic; until cited from stations in the North American Arctic (SCHUSTER, 1969, p. 534), it was not known north of Quebec and Newfoundland. What seems to be quite typical *L. longidens*, however, occurs as a rarity north to Inglefield Bredning and a larger-celled, probably polyploid variety occurs equally far north. Both taxa occur regionally; both here and in Inglefield Bredning, they are exceptionally rare.

ssp. *longidens* (LINDB.) MACOUN

Distribution (Map 20)

1B: Lyngmarken (66–0564). 6: Eqalúnguit (70–2228). 25: Sarfaq (70–2341). 26: Pâkitsup ilordlia (70–2285).

Known from 77°31′ N. at the east end of Inglefield Bredning (SCHUSTER, l.c.) and from the above stations.

This taxon is limited strictly to igneous regions and apparently restricted to sheltered but often quite dry sites. At Lyngmarken (66–0564), for example, it occurred on a thinly soil-covered, narrow shelf in a deep cleft, growing with *Cladonia*, *Stereocaulon*, *L. excisa*, *L. hatcheri*, and *Polytrichum*. At Eqalúnguit it also occurred in rather dry crevices of gneissic rocks, on north-facing ledges. As is noted in SCHUSTER (l.c.), in which the Arctic ecology is discussed, this species in the far north "is an 'ecological specialist' and seems to occur in only a limited series of biotypes". It never seems to produce sex organs, although the rust-red gemmae are common. Oil-bodies range from 5–12 per cell (in 70–2285) to 9–14 per cell (in 70–2228), which falls within the approximate range of the plants illustrated in SCHUSTER (l.c., fig. 199:9) from Lyngmarken.

ssp. *arctica* SCHUST.

Distribution (Map 20)

16: Manîtsoq (70–3006). 25: Sarfaq (70–2358a). 39: Tasiussaq (66–1257).

Additional collections:

17: Tupilak (K.J. 1304). 88: Christianshåb (K.H. 15.717d). 117: Sêrsínerssuaq (K.J. 629).

Previously known only from the types, from Inglefield Bredning and North Star Bay, in northwest Greenland (SCHUSTER, l.c., p. 539, fig. 199:1–8). The above plants agree in all points with the type collections, including the narrow leaves, often irregular and somewhat asymmetrically trifid; the deep sinuses, occasionally even extending to 0.6–0.7 the leaf length, although usually from 0.3–0.5; the very large, red gemmae; the large cell size and numerous oil-bodies; the erect growth among mosses and *L. hatcheri*.

It has already been noted (SCHUSTER, l.c., p. 541) that occasional individual plants "may prove difficult to separate" from the much more vigorous *L. rubrigemma*. It is possible—but hardly probable—that the present plants may prove to be a mod. *fissifolia-angustifolia-parvifolia-squarrosa* of *L. rubrigemma*, with which they basically agree in cell size, gemma color and size, and ecology. The narrow, polymorphous, often trifid leaves, however (compare fig. 199:6, in SCHUSTER, l.c.), which are

diagnostically squarrose at maturity, all argue for a closer affinity to *L. longidens*.

The local collections are from areas with igneous rocks. At Manîtsoq (70–3006) *L. hatcheri* was consociated; at Sarfaq (70–2358a) *L. hatcheri* and *Scapania mucronata praetervisa* were admixed. The association with *L. hatcheri* seems, so far, unusually constant: the types and cotypes also grew with this species (also *Anastrophyllum minutum*, *Gymnomitrion corallioides*, *L. barbata*, and *Plagiochila asplenioides*—all but the last are tolerant of highly intermittent moisture conditions).

Lophozia subapiculata sp. nov. (Fig. 5)

Gemmis viridulis numerosis *L. ventricosae* similis, foliis oblongis, corpusculis oleiferis paucioribus (3–9 in quaque cellula) ab ea diversa. Lobi foliorum saepe apiculis bicellulis terminati. Bracteae femineae valde crispae, crasse dentatae. Ostium perianthii ciliatum.

Distribution (Map 25)

26: Pâkitsup ilordlia (70–2304).

Plants small, prostrate, ca. 1–1.25 mm wide (at the ± crispate gynoecial apices to 1.7–2.0 mm wide), light green, the leaves occasionally light brownish (or brownish with a faint reddish tint) on the margins; stem green to brownish with age (never with vinaceous pigmentation), ca. 270–340 μ in diam. Leaves contiguous to moderately imbricate, laterally patent to more often somewhat antically secund, varying from patent (the adaxial surface visible from above) to subvertically oriented, ranging from nearly flat to loosely caniculate, the lobes usually spreading, rarely feebly incurved, the sinus descending 0.2–0.25, flat to somewhat gibbous (towards apices of ♀ plants becoming strongly gibbous), usually semilunar to obtusangular with a rounded base, occasionally ± sharp; leaf shape oblong to oblong-ovate, ranging from 800–850 μ wide × 830–1000 μ long (width from 0.83–0.98 the length), lateral margins weakly convex, locally almost parallel-sided; lobes mostly obtuse to rectangular, infrequently acutely angular, very often ending in 2 superimposed cells, thus forming a slight apiculus, but occasional lobes blunt at the tips; ventral leaf bases always colorless. Underleaves absent. Cells moderately collenchymatous with flat to moderately convex-sided trigones, along margins averaging 22–26 μ in the lobes (on gemmiparous leaves sometimes slightly larger and 24–28 μ); median cells 23–26 μ wide × 25–35 μ long; basal cells a little larger, ca. 25–30 × 33–48 μ; cuticle smooth. Oil-bodies colorless, finely and consistently granular botryoidal, (2)3–9(11) per cell, mostly ovoid or ellipsoidal, from 4–4.5×6–8.5 to 5–5.5×6.5 to 6–7×8–10 μ, occasional ones spherical and 4–5 μ. Rhizoids colorless, with age brownish at base. Gemmae greenish

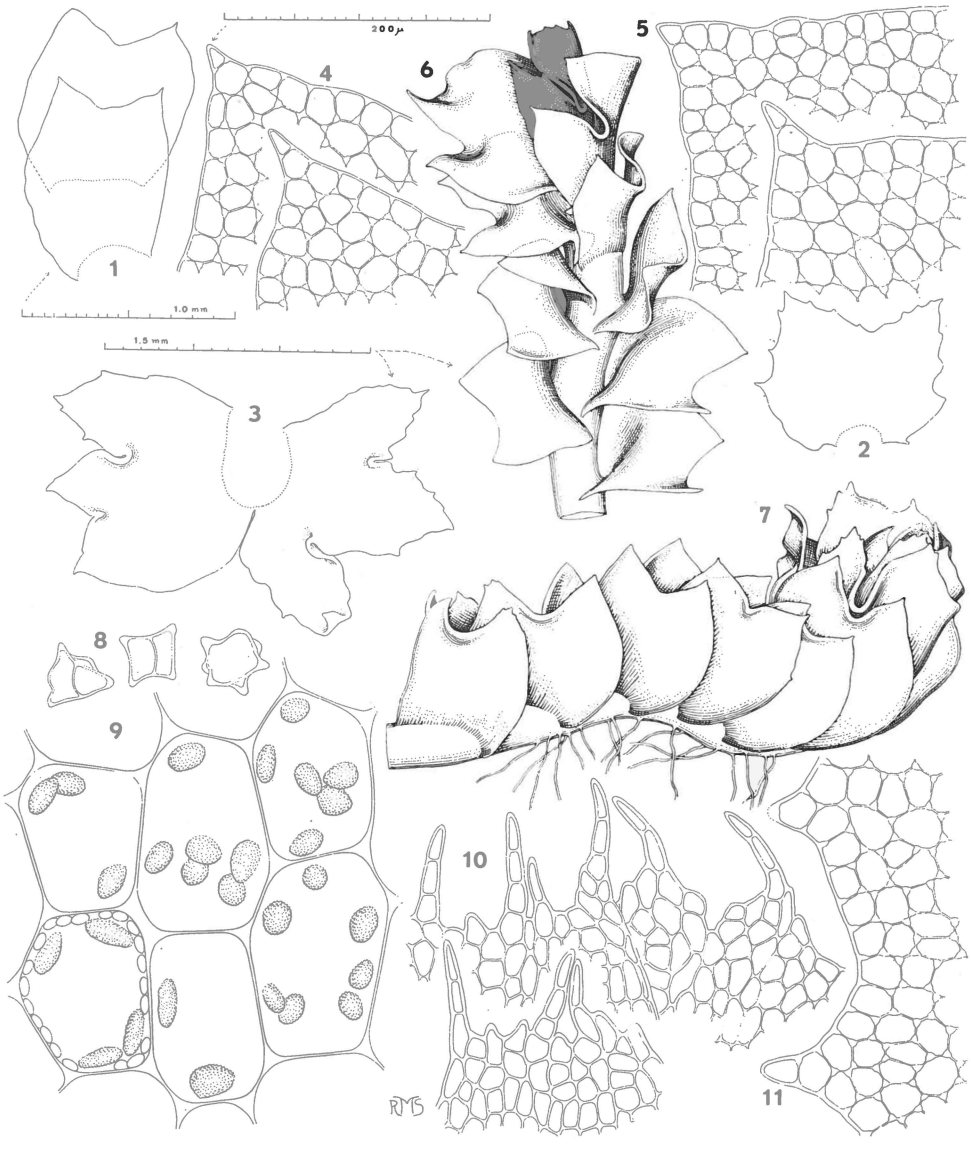


Fig. 5. *Lophozia subapiculata* Schust. & Damsholt. (1) Leaves (×28). (2) Young ♀ bract (×23). (3) Bracts and, lower right, bracteole (×23). (4) Leaf lobe apices, lower leaf in fig. 1 (×175). (5) Same (×175). (6) Shoot apex, antical aspect (×23). (7) Gynoecial shoot apex, showing ♀ bracts (×23). (8) Gemmae (×340). (9) Cells with oil-bodies and, lower left, chloroplasts (×685). (10) Perianth mouth sectors (×175). (11) Teeth from left margin of ♀ bract in fig. 2 (×175). [All from type, 70–2304; 1, drawn to 1 mm scale; 2, 3, 6, 7, drawn to 1.5 mm scale; 4, 5, 10–11, drawn to 200 μ scale].

at maturity, polygonal to sharply stellate, from 19×21 to 25×25 up to 26–27×27–29 μ, usually 2-celled at maturity, the projecting angles thick-walled.

Dioecious. ♂ Plants unknown. Gynoecial plants diagnostically crispate distally, at least on well-developed gynoecia; often with subfloral innovations when unfertilized; upper leaves below bracts somewhat larger, very often strongly gibbous in the sinus, often with reflexed margins, usually bifid, with sharp but edentate lobes. Bracts green or with brownish distal portions, one free, the other fused with the bracteole, or both fused up to 0.4 length of the bracteole, rather strongly crisped with reflexed sinuses and margins, typically one bract bifid, the other trifid, sinuses descending to 0.2–0.35(0.4), ovate-quadrate to broadly quadrate in outline, 820–1285 μ wide, 1025–1200 μ long, the lobes typically acute, the outer bract margins usually with 1 or 2, or sometimes several, coarse to small teeth, one or the other of the bract bases occasionally with a small tooth; bracteole typically oblong and to 635 μ wide × 850 μ long, then bifid for 0.2–0.3 its length, ranging to lanceolate and 290 μ wide × 1025 μ long, mostly edentate on the margins. Perianth (known only immature) strongly pluriplicate distally, the mouth shallowly plurilobulate and closely ciliate, the cilia often crowded, uniseriate for most of their length, frequently 2 cells wide at base and to 110–135 μ long, uniseriate distally for (2)3–4–5 cells, the terminal cells often strikingly elongate, up to 30–36 μ long × 12–14 μ wide; on some perianths the lobulate mouth more remotely ciliate with the broad-based lobes mostly ending in cilia formed of only 2–3(4) superimposed elongate cells and 60–70(90) μ long only.

Type. 26: Pâkitsup ilordlia, Qissugssalik (70–2304).

Known only from the type which occurred mixed with *L. polaris*, *Scapania curta*, and *L. heterocolpos*.

This small, green *Lophozia*, bearing only limited brownish pigmentation of the upper leaf lobes and bract margins, is difficult to place. The abundant greenish gemmae give the initial impression of a small form of *L. ventricosa;* the rather oblong leaves of sterile stems suggest *L. ventricosa* var. *silvicola*. Closer inspection, however, makes such a disposition impossible to maintain, for the following reasons: (1) ♀ Bracts show striking, if sporadic, dentition on the distal margins—at least one bract in every gynoecium being thus dentate. (2) Bracts and subfloral leaves have markedly gibbous sinuses (and often reflexed margins), and, under optimal conditions, appear crisped and fluted. (3) Dentition of the perianth mouth, when optimally developed, exceeds anything found in *L. ventricosa s.l.* Although *L. v.* var. *confusa* may have perianth teeth 2–3–4 cells long, these never attain a length of 5 cells and are never accompanied by den-

tate bracts. (4) The typically oblong leaves, with slightly convex margins, recall those of *L. porphyroleuca*, but that species never has gibbous sinuses, always has strong reddish pigmentation ventrally, and has narrow bracts with edentate margins. (5) The few oil-bodies per cell—mostly 3–9—recur again in *L. porphyroleuca* and *L. v. confusa*, but the average number of oil-bodies per cell in these taxa is still somewhat higher. (6) Lobes of leaves from nongemmiparous shoot sectors are often diagnostically apiculate with a 2-celled apiculus; such sharp tips are quite exceptional in other taxa of the *Ventricosae*. Thus it seems impossible to "force" the present plants anywhere within the precincts of the *L. ventricosa-porphyroleuca* complex. Indeed, dentition of the ♀ bracts is found again within sect. *Lophozia (Ventricosae)* only in *L. rubrigemma*, a species with much larger cells, many more oil-bodies per cell, and large, bright red gemmae. Thus, even though the sterile dead plant may be impossible to place, it seems that a well-defined new species is at hand.

Lophozia ventricosa (Dicks.) Dumort. *s.l.*

Distribution (Map 22)

1A: Behind Arctic Station (66–0185). 6: Eqalúnguit (70–2245). 15: Kronprinsens Ejland (70–2125). 17: Tupilak (66–0019a, 66–0117, 66–0118, 66–0121). 18: Grønne Ejland (70–2814). 23: Kangersuneq (70–3142). 24: Jakobshavn (66–0225b, 66–0246, 66–0247). 26: Pâkitsup ilordlia (70–2256, 70–2260, 70–2317a). 29: Ritenbenk (66–0270). 31: Anap nunâ (70–2425). 36: Umanak (66–1471). 37: Agpat (66–1436). 46: Qalatôq (66–1110). 48: Amitsup (66–0813). 53: Søndre Strømfjord (66–0051).

This *typus polymorphus*, perhaps the most malleable Greenland hepatic, is here very broadly defined (as in Schuster, 1969) to include essentially all plants with (1) green (rarely tardily fuscous) gemmae; (2) ♀ bracts with the lobe margins consistently edentate; (3) leaves whose lobe tips are rarely incurved and vary from blunt to sharp but never bear apiculate lobes with tips formed by 2 sharp superposed cells; (4) leaves, admittedly variable in shape, usually canaliculate or loosely folded and never spoon-shaped or strongly concave; (5) leaves never narrowly oblong as in *Lophozia porphyroleuca*.

Criteria 2 and 3 separate all phenotypes from the puzzling *L. subapiculata;* criteria 3 and 4 separate all phases from those of *L. wenzelii*. Nonetheless, phases of *L. ventricosa confusa* may approach *L. subapiculata*, and the larger-celled *L. ventricosa rigida* may be almost inseparable from *L. wenzelii lapponica*. Our only reason, actually, for maintaining a distinction between *L. ventricosa* and the other three taxa *(L. porphyroleuca, L. subapiculata, L. wenzelii)* with greenish gemmae, lies in the fact that, as defined here, *L. ventricosa* is already a tremendously variable entity.

The seven extremes recognized may be separated in the key on p. 109 (modified from SCHUSTER, l.c. with addition of v. *grandiretis*, newly reported for the North American Arctic).

In a strictly biological sense, it seems probable to us that several of the taxa recognized in the following key represent good species, albeit "microspecies". Thus, var. *confusa*, which typically quite lacks any reddish pigmentation, may, in extreme sun forms, develop fuscous gemmae (p. 111) which, along with the longly dentate perianth mouth and the rather few oil-bodies per cell, almost suggest that the plant be given the status of a *bona-fide* species. Similarly, Arctic populations we attribute to varieties described from temperate-boreal populations (e.g., var. *silvicola*), may deviate perceptibly in one or more respects. Thus, on p. 117, we show that at least some plants (70–2538) attributed to var. *silvicola* have a lobulate-ciliate perianth mouth such as never seems to occur in "normal" *silvicola* and that, in the combination of biconcentric oil-bodies and longly dentate perianth apex, these plants agree with those Japanese populations segregated as "*L. silvicoloides*". The entire point—one repeatedly stressed in the discussion of the "*L. ventricosa* problem"—is that *L. ventricosa*, which appears subcosmopolitan in the cool to frigid parts of the northern hemisphere, has imperfectly broken up into a series of genetically distinct populations or perhaps "microspecies". When BUCH (1933) showed that some of these (his *L. ventricosa* and *L. silvicola*) remained distinct in culture (the same "experiment" can be repeatedly observed in nature; thus, in Fig. 6:1–2 we show instances where two obviously distinct taxa, both referred to *L. ventricosa s.l.*, occur intermingled and remain distinct), he demonstrated that he was dealing with distinct genotypes but not, as he claimed, with distinct species. As a consequence, the problem of how to circumscribe *L. ventricosa* must remain fluid; any solution other than the pragmatically-inspired one (in SCHUSTER, l.c.) which is followed here, will be found only as a result of prolonged culture work, in addition to cytological and genetical studies of a large number of populations from the whole range of the species.

If living plants, in good condition, preferably with perianths, are available, then naming these to the varietal level is ordinarily feasible and mostly rather easy. Living material without perianths can ordinarily be placed with use of the following key; we think it is not feasible to name more than a small fraction of plants lacking oil-bodies. As a consequence, we have named, to species only, a rather large number of usually sterile collections (cited above under the species, not under any specific variety). In SCHUSTER (l.c.) no West Greenland plants are referred to var. *ventricosa;* the three collections cited from northwest Greenland are stated to "surely" represent a form "genetically distinct" from var. *ventricosa*. The pigmentation pattern is that of var. *confusa*, of which

they are probably extreme outliers. With this reservation, then, one can state that var. *ventricosa* is unknown from Greenland north of 65° N.

Two of the collections mentioned above, seem to fall reasonably close to var. *ventricosa* itself:

15: Kronprinsens Ejland (70–2125). 26: Pâkitsup ilordlia (70–2317 a).

The first collection usually has spherical oil-bodies, 3.6–5.5 μ, rarely biconcentric, mostly 15–20, rarely 10–15 per cell; perhaps a mod. *viridis* of var. *silvicola* is at hand. The second collection has mostly ± ovoid oil-bodies, (9)10–16(20) per cell.

Key to varieties of *Lophozia ventricosa*

1. Cells small: marginal 20–26 μ, median ca. 20–25×23–28 up to 25–30 ×30–38 μ; gemmae ca. 18–20×20–25 μ.
   2. Leaves generally broad (on mature axes): 0.95–1.25× as wide as long; oil-bodies (2–5)6–18(20) per median cell, many ovoid to elliptical, never biconcentric; rarely if ever with strong vinaceous or carmine pigmentation of leaf bases. . . . . 3.
      3. Perianth mouth armed with 1(2–3)-celled teeth, hardly lobulate; cells mostly with 9–16 (occasional cells with 17–21) oil-bodies . . . . . 4.
         4. Leaf lobes usually sharp and sinuses never gibbose; lobes almost uniformly 2; rarely reddish or pinkish locally, with perianths rarely strongly reddish; oil-bodies to 5–6×6–8 μ; gemmae abundant. (Absent in Arctic?) v. *ventricosa*
         4. Leaf lobes often blunt to narrowly rounded, sinuses often gibbose; leaf lobes sporadically 3; usually dense-leaved and with subvertical leaves; often strongly reddish tinged and with red perianths (bleached at mouth); oil-bodies to 7–8× 9–12 μ; gemmae rare. v. *longiflora*
      3. Perianth mouth armed with (1)2–3(4–5)-celled teeth, often arising from a broad base, the mouth ± lobulate; cells with (2–5)6–12(13–15) oil-bodies each. Pigmentation brown to warm brown (rarely fuscous) distally, the leaf bases usually lacking wall pigments (rarely feebly reddish). . . . . 5.
         5. ♀ Bracts with lobes and margins edentate, noncrispate; nongemmiparous leaf lobes not apiculate; oil-bodies (2–5)6–12(13–15) per cell; leaves of sterile shoots mostly 0.95–1.2× as wide as long, 0.25–0.45(0.5) bilobed . . . . . v. *confusa*. . . . . a.
            a. Leaves hardly wider than long, bilobed 0.3 or less; lobes rarely ending in 2 superposed cells. f. *confusa*

a. Leaves broadly quadrate, 1.1–1.2× as wide as long, bilobed 0.35–0.45(0.5) their length; lobes often ending in 2 superposed cells. f. *discoensis*

5. ♀ Bracts with lobes ± dentate to repand-dentate, crispate, with gibbose sinuses and ± reflexed margins; nongemmiparous leaf lobes sharp, ± apiculate; oil-bodies (2)3–9(11) per cell; leaves of sterile shoots mostly 0.8–1.05× as wide as long, 0.2–0.25 bilobed.
see *L. subapiculata*

2. Leaves generally narrow, oblong to oblong-ovate, (0.75)0.8–0.95 (1.05)× as wide as long; oil-bodies (4–6)7–21(24) per cell, usually spherical and to 5–6×5–7 μ or less, biconcentric in all or most cases. Light green, often with brilliant red pigmentation (especially of leaf bases). v. *silvicola*

1. Cells large: marginal cells of distal half of leaf (28) 30–34 (38) μ, median (28) 30–38 × (30) 35–45 (50) μ; gemmae ca. (26) 28–31 (33) × (31) 34–36 (38) μ at maturity. Leaves quadrate-ovate to broadly orbicular, with ± strongly arched sides, 1.05–1.35(1.5)× as wide as long, with sharp lobes. Oil-bodies (14)15–25 per cell or more..... 6.

6. Oil-bodies (25)30–50(55) per cell, only 3.5–4.5 μ, biconcentric, spherical. Ventral leaf bases vinaceous, distal parts of leaves ± reddish or purplish red (in part mixed with brown). v. *grandiretis*

6. Oil-bodies (14)15–20 to 21–25 per cell, the larger to 5–7×9–10 μ, ovoid to elliptical, nonbiconcentric. Ventral leaf bases and stem surface dull purplish; leaf lobes ± light brown, usually with no trace of reddish. v. *rigida*

Lophozia ventricosa v. *confusa* SCHUST. (Fig. 6:2)

Distribution (Map 21)

1A: Behind Arctic Station (70–2019a, 70–2022, 70–2029, 70–2035a, 70–2043a, 70–2050). 1B: Lyngmarken (66–0159, 66–0558). 1D: Skarvefjeld (66–0311a). 6: Eqalúnguit (70–2214a, 70–2227g). 7: Angûjârtûtit (70–2161c, 70–2175, 70–2181a). 9: Eqaluit (70–2522, 70–2529a, 70–2532, 70–2534, 70–2535, 70–2536a, 70–2541, 70–2550b). 14: Hareøen (70–2618, 70–2620). 15: Kronprinsens Ejland (70–2073, 70–2099). 16: Manîtsoq (70–3003a, 70–3002a). 17: Tupilak (66–0020 f. *discoensis*). 21: Umiasugssûp (70–2939a). 22: Orpigsôq (70–3108a). 24: Jakobshavn (66–0219, 66–0222). 25: Sarfaq (70–2347, 70–2364). 26: Pâkitsup ilordlia (70–2302, 70–2387). 29: Ritenbenk (66–0263). 30: Eqe (66–0328). 31: Anap nunâ (70–2412a). 32: Qôrorssuaq (70–2440d, 70–2471a). 46: Qalatôq (66–1102c).

This appears to be the common Arctic replacement for var. *ventricosa*, from which it differs (SCHUSTER, l.c.) principally in (a) lower average

number of oil-bodies per cell (see SCHUSTER, l.c., fig. 210:1–6); (b) general lack of reddish pigmentation—the leaf bases usually being quite devoid of reddish pigmentation, the distal portions of leaves becoming brownish in sun forms; in some cases limited amounts of admixed purplish or red pigment occur; (c) much more strongly armed perianth mouth (see fig. 209:1–4, 8–10, in SCHUSTER, l.c.). Oil-body number shows some deviation: in 70–2534 there are (2–3)4–12 per cell; in 70–2175 and 70–2541, (2)3–9(12); in 66–0263, 70–2471a, and 70–2019a, (2)3–9; in 70–2618, 5–10; in 70–2214a, 70–2347, and 70–2535, (2)3–8(10); in 70–2550b, (2–3)4–9(10); in 70–2181a, (3)4–11(12); in 70–3108a, (3–4)5–14(16); in 70–2227g, (3)4–10(12); in 70–2161c, (3)4–13(15–17) per cell. These counts are in addition to those published in SCHUSTER (l.c.) based on the 1966 collections. Maximal oil-body sizes range from 5–6×9–12 μ (70–2471a), 7×13 to 8×15 μ (70–2161c), 7×14 μ (70–2181a), 5×8–10 μ (70–2043a, 70–2019a) to 5–6×10–11 μ (70–2175); no oil-bodies are ever biconcentric. These figures are cited to more accurately establish varietal perimeters than could be determined from the few living collections earlier available. Critical in placing all these collections here is the fact that in all collections studied, some median cells bear only 2 or 3 oil-bodies. Also, the perianth mouth is armed with teeth of 1–2–3 cells (66–0263) or 2–3 cells to 2–3(4) cells (in 70–2347 and 70–2227g) and only occasionally with 1–2-celled teeth (in 70–2534). These figures are in agreement with the illustrations in fig. 209:1–4, 8–10 in SCHUSTER (l.c.).

Two notable deviations occur: (1) In 70–2550b there is some red pigmentation of the ventral side of the stem and, rarely, ventral leaf bases; in 70–2175 (which in some ways is transitional to var. *longiflora*) we find a little carmine pigmentation of the upper leaf lobes. (2) In two collections, from insolated, xeromorphic sites (associated with *L. hatcheri*, *Gymnomitrion concinnatum*, etc.) the gemmae becoming fuscous at maturity. The collection from Dundas, Wolstenholme Fjord (cited on p. 566 in SCHUSTER, l.c.), also with "initially green gemmae" that are "dull brown to purplish brown" with maturity like the leaf lobes, surely represents a similar phenotype. If the ability, in extreme sun forms, to develop fuscous pigmentation of the gemmae is a constant for var. *confusa*, its elevation to species status could probably be justified. In any event, "normal" phases, growing in less extreme sites, show gemmae that remain greenish at maturity, even when (as is normal) the distal portions of the leaves develop brownish pigmentation. Apparently only in the extremes, from very dry, exposed niches (e.g., 70–2035a, with *Gymnomitrion concinnatum*, *Scapania lingulata*, *L. kunzeana acuta*) do we find the mod. *fuscata-angustifolia-parvifolia*, in which the gemmae tend to become fuscous.

The var. *confusa* is the most common, most nearly ubiquitous phase

of the species in West Greenland. Plants occur mostly on damp soil or peat, sometimes moist sand, or between rocks, amidst mosses and other *Hepaticae*, usually in medium to strongly acidic sites. Commonly associated are *Pleuroclada albescens* (in 6 collections), *L. hatcheri* (2 collections), *L. kunzeana* (4 collections), *Blepharostoma trichophyllum brevirete* (3 collections), *Anastrophyllum minutum* (3 collections), less often: *Calypogeia sphagnicola*, *L. quadriloba*, *L. excisa*, *L. opacifolia*, *L. elongata*, *L. cavifolia*, *L. latifolia*, *Odontoschisma elongatum*, *Cephalozia pleniceps*, and *Scapania hyperborea*. The last 4 taxa are associated chiefly in acid, peaty, often irrigated sites. The sporadic occurrence with *L. heterocolpos* and *L. grandiretis* suggests the plant can tolerate feebly basic conditions; it seems, however, by far most frequent in areas with gneiss and other igneous rocks. Perianths and androecia are frequent; capsules are rare. In addition to the various phenotypes accounted for above, an extreme is formed by:

f. *discoensis* SCHUST.

Known only from the type, with its distinct leaves usually 1.1–1.2× as wide as long and bilobed 0.35–0.45(0.5) into two broadly triangular, often apiculate lobes which usually end in 2 superposed cells. Associated were *Blepharostoma trichophyllum brevirete* and *L.* cf. *groenlandica*.

v. *rigida* SCHUST. (Fig. 6:1)

Distribution (Map 21)

1B: Lyngmarken (66–0563). 9: Eqaluit (70–2530a, 70–2546b, 70–2552). 15: Kronprinsens Ejland (70–2063a). 16: Manîtsoq (70–3020a). 17: Tupilak (66–0115). 21: Umiasugssûp (70–2939a). 25: Sarfaq (70–2356, 70–2357, 70–2361). 26: Pâkitsup ilordlia (70–2267a, 70–2300, 70–2308a, 70–2387a). 28: Atâ (70–2512a). 32: Qôrorssuaq (70–2440c).

This variant was described from 66–0563 in SCHUSTER (1969) on the basis of the combination of (a) large cell size—suggesting a polyploid; (b) no trace of clear red pigments, the ventral leaf bases "dull purplish"; (c) the leaf cells with mostly 14–20 nonbiconcentric oil-bodies, often irregularly ellipsoidal in shape; (d) large gemmae. In 1970 a considerable suite of additional collections was made, all from acidic sites. The plants occur mostly with *Pleuroclada*, *Anthelia*, *L. kunzeana*, *L. hatcheri*, *Scapania hyperborea*, *Cephalozia bicuspidata*, *L. cavifolia*, *Tritomaria quinquedentata*. Also associated are *L. wenzelii wenzelii* (70–2546b), *L. alpestris* (70–2440b) and *L. ventricosa grandiretis* (70–2440c). The ability of the two large-celled phases of *L. ventricosa*—one a presumed polyploid of var. *confusa*, the other a presumed polyploid of var. *silvicola*—to occur together (as at Qôrorssuaq; 70–2440c) seems to suggest that perhaps the *silvicola-grandiretis* complex should be divorced from *L. ventricosa*. In

70–2512a var. *rigida* occurs with plants having red leaf apices and smaller cells; these appear to represent *L. v. longiflora*—again suggesting the last perhaps ought to be treated as a separate species. In 70–2387a a trace of *L. v. confusa* is admixed.

The additional collections somewhat broaden the perimeters of this variant. Oil-bodies range from (8)12–18 or more (70–2546b) to (5–6)7–15 (70–2440c) to 6–18 per cell (70–2512a) or 14–18 (70–2356) or 16–21 (70–2552) per cell. Although leaf bases and the ventral side of the stem may be dull purplish, in 70–2356 leaf bases lack such purplish pigmentation.

One atypical gathering is 70–2357, sharing with *L. heteromorpha* the occasional presence of underleaves—sometimes large—near the shoot apex; the occasionally trilobed leaves; leaf lobes and margins often purplish pigmented towards the shoot apex; nonbiconcentric oil-bodies. The plants of 70–2357, however, approach typical var. *rigida* in: large cells, those of margins in lobes (26)30–35 μ; median cells (28)30–33 × 35–39 μ or larger; polygonal-substellate gemmae, (20)22–25 × 34–44 μ. In all of these characters it is quite distinct from *L. heteromorpha*, in spite of the superficial similarity on the basis of pigmentation.

Lophozia ventricosa v. *longiflora* (Nees) Macoun (Fig. 6:6–9)

Distribution (Map 12)

1A: Behind Arctic Station (70–2042, 70–2056). 1B: Lyngmarken (66–0551, 66–0557). 6: Eqalúnguit (70–2238a). 15: Kronprinsens Ejland (70–2060a, 70–2067). 18: Grønne Ejland (70–2815a). 22: Orpigsôq (70–3106). 32: Qôrorssuaq (70–2440d).

Additional collections:

6: Eqalúnguit (M.P.P. 3848). 17: Tupilak (K.J. 1445, K.H. 13.015). 24: Jakobshavn (K.H. 16.043). 90: Tasiussaq (S.B. July 1870). 112: Umiartorfik (K.J. 605). 122: South of Eqaluit (K.H. 13.353). 131: Storø (A.R. July 1954). 142: Niaqornánguaq (K.H. 14.949b).

This well-marked phenotype usually occurs in acidic, most often boggy, sites amidst *Sphagnum* or *Aulacomnium*, associated with *Cephalozia pleniceps*, *C. bicuspidata*, *L. wenzelii wenzelii*, *L. binsteadii*, *Pleuroclada albescens*, *Scapania paludicola*, *S. curta*, *Anastrophyllum minutum*, *Riccardia sinuata*, *Mylia anomala*, and *Calypogeia sphagnicola*. It occurs with *L. heterocolpos*, a plant often found on peaty ground over basic substrates, but otherwise it never occurs with Ca-demanding taxa.

Known from Greenland only from the above localities. The Disko material was described and illustrated in Schuster (l. c.), where the blunt to obtuse—or even rounded—leaf lobes and gibbous sinuses of the leaves were emphasized as diagnostic for this variety (compare fig. 208:7–8, 10–11 in Schuster, l. c.); the perianth mouth was described as with low, "remote to locally subcontiguous, small, almost uniformly 1-celled

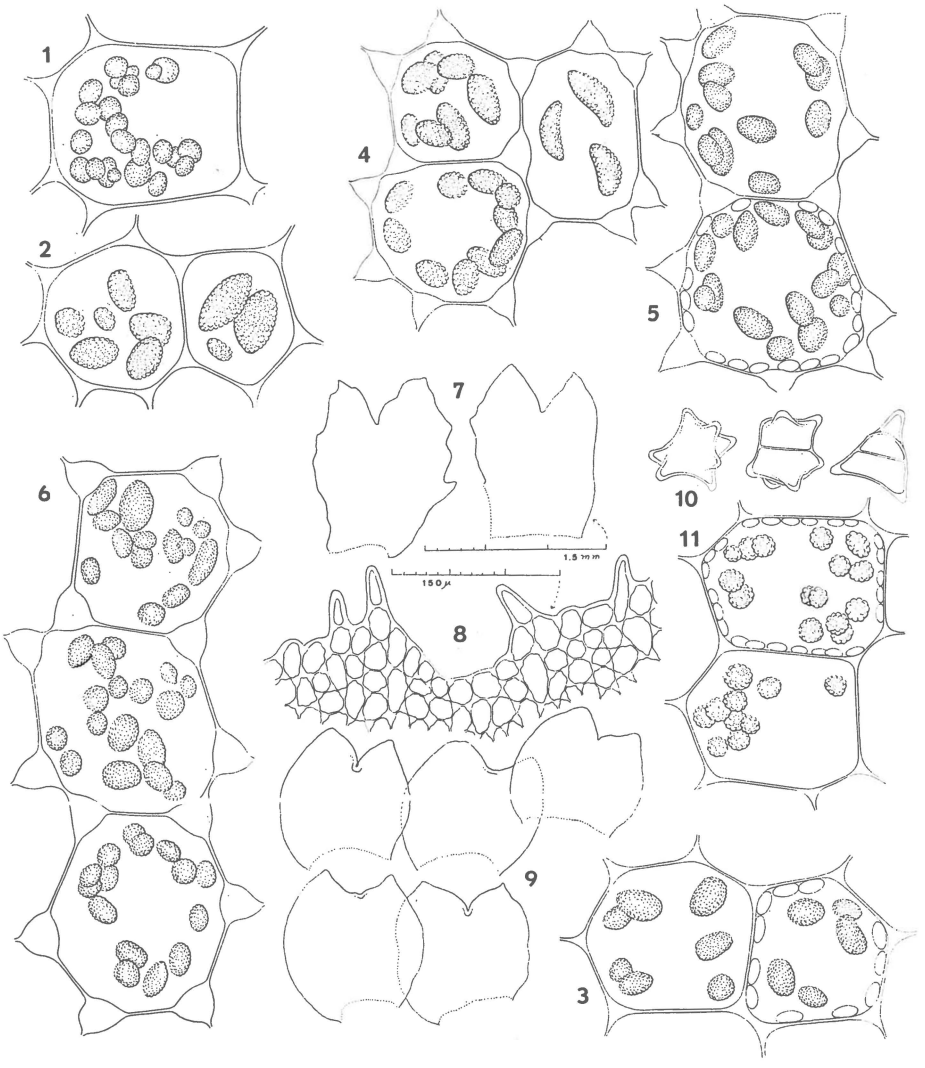


Fig. 6. *Lophozia* subg. *Lophozia:* Sectio *Ventricosae.* (1) *L. ventricosa v. rigida*, median cell (×615). (2) *L. ventricosa v. confusa*, from plant growing amidst that shown in fig. 1, median cell (×615). (3) *L. wenzelii v. wenzelii*, typical, median cells (×815). (4) *L. wenzelii v. wenzelii*, atypical, median cells (×735). (5) *L. ventricosa v. rigida* (questionable; phase like *L. v. longiflora* in color), median cells (×615). (6–9) *L. ventricosa v. longiflora*, typical coloration. (6) *L. ventricosa v. longiflora*, typical, median cells (×690). (7) ♀ Bracts (×16). (8) Perianth mouth cells (×145). (9) Leaves (×16). (10–11) *L. pellucida v. minor.* (10) Gemmae (×350). (11) Median cells (×705). [1–2, from intermixed plants, Pâkitsup ilordlia, 70–2387; 3, Eqaluit, 70–2531; 4–5, 70–2530; 6–9, 70–2815a, Grønne Ejland; 10–11, 70–2739a, Qasigíssat, Disko; 7, 9, drawn to 1.5 mm scale; 8, drawn to 150 μ scale].

teeth that are not conspicuously elongated." Also emphasized was the tendency towards formation of "yellow-brown, warm pigmentation of distal parts of leaves" which, on the type material (and the Disko material) is mixed with reddish pigmentation, while the ventral side of the stem is deep red, with the red color spreading to the ventral leaf bases. Plants from Grønne Ejland (70–2815a) agree in most respects: leaf form; blunt to rounded lobes; often strongly gibbose sinuses; coarse trigones; large number of oil-bodies [9–16(17–21) in the Disko plants; (9)14–18(22) in the Grønne Ejland plants] that are variable and nonbiconcentric, the largest oil-bodies to $7 \times 10\ \mu$ (Grønne Ejland plants) or even $7.5–8 \times 9–12\ \mu$ (Disko plants); ♀ bracts with blunt to rounded lobes; the warm, light brown tint to the upper parts of leaves; the rarity of gemmae. In other respects the Grønne Ejland plants differ appreciably: they lack all reddish pigments and have a slightly more dentate perianth mouth, with teeth alternately 1- and 2-celled. The dentition of the perianth mouth, however, remains by far the weakest in all Arctic phases of *L. ventricosa s.l.* seen.

This variety, found only in the Precambrian region, often gives the impression of being a well-defined, independent species, with its own range of variation. Plants often occur in exposed rich fens, or over *Sphagnum* on peaty slopes, in full sun. They are then usually pinkish- to reddish-tinged (as 70–3106); the pigmentation is never confined to the ventral leaf bases, but occurs on lobes and marginal portions of leaves and bracts as well. Diagnostic is the gynoecium which is strongly crispate prior to perianth elongation. Equally diagnostic are the few greenish gemmae and the quadrate to broadly quadrate leaves, usually with an angular sinus that is often rounded at the base and very often conspicuously gibbous. Finally, the very small and often minutely projecting, remote perianth mouth teeth, are often formed in large part of mere projecting free ends of laterally coherent cells, although scattered 1- and occasionally even 2-celled teeth may occur. All of these features are well marked in the luxuriant and copious plants of 70–3106 (with *Calypogeia sphagnicola*, *Mylia anomala*, in a boggy slope with *Ledum*).

In these plants leaves tend to be considerably broader than long—broader than figured in Schuster (l.c.) for the variety. The oil-bodies are somewhat troublesome: they are very preponderantly spherical, occur (7)8–16(20) per cell and although usually formed of similar-sized spherules throughout, occasionally have a centric or excentric larger sphere—hence, in number and form some slight transition to *L. v. silvicola* occurs. It is the existence of such partial transitions that dictates treatment of *longiflora* as a variety rather than species.

The variety often bears perianths and androecia and has been found (66–0557; July 30–31) with capsules.

Lophozia ventricosa v. *silvicola* (BUCH) JONES (Fig. 7:1–7)

Distribution (Map 21)

2: Fortunebay (66–0208a). 9: Eqaluit (70–2538). 16: Manîtsoq (70–3013). 17: Tupilak (66–0006, 66–0014b). 18: Grønne Ejland (70–2810d). 19: Nûk (70–2869b, 70–2885b). 21: Umiasugssûp (70–2941, 70–2948f). 22: Orpigsôq (70–3109). 25: Sarfaq (70–2365a). 26: Pâkitsup ilordlia (70–2294d). 29: Ritenbenk (66–0257a). 31: Anap nunâ (70–2405). 32: Qôrorssuaq (70–2483). 37: Agpat (66–1422a, 66–1451).

Additional collection:

88: Christianshåb (K.H. 16.824a).

This variant is apparently rather frequent in the Disko Bugt region, almost exclusively in areas with acidic rocks, often occurring in well-lit, rather helophytic sites as in boggy meadows traversed by rills and pitted by pockets of standing water, associated with *Mylia anomala*, *Calypogeia sphagnicola* (70–3109) or *C. sphagnicola*, *L. opacifolia*, *L. polaris sphagnorum*, *Cephaloziella subdentata* (70–2885b), or *Mylia*, *Blepharostoma t. trichophyllum*, *Cephalozia leucantha*, *C. lunulifolia*, *C. bicuspidata*, *Anastrophyllum sphenoloboides* (70–2810d); the last two taxa, plus *A. minutum*, *Calypogeia sphagnicola*, and *L. binsteadii* occur associated in 70–2294d. Less often, on acid, peaty soil, *Pleuroclada albescens*, and *L. cavifolia* may be associated (70–2538, 66–0257a, 70–3013). Relatively rarely found in rather xeric sites (70–2483, with *L. hatcheri;* 70–2948f, with *Prasanthus*, *Gymnomitrion concinnatum*, *Solenostoma sphaerocarpum*, *L. excisa*, *Anastrophyllum sphenoloboides*, *Scapania parvifolia*). Similarly, it is more frequent on exposed hummocks in helophytic areas, where subject to partial desiccation; an exception is 70–2869b, in wet ground around tarns, with *Scapania hyperborea*, *S. paludicola rotundiloba*, and *Odontoschisma macounii.*

All plants placed here bear biconcentric oil-bodies, almost always spherical; they ranged from typically (12)13–20 per cell (70–2869b, 70–2941) to (7–9)12–19(22) per cell (70–2885b, 70–3109), to 15–19 per cell (70–2483), to 15–25 per cell (70–2948f), to 12–18 per cell (70–2365a), to (10)15–23 per cell. In only one collection (70–2810d), in which all or most oil-bodies are of the biconcentric, *silvicola* type, are there only (4–5)6–15(16) oil-bodies per cell; see Fig. 7:7. In a few other cases, the oil-bodies, although essentially all spherical and rather small, are only in part biconcentric (Fig. 7:1). In 70–3109 60–80 % of the oil-bodies are biconcentric. Varying amounts of strong reddish pigmentation, especially of ventral leaf bases, have been seen in all of the collections.

The plants of 70–2538 are pertinent in evaluating *L. silvicoloides* KITAGAWA (1965), which was placed in "provisional synonymy" under *L. ventricosa* var. *silvicola* in SCHUSTER (1969, p. 570); therein is expressed the opinion that "possibly" the plant "should be regarded as a discrete variety, parallel with var. *silvicola*", on the basis of the "ciliate-laciniate

perianth mouth with teeth 3–6 cells long". In 70–2538 the perianth apex is lobulate-laciniate with narrow laciniae or teeth 5–6 cells long, with the apex uniseriate for 2–3 cells; the terminal cell, furthermore, is strongly elongated and to 16.5×67 μ, although usually much shorter. Correlated are: (1) narrow, rather patent, ovate leaves, ranging from 860 μ wide × 820–960 μ long to 1030 μ wide × 1100 μ long (width 0.9–1.05 length, averaging slightly longer than wide), with a normally angulate sinus descending 0.25; (2) brilliant red coloration which varies a good deal, depending on exposure: plants growing exposed first develop intensive red pigmentation of distal portions of the leaves which, not far behind the apex, is partially masked by yellow-brown pigments, resulting in a brownish red to dull red coloration; initially no pigment of the leaf bases is present, but vinaceous pigmentation, often very intensive, develops not far behind the apex and spreads to the postical (and sometimes entire) leaf bases. In shade forms no secondary pigments develop except for this last type of often exceedingly intense coloration. (3) Most, but not all, oil-bodies are spherical, ca. 13–24 per cell, some biconcentric, but in many cells most or even all are formed of similar-sized spherules throughout. Such plants suggest that *L. silvicoloides* is best regarded as one of several extremes of v. *silvicola*.

Although the status of *L. silvicola* as a species has been defended on the basis of study of only non-Arctic material (Schuster, 1953), more exhaustive study (Schuster, 1969) has shown that there is very imperfect correlation between the two principal features regarded as diagnostic of "*L. silvicola*": rectangulate leaves that are slightly to clearly longer than wide; many, spherical, biconcentric oil-bodies per cell. This examination of several West Greenland collections reinforces the wisdom of considering "*L. silvicola*" as a variety within a broadly conceived *L. ventricosa*. Thus occasional plants (e.g., 70–2294d) show, on young growth, the strong, rose-red coloration typical of v. *silvicola*, with the postical bases usually more strongly vinaceous; on old growth, however, these pigments are often lacking, with a brown pigment developed. Leaves may range, in allometric pattern, from narrower than long (weak shoots) to quadrate-orbicular and fully as wide as long or more (robust shoots). Oil-bodies are a problem: some shoots show no biconcentric oil-bodies, others have them biconcentric in younger leaves, nonbiconcentric in older leaves. With few exceptions oil-bodies are spherical and usually occur 12–22 per cell. The sharp lobes, relatively flat leaves and their orientation, the form of the sinus, color, and aspect all speak for var. *silvicola*, but the leaf shape and oil-bodies allow no such easy placement. [Plants from Grønne Ejland (70–2810d) are rather similar but are atypical in that oil-body number is often lower, on some leaves only (4–5)6–15(16) occur per cell, on other leaves (5–8)9–17(18) per cell, and in that some oil-bodies

are not biconcentric, while many are rather indistinctly so (Fig. 7:7)]. Such collections serve to reinforce the conservative position taken which relegated "*L. silvicola*" to the status of a variety of *L. ventricosa*. The present plants could be considered as transitional to var. *ventricosa* itself.

Equally problematic is 70–3013: it has the narrow leaves BUCH (1933) regarded as typical of this taxon and the many, small, spherical oil-bodies, each biconcentric, normal to var. *silvicola*. Very intense, vinaceous red pigmentation at the ventral leaf bases is also produced, even in otherwise green forms. In other respects the plants diverge strongly: sinuses are usually lunate and shallow, although sometimes angular; cells vary in size and are, in part, appreciably larger (ranging towards var. *grandiretis* in size); leaves, associated with creeping growth on exposed dead peat, are strongly concave in many cases and quite small (indeed, the plants as a whole are atypically small). Most strongly divergent of all are the distinctly striolate leaves—a feature not seen elsewhere within subg. *Lophozia*.

We have presented the above evaluation of several "*silvicola*" phenotypes in order to reinforce the treatment of this taxon as simply a variety of the malleable and almost incomprehensibly polymorphic *L. ventricosa* (see SCHUSTER, l.c.). It is perfectly obvious that each of these gatherings diverges from the others at one or more salient points and, without question, renders recognition of varieties within *L. ventricosa* a matter of great difficulty. In fact, without oil-bodies available for study, determination of *L. ventricosa* to the varietal level is, we think, impossible. Even with oil-bodies present, some gatherings will remain unplaceable since they combine characters of the various phenotypes here recognized as varieties of *L. ventricosa*.

v. *grandiretis* (BUCH & S. ARN.) SCHUST. & DAMSHOLT, comb. n. (Fig. 7:8–13)

Basionym: *Lophozia silvicola* v. *grandiretis* BUCH & S. ARN., Sv. Bot. Tidskr. 44:82, 1950.

Distribution (Map 22)

15: Kronprinsens Ejland (70–2101). 16: Manîtsoq (70–3003a). 17: Tupilak (66–0023). 32: Qôrorssuaq (70–2440a, 70–2441, 70–2450a, 70–2461, 70–2462, 70–2464, 70–2468, 70–2469, 70–2470, 70–2473, 70–2474).

This variant is known from a few localities only, but it has probably been repeatedly overlooked. It is known only from acidic (igneous and metamorphic) regions; at Qôrorssuaq, where apparently frequent, it occurred on peaty-rocky borders of a rushing, intermittent rill, associated with *L. alpestris*, *L. excisa*, *Marsupella boeckii*, *Gymnomitrion concinnatum*, *Tritomaria quinquedentata*, *L. kunzeana*, *Cephalozia bicuspidata*, and *Pleuroclada albescens*—in part admixed with *Sphagnum*. Less often (70–

2450a) *Scapania subalpina* was associated or (70–2441) *L. wenzelii lapponica.* Almost all collections, including the last two, occurred in admixture with *Tritomaria quinquedentata.* At Manîtsoq it occurred on peaty soil over gneiss, with *Scapania hyperborea, L. alpestris, L. hatcheri, Pleuroclada, Gymnomitrion concinnatum,* and *Tritomaria quinquedentata,* as well as *L. ventricosa confusa. L. v. grandiretis* had 25–35 biconcentric oil-bodies per cell; admixed *L. v. confusa* 3–12 nonbiconcentric oil-bodies. Our plants appear to quite agree with ARNELL's concept of var. *grandiretis* (ARNELL, 1956, p. 118), except that they have larger gemmae; ARNELL gives them as only 18–24 μ.

Var. *grandiretis* has been known only from alpine regions in Sweden and Norway; it is new to the western hemisphere. The following diagnosis is therefore needed:

Plants rigid, brittle, similar to var. *rigida* in aspect and size, but with ventral leaf bases intensely vinaceous and distal parts of upper leaves bright purplish red (often ± mixed with brown) in color; leaves usually broader, most often with a lunate sinus and broadly arched lateral margins; from (800)1175–1500 μ wide × (740)860–1050 μ long, width-length ratio (1.12)1.24–1.5:1; leaves obliquely oriented rather than subvertical, at most shallowly to moderately concave, lobes not or hardly incurved, broadly and obtusely triangular but usually distinctly pointed rather than blunt; sinus usually descending only 0.1–0.2(0.25), lunate to obtusely angular with (usually) a rounded base. Cells large, moderately strongly collenchymatous, with (distally) reddish purple walls on upper parts of apical leaves, on older leaves with reddish brown to brown pigmentation; marginal cells in distal half of leaf (25)28–34(36) μ, median cells 28–38 × 30–40 μ. Oil-bodies very numerous, in lobe and median cells (25)30–50(55) per cell and, perhaps, in some cells more, small (3.5–4 μ) to ovoid and 4–4.8 × 4–6 μ, biconcentric (with a homogeneous centric or excentric "eye" and a finely granular mantle). Gemmae infrequent, green at maturity, 1–2-celled, large (ca. 28–31 × 31–36 μ), pluriangulate-stellate.

The discovery of this vigorous plant was nevertheless the cause of some distress: *L. ventricosa* (with inclusion of *L. silvicola* and *L. longiflora* as varieties and addition of vars. *confusa* and *rigida*) thus acquires almost incomprehensible perimeters. It would appear that var. *confusa* as well as var. *silvicola* has undergone polyploidy (giving rise to var. *rigida* and var. *grandiretis*, respectively). This may be an overly simplified hypothesis, but, until the requisite cytological work can be done, it will need to suffice. Since we know that allometric growth takes place in the leaves, the associated vigor, with polyploidy, would account for the drastically broader leaves.

However, pigmentation patterns are not quite identical to those of var. *silvicola:* the stem may be black purple beneath and reddish-purplish

near the shoot tips, with rhizoid bases purplish, but reddish color at the postical leaf bases, if well developed, is intensely vinaceous. Gemmae in this variety are much larger than in var. *silvicola*, averaging 28–31 × 31–36 μ at maturity [vs. 16–23 × 18–26(35) μ in var. *silvicola*]; in size they agree approximately with those of var. *rigida*.

We think this variety will remain indeterminable in the absence of living cells for study. It may occur with *L. wenzelii* var. *lapponica* (and then has cells almost or quite as large), and both taxa may show some reddish leaf pigmentation. Where mixed (as in 70–2441), living plants showed the following distinctions:

L. ventricosa grandiretis	*L. wenzelii lapponica*
Leaf bases, at least locally, reddish.	No red color of ventral leaf bases.
Oil-bodies small, dense, usually spherical, 25–40 or more (50–55 extreme) per cell, clearly biconcentric.	Oil-bodies mostly ovoid, variable in size and shape, usually 16–20 or fewer per cell, nonbiconcentric.
Leaves broadly quadrate-rounded, sinus occasionally angular, 880 × 740 μ and larger (width ca. 1.2:1).	Leaves very broad, transverse, convex-margined, lunate sinus, 1370 × 1050 μ (width ca. 1.3–1.4:1).

We also place here, with reservations, plants from Manîtsoq (70–3003a, mixed with *L. alpestris*, *L. ventricosa confusa*, *Tritomaria quinquedentata*, and *Pleuroclada*, from a moist, shaded gneiss cliff face) which are purplish ventrally, rather than red (with the purplish or vinaceous color extended to rhizoid and postical leaf bases). These plants quite agree in the large cells and the numerous (25–35 or more) *silvicola*-like, biconcentric oil-bodies, but, if dead, would not be surely placeable; they could be confused with either *L. ventricosa rigida* or, less so, with *L. wenzelii lapponica*. From the latter they differ in the rather frequent angular sinuses and the much less convexly arched sides of the leaves.

Lophozia groenlandica (NEES, in GOTT., LINDENB. & NEES) MACOUN

Distribution (Map 19)

17: Tupilak (66–0017a with *Tritomaria exsectiformis*, 66–0020a).

Additional collection:

88: Christianshåb (K.H. 16.617).

This species is "poorly known and long-forgotten," and probably "Arctic-alpine" in range (SCHUSTER, 1969). It is reported from as far north as 82°26′N, in Ellesmere Island, southward to "microclimatic" tundra areas at the shore of Lake Superior in Michigan and Minnesota. In Greenland known north to Siorapaluk, Robertson Bugt (SCHUSTER, l.c.). The report from East Greenland in JENSEN (1900) is based on plants of *T. polita* (see pp. 148–149).

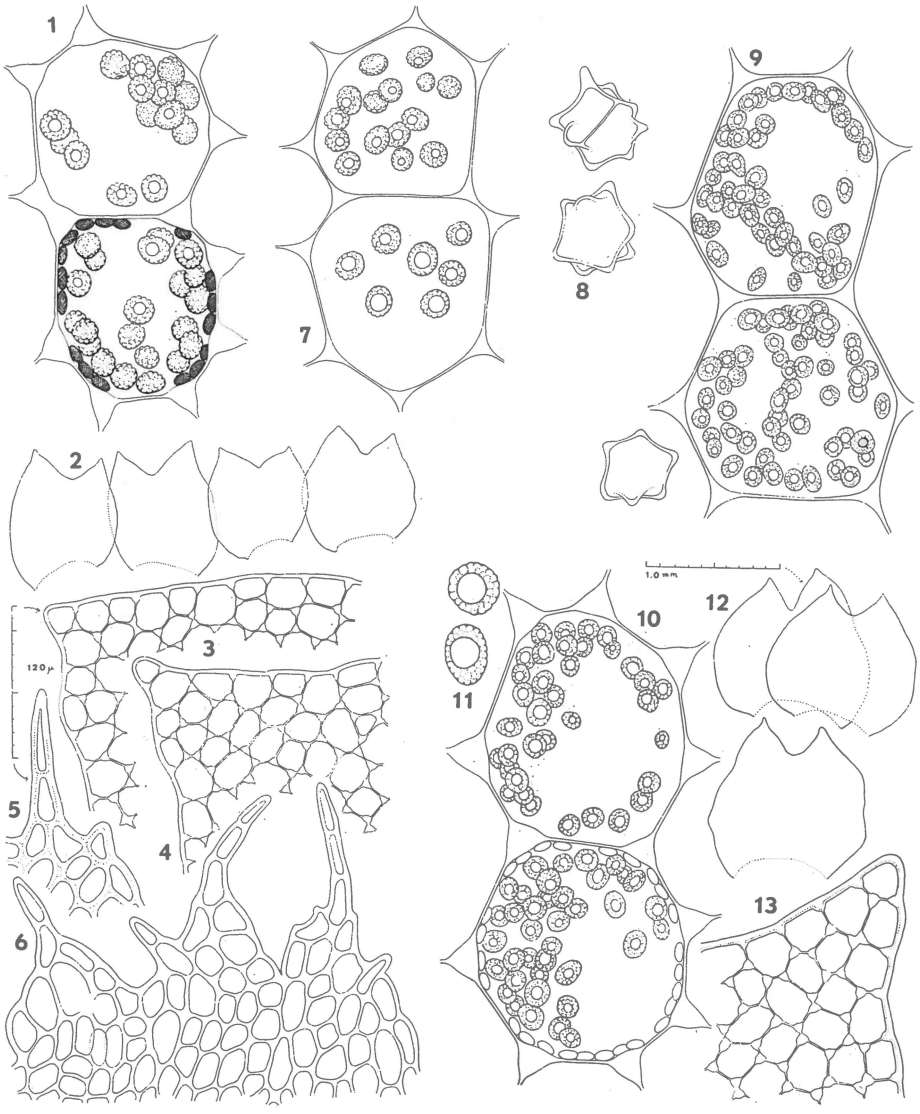


Fig. 7. *Lophozia ventricosa.* (1–7) *v. silvicola*; (8–13) *v. grandiretis.* (1) Cells with oil-bodies [13–22 per cell] and, below, chloroplasts (×640). (2) Leaves (×18). (3, 4) Leaf lobe apices (×165). (5, 6) Teeth of perianth mouth (×165). (7) Cells with oil-bodies, (4–5)6–15(16) per cell (×760). (8) Gemmae (×390). (9) Two median cells with oil-bodies, 46–52 per cell (×720). (10) Median cells with oil-bodies (30)32–38(45) per cell, and, below, chloroplasts (×675). (11) Individual oil-bodies (×1200). (12) Leaves (×18). (13) Leaf lobe (×165). [1–6, 70–2538; 7, 70–2810d, Grønne Ejland; 8–9, 70–2440a; 10–13, 70–2470, Qôrorssuaq; 2, 12, drawn to 1 mm scale; 3–6, 13, drawn to 120 μ scale].

[The plants (66–0017a) reported as *L. groenlandica* (SCHUSTER, l.c.) had biconcentric oil-bodies and mostly very broad leaves with shallow, crescentic sinuses; cells of leaf margins in lobes are 20–29 μ, median cells 23–29 × 20–33μ; gemmae are ca. 23 × 29μ; leaf width-length is ca. 1.1–1.3:1. On that basis, and lack of reddish pigmentation, it seems safe to attribute this collection here.—A second collection (66–0023) from the same locality, cited as "xeromorphic form", in SCHUSTER, l.c., also with many biconcentric oil-bodies, is labeled as "*Lophozia cf. groenlandica*". This plant has pinkish leaf bases and much larger cells, 28–33μ in lobe margins, 30–34 × 32–40μ medially; gemmae 30 × 30μ or even larger; it clearly represents *L. ventricosa var. grandiretis* (see p. 119)].

All collections agree in the broad, rotund-quadrate leaves, much as in *L. wenzelii*, associated with numerous, small, biconcentric oil-bodies. Gemmae are normally greenish to maturity, but in one collection from northwest Greenland (Kânâk, RMS 46160a, from an exposed site, with *Prasanthus*) cell walls of mature gemmae are "slightly to distinctly brownish, ... almost or quite matching (in color) those of the leaf cell walls." We have seen a small amount of the type of *L. groenlandica* (in Groenlandia, rev. Breutel & Curie"); this also shows a few old, ± persistent, pale brownish gemmae below the shoot tip. On that basis we must assume that, as in *L. ventricosa confusa*, extreme sun forms of *L. groenlandica* of exposed sites—where, i. a., *Prasanthus* occurs—may tardily develop brownish (not reddish or red-brown) pigmentation of the gemmae. The problem of gemma color is complex: normally in plants with green gemmae the leaf cells, even in the gemma-bearing lobes, may develop wall pigments, but these pigments do not "go over" to the gemmae themselves. In *L. ventricosa confusa* and evidently in *L. groenlandica*, the brownish coloration of the leaves "goes over" to the stalk cells of the gemmae and—at least on leaves some distance back from the apex—residual gemma development may involve some pigmented gemmae being cut off. The same appears to characterize *L. heteromorpha*, but here the purplish color of the lobes "goes over" to the older, still attached gemmae. These instances differ from those of *L. pellucida*, in which cell wall response within the leaf and within the gemma mass is similar (or at best, wall pigmentation in the leaves is somewhat more intense) and from the taxa with reddish gemmae (e.g., *L. polaris*) in which wall pigmentation of gemmae is initiated even when in shaded sites, where wall pigmentation of leaf cells does not occur.

L. groenlandica continues to be a critical species: the broad and subrotund-quadrate leaves suggest *L. wenzelii;* from this it differs in the more oblique leaves and lack of clear pink to reddish coloration of the ventral leaf bases, as well as in the biconcentric oil-bodies. In turn, the broad leaves and biconcentric oil-bodies are as in *L. ventricosa grandiretis*, from which *L. groenlandica* differs in (a) lack of red coloration of ventral leaf bases; (b) usually more lunate sinuses; (c) clearly smaller leaf cells.

On the basis of the green gemmae, which may become light brownish in sun forms, there might also be potential confusion with *L. pellucida minor*. The latter, however, has few and nonbiconcentric oil-bodies.

Lophozia wenzelii (NEES) STEPH. (Fig. 6:3–4)

Distribution (Map 23)

1B: Lyngmarken (66–0557b). 2: Fortunebay (66–0130, 66–0133, 66–0145a). 9: Eqaluit (70–2520a, 70–2523, 70–2529a, 70–2530a, 70–2531, 70–2532, 70–2533c, 70–2546c, 70–2551a, 70–2558a). 10: Enoks Havn (70–2778c). 12: Perdlertut (70–2694). 14: Hareøen (70–2607). 16: Manîtsoq (70–3002a, 70–3015, 70–3020a, 70–3021, 70–3022a). 17: Tupilak (66–0001a). 17A: Egedesminde (66–0945). 18: Grønne Ejland (70–2815c). 22: Orpigsôq (70–3113b). 23: Kangersuneq (70–3126a). 24: Jakobshavn (66–0223). 26: Pâkitsup ilordlia (70–2393). 29: Ritenbenk (66–0253b, 66–0254a). 32: Qôrorssuaq (70–2476, 70–2477). 53: Søndre Strømfjord (66–0051).

Additional collections:

60: Kûgssuaq (M.P.P. 1707). 86: Seqíneqârajutoq (L.H. Aug. 1932). 90: Tasiussaq (S.B. 1870 recorded by S.B. 1875 was *L. ventricosa longiflora*).

L. wenzelii remains a poorly known and understood species and any statements on range are apt to be misleading (SCHUSTER, 1969, p. 596). It extends northward at least as far as 79° N. in Spitsbergen (ARNELL & MÅRTENSSON, 1959), but in Greenland it is not known from farther north than the above stations; southward it is reported to Newfoundland and Ontario, and (rather atypical, hence questionable material) from alpine summits in New Hampshire and Maine.

In our area it is apparently infrequent and usually confined to areas with acidic rock exposures, but most often in permanently moist, poorly drained, moory areas, often on peaty soil between rocks and boulders, but is typically not truly helophytic. Frequently associated are *L. binsteadii*, *L. kunzeana*, *L. ventricosa longiflora* (occasionally, *L. v. confusa*), *L. wenzelii lapponica* (70–2546, 70–2551 a), *Anastrophyllum minutum*, *Cephalozia pleniceps*, *Scapania curta*. Occasionally (66–0001 a) it is found in thin patches over rocks where subject to drying out, then with *Chandonanthus setiformis* and *Gymnomitrion concinnatum*. At the opposite extreme, on moist peaty ground around margins of shallow lakes (66–0945), with *Gymnocolea inflata* and *Scapania hyperborea;* also on peaty soil over rocks at the margins of cold cascading rills (as at Qôrorssuaq, 70–2476), with *L. opacifolia*, *Anastrophyllum assimile*, *A. minutum*, *Tritomaria quinquedentata*, *Pleuroclada*, and *Scapania serrulata*. Often frequent on moist, sandy, low-lying "plains" peripheral to the mouths of rivers (as at Eqaluit), associated with *Pleuroclada*, *Lophozia cavifolia*, *L. kunzeana*, *L. alpestris*, *L. ventricosa confusa*, *Gymnomitrion concinnatum* (rarely *Marsupella condensata*, when on adjoining rocky-sandy slopes), *Cephalozia bicuspidata*, *C. pleniceps*, *Anthelia*, *Scapania hyperborea*, *S. curta*,

S. irrigua rufescens, and *Nardia geoscyphus*. In rich, densely vegetated, moory areas with pockets of standing water, often with *Scapania paludicola s.l.* (70–3113b, 70–2815c), *L. kunzeana*, *L. ventricosa longiflora*, and *Gymnocolea*.

Oil-bodies are usually (2–3)4–9(10–12) per cell (SCHUSTER, l.c.); in the 1970 collections minor deviations from these figures were noted: in 70–3002a there are (4)6–12(13) oil-bodies per cell; in 70–2476, 9–12; in 70–2530a, 2–9; in 70–2529a, (3)4–9; in 70–2546c, 3–9(14) per cell. In none of our collections are oil-bodies ever biconcentric. Pigmentation occasionally (as in 70–3002a) involves some red at the postical leaf bases and ventral stem surface. Perianths are common, capsules rare (Aug. 8; 70–2523).

L. wenzelii occasionally presents major taxonomic problems. Several collections are atypical, but on the basis of aspect can hardly be "forced" elsewhere, e.g. (1) 70–3126a, a fuscous phase without the red color often present; (2) 70–2477, a phase, mixed with *L. hatcheri*, in which there are 8–18 variably shaped, nonbiconcentric oil-bodies per cell; (3) 66–0133, a plant of an exposed site, with gemmae in part pale brownish at maturity. Adding to the complexities involved in understanding this species is the fact that other allied taxa of *Lophozia* with greenish gemmae are often intermingled; on the basis of dead material, without oil-bodies available for examination, an understanding of such "mixed" collections is impossible. Thus in 66–0254a and 70–2551a some of the admixed material is var. *lapponica* (marginal cells ca. 30–32 μ; oil-bodies mostly 10–15 per cell); in 70–2815c, *L. ventricosa longiflora* is admixed; in 70–3002a, 70–2532, and 66–0557b, *L. ventricosa confusa* is admixed (and in 70–3022a probably the same admixture occurs); in 70–2546c, *L. ventricosa rigida* is intermingled. When one considers the plasticity of these various taxa, discrimination of the various components in a collection becomes almost impossible.

L. wenzelii is notoriously difficult to separate from *L. ventricosa s.l.* and occasional individual gatherings will prove almost unplaceable. We have assumed—perhaps incorrectly so—that if plants with the saucer-shaped, subvertical, orbicular leaves, with arched flanks diagnostic of this species are present, assignment to *L. wenzelii* is "safe". When the plants grow in partial shade amidst coarser mosses (as in 70–2815c), only a minority may show such hollow subvertical leaves with the broad, shallow lobes somewhat incurved; others may have almost flat leaves, and in some instances the distal portions of subhorizontal (rather than subvertical) leaves are squarrose, as in *L. longidens*, so that the leaf actually becomes adaxially convex. All of these conditions may, indeed, occur on one plant and seem partially to represent seasonal response. No matter what the orientation of the leaf, there is, however, persistence

of the broad and broadly rounded leaf form. We regard the strongly convexly arched leaf margins as diagnostic—more so than the sinus, which, although usually broad and shallowly lunate, may occasionally become angulate. In the above collection (70–2815c) oil-bodies are typical for *L. wenzelii:* normally (6)8–12 per cell and typically quite variable in form and size, usually within a single cell; the smallest may be under 3.5–4.5×4–5 μ, the largest range up to 5–6×10–12 μ; none are biconcentric.

Var. *wenzelii* is often difficult to separate, when relatively lax, from *L. ventricosa* var. *confusa.* When growing on sandy-peaty, low ground however, as at Eqaluit (70–2531, 70–2532), plants may be completely typical and recognizable at a glance: the shoots are almost terete, dense-leaved, with the concave leaves rather subvertically oriented. Such phases, of exposed ground, subject to at least sporadic desiccation, may be almost julaceous in aspect; they grow amidst (in 70–2532) *L. ventricosa confusa*, *L. alpestris*, *Pleuroclada albescens*, and *Nardia geoscyphus*, forming mats in which *Salix herbacea* grows, adjoining low dunes at the head of a fjord.

In 70–3002a, there occurs besides typical var. *wenzelii*, a laxer-leaved plant, with flatter leaves and angular, deeper sinuses. This we have referred, with some misgivings, to *L. ventricosa confusa;* it may approach f. *discoensis* in the occasionally trifid leaves and in the sharp sinuses going as deep as 0.45 the leaf length. The *L. wenzelii* plants, growing in a boggy, late snow area around a lake, mixed with *Salix herbacea*, are rather poorly pigmented, with leaf margins and apices often a light brown, but ventral stem surfaces and occasionally postical leaf bases distinctly reddish. Oil-bodies correspond to the description in Schuster (l. c.): (3–4)6–10 (13) per cell, in part spherical, but mostly ovoid, grossly variable in size, ranging to 6×8–9.5 μ.

v. *lapponica* Buch & S. Arn.

Distribution (Map 23)

1D: Skarvefjeld (66–0311a). 9: Eqaluit (70–2549, 70–2553a, 70–2559). 21: Umiasugssûp (70–2947a). 23: Kangersuneq (70–3135b). 24: Jakobshavn (66–0246). 29: Ritenbenk (66–0253b, 66–0254). 32: Qôrorssuaq (70–2441, 70–2447).

Range poorly known: Finland and Sweden, with a few reports from West Greenland and one from Quebec (Schuster, 1969). The variety gives the impression of being a polyploid derivative of var. *wenzelii*, analogous in its origin to var. *rigida* and var. *grandiretis* (vis à vis, respectively, *L. ventricosa* var. *confusa* and var. *silvicola*). Owing to the very large cells and green gemmae, apt to be confused with only these two taxa, especially (because of the variable, never biconcentric oil-bodies) with *L. ventricosa* var. *rigida.* We are not certain that it is always possible

to sharply discriminate between these two—in the same manner that a consistent separation between *L. v. ventricosa* and *L. w. wenzelii* is seemingly impossible to carry through.

The var. *lapponica* has the same ecology, apparently, as var. *wenzelii* and may occur admixed with it (e.g., in 66–0253b, 66–0254). Other associates noted are principally *Scapania irrigua rufescens*, *S. hyperborea*, *L. kunzeana*, *Pleuroclada*, *Nardia geoscyphus*, *Cephalozia bicuspidata*, *C. pleniceps*, *L. ventricosa grandiretis*, *L. kunzeana*, and *Gymnocolea inflata*. Frequent in rather moory, permanently moist, peaty sites, but the plant rarely occurs in truly helophytic niches; alternatively it is found on more nearly mineral soils, where damp (then typically with *Nardia geoscyphus*).

Oil-bodies are stated to occur (9)12–20(23) per cell (SCHUSTER, l.c.). In the 1970 gatherings slight deviations in number occur: thus, in 70–2947a, there are 12–24 per cell; in 70–2549, 10–24; in the somewhat doubtful 70–3135b, (6)8–16(18); in 70–2441, at most 16–20 per cell. In SCHUSTER (l.c.) the color is noted to "rarely" include any reddish tinge, but, in 70–2447 we have a forma with ± reddish pigmentation of the leaves; in 70–2947a the leaf bases are also reddish. In, i.a., 70–2441, however, no red wall pigments of the ventral leaf bases are produced. The possibility that red-pigmented forms may be closer to *L. ventricosa rigida* cannot be dismissed: the differences in leaf form and orientation are sufficiently subject to environmental modification that these two taxa are often very hard to separate.

Lophozia alpestris (SCHLEICH. ex WEB.) EVANS (sensu EVANS) (Fig. 8:1–4)

Distribution (Map 24)

1A: Behind Arctic Station (70–2050). 6: Eqalúnguit (70–2221, 70–2240a, 70–2254). 9: Eqaluit (70–2531, 70–2532, 70–2540a). 15: Kronprinsens Ejland (70–2110a, 70–2120). 16: Manîtsoq (70–3001c, 70–3003). 21: Umiasugssûp (70–2948a). 25: Sarfaq (70–2366a, 70–2371, 70–2377a). 26: Pâkitsup ilordlia (70–2256, 70–2260a, 70–2395). 32: Qôrorssuaq (70–2438a, 70–2439, 70–2440b, 70–2445, 70–2450b, 70–2453, 70–2457a, 70–2461, 70–2462, 70–2464, 70–2466, 70–2467, 70–2478a, 70–2480, 70–2482). 45: Sagdliaruseq (66–1101). 48: Amitsup (66–0818).

Additional collections:

6: Eqalúnguit (M.P.P. 2063). 17: Tupilak (K.H. 16.995). 67: Asuk (M.P.P. 135d). 84: Qeqertasugssuk (L.H. Aug. 1932). 88: Christianshåb (K.H. 15.717). 90: Tasiussaq (S.B. 1870). 99: Sarqaq valley (K.J. 186c). 106: Nûgssuaq (K.J. 39). 112: Umiartorfik (K.J. 604a). 115: Kûgssuaq (K.J. 744). 123: Uigordleq (K.H. 12.889). 129: Avataussaligssuaq (K.J. 914c). 141: Inukavsait qáqarssue (K.H. 16.286f). 145: Uligssat (K.J. 10.186f).

Taken in a very broad sense (e.g., in SCHUSTER, 1969), this polymorphous species is one of the "critical" taxa in the Arctic. It is subject to extraordinary environmental modification, even in lower latitudes.

We have narrowed down the "old" concept of this species, as found in the Arctic, by segregating some plants with unisexual inflorescences and reddish gemmae as (1) *L. longidens;* (2) *L. rubrigemma;* (3) *L. latifolia.* What remains is still distressingly variable and includes, basically, three entities, recognized in SCHUSTER (l.c.):

1. A normally small plant with small cells, with mostly large, very variable, finely granular-botryoidal, opaque oil-bodies (and rather opaque cells), "Ca-intolerant" and seemingly relatively infrequent in the high Arctic. It represents ssp. *alpestris* of SCHUSTER (l.c.).

2. A large plant, often like 3, but pigmentation usually lacking the intense reddish complement of ventral leaf bases, ♀ bracts, perianths, and stem surfaces found in *L. polaris sphagnorum;* the large cells have oil-bodies similar to 1 in being finely granular or granular-botryoidal; because of the large cell size, they seem to occlude the cell lumen to a lesser degree. This plant is strongly limited by a seemingly consistent "dependency" on Ca-rich sites. It represents ssp. *polaris* of SCHUSTER (l.c.), after exclusion of f. *sphagnorum;* it is now treated as an autonomous species *L. polaris.*

3. A large plant, with flatter leaves, often light green but with ventral stem surfaces and postical leaf bases very intensively red to deep red-pigmented, varying almost to piceous; it has large cells, large gemmae, and quite diagnostically coarse-botryoidal, small, rather uniformly sized oil-bodies (Fig. 8:5–19; see also fig. 218:15 in SCHUSTER, l.c.). This phenotype is almost always helophytic, confined to acid sites, and usually grows over *Sphagnum* hummocks. It represents ssp. *alpestris* f. *sphagnorum* of SCHUSTER (l.c.). This seems best elevated to the status of a variety of *L. polaris.*

As here narrowed down, *L. alpestris s.str.* is a generally Ca-intolerant plant whose Arctic distribution is actually very poorly known because, prior to the treatment of SCHUSTER (1959, 1969), all unisexual collections from the Arctic with polygonal, red gemmae were almost automatically referred to "*L. alpestris*", or "*L. alpestris* v. *major*" (the latter, as regards type plants, is shown in SCHUSTER, l.c., to represent an admixture of two taxa, *L. excisa* and *L. latifolia*). Only several collections from Kânâk, Inglefield Bredning (RMS 45724b, 45632a, 45729, 46160b, 46161a, occurring in strongly acidic sites; RMS 45724b in a *Dryas-Cassiope-Vaccinium* heath on an arid plateau traversed by rills; 45632a, 46160b, and 46161 a, on damp silty soil from the adjoining glacier, with *Marsupella ustulata, Gymnomitrion apiculatum, Prasanthus, Scapania obcordata, Lophozia groenlandica,* and other Ca-intolerant taxa) and a single collection from near Alert, Ellesmere Island, at 82°25′N. (RMS 35302a) appear to clearly represent *L. alpestris s.str.* while essentially all of the many collections studied from the northern half of Greenland seem to be misidentified.

Thus HESSELBO (1923) reported *L. alpestris* from Kap Salor, 82°54′N. (leg. TH. WULFF), which ARNELL (1960) "shifted" to *L. latifolia;* the plant is sterile and almost impossible to determine and is probably *L. polaris* (SCHUSTER, l.c., p. 527). We are also sceptical of two reports by ARNELL (1960) from Peary Land, but have not rechecked the material. Any report of *L. alpestris* from basic sites is open to suspicion; the sole report from the basic rock regions in northeast Ellesmere Island (SCHUSTER, l.c., p. 610) is clearly cited from leached and "weathered slopes".

L. alpestris s. str. is relatively infrequent in West Greenland. It is ecologically strictly confined, usually to noncalcareous areas, typically (1) submerged and emergent areas along a rocky rill (summer dry ?), then forming spongy masses, associated with *Marsupella boeckii*, *Scapania subalpina*, *S. obscura*, *S. serrulata*—and where clearly emergent, *Tritomaria quinquedentata*, *Gymnomitrion concinnatum*, *Cephaloziella byssacea*, *Pleuroclada*, *Cephalozia bicuspidata*, as at Qôrorssuaq; (2) on exposed stony slopes, subject to desiccation, growing amidst *Gymnomitrion concinnatum*, with *L. cavifolia*, *Pleuroclada albescens*, and lichens, as at Eqaluit; on exposed, sandy-peaty ground, head of a valley, with *Lophozia wenzelii wenzelii*, *L. ventricosa confusa*, *Cephalozia bicuspidata*, and *Pleuroclada*; (3) intermittently dry, exposed, fine broken soil (often of stony polygons) on acidic slopes (as at Qôrorssuaq 70–2457a, and Pâkitsup ilordlia, 70–2260a), associated with *Prasanthus*, *Cephalozia bicuspidata*, *Gymnomitrion corallioides*, *Anastrophyllum minutum grandis*, less often *Anthelia*, *Nardia geoscyphus*, and *L. alboviridis*; (4) thin, intermittently wet, peaty soil over north-facing, cold, shaded cliff walls, with *Anthelia*, *Gymnomitrion corallioides*, *G. concinnatum*, *Diplophyllum albicans*, *Cephalozia bicuspidata*, and *Scapania spitzbergensis*.

Plants growing in the type 1 site are thoroughly "typical": brown, with very little reddish in the pigment complement, with saucer-shaped leaves with incurved lobes; these plants are relatively large, lax, mostly gemma-free. Plants from sites of the second type are totally deviant: small, rigid, brittle, with stout fleshy stems and relatively small leaves folded in the sinus so that they appear at times loosely conduplicate; intensively reddish colored, the red pigmentation in the distal parts of shoots masking any brown pigment that may be present; shoots may appear chestnut-red to almost piceous; gemmae are rare, bright red, ca. 19–21 × 20–22 μ to 22–24 × 20–24 μ.

We were initially inclined to believe that the rigid, bright red (in drying almost piceous) plants of the second type could not be referred to *L. alpestris*. The cells, however, are typical of this species: each has (9)10–17(20) oil-bodies of diagnostically grossly differing shape and size. Within a single cell some oil-bodies may be irregularly ovoid to fusiform-elliptical and 5–6.5 × 8–11 μ, others only 3–4 μ and spherical to 3 × 5 μ

and ellipsoidal. The oil-bodies, as is typical of non-Arctic populations of this species, are very finely granular-botryoidal.

Cell size in most Greenland extremes of *L. alpestris* seen averages a little larger than in plants from boreal sites; those of the leaf margins distally, and in the lobe apices are (18)20–24 μ usually, rather than 18–21 μ. Otherwise no obvious distinctions occur.

Nomenclature of *L. alpestris*: We continue the time-honored usage of *L. alpestris* sensu MÜLLER (1905–16, 1951–58), MACVICAR (1926), BUCH (1933), ARNELL (1956), ARNELL & MÅRTENSSON (1959), KITAGAWA (1965), SCHUSTER (1953, 1969) and of innumerable authors since the time of NEES (1836). The reasons are: (a) the manuscript was ready for the printer prior to the appearance of the paper by GROLLE (1971); (b) the discrepancies in lectotypification in GROLLE (1968) and GROLLE (1971) are such—he has drastically changed his mind as to the nature of the type of *Jungermannia ehrhartiana* WEB. (1815)—as to leave a large residue of doubt as to what, if one wishes to be a nomenclatural "purist", one must call the well-known and almost ubiquitous *L. alpestris*.

Pertinent—if one wishes to supplant the name *L. alpestris*—are the following facts. (1) Extant usage is based on what NEES (1836) regarded as *J. alpestris*; NEES's description and treatment of *J. alpestris* leave no doubt but that he had before him the plant with rusty gemmae now generally known as *Lophozia alpestris*; as GROLLE (1971) admits, there is no specimen of *J. alpestris* SCHLEICH. ex WEB. in the NEES herbarium, labeled as such, that represents part of the type [Pl. Crypt. Helvet. Exs., Cent. 2, no. 59]. Yet NEES stated clearly, in the synonymy of *J. alpestris*, after the citation: SCHLEICH., Pl. Crypt. Helvet. Exs., Cent. 2, no. 59, "*fide speciminis*". NEES was much too acute a Hepaticologist to confuse *Lophozia* (*Leiocolea*) *collaris*, which is gemma-free, with the constantly gemmiparous *L.* (*Lophozia*) *alpestris*. It seems a reasonable assumption that the original material distributed by WEBER was heterogeneous and that NEES's specimen—which has apparently disappeared—conformed with *L. alpestris sensu* NEES [and sensu many subsequent authors!]. If—as is so often the case with old exsiccatae—the no. 59 of WEBER's exsiccatae was a mixed collection, NEES was within his rights to select whichever element of it he wished to as the lectotype. In order to retain any sanity whatsoever in our nomenclature, it is absolutely necessary to assume, therefore, that the type of *L. alpestris*—namely, the example of WEBER's no. 59 that is, or was, in NEES's herbarium—corresponds with *L. alpestris* as usually accepted, and the specimen in WEBER's own herbarium [at S–PA], which is identical with *L. collaris*, represents a second element distributed under that same number. To now regard the specimen at S–PA as the holotype and, after nearly one and one-half centuries, alter our whole nomenclature on that basis, seems extremely unwise. (2) GROLLE

(1968, p. 542) earlier dealt with the synonymy of *L. alpestris* [which he then accepted in its usual sense, as it is accepted here, and in MÜLLER (1951–58) and SCHUSTER (1969)]. He here places under *L. alpestris* [Basionym: *Jungermannia alpestris* SCHLEICH. ex WEB., Hist. Musc. Prodr., p. 80, Kiel, 1815], as a synonym, *Jungermannia ehrhartiana* Web., Hist. Musc. Prodr., p. 81, Kiel, 1815. He states that this last plant was based on plants from Uppsala, Sweden, issued by EHRHART, Pl. Crypt. Linn. Exs. no. 292, as "*Jungermannia bicuspidata*". Further noted was the fact that *J. ehrhartiana* has been variously placed subsequently as a synonym of *J. excisa* DICKS., *J. ventricosa* DICKS., and *J. porphyroleuca* NEES. GROLLE formally designated as "Lectotypus (nov.)" of *Jungermannia ehrhartiana* Web. a specimen at S–PA labeled "*Lophozia porphyroleuca*" "ab/ipso *Jung. ehrhartiana* Herb. WEBER, Herb. LEHMANN". This lectotype is specifically stated to be (a) dioecious; (b) with stellate, reddish gemmae, 17–20 μ; (c) with small, median cells, 20–25 μ, with small trigones. We agree that these criteria speak unambiguously for *L. alpestris* (*sensu* NEES, 1836). This selection of a lectotype, in our opinion, must stand. Yet GROLLE (1971) would now abandon his own lectotypification because, as he says, he could find in the interim "einen wesentlich besseren Isotypus von *J. ehrhartiana* mit ... reingrüner Gemmen aus LINN (Hb. SMITH no. 14: EHRHART, Pl. Crypt. Exs. no. 292, 1793, als *J. bicuspidata*)".

It is our contention that (a) the distributed "originals" of *J. ehrhartiana* clearly consisted of a mixture of plants; (b) after a valid lectotypification of *J. ehrhartiana* by GROLLE (1968) to correspond with the red-gemma plant here called *L. alpestris*, and so placed by him, it is invalid for him (GROLLE, 1971) to discard his own lectotypification in favor of a plant with green gemmae that evidently corresponds with *L. ventricosa*—especially for the reasons stated: the isotype at LINN is "wesentlich besser".

Major problems ensue, therefore, if one is to accept the reasoning of GROLLE (1971) that (1) in the absence of NEES's own portion of the type of *J. alpestris* (leaving us in doubt as to the proper provenance of the name *J. alpestris*) we should adopt as the holotype of *J. alpestris* the specimen at S–PA; (2) the S–PA specimen is identical with *J. collaris*; (3) therefore *J. alpestris* should be thrown on the scrap-heap as a "nomen ambiguum". One can argue that, until lectotypified by GROLLE (1971), *J. alpestris* was one of the least ambiguous of holarctic taxa; that, like most such taxa based on old exsiccatae, its antecedents are likely to be ambiguous, depending on which example of the exsiccatae one examines; that, therefore, following the sentiments of JONES (1958) such lectotypification is a "mischievous game better left unplayed". If, however, we are to play it, then the ICBN demands that we play it once for each species. NEES (1836), as is clear from his treatment, adopted a functional lectotypification of

J. alpestris as a plant with reddish gemmae; the fact that other—even perhaps most—numbers of the pertinent exsiccatum contain other taxa is not pertinent; the fact that NEES's example of the original has disappeared is, we think, also not necessarily critical. We consider it more likely that NEES had before him a specimen of SCHLEICHER's Pl. Crypt. Exs. Ser. 2, no. 59 which corresponds with our modern *L. alpestris* than that he made the egregious error of which GROLLE accuses him. [Indeed, GROLLE states "Es bleibt ein Rätsel, wie NEES (1836) zu seiner irrigen Fassung von *J. alpestris* ... langte."]. The key to the mystery is, we think, obvious—from the fact that of the two "lectotypes" of *J. ehrhartiana* WEB. which GROLLE (1968, 1971) selected, one is *L. alpestris*, the other *L. ventricosa*. With the broad "species concepts" and the almost macroscopic distinctions then employed, plus the fact that *Hepaticae* notoriously tend to occur in mixed mats, "types" based on exsiccatae—which, being issued in numerous examples, are particularly subject to being based on admixtures—are often an admixture. Lectotypifications based on such old exsiccatae, a century and more after the fact, must be carried through with a major emphasis on maintaining some sanity in our taxonomy. The implications of all this seem, also, to have restrained GROLLE to the point where he frankly states his solution is proposed only as a "vorläufige Lösung". Since, in the interval of three years, he has given us one lectotypification of *J. alpestris* that can have only distressing taxonomic consequences and two lectotypifications of *J. ehrhartiana* that are diametrically opposed—the confusion is now so great that retention of the *status quo ante* seems the only sane thing to do.

For these reasons we are retaining the usage of *L. alpestris* (SCHLEICH. ex WEB., emend. NEES, 1836) EVANS in KENNEDY & COLLINS, Rhodora 3:181, 1901—a usage which has been singularly free of doubt.

If, however, the purist would wish to discard *J. alpestris* as a "*nomen ambiguum*", following GROLLE (1971), then the "vorläufige Lösung" proposed by GROLLE (1971) becomes illegitimate. GROLLE would supplant *L. alpestris*, in the above sense, with *L. sudetica* (NEES in HÜB.) GROLLE [Basionym: *Jungermannia sudetica* NEES, in HÜB., Hep. Germ., p. 142, Mannheim (1834)]. However, *Jungermannia ehrhartiana* WEB. [Hist. Musc. Prodr., p. 81, Kiel, (1815)], as validly lectotypified in GROLLE (1968, p. 54) would then be the first valid name for *J. alpestris*; the second lectotypification in GROLLE (1971, p. 263) is invalid, as noted above.

Lophozia polaris (SCHUST.) *stat. nov.*

Basionym: *L. alpestris* ssp. *polaris* SCHUST., HEP. & ANTHOC. N. A. 2:614, 1969.

Distribution (Map 24)

1A: Behind Arctic Station (66–0281, 66–0287). 1B: Lyngmarken (66–0342, 66–0569). 2: Fortunebay (66–0203a). 4: Flakkerhuk (66–0173b). 6: Eqalúnguit

(70–2221, 70–2239b). 7: Angûjârtûtit (70–2168a, 70–2177). 9: Eqaluit (70–2521a, 70–2545, 70–2560). 10: Enoks Havn (70–2771). 11: Qasigíssat (70–2738a). 12: Perdlertut (70–2681, 70–2687, 70–2693a). 13: Jens Vahls Dal (70–2631, 70–2636, 70–2639, 70–2646c, 70–2649, 70–2650, 70–2651a, 70–2653). 14: Hareøen (70–2570, 70–2587, 70–2589, 70–2591, 70–2595, 70–2605, 70–2615). 17: Tupilak (66–0013). 25: Sarfaq (70–2362, 70–2364, 70–2373, 70–2374b). 26: Pâkitsup ilordlia (70–2315, 70–2287, 70–2304, 70–2308). 30: Eqe (66–0322a, 66–0323, 66–0336). 31: Anap nunâ (70–2419). 35: Hollænderbugt (66–1500, 66–1503). 36: Umanak (66–1478). 37: Agpat (66–1464). 38: Uvkusigssat (66–1385). 45: Sagdliaruseq (66–1057). 46: Qalatôq (66–1101). 48: Amitsup (66–0771). 49: Skalø (66–1014). 51: Simiútap kûa, shore (66–0836). 53: Søndre Strømfjord (66–0087).

Additional collections:

8: Kuánerssuit (M.P.P. 3933, 3941). 57: Nipisat (K.H. 14.583). 64: Ingigigsoq (M.P.P. 3114a). 65: Ûnartuarssuk (M.P.P. 667b). 66: Gamle Qutdligssat (M.P.P. 126). 70: Sarqardlît (M.P.P. 657c). 106: Nûgssuaq (K.H. 15.616, 15.662). 122: South of Eqaluit (K.H. 13.353). 129: Agatdalen (K.H. 13.964). 131: Storø (A.R. July 1954). 147: Amitsoq (K.H. 14.646).

Note added (Feb. 1974) in proof: SCHLJAKOV (1973) proposes "*Lophozia major* (JENS.) SCHLJAKOV" based on *L. alpestris* var. *major* JENSEN, 1906. He places *L. alpestris* ssp. *polaris* SCHUST. in synonymy under *L. major* (JENS.) SCHLJAKOV. SCHLJAKOV overlooked the following points in this erroneous and untenable treatment: 1. SCHUSTER (1969, p. 515) selected as the *lectotype* of *L. alpestris major* JENS. a specimen from Kap Brewster, E. Greenland (HARTZ, 1900), labeled by JENSEN as the "var. *major*." This plant is, as SCHUSTER notes, a "mod. *laxifolia-latifolia* of *L. excisa*. . . . On two plants with gynoecia at the mature-archegonial stage. . ." it was possible to "find (1)2-3 antheridia per bract in 2 pairs of subfloral leaves." On that basis the material is unquestionably identical to *L. excisa*. Hence, placing *L. alpestris* var. *major* JENS. as a synonym of *L. excisa* (DICKS.) DUMORT., as in SCHUSTER (1969, pp. 512, 515) is correct. Therefore, placing the dioecious taxon *L. alpestris* ssp. *polaris* SCHUST. = *L. polaris* (SCHUST.) SCHUST. & DAMSH. as a synonym of the paroecious taxon *L. alpestris* var. *major* (= *L. excisa*), as in SCHLJAKOV (1973) is patently untenable. 2. The second specimen cited under *L. alpestris* v. *major* by JENSEN (1906) was one from Hurry Inlet. Of this SCHUSTER (1969, p. 528) reports seeing two slides at Copenhagen, mostly of sterile plants, but with a few gynoecia, "hence the Kap Brewster plant was selected as the lectotype of var. *major*." This second plant is unquestionably identical to *L. latifolia*. The choice of lectotypes was dictated by the fact that the Hoyers Fluid slides of the second specimen (no herbarium specimen could be found in the Copenhagen herbarium) did not constitute, in the opinion of SCHUSTER (l. c.), an adequate lectotype. 3. With either specimen selected as lectotype, the synonymy proposed by SCHLJAKOV is untenable.

L. polaris, known at least to 82°55′ N. in North Greenland (SCHUSTER, l. c., p. 615) and to 82°25′ N. in Ellesmere Island (SCHUSTER *et al.*, 1959), may be a purely Arctic derivative of the Ca-intolerant *L. alpestris*. It is possibly polyploid, but this needs substantiation. It differs strikingly from *L. alpestris* in being very much limited to Ca-rich sites; in areas with acidic rocks it seems linked to small "niches" where some basic seepage occurs, or where small basalt dikes are found (as at Eqe).

L. polaris is found with a wide range of Ca-tolerant or -demanding taxa. When on soil in creviced rocks in ravines cut through basalt, found with *L. excisa*, *Scapania cuspiduligera*, *L. quadriloba* (as above Godhavn). When on irrigated, wet, poorly drained slopes below basalt mountains, in hummocky, rich moss-tundra, it is found with *L. grandiretis*, *L. heterocolpos*, *L. quadriloba* (70–2239b), and *Tritomaria polita polymorpha*. When in intermittently dry sites, on well-drained, steep clayey-rocky slopes (as at Jens Vahls Dal and at Hollænderbugt), *L. pellucida*, *L. gillmani*, *L. heterocolpos harpanthoides*, *L. quadriloba glareosa*, *Arnellia fennica*, occasionally also *Scapania lingulifolia* and *S. gymnostomophila* are associated; in rather similar sites (at Perdlertut) it is found with *Tritomaria scitula* and *L. heterocolpos*.

Occasional occurrences away from Ca-rich sites are: (a) at Sarfaq (70–2374b), with *Scapania mucronata praetervisa*, *S. paradoxa*, *Cephalozia pleniceps*; (b) on low, wet, sandy-peaty, flat plains at Mudderbugten (66–0173b), with *L. opacifolia*, *L. hatcheri*, *L. excisa*; (c) in similar sites at Eqaluit (70–2521a), the last two species occur consociated. When, rarely, the plant is found on exposed cliffs (with cells of leaf lobe margins 23–25 μ, gemmae 24–25 × 24–27 μ), as on Tupilak (66–0013), *Gymnomitrion concinnatum* and *Anastrophyllum minutum* are associated. Such plants, in the final analysis, come sufficiently close in aspect to *L. alpestris* that one might retain *L. polaris* as a mere subspecies of *L. alpestris s. l.* However, this purely Arctic plant, to date known only from the North American Arctic, evidently deserves the standing of a wholly distinct species: unlike *L. alpestris s. str.*, it is usually unable to develop intense brown pigments (if at all present, their traces are limited mostly to the distal marginal portions of leaves), and has little or no reddish pigmentation (except for occasional traces along the postical side of the stem, which may extend to the leaf bases). Like *L. alpestris*, it has very broad leaves, with the sides, especially the ventral margins, strongly convex and ampliate—but the leaves are normally only shallowly concave. Gemmae are always very common, often in immense reddish masses at the tips of uppermost lobes.

When *L. polaris* grows mixed with *L. excisa* the distinction between these two taxa is immediately perceptible. The following table shows the distinctions as they appear in 70–2521 and 70–2521a:

L. polaris	*L. excisa*
Habitually sterile	Freely fertile and with capsules
Pale green, not brittle	Grass green, strongly chlorophyllose, brittle
Gemmae abundant, in copious mealy masses	Gemmae rare, in small clusters, usually inconspicuous
Leaves of sterile shoot sectors very broad, to 1.5X as wide as long, with very convex margins (particularly the ventral)	Leaves of sterile shoots quadrate, 1.0–1.3X as wide as long, with margins slightly or hardly convex
Sinus lunate, shallow, 0.15–0.2 leaf length	Sinus angular, usually, often sharply so, 0.25–0.4 leaf length
Ventral face of stem and ventral leaf bases occasionally red	Ventral side of stem and leaf bases never reddish
Oil-bodies (2–4)5–13(15–18) per cell, average 6–11	Oil-bodies (12)14–18(24) per cell, average 12–17

L. polaris may, at times, be difficult to separate from *L. latifolia*; this problem is discussed in SCHUSTER (l. c., pp. 618–19). We have seen four recent collections with androecia (66–1014, 70–2221, 70–2239b, 70–2738a), and in all of these collections the androecia, which may be slender as in *L. latifolia*, allow a clear and unambiguous separation from *L. latifolia*: the ♂ bracts always lack a tooth of the antical base (while such a tooth, often inflexed and hidden, is always present in *L. latifolia*) and the ♂ bracts are 2–3-androus.

L. polaris often quite lacks reddish pigments except for the red-colored gemmae. As is noted in SCHUSTER (l. c., p. 618), however, ventral leaf bases may occasionally show some reddish or vinaceous pigmentation (such pigments are present in isolated plants of 66–1014). It is not possible to definitely separate such plants from *L. polaris sphagnorum* when oil-bodies are no longer present, since this latter plant, when growing not or hardly exposed, may show only weak and localized reddish pigmentation. When optimally pigmented, *L. polaris sphagnorum* is so distinct—and seems constantly distinct in oil-body form—that a specific identity with *L. polaris* is hard to defend.

v. *sphagnorum* (SCHUST.) stat. n. (Fig. 8:5–21)

Basionym: *Lophozia alpestris* ssp. *polaris* f. *sphagnorum* SCHUST., HEP. & Anthoc. N. A. 2:619, fig. 218:15–19, 1969.

Distribution (Map 24).

16: Manîtsoq (70–3016b). 19: Nûk (70–2870, 70–2885a), 48: Amitsup (66–0790, 66–0791, 66–0797, 66–0798, 66–0802, 66–0816).

Additional collection:

45: Sagdliaruseq (K.H. 13.206).

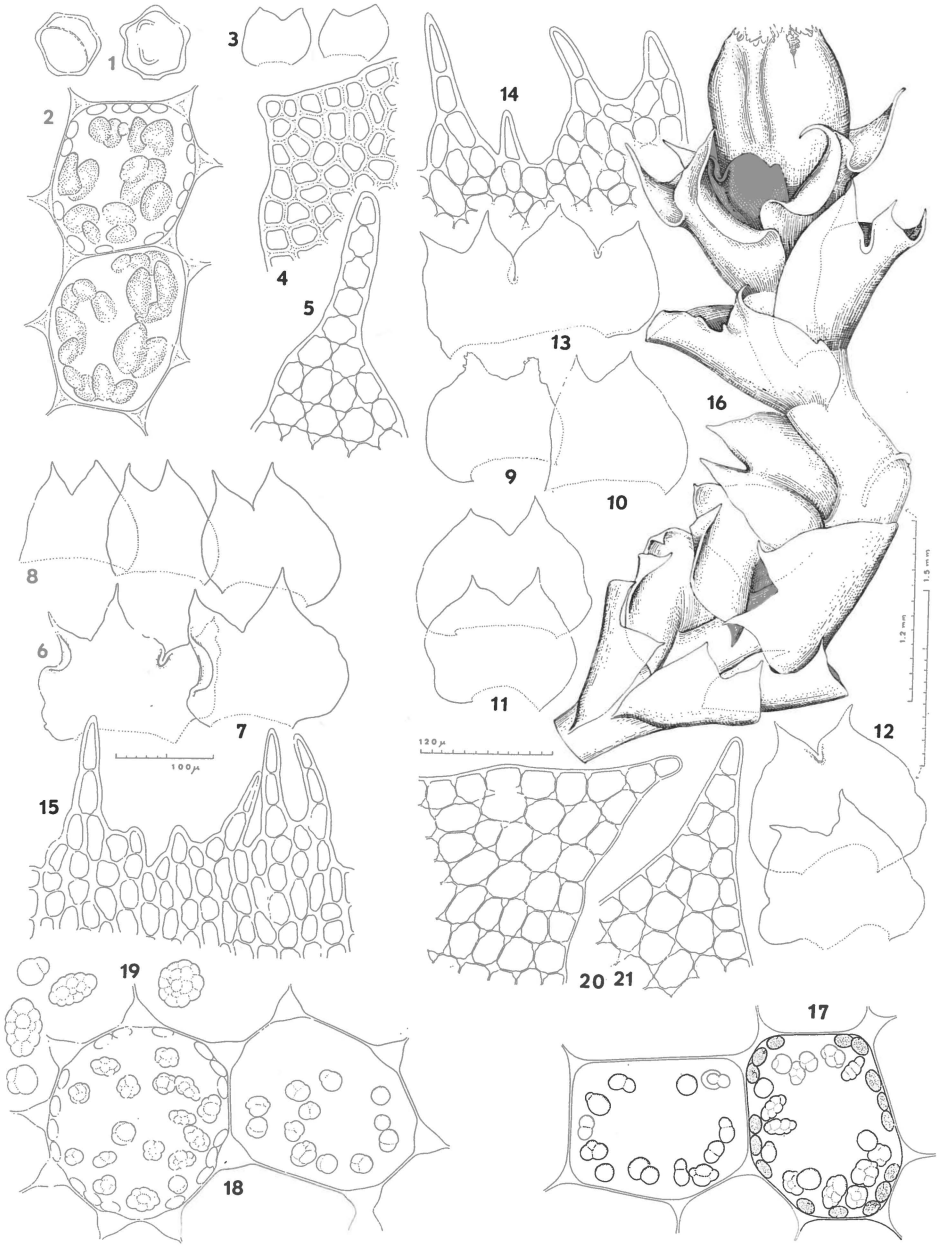


Fig. 8. *Lophozia alpestris* (1–4) and *L. polaris v. sphagnorum* (5–21). (1) Gemmae (×450). (2) Cells with oil-bodies and, above, chloroplasts (×675). (3) Mature leaves (×15). (4) Leaf lobe (×145). (5) Tip of ♀ bract lobe (×145). (6–7) ♀ Bract at left, subfloral leaf at right (×15). (8) Leaves (×15). (9–10) Leaves, the left a gemmiparous one (×15). (11–12) Subfloral leaves (×15). (13) ♀ Bracts (×15). (14–15) Sectors of perianth mouth (14, ×145; 15, ×130). (16) Shoot apex with young perianth (×20). (17) Median cells with oil-bodies, at right also chloroplasts (×680). (18) Same, chloroplasts in left cell (×680). (19) Individual oil-bodies (×875). (20–21) Leaf and ♀ bract lobe apices, respectively (×145). [1–4, 70–2540a; 5–17, 20–21, 70–2870; 18–19, 70–2885, last two from Nûk, Disko Bugt; 3, 6–13, drawn to 1.5 mm scale; 4, 5, 14, 20, 21, drawn to 120 μ scale; 15, drawn to 100 μ scale; 16, drawn to 1.2 mm scale].

Plants with aspect of *L. polaris*: leaves broad-based, ovate to broadly ovate; gemmae brilliant to intensely deep red in color; marginal cells in lobes ca. 22–27 μ. Differing from var. *polaris* in: leaf sinuses often angulate; leaf lobes, especially on ♀ plants often sharply apiculate to short-acuminate, ending in 2–3 single cells; leaf sinuses of ♀ bracts and subinvolucral leaves usually reflexed, the lobes acuminate-caudate, often sulcate; perianth mouth lobulate-ciliate, the teeth in part 2–3 cells broad at base, formed at apex of 2–3 rigid, thick-walled elongated cells; cells with mostly 12–17 (18–20) coarse-botryoidal oil-bodies of small size (mostly 3–4.5 × 4.5–6 up to 7 μ and 6 × 8 μ). ♂ Plant with androecia loosely spicate, eventually intercalary, bracts in 3–5 pairs; bracts suberect, base strongly ventricose antically, strongly vinaceous (distally the vinaceous pigments sometimes diluted by pale brown pigmentation); bracts normally 2–3 androus; bract insertion running obliquely up stem, at antical base never with a tooth. Gynoecia with bracts 2–4-lobed, the lobes ± sulcate (sinus bases often recurved), acuminate to cuspidate at apex, otherwise usually unarmed; bracteole distinct, broadly united with one bract, bifid, lobes as on bracts. Perianth cylindrical-ellipsoidal, often strikingly vinaceous, but towards apex the vinaceous color mixed with brown pigmentation and mouth often decolorate; mouth dentate with variable teeth, 1–3 cells long, formed of rigid thick-walled cells (terminal cell of teeth triangular, sharp-pointed).

Type. Kânâk, Red Cliffs Peninsula, Inglefield Bredning (RMS 45610c); the type is illustrated in SCHUSTER (l. c., fig. 218:15–19).

This plant, previously known only from a few collections from Inglefield Bredning, is strictly limited to acidic sites. It is basically helophytic, occurring admist *Sphagnum* and *Aulacomnium* tussocks and hummocks in irrigated and/or poorly drained areas, often around shallow lakes or tarns. Associated locally are: *Calypogeia sphagnicola*, *L. ventricosa silvicola*, *L. excisa*, *Cephaloziella subdentata*, *Cephalozia pleniceps*, *C. bicuspidata* (70–2870, 70–2885a) or *C. pleniceps*, *Pleuroclada*, and *Calypogeia sphagnicola* (70–3016b).

Plants of 70–3016b are largely sterile, although two aborted gynoecia with subfloral innovations were seen. They also lack gemmae, hence their placement is slightly uncertain. Many leaves, however, have a lunate sinus and convex sides, as in *L. polaris*, and the diagnostic coloration is present: reddish pigments of ventral side of stem, spreading to postical leaf bases; some leaves, at shoot tips, also with reddish pigmentation of distal sectors of leaves. The plants do not have the facies of *L. latifolia*, with which they might be confused, except for the deviant pigmentation.

By contrast, 70–2885a and 70–2870 bear abundant but unfertilized gynoecia. Study of these plants strongly suggests that perhaps var. *sphagnorum* should be raised to separate subspecies rank (or is perhaps even

an independent species). In spite of the characters reminiscent of *L. polaris s.str.* [leaf form; red gemmae averaging (16) 18–24×20–26 μ; marginal cells in leaf lobes 23–27 μ] there are several criteria that strongly isolate the plant, chiefly: (1) the coarsely botryoidal oil-bodies that "seem distinctive" as stated in the original discussion of the plant (SCHUSTER, l. c. p. 620; in the type the oil-bodies are all more or less coarsely botryoidal; see fig. 218:15 in Schuster, loc. cit.) and range to only 4.5×6 μ, on an average. In 70–2885a the oil-bodies are even more coarsely botryoidal, in part formed of only 2–4 segments, a few larger ones range to 7 μ or 6×8 μ. The apparent constancy in the coarse-botryoidal nature of the oil-bodies and the absence of isolated, very large ones (compare figs. 217:9 and 218:1, 14, 23 in Schuster, l.c.) suggest a very different taxon is involved. In 70–2870 younger leaves show *Calypogeia*-like oil-bodies, in large part glistening, homogeneous spheres 4–5 μ in diam., in part twinned (with equal or unequal halves), and 5×7 μ, in part of 4–7 segments and then 5–5.5×6–8 μ. The oil-bodies show no parallel to those of any other *Lophozia* familiar to us, except for the unallied *L. grandiretis* (compare Figs 3:16–17 and 8:17–19); (2) the broad-triangular to triangular lobes of leaves immediately below the ♀ bracts, and of the gynoecial bracts that are almost caudate-apiculate, being abruptly narrowed into a frequently hyaline apex formed by 2–4 superposed single, subisodiametric cells; this feature clearly shows in the type (see fig. 218: 16, in SCHUSTER, l. c.); (3) the rather more strongly dentate perianth mouth, the teeth "in large part formed of 1–2 elongated, tapered, thick-walled cells" (type; 70–2870), or even in part formed of teeth 3 cells long and 2 (3) cells broad at base (70–2885); see Fig. 8:14–15.

The gynoecial bracts in the type were quite crispate (as is indicated in SCHUSTER, l. c.). In plants with the most mature gynoecia (in 70–2870) we find similarly 2–3-lobed crispate bracts with reflexed margins and sinuses, and longly acute to short-acuminate and often arcuate or coiled apices.

The androecial (and in part gynoecial) diagnosis is based on the plant from Amitsup (66–0790); here we found a number of plants with 3–5 to even 8–12 pairs of remote to contiguous, mostly highly pigmented bracts per androecium. Of major importance—the bifid ♂ bracts, with their strongly saccate antical bases, were in at least large part 2–3-androus, and the bracts antically were inserted on an oblique line running towards the stem apex; there was no trace of an antical tooth. These features wholly preclude confusion with the dioecious *L. latifolia*—a plant often with a similar ecology. Perianths seen were very strikingly vinaceous in the basal half or more, with the vinaceous pigments diluted distally and, in part, masked by light brownish pigments. A similar change in pigmentation often characterizes the ♀ bracts: vinaceous basally, but vinaceous mixed with brownish distally. Perianth mouth of the mature gynoecia of

66–0790 are exactly as in the type: 1– and 2–3-celled sharp teeth intermixed, with the end cells sharp-pointed, thick-walled. This, also, precludes confusion with *L. latifolia* (and *L. exisa*). As a consequence, this plant, technically, is closest to *L. polaris*. We retain it there, in spite of the deviant cytological features, and the very different ecology, because there is apparent transition in pigmentation, and, when only dead material is available, a certain separation is not always possible.

Lophozia rubrigemma SCHUST.

Distribution (Map 25)

11: Qasigíssat (70–2723). 24: Jakobshavn (66–0227). 25: Sarfaq (70–2360). 26: Pâkitsup ilordlia (70–2318). 29: Ritenbenk (66–0270). 32: Qôrorssuaq (70–2456a, 70–2459a).

Additional collections:

17: Tupilak (K.H. June 1956). 113: Nugfiumaneq (K.J. 824).

This species, recently described and illustrated in SCHUSTER (1969, p. 621, figs. 219, 222:1–7), is known only from the Inglefield Bredning area (type) and West Greenland. It will surely prove more widespread in Arctic areas with acidic rocks; in our area confined to the eastern, Precambrian region.

The ecology of this strictly oxylophytic species is distinctive: it occurs, often mixed with mosses, on dry, sometimes rather peaty soil in crevices between boulders or bed-rock crevices, where subject to desiccation. Associated are xerophytic mosses such as *Dicranum* spp. and *Racomitrium canescens*, various lichens and various *Hepaticae*, i.a. *L. hatcheri*, *Ptilidium ciliare*, *L. kunzeana*, *Cephaloziella byssacea*, *C. rubella arctogena*, *Chandonanthus setiformis*, *Anastrophyllum minutum*, occasionally *L. ventricosa s.l.* The first two of these species are almost constantly consociated.

Plants of 70–2456 are gynoecial, densely caespitose, forming rather large, pure patches in crevices of compact soil among stone polygons in a sparingly vegetated fell field; they are very typical of the species in (1) the crispate gynoecial bracts, with 2–3–4 lobes, the lobes bearing a few coarse, broad-based teeth; (2) cell size and the 16–25 oil-bodies per cell; (3) the juvenile perianths with a claret-red mouth, the mouth armed with short teeth of 1–2(3) superposed cells, the terminal cells often tear-drop shaped, to 20–22×48–55 μ. Occasional terminal cells were somewhat smaller than in the fragmentary type material described and illustrated in SCHUSTER (l. c.), but the differences seem trivial and well within the range of variation to be expected.

Growing adjacent to the plants forming pure patches in relatively sheltered microenvironments were patches of more exposed, denser-

leaved plants, closely appressed, erect, and caespitose in growth, found mostly with *Cephaloziella* and *Dicranum*. These plants were more rigid, stiffer-leaved extremes, often with leaves more transversely oriented, often a little narrower (but retaining a broadly angulate or, rarely, even lunate sinus) and with a *L. longidens*-like aspect on the smallest, most juvenile shoots. They also had smaller cells, often only (23)24–28 μ on the lobe margins and (23)24–28×25–35 μ medially. Associated with the smaller cells of these xeromorphic extremes were fewer oil-bodies, often only (9)12–16(18) per median cell. Such phases, as stated in SCHUSTER (l. c., p. 541), may easily be confused with *L. longidens* ssp. *arctica*, but the latter, on the largest shoots seen, retains the narrow leaves, with narrow and drawn-out lobes diagnostic of the species. Also, *L. longidens* was never collected in such exceedingly exposed sites, in dense, mutually appressed, caespitose groups of individuals. Plants of 70–2459 are very much similar to this last, juvenile, rigid extreme, but larger individuals have leaves clearly broader than long, with broad lobes; they grew in clefts between rocks in a fell field, associated with the typical fell field drought-tolerant *Chandonanthus setiformis* and *L. hatcheri*.

Lophozia pellucida SCHUST.

Distribution (Map 26)

12: Perdlertut (70–2689). 13: Jens Vahls Dal (70–2637, 70–2646b, 70–2651a). 35: Hollænderbugt (66–1512, 66–1513, 66–1518, 66–1523). 40: Mârmorilik, head of the Fjord (66–1199). 43: Kangerdlugssuakavsak (66–1288). 52: Umîarfik, Qôrnoq (66–0978). 53: Søndre Strømfjord (s.n.).

Additional collections:

39: Tasiussaq (K.H. 13.523). 40: Mârmorilik, head of the Fjord (K.H. 13.730).

A species best diagnosed by its highly specific ecology; it was described (SCHUSTER, 1959, 1961) from northern Ellesmere Island, from plants on seepage-moist, clay-shale solifluction slopes rich in *Orthothecium chryseum*, *Equisetum variegatum*, and other Ca-tolerant or "demanding" taxa. These were laxly leafy, robust, rather distinctly clear yellow-brown to chestnut-pigmented plants, with gemmae similar to rusty orange in color. Subsequent collections have almost all been from well-drained, steep, highly calcareous mineral soil slopes (most often fast-drying clays, with intermixed rock fragments), on which the species may occur in "phenomenal quantities" bearing "masses of usually orange-colored gemmae" (SCHUSTER, 1969). In such sites the species may occur straggling amidst other bryophytes, in sheltered crevices between stones, etc., and is then most often a light, pellucid green with very local leaf pigmentation. Such pellucid, nearly pigment-free phenotypes are, indeed, the commonest ones seen in West Greenland. They may occur as very weakly developed,

almost juvenile phases, and are then difficult to recognize in the field except for one distinguishing feature: the very diagnostic orange- or rust-yellow gemmae. Typical of such occurrences was on the northeast-facing slopes of Jens Vahls Dal (70–2637), among *Distichium capillaceum* and numerous admixed hepatics (*L. quadriloba*, *L. heterocolpos* var. *harpanthoides*, *Scapania cuspiduligera*, *S. ligulifolia*, *Blepharostoma t. brevirete*, *Arnellia fennica*, *Tritomaria scitula*, traces of *L. polaris*). The last five taxa, and the *L. heterocolpos harpanthoides* are, indeed, almost constant associates of *L. pellucida*, together with *Saxifraga oppositifolia*.

Even the weakest phases of this species are distinct in the gemma color and in the large, pellucid cells and even the feebly developed plants cited above have median cells 35–45 μ wide, marginal cells mostly 30–35 μ (tangentially measured) or larger. Associated with the large cell size are the seemingly minute chloroplasts and oil-bodies; the last, for a species with such large cells, are very few (in 70–2637 they are mostly 9–16 per cell, obscuring less than 0.2 of the cell surface).

v. *minor* SCHUST. (Fig. 6:10–11)

Distribution (Map 26)

7: Angûjârtûtit (70–2179). 10: Enoks Havn (70–2766). 11: Qasigíssat (70–2739a, 70–2744b). 14: Hareøen (70–2571). 26: Pâkitsup ilordlia (70–2258d). 35: Hollænderbugt (66–1503, 66–1524). 40: Mârmorilik, head of the Fjord (66–1209). 47: Íngia (66–1031, 66–1036).

This plant, described in SCHUSTER (1961) and in more detail, with illustrations, in SCHUSTER (1969, p. 634, fig. 221) has been previously cited only from the type material, from the north coast of Ellesmere Island, and from Nûgssuaq in West Greenland. It appears to be a common component of "difficult" sites in exposed, highly calcareous, usually steeply sloping and intermittently dry sites. Basically the var. *minor* encompasses a difficultly comprehensible ensemble of plants which agree in two essentials: gemmae that, even with limited insolation, turn yellowish-orange to rusty orange (but never deep red) and which maintain the same, or almost the same reaction to insolation as the leaves themselves; leaf cells that never develop conspicuous trigones (they always remain concave-sided) and which are usually smaller than in the "normal" variety. Cell size, in the species as a whole, is so variable that it is of limited significance; perhaps *L. pellucida s.l.* is a derivative of *L. alpestris*. The fact that *L. pellucida* may occur intimately intermingled with *L. polaris* and is at once distinct in gemma color (see p. 629 in SCHUSTER, l. c.) alone seems to preclude specific identity of these two taxa. (This is not the only instance in which the two taxa occur intermingled; they do so often as, e.g., at the mouth of Jens Vahls Dal, see p. 133). Nevertheless

plants of 70–2739a, in fact, indicate a possible closer relation between the two taxa, with cells smaller than in the type of var. *minor*, 19–24 μ on the margins distally [vs. 23–28 (30) μ in the type], 21–26 (27) × 22–29 (33) μ medially [vs. 23–30 × 23–34 (38) μ in the type]. Leaves of these plants, a mod. *colorata-parvifolia-angustifolia*, are ca. (900) 1320–1350 μ wide × (840) 1100–1150 μ long (ca. 1.1–1.2 × as wide as long); and are also somewhat narrower, more nearly *alpestris*-like in form, with convex and strongly arched sides, and a shallow, usually lunate sinus. If it were not for the habitat (clayey, basic soil in a steep, shallow, south-facing "draw" in a late-snow area, with a dense growth of *Salix herbacea*), the light rust-colored gemmae, and the rather large, diagnostically bluntly to sharply stellate gemmae (ca. 24–25 × 25–35 to 28 × 30–34 μ), one might be tempted to dismiss these plants as a form of *L. alpestris*. Plants from Enoks Havn (70–2766) are almost an exact match for those just described, but, if anything, are even more gracile, with ovate leaves. Cells are no larger: 19–23 μ marginally, occasionally less; 22–25 × 24–27 μ medially. Oil-bodies are only 5–14 per cell (reflecting the greatly reduced cell volume). Strikingly enough, however, the large gemma size is hardly affected: the larger of the light rusty orange gemmae are ca. 33 × 35 μ. The plants, like those just described from Qasigíssat, come from a difficult site where the dominant angiosperm is *Salix herbacea* and where a common associate is the equally tolerant *Nardia geoscyphus*; in both places the latter occurs, in part, as a mod. *colorata* with reddish local pigmentation.

Ironically, with a comprehension of the ecology plus attention to the crucial matter of gemma response to illumination, one can easily recognize *L. pellucida s.l.* in the field.

This plant has been found fertile a single time (66–1209; Mârmorilik), in what appears to be a typical manifestation of var. *minor*: gemmae are green to orange, to 33–34 × 45–47 μ, and median cells vary from a low of 22–25 × 22–29 to 28–31 × 28–36 μ, showing the usual striking range in cell size noted above. The ♂ plant has 2–3 pairs of intercalary bracts forming a rather lax androecium. Bracts are leaflike but more transverse, with a moderately ventricose antical base (which is typically deeper pigmented, from light to deep reddish-castaneous) in which there are (1) 2–3 antheridia. Antheridia have the stalk 1-seriate, or sometimes locally 2-seriate; the ovoid or short-ellipsoidal body is ca. twice as long as the stalk, formed of relatively large, polyhedral jacket cells. There is no trace of paraphyses and the bract lacks any trace of an antical tooth. Gynoecial plants are somewhat fleshier and larger, with the upper, subfloral leaves rather dense, fluted-plicate, often with a large antical tooth or small lobe in addition to the two normal, lanceolate-triangular, entire-margined lobes; one or the other lobe may bear a tooth near its base. Subfloral, bifid bracteoles occur for 1–2 cycles below the ♀ bracteole. ♀ Bracts are sheathing, erect,

plicate and fluted, polymorphic: one bract is free and typically quadrate (when flattened); it is 0.35–0.45 quadrifid. The other is mostly trifid 0.35–0.45, but is united at base with the bracteole which is free for usually 0.65–0.85 its length—a very unusual feature—and is lanceolate or symmetrically to asymmetrically bifid. Bract and bracteole lobes are narrow-triangular to lanceolate-triangular, separated by narrow, V-shaped sinuses, are entire to sinuous on their margins, and the tips are acute (ending in 1, less often 2, superposed cells). The perianths deeply 3–4-plicate to near the base, rather wide open at the mouth (much as in *Tritomaria polita*), with the mouth shallowly sinuous-lobulate, the shallow lobes subentire to remotely denticulate with 1–2-celled, polymorphic, irregular and hardly sharp, often only sporadically produced teeth—the general aspect is of a sinuous-lobulate, wide, and essentially edentate perianth mouth. Gynoecia, like upper leaves, are orange-yellow-tinged but may also show very weak vinaceous pigmentation basally; perianths are an orange, rusty to orange-brown color.

Tritomaria SCHIFFN.

Subg. ***Tritomaria*** SCHIFFN.

Tritomaria exsectiformis ssp. *arctica* SCHUST.

Distribution (Map 27)

17: Tupilaq (66–0017). 22: Orpigsôq (70–3116). 24: Jakobshavn (66–0226).

This distinctive plant seems to be very rare in West Greenland; it was described from Siorapaluk, Robertson Bugt, in northwest Greenland and is known otherwise only from the above stations, all areas with acidic rocks. The type occurred over peaty slopes enriched by leachings from dovekie roosts. Regional plants are from (1) peaty soil over or between rocks adjoining standing water (66–0226, 66–0017), associated with *Lophozia groenlandica*, *Cephalozia bicuspidata*, and *Scapania lingulata microphylla*, and (2) poorly drained, level, peaty ground, in wet pockets, associated with *Anastrophyllum minutum minutum* (70–3116). The plant has also been collected from peaty soil in crevices of exposed bedrock, at Ritenbenk (material not studied).

Plants are always sterile and always freely bear the diagnostic, bright reddish gemmae.

Tritomaria scitula (TAYL.) JOERG.

Distribution (Map 27)

1A: Behind Arctic Station (66–0150, 66–0166, 70–2182). 1D: Skarvefjeld (66–0314). 6: Eqalúnguit (70–2247a). 8: Kuánerssuit (70–2138a, 70–2151, 70–2155). 12: Perdlertut (70–2670a, 70–2671, 70–2672, 70–2675a, 70–2681, 70–2685, 70–2696). 13: Jens Vahls Dal (70–2630, 70–2632, 70–2637d, 70–2638, 70–2641, 70–2643, 70–2644,

70–2645, 70–2647, 70–2651a, 70–2653, 70–2654, 70–2655, 70–2658, 70–2659, 70–2663, 70–2667). 14: Hareøen (70–2571, 70–2573, 70–2582, 70–2605, 70–2610, 70–2613, 70–2619, 70–2621). 29: Ritenbenk (66–0264). 31: Anap nunâ (70–2406a, 70–2417, 70–2420, 70–2427, 70–2432). 35: Hollænderbugt (66–1505a, 66–1507, 66–1513, 66–1517). 38: Uvkusigssat (66–1389, 66–1390). 39:Tasiussaq (66–1262). 40: Mârmorilik, head of the Fjord (66–1204, 66–1206, 66–1207). 42: Magdlak (66–1357g, 66–1364, 66–1367, 66–1372). 43: Kangerdlugssuakavsak (66–1286, 66–1287c). 44: Akuliarusikavsak (66–1320). 45: Sagdliaruseq (66–1076). 49: Skalø (66–1006). 50: Simiútap kûa, valley (66–0866). 51: Simiútap kûa, shore (66–0916c, 66–0917, 66–0826, 66–0836). 52: Umîarfik, Qôrnoq (66–0976).

Additional collections:

39: Tasiussaq (K.H. 13.522, 16.857). 65: Ûnartuarssuk (M.P.P. 667a). 83: Angnertussoq (L.H. Aug. 1932). 84: Qeqertasugssuk (L.H. Aug. 1932). 99: Sarqaq valley (K.J. 186f). 100: Iperqarfiunge (L.H. July 1932). 103: Qapiortoq kitdleq (K.J. 1043, 1052b, 1062). 127: Kangersôq (K.J. 1091). 128: Agatdalen (K.H. 13.968c). 129: Avataussaligssuaq (K.J. 892). 145: Uligssat (K.J. 10.186).

This species is imperfectly Arctic-alpine in range, with its distribution limited because of a sharp restriction to sites with basic rocks. In the Arctic found north to Kangerdlugssuak, Inglefield Bredning (Schuster, 1969), at 77°23′N.; southward it is found to Quebec, Ontario, and the Lake Superior margin in Michigan, Wisconsin, and Minnesota.

It is frequent in areas with basaltic or basic sedimentary rocks under two sets of conditions: (1) in damp, sheltered crevices of basalt, often with *Scapania gymnostomophila* (less often *S. cuspiduligera*) where it occurs chiefly as a "normal" green modification. In such sites it may also occur (with minimal soil accumulation, often in crevices) with *Peltolepis grandis* (70–2247a) and with *Mannia pilosa*, *Solenostoma pumilum polaris*, *Lophozia badensis*, *Sauteria alpina*, *Athalamia hyalina*, *Scapania gymnostomophila*, *Plagiochila asplenioides* (66–1357g), *Lophozia heterocolpos*, *Scapania curta* (66–0150), *Blepharostoma trichophyllum brevirete*, *L. heterocolpos*, and *L. opacifolia* (66–0314). Under intermediate conditions, with regard to exposure (as on irrigated, steep, calcareous slopes; 70–2632, 70–2407a, 70–2645), *Plagiochila asplenioides*, *L. grandiretis*, *L. heterocolpos*, *L. gillmani*, *L. quadriloba*, *L. opacifolia*, *Cephalozia pleniceps*, and *Odontoschisma macounii* are also associated. (2) On exposed, often periodically desiccated, steep, insolated slopes, often on fast-drying clayey soils or gritty, sandy, weathered mineral soils. In the last type of habitat it is often abundant and typically associated with a series of taxa either confined to such sites (*Arnellia fennica*, *L. pellucida*) or frequent there (*L. heterocolpos harpanthoides*, *L. gillmani f. apiculata*, *Solenostoma pumilum polaris*, *Blepharostoma trichophyllum brevirete*, *Scapania ligulifolia*, *S. gymnostomophila*, *L. polaris*, *L. quadriloba*, rarely *Cephalozia pleniceps*).

In sites of the second type the species is often strongly modified and may approach *T. heterophylla* in facies. It acquires a chestnut-brown

pigmentation of a least upper sectors of leaves and bracts (and, in extreme cases, the tips of these may become decolorate); the ventral stem surface may become blackish purple, and a small amount of purplish pigments may "creep" on to the ventral leaf bases. The plants also become denser-leaved, more compact, and shorter-leaved (associated with which the width becomes proportionally greater); the leaves, especially near the gynoecia, may become distinctly fluted. Plants of 70–2644 are typical of this last type and are also notable for the development of some purplish red color of the ♂ bracts (which seem to be usually 1-androus) and for deviations in the gynoecia. ♀ Bracts are strongly fluted, broader than in the phenotype illustrated in SCHUSTER (l. c., fig. 228:4), with one bract 3–4-lobed, with convex, fluted, sharp lobes, of which 1 or 2 may bear a vestigial 1-celled tooth (but are never spinose-dentate as in *T. heterophylla*). The perianth mouth may be unusually weakly toothed with remote, mostly 1–2–, a few 3–4-celled teeth 2 cells wide at the base.

Although extremes of *T. scitula* may prove difficult to separate from *T. heterophylla*, the distinctness of the two is clear from 66–1287c, in which they occur admixed (together with *T. quinquedentata*, *Lophozia excisa elegans*, *Scapania mucronata praetervisa*, *Solenostoma sphaerocarpum*) on intermittently dry soil between rocks on a steep, basic slope. The distinctness, under such conditions, is clear from the table given on p. 671 in SCHUSTER (l. c.).

Tritomaria heterophylla SCHUST.

Distribution (Map 27)

26: Pâkitsup ilordlia (70–2266a). 30: Eqe (66–0249c, 66–0251, 66–0289b). 31: Anap nunâ (70–2409c). 38: Uvkusigssat (66–1393a). 43: Kangerdlugssuakavsak (66–1280b, 66–1281, 66–1283, 66–1287c). 51: Simiútap kûa, shore (66–0836).

Additional collections:

12: Perdlertut (M.P.P. 480a). 145: Uligssat (K.J. 10.188a).

T. heterophylla is known from as far north as Low Point (83°06′ N.) in Peary Land and 82°26′ N. in Ellesmere Island (SCHUSTER, 1969); it is scattered in the Inglefield Bredning region, widespread in the Disko Bugt area, and otherwise known only from Southampton I. (SCHUSTER, l. c.; PERSSON & HOLMEN, 1961). It appears to be a strictly Arctic and chiefly high Arctic taxon, which probably survived the Pleistocene north of the region of continental glaciations.

Regionally the species is confined to basic sites, most often in areas subject to intermittent desiccation; it may then be light green (because of the enormous, hyaline trigones) and quite small in size. Such plants, of the mod. *viridis-parvifolia*, may occur on stony, fragmented clay-rock slopes,

in crevices, associated with *Solenostoma pumilum polaris*, *Scapania mucronata praetervisa*, *S. gymnostomophila*, *Anthelia juratzkana*, and *Cephaloziella uncinata*. It is also found in wet, sandy depressions in low moss-heath tundra, peripheral to shallow lakes (in 70–2266a), where localized basic seepage must have been present, judging from the occurrence with *Pinguicula vulgaris* and *L. rutheana*; admixed were *L. cavifolia*, *Cryptocolea imbricata*, *Nardia geoscyphus*, and *Anthelia*. On soil over basic ledges (in 70–2409c) it occurred with *Peltolepis grandis*, *Solenostoma subellipticum*, and *Scapania mucronata praetervisa*.

The species may occur in areas with igneous rocks, if local basalt dikes are present, as at Eqe. Here it may grow on peaty soil along a rill, mixed with *Prasanthus*, *Cryptocolea*, *Anthelia*, *Odontoschisma macounii*, *Aneura pinguis*, *Lophozia quadriloba*, *L. heterocolpos*, and *Cephalozia pleniceps*.

Plants of 70–2409c are gynoecial; they are the first collections of fertile plants made since the type was described (SCHUSTER, 1958) and match exactly the figures given there and in SCHUSTER (l. c.). They have the same crenulate, bleached perianth mouth as in the type plants, show 2–3-lobed, broad bracts, often with crispate lobes and/or reflexed margins which bear sharp, spinose teeth on some—but not often all lobes—and end in a setose, stiff cilium. The only notable difference lies in the trigones: these are even coarser and more nodose than in the type plants (or in any other known *Tritomaria*), so that the plants seem lighter green in aspect than the type.

Tritomaria quinquedentata (HUDS.) BUCH

Distribution (Map 28)

1A: Behind Arctic Station (66–0146, 66–0176, 66–0271, 70–2040, 70–2046). 2: Fortunebay (66–0128a, 66–0131, 66–0135a, 66–0139, 66–0140, 66–0141a). 6: Eqalúnguit (70–2215a, 70–2241, 70–2249a, 70–2254). 7: Angûjârtûtit (70–2167). 9: Eqaluit (70–2522, 70–2546, 70–2558a). 10: Enoks Havn (70–2762a, 70–2767, 70–2769, 70–2775a). 13: Jens Vahls Dal (70–2632). 14: Hareøen (70–2570, 70–2575, 70–2587, 70–2592a, 70–2599, 70–2601, 70–2614, 70–2621, 70–2622). 15: Kronprinsens Ejland (70–2070, 70–2071, 70–2077, 70–2088, 70–2100, 70–2119). 16: Manîtsoq (70–3003, 70–3014b). 17: Tupilak (66–0033b, 66–0111, 66–0115, 66–0117a, 66–0122). 19: Nûk (70–2845). 23: Kangersuneq (70–3137, 70–3138b, 70–3145c, 70–3159). 25: Sarfaq (70–2335, 70–2339a, 70–2345, 70–2354, 70–2361, 70–2362). 26: Pâkitsup ilordlia (70–2260, 70–2276, 70–2280b, 70–2381). 29: Ritenbenk (66–0264, 66–0273a). 30: Eqe (66–0249, 66–0327, 66–0332, 66–0333, 66–0336, 66–0339). 31: Anap nunâ (70–2412a, 70–2421, 70–2424). 32: Qôrorssuaq (70–2450a, 70–2464, 70–2469, 70–2471a, 70–2476c, 70–2480). 36: Umanak (66–1474, 66–1482). 37: Agpat (66–1434, 66–1461). 38: Uvkusigssat (66–1390). 40: Mârmorilik, head of the Fjord (66–1207). 43: Kangerdlugssuakavsak (70–1287c). 46: Qalatôq (66–1110). 48: Amitsup (66–0781, 66–0774, 66–0785, 66–0770, 66–0788, 66–0791, 66–0771, 66–0813). 51: Simiútap kûa, shore (70–914g). 52: Umîarfik, Qôrnoq (66–0976).

Additional collections:

1: Godhavn (S.B. 1870). 1B: Lyngmarken, Engelskmandens Havn (M.P.P. 2053). 17: Tupilak (K.J. 1345, K.H. June 1956). 24: Jakobshavn (K.H. 15.981). 34: Marrait kangigdlît (K.H. Sept. 1956). 44: Akuliarusikavsak (K.H. 15.872). 45: Sagdliaruseq (K.H. 16.956, 16.965). 52: Umîarfik, Qôrnoq (K.H. 16.362). 53: Søndre Strømfjord (K.H. 3123a). 57: Nipisat (K.H. 14.583a). 60: Kugssuaq (M.P.P. 737a). 74: Kangerdluarssuk (K.H. 14.495). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 83: Angnertussoq (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958). 88: Christianshåb (K.H. 15.445). 103: Qapiortoq kitdleq (K.J. 1048, 1057). 106: Nûgssuaq (K.J. 25, 37, K.H. 15.641, 62–938). 110: Ikorfat (K.J. 334). 112: Umiartorfik (K.J. 625). 114: Eqaluit (K.H. 13.219a). 115: Kûgssuaq (K.J. 743). 120: Itipilua qáqâ (K.J. 695a). 123: Uigordleq (K.H. 12.890). 124: Tasíngortaq (K.H. 13.304). 126: west of Sarqap taserssua (K.H. 13.425). 128: Agatdalen (K.H. 13.966, 13.981). 134: Umîvik (K.H. 13.870). 136: Small Island (K.H. 16.737). 137: Esersiutilik (K.H. 16.476). 139: Qaqortukavsaq (K.H. 16.075). 141: Inukavsait qáqarssue (K.H. 16.286b, 16.291). 143: Kangerdlugssuaq (K.H. 16.392). 145: Uligssat (K.J. 10.186a). 147: Amitsoq (K.H. 14.642, 14.644).

The above records include a wide array of phenotypes; only plants which clearly represent, respectively, var. *turgida*, var. *grandiretis*, and f. *gracilis* are cited under those specific taxa.

T. quinquedentata s.l. is subcosmopolitan in boreal to Arctic regions of the northern hemisphere, with disjunct occurrences in the region of Yunnan Prov., China, and northwestern India and the Himalaya (ssp. *papillifera* SCHUST.; see SCHUSTER, 1966a; 1969). Associated with its wide range and ability to invade the most diverse sites is a phenomenal variability.

Ecologically the species, *s.l.*, has such a wide range that a list of associates would include most of the regional *Hepaticae*—hence would be essentially meaningless. The plants have a "weak affinity" for basic rocks and are therefore clearly most common in regions, locally, where basaltic rocks occur, but are not limited to such areas. Statements (REIMERS, 1940, p. 207) that the species is a "Silikatmoos" are incorrect. It may occur over basic slopes, associated with *Lophozia polaris* and *L. quadriloba* (70–2570), or with *Scapania ligulifolia*, *S. cuspiduligera*, *L. grandiretis*, *L. gillmani* (70–2592a), or over rich, calcareous, moory ground or in fens, associated with *Cryptocolea*, *L. rutheana*, *L. heterocolpos*, *L. grandiretis*, *L. quadriloba*, *Aneura pinguis*, *Odontoschisma macounii*, and *Riccardia sinuata* (66–0914g). On basic, seepage-wet slopes *Scapania degenii dubia* and *L. quadriloba* may be admixed (70–2775a). However, occurrences over acid, peaty soil, sometimes over or between rocks along cascading rills (as at Qôrorssuaq; 70–2476c, 70–2450a) are equally typical; here may be associated *Pleuroclada*, *Lophozia wenzelii*, *L. opacifolia*, *L. alpestris*, *Anastrophyllum assimile*, *A. minutum*, *Scapania serrulata*, and *S. subalpina*. Similarly, the plant may occur in noncalcareous moors and fens, associated with *S. hyperborea*, *S. paludicola s.l.*, *L. kunzeana*,

Cephalozia bicuspidata, and *Gymnocolea inflata* (70–2070, 70–2276, 70–2280b, 66–0273a)—all taxa of acidic, helophytic sites. At the opposite extreme are xerophytic occurrences, in crevices between rocks (as in 70–2100), mixed with *Chandonanthus setiformis* or (70–2762a) mixed with *Ptilidium ciliare* and *Anastrophyllum minutum*.

f. *gracilis* (JENS.) SCHUST.

Distribution (Map 28)

1A: Behind Arctic Station (66–0195). 2: Fortunebay (66–0126, 66–0127). 6: Eqalúnguit (70–2218a). 8: Kuánerssuit (70–2154). 17: Tupilak (66–0037a). 18: Grønne Ejland (70–2811b, 70–2813a). 19: Nûk (70–2875). 22: Orpigsôq (70–3118b). 30: Eqe (66–0325). 37: Agpat (66–1467, 66–1438). 45: Sagdliaruseq (66–1063).

Additional collections:

128: Agatdalen (K.H. 13.863). 136: Kangerdluarssûp qeqertâ (K.H. 16.167a).

This poorly known plant at times gives the impression of being a mod. *angustifolia-parvifolia*. When typically developed, however, it is merely 0.25–0.35 as large as var. *quinquedentata*, with much less asymmetric leaves (see fig. 228:9–10 in SCHUSTER, 1969).

There are no obviously different ecological perimeters *vis à vis* var. *quinquedentata*. Plants may occur in "difficult" sites, as on cold north-facing ledges on gneissic hills, associated with *Prasanthus*, *Anthelia*, *Lophozia opacifolia*, *Anastrophyllum minutum* (70–3118b), or with *Gymnomitrion corallioides* (66–1467), or on soil over exposed cliffs, with *Scapania paradoxa* (70–2813a, 70–2811b). They can also occur, however, on irrigated, south-facing basaltic slopes, with *Preissia*, *L. heterocolpos*, *S. mucronata praetervisa* (70–2154), or over basalt dikes, with *Peltolepis grandis*, *Cephalozia pleniceps*, *L. quadriloba* v. *glareosa* f. *cephaloziellioides* (66–0325).

Most phases seen were of green plants, sometimes variously brownish pigmented. However, 66–0195 had more or less vinaceous postical leaf bases, a peculiarity rarely seen in typical *T. quinquedentata* itself.

Plants of 70–2813a are of an atypical, very richly ramified phenotype, with exclusively terminal, *Frullania*-type branches. The plants occur mixed with an equally copiously branched phase of *Scapania paradoxa* (but in this branches are basiscopic, *Radula*-type). The collection was made from soil over a cliff face, where possibly manured by birds, and the peculiar morphology and free branching may reflect nutritional peculiarities of the site. The stiff, brittle, thick stems and the rigid, concave leaves of this phenotype are all atypical. Leaves, although mostly broader than long, have the ventral lobe nonampliate; the dorsal lobe is always quite long, sharp, and well developed. The aspect is almost that of a fleshy, gemma-free phase of *L. hatcheri*.

v. *turgida* (LINDB.) WEIM.

Distribution (Map 28)

6: Eqalúnguit (70–2231). 14: Hareøen (70–2595).

This ill-defined variety, which perhaps ought to be considered a mere forma, usually occurs in relatively constantly moist, rich sites. Several other collections, cited under ordinary *T. quinquedentata*, verge on variety *turgida*. The collections cited here have very broad, asymmetric leaves, slightly larger cells, and often somewhat more numerous oil-bodies. In 70–2595 marginal lobe cells are 20–25 μ and oil-bodies occur (3)4–9(10) per median cell. Associates are *Lophozia polaris* and *Blepharostoma trichophyllum brevirete*.

This variant is known from Siberia (type), northern Scandinavia, a single station from the Alps, many stations in Alaska, and several from Greenland (SCHUSTER, 1969). MÅRTENSSON (1955) correctly doubts the validity of the taxon.

v. *grandiretis* BUCH & ARN.

Distribution (Map 28)

1B: Lyngmarken (66–0343a). 17: Tupilak (66–0014). 25: Sarfaq (70–2373).

This variant, a presumed polyploid, is treated in SCHUSTER (1958; 1969, figs 230:8–9, 231:9, 12–13). It is sporadically present within the Arctic range of the species proper; known to date from Novaya Zemlya, Sweden (Torne Lappmark), northwest Greenland and West Greenland (SCHUSTER, 1969), with the northernmost station at 82°24′ N. in Ellesmere Island (SCHUSTER *et al.*, 1959).

In our area known only from acidic (igneous) sites, where over peaty ground, around rills and tarns; associated are *Lophozia kunzeana* (66–0014, 66–0343a), *L. ventricosa* cf. *silvicola*, and *L. binsteadii*. Regional plants have from (8)10–16 to 9–15 oil-bodies per median cell (66–0014, 66–0343a) up to mostly 12–18 per cell (70–2373).

Subg. ***Saccobasis*** (BUCH) SCHUST.

Tritomaria polita (NEES) SCHIFFN.

This species, reported from as far north as 79° N. in Spitsbergen (ARNELL & MÅRTENSSON, 1959) is not known in the western hemisphere north of the stations cited below; on the east coast of Greenland it extends north to Scoresby Sund: Ryders Elv, Hurry Inlet, 70°54′ N., 22°25′ W. (Dusén, 1899). This material, mixed with *Anthelia juratzkana* and *Lophozia heterocolpos*, forms the basis for the report of "*Jungermannia groenlandica*" in JENSEN (1900, p. 800). JENSEN's figs. 1–15 clearly show a plant with

mostly subquadrate trilobed leaves with blunt, shallow lobes. The specimen is of a mod. *parvifolia* of *T. polita*, and is hardly determinable to subspecies. It is distinct at once from *Lophozia* in (a) the strikingly locally oblong cells at the leaf base; these range from a minimum of 21–25×31–36 μ or 22–26×34–42 to 20–22×39–48(62)μ; (b) striolate basal leaf cells and striolate, strongly elongated cortical cells; (c) the leaf basically transversely inserted in the antical half, with the line often somewhat obliquely inclined towards the stem apex—typical of subg. *Saccobasis*. Admittedly figs. 5–7 in JENSEN (l. c.) show a plant with oblong, bilobed leaves; this represents a juvenile plant—and such juveniles in *Saccobasis* often have transverse, bifid leaves. The few relatively mature shoots showed leaves which are broadly quadrate and 1.15–1.25 × as wide as long; they suggest the plant falls best under ssp. *polymorpha*. Cell sizes of the Hurry Inlet plant are clearly much smaller than those given for mature plants of *T. polita* in SCHUSTER (1969); they average 18–25 μ in subapical cells, 20–26×20–27 μ in median cells, 20–26×31–48(62) μ in basal cells. The small cell size seems to reflect the evidently difficult conditions under which the plants grow.

JENSEN's erroneous attribution of this transverse-leaved plant to *J. groenlandica* appears to have induced both STEPHANI (1898–1924) and MÜLLER (1916, in 1905–16) to place *J. groenlandica* into "*Sphenolobus*" —a genus which, at that time, also included *T. polita*.

Southward in North America it is found only to Newfoundland and Quebec (SCHUSTER, 1969), with a seemingly oceanic range. It is essentially oceanic-subarctic and low Arctic; reports from the interior of North America (e.g., Ontario, in CAIN & FULFORD, 1948) are based on errors in determination (SCHUSTER, l. c.).

T. polita is highly plastic in the north and, like several other taxa (e.g., *Solenostoma pumilum*, *T. exsectiformis*) generally develops much broader—and shorter—leaves and gynoecial bracts. With single exceptions (referred to ssp. *polita*), all collections seen belong to this broader-leaved phenotype. Some collections, however, are of weak plants whose subspecific attribution is somewhat uncertain. We cite these arbitrarily, as ssp. *polymorpha*, because this seems to be the dominant subspecies in the area.

ssp. *polita* (NEES) SCHIFFN.

Distribution (Map 29)

12: Perdlertut (70–2710).

The plants of 70–2710, growing with *Lophozia gillmani* and *L. heterocolpos* on damp, sandy soil of a steep slope, along a small temporary rill, appear to represent typical ssp. *polita* rather than ssp. *polymorpha*.

Gynoecia have bracts that are mostly 0.2–0.25 trilobed, with blunt to rounded but discrete lobes, and from the broad, truncate apex converge somewhat towards the base; they are about 1575 μ wide × 1600–1650 μ long to 1740 μ wide × 1500 μ long. Leaves, varying greatly with vigor, are subquadrate on mature plants from a somewhat narrowed base, are almost all trilobed, and average from 1230–1250 μ wide × 1230 μ long to 1300 μ wide × 1200 μ long, thus from as wide as long to slightly wider than long. On the basis of the gynoecial bracts these plants seem definitely much closer to ssp. *polita* than to ssp. *polymorpha*.

The sporophyte of this species (and subgenus) has not been described. In 70–2710 sporophyte details were as follows: The seta, ca. 300 μ in diam., had a cortical stratum of ca. 22 delicate cells, each similar in diam. to the medullary cells, which were ca. 5 cells across. The ovoid capsule had a wall that varied, on the same valve, from 3-stratose (ca. 48 μ thick) to 4-stratose (ca. 55–58 μ thick). Epidermal cells were 19–24 μ high, the internal cell strata were each subequally high, 10–12(13) μ. Epidermal cells, in surface view, in the basal two-thirds of the capsule were mostly subquadrate to short-oblong, but polyhedral ones were frequent; they averaged 20–36 μ wide × 36–48 μ long, with almost all longitudinal walls and many to most transverse walls with "nodular" (vertical) thickening bands that were neither very coarse nor confluent, nor more than minimally tangentially extended. Transverse walls often lacked thickenings or had them feebly developed and weakly pigmented. Inner cells, more irregular in shape, often so much so as to negate the value of any dimensional description, bore complete to incomplete semiannular bands (median sectors of the tangential walls often incomplete or lacking); the bands were frequent but not very thick or broad. Spores were 14–16 μ and covered by low markings that formed a granulate-vermiculate, dense surface. Elaters were 7–8.5 μ in diam., weakly tortuous, rather short (90–130 μ), bispiral.

ssp. *polymorpha* SCHUST.

Distribution (Map 29)

1A: Behind Arctic Station (66–0153, 66–0173a, 66–0196, 70–2004, 70–2008, 70–2030, 70–2038). 1B: Lyngmarken (66–0568). 2: Fortunebay (66–0142, 66–0144, 66–0200, 66–0371). 6: Eqalúnguit (70–2209, 70–2239a). 7: Angûjârtûtit (70–2169c). 9: Eqaluit (70–2537a). 12: Perdlertut (70–2700, 70–2703). 13: Jens Vahls Dal (70–2654, 70–2656). 14: Hareøen (70–2588, 70–2593, 70–2596, 70–2611). 17: Tupilak (66–0026, 66–0028, 66–0105b, 66–0113). 18: Grønne Ejland (70–2812). 26: Pâkitsup ilordlia (70–2263, 70–2264, 70–2269, 70–2380, 70–2383a). 31: Anap nunâ (70–2400b, 70–2403, 70–2408). 39: Tasiussaq (66–1263). 42: Magdlak (66–1354, 66–1364a). 45: Sagdliaruseq (66–1058). 48: Amitsup (66–0782, 66–0789, 66–1551, 66–1552). 51: Simiútap kûa, shore (66–0937).

Additional collections:

17: Tupilak (K.J. 1319, K.H. June 1956). 34: Marrait kangigdlît (K.H. Sept. 1956). 36: Umanak (K.H. 16.349). 68: Hammers Dal (M.P.P. 408). 75: Qârusuit

(L.H. Aug. 1932). 83: Angnertussoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 15.717c). 106: Nûgssuaq (K.H. 15.632a). 110: Ikorfat (K.J. 379, K.H. 62–1574a). 126: west of Sarqap taserssua (K.H. 13.414). 144: Igdlorssuit (K.H. & W.C.S. July 1962).

This Arctic subspecies of *T. polita* shows drastic polymorphism (hence the name), and, in the Disko Bugt area, at times grades into ssp. *polita*. Such gradation is seen, e.g. in Porsild 408. Here leaves are 3(4)-lobed and much wider than long, but ♀ bracts are more clearly 3–4-lobed than shown in Schuster (l. c. fig. 234:2). Plants usually occur in permanently moist sites: usually along small rills or around water-filled depressions in moss-tundra, or in rich calcareous fens, and only in areas with basic rocks, never directly on rocks or cliffs, but always over organic substrates irrigated by Ca-rich waters. Associated are usually *Lophozia heterocolpos* (rarely var. *harpanthoides*), *L. gillmani*, *L. grandiretis*, *L. opacifolia*, *L. quadriloba*, *L. polaris*, *Odontoschima macounii*, *Cephaloziella arctica*, *Cephalozia pleniceps*, *Tritomaria scitula*, and (rarely; when over peaty to sandy soil with a high mineral content) *Scapania irrigua rufescens* and *Nardia geoscyphus* (in 70–2537a) or *Cryptocolea* and *N. geoscyphus* (70–2269) or *L. rutheana* (70–2383a).

Certain phases, of moory holes in rich fens may cause difficulties; thus in 70–2812 the plants are a pitch-black, scorched, greasy phase (mod. *parvifolia-mesoderma-colorata*), with the leaves usually transversely inserted dorsally, except for the innermost edge which is abruptly short-decurrent. These plants are prostrate in growth and do not have the *T. polita* aspect at all. Leaves, however, are of the ssp. *polymorpha* type, averaging broadly quadrate (typical dimensions, width×length: 530×440 μ; 640×515 μ; 950×870 μ). Cells often have only weak trigones and unusually small oil-bodies in some cases; they are usually fewer than normal in ssp. *polymorpha*—median cells may bear only (2–3) 4–7 (8–11) oil-bodies.

Plants with gynoecia and androecia are common; capsules are relatively rare but produced from July 10 (70–2383a) to at least as late as Aug. 7 (70–2700, 70–2710). Gemmae seem to be very rarely produced (66–0568, 66–1364a, 66–1354; see fig. 234:8–9 in Schuster, 1969).

Anastrophyllum (Spr.) Steph.

Anastrophyllum assimile (Mitt.) Steph. (Fig. 9:7–8)

Distribution (Map 30)

21: Umiasugssûp (70–2927). 25: Sarfaq (70–2322, 70–2323a, 70–2354, 70–2370a, 70–2376). 32: Qôrorssuaq (70–2439, 70–2476b). 36: Umanak (66–1479, 66–1480, 66–1488). 46: Qalatôq (66–1100, 66–1114).

Additional collections:

24: Jakobshavn (S.B. 1870). 84: Qeqertasugssuk (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 97: Qôrorssuaq (S.B. 1870 as *Jungermannia plicata*). 114:

Eqaluit (K.J. 790, K.H. 13.219). 124: Tasíngortaq (K.H. 13.310). 131a: Agpat, Qaqortuatsiaq (K.H. & G.M. 71–1692). 141: Inukavsait qáqarssue (K.H. 16.252a).

A phytogeographically "critical" species in the region, it was first reported from Greenland (SCHUSTER, 1969) from two localities in Inglefield Bredning (77°23′–77°32′ N.) and from two sites in West Greenland, and has since been collected (by DAMSHOLT) in the Angmagssalik District. The plant is otherwise known from southern coastal Norway, the southern portions of the Alps (Austria, Switzerland, Italy; see map in MÜLLER, 1951–58), Nepal and Sikkim in the Himalaya, Korea, Japan, and Borneo (SCHUSTER, 1969, p. 720). In North America known only from coastal Alaska and British Columbia (Queen Charlotte Isls.).

A. assimile is restricted to regions with igneous rocks where typically found over cold, exposed but permanently moist (not necessarily strongly irrigated) rocks walls and cliffs; associated are, in such sites, *Marsupella revoluta*, *M. arctica*, *Cephaloziella byssacea s.l.*, *Gymnomitrion concinnatum*, *Anthelia juratzkana*, less often *Anastrophyllum minutum grandis*, and *Andreaea* spp. (as in 70–2323a, 70–2370a). It may also occur on steep slopes, in sheltered spots between rocks, along cascading rills, associated with *Scapania serrulata* (as at Qôrorssuaq), or over peaty soil between rocks along gently flowing rills (as at Qalatôq; here with *S. degenii*, *Marsupella arctica*, *Anastrophyllum minutum grandis*). Occasionally found in large, piceous mats over ledges where subject to prolonged inundation (as in Sydostbugt; here with *S. crassiretis*, *Marsupella arctica*, *Gymnomitrion concinnatum*). Occurrences with the last three taxa, plus *M. revoluta*, seem very constant and very typical; less often *Gymnocolea* and *Odontoschisma macounii* are admixed.

Earlier collections from Greenland were "uniformly ♂ or sterile" (SCHUSTER, l. c.). In the plants from Qôrorssuaq (70–2481) perianths and a few capsules were present; 70–2439, from the same area, had perianths. The sporophyte is undescribed. The seta is ca. 8–9 cells (240 μ) in diam., with ca. 24–25 rows of epidermal cells similar in diam. or slightly larger than the medullary cells. The capsule wall is 45–47 μ thick, 4–5-stratose, with epidermal cells about 2× as high as the average of the internal strata. Epidermal cells bear strong nodular thickenings, inner cells, semiannular bands. Spores are 12–14 μ and bear remote, small, sharp papillae on the exine surface. Elaters are 7–8 μ in diam., bispiral, with lax and narrow spirals, only 1.5–1.8 μ broad.

Anastrophyllum saxicolus (SCHRAD.) SCHUST.

Karajak Station (in Qarajaqs Isfjord, 70°27′ N., 50°36′ W.), *fide* STEPHANI (1897). We have not collected this species, otherwise known again only from South Greenland (Tunugdliarfik, J.V. 195). However, a single collection of this species is cited from "Tupilak, near Egedes-

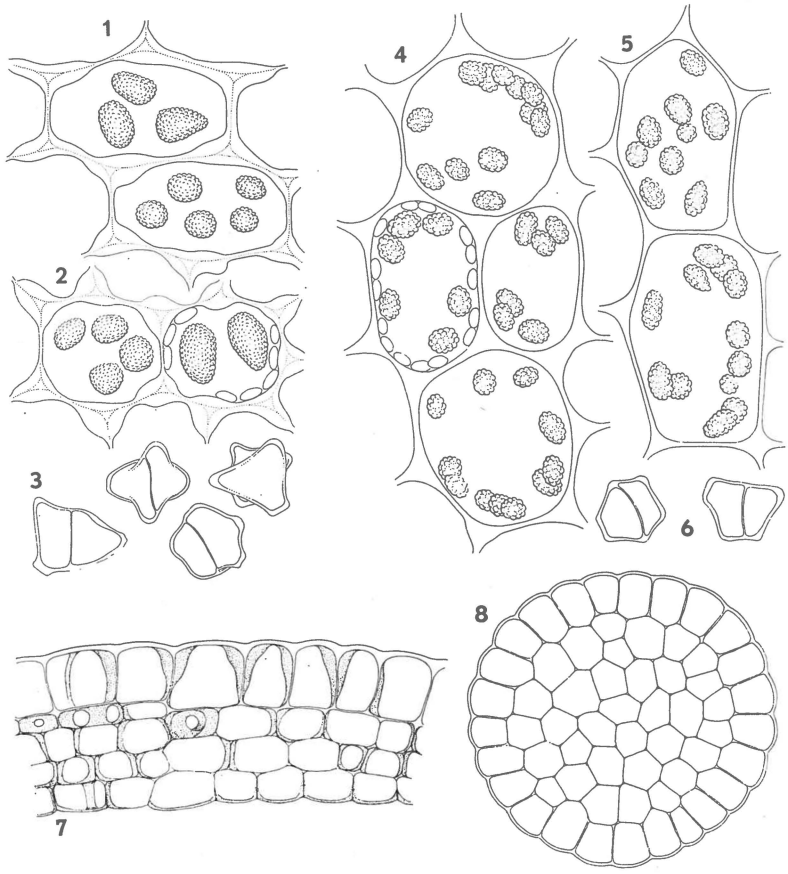


Fig. 9. *Anastrophyllum sphenoloboides* (1–3); *Lophozia cavifolia* (4–6); *A. assimile* (7–8). (1) Cells of leaf base, with oil-bodies (×800). (2) Median cells (×800). (3) Gemmae (×590). (4) Median lobe cells (×770). (5) Basal cells (×740). (6) Gemmae, vinaceous (×400). (7) Capsule wall cross section (×460). (8) Seta cross section (×165). [1–3, 70–2948c, Umiasugssûp; 4–6, 70–2540, Eqaluit; 7–8, 70–2481, Qôrorssuaq].

minde (HOLMEN)" in SCHUSTER (1969, p. 736). The absence of an accentuation mark indicated that the determination had not been verified. In June, 1970, the specimen in the Copenhagen herbarium was checked; it represents *Tritomaria quinquedentata*. As a consequence, *A. saxicolus* should be deleted from the West Greenland flora.

Anastrophyllum sphenoloboides SCHUST. (Fig. 9:1–3)

Distribution (Map 31)

6: Eqalúnguit (70–2225). 18: Grønne Ejland (70–2814d, 70–2816a). 21: Umiasugssûp (70–2948c). 25: Sarfaq (70–2344a). 26: Pâkitsup ilordlia (70–2294).

Additional collections:

17: Tupilak (K.H. June 1956). 79: Agpalilik (C.K. 1202). 90: Tasiussaq (S.B. July 1870). 112: Umiartorfik (K.J. 598). 147: Amitsoq (K.H. 14.645).

This stenotypic and highly diagnostic species, the only bisexual species of *Anastrophyllum* known, was described only recently from plants from northwest Greenland (type) and Alaska (SCHUSTER, 1969, p. 741); it is now also known from the Mackenzie R. District of northwestern Canada. The above reports represent the southernmost known from Greenland. *A. sphenoloboides* is apparently a strictly Arctic type, quite possibly a North American endemic whose post-glacial range emanates from unglaciated western North America.

Although rare, it has surely been previously mistaken for *A. minutum*, from which it differs in the field (under the hand lens) in the reddish cast of the plants—they are, distally at least, reddish or purplish brown or brownish red, rather than yellow-brown as in *A. minutum*—and in the glossier texture of the dry plant. Also, it is always freely fertile and the auto- and heteroecious inflorescences are easy to establish. Unlike in *A. minutum*, in which gemmae occur commonly in boreal populations, infrequently in Arctic ones, gemmae are very rare in *A. sphenoloboides*; they have been seen a single time and were not reported for the species in the original diagnosis. The gemmiparous plants from Sydostbugt (70–2948c) are sparse. Only androecia were found; apparently gynoecia had not yet formed. Gemmae occurred in small quantities at the tips of unmodified leafy shoots. They were intensely claret-red, (1)2-celled at maturity, bluntly to moderately sharply polygonal but hardly stellate, and averaged from 16–19×18–19 μ up to 16–17×19–21 μ. The plants were otherwise quite typical in the leaf cells and oil-bodies: median cells were quadrate to polygonal, ca. 16–21×18–24 μ, with 2–4 oil-bodies that ranged from 4–4.5×5 to 5×6 up to 5.5–7×8–9 μ; basal cells were relatively elongated, 15–17×25–30 μ, and had (2)3–6(9) oil-bodies similar to those of the median cells. The obvious, coarse trigones are diagnostic.

The plants from Grønne Ejland are of interest not only because of their abundance, but also in their associations. They occurred on moderately moist, acid peat, where snow lies late in the spring, associated with *Salix herbacea*, the mosses *Aulacomnium* and *Polytrichum*, *Sphagnum*, and a host of *Hepaticae*, some of southern range, i. a., *Calypogeia neesiana*, *C. sphagnicola*, *Mylia anomala*, *Cephalozia leucantha*, *C. lunulifolia*, *Lophozia ventricosa silvicola*, *L. opacifolia*, and *Anastrophyllum m. minutum*. By contrast, plants of 70–2948c occurred in small quantity on broken rocky ground, on soil between rock fragments, associated with the typical ensemble of soil-inhabiting taxa tolerating difficult conditions: *Prasanthus suecicus*, *Scapania parvifolia*, *Gymnomitrion concinnatum*, *Cephalozia bicuspidata*, *Solenostoma sphaerocarpum*, and *Anthelia juratzkana*. Possibly gemma production, noted only in these plants, needs the stimulus of strongly intermittent moisture conditions for its initiation.

Typically this species occurs over peaty, damp soil, often (as with

70–2225, 70–2294) with *Lophozia binsteadii* and *Anastrophyllum minutum*; less often *L. kunzeana*, *Cephaloziella hampeana*, *C. arctica*, *Pleuroclada albescens*, *Cephalozia bicuspidata*, *C. pleniceps*, and *L. ventricosa silvicola* are consociated (as in 70–2344a, 70–2294).

Anastrophyllum minutum (Schreb. ex Cranz) Schust.

Distribution (Map 31)

1A: Behind Arctic Station (66–0102a, 70–2042). 1B: Lyngmarken (66–0557). 2: Fortunebay (66–0123, 66–0209a, 66–0215). 6: Eqalúnguit (70–2225, 70–2227d, 70–2238, 70–2243b, 70–2249b). 7: Angûjârtûtit (70–2164). 9: Eqaluit (70–2548a). 10: Enoks Havn (70–2762b). 14: Hareøen (70–2572, 70–2574). 15: Kronprinsens Ejland (70–2067, 70–2071, 70–2084, 70–2089a, 70–2101, 70–2102, 70–2103, 70–2111, 70–2123). 16: Manîtsoq (70–3007, 70–3022). 17: Tupilak (66–0012a, 66–0013b, 66–0022, 66–0023a, 66–0033b, 66–0108). 17A: Egedesminde (66–0948b). 18: Grønne Ejland (70–2816a). 19: Nûk (70–2837a). 22: Orpigsôq (70–3118c, 70–3116a). 24: Jakobshavn (66–0235, 66–0243a, 66–0245). 25: Sarfaq (70–2351, 70–2352a, 70–2353, 70–2359a). 26: Pâkitsup ilordlia (70–2294b, 70–2319). 30: Eqe (66–0249, 66–0289). 31: Anap nunâ (70–2414a, 70–2421, 70–2424, 70–2429, 70–2434). 32: Qôrorssuaq (70–2457, 70–2459c, 70–2476b, 70–2480). 36: Umanak (66–1471, 66–1493). 37: Agpat (66–1438, 66–1467b). 42: Magdlak (66–1375). 48: Amitsup (66–0818). 51: Simiútap kûa, shore (66–0919). 53: Søndre Strømfjord (66–0050, 66–0072, 66–0073, 66–0075, 66–0076, 66–0082, 66–0090, 66–0095, 66–0096, 66–0101).

Additional collections:

17: Tupilak (K.J. 1342, 1349, 1350, 1354, 1449, K.H. 17.006). 44: Akuliarusikavsak (K.H. 15.868, 16.689). 56: Ujarasugssuliup qáqâ (L.K.R. Aug. 1886). 57: Nipisat (K.H. 14.577). 60: Kugssuaq (M.P.P. 737). 74: Kangerdluarssuk (M.P.P. 1766a). 79: Agpalilik (C.K. 1202a). 83: Angnertussoq (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 87: Kangersuneq (K. Hansen Aug. 1958). 88: Christianshåb (K.H. 16.675). 90: Tasiussaq (S.B. July 1870). 95: Pâkitsoq (J.V. 167, 177). 98: Sarqaq (J. V. 247a). 106: Nûgssuaq (K.J. 39a). 112: Umiartorfik (K.J. 627, 876a, 882). 115: Kûgssuaq (K.J. 749). 116: Puiagtukavsak (K.J. 679). 117: Sêrsínerssuaq (K.J. 616). 125: Eqaluit (K.J. 510, 541, K.H. 13.245). 131: Storø (A.R. July 1954). 137: Esersiutilik (K.H. 13.802).

The above range includes all plants which represent typical var. *minutum* and any borderline specimens that verge on var. *grandis*. The species, *s.l.*, has a subcosmopolitan range in boreal and Arctic regions of the northern hemisphere, with disjunct stations in the Azores, South Africa (Arnell, 1963), and (?) Kerguelen I. (G., L. & N., 1844–47); the last two citations must be regarded with doubt. The species is also known southward to Mexico (and as ssp. *novoguineanensis* Schust.; see Schuster, 1968) from high elevations in New Guinea; also reported from Borneo (Kitagawa, 1970).

A. minutum is so nearly ubiquitous in the Arctic that any detailed statement about environmental restrictions and associates would be self-defeatingly comprehensive. The plant is common in all areas, but perhaps more so in acidic regions. It is particularly ubiquitous among mos-

ses in deep, peaty moss-tundra, often with *Lophozia binsteadii*. Common associates are *L. polaris*, *Gymnomitrion concinnatum*, *G. corallioides*, *Tritomaria quinquedentata*, *Scapania crassiretis*, *S. serrulata*, *Anastrophyllum assimile*, less often *S. hyperborea*, *S. mucronata*, *Cephalozia bicuspidata*, etc.

This is one of few taxa able to tolerate strikingly dry conditions and may occur as erect, straggly plants amidst deep mats of *Chandonanthus setiformis* and *Lophozia hatcheri* (as in 66–0243a), or with these taxa and *L. rubrigemma* and *L. kunzeana* (70–2459c). It may also occur over exposed gneissic rocks with *Chandonanthus* and *Gymnomitrion corallioides* (66–0948b), or with *Prasanthus*, *Anthelia juratzkana*, *L. opacifolia*, *Tritomaria quinquedentata* (70–3118c).

Perianths are frequent; capsules are rare; gemmae are very infrequent in regional plants (but are present in 66–0012a, 66–0140), except when these occur in almost pure, caespitose, vigorous patches under somewhat helophytic conditions (then often with *L. binsteadii*).

v. *grandis* (GOTT. ex. LINDB.) SCHUST.

Distribution (Map 31)

1A: Behind Arctic Station (70–2012d, 70–2039b, 70–2056). 2: Fortunebay (66–0136, 66–0139, 66–0140). 10: Enoks Havn (70–2759a, 70–2762b). 14: Hareøen (70–2609, 70–2618). 15: Kronprinsens Ejland (70–2064, 70–2073, 70–2077, 70–2078, 70–2095). 17: Tupilak (66–0032c). 19: Nûk (70–2835). 22: Orpigsôq (70–3115b). 23: Kangersuneq (70–3145c). 25: Sarfaq (70–2338b, 70–2345, 70–2353, 70–2354, 70–2365, 70–2366a). 26: Pâkitsup ilordlia (70–2260d, 70–2264c, 70–2272a, 70–2274, 70–2301a, 70–2316a, 70–2388). 30: Eqe (66–0293b). 31: Anap nunâ (70–2416, 70–2435). 32: Qôrorssuaq (70–2448c, 70–2456). 36: Umanak (66–1481a, 66–1561). 45: Kangerdlugssuakavsak (66–1078). 46: Qalatôq (66–1100). 48: Amitsup (66–0776, 66–0781). 53: Søndre Strømfjord (66–0075, 66–0096).

Additional collections:

45: Sagdliaruseq (K.H. 16.933c). 73: Igdlokasik (K.H. 14.497b). 88: Christianshåb (K.H. 16.655). 99: Sarqaq valley (K.J. 241, 989). 106: Nûgssuaq (K.H. July 1956). 112: Umiartorfik (K.J. 876b). 122: South of Eqaluit (K.H. 13.345a). 125: Sarqap taserssua (K.H. 17.114). 136: Kangerdluarssûp qeqertâ (K.H. 16.162). 139: Qaqortukavsak (K.H. 16.121). 141: Inukavsait qâqarssue (K.H. 16.277a). 142: Niaqornánguaq (K.H. 14.949).

This almost exclusively Arctic plant is perhaps no more than a luxuriant extreme of var. *minutum*; the distinctions are given in SCHUSTER (1969, table 6, p. 769). Insofar as the plant may be distinct, the above cited collections belong to it.

Var. *grandis* may be a mere forma of richer, less arid sites, where it may occur under almost helophytic conditions (with *Lophozia ventricosa longiflora*, *L. binsteadii*, in 70–2056, 70–2064), or in peaty depressions between rocks, where there is weakly basic seepage (then with *Odonto-*

schisma macounii, *Scapania degenii dubia*, *Gymnomitrion corallioides* and *concinnatum;* in 70–2012d). It may also occur, however, on cold, wet cliffs, with *Marsupella revoluta* and *Gymnomitrion concinnatum* (70–2338b), or over rather dry rocks, amidst mosses and *Cephaloziella rubella arctogena*, *L. rubrigemma*, *L. kunzeana*, *L. excisa*, *Chandonanthus*, and *Ptilidium ciliare* (70–2456; 70–2039b). Occasionally, however, under very exposed conditions, in heaved ground of soil-stone polygons, associated with *L. alboviridis*, *Scapania parvifolia*, *Nardia geoscyphus*, *Cephalozia bicuspidata*, and *Gymnomitrion corallioides* (70–2448c); the last three species also are found admixed on broken stony soil slopes (70–2260d). By contrast, on more or less permanently damp, sandy depressions in moss-heath tundra, the species sometimes occurs with *Cryptocolea*, *Odontoschisma macounii*, and *Cephalozia pleniceps* (in 70–2272a) or with *L. rutheana* (in 70–2264c)—species usually found in at least slightly calcareous sites.

The plants, in general, have slightly larger cells and more numerous oil-bodies than in var. *minutum*; in 70–2416 marginal lobe cells are 17–19 μ, oil-bodies are 3–6 per lobe cell but (4)5–7(8) per basal cell; in 70–2759a there are only 2–4 oil-bodies per lobe cell; in 70–2365, 3–6 per lobe cell; in 70–2264c, (2)3–4 per lobe cell; in 70–2272a, 2–5 per lobe cell; in 70–2456, 3–6 per lobe cell; in 70–2095, 3–6(7) per median cell; in 70–2762b, (2)3–4(5) per lobe cell.

Occasionally we find what appears to be an admixture (or intergradation ?) between var. *minutum* and var. *grandis*. Thus in 70–2353 some plants have marginal lobe cells 12–15 μ (= var. *minutum*), others 17–18 μ, and have 2–5 oil-bodies per lobe cell (= var. *grandis*).

A. minutum grandis rarely occurs admixed with the deceptively similar *Lophozia cavifolia* (as in 70–2301a). The two are then distinct on the basis of the criteria used in Schuster (1969, p. 769). In the collection cited, var. *grandis* had cells without obvious trigones and only (2)4–5 oil-bodies per lobe cell; in the *L. cavifolia*, cells were larger, the marginal ones were to 21–24 μ, and had conspicuous trigones; the lobes usually had 4–7 oil-bodies per cell.

Gymnocolea (Dumort.) Dumort.

Gymnocolea inflata (Huds.) Dumort.

Distribution (Map 32)

1A: Behind Arctic Station (66–0102d, 66–0193a, 66–0197, 70–2007, 70–2009a, 70–2037, 70–2041, 70–2046). 1B: Lyngmarken (66–0344, 66–0555). 15: Kronprinsens Ejland (70–2068b, 70–2069, 70–2075, 70–2081, 70–2084). 16: Manîtsoq (70–3000, 70–3012a, 70–3024a, 70–3007c). 17: Tupilak (66–0001a, 66–0002a, 66–0009a, 66–0010, 66–0011, 66–0016, 66–0024a, 66–0105a, 66–0109a, 66–0028b). 17A: Egedesminde (66–0945). 19: Nûk (70–2874c, 70–2879). 21: Umiasugssûp (70–2926). 22:

Orpigsôq (70–3113a, 70–3119c). 23: Kangersuneq (70–3130, 70–3134b, 70–3157, 70–3158a). 25: Sarfaq (70–2366a, 70–2375, 70–2377a). 26: Pâkitsup ilordlia (70–2276a, 70–2305, 70–2314). 32: Qôrorssuaq (70–2442b, 70–2452, 70–2455b). 36: Umanak (66–1486). 37: Agpat (66–1468, 66–1426, 66–1434). 45: Sagdliaruseq (66–1052).

Additional collections:

16: Manîtsoq (W. & H. 1884). 28: Atâ (LÆGAARD July 1962). 45: Sagdliaruseq (K.H. 14.593). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.631). 106: Nûgssuaq (K.H. 15.589). 112: Umiartorfik (K.J. Aug. 1947). 126: west of Sarqap taserssua (K.H. 13.414a). 136: Kangerdluarssûp qeqertâ (K.H. 16.143). 142: Niaqornánguaq (K.H. 14.929, 14.930b).

G. inflata is a subcosmopolitan species in cool to Arctic regions of the northern hemisphere; its distribution in Asia is not clearly defined because of disparate taxonomic treatments by the Japanese bryologists who have recognized "*Gymnocolea montana*" or "*G. inflata* ssp. *montana*"; SCHUSTER (1969, p. 789) was unable to find consistent differences between the Japanese and American plants. To add to the confusion, KITAGAWA (1965) recognizes a *G. marginata* (STEPH.) HATT., following HATTORI, and places *G. montana* under it as a simple synonym. SCHUSTER (1965, p. 274) has expressed reservations about any attempt at a distinction at the species level.

Almost equally ambiguous is the difference between *G. inflata* and *G. acutiloba* (SCHIFFN.) K. MÜLL., a plant reported from Godhavn (PERSSON, 1942) and supposedly distinct in the sharp leaf lobes. We regard all regional plants as representing the single species, *G. inflata*. Broadly defined, it extends north to ca. 77°23–33′ N. in the Inglefield Bredning area (SCHUSTER, l. c.), and south to North Carolina and Arkansas.

Regionally almost always limited to exposed sites (hence usually a fuscous to scorched-appearing mod. *colorata*), most often where kept wet by seepage; usually on bare rocks or thinly soil-covered rocks in and on the margins of rills, or on cliff faces, associated with *Marsupella boeckii*, *M. arctica*, *Scapania hyperborea* (70–2442b) or also *Cephaloziella byssacea* and *Gymnomitrion concinnatum* (70–2455b). On peaty low ground, amidst boulders or rocks near tarns, it is often with *G. apiculatum*, *G. concinnatum*, *Odontoschisma elongatum*, *Cephalozia bicuspidata* (70–2068b, 66–0193a). Equally often on peaty, often mucky wet soil around tarns, sometimes submerged, associated with *Anthelia*, *S. hyperborea*, *S. paludicola rotundata*, *Lophozia alpestris*, *L. kunzeana*, *Cephalozia bicuspidata*, and occasionally (when emergent) *L. binsteadii*. Around sunny, acid tarns it is also sometimes found with *Marsupella arctica* and *Odontoschisma elongatum*—both of which may be equally piceous in color.

The species exceptionally occurs, as a small, scorched phase, on broken, rocky soil where subject to desiccation; it is then associated with

Prasanthus, *L. excisa succulenta*, *Solenostoma sphaerocarpum*, *Nardia geoscyphus*, and *Pleuroclada* (70–3007c). In this, and all other sites, it is clearly restricted to regions with acidic rocks and with acidic seepage. Only once were collections made on irrigated, peat-covered slopes dotted with small pools, where perhaps a slight amount of basic seepage was present; here (66–0105a) *Aneura pinguis* and *Solenostoma subellipticum* were consociated.

Sterile (inflated) perianths and androecia are common; we have not seen capsules in the West Greenland plants. Most plants correspond to "normal" *G. inflata*, but in areas with some basic seepage and when admixed with *Aneura pinguis*, *Tritomaria polita polymorpha*, and *Drepanocladus*, larger forms occur (see SCHUSTER, l. c., p. 793). These plants, to 2.6 mm wide or more, have horizontally patent leaves and produce fertile perianths that are strongly 5–6-plicate in the distal 0.2–0.25. Such plants may have only 1–5 oil-bodies per cell, with some cells bearing 1–2 very large oil-bodies (see fig. 251:14–18, in SCHUSTER, l. c.).

Subfamily *Jamesonielloideae* INOUE emend. SCHUST.

Jamesoniella (SPR.) SCHIFFN.

Jamesoniella undulifolia (NEES) K. MÜLL.

Distribution (Map 33)

24: Jakobshavn (K.H. 15.994).
87: Kangersuneq? (J.V. 108, 111).

J. undulifolia is an exceptionally rare plant in the western hemisphere. It is known only from the above collections, which we have verified, and from Siorapaluk, in northwest Greenland (SCHUSTER, 1969). VAHL 111 has a "crenulate perianth mouth" (SCHUSTER, l. c., p. 831). A small mount of *J. undulifolia* was also detected in VAHL 108, presumably from the same locality, mixed with *Lophozia binsteadii* and *Calypogeia sphagnicola*. VAHL 111 is cited from "Moser, ofte mellem Sphagna". The Siorapaluk plant occurred with *Sphagnum balticum*, *Polytrichum*, *Anastrophyllum minutum grandis*, *A. sphenoloboides*, *L. groenlandica*, etc., on wet, peaty ground.

We have searched in vain for this species in West Greenland.

Plants of HOLMEN 15.994 are fertile: both perianths and androecial plants are present. In these plants we have seen not only the "frequently furcate and terminal" branches noted for the species in SCHUSTER (1969), but also branches of the *Radula* type: smoothly originating, without a collar, from the stem near its juncture with the abaxial leaf base. In such

cases there is no modification of the associated leaf, or of that lying posterior to the branch. Such branching is rare in *Jungermanniaceae*, *s.l.*, but has been noted by SCHUSTER in *Tritomaria*; we have also seen it in *Solenostoma cordifolium*.

Subfamily *Jungermannioideae* DUMORT. emend. SCHUST.

Solenostoma MITT.

Arctic populations of *Solenostoma* (*s.l.*, as in SCHUSTER, 1969) pose major taxonomic problems. They often simply fail to match the stereotypes derived from temperate and boreal European populations. Thus few collections can be attributed to "normal" *S. pumilum* (see detailed discussion of this species and its "problems" in the Arctic, in SCHUSTER, l.c.); large-celled populations exist which are very close to the dioecious *S. oblongifolium* but which are clearly heteroecious. The question is: what significance should be put upon this, taxonomically? Also, the *S. sphaerocarpum* (incl. var. *nana*)-*pyriflorum*-*pusillum* complex in Greenland is complex almost beyond belief. In many cases the plants do not at all correspond to non-Arctic taxa. We meet here again the problem of going, seemingly by stages, from purely paroecious plants (*S. sphaerocarpum* and *S. pusillum*) to heteroecious or possibly partially dioecious plants (*S. pyriflorum* ssp. *purpureum*).

Within the *S. sphaerocarpum-pusillum-pyriflorum* complex we find that pigmentation patterns "fail" as a taxonomic criterion. Thus we have the "boreal-temperate stereotype" of a green *S. sphaerocarpum* whose sun forms become brown to fuscous distally, and a "temperate" *S. pusillum* that becomes bright red to claret colored, whereas the Appalachian-Asiatic *S. pyriflorum* is green, with intensive to dull purple distal sectors in sun forms. With such non-Arctic derived stereotypes at hand, where do we place the small Arctic plants, here called *S. pyriflorum* ssp. *purpureum*, which are intensively purplish-pigmented?

The taxonomic meaning of these different criteria, which we have had to evaluate pragmatically (and surely not fully satisfactorily), will need to be eventually re-examined by means of culture experiments and possibly reciprocal transplant experiments.

Obviously the genetics of the *S. pumilum* and *S. sphaerocarpum*, as well as the *S. cordifolium-oblongifolium* complexes, demand detailed study. With the demonstration (SCHUSTER, 1972) that in the allied genus *Jungermannia* we can easily go from dio- to paroecious populations, sexuality as a species criterion in *Solenostoma* must undergo very critical re-evaluation. It is possible that the extreme environmental conditions of the Arctic have induced either physiological suppression of potentially monoecious conditions, or vice versa, or that there has been imperfect genetic

segregation of differences in sexuality. Perhaps both factors are operative —leading to a hopeless taxonomic situation.

Subg. ***Luridae*** (Spruce) K. Müll.

Solenostoma pumilum (With.) K. Müll.

Distribution (Map 34)

1A: Behind Arctic Station (66–0150c, 66–0153b, 66–0177, 66–0183, 66–0276). 1D: Skarvefjeld (66–0231, 66–0307, 66–0308). 17: Tupilak (66–0026a). 23: Kangersuneq (70–3127a, 70–3129 f. *rivularis*). 30: Eqe (66–0322c). 38: Uvkusigssat (66–1393). 42: Magdlak (66–1356d). 43: Kangerdlugssuakavsak (66–1284, 66–1290).

Additional collection:

111: Kûtsiaq (Sørensen Aug. 1947).

This plastic species is one of the most variable and difficult to interpret if we try to use the same standard of comparison for Arctic populations as for European ones (see Schuster, l. c., pp. 909–911, and Schuster *et al.*, 1959). The "usual" criteria relied on to separate two (*S. pumilum*, *S. schiffneri*) or more (*S. pumilum*, *S. schiffneri*, *S. polaris*, *S. atrovirens*) species for Arctic populations seem foredoomed to failure; there is no clear linkage between criteria relied upon for species discrimination. Leaf shape (and width-length ratios), perianth shape, cell size, capsule wall ornamentation—all are highly variable and all, seemingly, vary largely independently. If any linkage occurs it is so imperfect that we have been unable to perceive it. Even the partial linkage suggested in the key in Schuster (l. c., p. 907) frequently breaks down: it expresses an ideal the material only in part adheres to.

Key to Variants of *S. pumilum*

1. Cells small: those of distal margins of leaves, at apices, 16–18 μ or less. Cortical cells dorsally ca. (15)17–21(23) μ wide . . . . . 2.

2. Leaves of sterile stems ± elliptical (in Arctic phases ranging to ovate); perianth typically fusiform, the distal one-fourth or more conically tapered; cells with (2)3–6 or more oil-bodies; apical leaf cells ca. 16–18 μ, median to 23–25 × 25–30(35) μ.
ssp. *pumilum* . . . . . a.

a. Perianth fusiform, conically pointed, tapered in at least the distal one-fourth. f. *pumilum*

a. Perianth strongly inflated, oblong-ovoid to obovoid, abruptly rounded to mouth. f. *rivularis*

2. Leaves of sterile stems rotundate to broadly ovate; perianth broadly clavate or obovoid, abruptly narrowed to mouth; cells

with (1)2–4(5) oil-bodies per cell; apical leaf cells usually ca. 13–17 μ, median (12–13)14–18×16–22(24–26) μ.
ssp. *polaris* . . . . . b.

b. Leaves broadly ovate, usually narrowed from middle to rounded or blunt apex. f. *polaris*

b. Leaves broadly subrotund, wider than long, strongly concave to hemispherical. f. *cavifolius*

1. Cells large: distal marginal cells ca. (18)19–25(27) μ, median 21–25× 25–36 μ; perianths obovoid; leaves ovate-pointed, longer than wide, concave, spoon-shaped. Cortical cells ca. 20–34×50–60 μ.
ssp. *anomalum*

ssp. *pumilum* (WITH.) K. MÜLL. (Fig. 10:8–9, 11–12)

This is to a large extent supplanted by ssp. *polaris* in the Arctic. The plant is perhaps most frequent in admixture, often over exposed peaty soil, in permanently wet areas, at other times over sheltered, moist to wet rocks or in rock crevices, often along rills; it is common on basaltic cliffs. At least in Arctic and subarctic sites, it is strongly Ca-tolerant and associated with a wide range of calciphytes, e.g., *Tritomaria scitula*, *Lophozia heterocolpos*, *Scapania curta*, *S. cuspiduligera*, *Sauteria alpina*, *Preissia quadrata*, very often occurring in small quantity, growing in the interstices left between the thalli of the last two marchantioids.

In the Arctic ssp. *pumilum* tends to grade gradually into ssp. *polaris*; both leaves and perianths become abbreviated, and on the latter, the conoidally tapered apex undergoes progressive abbreviation until an obovoid perianth, with the apex rather suddenly contracted, results. As a consequence, transitional specimens (e.g., 66–0280) are frequent, and even the most nearly typical collections have leaves somewhat broader and more ovate than in "typical" plants (such as are shown in SCHUSTER, 1969, fig. 273:1–4) from temperate zones. Thus the Kûtsiaq specimen (inter *Sauteria alpina*) has the rather narrowly pointed perianths typical of *S. pumilum*, and, on that basis, it is placed here rather than with ssp. *polaris*; it is definitely paroecious. Sterile shoot sectors are few and—as in almost all Arctic forms we have seen referred to *S. pumilum*—have ovate leaves, much as in ssp. *polaris*.

Two other notable variations exist in local populations: (1) on thin, wet sandy soil along cascading streams cutting through igneous rocks, as in Kangersuneq (70–3129, 70–3127a) we find the f. *rivularis*, a plant which tends to be slightly larger, with larger and more obovoid perianths. Associated are other rather Ca-intolerant taxa, e.g., *Scapania irrigua rufescens*, *S. subalpina*, *S. tundrae*, *Solenostoma subellipticum*, as well as more tolerant species: *Nardia geoscyphus*, *Cephalozia pleniceps*, *C. bicuspidata*, *Pleuroclada albescens*, *Anthelia juratzkana*. (2) On moist rocks in

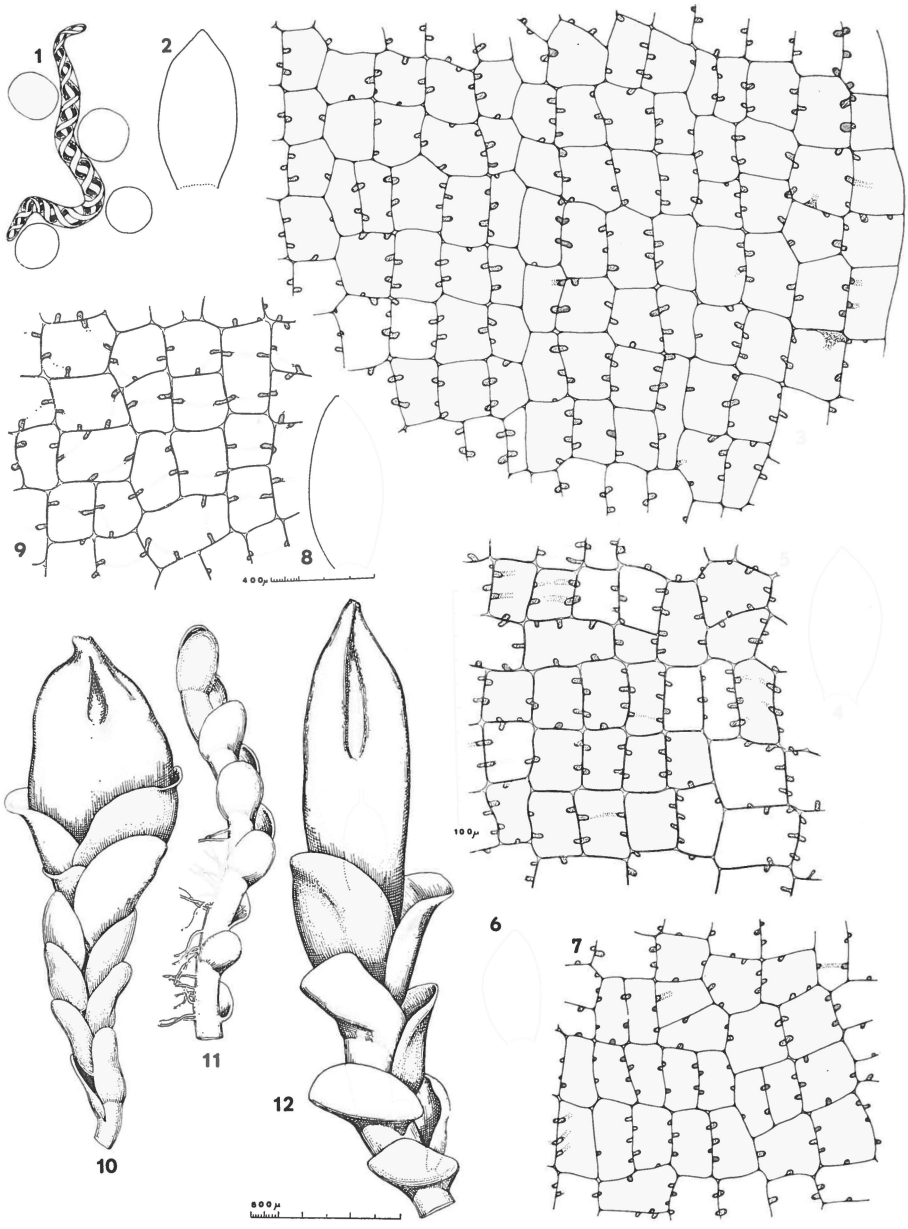


Fig. 10. *Solenostoma pumilum.* (1–7, 10) ssp. *polaris;* (8 9, 11) s p *p* phase with "*pumilum*-like" perianth but broad, "*polaris*-like" leaves. (1) S outline, and elater (×305). (2) Valve of capsule, large sporophyte (×33). (3 epidermal cells from preceding valve (×305). (4) Valve, medium-sized capsu (5) Epidermal cells from preceding valve (×305). (6) Valve from small capsu (7) Median epidermal cells from preceding valve (×305). (8) Valve from larg (×33). (9) Median epidermal cells from preceding valve (×305). (10) Periant shoot apex from phenotype shown in figs. 1–7 (×33). (11–12) Sterile a shoots, from phenotype shown in figs. 8–9 (×33). [1–7, 10, from 66–0283a, Bl Godhavn; 8–9, 11–12, from 66–0026a, Tupilak; for discussion of the unreli sporophyte-derived criteria and a discussion of 66–0283a, see p. 910 in S 1969; 1, 3, 5, 7, 9, drawn to 100 μ scale; 2, 4, 6, 8, drawn to 400 μ scale; 10– to 600 μ scale].

the igneous-basalt transition at Lyngmarksfjeld (66–0177), a population of clearly heteroecious plants occurs. These have the (2)3–5 oil-bodies per cell, as shown for ssp. *pumilum* (SCHUSTER, l. c., fig. 273:3). They also often have the leaves quite narrow and elongated, and have rather clearly pointed perianths, as in typical ssp. *pumilum*. Their sexuality, however, is very variable. In addition to "normal" paroecious plants we find plants with intercalary ♂ bracts, succeeded by a variable number of sterile leaves prior to initiation of a gynoecium. We also find plants in which an intercalary androecium is succeeded by several pairs of sterile leaves, then by another androecium, then again by sterile leaves. It is very doubtful if the last type represents unisexual individuals, however. This conclusion seems warranted by the presence of a third kind of individual: plants with leading axes that lack ♂ bracts, but end in a gynoecium, and which develop paired innovations that are eventually androecial. Such plants, with death of the older, gynoecial axis, might simulate unisexual individuals.

ssp. *polaris* (BERGGR.) SCHUST. (Figs. 10:1–7, 10; 11: 11–12)

Distribution (Map 34)

1A: Behind Arctic Station (66–0280, 66–0283a, 66–0286, 70–2030a). 11: Qasigíssat (70–2739b, 70–2744c). 12: Perdlertut (70–2689, 70–2703a). 13: Jens Vahls Dal (70–2643, 70–2651a, 70–2666). 14: Hareøen (70–2592c, 70–2608a, 70–2613, 70–2619). 30: Eqe (66–0290b f. *cavifolius*). 31: Anap nunâ (70–2408a). 35: Hollænderbugt (66–1507b). 40: Mârmorilik, head of the Fjord (66–1198). 42: Magdlak (66–1357a). 43: Kangerdlugssuakavsak (66–1281, 66–1281a f. *cavifolius*, 66–1283a, 66–1288, 66–1292a). 47: Íngia (66–1032, 66–1034). 49: Skalø (66–1022). 51: Simiútap kûa, shore (66–0826, 66–0836). 53: Søndre Strømfjord (66–0041a).

Additional collections:

70: Sarqardlît (M.P.P. 657b). 90: Tasiussaq (S.B. 1870). 92: Claushavn (S.B. 1870). 103: Qapiortoq kitdleq (K.J. 1052d). 110: Ikorfat (K.J. 334c, K.H. 62.1567b). 129: Avataussaligssuaq (K.J. 924a). 143: Kangerdlugssuaq (K.H. 16.406). 145: Uligssat (K.J. 10.186e).

Stated (SCHUSTER, 1969, p. 921) to be the "commonest and most variable member of the genus in the Arctic, with corresponding wide ability to undergo ecesis in the most diverse sites. The plant is almost "weedy in sites where a dense ... vegetation cannot (or has not yet) succeeded, often forming small, diffuse colonies on difficult or temporary sites". As the associates and map show, the plant is Ca-tolerant. Typical occurrences are: (a) on sunny, south-facing slopes in continental areas (as at Søndre Strømfjord, 66–0041a, with *Mannia pilosa*), on soil over ledges; (b) in crevices of moist rocks, around cascades and waterfalls (as at Magdlak; 66–1357a, with *M. pilosa*, *Athalamia hyalina*, *Preissia*, *Tritomaria scitula*, *Scapania cuspiduligera*, *Plagiochila asplenioides*; the plant occurs here in a phase most nearly matching *S. "schiffneri"*); (c) on fast-drying, often calcareous, stony clay slopes (66–1507b, 70–2739b,

associated with *S. sphaerocarpum nana*, *Lophozia heterocolpos s.l.*, *L. pellucida minor*, *Scapania curta isoloba*, *Nardia geoscyphus*, *Tritomaria scitula*); (d) in sites similar to (c) but strongly calcareous and more permanently damp to moist [70–2613, 70–2608a, 70–2592c, associated with *Scapania cuspiduligera*, *S. ligulifolia*, *T. quinquedentata*, *T. scitula*, *Lophozia gillmani*, *L. grandiretis*, *L. quadriloba glareosa*, *L. heterocolpos harpanthoides*, *Anthelia*; in similar sites (70–2703a), where apt to be kept wet or damp by seepage, with *Cryptocolea*, *T. polita s.l.*, *L. heterocolpos*, *Cephalozia pleniceps*]; (e) on "difficult" sites over bare, peaty ground along rills, subject to inundation by Ca-enriched waters, with *T. polita polymorpha* and *Scapania obcordata s.l.* (70–2030a); (f) over soil in crevices between calcareous rocks, subject to periodic drying out (66–1283a, with *T. heterophylla*, *Scapania gymnostomophila*, *S. mucronata praetervisa*, *Cephaloziella uncinata*). Other sites invaded are discussed in SCHUSTER (l. c., p. 922). Capsules are very abundantly produced from July 5–Aug. 7.

The plants are all demonstrably paroecious, although some collections (e.g. 70–2030a) are heteroecious—some purely androecial branches being present. Occasionally we find striking suppression of antheridium formation, without development of purely androecial branches. Thus in 66–1281 (Kangerdlugssuakavsak; a lax, mesic phase, with *Scapania gymnostomophila* and *Plagiochila*) we find many gynoecial axes which, in almost all cases, lack any trace of ♂ bracts. This is true of young gynoecia, with archegonia at the point where they are ripe for fertilization. In such cases one can search for a long time before finding a paroecious plant—and then there may be only a single ♂ bract developed! Such plants are likely to be mistaken for *S. atrovirens* but differ in (a) lacking the long ♂ spikes; (b) having somewhat larger cells, (17)19–23(26) μ marginally, 17–20 × 19–28 μ medially; cortical cells 16–20 × 62–85 μ. These measurements (taken from 66–1281) show clearly that ssp. *polaris*, when growing in mesic loci, may develop larger than normal cells. Indeed, cells size in *S. pumilum s.l.* seems highly variable, subject to vigor of the plant.

In difficult sites ssp. *polaris* tends to develop remote, very broad, strongly hollowed-out, often wider than long leaves; this represents:

f. *cavifolius* (SCHUST.) SCHUST.

This phenotype occurs usually under extreme conditions. The plant from Eqe (66–0290b) is from an exposed, cold, cliff wall adjoining a small basalt dike, with *Marsupella revoluta*, *Anomomarsupella cephaloziellioides*, and *Cephaloziella arctica* admixed.

ssp. *anomalum* SCHUST. & DAMSH., *ssp. nov.* (Fig. 11:8–10)

Subsp. *pumilo* simile sed omnino majus, cellulis corticis majoribus (20–34 × 50–60 μm) foliorum multo majoribus (21–25 × 25–36 μm).

Plants similar to *S. pumilum* f. *rivularis*: leaves ovate, longer than wide on sterile shoot sectors; perianths obovoid. Differing in the somewhat larger cells (especially of leaf tips) and in the strongly concave, spoon-shaped leaf form.

Type. 26: Pâkitsup ilordlia (70–2390a), Qissugssalik, trace over wet sand, shallow depression near lake shore, among *Scapania irrigua rufescens*, *Nardia geoscyphus*. (Map 34).

The Qissugssalik material represents the only collection of this taxon seen. The very few plants suggest the doubtful *S.* "*rivularis*" phase. Sterile leaves are ovate-pointed and ca. 655 μ wide × 700–725 μ long, but seem much narrower because they are quite concave and spoon-shaped, with conspicuously narrowed ends. The flattened leaf is similar in shape to that of *S. oblongifolium*. Cells are unusually large: marginal cells distally average mostly (18)19–25(27) μ, median (19)20–25×25–36 μ, basal from 20–25×34–40 μ up to 28–33×36–55 μ on some leaves. The few, rather malformed perianths seen are obovoid in shape, as in the "*rivularis*" phase of *S. pumilum*. The identity of the material with *S. pumilum s.l.* is definitely established, since a paroecious inflorescence was twice demonstrated. Also, plants are dwarf, being much smaller than the large-celled plants here attributed to *S. oblongifolium*. If we compare the cell sizes, however, of both leaf and stem (dorsal cortical cells), it is clear that *S. pumilum anomalum* closely matches *S. oblongifolium heteroicum*.

The choice thus seems to be between placing these plants under *S. pumilum* or *S. oblongifolium*. Since the obovoid perianths, small size of the plant, and clearly paroecious inflorescences (with ♂ bracts just below the ♀ ones) clearly correspond to *S. pumilum s.l.*, we place the plants here as a large-celled Arctic derivative. More copious collections may necessitate a re-examination of this placement. It is also not impossible that a large-celled extreme of f. *rivularis* is at hand.

Solenostoma oblongifolium (K. MÜLL.) K. MÜLL.

Distribution (Map 33)

114: Eqaluit (K.J. 830b).

This poorly understood species has been reported from Greenland only from the type station (VAHL 236, 1829, cited in SCHUSTER, 1969, p. 937, as from the "east coast", but the VAHL collection was from Frederiksdal in south Greenland), and is otherwise cited only from Siberia (ARNELL, 1913), the Hudson Bay area (SCHUSTER, 1951) and from Scotland (PATON, 1968).

The plant of JAKOBSEN (830) from Nûgssuaq was found amidst *Marsupella arctica* and *Scapania serrulata* from the igneous rock area;

only a few sterile stems were found, hence—although attribution to *S. oblongifolium* is certain, we cannot be sure if it is the typical, dioecious subspecies, or the heteroecious ssp. *heteroicum*. Leaves are 1145 μ long × 1060 μ wide; marginal cells in the median half of the leaf are 17–22 μ; median cells are 21–27 × 26–33 μ. This contrasts to leaves 660 μ long × 515 μ wide in the type of *S. oblongifolium*, with marginal cells 19–25 μ, median cells 19–23 × 31–37 μ. In view of the great variation in cell size and leaf size in these aquatic and subaquatic plants, these measurements mean very little.

ssp. *heteroicum* SCHUST. & DAMSH. *ssp. nov.* (Fig. 11:1–7)

Subsp. *oblongifolio* dioico forma foliorum, magnitudine cellularum, colore, habitu simile, inflorescentiis heteroicis ab eo diversum.

Distribution

21: Umiasugssûp (70–2951a).

Additional collection:

32: Qôrorssuaq (S.B. 1870; publ. as "J. cordifolia" by BERGGREN, 1875).

[A final answer as to where S. BERGGREN collected his specimen of *Solenostoma "cordifolium"* is impossible to give. BERGGREN (1875) mentions "*J. cordifolia*" from Qôrorssuaq (the land north of Kikertak = Qeqertaq) but all collections studied (in Stockholm, Lund, and Copenhagen) have Ritenbenk cited as the collecting station. A possible answer to this problem is suggested by a study of a BERGGREN collection, still unlabeled, in the Botanical Museum at Lund. On a sheet containing "*J. cordifolia*" is a small slip of paper with a "R" for Ritenbenk, but a part of the collection has a Kikertak-label. We conclude that his collection, labeled Ritenbenk, was thus labeled by mistake and that Kikertak (or Qeqertaq) is the collecting place. This mistake could easily have been made as BERGGREN visited the Nûgssuaq area only one day and stayed at Ritenbenk both before and after this visit. The second BERGGREN report of "*J. cordifolia*", from Jakobshavn has not been checked by us.]

The following diagnosis is based on the type; slightly deviant details of the Berggren specimen are added in brackets.

Plants green to olive-green, medium-sized, leafy shoots 10–15 mm tall up to 1.4 to 1.65(1.9) mm wide, erect in growth, sporadically branched, with intercalary branches; branches dimorphic, some microphyllous, geotropic, stoloniform, others initially small-leaved and eventually leafy, others of the *Radula* type (terminal-basiscopic). Stem soft and slender (150–170 μ in diam.), cortical cells oblong, the dorsal 24–28(32) μ wide × 60–75 μ long. Leaves subvertical, remote to contiguous, showing gross seasonal variation in form; smaller leaves ovate, 575 μ wide × 700 μ long, larger leaves ovate and to 925 μ wide × 1100 μ long (0.8–0.85 as wide as

long), occasional leaves suborbicular, 800 μ wide × 760 μ long [1155 μ wide × 1310–1430 μ]. Leaves from slightly concave and widely patent to rather spoon-shaped and suberect. Cells rather large, marginal cells subquadrate, (19)22–25 μ [18–23 μ], median ± oblong, 21–28×30–36(55) μ long [21–28 × (29)32–43(46)]. Walls thin to slightly thickened, trigones very small; cuticle smooth distally, obscurely striolate near leaf base. Oil-bodies colorless, finely granular, variable, mostly 2–4 per cell (on some leaves accompanied by 2–4 much smaller accessory oil-bodies), mostly elliptical to bacilliform, from 4.5×9 to 7×10–12 μ, a few spherical to subspherical and 5–6×5–7 μ.

Heteroecious. Some plants apparently dioecious (gynoecial plants without subtending ♂ bracts, with subfloral innovations that are again gynoecial; androecial shoots with 2–3 [to 9–12] pairs of intercalary ♂ bracts), others with bisexual shoots; bisexual plants usually with 1–2 pairs of ♂ bracts followed by several pairs of sterile leaves before gynoecia are produced; rarely with 2–3 pairs of ♂ bracts immediately below the ♀ bracts; occasionally with androecial subfloral innovations. ♂ Bracts vertical, quite concave at base, their insertion running a little up stem, monandrous. ♀ Bracts leaf-like, vertical, concave, and loosely sheathing at base, errect to suberect. Perianths ± obovate, often slenderly so, widest within 0.3–0.4 of apex, the distal fourth contracted and often subconoidally narrowed, plicate, and with an antical furrow; perianth to 825 μ wide × 1850 μ long. Seta 330–350 μ in diam., with ca. 20 rows of epidermal cells surrounding ca.16 rows (in two concentric rings) of almost equally large to moderately small internal cells. Capsule wall 2-stratose, epidermal cells mostly short-oblong, 18–24 μ wide, 34–40 μ long (distally becoming subquadrate). All but scattered longitudinal walls with 2–3 very strong nodular thickenings per face; transverse walls without thickenings or with 1 or rarely 2 per wall. Inner cells irregular, strongly elongated, mostly 10–14 μ wide × 45–70 μ long, with many complete to incomplete tangential bands. Spores brown, densely granular-punctate, large, (19) 20–23(24) μ in diam., elaters contorted, 8–9.5 μ in diam., 2-spiral, the spiral ca. 3.5–4.5 μ wide; elater apices strongly narrowed and arched, often with spiral thickenings becoming obsolete.

Type. 21: Umiasugssûp (70–2951a), Disko Bugt, stream valley S. of Umiasugssûp tunua. The type occurred mixed with *Marsupella arctica* on irrigated rocky ground.

This perplexing plant fails to conform to any of the stereotypes that pass for species in the subg. *Luridae*. Its size essentially eliminates *Solenostoma pumilum*, although one might be tempted to place it as a *rivularis*-like phenotype of that species. The heteroecious inflorescences are occasionally found again in *S. pumilum* ssp. *polaris* (SCHUSTER *et al.*, 1959). The larger cell size, however, with the marginal cells mostly 20 μ or larger,

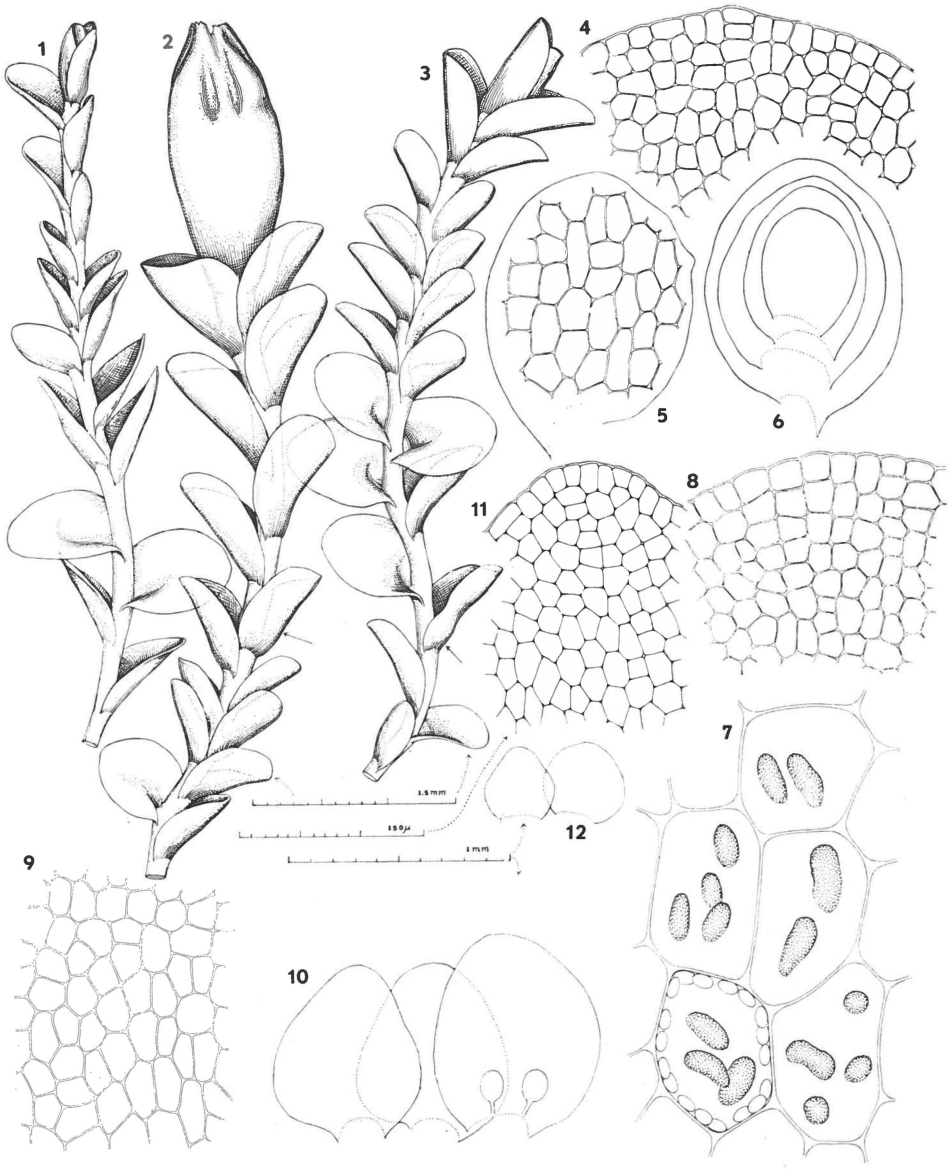


Fig. 11. *Solenostoma* species. (1–7) *S. oblongifolium* ssp. *heteroicum;* (8–10) *S. pumilum* ssp. *anomalum;* (11–12) *S. pumilum* ssp. *polaris.* (1–3) Sterile, paroecious, and ♂ shoots; ♂ bracts at arrows (×18). (4) Cells of leaf apex (×160). (5) Leaf (×29) and, within, median cells (×160). (6) Four leaves, showing variation in size (×29). (7) Median cells with oil-bodies and, lower left, chloroplasts (×645). (8) Cells of leaf apex (×160). (9) Median cells (×160). (10) Two leaves and a ♂ bract (×29). (11) Cells of leaf apex and middle (×160). (12) Leaves (×29). [1–7, from 70–2951a; 8–10, 70–2390a; 11–12, 66–0283a; 1–3, drawn to 1.5 mm scale; 4, 5, 8, 9, 11, drawn to 150 μ scale; 6, 10, 12, drawn to 1 mm scale].

and the large spores would seem to eliminate any phase of *S. pumilum.* The plant has much in common with *S. triste* and both cell size and oil-body form and number suggest this species; *S. triste*, however, is apparently consistently dioecious and has the spores usually 14–17 μ.

The spores, averaging 20–23 μ in diam., plus leaf shape, cell size, oil-body form and number agree quite closely with *S. oblongifolium* as that species is described in PATON (1968); vegetatively the plant closely approaches *S. oblongifolium* as described in SCHUSTER (1969). In particular, leaf size in the latter ("800–1000 μ long × 670–800 μ wide") and leaf shape, plus the cuticle, which is smooth distally on the leaves and striolate towards the base, is much as in *S. oblongifolium.* There are slight differences, however, in cell size: in the type plant of *S. oblongifolium* ssp. *heteroicum* we find apical cells averaging 22–25 μ (in the BERGGREN specimen, however, they are 18–23 μ); in *S. oblongifolium* ssp. *oblongifolium* PATON (1968) states they are "12–20(24) × 16–20 μ" and Schuster (l. c.) gives them as "15–19 to 20 μ". There are also differences in number of ♂ bracts on purely androecial shoots: in the BERGGREN material there are mostly 6–9 pairs per androecium; PATON (1968) states that the few perigonial bracts ("bracts in 2–4 pairs") of the androecium are "sufficiently distinct" in typical *S. oblongifolium* to enable one "to determine material in the absence of perianths".

The most obvious and impressive difference between typical (dioecious) *S. oblongifolium* and the plant described above, ssp. *heteroicum*, however, is the heteroecious inflorescence of the latter. This is very obvious in the type; it is less so in BERGGREN's material, but even here we found plants with a main stem on which after a zone of vegetative leaf development, several ♂ bracts were formed, succeeded by one or several sterile pairs of leaves, and then by ♀ bracts and a perianth. Such plants may produce lateral-intercalary branches which also show the same intercalary androecium of 2–6 pairs of bracts, followed by sterile leaves, and eventually ending in an androecium. Also, many shoots which were purely androecial were seen (which had up to 7–9 to 9–12 pairs of bracts); it is assumed that, in the demonstrated ability of shoots to develop androecia and later gynoecia, such androecial "plants" are also genetically able to develop gynoecia.

On balance, we feel that the plants here described and illustrated are best considered to be a heteroecious subspecies of dioecious *S. oblongifolium.* Elsewhere in the *Jungermanniaceae* similar variation in sexuality is known, e.g., in the paroecious *Jungermannia lanceolata* L. ("*J. leiantha* GROLLE") vs. the dioecious *J. lanceolata* ssp. *stephanii* AMAKAWA. [The case of this last plant is examined in detail by SCHUSTER (1972); it is shown there that the only reliable difference between the two lies in the sexuality.

SCHUSTER (1969, p. 839) considered *J. lanceolata* as paroecious but as "rarely with some purely ♀ branches, or with purely ♂ branches" and stated that gemmae were rarely present. GROLLE, although once insisting that there was a dioecious plant, *J. amakawana* GROLLE, which produced gemmae vs. a monoecious *J. lanceolata* ("*J. leiantha*") which was unable to produce gemmae, now admits that this last monoecious plant may produce gemmae. This is in accord with the statement (SCHUSTER, l. c., p. 839), that asexual reproduction is "rarely present!" In the opinion of SCHUSTER (1972) the mere difference in sexuality, for which a simple genetic model can be given, is not sufficient to distinguish species; it may, as there stated, not even be enough to distinguish subspecies. As a practical step in the deliniation of these taxonomic problems, however, some type of nomenclatural recognition is at least useful—and appears to reflect a more acceptable hierarchial status.]

The BERGGREN material, which is quite copious, is of interest in that terminal branching of the modified *Radula* type, as described by SCHUSTER (1974a) for the allied *S. cordifolium*, is abundantly present. These branches, which are much weaker than the main axis, issue smoothly from near the abaxial base of the leaves, from loci situated not only behind the leaf but near the ventral end of its line of insertion. As in *Radula*, they thus develop from the basiscopic portion of a segment, and from the ventral portion of the segment.

Subg. ***Solenostoma*** MITT.

In the Arctic, speciation in this subgenus seems to be imperfect at best. In SCHUSTER (1969) only *S. sphaerocarpum* and *S. pusillum* are recognized from the North American Arctic; the first supposedly has only brownish secondary wall pigments, the latter has them carmine to reddish. Both taxa are paroecious. The situation is, however, much more complex: there are, in addition, populations which defy placement into the usual species perimeters and which develop the purplish pigmentation of the dioecious Appalachian-East Asiatic, temperate zone, *S. pyriflorum*. They furthermore approach this species in (a) oil-body form and number; (b) leaf form; (c) lack of paroecious inflorescences. Such purplish-pigmented plants produce either dioecious inflorescences (70–3148) or pseudodioecious —or perhaps truly dioecious—to autoecious inflorescences (70–3145a). Complicating matters further is the fact that there are gross differences in cell size between these two phenotypes. The problems of where to place such purple-pigmented plants and whether to treat them as members of a single species, or not, are acute. A definitive resolution of the problem is impossible until many more collections come to light. An attempted resolution is outlined in the following key:

1. Paroecious; secondary pigmentation brown or reddish; ♂ bracts 2–3-androus . . . . . 2.
   2. Secondary pigments, if any, brownish or purplish-brown, dull; shoots usually not dimorphic (flagella absent or rare); leaves of sterile shoots usually rotundate, 1.0–1.2(1.3) × as long as wide. 3.
      3. Perianth ± emergent, without a perigynium at base or with a vestigial one; plants usually vigorous.
         S. sphaerocarpum v. *sphaerocarpum*
      3. Perianth ± included, with distinct perigynium at base; plants compact, dwarf, usually broad-leaved, leaves to 1.2–1.3 × as wide as long. *S. sphaerocarpum* v. *nana*
   2. Secondary pigments reddish to claret-red; shoots usually dimorphic, with ± distinct, small-leaved flagella; leaves to 1.4–1.75 × as wide as long; perigynium distinct. *S. pusillum*

1. Autoecious, pseudodioecious and/or dioecious; androecial shoots distinct, with intercalary bracts; bracts 1-androus, small; androecial shoots slender, with slenderly compact androecia; secondary pigments (of perianth apices and bract and leaf apices) always purplish.
   S. pyriflorum ssp. *purpureum* . . . . . 4.
      4. Cells smaller: median 17–23 × 16–21(26) μ; at least sporadically (perhaps normally) autoecious; plants dwarf, innovation-free. v. *purpureum*
      4. Cells larger: median (24)26 28(30) × (26)28 30(35) μ; apparently uniformly dioecious (♂ shoots rare); plants larger, with abundant innovations. v. *innovatum*

Solenostoma (*Solenostoma*) *sphaerocarpum* (HOOK.) STEPH.

Distribution (Map 35)

1A: Behind Arctic Station (66–0146a, 70–2021). 6: Eqalúnguit (70–2213). 9: Eqaluit (70–2541b). 13: Jens Vahls Dal (70–2641, 70–2643). 21: Umiasugssûp (70–2948b). 24: Jakobshavn (66–0230). 32: Qôrorssuaq (70–2438b, 70–2465). 42: Magdlak (66–1356c, 66–1359a). 38: Uvkusigssat (66–1393). 43: Kangerdlugssuakavsak (66–1281, 66–1287b, 66–1289, 66–1290). 45: Sagdliaruseq (66–1091). 46: Qalatôq (66–1101). 48: Amitsup (66–0780).

Additional collections:

28: Atâ (LÆGAARD July 1962). 64: Ingigigsoq (M.P.P. 3114b). 88: Christianshåb (K.H. 16.824). 116: Puiagtukavsak (K.J. 671a). 124: Tasíngortaq (K.H.13.302). 142: Niaqornánguaq (K.H. 16.756). 144: Igdlorssuit (K.H. & W.C.S. July 1962).

S. sphaerocarpum is a common and malleable species in the Arctic, most often found on broken, exposed, circumneutral, acid or weakly basic, mineral soil, often in crevices, associated, i. a., with *Lophozia excisa*

(small compact forms), *Nardia geoscyphus*, *Gymnomitrion*, *Prasanthus*, etc. It then often, but not always, occurs as var. *nana*. Fuscous extremes may occur on thin peaty soil over and amidst rocks, at the edges of rivulets and small cascades (as at Qôrorssuaq; 70–2438b), associated with *Scapania serrulata*, *S. subalpina*, *Pleuroclada*, *Lophozia alpestris*, and other oxylophytic taxa. It may also occur, however, in weakly basic sites (Magdlak; 66–1359a), associated with *L. grandiretis*, *Cephalozia pleniceps*, and *Anthelia jurtazkana*, on moist, somewhat peaty soil; also over soil, between basic rocks, where subject to desiccation, with *Tritomaria scitula*, *T. heterophylla*, *T. quinquedentata*, *Solenostoma subellipticum*, *L. excisa elegans*, *Anthelia*, and *Scapania mucronata praetervisa* (in 66–1287b).

A peculiar extreme, not again met with, is that of 70–2948b (Sydostbugt, stream valley S. of Umiasugssûp tunua). The plants occurred here on frost-heaved, broken soil over ledges, associated with *Prasanthus*, *Gymnomitrion concinnatum*, *Scapania parvifolia*, *Anthelia juratzkana*, *L. alpestris*, *Andreaea*, etc. In sheltered soil crevices, green to lightly brownish-tinged, fertile plants occurred, always with the apical portions of the long-emergent perianth brown-tinted. On exposed, more level patches of ground, however, a highly reduced, creeping, arcuate, almost filiform, sterile phase occurred, largely microphyllous and (in itself) hardly recognizable. Such slender, often whiplike, small-leaved shoots, common in the allied *S. pusillum*, were not seen elsewhere in *S. sphaerocarpum*. They were often intensely brown-tinged, almost chocolate-brown, often with the color of deeper pigmented forms of *Odontoschisma elongatum*, but much smaller. In spite of the dwarfed, atypical form, their leaves had typical cells: the marginal 23–27 μ, the median with intermingled 2–3 large, ellipsoidal to fusiform oil-bodies, others with up to 4–6, usually smaller, ovoid to subglobose oil-bodies.

Although normal sun phases of this species develop brown to fuscous pigmentation (as, e.g. 70–2438b, 70–2948b, cited above), we find occasional phenotypes with the perianth tips tending to develop a little dull purplish pigmentation (e.g., 70–2213, from a feebly basic site, with *Lophozia heterocolpos*).

Plants of 70–2438b (Qôrorssuaq, on silty soil subject to submersion, edge of rill, among *Pleuroclada albescens*, *Scapania serrulata*, *S. subalpina*, *Lophozia alpestris*) are of a typical, robust phase, without any trace of basal perigynium and with only the distal 0.25–0.35 of the perianth at all plicate. Leaves, which are rather long-decurrent antically, are no wider than long and have cells well within the sizes specified in Schuster (1969) for this species. Notable are two features: the extensive brown pigmentation of perianths, bracts, and leaves (except for their bases), and the often creeping, remote-leaved, sterile axes. Stoloniform, microphyllous axes, however, could not be found. The occurrence of such strongly

brownish-pigmented plants, without trace of vinaceous pigmentation, suggests that the often questioned distinction between *S. sphaerocarpum* and the usually much smaller *S. pusillum* is a real one. As is noted under the latter, intense vinaceous red pigments are commonly produced in sun forms of *S. pusillum.* Similarly, the intensive purple pigmentation of *S. pyriflorum* ssp. *purpureum* (described below) also can hardly be interpreted as due to other than genetic causes.

v. *nana* (NEES) SCHUST. (Fig. 12:10–16)

Distribution (Map 35)

11: Qasigíssat (70–2744, 70–2728). 14: Hareøen (70–2583). 16: Manîtsoq (70–3007d, 70–3013a).

Additional collections:

12: Perdlertut (M.P.P. 480b). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 99: Sarqaq valley (K.J. 186e). 103: Qapiortoq kitdleq (K.J. 1055). 115: Kûgssuaq (K.J. 744a).

The var. *nana* is a compact extreme, often of sites subject to desiccation. It may occur on weakly to distinctly basic slopes, on soil between rocks, with *Lophozia heterocolpos*, *L. quadriloba*, *L. opacifolia*, and *Cephalozia pleniceps* (70–2583), or *L. heterocolpos s.l.*, *L. pellucida minor*, *Solenostoma pumilum polaris* (70–2744). Or it may occur on broken soil over acidic rocks, as noted specifically below.

The plants of 70–2728 represent a firm, erect, rigid and terete, caespitose growing phase of var. *nana*, developed to its optimal extent. In all longisected gynoecia a very distinct, ringlike to short-tubular stem perigynium is distinct, and the deeply 4-plicate perianth is relatively short, often largely included within the erect and sheathing bracts. Perianth apices are often locally brownish to purplish brown, otherwise wall pigments are lacking or nearly so. The subfloral (♂) bracts and uppermost leaves are relatively broadly reniform-rotundate with a broad, arcuate insertion; leaves are ca. 1400 μ wide × 980 μ long (measured along leaf midline), while bracts range to 1600 μ wide × 840 μ long. Oil-bodies seem to show points of distinction from var. *sphaerocarpum*: they are distinctly larger and fewer, mostly 2–5(6) per cell, in rare cells 7 (they are then subspherical to short-ovoid and 6–7 × 7–8 μ). When 2–4 per cell, as is most common, they are ellipsoidal to almost bacilliform and range from 6–7 × 11–13 μ to 7 × 18–20 μ to 8–9 × 17–18 μ. They are obscurely, faintly botryoidal but essentially smooth-surfaced. Capsule wall anatomy agrees in all essential details with that found in var. *sphaerocarpum*: spores are 16–17 μ in diam., weakly granular-punctate; elaters, which are strongly contorted and rather short, are 7.5–8.5 μ in diam., bispiral, with the rather narrowed tips forming at best a short, feebly thickened spur in

which a single, coalescent spiral ends. The bistratose capsule wall is 38–42 μ thick and shows a very sharp distinction between tall epidermal cells (25–28 μ high) with nodular thickenings of essentially all walls, and a much lower (11–14 μ high) stratum of interior cells, with nodular to semiannular bands.

Plants of 70–3007d are essentially similar but have no purplish complement in the pigmentation, are a clear chestnut brown and, here and there, a little glossy. They show a distinctly lower perigynium, and, in general, have more distinctly exserted perianths, plicate only in the distal third or less. Oil-bodies are exactly as in 70–2728. These plants are from a solifluction slope, on soil between rocks, associated with other taxa of "difficult" sites, e.g., *Prasanthus suecicus*, *Nardia geoscyphus*, *Lophozia excisa succulenta*, *Gymnocolea inflata*, and *Cephalozia bicuspidata*. The reaction to exposure of the *Solenostoma* and the *Nardia* are strikingly different: the former develops brown pigments, the latter dull carmine ones, with age mixed with some brown.

Solenostoma (*Solenostoma*) *pusillum* (JENS.) STEPH.

Distribution (Map 35)

6: Eqalúnguit (70–2223).

This species has been known only from three localities in North America: Steensby Land in northwest Greenland (SCHUSTER, 1969), the Ungava Distr. of Quebec (LEPAGE, 1953; based on an S. Arnell determination), and Alger Co., Michigan (AMAKAWA, 1960).

At Eqalúnguit it occurs in a rich, irrigated meadow, fed with melt water from basaltic cliffs above; it is found here over peaty ground, mixed with *Cephalozia pleniceps*, *Pleuroclada albescens*, and *Lophozia heterocolpos*.

The plants are strongly reddish-tinged, smaller than "normal" *S. sphaerocarpum*. Although usually paroecious, a few slender, purely androecial shoots were found—hence the species shows a tendency towards becoming heteroecious. Capsules were freely produced (July 11).

The status of *S. pusillum* as a distinct species is not above question; the various opinions expressed are summarized in SCHUSTER (l. c., p. 956). Insofar as the species is distinct, the strongly reddish color, compact build, and generally paroecious inflorescences of the present plants clearly place them here rather than with *S. sphaerocarpum*.

Solenostoma pyriflorum STEPH.

Described from east Asia and first reported from North America by SCHUSTER (1969) from the southern Appalachians, with an isolated population from Michigan; it does not occur in Europe. The species *s. str.* differs from the *S. sphaerocarpum-pusillum* complex in two obvious fea-

tures: (a) purple to dark purple secondary pigments of the otherwise green to yellow-green plants; (b) dioecious inflorescences.

With some reluctance we place three collections, from two localities, as an Arctic subspecies of *S. pyriflorum*, distinct from this in the at least occasionally autoecious inflorescences and in the slender androecia, with usually monandrous ♂ bracts. The Arctic plants are much smaller than the temperate zone ssp. *pyriflorum*. Further complicating the situation is the fact that cell size seems to be quite different in the two Greenland collections which are, as a consequence, attributed to separate varieties.

We admit that this is perhaps only a temporary solution to the problem; chromosome counts and culture experiments are needed.

Key to Taxa

1. Non-Arctic plants; uniformly dioecious; ♂ bracts large, often 2-androus; plants relatively vigorous. ssp. *pyriflorum*

1. Arctic plants; dioecious ranging to (rarely?) autoecious, but never paroecious; ♂ bracts small, normally monandrous; plants small, compact. ssp. *purpureum*.... 2.

   2. Cells larger: marginal near apex (18)20–26(27) μ, median (24) 25–30(32) × (26)28–34(35) μ; with numerous erect to creeping, microphyllous branches. Uniformly dioecious. v. *innovatum*

   2. Cells smaller: marginal near apex (15) 17–20 (21) μ, median 17–23 × 16–21 to 20–24 (28) × 22–28 μ; no microphyllous branches. Dioecious to (rarely) autoecious. v. *purpureum*

Solenostoma (*Solenostoma*) *pyriflorum* ssp. *purpureum* SCHUST. & DAMSH. *ssp. nov.*(Fig. 12:1–9)

Pigmento saturate purpureo partium superiorum subsp. *pyrifloro* simile, foliis orbicularibus non orbiculari-reniformibus, statura multo minore, inflorescentiis heteroicis raris ab eo diversum.

Plants light green to green, with intense purplish pigmentation of (at least) distal half of perianth and distal portions of bracts and leaves. Leaves subrotundate, width 1.1–1.2:1. Cells relatively small: apical marginal cells (15) 17–20 (21) μ; marginal cells midway from leaf tip to base, 16–20 μ; median cells 17–23 × 16–21 (26) μ. Plants (at least usually) lacking small-leaved innovations. At least sporadically autoecious, but (most often) with no evident connection between androecia (which are intercalary) and gynoecia (which are terminal on leading axes).

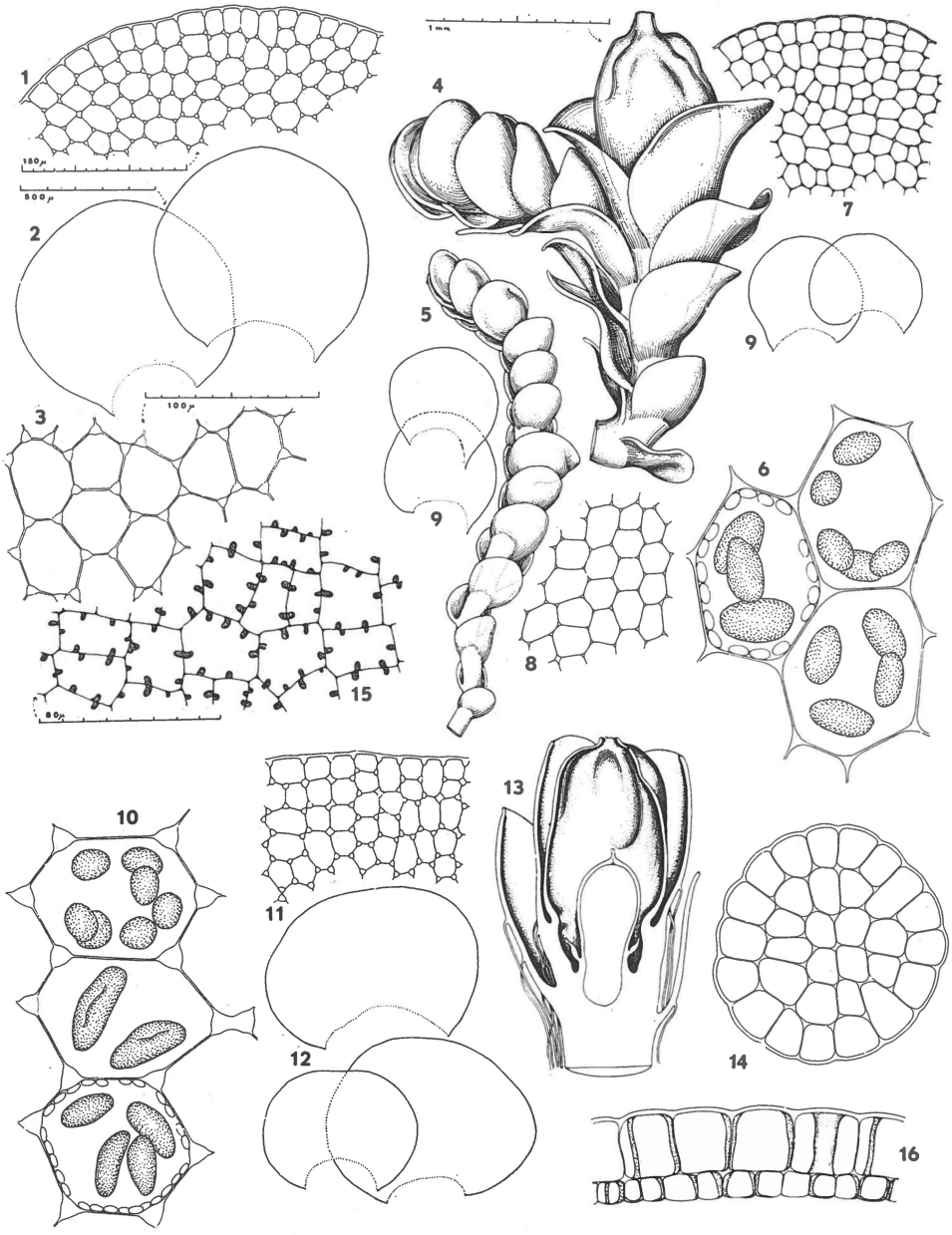


Fig. 12. *Solenostoma.* (1–9) *S. pyriflorum* ssp. *purpureum.* (1) Leaf cells of leaf apex (×145). (2) Two leaves (×35.5). (3) Median leaf cells (×230). (4) Shoot with perianth and subfloral innovation (×24). (5) Androecial shoot apex, lateral aspect (×24). (6) Median cells with oil-bodies (×560). (7) Leaf apex, cells (×145). (8) Median cells (×145). (9) Leaves (×24). (10–16) *S. sphaerocarpum v. nana.* (10) Median cells with oil-bodies and, lower cell, chloroplasts (×665). (11) Cells of leaf apex (×145). (12) ♀ Bract, above, and ♂ bract and leaf, below (×20). (13) Longisection through perianth-bearing shoot apex (×20). (14) Seta cross section (×145). (15) Cells of epidermal layer, capsule wall (×300). (16) Cross section, capsule wall (×300). [1–6, 70–3148; 7–9, 70–3145a, 10–16, 70–2728; 1, 7, 8, 11, drawn to 150 μ scale; 2, drawn to 500 μ scale; 4, 5, 9, drawn to 1 mm scale; 15, drawn to 80 μ scale].

Distribution (Map 36)

23: Kangersuneq (70–3145a).

Additional collection:

147: Amitsoq (K.H. 14.643).

Two plants from Kangersuneq, placed here as ssp. *purpureum*, pose problems: they are green, with the distal portions of perianths, upper leaves, and ♂ bracts intensely purplish-pigmented (not the intense claret red to red of *S. pusillum*). In 70–3148 the plants seem to be wholly unisexual. In 70–3145a we have seen many plants with intercalary androecia, followed by several sterile leaves; no gynoecia could be found on the last type of plant. Also, many gynoecial plants with well-developed perianths, all purplish distally, were seen; not one of these had antheridia or antheridial remains in the leaf axils below the perianth; these leaves, furthermore, were no more concave than the hardly concave vegetative ones. A single individual with an old capsule was seen, however, which was surely autoecious: a long, gynoecial axis had several lateral-intercalary branches, one of which had an intercalary androecium. Thus we must assume that, genetically, these plants are able to be bisexual, although the majority seemed to be unisexual. It is possible that the dioecism is a pseudodioecism—older shoot sectors connecting ♂ and ♀ branches having decayed. Although this interpretation may be valid for 70–3145a, 70–3148 as indicated above, seems to be wholly unisexual.

The specimens were collected on a moist, silty glacial deposit (rock meal) in a raised glacial valley adjoining a small lake, growing in full sun; associated were *Nardia geoscyphus*, *Prasanthus suecicus*, *Scapania curta grandiretis*, *Anthelia juratzkana*, and traces of *Riccardia sinuata*.

Only *S. sphaerocarpum* and *S. pusillum* have been reported from Greenland (Schuster, 1969) and are here also recorded from West Greenland; both species are apparently consistently paroecious and paroecious inflorescences are always obvious and readily demonstrable. The clearly unisexual plants of 70–3148 bear abundant perianths, all unfertilized so far as we could see; no trace of antheridia was seen in axils of subfloral leaves, nor could antheridia be found in axils of leaves of subfloral innovations, many of which had archegonia (and a rudimentary perianth) present at the tips. Except for this the plants closely match *S. sphaerocarpum*, although, unlike this the perianth apices are colored purplish or purplish brown at times—a feature noted in SCHUSTER (l. c.) as typical of sun forms of *S. pyriflorum*.

The type (70–3145a) bears (2)3–6(7) subhomogeneous oil-bodies per cell, which is 1–2 less than the maximum recorded for typical *S. pyriflorum*. They also have somewhat less broad leaves, a feature associated with less vigorous growth. Except for this, only minor points of difference have

been noted, which, in our opinion, warrant at best recognition of an Arctic subspecies. The material of HOLMEN 14.643 seems quite identical to the type of ssp. *purpureum*—including leaf shape, cell size, and intense purplish color; it also had only unfertilized perianths, and seemed largely dioecious, although again one ♀ shoot with unfertilized archegonia bore subfloral innovations that bore androecia, hence some autoecious (or perhaps heteroecious) inflorescences must occur. The only other point of deviation noted: although most ♂ bracts were monandrous, one diandrous ♂ bract was seen. Both collections, as well as the following one referred to var. *innovatum*, appeared to rather uniformly lack rhizoids from abaxial leaf faces, and from the perianths. This may constitute an additional distinction from *S. sphaerocarpum*, in which rhizoids from perianths and abaxial leaf surfaces are often abundant (see fig. 280:6 in SCHUSTER, l. c.).

ssp. *purpureum* v. *innovatum* SCHUST. & DAMSH. *var. nov.* (Fig. 12:1–6).

Colore, magnitudine, foliis orbicularibus var. *purpureo* simile, innovationibus numerosis ab eo diversum; dioicum.

Distribution:

23: Kangersuneq (70–3148).

Plants light to clear green, with perianth tips and leaf margins intensely purplish, less vigorous than in *S. pyriflorum*, typically only 0.6–1.2 mm wide on leading stems and 5–10 mm high; freely producing subfloral innovations with numerous erect or creeping, small-leaved, almost microphyllous branches, often purplish-tinged, which bear ± erect, concave leaves only 275–350 μ long and which are, with the leaves, only 350–510 μ wide. Leaves orbicular rather than reniform, to ca. 950–1000 μ wide and 820–875 μ long, near the gynoecia becoming somewhat broader and 1050 μ wide × 800 μ long. Marginal cells ca. (18)22–27 μ, the median 24–32×26–35 μ. Oil-bodies in median cells (2)3–6(7) per cell, usually ovoid to ellipsoid, faintly granulate and colorless, ca. 5–5.5 ×8–10 to 6×10–12 up to 9×13–15 μ. Perianths obpyriform to slenderly obpyriform, without antheridia in the subfloral leaves, the plants never paroecious. ♂ Branches with intercalary androecium of small, purplish, saccate contiguous bracts in 3–5 pairs; monandrous (as far as seen).

Type. Kangersuneq (70–3148). Valley E. of Ivnarssuâq.

This plant has the aspect of a freely microphyllous-branch-bearing *S. sphaerocarpum*, from which it differs in the intense purplish color and in being dioecious. The small size, presence of small-leaved branches, and the more orbicular and less broad leaves and bracts distinguish the plant from *S. pyriflorum*. Habitat, size, and other criteria suggest *S. pusillum*,

but that plant is paroecious, has reddish rather than purplish pigmentation, and has much broader, almost reniform leaves and bracts.

Subg. ***Plectocolea*** Mitt.

Solenostoma subellipticum (LINDB.) SCHUST.

Distribution (Map 36)

1A: Behind Arctic Station (70–2017b, 70–2047e). 14: Hareøen (70–2597). 17: Tupilak (66–0105b). 21: Umiasugssûp (70–2940). 23: Kangersuneq (70–3127a). 25: Sarfaq (70–2364, 70–2367). 26: Pâkitsup ilordlia (70–2270, 70–2306, 70–2313a). 30: Eqe (66–0289, 66–0322b, 66–0326, 66–0340a). 31: Anap nunâ (70–2409b). 42: Magdlak (66–1356c). 43: Kangerdlugssuakavsak (66–1281, 66–1287c, 66–1289). 45: Sagdliaruseq (66–1074a). 46: Qalatôq (66–1101). 53: Søndre Strømfjord (66–0059, 66–0060, 66–0088a).

This rather infrequent Arctic-alpine and subarctic species occurs north as far as Spitsbergen and to the Inglefield Bredning region of northwest Greenland (a number of the above reports are first cited in SCHUSTER, 1969). Otherwise known from East Greenland, southward to Quebec and Nova Scotia; also in Iceland, and in Europe from Spitsbergen to north Italy.

S. subellipticum is a relatively tolerant species that occurs mostly in acidic regions but may also be found over moist, sheltered basic soil where (at least locally) basaltic dikes occur. Sites of the last type are at Anap nunâ (70–2409b) and Eqe (66–0340a); in such places *Peltolepis grandis*, *Lophozia quadriloba*, *Odontoschisma macounii*, *Tritomaria heterophylla*, *Cephalozia pleniceps*, etc., may be associated. More typically it occurs on moist soil with a high mineral content, or on circumneutral or acidic soil between rock crevices. Then *Scapania irrigua rufescens*, *S. curta*, *Calypogeia muelleriana*, *Nardia geoscyphus*, *Cephalozia pleniceps*, and other taxa are associated; less often, under more helophytic conditions, with *Scapania paludicola* (70–2940) or *S. degenii dubia* (70–2017b). Rarely found in insolated, exposed sites, on thin, often irrigated soil of exposed acidic cliffs, associated with *Gymnocolea inflata* and *Aneura pinguis* (Tupilak, 66–0105b). The species usually grows scattered, mostly as small gregarious patches or as isolated individuals. Cells almost always have 2–5 (6) large, faintly to distinctly granular oil-bodies; the cuticle is often rather perceptibly striolate (as, e.g., in 70–2270). Branches seen have all been lateral-intercalary. Plants are always fertile; paroecious inflorescences are always easily demonstrated. Capsules are not rare and once (in 70–2047e, July 5) we saw a perianth-perigynium complex from which two sporophytes issued. Sporophyte production extends to at least July 20 (70–2367).

Phenotypes of sheltered sites are all yellowish green; in exposed sites, however, we find a mod. *colorata-vinacea*. Such plants tend to be

small and may occur mixed with *Anthelia juratzkana*. The two extremes—shade and sun forms—may be drastically different (see discussion and key on p. 1026 in SCHUSTER, 1969), the former lacking trigones, while the last has them nodular (compare fig. 278:16–17 in SCHUSTER, l. c.).

The plant with distinct trigones usually has strong reddish pigmentation linked with a fleshy stem, rotundate leaves that may average wider than long, and a perianth mouth with cells averaging only 1.5–2 × as long as wide. Such compact plants may occur on exposed soil, with *Anthelia juratzkana*, *Scapania obcordata*, *S. serrulata*, *Cephalozia bicuspidata* admixed (as in 66–1074); they correspond exactly to the "mod. *colorata-densifolia*" of SCHUSTER (l. c., p. 1026) and—chiefly because of the rotundate, abbreviated leaves, may be sought under *S. sphaerocarpum* and its allies.

Nardia S. F. GRAY

Nardia geoscyphus (DE NOT.) LINDB. in CARR.

Distribution (Map 37)

1A: Behind Arctic Station (66–0102c, 66–0146a, 66–0154a, 66–0159, 66–0175, 66–0182, 70–2015, 70–2016, 70–2026c, 70–2028a, 70–2044a, 70–2045, 70–2050). 2: Fortunebay (66–0199a). 6: Eqalúnguit (70–2226a). 7: Angûjârtûtit (70–2157a). 9: Eqaluit (70–2522, 70–2523, 70–2526b, 70–2527, 70–2530a, 70–2537a, 70–2539, 70–2542, 70–2543a, 70–2547, 70–2549a). 10: Enoks Havn (70–2763c, 70–2776a, 70–2770b). 11: Qasigíssat (70–2739c). 14: Hareøen (70–2596, 70–2597a, 70–2607). 15: Kronprinsens Ejland (70–2073). 16: Manîtsoq (70–3008, 70–3007a, 70–3015c). 21: Umiasugssûp (70–2935, 70–2936, 70–2942, 70–2943, 70–2946, 70–2945a, 70–2951c). 23: Kangersuneq (70–3127b, 70–3129b, 70–3135a, 70–3136, 70–3138a, 70–3140a, 70–3143a, 70–3144, 70–3145, 70–3149b, 70–3153a). 24: Jakobshavn (66–0230). 25: Sarfaq (70–2336d, 70–2359). 26: Pâkitsup ilordlia (70–2258a, 70–2259, 70–2266b, 70–2269a, 70–2270a, 70–2283a, 70–2288a, 70–2291, 70–2299a, 70–2300, 70–2310, 70–2313a, 70–2386a, 70–2388). 30: Eqe (66–0249f, 66–0250). 32: Qôrorssuaq (70–2448a, 70–2457b, 70–2458). 36: Umanak (66–1474). 43: Kangerdlugssuakavsak (66–1285b, 66–1290). 45: Sagdliaruseq (66–1074, 66–1091, 66–1093). 46: Qalatôq (66–1101). 48: Amitsup (66–0782, 66–0785).

Additional collections:

6: Eqálunguit (M.P.P. 2620). 17: Tupilak (K.J. 1364). 83: Angnertussoq (L.H. Aug. 1932). 84: Qeqertasugssuk (L.H. Aug. 1932). 88: Christianshåb (K.H 16.675b). 125: Sarqap taserssua (K.H. 17.113). 139: Qaqortukavsaq (K.H. 16.079). 142: Niaqornánguaq (K.J. 14.988).

A frequent and widely dispersed plant of circumboreal-circumarctic range, absent from most highly continental regions; it occurs south to New England and, in Europe, to the Alps, and recurs in Macaronesia.

Seemingly frequent along the entire Greenland coast, reported by SCHUSTER (1969, p. 866) from Peary Land as far north as 81°48′ N. It is usually found on mineral soil or humus, more rarely on purely organic

substrates, often in difficult sites (e.g., heaved and broken, stony ground and stone polygons, where on soil in pockets between rocks, associated with hardy taxa such as *Prasanthus suecicus*, *Solenostoma sphaerocarpum nana*, *Gymnocolea inflata*, and *Anthelia*, or on compact soil between stones along river terraces, where subject to alternate flooding and drying, then with *A. juratzkana*, *Cryptocolea imbricata*, *Cephalozia pleniceps*, *C. bicuspidata*, *Scapania perssonii*), where it may occur as very small, compact, fleshy, rigid forms. At the opposite end are relatively luxuriant forms, with elongated sterile stems, growing on a sand-peat mixture on low plains at the head of inlets or fjords (as at Eqaluit and at Eqalúnguit, both on Disko), where associated with *A. juratzkana*, *C. bicuspidata*, *Pleuroclada albescens*, *Lophozia wenzelii lapponica*. The luxuriant forms occasionally approach *N. scalaris* in vigor, and may have minute underleaves all along the sterile axes, as that species; they differ, however, in the high incidence of retuse leaves, especially towards the fertile shoot tips and in the paroecious inflorescences. Oil-bodies in all living Greenland plants studied showed a high level of consistency in form and number: almost always 2, less often 3, very sporadically 1 or 4 per cell, usually elongate and often bacilliform, almost homogeneous to faintly granular-botryoidal. They are ellipsoidal and range to 6–7 × 10–13 μ when 1–3 per cell, spherical to ovoid when 3–4 per cell, and 5.5–6 × 6–7 μ.

On compact mineral soils the species is sometimes mingled with *Cryptocolea* (as at Enoks Havn), and then the sterile shoots are at times superficially similar. The *Nardia*, however, develops quite intense carmine-red pigmentation in sun forms, at least late in the season, while the intermingled *Cryptocolea* is more nitid and develops a light, yellowish brown color. The two taxa are clearly separable on cytological grounds: in *Cryptocolea*, although some cells may have 2–3 large, ellipsoidal to fusiform oil-bodies, some or most cells bear 4–6(7) smaller, spherical to ovoid oil-bodies each.

In "difficult" sites, as on broken soil on stony solifluction slopes, associated with *Prasanthus*, *C. bicuspidata*, and other taxa, *Nardia geoscyphus* may grow mingled with *Solenostoma sphaerocarpum* var. *nana* (as on Manîtsoq, 70–3007). The *Nardia* and the *Solenstoma* are then, when sterile, deceptively similar—both having orbicular leaves. *N. geoscyphus*, however, becomes dull carmine in such exposed sites, the *Solenostoma* a clear chestnut brown; the *Nardia* has 2(3) oil-bodies per cell, the *Solenostoma* (2)3–6(7) per cell. In such exposed environments the plants of *N. geoscyphus* are closely prostrate, including the fertile ones, which develop a very conspicuous marsupium ventrally.

Contrasting forms are the pure green robust plants growing on wet peat in boggy depressions around the margins of tarns and small lakes (70–3015c, Manîtsoq, associated with *Anthelia*, *Diplophyllum taxifolium*,

Pleuroclada albescens, *Cephalozia pleniceps*), in which even sterile shoots may show rounded-quadrate leaves that are retuse apically and may show distinct underleaves. Such plants tend to have slightly more numerous oil-bodies (2–3 per cell in distal leaf sectors, 3–4 in the basal halves), and the proximal halves of the leaves are fleshy and bistratose. Such phases, because of competition and largely erect growth, show no trace of a marsupium, the perigynium lying in the stem axis.

Nardia scalaris (SCHRAD.) S. F. GRAY

Distribution (Map 37)

1A: Behind Arctic Station (70–2059a).

N. scalaris is a plant of basically temperate range, found here at its northern periphery; it is basically circumboreal and extends in North America south, in the Appalachian moutains, as far as North Carolina and Tennessee.

The above is the northernmost collection of the species from the west coast of Greenland, although JENSEN (1906) reports it from the east coast as far north as Angmagssalik District. It is apparently rare so far north; the collection of typical material from Disko occurred mixed with *Gymnomitrion corallioides* and *Cephalozia bicuspidata* ssp. *ambigua*; it bore capsules on the date of collection, July 5.

Typical *N. scalaris* is at once distinct from other taxa with entire lateral leaves and distinct underleaves in the oil-body form. In 70–2059a, as in material from temperate sites (see fig. 260:4–5 in Schuster, 1969), oil-bodies occur 2(3) per cell and are either quite homogeneous and glistening, or clearly 2–3-segmented.

In addition to typical (ssp.) *scalaris*, a single collection has been made of ssp. *botryoidea*.

ssp. *botryoidea* SCHUST.

Distribution (Map 37)

17: Tupilak (66–0027).

The single collection, of sterile plants, was studied while living; the 2(3) oil-bodies per cell were clearly botryoidal (see fig. 258:5 in SCHUSTER, 1969, derived from the Tupilak plant). The plants are similar in oil-body form to *N. geoscyphus* but differ in (a) being dioecious; (b) the underleaves distinct throughout; (c) no retuse leaves. This subspecies was described from the summits of the Appalachian Mts. in Tennessee; it is again known from coastal Nova Scotia. As pointed out in SCHUSTER (l. c., p. 862), the "occurrence of ssp. *botryoidea* together

with ssp. *scalaris* suggests the former may represent an independent species". Until more collections come to light, any change in status seems premature.

Cryptocolea SCHUST.

Cryptocolea imbricata SCHUST.

Distribution (Map 38)

10: Enoks Havn (70–2770c). 12: Perdlertut (70–2693b, 70–2703). 22: Orpigsôq (70–3118e). 26: Pâkitsup ilordlia (70–2257, 70–2266b, 70–2269a, 70–2272b, 70–2274, 70–2313a). 30: Eqe (66–0249e, 66–0289a). 40: Mârmorilik, head of the Fjord (66–1206). 43: Kangerdlugssuakavsak (66–1204, 66–1205, 66–1281b, 66–1289, 66–1290a). 46: Qalatôq (66–1101, 66–1109, 66–1138). 51: Simiútap kûa, shore (66–0911, 66–0914, 66–0915, 66–0916, 66–0917, 66–0919). 52: Umîarfik, Qôrnoq (66–0980).

Additional collections:

125: Sarqap taserssua (K.H. 17.115). 128: Agatdalen (K.H. 13.971).

This species, described from the Lake Superior region of Minnesota and Michigan (SCHUSTER, 1953), was shown to possess a chiefly Arctic range, including northern Ellesmere Island (SCHUSTER *et al.*, 1959) and northern Greenland, as well as northwest and West Greenland [SCHUSTER, 1969; a report of the species from Peary Land (ARNELL, 1960) is based on *Plagiochila arctica*, SCHUSTER l. c.]. The species seems to be frequent but not common in all basic regions of West Greenland. It usually occurs in rich, moist moss-tundra, sometimes on peaty soil irrigated by melt water from basalt cliffs above, sometimes on peaty soil in basaltic regions (as at Simiútap kûa valley; 66–0919), around shallow lakes. At other times it is found on damp, sandy depressions in local basic niches (associated with *Pinguicula vulgaris*) in acidic regions, as at Qissugssalik (70–2272b), where, on sandy-peaty ground, mixed with *Odontoschisma macounii*, *Cephalozia pleniceps*, *Anastrophyllum minutum grandis*. These species, as well as *Anthelia juratzkana*, *Nardia geoscyphus* (less often *Solenostoma sphaerocarpum* and *S. pumilum*), *Arnellia fennica*, *Tritomaria scitula*, and others, may occur mixed with it in exposed sites. In richer sites, as in wet calcareous fens, we find admixed *Tritomaria polita* (rarely *T. heterophylla*), *Lophozia grandiretis*, *L. heteroçolpos*, *L. quadriloba*, *L. rutheana* (rarely *L. cavifolia*), *Aneura pinguis*, as well as most of the previous species. Occasionally (as at Kangerdlugssuakavsak; 66–1290a) *Solenostoma sphaerocarpum*, *S. pumilum*, and *Nardia geoscyphus* are associated, as well as *Blasia pusilla*; the species then grows over damp, basic mineral soil. There is a single occurrence away from localized basic substrata, from gneiss hills, at the juncture of Qarajaq and Orpigsôq (70–3118e), where a small amount was collected over rather exposed, vertical, thinly soil-covered cliffs, amidst *Prasanthus suecicus* and *Anthelia juratzkana*. All other records are from basic sites.

C. imbricata has been found a single time with mature capsules (66–1289; see fig. 270:3–5 in SCHUSTER, 1969). There is a long discussion of the variation, particularly of the oil-bodies and of the gynoecial region, in SCHUSTER (l. c., pp. 894–97), hence further discussion here is superfluous.

Subfamily *Mylioideae* GROLLE

Mylia S. F. GRAY emend. CARR.

Mylia anomala (HOOK.) S. F. GRAY

Distribution (Map 38)

1B: Lyngmarken (66–0561). 17A: Egedesminde (66–0951). 18: Grønne Ejland (70–2810, 70–2814c, 70–2816c). 19: Nûk (70–2871a, 70–2877b). 21: Umiasugssûp (70–2949). 22: Orpigsôq (70–3106b, 70–3109a). 37: Agpat (66–1422).

Additional collections:

17: Tupilak (K.H. June 1956). 24: Jakobshavn (S.B. 1870).

This helophytic species, of southern affinity, occurs at its northernmost known station at Agpat, N. of Nûgssuaq; it is imperfectly holarctic, with southern, isolated stations in North America in peat bogs as far south as Pennsylvania, New Jersey, and West Virginia (SCHUSTER, 1969). It typically occurs in permanently moist, richly vegetated, peaty sites around shallow lakes and tarns, always where well illuminated, and there over and amidst *Sphagnum* and *Aulacomnium* and various *Hepaticae*, principally: *Calypogeia sphagnicola*, *Riccardia sinuata*, *Lophozia binsteadii*, *L. ventricosa silvicola*, *L. v. longiflora*, *Cephalozia bicuspidata*. Less often *C. pleniceps* and *Cephaloziella subdentata* are associated (in 70–2871a). Occasionally, when in low, peaty areas, but away from any standing water, *Cephalozia leucantha*, *C. lunulifolia*, *Anastrophyllum sphenoloboides*, *A. minutum*, *Calypogeia sphagnicola*, *C. neesiana*, *Pleuroclada*, *Lophozia opacifolia* and *L. v. silvicola* are intermingled.

M. anomala is always sterile locally, but invariably bears the diagnostic masses of gemmae. Plants rarely show any strong brownish pigmentation and are often present only as isolated, straggly stems.

Family ***Gymnomitriaceae*** KLINGGR.

Marsupella DUMORT.

Marsupella emarginata (EHRH.) DUMORT. v. *aquatica* (LINDENB.) DUMORT.

Distribution (Map 39)

95: Pâkitsoq (K.H. & G.M. 71–1929, 71–2027).

M. emarginata s.l. is a chiefly southern plant, extending in eastern North America south, as ssp. *tubulosa* var. *latiloba* SCHUST. (1974), to

northern Georgia, at the south rim of the Appalachian Mts. It is a genetically complex and variable species, with the southern populations in North America approaching the east Asiatic subspecies *tubulosa*. Northward this subspecies, characterized by the V-shaped deep sinuses and rounded lobes, fails to occur—or at least grades into ssp. *emarginata*, and its var. *aquatica*. Poor material, hardly determinable to subspecies or variety, of *M. emarginata s.l.* is known in Greenland as far north as the Thule region (W. of Nuna Lake, Benninghof 8608), but the species proper is extremely infrequent north of southern Greenland and is primarily subarctic in range.

The only two collections (HOLMEN & MOGENSEN 71–1929, 71–2027; the former with *Hygrobiella laxifolia* and *Solenostoma pumilum pumilum*; the latter with *M. arctica*) here reported clearly represent quite typical var. *aquatica*, showing rounded to blunt and very shallow lobes and a correspondingly shallow leaf sinus, as well as narrowly but tightly revolute leaf margins. Probably more widespread in the more continental, acidic portions of our range.

Marsupella arctica (BERGGR.) BRYHN & KAAL.

Distribution (Map 39)

1A: Behind Arctic Station (66–0188, 66–0196, 70–2005, 70–2006). 6: Eqalúnguit (70–2224). 15: Kronprinsens Ejland (70–2078, 70–2080, 70–2085). 16: Manîtsoq (70–3012c). 17: Tupilak (66–0028a, 66–0030a, 66–0116, 66–0119). 19: Nûk (70–2874a). 21: Umiasugssûp (70–2926, 70–2927a, 70–2934, 70–2949, 70–2951a). 23: Kangersuneq (70–3158). 25: Sarfaq (70–2322, 70–2323a, 70–2354, 70–2370). 32: Qôrorssuaq (70–2442a, 70–2451). 36: Umanak (66–1479c). 46: Qalatôq (66–1100a, 66–1114).

Additional collections:

1: Godhavn (K.H. & W.C.S. 62.1406). 1B: Lyngmarken (M.P.P. 67, part of type of *M. groenlandica*). 17: Tupilak (K.H. June 1956). 28: Atâ (LÆGAARD July 1962). 29: Ritenbenk (S.B. 1870). 85: Sarpiussat (L.H. Aug. 1932). 88: Christianshåb (K.H. 15.458, 15.719). 90: Tasiussaq (S.B. July 1870). 92: Claushavn (S.B. Aug. 1870). 95: Pâkitsoq (K.H. & G.M. 71–2027). 112: Umiartorfik (K.J. Aug. 1947). 114: Eqaluit (K.J. 830, K.H. 13.224, 13.240). 116: Puiagtukavsak (K.J. 671). 141: Inukavsait qáqarssue (K.H. 16.252). 142: Niaqornánguaq (K.H. 16.252).

A strictly Arctic taxon, known from as far north as Low Point (83°06′N.) in Greenland, southward only to northernmost Quebec (SCHUSTER, 1951); unknown outside of Spitsbergen, Greenland, Ellesmere Island, Baffin Island, northern Quebec, Southampton Island, and Alaska (PERSSON & HOLMEN, 1961). The species is rather frequent in our region in areas with acidic rocks; it seems to have a very low toleration for sites with Ca-enriched seepage.

M. arctica typically occurs in insolated, acidic, and at least intermittently wet sites, in blackish mats, often submerged or barely emergent.

At the edges of rock pools and tarns it is associated most often with *Scapania hyperborea*, *S. paludicola s.l.*, *Odontoschisma elongatum*, *Cephalozia bicuspidata*, *Cephaloziella arctica*, *Gymnocolea inflata*, and *Anthelia juratzkana*; less often (and, perhaps, where there are minimal traces of calcareous seepage) *Odontoschisma macounii* may be consociated (70–2005). This last situation can occur only in areas like Lyngmarksfjeld, where igneous rocks, with sunny rock pools, are found juxtaposed to basaltic intrusions.

The species is also found along rills or in stream valleys, over exposed rocks where (intermittently) submersion may occur, here associated (70–2927a) with *Anastrophyllum assimile*, *Cephaloziella* cf. *arctica*, *Scapania crassiretis*, and *Gymnomitrion concinnatum*; the first two taxa are also consociated in 66–1100a; the last and *Marsupella boeckii* are associated in 70–2451. When more frequently exposed to desiccation, as in peaty depressions of low tundra, the species may occur with *Gymnocolea* and *Gymnomitrion corallioides* (70–3158). Occasionally also on cold, permanently moist or seepage-damp rock walls, then with *Anastrophyllum assimile*, *Gymnomitrion concinnatum*, *Marsupella revoluta*, and *Cephaloziella byssacea* var. *scabra*; all but the last species are again consociated in 66–1479c. Indeed, the association with *Anastrophyllum assimile* and *Marsupella revoluta* is a very diagnostic one, and probably phytogeographically relevant. It is possible that all three taxa represent remnants of a pre-Pleistocene flora that survived the Pleistocene somewhere in Greenland. There is no evidence that any of the three taxa represents a post-Pleistocene immigration from the south.

The species is almost always sterile; only in 66–0188 could we find gynoecia.

Marsupella revoluta (Nees) Lindb.

Distribution (Map 40)

25: Sarfaq (70–2322, 70–2323, 70–2337b, 70–2338, 70–2340, 70–2354, 70–2370b, 70–2376a). 30: Eqe (66–0290a). 36: Umanak (66–1479a, 66–1481, 66–1493).

Additional collections:

1B: Lyngmarken, Engelskmandens Havn (M.P.P. 2388). 24: Jakobshavn (S.B. Aug. 1870). 84: Qeqertasugssuk (L.H. Aug. 1932). 90: Tasiussaq (S.B. July 1870). 114: Eqaluit (K.H. 13.219). 131a: Agpat, Qaqortuatsiaq (K.H. & G.M. 71–1687). 141: Inukavsait qáqarssue (K.H. 16.253). 142: Niaqornánguaq (K.H. 14.930).

This species, which has a scattered and probably relict distribution in Greenland (Inglefield Bredning, at 77°30′N. near Kânâk [northernmost station]; East Greenland; West Greenland) is known again only from Baffin Island (Schuster, 1974) in the western hemisphere. It occurs in western Europe from the Alps and Tatra Mts. to Great Britain, and then recurs in the Himalaya, Japan, Taiwan, and (Schuster, 1968) is

common at high elevations (13.500–14.900 ft) in Australian New Guinea. Greenland plants are almost uniformly sterile; only in 70–2340 did we find unfertilized gynoecia.

M. revoluta typically occurs on seepage-moist, cold, acidic rock walls and cliffs, in places where it rarely, if ever, dries out, often (as in 70–2323, 70–2370b) with *M. arctica*, *Anastrophyllum assimile*, less often (70–2338) with *Gymnomitrion concinnatum*, *A. minutum grandis*, and *Cephaloziella byssacea scabra*; rarely *Scapania curta grandiretis* and *Anthelia juratzkana* may be associated (70–2340), or *Gymnomitrion corallioides* and *G. concinnatum* (70–2337b). The last two taxa are also associated with the HARMSEN collection (1932). When, rarely, we find the plant in sites where there is seepage with probably some Ca present, then *Odontoschisma macounii* may be associated (66–1481) or *Lophozia quadriloba*, *Cephaloziella arctica*, *Solenostoma pumilum polaris*, and *Anomomarsupella cephaloziellοides* (66–0290a).

Marsupella ustulata (HUEB.) SPR.

Distribution (Map 40)

1A: Behind Arctic Station (70–2053a). 25: Sarfaq (70–2348). 32: Qôrorssuaq (70–2448g).

Additional collections:

82: Sarqardlîp nunâ (L.H. Aug. 1932). 90: Tasiussaq (S.B. July 1870). 119: Itipilauta (BESCHEL 12.300h). 122: South of Eqaluit (K.H. 13.336a).

This species, broadly interpreted here (to include *M. sprucei*), has a scattered range in much of the Holarctic, outside of Asia, and recurs again in Tierra del Fuego and New Zealand (SCHUSTER, 1968, p. 500). The northernmost report is from Ellesmere Island at 82°26′ N. (SCHUSTER *et al.*, 1959); the southernmost ones in the Holarctic are in Madeira, the Pyrenees, and New Hampshire.

M. ustulata is rare in both West and northwest Greenland (where it has been found near Kânâk by SCHUSTER). It usually occurs in acidic, low moss-tundra, often where irrigated by snow melt, mixed with a wide array of other species (*Scapania spitzbergensis*, *Diplophyllum obtusifolium*, *Anthelia*, *Gymnomitrion concinnatum*, *Lophozia groenlandica*, *Cephalozia bicuspidata*, etc., in Inglefield Bredning; *D. taxifolium*, *Scapania lingulata*, *S. mucronata praetervisa*, in 70–2053a; *C. bicuspidata*, in 70–2348). Rather rarely found on exposed, compact soil of stone polygons (70–2448g), where in small quantity amidst *D. obtusifolium*, *Prasanthus suecicus*, *L. alboviridis*, *L. excisa*, *Nardia geoscyphus*, *Anastrophyllum minutum*, *Gymnomitrion corallioides*, *S. parvifolia*, *C. bicuspidata*, here as isolated plants in small, damp, relatively sheltered depressions. The species, generally, seems to occur in "difficult" and exposed sites and is always limited to areas with acidic rocks.

M. ustulata always seems to be found in minute amounts, mostly only some 10–16 plants at each station, always as solitary stems amidst other, more ubiquitous taxa. For this reason it has surely been overlooked. In 70–2448g, for example, a single fertile (paroecious) plant was found, together with a few sterile ones. The regional plants are usually (e.g., 70–2348) provided with sharp lobes of the bracts, and have marginal cells only 11–14 μ; this corresponds with f. *neglecta*, a plant that approaches "*M. sprucei*".

Marsupella boeckii (AUST.) LINDB.

Distribution (Map 41)

15: Kronprinsens Ejland (70–2061). 32: Qôrorssuaq (70–2440, 70–2442a, 70–2445, 70–2451a, 70–2453, 70–2455c, 70–2462, 70–2464, 70–2467, 70–2478, 70–2480, 70–2482a, 70–2484).

A local and often Arctic-alpine species in Europe and, although widely scattered, never common; extending from northern Fennoscandia to Wales and Scotland, it recurs in the Pyrenees, Carpathians, and the Alps [the report by ARNELL (1957) from Equatorial Africa represents *Nardia arnelliana* Grolle]. In our opinion *M. stableri* Spr. from Great Britain is probably identical. In North America cited previously from a single, indefinite station from "Greenland". It occurs in the Angmagssalik District of East Greenland, from 60°06–50′ N. in South Greenland, and from the two above stations in the Disko Bugt region, the northernmost reports of *M. boeckii*.

At Nunarssuaq (70–2061) found in a relatively arid site, in thin patches on shaded rocks, associated with *Scapania lingulata* and *Cephaloziella arctica*, as a grey-green phenotype very similar to a *Cephaloziella* in aspect. At Qôrorssuaq, where rather frequent, it occurs over thin layers of peat over rocks at the edge of a steep, cascading rill, where subject to periodic submersion. Associated here are *Lophozia alpestris*, *Cephaloziella byssacea*, *Gymnomitrion corallioides*, *G. concinnatum*, *Gymnocolea inflata*, *Scapania obscura*, *Lophozia ventricosa grandiretis*, *L. v. rigida*, *L. opacifolia*, *Anthelia*, *Pleuroclada* and, occasionally, *Marsupella arctica* and *S. hyperborea*.

Plants are usually quite small (stems 70–80 μ in diam.; leafy shoot 110–130 μ wide in 70–2442a); they are often gynoecial, but no fertilized gynoecia have been seen, nor have androecial plants. West Greenland plants represent the remote-leaved "*boeckii* phase", but in southwest Greenland phases (the "*stableri* phase") occur with denser, narrower, more deeply bifid leaves that have sharper and longer leaf lobes.

Marsupella condensata (ÅNGSTR. ex HARTM.) KAAL.

Distribution (Map 41)

9: Eqaluit (70–2544, 70–2551, 70–2554, 70–2556).

M. condensata is known from northernmost Europe, Spitsbergen, Scotland, the Alps and Tatra Mts. and Cantal, France; recurring in Iceland. Unknown from North America except for the Greenland stations: Fiskenæsset District (Tasiussarssuaq, 62°49′N., 50°10′W. KD 71–436) and the west coast of Disko, Eqaluit; at the last station on thin soil, stony north-facing slope near persistent snow banks, with *Gymnomitrion concinnatum*, *G. apiculatum*, *Anthelia juratzkana*, and xeromorphic extremes of *Lophozia hatcheri* and *Andreaea*. Sporadically *L. wenzelii* and *Pleuroclada* may be associated. Capsules are present (Aug. 8.) in 70–2556.

JØRGENSEN (1934) states that the species is an extremely high mountain plant in Norway, occurring on moist, sandy earth, mostly in places where the soil is continuously irrigated by melting snow fields. This almost exactly describes the West Greenland site, where the species occurs with late snow taxa, such as *A. juratzkana* and *G. apiculatum*. At least in our limited experience, the species occurs in noncalcareous areas (in the Disko Station, although in a basalt region, the plant was found on thoroughly leached ground).

The ecology is apparently closely similar to that of the superficially similar *G. apiculatum*. JØRGENSEN (l.c., p. 89) states that *M. condensata* "looks to a very high degree" like *G. apiculatum*, "with which it was earlier confused ... In most cases it is possible to readily separate it in the field" from *G. apiculatum* on the basis of the "often darker brown or black color (in *G. apiculatum* more yellow- or reddish brown) and slenderer shoots. ... Under the microscope it is easily separated by the never hyaline margins of uninjured leaves and in the characteristic lunulate sinus—which is extremely different from the angulate, often sharp sinus of *G. apiculatum* (*Marsupella condensata* always has the sinus lunate, and at shoot tips, owing to the strongly concave leaves with incurved lobes, the lobe apices may be actually connivent; in *G. apiculatum* it is often also lunate, although not consistently so). It varies very little except in size. Transition forms to *G. apiculatum* do not occur. Fresh plants, when crushed, have the same terpene-like odor as the species of *Gymnomitrion*, which does not occur elsewhere in *Marsupella*."

In the Greenland material of *M. condensata* the shoots are clearly nitid and chestnut brown, with leaves neither appressed nor imbricate to the point that their perimeters are indistinct; by contrast, in *G. apiculatum* (including the admixed plants of 70–2556a) the shoots are dull, more

red-brown to fuscous, with more tightly imbricate-appressed leaves whose outlines, *in situ*, are almost indistinguishable.

Marsupella sparsifolia (LINDB.) DUM.

Distribution (Map 40)

29: Ritenbenk (S.B. 1870).

An infrequent to rare species of bipolar range, reported from subarctic to low Arctic loci in western Europe south to the Azores, and in eastern North America from New Hampshire west to Michigan, north to Nova Scotia, Quebec, and Ontario. In Greenland, for which no prior reports exist, it occurs in the south from 59°54′ N. to 62°49′ N. and in the east from 65°35′ N. to 66°06′ N. (in the Angmagssalik District; KD 69–337). The report from Ritenbenk is the northernmost one of the species, but we have been unable to find it ourselves.

The Ritenbenk plant occurred under evidently exposed conditions, associated with *Gymnocolea inflata* and *Cephaloziella arctica*, in an area with acidic rocks. Associated with the evidently exposed mode of growth is the relatively small size (3–6 mm tall × 0.5–0.8 mm wide, at the apex of the paroecious inflorescence to 1.1 mm wide); plants are more compact; leaves are denser and obliquely patent and the lobes are not widely patent to squarrose, as is typically the case with "normal" *M. sparsifolia*. As seems to be the case with several other species at their northern perimeters (see, e.g., discussion of *Solenostoma pumilum* and *Tritomaria polita* in SCHUSTER, 1969), the leaves tend to become somewhat shorter and leaf lobes are consistently blunt to narrowly rounded, rather than sharp, as is normally the case in *M. sparsifolia*.

As a consequence of these divergences, we initially were doubtful about the wisdom of placing the plant here. The relatively wider leaves (width: length ca. 0.9–1.1:1 *vs.* 0.8–1:1 in Angmagssalik plants) seem to result from abbreviation of the leaves. As a consequence, median cells are only ca. 13–17×15–20 μ (16–18×21–25 μ in Angmagssalik material). Associated with the rather stiff growth and depauperate aspect, cell size as a whole is slightly smaller (marginal cells, 12–17 μ vs. 13–16 μ in Angmagssalik material, however, are essentially identical). There is already a feeble tendency in some Angmagssalik plants for some leaf lobes to become blunt, and the blunt to narrowly rounded lobes of the Ritenbenk material seems a mere accentuation. As a consequence we feel certain that this paroecious material from Ritenbenk must be referred to *M. sparsifolia*. The relatively patent leaves, not strikingly smaller below, and never scalelike nor semiappressed, at once exclude *M. ustulata* from consideration—the only other paroecious species with which it might be confused.

Gymnomitrion Corda

Gymnomitrion apiculatum (SCHIFFN.) K. MÜLL.

Distribution (Map 43)

1A: Behind Arctic Station (66–0193). 1B: Lyngmarken (66–0344, 66–0555). 9: Eqaluit (70–2544a, 70–2554, 70–2556a, 70–2783). 15: Kronprinsens Ejland (70–2068, 70–2105a, 70–2122). 16: Manîtsoq (70–3005, 70–3014, 70–3017). 32: Qôrorssuaq (70–2472, 70–2481a). 37: Agpat (66–1434). 45: Sagdliaruseq (66–1073, 66–1074). 52: Umîarfik, Qôrnoq (66–0933).

Additional collections:

17: Tupilak (K.J. 1308). 29: Ritenbenk (S.B. 1870). 45: Sagdliaruseq (K.H. 16.963, 16.970). 76: Ivnârssulik (C.K. 834). 119: Itipilautâ (Beschel 12.300g). 142: Niaqornánguaq (K.H. 14.939, 16.757).

This Arctic-alpine species has a restricted range in northern Europe (Fennoscandia, northwestern Russia, Scotland, the Alps, Tatra Mts.) and Spitsbergen; also in Siberia, Japan, and Alaska. Reported from Angmagssalik District (Qordlortoq Sö, JENSEN 1906) in E. Greenland, and recurring near Kânâk, Inglefield Bredning (SCHUSTER l. c., northernmost Greenland stations), and from the West Greenland stations cited above. Otherwise unknown from the eastern North American Arctic. The species is not rare in West Greenland but has a peculiar ecology which must be appreciated and understood or the plant will be repeatedly overlooked in the field.

G. apiculatum usually occurs on acid, often peaty soil (never, unlike our other *Gymnomitria* as a pioneer over rocks or cliffs), often on level or gently sloping ground, sometimes where nearly continuously irrigated during the growing season, and not infrequently in late snow areas, or below beds of persistent snow. Here may be associated *G. concinnatum*, *Gymnocolea*, *Cephalozia bicuspidata*, *Odontoschisma elongatum* (70–2068), or, infrequently (66–0555), *Gymnocolea* and *Pleuroclada*. Occasionally also on gentle slopes below persistent snow fields, on soil between rocks, associated with *G. concinnatum*, *Marsupella condensata*, and *Anthelia juratzkana* (70–2556). The species may also be found in depressions between rocks in broken, rocky fell fields, over silty soil, where (as at Qôrorssuaq; 70–2472) it may form very large, pure patches in sites with late persisting snow and where, at times, submersion is possible; here it is associated with *G. concinnatum* and *Cephaloziella arctica*. At the opposite extreme are occurrences (as on Manîtsoq; 70–3014) on broken rocky ground, over fine, compact but heaved soil, associated with *Prasanthus*, *G. concinnatum*, *Pleuroclada*, and *Tritomaria quinquedentata*. The almost constant association with *G. concinnatum* is noteworthy.

Gynoecia are not rare on local plants; we have seen no evidence of sporophyte production.

Gymnomitrion concinnatum (LIGHTF.) CORDA

Distribution (Map 44)

1A: Behind Arctic Station (66–0197, 70–2006, 70–2007a, 70–2012a, 70–2035b, 70–2046). 1B: Lyngmarken (66–0344a). 6: Eqalúnguit (70–2224a, 70–2242b, 70–2249, 70–2251). 9: Eqaluit (70–2529, 70–2540, 70–2544, 70–2548a, 70–2550, 70–2554, 70–2556b, 70–2559, 70–2561). 10: Enoks Havn (70–2778b). 14: Hareøen (70–2575). 15: Kronprinsens Ejland (70–2068a, 70–2075, 70–2079b, 70–2105a, 70–2110a, 70–2113, 70–2120, 70–2122). 16: Manîtsoq (70–3001a, 70–3010a, 70–3014b, 70–3015c). 17: Tupilak (66–0001, 66–0003, 66–0013a, 66–0033). 19: Nûk (70–2875b, 70–2835). 21: Umiasugssûp (70–2927a, 70–2948a). 25: Sarfaq (70–2320b, 70–2323b, 70–2337a, 70–2338a, 70–2368, 70–2370, 70–2376). 26: Pâkitsup ilordlia (70–2281, 70–2388). 30: Eqe (66–0249d, 66–0293, 66–0294, 66–0328a, 66–0331, 66–0334, 66–0336a). 31: Anap nunâ (70–2424). 32: Qôrorssuaq (70–2451a, 70–2453, 70–2455a, 70–2458, 70–2462, 70–2464, 70–2467, 70–2472b, 70–2480, 70–2481a, 70–2484b). 36: Umanak (66–1479b, 66–1480, 66–1491). 37: Agpat (66–1438, 66–1440). 47: Íngia (66–1056, 66–1057, 66–1078, 66–1084). 46: Qalatôq (66–1102a, 66–1110). 48: Amitsup (66–0788, 66–0818). 52: Umîarfik, Qôrnoq (66–0933).

Additional collections:

16: Manîtsoq (W. & H. July 1884). 17: Tupilak (K.J. 1290, K.H. June 1956). 28: Atâ (LÆGAARD July 1962). 29: Ritenbenk (S.B. 1870). 44: Akuliarusikavsak (K.H. 15.867). 52: Umîarfik, Qôrnoq (K.H. 12.697). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 84: Qeqertasugssuk (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 88: Christianshâb (K.H. 15.709, 16.630c). 90: Tasiussaq (S.B. July 1870). 95: Pâkitsoq (J.V. Aug. 1835). 98: Sarqaq (J.V. 247). 112: Umiartorfik (K.J. 622, 634). 114: Eqaluit (K.H. 13.232). 120: Itipilua qáqâ (K.J. 695). 122: South of Eqaluit (K.H. 13.232). 131: Storø (A.R. July 1954). 131a: Agpat, Qaqortuatsiaq (K.H. & G.M. 71–1681). 139: Qaqortukavsak (K.H. 16.079a). 141: Inukavsait qáqarssue (K.H. 16.250, 16.286e). 143: Kangerdlugssuaq (K.H. 16.386).

This abundant species is strictly Arctic-alpine and essentially holarctic in range; reports from the southern hemisphere (Tasmania, Tierra del Fuego) are all based on errors in determination. It is found as far north as 82°53′N. in Peary Land (ARNELL, 1960) and 82°25′N. in Ellesmere Island (SCHUSTER *et al.*, 1959), extending southward in North America to New Hampshire and Vermont, where it is strictly alpine.

G. concinnatum shows a much wider ecological "spread" in the Arctic than further southward and than noted in Fennoscandia by HAAPASAARI (1966). As noted under *G. apiculatum*, it often occurs with that species in late-snow areas, over mineral or peaty soil, often on level ground or gentle slopes, where moist throughout the growing season; here *Gymnocolea inflata*, *Cephaloziella arctica*, and *Pleuroclada* may be associated (66–0344a, 70–2481a, 70–2472b), rarely also *Prasanthus* (70–3014b) or *Marsupella condensata* (70–2556). At the opposite extreme, it occurs on exposed, often heaved and unstable mineral soil in exposed, rocky ground, then associated with *Prasanthus suecicus* and occasionally *G. corallioides* (66–0336a) or *G. corallioides* and *Gymnocolea* (70–2075). Occasionally also

Lophozia alpestris and *G. corallioides* occur together with *G. concinnatum* (70–2110a). At times it is found on fine sandy silt, on heaved ground, with *Prasanthus*, *L. alpestris*, *L. excisa*, *L. ventricosa silvicola*, *Scapania parvifolia*, *Solenostoma sphaerocarpum*, and *Anastrophyllum sphenoloboides* (70–2948a). The common denominator for all but the first of these stations is exposure of the plants to possible desiccation.

The species may also be found, however, over insolated peaty ground around rock pools, then with *Odontoschisma elongatum*, *Gymnocolea*, and *Pleuroclada* (66–0197), or on peaty ground in similar but less moist sites, with *Diplophyllum albicans*, *D. taxifolium*, *Gymnocolea*, *Cephalozia pleniceps*, and *O. elongatum* (70–2007a). Similarly, occurrences over peaty soil on rocks edging cold, cascading rills are frequent (as in 70–2455a, 70–2484b), associated with *Cephaloziella byssacea*, *Marsupella boeckii*, *Anthelia*, *Gymnocolea*, *Lophozia opacifolia*, etc.

G. concinnatum may persist beyond the initial states in succession on exposed cliffs, where it is very common, occurring in large sheets, sometimes with *G. corallioides* (especially when growing very exposed). Under these conditions it may occur in deep mats, associated with *Scapania crassiretis* (in 70–2249) or *S. spitzbergensis* and *D. albicans* (in 70–3001 a). When a pioneer or near-pioneer on permanently humid or moist cliff walls it occurs not only with *G. corallioides* but with *Marsupella revoluta*, *M. arctica*, *Anastrophyllum assimile*, and *Cephaloziella byssacea scabra* (70–2323b, 70–2337a). Rarely on cliffs walls it may occur mixed with *Chandonanthus* (66 0003) or *L. hatcheri* (70 2251). Similar but much more extreme pioneer conditions obtain on damp, windblown, fine sand deposited from the nearby Inland Ice, as at Eqe (66–0293d), where *G. concinnatum* is found mixed with *Prasanthus*, *G. corallioides*, *Lophozia cavifolia*, *A. minutum grandis*, *L. excisa*, and *S. obcordata.*

Although very largely restricted to areas with acidic rocks—where the plant may be almost ubiquitous—there are a few collections from sites which show association with Ca-tolerant or Ca-demanding taxa: *O. macounii* (in 70–2251, 70–2778b, 70–2242b), rarely *L. heterocolpos* (70–2242b; there also with *S. mucronata praetervisa*). In a single case, under conditions where oxylophytes dominated but where slight basic seepage must have been present, on the Nûk (70–2875b), both the oxylophyte *O. elongatum* and the basiphyte *O. macounii* were intermingled, under relatively mesic conditions. Finally, *G. concinnatum* may occur over peaty, exposed hummocks along rills, where some Ca-enriched seepage occurred, together with *Prasanthus*, *Tritomaria quinquedentata*, *T. heterophylla*, *O. macounii*, *Cryptocolea*, and *Anthelia* (66–0249d).

The preceding selection of sites and associates by no means exhausts the types of areas that may be invaded. In most of these sites the species freely develops capsules. Both tawny-green and green-brown phenotypes

are common, as well as, rarely, strongly brown phenotypes (e.g., 66–0331). Plants of the last type may be mistaken for *G. apiculatum*, from which they are distinct in the rough cuticle and greater diameter of the leafy shoots. Except for differences in pigmentation, associated with differences in exposure, the species seems to vary within narrow limits, when we consider its phenomenal ability to invade diverse habitats.

Gymnomitrion corallioides Nees

Distribution (Map 44)

1A: Behind Arctic Station (70–2011, 70–2012a, 70–2059). 2: Fortunebay (66–0209). 6: Eqalúnguit (70–2240a). 9: Eqaluit (70–2548). 15: Kronprinsens Ejland (70–2065, 70–2075, 70–2079, 70–2102, 70–2110). 16: Manîtsoq (70–3001b). 17A: Egedesminde (66–0948). 22: Orpigsôq (70–3110b, 70–3112a, 70–3118d). 23: Kangersuneq (70–3158b). 25: Sarfaq (70–2337a, 70–2341, 70–2371). 26: Pâkitsup ilordlia (70–2260c, 70–2388, 70–2394). 29: Ritenbenk (66–0265). 30: Eqe (66–0293a, 66–0328b, 66–0335, 66–0336a). 31: Anap nunâ (70–2405b). 32: Qôrorssuaq (70–2448d, 70–2457d, 70–2480). 37: Agpat (66–1434, 66–1467c). 45: Sagdliaruseq (66–1056, 66–1078). 46: Qalatôq (66–1102a). 48: Amitsup (66–0818).

Additional collections:

6: Eqalúnguit (M.P.P. 1653). 45: Sagdliaruseq (K.H. 16.969). 84: Qeqertasugssuk (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.630). 95: Pâkitsoq (J.V. Aug. 1833). 112: Umiartorfik (K.J. 573, 621). 115: Kûgssuaq (K.J. 747). 116: Puiagtukavsak (K.J. 670). 119: Itipilautâ (Beschel 12.300f). 131: Storø (A.R. July 1954). 137: Esersiutilik (K.H. 16.460). 139: Qaqortukavsaq (K.H. 16.079c). 141: Inukavsait qáqarssue (K.H. 16.250a).

A strictly circumpolar, Arctic-alpine species, which extends north to at least 82°30′N. in Ellesmere Island (Schuster *et al.*, 1959); in eastern North America it extends south to New Hampshire (where at over 5200 ft) and New York; in Spitsbergen it is found north of 79° and in Siberia to 78°20′N. In Greenland occurring as far as north of Saxifragadal, Independence Fjord, at 81°51′N. (Holmen !). Common in our area, almost exclusively in regions with acidic rocks.

G. corallioides is often essentially a pioneer under very difficult conditions. It often occurs in nearly pure patches on exposed rocks and cliff walls, sometimes with *G. concinnatum*, small forms of *Lophozia alpestris*, with various mosses (*Andreaea*), and occasionally with *Anastrophyllum minutum*. It is frequent in late snow areas, where on damp soil between boulders and bedrock ledges, with mosses, *A. minutum*, *Anthelia juratzkana*, *Cephaloziella arctica* (sometimes *C. grimsulana*), and also on exposed, heaved, compact soil of stone polygons, where sometimes associated with a wide range of species typical of such extreme sites (in 70–2448 and 70–2457d): *L. alboviridis*, *Nardia geoscyphus*, *Cephalozia bicuspidata*, *L. excisa*, *Diplophyllum obtusifolium*, *Anastrophyllum minutum*, *Cephalozia bicus-*

pidata s.l., *L. alpestris*, *Anthelia juratzkana*, and *Prasanthus suecicus*. The last five taxa also occur admixed in 70–2260c, from fine silty, heaved soil on a rocky, exposed slope, where subject to desiccation. Occasional also in more permanently damp sites, as on peaty ground between rocks, with *Marsupella arctica* and *Gymnocolea* (70–3158b), or with *L. binsteadii* (70–3112a) or *Tritomaria quinquedentata gracilis*, *C. bicuspidata*, *Scapania mucronata* (66–1467c); rarely with *C. bicuspidata ambigua* and *Nardia scalaris* in patches on exposed peaty ground (70–2059).

Perhaps the most extreme site invaded is barely damp, hardly consolidated wind-blown, fine sand, adjacent to the Inland Ice (at Eqe), here associated with *G. apiculatum*, *Prasanthus*, *L. excisa*, *S. obcordata*, together with *Saxifraga oppositifolia*, a plant with an equal ability to invade "impossible" sites.

Anomomarsupella SCHUST.

Anomomarsupella cephaloziellloides SCHUST.

Distribution (Map 42)

1A: Behind Arctic Station (66–0189). 30: Eqe (66–0290). 42: Magdlak (66–1356a). 43: Kangerdlugssuakavsak (66–1285).

Additional collection:

36: Umanak (K.H. 16.331).

This minute species, known only from the above collections, is so easily overlooked that, although collected from four localities in 1966, it was not again seen in 1970. As the species name connotes, it resembles a *Cephaloziella*—and a sterile, fuscous green, particularly nondescript one at that. Hence its range is quite unknown.

The plant seems to occur principally in permanently moist, basic areas—the type came from the edge of a basalt dike, on a seepage-moist cliff face, associated with *Lophozia quadriloba*, *Cephaloziella arctica*, *Solenostoma pumilum polaris* (all Ca-tolerant taxa), and *Marsupella revoluta* (a species which is usually absent from basic sites). The plant of 66–1285 was from soil between rocks, associated with *Nardia geoscyphus* and *Cephaloziella uncinata*; that of 66–1356a was associated with *Solenostoma sphaerocarpum*, *S. subellipticum*, *S. pumilum*, *Scapania cuspiduligera*, *Lophozia gillmani*, *L. heterocolpos* (all Ca-tolerant), as well as *Scapania serrulata*, a plant which (in our limited experience is usually Ca-intolerant. The paratype occurred over peaty, bare, black soil, together with *Anthelia*, along a rill draining basalt cliffs.

We have no additional information to that given in SCHUSTER (1969b, 1974).

Prasanthus LINDB. & ARN.

Prasanthus suecicus (GOTT.) LINDB. & ARN.

Distribution (Map 42)

1A: Behind Arctic Station (66–0102). 16: Manîtsoq (70–3007, 70–3014a). 21: Umiasugssûp (70–2948). 22: Orpigsôq (70–3118). 23: Kangersuneq (70–3145, 70–3148, 70–3149, 70–3154). 25: Sarfaq (70–2320, 70–2364a). 26: Pâkitsup ilordlia (70–2260, 70–2277). 28: Atâ (70–2498). 30: Eqe (66–0249a, 66–0293, 66–0336). 32: Qôrorssuaq (70–2448, 70–2457, 70–2480). 37: Uvkusigssat (66–1434). 45: Sagdliaruseq (66–1073). 46: Qalatôq (66–1102).

Additional collections:

29: Ritenbenk (S.B. 1870). 57: Nipisat (K.H. 14.369). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 90: Tasiussaq (S.B. 1870). 112: Umiartorfik (K.J. 553, 556). 117: Sêrsínerssuaq (K.J. 616).

A strictly circumpolar Arctic-alpine species. Reported from Siberia, the high mountains of Scandinavia, Jan Mayen, E. Greenland and the Alps.

In Greenland occurring as far north as Inglefield Bredning (Kangerdlugssuak 77°23′N.; SCHUSTER, 1974) and reported from E. Greenland (Scoresby Sund area; JENSEN, 1897 and 1900), and collected as well in S. Greenland (Kangikitsoq 60°20′N.; P.M.P. 338) and in SW. Greenland (Perserajôrssuaq 63°02′N.; KD 71–195).

Prasanthus is often a pioneer under very difficult conditions especially in areas with acidic rocks. In our area collected at sea level, while in SW. Greenland it occurred only at higher elevations often in places where the soil was continuously irrigated by melting water.

Prasanthus occurs on exposed compact soil often, as at Sagdliaruseq (66–1073), associated with *Gymnomitrion concinnatum*, *G. corallioides*, *Cephalozia bicuspidata ambigua*, *Lophozia ventricosa confusa*. Sometimes it is also associated with *Gymnomitrion apiculatum* and *Nardia geoscyphus*, as at Uvkusigssat (66–1434) and Sagdliaruseq (66–1073), but rarely, as at Qôrorssuaq (70–2448), it occurs together with *Lophozia alboviridis*, *Scapania parvifolia*, *Diplophyllum obtusifolium* and, *Marsupella ustulata*. At Umiasugssûp (70–2948) it occurred together with *Anastrophyllum sphenoloboides* and *Solenostoma sphaerocarpum*.

Family ***Scapaniaceae*** MIGULA

Diplophyllum DUMORT.

Diplophyllum albicans (L.) DUMORT.

Distribution (Map 45)

1A: Behind Arctic Station (70–2007, 70–2046). 16: Manîtsoq (70–3001).

Additional collections:

1A: Godhavn (S.B. 1870, specimen not seen). 6: Eqalúnguit (M.P.P. 3859a). 54: Holsteinsborg (W. & H. 1884).

This suboceanic species is of essentially temperate range; in Europe it extends south to the Pyrenees and Sierra Cantabrica, Portugal, and Italy; it occurs northward chiefly in the southern parts of Fennoscandia and ranges south to Madeira, the Azores, and the Canary Islands, and east to the Black Sea; it recurs in Iceland, Japan, Kamchatka, Korea, Formosa, and Hawaii. The northernmost station is in Spitsbergen (BERGGREN, 1875; ARNELL & MÅRTENSSON, 1959). In West Greenland it is found north only to Disko—Disko Bugt region, where it is local and rare; it was first collected in our region at Holsteinsborg (WARMING & HOLM, 1884).

The species is limited to areas with acidic rocks, where it may occur over ledges with *Scapania crassiretis* (PORSILD, 1898), but occurs more commonly (both at Godhavn and Manîtsoq) over damp but exposed moss-tundra in depressions in peaty ground around tarns and rock pools. Here the plants are found principally as a strongly infuscated phase, which may even produce infuscated gemmae. Associates are usually *Diplophyllum taxifolium*, *Gymnocolea inflata*, *Gymnomitrion concinnatum*, *G. corallioides*, *Odontoschisma elongatum*, *Anthelia juratzkana*, *Cephalozia bicuspidata*, *C. pleniceps*, *Lophozia alpestris*, and *Scapania spitzbergensis*.

Local plants show a marked tendency to become infuscated and may nearly or quite lack the reddish color of the leaf bases often diagnostic of the species. Then several rows of marginal cells become decolorate and lack oil-bodies. Even on young leaves the oil-bodies may be lacking from all or most leaf cells, except for the strongly elongated cells of the vitta (in which they persist until the leaves begin to die). No sex organs have been seen on regional plants, although gemmae are always present.

Diplophyllum taxifolium (WAHL.) DUMORT.

Distribution (Map 45)

1A: Behind Arctic Station (66–0184, 70–2007b, 70–2053b, 70–2047d f. *macrosticta*). 1B: Lyngmarken (66–0559). 16: Manîtsoq (70–3009a, 70–3010a, 70–3015, 70–3021).

D. taxifolium is a more northern species than *D. albicans* but hardly an Arctic species; it is also much more common in continental areas than *D. albicans* and generally more tolerant and widespread. It extends north to Spitsbergen and Siberia in Eurasia, south to the Black Sea in Turkey, to the Spanish Pyrenees, and recurs in the North Pacific Arc from alpine regions of Japan to Kamchatka, Korea, Sakhalin, and Alaska, south to California. In our area it is found north only to Godhavn (69°14′N.) and south in eastern North America to Tennessee and North Carolina along the crest of the Appalachians; limited strictly to areas with acidic rocks.

In our area it occurs in pure thin patches in damp clefts of gneiss cliffs (66–0559), also a typical habitat of the species in forested regions. More frequent, in admixture, in exactly the type of site where *D. albicans* occurs (admixed in 70–2007b); other associates then are *Gymnomitrion concinnatum*, *Gymnocolea*, *Odontoschisma elongatum*, *Cephalozia pleniceps*, *Lophozia cavifolia*, *L. wenzelii*, and *Anthelia juratzkana*. When over damp but exposed peaty ground, amidst rocks, often in shallow depressions, sometimes also with *Scapania mucronata praetervisa*, *S. lingulata*, *Marsupella ustulata*, *Pleuroclada*, *Anthelia*, *Nardia geoscyphus*, *C. pleniceps*, and *Calypogeia integristipula* (70–3009a, 70–3015, 70–2053b).

D. taxifolium locally often has the cuticle very coarsely papillose ("var. *macrosticta* Buch"—a plant here considered as at most a mere *forma*). Often 1–4 marginal cell rows lack oil-bodies, although all others have them present. Gemmae are common; we have not seen sex organs in regional plants.

Diplophyllum obtusifolium (Hook.) Dumort.

Distribution (Map 45)

32: Qôrorssuaq (70–2448g).

This species, which is frequent and often, indeed, almost weedy in temperate areas of Europe, occurs from southern Fennoscandia to the Spanish Pyrenees, the French Maritime Alps, northern Italy, Croatia, the Carpathians, westward to Wales, Scotland and Ireland; reported from Iceland. It recurs along the North Pacific Arc from Japan to British Columbia and northern California. In eastern North America it is almost wholly replaced by the autoecious *D. obtusatum* (Schust.) Schust., which extends from Minnesota and Newfoundland to North Carolina and Tennessee. However, typical *D. obtusifolium* recurs, far out of its expected range, in two localities in Greenland; the northernmost is at Kânâk, Inglefield Bredning and the other noted above. We have no explanation for the anomalous Arctic occurrences of this species which hardly penetrates the northern half of Fennoscandia (and, in the North Pacific Arc fails to extend to Alaska). It is not impossible that *D. obtusifolium* is a pre-Pleistocene relict species in Greenland. In any event, it is not only very rare, but has been found in only minute amounts in the two Greenland stations.

D. obtusifolium is stated by Müller (1905–16, p. 364) to occur almost constantly on sandy-loamy soil, with *Scapania curta* (*s.l.*), *Cephalozia bicuspidata*, and *Nardia scalaris*, often forming red-brown (in shaded areas green) patches. Müller (as well as Buch, 1928, pp. 26–27) emphasizes that the species is almost constantly on Ca-poor soils; both Müller and Buch emphasize the frequent occurrence (at least in the lowlands) on sides of ditches, often in shaded sites.

The ecological distribution in West Greenland is drastically different. The species here occurs on exposed clayey soil, in crevices between rock fragments and boulders, in frost-heaved soil-stone polygons, associated with a whole series of taxa typical of such sites: *Prasanthus suecicus*, *S. parvifolia*, *Lophozia alboviridis*, *L. excisa*, *Nardia geoscyphus*, *Gymnomitrion corallioides*, *Anastrophyllum minutum*, *Cephalozia bicuspidata*, *Marsupella ustulata*, etc. (in 70–2448g). Here the plants occur as a golden brown and very dense-leaved, compact phase, quite devoid of the claret-red or purplish color typical of the temperate zone, European phases. The few plants seen are all clearly paroecious, but lack gemmae.

By contrast, the plants from northwest Greenland (RMS 45635a) are a sterile mod. *viridis*, occurring amidst *Marsupella ustulata*, *Scapania spitzbergensis*, *Polytrichum*, *L. alpestris*, *C. bicuspidata*, and *G. concinnatum* on steep, consolidated clayey soil, in a late snow area irrigated from an adjacent, local ice cap. These plants show abundant gemma production.

The Greenland plants are notable in the densely and coarsely papillose cuticle. On this basis they perhaps should be segregated as a distinct subspecies from Eurasian-temperate, "typical" *D. obtusifolium*, which is stated to have the cuticle weakly striolate to "fast glatt" (MÜLLER, 1905–16). MACVICAR, however, notes that in plants from Great Britain the cuticle is "*strongly verruculose*" (emphasis his).

Scapania (DUMORT.) DUMORT.

The large genus *Scapania* is the most difficult genus of *Hepaticae* in Greenland. The problems are innumerable and we have not, by any means, been able to resolve them in many instances. Since many of these taxonomic problems are discussed in detail in SCHUSTER (1974), we will limit ourselves here to treatment of those specific problems for which there was insufficient space in the aforementioned work.

These taxonomic problems reside, to a large extent, in the following factors: (a) a very high intrinsic malleability in almost all species; (b) development of series of phenotypes which fail to correspond in all points to "temperate zone" phenotypes that have been, in all but a few cases, the basis for establishment of the species; (c) apparent autopolyploidy, leading to large-celled races with larger gemmae and more numerous oil-bodies; (d) development of larger dorsal lobes (and longer keels) *vis à vis* the "temperate zone" populations, as an apparent adaptation to the Arctic environment; examples are *Scapania mucronata praetervisa* and *Scapania curta isoloba*; (e) Arctic populations often developing rounded and edentate leaf lobes, in contrast to "temperate zone" populations, as, e.g., *S. irrigua rufescens vs. S. i. irrigua* and *S. paludicola rotundiloba vs.*

S. p. paludicola; (f) Arctic populations sometimes developing reddish to vinaceous pigments, the "parent" species failing to exhibit such coloration, as in, e.g., *S. lingulata*, *S. irrigua*, *S. paludicola*, etc.; (g) frequent loss, perhaps a result of the "hostile" Arctic environment, of "normal" branching patterns, replaced by terminal, *Radula*-type branching. We do not know how to fully, taxonomically, evaluate such differences in branching.

One of the major taxonomic problems is that, not infrequently, two or more species of a single section may occur admixed. The extreme is reached in 70–2940a, in which we find *S. paludicola rotundiloba*, *S. irrigua rufescens*, *S. hyperborea*, and a plant near *S. tundrae* (the last a large-celled plant)—all species of the single sect. *Irriguae*. With the malleability of the species, separating these is a problem. For example, lateral-intercalary branches of *S. paludicola*, which are rather weak, may have a weakly arched and rather elongate keel—and simulate *S. irrigua*! The "*S. tundrae*"-like plant, which we do not cite under that species, is so deviant that possibly a new species is at hand—but the material is much too sparing to warrant any definite conclusion.

Subg. ***Jensenia*** S. Arn.

Under this "subgenus" we have placed a large series of phenotypes which constitutes by far the most puzzling, variable, and taxonomically intractable complex we have thus far found in Arctic *Hepaticae*. The following attempt to a solution represents the best that we can do, but we realize that, in essence, we have abandoned the problem at an unsatisfactory level; further resolution must involve culture experiments, chromosome counts, and reciprocal transplant experiments.

We have critically studied all pertinent material: types of *S. lapponica*, *L. jenseni*, *S. obcordata*, *S. paradoxa*, and *S. paradoxa v. ramosa*; we have also seen essentially all collections of all these taxa that have been made. It is noteworthy that while we saw few specimens, taxonomic and morphological discontinuities seemed obvious; the more material we saw, the greater the breakdown in these discontinuities until it almost seemed that we were dealing only with plastic populations forming a single immense *typus polymorphus*. At the same time, it is almost impossible to conceive that a single species should show a level of variation exceeding the generic limits established by Buch (1928) in the *Scapaniaceae*. For example, in the following key to phenotypes we find both plants with a sharp leaf keel ("genus *Scapania*") and those which quite lack it ("genus *Scapaniella*"). Even such criteria as cell size and oil-body number which Buch (l. c.), Müller (1951–58) and Schuster (1953) employed as definitive species criteria, break down. Thus, in *S. paradoxa* (Fig. 13:8–9;

see p. 215), cell size and oil-body number are both distressingly variable, sometimes, with seasonal conditions, on one plant. For this reason we have employed such criteria here only as supplementary criteria and do not maintain the "usual" distinction between *S. obcordata* and *S. lapponica.*

Part of the problem, of course, lies in the fact that most, if not nearly all, plants assigned here are "specialists" that invade the most inhospitable sites in a difficult general habitat. It is almost as if the inherent harshness of the Arctic environment is not enough; these plants seem to "seek out" the most intractable microhabitats: sandy or silty sites where they are often covered by washed or blown sand or silt; late snow areas where water-carried silt tends to overwhelm them; late snow areas where the growing season is reduced to the minimum—perhaps no more than 3–4 weeks per year. Thus at the type locality of "*Lophozia jenseni*"—which belongs here—one of us (DAMSHOLT) had repeated opportunity to observe the plant; during the growing season, the plants, which grow near the mouth of a glacier, are covered daily by water-carried fine sand. Every day, towards morning, the plants are uncovered; as the day proceeds and the temperature rises, ice melt from the glacier front, carrying fine sand, invades the habitat, covering the plants so that in the afternoon it is physically impossible to collect them. Here we find, during the growing season, daily disturbances that threaten to overwhelm the population; in other instances, as with *S. paradoxa*, melt water from hanging or late snow banks, carrying silt, tends to continuously bury the plants whose survival seems to depend on a very vigorous growth rate during the growing season. Possibly the ill-coordinated growth which has been observed in both *S. obcordata* and *S. paradoxa* results from this. The impression is, almost, as if the plants were desperately growing to avoid destruction—and in the process ordinary "controls" over growth and differentiation tend to break down. The analogy is, clearly, to the "breakdown" in ordinary morphology which BASILE (1967, 1969) cites he achieved experimentally with *S. nemorosa* by chemical alteration of the "environment".

The problems involved with *Jensenia* are, inferentially, well demarcated through a consideration of the history of the complex. The type of *Jensenia* was described by BERGGREN (1875a, p. 96) as "*Sarcoscyphus obcordatus*", from Spitsbergen. This was not referred to *Scapania* until ARNELL, in ARNELL & MÅRTENSSON (1959) made the proper combination; he then suggested that *S. lapponica* was allied to *S. obcordata.*

Our researches on this complex suggest that both of these species may represent but two of many extremes of a single, plastic, species which, because of its ability to survive under unusually difficult conditions, often occurs as hardly recognizable forms. This is clear from the following history:

(1) BERGGREN (1875a) described the first binomial in this complex as a species of *Sarcoscyphus* (= *Marsupella*). MÜLLER (1915, in 1905–16, p. 424) stated that this plant was apparently "near" *Marsupella sullivantii* and that LINDBERG was incorrect in considering it a form of *Scapania irrigua*; later (l. c., p. 740) he stated that in all probability *Sarcoscyphus obcordatus* should be placed as a synonym of *M. sullivantii*. In MÜLLER (1951–58, p. 777) the plant is in turn placed, with a question mark, into the synonymy of *M. sphacelata*! (2) The second binomial described in the complex was *Jungermannia globulifera* JENSEN (1906, p. 306, with 2 good figures); JENSEN implied an affinity to *Lophozia alpestris*. MÜLLER (1910, p. 685, in 1905–16), noting that *J. globulifera* was pre-occupied, gave it the new name "*Lophozia jenseni*", but stated that it would be necessary to find perianths before one could decide whether the plant is a *Lophozia* or a *Scapania*; he correctly noted a similarity to *S. lapponica*. The species reappears in FRYE & CLARK (1937–47, p. 357) as "*L. jenseni*". (3) The third binomial described in the complex was *Martinellia lapponica*, by ARNELL & JENSEN (1907, p. 93, fig. 6), which they stated was similar to a minute form of *L. alpestris* and which appeared to be intermediate between *Jungermannia* (*Lophozia*, in our sense) and *Scapania* (= *Martinellia*). MÜLLER (1915, in 1905–16, p. 419) "confirmed" the possibility, admitted by ARNELL & JENSEN, that the plant is not a *Scapania*, and assumed it was a *Lophozia* subg. *Leiocolea*. This opinion is reiterated in 1947, in a special, illustrated account of the species. BUCH (1928) believed it might be a juvenile of the sect. *Irriguae* of *Scapania* and MÜLLER (1956, in 1951–58) later tentatively placed the species in the *Irriguae*.

It is thus clear that taxa which we would assign to *Jensenia* have been attributed to (or to the vicinity of) the genera *Marsupella*, *Lophozia* subg. *Lophozia*, *Lophozia* subg. *Orthocaulis*, *Lophozia* subg. *Leiocolea*, and *Scapania* sect. *Irriguae*—in other words, to taxa belonging in three different families. The situation, taxonomically, stood at this point when the senior author first became familiar with the species in Ellesmere Island in 1955, and in northwest Greenland in the summer of 1960, when he found material that seemed to belong to a species of *Scapania* of the sect. *Curtae*, perhaps allied to *S. scandica*. The combination of relatively narrow leaf lobes, local reddish pigmentation, non-marginate leaves, and, typically, rounded ventral lobes was suggestive of *S. scandica*, especially when weak plants were examined. Plants with young perianths clearly agreed with those of the *Curtae* in the wide mouth, with the edentate to subdenticulate mouth ± compressed. Not having yet seen the paper by ARNELL & MÅRTENSSON (1959), he believed a new species of the *Curtae* was at hand—*S. obcordata* being "lost" in *Marsupella*, "*Lophozia*" *jenseni* being lost in *Lophozia*, *Scapania* "*lapponica*" being placed alternatively in the *Irriguae* of *Scapania* or into *Leiocolea*—and named the plant *S. perssonii* in manu-

script. In 1955 one of us (RMS) had collected a plant of the same complex in northern Ellesmere Island and had (1959) referred this provisionally to *S. lapponica*. No similarity between *S. lapponica* and the West Greenland plant was then assumed since the first "looked" *Lophozioid*, the second was clearly closer to *Scapania* sect. *Curtae* in aspect. As will be shown, juvenile phases of this entire complex nearly always look *Lophozioid*; mature plants acquire a *Scapanioid* aspect. Much of the difficulty with which this admittedly refractory complex has been invested resides in this simple fact. A solution to this problem did not really become apparent until one of us (KD) made massive collections at the type locality of "*Lophozia jenseni*". Plants with clearly *Scapanioid* perianths and androecia were then found; admixed were juvenile plants with equally or subequally bilobed, nonconduplicate "*Lophozioid*" leaves. Furthermore, cultivated material formed a mod. *viridis-laxifolia*, totally *Lophozioid* in aspect, except for the almost transverse orientation of the shallowly concave, nonconduplicate, symmetrically bilobed leaves. Thus with study of abundant fertile material, placing of at least *L. jenseni* into *Scapania*, in the vicinity of *S. obcordata*, became feasible and part of the interlocked series of mysteries was resolved.

However, other problems remained. An immediate question was: What are the affinities of *S. obcordata*, *S. lapponica*, *L. jenseni*? As will be developed, we were able to show that the last is undoubtedly very close, if not identical, to *S. obcordata*. In the following pages we shall attempt to show that there is no sound basis for recognizing more than a single species in this entire complex, for which the correct name is *S. obcordata* (BERGGR.) S. ARN., with the following taxa as synonyms: *L. jenseni* MÜLL., *Jungermannia globulifera* JENS., *Martinellia lapponica* ARN. & JENSEN. Since the plasticity of this protean species is such that the best Hepaticologists of the 19th and early 20th centuries misunderstood the plant, and since its variability is so great that it has been a source of confusion for almost a century, the following detailed treatment is offered in the hope that finally some of the leading problems inherent in this species can be resolved. What we have not been able to resolve is (a) whether more than one genetically distinct form is involved; (b) how much of the obvious variability in all features is due to environment, how much is genetic. The species often occurs on irrigated sand near active glaciers, under exceptionally difficult conditions; the often "juvenile" facies appears to reflect its inability to attain a recognizable *Scapanioid* aspect. The question naturally arises: Is the subg. *Jensenia* S. ARNELL (1956, pp. 173, 309) valid?

Diagnostic for the subgenus are not only the unkeeled leaves, but the (a) tendency for the leaf lobe cells below gemmiparous regions to become mammillate (which is equally distinct in the topotypic material of "*J.*

globulifera" from E. Greenland); (b) gynoecial bracts—one or both—often somewhat smaller than the leaves below, often one or both suberect and rather sheathing, hardly *Scapanioid*; (c) delicate, ovoid, 2-celled gemmae, pale green to, in part, violet-tinged; (d) tendency for basal leaf cells to be notably larger and sometimes rather gibbous; (e) undefined cortical cells, in cross section—at most 1 stratum being thick-walled; (f) strongly saccate and often rather reduced, often deep-pigmented and ± vinaceous or purple-brown ♂ bracts, each with 1(2) antheridia; (g) perianth at best moderately *Scapanioid*, not strongly compressed, even distally (section elliptical to near mouth), the moderately wide and ± truncate apex with usually a shallow, long or short dorsal furrow; (h) frequent occurrence of furcate terminal branching of the *Radula* type, i.e., from the basiscopic end of a segment, below a normal leaf. [Branching of this type is rare and sporadic elsewhere in *Scapania*. In *Jensenia* it occurs in the type of *S. obcordata* (Nord Kap, BERGGREN) and other BERGGREN collections e.g., Green Harbour (BERGGREN 1868); also common in the Disko collection from Kugssuaq (*S. paradoxa ramosa*, PORSILD 742), in material from Advent Bay, Longyearbyen, Spitsbergen (ARNELL & MÅRTENSSON, 1959), and in the type of *S. lapponica*, from the Sarekgebiet. Also in DAMSHOLT's specimens from Angmagssalik (KD 69–142, etc.). After studying the types of all these plants, we are convinced that no good species distinctions within this complex are possible].

Although *Jensenia* was once confused with *Lophozia*, only the weakest shoots, and, in particular, innovations are clearly *Lophozioid* in aspect. Mature plants—especially gynoecial ones—leave no doubt as to its true affinity.

Scapania (*Jensenia*) *obcordata* (BERGGR.) S. ARN.

Distribution (Map 46)

1A: Behind Arctic Station (70–2030). 26: Pâkitsup ilordlia (70–2386a). 30: Eqe (66–0329). 45: Sagdliaruseq (66–1074a).

Additional collections:

26: Pâkitsup ilordlia (S.B. 1870). 45: Sagdliaruseq (K.H. 14.597, 15.598, 16.754, 16.971). 90: Tasiussaq (S.B. 1870). 112: Umiartorfik (K.J.604). 122: South of Eqaluit (K.H. 13.336c). 124: Tasíngortaq (K.H. 13.311).

This hardly definable species—or rather complex of phenotypes gathered up under this name—includes a series of plants found in difficult sites (sandy areas, where sand accumulation is a problem; areas where periodic silting may occur; late snow areas), most of which are characterized by periodic irrigation. Often associated are taxa which also survive such sites, especially *Anthelia juratzkana*. At Eqe (66–0329) plants occurred over fine, wind-blown, barely damp sand, perhaps one mile from the In-

land Ice; associated were extreme forms of *Gymnomitrion corallioides*, *G. apiculatum*, *Prasanthus suecicus*, and a trace of a very compact phase of *Lophozia excisa*.

S. obcordata, if it is indeed a single, widely defined species, is here taken (following SCHUSTER, 1974) to include *J. globulifera* JENS. (= *L. jenseni* K. MÜLL.), *L. violascens* BRYHN & KAAL., and *S. lapponica* (ARN. & JENS.) STEPH. It shows an almost incomprehensible range of variability, from small, *Lophozioid* plants to those which are clearly *Scapania*-like. All of the various phenetic expressions gathered together as *S. obcordata* agree in: (1) freely developing *Radula*-type branching; (2) representing rather small plants; (3) presence of a rather thin cortex, either of hardly differentiated cells, or cells thick-walled in 1(2)-strata. [The stem anatomy, like everything else, is distressingly variable. In most phenotypes seen the cortex is either hardly distinct, or a yellowish, 1-layered cortex of thicker-walled, smaller cells is present. In some plants from the Angmagssalik District (KD 69–141), however, the cortex is (1)2-stratose and unusually well defined. In *S. obcordata* we find that the ventral portion of the stem medulla usually becomes mycorrhizal with age (as, e.g. in 70–2386a, and in KD 69–142), but in plants from the same locality (KD 69–141) the medullary infection is slight or nonexistent]; (4) leaves that, aside from gemma-stalk cells, lack dentition of the lobes and normally have rounded ventral lobes (dentition of the leaves near gemmiparous regions may, sporadically, be present; thus in KD 69–140 scattered 1-and rarely even 2-celled teeth of the dorsal lobe are present on leaves adjoining the gemmiparous zones); (5) usual presence of reddish to violet to purplish pigmentation which may be variously mixed with brownish pigments, especially of the distal portions of the leaf lobes; (6) dorsal lobes averaging at least two-thirds the ventral in size [this criterion—like all others—is subject to variation; in 70–2386a, for example, although most plants have dorsal lobes 0.65–0.75 (0.8) the ventral in area, here and there reduced dorsal lobes, only 0.45–0.55 the ventral in size occur].

In addition to the variability discussed above, the various collections of *S. obcordata* studied show other, often distressingly complex patterns of variation, which cast doubt upon the very value of the subg. *Jensenia*. (1) Vigorous plants show a distinct, sharp keel at least in the distal 0.2 of the keel (SCHUSTER, 1974). The keels may be formed locally of 3–5 cell-strata. In all but juvenile, *Lophozioid* plants, the basal portion of the keel is rounded and 2(3)-stratose, much as is "normal" for *S. lingulata s.l.* Thus, on vigorous plants, the keel is unistratose only in the median sector. (2) The stem cortex, although not or hardly differentiated in the leptodermous "*lapponica*" extreme frequently may be reasonably distinct even in plants referable to "*lapponica*" (e.g., material leg. S. ARNELL, Härjedalen, Sweden), although thick-walled in only one stratum. In

vigorous plants, as of KD 69–141, we may find, dorsally and laterally, a 2-stratose cortex developed. (3) Leaf lobes, although mammillose with gemma formation in the "*lapponica*" extreme, frequently may undergo severe reduction, with formation of triangular, large-celled, *Scapaniella*-like or *S. scandica*-like abbreviated lobes that fail to show mammillose cells. (4) Branching, although usually of the *Radula* type, may occasionally be of the terminal, *Frullania* type. (5) Androecial plants may be slender, strongly pigmented, with monandrous or 1–2-androus bracts; large, *Scapanioid* ♂ plants, with hardly differentiated and not especially pigmented ♂ bracts may occur in the same population (often all ♂ plants seen are of the "undifferentiated" type. Thus in 70–2386a isolated ♂ bracts, preceded and followed by vegetative leaves, may occur; these may bear a single, usually deeply purplish, antheridium). (6) Spores in *S. obcordata* from the type region are "remarkably large ..... 18–20 μ in diameter" (ARNELL & MÅRTENSSON, 1959); in KD 69–142 we have seen spores, from two capsules, which range from 11–12.5 μ. (7) The perianth mouth, although usually merely repand-sinuate to repand-lobulate, varying to entire, may be lobulate-dentate or dentate with 1–3(4)-celled teeth.

As earlier mentioned, perhaps the problem is that basically we are dealing with a complex which, responding to phenomenally difficult environmental conditions, survives only because of its ability to retain an exceptionally high level of phenetic response.

It is quite possible that we have tried to "force" too wide a range of phenotypes into *S. obcordata*: it is not impossible that a series of poorly delimited microspecies exists here. Phenetic variability, however, is so enormous that any genotypic diversity is effectively masked. We have spent (summers 1960, 1966, 1970, in Greenland) literally weeks puzzling about this complex; it has been attacked again in the laboratory. At this point, no more definitive appraisal of the complex seems possible. Indeed, we are not fully convinced that the much larger *S. paradoxa* can always be kept separate from the usually small *S. obcordata*. In effect, the concept of *S. obcordata*, now, is that of a receptacle into which the residium of ill-defined, small phenotypes, which cannot be "forced" into the *Curtae* nor seem to belong elsewhere, are placed. Reasonably constant are only (a) the always demonstrable terminal branching; (b) lack of dentition of the leaves away from gemmiparous zones; (c) rounded ventral leaf lobes but usually bluntly to sharply pointed dorsal lobes; (d) non-margined leaves; (e) oil-bodies normally (2)3–6(7) per lobe cell; (f) gemmae, when produced in exposed loci, tending to be small (under $17 \times 25\ \mu$, usually), often spherical to short-ovoid and under 1.5 × as long as wide.

This distinction, in particular, seems important in separating *S. obcordata* from *S. perssonii*. In the former, pigmented gemmae, produced

where exposed, are always broad and short, never fusiform; in the latter, even in highly pigmented plants from the most exposed niches (at Kânâk), the gemmae are ellipsoidal to ellipsoidal-fusiform, averaging 2 × as long as wide, or occasionally longer, and range to 16–19 (22) × 30–35 (39) μ. It is important that the smaller (and presumably immature) gemmae be neglected in these measurements; to include these can lead only to misunderstanding. Also, in the large, *Scapanioid* plants of *S. obcordata*, with complanate leaves, we occasionally find thin-walled, colorless, large and ellipsoidal gemmae produced; these are formed in plants of the same phenotype, growing intermingled with smaller, "*Lophozioid*" plants with "normal" (broad, small), pigmented gemmae.

Scapania perssonii SCHUST.

Carinis foliorum paulum manifestis, pigmentis saepe rubentibus subgeneri *Jenseniae* similis; lobi ventrales foliorum plus minus assidue apiculati, integerrimi nisi gemmipari; corpuscula oleifera in quaque cellula (5)6–10(13); cellulae marginales circiter 20–23μm diam. vel ultra; ostium perianthii subintegerrimum vel denticulatum.

Distribution (Map 46)

10: Enoks Havn (70–2763a). 26: Pâkitsup ilordlia (70–2256a). 30: Eqe (66–0293e). 36: Umanak (66–1478).

The few collections from West Greenland placed here give no clear idea of their ecology and associates. In 70–2256a *S. mucronata* ssp. *praetervisa* is intimately admixed. Plants of 70 2763a occurred on the slope of a river terrace, with *Salix herbacea*, associated with *Cephalozia bicuspidata*, *C. pleniceps*, *Nardia geoscyphus*, and *Anthelia juratzkana*; here the plants were on fine mineral soil, water-deposited, in sites where seasonal flooding may occur. Like *S. obcordata*—from which we are still not certain it is always distinct—it is evidently a plant of very difficult sites. In Kânâk, where apparently common, it is usually in small quantity in extreme loci: fine, silty soil, where subject to inundation by melt water from adjacent ice caps, and similar "unattractive" pioneer sites.

This controversial plant occupies in some respects a difficult midground between *S. obcordata* and *S. lingulata* v. *microphylla*, and can be confused with both taxa. Its primary criteria include (a) vinaceous color of the ventral leaf bases in all but extreme shade forms; (b) large, rather hyaline cells with usually 6–12, rarely even to 15 oil-bodies each; (c) ability to develop only a moderate amount of collenchyma and only a rather delicately roughened cuticle; (d) a sinuous to sinuous-lobulate, subentire perianth mouth, or with remote to rare, 1–2-celled teeth; (e) leaves showing much variability, even in one population, in width of the lobes, especially of the dorsal lobes which may range (on weak plants) from 0.4–0.5 (the length) up to (vigorous shoots) 0.75–0.85 (the length);

(f) dorsal lobes, except on weakest shoots, where under 0.65 the ventral in size, usually 0.65–0.75(0.8) the ventral in area; (g) dorsal lobes at least bluntly pointed, often sharply so, and ventral lobes which are ovate (but not or exceptionally obovate-lingulate), mostly blunt to ± apiculate; (h) the dorsal lobes, and less so the ventral ones, showing a marked tendency, especially near gemmiparous zones but occasionally remote from them, to develop a few small, rarely coarse, teeth; (i) elliptical, light green to rose-red or vinaceous (in sun), large gemmae—the larger always 16–19(22) × (25)30–35(39) μ.

As demonstrated under *S. obcordata*, larger phenotypes of that species have a *Scapanioid* aspect resembling that of *S. perssonii*; they may also show similar pigmentation and cells of similar size; they also tend to develop only small or medium-sized, rarely distinctly bulging, trigones and have a smooth to finely verruculose cuticle; they also have a subentire perianth mouth and, finally, leaves with the dorsal lobes mostly at least 0.65 the ventral in area. One is tempted, on that basis, to equate *S. obcordata* with *S. perssonii* and we have repeatedly attempted to unite them. *S. obcordata*, however, seems distinct from *S. perssonii* in criteria b [oil-bodies are only 2–6(7) per cell usually], g [the ventral lobes are rather consistently rounded], h [except adjoining or in gemmiparous zones, leaves are constantly edentate], and i [gemmae are usually broader and shorter and are 12–17(19) × 12–25(29) μ, with the majority well below 14 × 25 μ]. These four criteria seem important enough to warrant segregation of *S. perssonii*. Two final, subtle criteria may be of significance: (1) In *S. perssonii* no plants are ever "*Lophozioid*", and on the weaker stems we find leaves that have narrow lobes, with the dorsal lobes relatively small at times. (2) Perianths—all juvenile and unfertilized—have large, widely spreading bracts (in *S. obcordata* often smaller, sheathing).

Separation from *S. lingulata* is, at times, almost as difficult. With this *S. perssonii* agrees in the large gemmae and their mostly slender form; the vinaceous color of the leaf bases (of var. *microphylla*); the proclivity to tooth formation (although in *S. lingulata microphylla* teeth tend to become both sharper and much more numerous, especially with gemma formation); the generally apiculate or variously pointed ventral leaf lobes; rather large cells; consistently "*Scapanioid*" aspect, even of smaller plants. It is clear, however, that two well-separated taxa are at hand since *S. lingulata* normally has (a) coarser trigones and a much more distinctly papillose cuticle; (b) usually freer and sharper dentition of leaves, especially with gemma formation; (c) a distinctly, closely ciliate-dentate to dentate perianth mouth; (d) a shorter keel and, on mature leaves, smaller dorsal lobes [the distinctions are obvious if one compares plants growing in the same locality (Qissugssalik, 70–2256a and 70–2255).

In the first cells are somewhat larger, essentially smooth, hyaline, with concave-sided trigones, and with very limited dentition, the leaf lobes rarely sharp; these highly colored plants with subentire perianth mouths are clearly *S. perssonii*. By contrast, in 70–2255 plants were growing less exposed (mod. *viridis*), with slightly smaller cells which are rather opaque owing to the densely papillose cuticle, but trigones are coarse and bulging; dentition of the leaves is unusually sharp, even for *S. lingulata*, and copious, and leaf lobes are almost always quite sharp; these plants clearly represent *S. lingulata s.l.*, and because of the dentition they possibly should be referred to v. *microphylla*; in the absence of wall pigments they have been left in *S. lingulata s.l.*].

Critical in the evaluation of this taxon are the plants from Qissugssalik (70–2256a), which occur mixed with *S. mucronata praetervisa*. These plants have the combination of brown pigments of the leaves distally and violet to purplish pigments toward the ventral leaf bases that also occurs in some phenotypes we refer to *S. obcordata*. They often tend to be infuscated when these two pigments are intense. Some mature gemmae are vinaceous to purplish, only ca. $16 \times 25\ \mu$. The keel is ill developed and bluntly folded, only 2-stratose locally, although the bistratose area may be rather broad (not forming a sharp, well-defined keel). Plants of 66–1478 (Umanak) are very similar, except that reddish pigmentation is only local and weak. We have tried to "wedge" such plants into *S. obcordata* and (because of the large cells and purplish pigments of ventral leaf bases) into *S. lingulata* var. *microphylla*. The tendency for sporadic tooth formation, away from gemmiparous regions, suggests the latter taxon. The bluntly, rather remotely lobulate-dentate to repand-lobulate perianth apex, however, excludes *S. lingulata s.l.* (but not *S. obcordata*). *S. obcordata* is excluded by the apiculate to pointed ventral leaf lobes, the rather frequent lateral-intercalary branching (with no *Radula*-type branching visible), and the frequent, if sporadic, dentition away from gemmiparous zones.

Admittedly, juvenile plants and those from difficult sites will remain almost impossible to place at times. Thus, at the northern edge of the range of *S. perssonii*, in the Kânâk region, plants are generally highly colored but so poorly developed that a decision to place them under *S. perssonii vs. obcordata* is almost impossible to carry out. For example, in RMS 46154a the plants are small, compact, with almost unkeeled leaves—although a *Scapanioid* aspect persists; they are so malformed in aspect that certain placement is almost impossible and is made essentially on three tenuous bases: (a) the larger gemmae exceed $16–17 \times 32\ \mu$; (b) other, more "normal" plants from the area have even larger gemmae and tend to develop isolated teeth of the leaves; (c) some ventral lobes

are pointed—although many are erose and malformed with gemma formation. Placement of such extremes of such difficult sites is almost impossible.

There are differences between the plants from Kânâk and vicinity, assigned to *S. perssonii*, and those above from West Greenland; these emerge from the following key:

a. Perianth mouth (juvenile) mostly subentire or remotely dentate with 1–2-celled teeth; ventral lobes usually apiculate or at least bluntly pointed; dorsal lobes often apiculate with a 2-celled tooth; leaves rather frequently tending to develop 1-several accessory teeth. Leaves usually clearly, rather sharply folded.

West Greenland phenotype (70–2763a, 70–2256a).

a. Perianth mouth (juvenile) with ± close, 1–3(4)-celled teeth; ventral lobes usually blunt to rounded, except on weak leaves (where ± apiculate); dorsal lobe apiculum not 2-celled; accessory teeth of leaves, not associated with gemma fascicles, rare or absent. Leaves most often concave, vertical, hardly conduplicate.

Northwest Greenland (Kânâk) phenotype (RMS 46159, 46154a, etc.).

The color of the latter is usually extraordinarily vivid: the reds are much more intensely developed, especially at the shoot apices. The plants "look" different—although this is almost impossible to express in words. In the paucity of any dentition, in the tendency for the ventral lobes to be rounded or blunt, rarely sharp, and in the lack of a sharply developed dorsal lobe apiculum, these plants suggest *S. obcordata*, but differ in the much larger average gemma size, in the spreading ♀ bracts, and in the more closely dentate perianth mouth.

Scapania (*Jensenia*) *paradoxa* Schust. *sp. nov.* (Fig. 13:11–13)

Ramis radulaceis saepe formatis *S. obcordatae* similis, statura multo validiore ab ea diversa; laete viridis praeter lobos foliorum apice saturate purpureos vel fusco-purpureos, bases foliorum ventre colore carentes.

Distribution (Map 46)

12: Perdlertut (70–2694). 18: Grønne Ejland (70–2811, 70–2813). 25: Sarfaq (70–2334a, 70–2362, 70–2374). 37: Agpat (66–1464).

Additional collections:

84: Qeqertasugssuk (L.H. Aug. 1932). 90: Tasiussaq (S.B. 1870). 106: Nûgssuaq (K.H. July 1956).

Type. 25: Sarfaq (70–2374) with *Scapania mucronata praetervisa*, *Lophozia polaris*, and *Cephalozia pleniceps*.

Known only from a few collections; all are from "difficult" sites. The type grew on sandy-silty ground near a small rill; the plants from Perdlertut grew with *L. wenzelii* and *L. excisa*.

S. paradoxa is a soft-textured plant, abundantly provided with *Radula*-type branching. It is succulent and typically grows on fine, silty ground, probably where occasionally submerged (as at Sarfaq). The plants from Grønne Ejland, however, grew, with *S. mucronata praetervisa*, on steep, hanging, soil-covered cliffs and ledges, where probably somewhat manured by birdlime leachings.

Type plants were green except for weak brownish pigmentation of older stem sectors and leaf lobes near and in the distal, gemmiparous zones, which were intensely violet-pigmented. In these plants, as well as all others of the species seen, pigment initiation starts in marginal portions of the leaf lobes; the leaf bases are normally all devoid of cell wall pigments and diagnostically whitish green. As a result of growth under conditions of repeated silting, the plants are often straggly and rather ill developed. Gemmae are freely produced, range from light green to violet-red or red, and are mostly broad-ovoid (19×20 to 19×21.5 to 24–28.5 μ), but a few are elliptical (to 16.5×31 μ).

The plants from Disko, although more abundant, in part more "typically" *Scapanioid* in development, deviate sufficiently so that one might doubt their conspecificity with the Sarfaq material. They differ in having upper leaf lobes a dull fuscous-pigmented (or, at times, bear some purplish pigment with the fuscous); they have almost wholly elliptical to narrowly ovoid gemmae, mostly 16–19(20)×31–36 μ, some ovoid and 21–22×28–30 μ; leaves are less variable and give the impression of exhibiting less malformation, and are usually less bifid (keel 0.6–0.7 length of ventral lobe); the gemmiparous leaves fail to show the mammillate, gibbous cells of the lobe margins. Until the significance of vinaceous vs. fuscous pigment production is known, it seems best to de-emphasize this. In any event, the rather intensely fuscous or more intensely violet pigmentation of upper portions of upper leaves is quite diagnostic. So are the enormous masses of light green, very large gemmae, with a few older ones always vinaceous.

An additional collection is from damp soil over cliffs on Grønne Ejland (70–2811). These plants (in part androecial) are critical in that they are mixed with fertile, perianth-bearing individuals of *S. mucronata* cf. ssp. *praetervisa*. The two taxa are distinct at both macroscopic and microscopic levels, and plants of the two may be intimately admixed; the distinctions (drawn from admixed individuals) follow:

S. paradoxa	*S. mucronata praetervisa*
Often vigorous, to 2.5 mm wide.	Plants usually to 1.8 mm wide.
Gemmae masses large, greenish (a few gemmae dull purple or brownish with age).	Gemmae masses much smaller, the older gemmae bright reddish.
Leaves away from gemmiparous zones with ventral (and sometimes dorsal) lobes narrowly rounded to blunt.	Ventral lobes at least weakly mucronate, dorsal lobes always sharp.
Gemmae to 19–20×27–30μ to 16×31μ.	Gemmae to 13–14×24–25μ.
Leaves near gemmiparous zones often locally purplish, sometimes very intensely so, plants otherwise dull fuscous brown tinted, where not green.	Never with purplish pigmentation: aside from gemmae, which are pink at maturity, only brown pigments produced.
Leaf margins with gemma formation never sharply dentate on margins, but abaxial lobe apices often mammillate or even appendiculate.	Leaf margins with gemma formation often with sharp, scattered marginal teeth; never with lamella or spines of abaxial lobe tips.
Cell size grossly variable (see below); many plants large-celled and with 5–9 oil-bodies per lobe cell; ventral marginal cells often 20–25μ.	Cells uniformly small, marginal cells on middle of ventral margin only (14)15–19μ, with (2)3–6 large oil-bodies in lobe cells.
Radula-type branching common.	No *Radula*-type branching.

Ironically, in spite of the fact that it is obvious from the first two criteria cited that two obviously distinct taxa are at hand (the color of the gemma masses at once affords a conspicuous distinction), both taxa are so variable in their microscopic characters that a distinction between individual plants is often almost impossible to effect. The malleability of *S. paradoxa* is so phenomenal that it can hardly be readily defined in rigid terms. The combination of local, intense purplish coloration and at least occasionally broadly rounded ventral (and, more rarely, dorsal) lobe apices on mature nongemmiparous leaves, however, is diagnostic. Admittedly, with copious gemma production, finding such leaves is often difficult.

Because of the leaf form, the large cells, the large green gemmae (which may be vinaceous with age), and the many oil-bodies per cell, *S. paradoxa* is apt to be confused with robust phases of *S. perssonii*. *S. paradoxa*, however, is either strongly vinaceous or fuscous-tinted on distal portions of upper leaves, whereas basal sectors of the leaves and ventral faces of the stem are nearly uniformly devoid of vinaceous or reddish pigments. In *S. perssonii*, by contrast, distal portions of leaves, if pigmented at all, are mostly a light warm brownish or golden-brown pigmented, and some, most, or all upper leaves have vinaceous bases,

the pigment spreading from the ventral stem faces to the leaf bases. Also, in *S. perssonii*, *Radula*-type branches, although occasionally present, are usually rare.

S. paradoxa shows bewildering variation, with the two most obvious extremes separable as follows:

Key to varieties of *Scapania paradoxa*

1. Cells with (5–6) 7–10 (12) oil-bodies in free lobe cells; gemmae large, 19–21.5×20–28.5 up to 16.5–24×31 μ; cells relatively large, on vigorous leaves marginal cells 18–25 (29) μ. v. *paradoxa* (see above)

1. Cells with (1)2–4 (5–6) oil-bodies in free lobe cells; gemmae small, ovoid, 13×16 to 12–14×16–23 μ; cells smaller usually, on vigorous leaves marginal cells 14–21 (23) μ. v. *ramosa*

v. *ramosa* SCHUST. *var. nov.* (Fig. 13:1–10)

A var. *paradoxa* corpusculis oleiferis paucioribus (in quaque cellula plerumque 1–5), cellulis foliorum minoribus imprimis diversa. Rami *radulacei* numerosi, saepe erecti.

Distribution (Map 46)

1A: Behind Arctic Station (66–0285). 14: Hareøen (70–2602).

Additional collection:

60: Kugssuaq (M.P.P. 742, 746).

Type. 14: Hareøen (70–2602).

The type occurred on clayey soil between rocks in a late snow area, on an east-facing slope, just recently free of snow.

Var. *ramosa* has been given its name because of the extremely copious branching, mostly of the *Radula* type. Typically even the shoot tips, when dissected free, show rudiments of such branches initiated posterior to the keel insertion. Indeed, a single season's growth will normally produce 2–3 such terminal branches as well as 1–2 or more lateral-intercalary ones. The PORSILD specimens (742, 746) are, if anything, even more copiously and fastigiately branched than the type; they have branches usually stiffly erect, juxtaposed, and of *Radula*-type origin; however, one *Frullania*-type branch has been seen. These collections had marginal cells at the lower end of the spectrum: 15–18 μ; gemmae ranged from 12–14×21–23 μ. The plants showed the usual purplish to fuscous-purple pigmentation on and near gemmiparous leaves—initially on the lobes and not attaining the leaf bases. One plant, however, showed slight vinaceous red pigmentation of some postical leaf bases—a pigmentation otherwise not known for *S. paradoxa* as a whole.

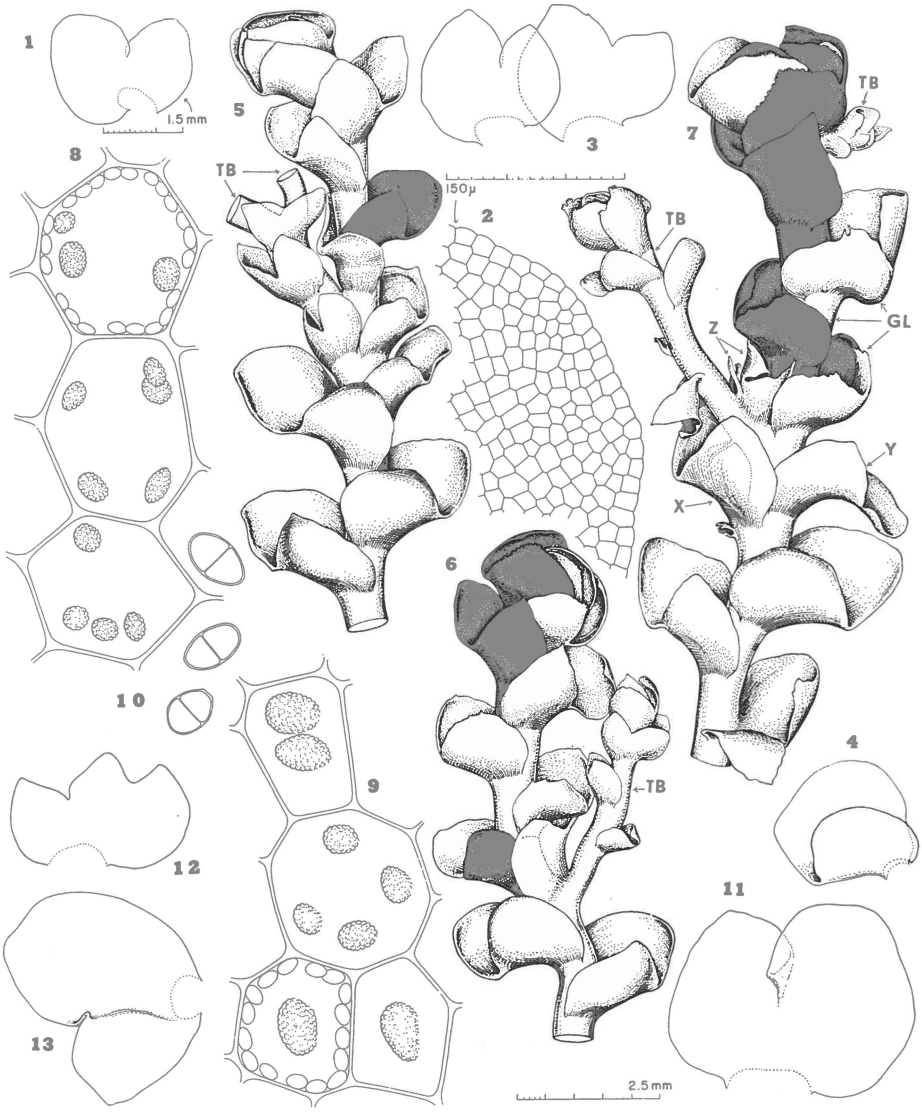


Fig. 13. *Scapania paradoxa.* (1–10) v. *ramosa;* (11–13) v. *paradoxa.* (1) Small leaf (×7). (2) Cells of apex of ventral lobe in fig. 1 (×155). (3–4) Leaves (×7.5). (5) Shoot with terminal branch bifurcate (at TB) (×7.5). (6) Shoot with *Radula*-type terminal branch at TB (×7.5). (7) Ramified shoot: at TB, *Radula*-type terminal branches; X, Y, Z, leaves, with a dormant branch associated with leaf X and a nondormant branch associated with leaf Z, the latter highly modified and abnormal; note modified gemmiparous leaves at GL (×7.5). (8) Cells of lobe middle, with oil-bodies and, above, chloroplasts (×770). (9) Cells with oil-bodies, showing isolated cells with solitary oil-bodies (×930). (10) Gemmae (×405). (11, 13) Normal leaves (×7.5). (12) Abnormal, trilobed leaves (×7.5). [1–10, type of v. *ramosa*, from Hareøen; 11–13, type of *S. paradoxa;* 1, drawn to 1.5 mm scale; 2, drawn to 150 μ scale; 3–7, 11–13, drawn to 2.5 mm scale].

This variety may possibly prove to merit the rank of an autonomous species, when better material becomes available. The few oil-bodies per cell (it is, *S. gymnostomophila* aside, the only known *Scapania* with a high incidence of cells containing single oil-bodies) and the considerably smaller gemmae suggest an autonomous species may be involved. As is shown under var. *paradoxa*, however, the species as a whole is so plastic that a "conservative" approach to species delimitation surely seems best.

As with var. *paradoxa*, which often occurs on sandy soil apparently washed in by melting snow water, the var. *ramosa* occurs under difficult conditions. The type of var. *paradoxa*, indeed, gives the impression of having grown on damp sand; with each year the plant is almost covered by an annual increment of new sand washed in—so that the plant has to make a valiant effort to keep from being buried. With var. *ramosa* we deal with hazards of a rather different type: the plant occurs in a late-snow area, just free of snow (on Aug. 5), together with *Salix herbacea*, on wet, clayey soil which probably is deposited in layers each year so that plants occur semisurrounded by clay.

Subg. ***Kaalaasia*** BUCH emend. SCHUST.

Scapania (*Kaalaasia*) *gymnostomophila* KAAL.

Distribution (Map 47)

1A: Behind Arctic Station (66-0152, 66-0169, 66-0171, 66-0277, 66-0282a, 70-2057a, 70-2182). 1C: Blæsedalen (66-0303). 1D: Skarvefjeld (66-0298, 66-0316a, 66-0317b, 66-0320a). 6: Eqalúnguit (70-2211). 8: Kuánerssuit (70-2126, 70-2153a, 70-2155). 12: Perdlertut (70-2670b, 70-2671a, 70-2673, 70-2676, 70-2685). 30: Eqe (66-0289, 66-0295). 31: Anap nunâ (70-2406a, 70-2417, 70-2430). 34: Marrait kangigdlît (66-0726b). 35: Hollænderbugt (66-1505b). 38: Uvkusigssat (66-1387, 66-1388, 66-1392). 39: Tasiussaq (66-1262). 40: Mârmorilik, head of the Fjord (66-1199, 66-1205). 42: Magdlak (66-1353, 66-1357b, 66-1372). 43: Kangerdlugssuakavsak (66-1280, 66-1281, 66-1283b). 45: Sagdliaruseq (66-1079). 50: Simiútap kûa, valley (66-0862a). 51: Simiútap kûa, shore (66-0916c, 66-0917a). 53: Søndre Strømfjord (66-0046, 70-3216).

Additional collections:

95: Pâkitsoq (K.H. & G.M. 71-1930). 100: Ipeqarfiunge (L.H. July 1932). 110: Ikorfat (K.H. 62.1567a). 127: Kangersôq (K.J. 1089a). 132: Akuliarusikavsak (K.H. 13.764). 143: Kangerdlugssuaq (K.H. 16.397a).

A strict basiphyte, found as far north as there is land (to 83°06′N. in Peary Land; to 82°32′N. in Ellesmere Island; SCHUSTER, 1974). It is imperfectly circumarctic and alpine in range, occurring in Eurasia from Spitsbergen and Siberia south to the French Pyrenees; in North America it is found southward, as a rare disjunct, to Vermont, Massachusetts, and Minnesota.

S. gymnostomophila is a common species in the basaltic areas around Disko Bugt and on Disko, although there are very few previously known stations from Greenland. It occurs at times in crevices of basaltic rocks particularly where shaded and protected, and permanently damp, then mostly with *Tritomaria scitula* (70–2417, 66–1357b) and less often also *Lophozia badensis*, *Solenostoma pumilum polaris*, *Plagiochila asplenioides*, *Athalamia*, *Sauteria*, *Preissia*, *Mannia pilosa*, and *S. cuspiduligera* (66–1357b) or *S. mucronata praetervisa* (70–2057a). It may also be found on basalt dikes with *Preissia* (66–0295). *S. gymnostomophila* is perhaps even more frequent on mineral soils derived from disintegration of basic rocks; here it is frequent in and around run-off crevices on steep, stony soil slopes, often associated with *S. ligulifolia* (70–2406a, 70–2671a, 66–1505b), *Tritomaria scitula*, *Arnellia*, *Lophozia heterocolpos*, *L. quadriloba glareosa*; in more permanently damp sites on such slopes these species, plus *S. cuspiduligera*, may be associated (70–2126) and the *S. gymnostomophila* is then developed to its optimal degree. Occasionally on basic soil between rocks, *T. scitula* is supplanted by *T. heterophylla* (66–1280, 66–1283b), with *S. mucronata praetervisa*, *Solenostoma pumilum*, and *Cephaloziella uncinata* as other associates. Finally, relatively exceptionally, when under ecologically advanced conditions on humus over basalt ledges, *S. brevicaulis* may be associated (66–0282a).

S. gymnostomophila is singularly unvariable locally; the f. *incurva* (Bryhn & Kaal.) Schust. of high Arctic sites, has not been encountered locally. Gemmae always occur, but sex organs are never found in local populations.

Scapania (*Kaalaasia*) *ligulifolia* Schust. (Fig. 14)

[syn.: *Scapania calcicola* (Arn. & Perss.) K. Müll. var. *ligulifolia* Schust. 1951].

Planta compacta satis carnosa, corpusculis oleiferis fuscis persistentibus, foliis integerrimis, gemmis fuscis, ostio perianthii incise lobulato ciliato-dentato *S. gymnostomophilae* similis, corpusculis oleiferis in quaque cellula 2–5, lobo dorsali folii plerumque 0.5–0.6 ventralis longitudinis, carina longiore, cellulis majoribus, gemmis multo majoribus ab ea diversa.

Distribution (Map 47)

1A: Behind Arctic Station (66–0148, 66–0171, 70–2057). 1C: Blæsedalen (66–0303). 1D: Skarvefjeld (66–0316a, 66–0317b). 12: Perdlertut (70–2670b, 70–2671a, 70–2672, 70–2685). 13: Jens Vahls Dal (70–2637c). 14: Hareøen (70–2582, 70–2592b, 70–2603, 70–2608). 29: Ritenbenk (66–0264). 31: Anap nunâ (70–2406). 35: Hollænderbugt (66–1503a, 66–1505). 47: Íngia (66–1033, 66–1034, 66–1035, 66–1032, 66–1036). 49: Skalø (66–1007, 66–1018). 50: Simiútap kûa, valley (66–0866).

Additional collections:

129: Avataussaligssuaq (K.J. 924). 143: Kangerdlugssuaq (K.H. 16.385).

The type of this distinctive species (Godhavn, 66–0148) grew in damp, basalt crevices and was provided with perianths, which also occur in 70–2670b and 66–1007. *S. ligulifolia* is known thus far only from the New World but may also occur in Arctic sites in Eurasia. It extends north to at least 82°26′ N. on the south coast of Independence Fjord [HOLMEN 7717; the Peary Land plants were all reported as *S. calcicola* by ARNELL (1960)] and is known from Inglefield Bredning (RMS 46.048a), where it is very rare, from Nathorst Land in East Greenland (HOLMEN 18.690), from Ungava Bay, Labrador Peninsula (Quebec), and the Belcher Islands in Hudson Bay (SCHUSTER, 1951). It is probably frequent in all basic regions of the high Arctic and is, seemingly, a consistently Arctic species, not found so far in southern Greenland.

S. ligulifolia may occur in damp crevices of fissured, weathered basalt, then (66–0171, 70–2406) often with *S. gymnostomophila*, sometimes also *Peltolepis grandis* (66–0316a). It is more common, however, along drainage crevices of intermittently desiccated, stony, clayey, steep, weathered slopes, where found with a diagnostic ensemble of associates: *Tritomaria scitula*, *Arnellia fennica*, *S. gymnostomophila*, *Lophozia quadriloba glareosa*, *L. heterocolpos harpanthoides*, *Blepharostoma trichophyllum brevirete*, more rarely small forms of *S. cuspiduligera* (66–1503a, 66–1505, 70–2637c), occasionally *L. pellucida*, and *L. polaris*. When on such basic slopes, under somewhat moister (and better vegetated) conditions, *S. cuspiduligera*, *B. trichophyllum brevirete*, *Solenostoma pumilum polaris*, *L. heterocolpos harpanthoides*, *L. quadriloba*, *L. grandiretis*, *L. gillmani*, *Tritomaria polita*, *T. quinquedentata* (less often *T. scitula*) are associated (70–2582, 70–2608, 70–2603, 70–2592b).

Although perianths (unfertilized gynoecia only!) occasionally occur, we have seen no ♂ plants. Cells always have (1)2–4(5) very large, brownish, persistent, opaque oil-bodies almost filling the lumen, except for a distinct, hyaline, "dead" region of the cells of the postical leaf base. The only noteworthy deviation occurred in 70–2406, in which gemmae were unusually small (mostly 12–14 × 20–28 μ); they range mostly up to 17–19 × 35–39 μ and may show nipple-like projections or angles (as in 66–1007). Perianths, in so far as they have been found, are all of the *S. gymnostomophila* type: strongly incised-lobulate, with the small acute lobes diagnostically dentate to ciliate-dentate on their flanks, and ending in terminal cilia, in part often arched or hooked.

This species serves to connect *S. calcicola* with *S. gymnostomophila*. At times gemmiparous, sterile plants are very hard to separate from *S. gymnostomophila*; both taxa tend to be deep green, with brown gemma masses; both have the ventral leaf bases characteristically decolorate. At times *S. gymnostomophila* has the dorsal lobes somewhat larger, fully 0.35–0.5 the ventral lobes in area, and may then acquire a *S. ligulifolia*-

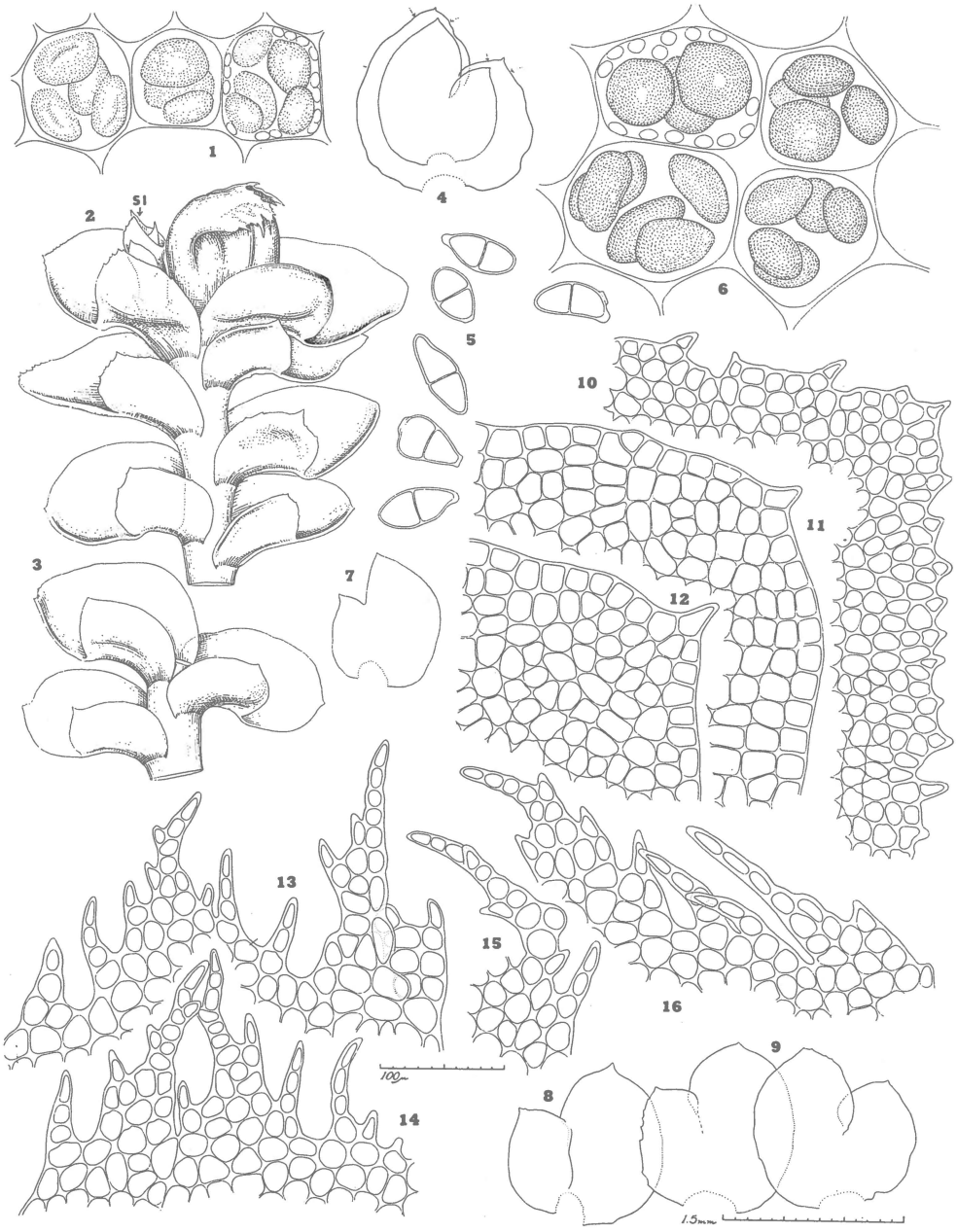


Fig. 14. *Scapania* (*Kaalaasia*) *ligulifolia*. (1) Cells with oil-bodies and, at right, chloroplasts (×615). (2) Shoot apex with young perianths; at SI a subfloral innovation (×20.5). (3) Sterile shoot sector, antical aspect (×20.5). (4) Two leaves, the larger an upper leaf from ♀ plant, the lobe tips of which are shown in figs. 11–12 (×16.5). (5) Gemmae (×310). (6) Cells with oil-bodies and, upper left, chloroplasts (×845). (7) Small leaf, sterile shoot (×16.5). (8) Leaf (×16.5). (9) Two ♀ bracts (×16.5). (10) Apex of lobe of ♀ bract (×168). (11–12) Ventral and dorsal lobe tips, respectively, from leaf in fig. 4 (×168). (13–16) Sectors of mouths from several immature perianths (×168). [1, 46048a, Kekertat, Inglefield Bredning, NW. Greenland; 2–6, 13–16, 66–0148 and 7–12, 66–0317, Godhavn; 4, 7–9, drawn to 1.5 mm scale; 10–16, drawn to 100 μ scale].

like aspect. The long-persistent brownish oil-bodies, however, afford a wholly unambiguous method of separating *S. ligulifolia* from *S. gymnostomophila*: in the former there are 2–4(5) oil-bodies per cell, in the latter 1 (in rare cells 2) per cell. Although oil-body criteria and gemma size suggest a close affinity between *S. ligulifolia* and *S. calcicola*, the two taxa appear to be wholly different in the perianth mouth. The incised, *S. gymnostomophila*-like perianth mouth of *S. ligulifolia* is very different from the unlobed and merely finely dentate perianth mouth of *S. calcicola*. Furthermore, we have never seen dentition of the leaf lobes, as shown by BUCH (1928, fig. XVIII:7) for *S. calcicola*, in any phase of *S. ligulifolia*—the latter, except associated with ♀ bracts, normally is quite edentate-margined, exactly like *S. gymnostomophila*.

Subg. ***Scapaniella*** (BUCH) JOERG., emend. SCHUST.

Scapania invisa SCHUST. (Fig. 15)

Planta parva, laete viridis, gemmis saturate fuscis; subgeneri *Scapaniellae* foliis plus minus manifesto marginatis lobis angustis similis, cellulis foliorum majoribus plura corpuscula oleifera continentibus ut gemmis majoribus semper bicellulis ab omnibus speciebus illius subgeneris diversa, ab omnibus speciebus illius subgeneris adhuc descriptis diversa.

Distribution (Map 49)

1A: Behind Arctic Station (66–0287a). 1B: Lyngmarken (70–2023). 12: Perdlertut (70–2675).

Type 1A: Behind Arctic Station (66–0287a). Mouth of Blæsedalen at Lyngmarksfjeld, in and near small ravine running into Rødeelv. Together with *S. hyperborea*, *Lophozia polaris*, and *L. heterocolpos*.

This species is known only from the above stations; it is probably more common than the few reports suggest. It seems to be an ecological specialist with narrow tolerations. The plant seems confined to basaltic cliffs, usually in sheltered sites, in places where humidity is high and usually near flowing water—hence it typically occurs in pockets of basaltic cliffs, often along small ravines. Associates are usually *S. cuspiduligera*, *Tritomaria scitula*, *Sauteria*, *Lophozia heterocolpos*, *L. polaris*, *Blepharostoma trichophyllum brevirete*, and (once; surprisingly) *S. hyperborea*.

S. invisa occurs only sterile but always has the diagnostic reddish brown to deep brown, 2-celled gemmae. Copious gemma production (as in 70–2675) may lead to development of serrulate dentition of the dorsal lobes, but leaves away from gemmiparous zones always show ± broadly rounded ventral lobes (and at most 1–3 minute, 1-celled denticulations of the dorsal lobes). Plants are usually a light, rather translucent green (gemmae aside); leaf cells have (5)6–9(10–12) oil-bodies each, separating *S. invisa* at a glance from any possible taxa that could be confused (*S. gymnostomophila*, *S. ligulifolia*, *S. mucronata praetervisa* and *S. brevicaulis*).

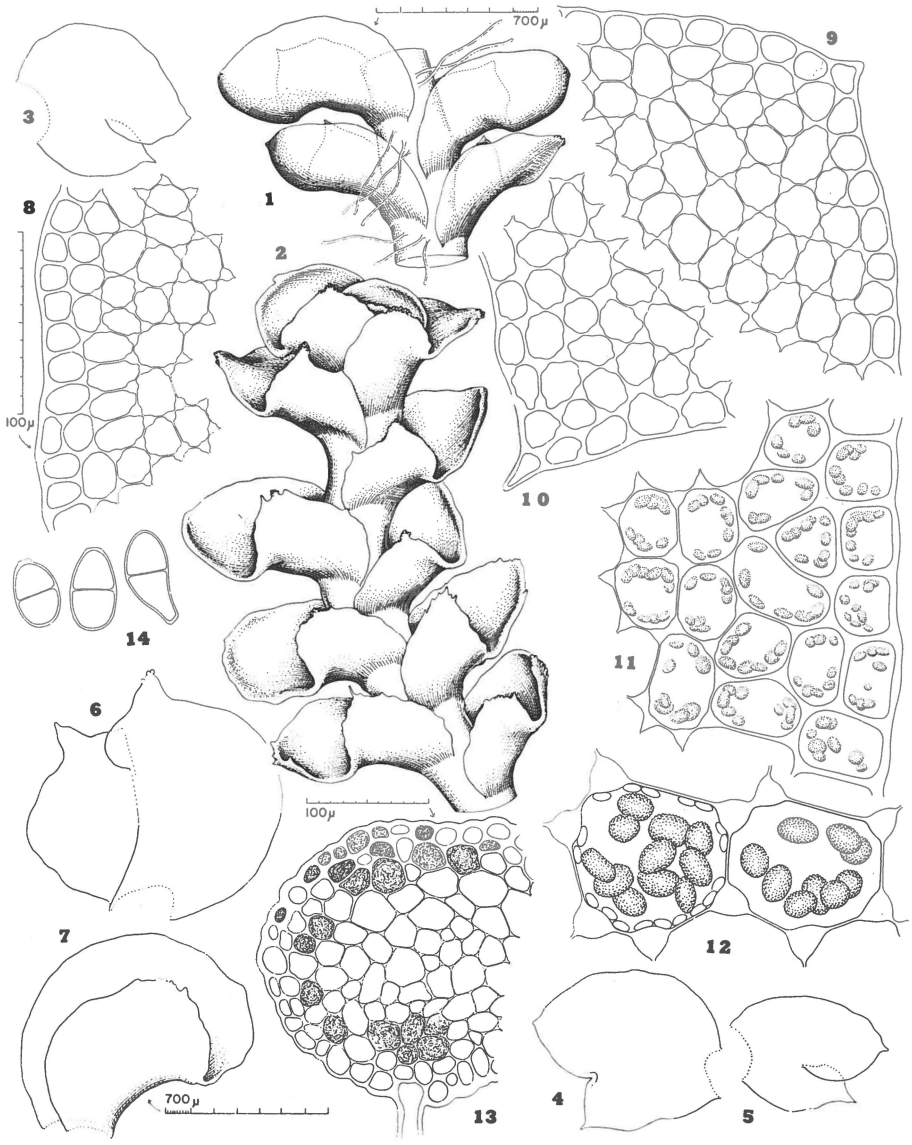


Fig. 15. *Scapania invisa*. (1) Shoot sector, ventral aspect (×30). (2) Gemmiparous plant, antical aspect (×30). (3–5) Leaves from smaller, nongemmiparous shoot sectors; leaf in fig. 5 juvenile (×30). (6) Large leaf from gemmiparous shoot apex, showing triangular, larger-celled, gemmiparous lobe tips (×30). (7) Large, gemmiparous leaf (×30). (8) Cells along ventral leaf margin, near middle (×240). (9–10) Ventral and dorsal leaf lobes, respectively (×240). (11) Cells along middle of ventral leaf margin, with oil-bodies drawn in (×365). (12) Cells from middle of ventral lobe with oil-bodies and, at left, chloroplasts (×720). (13) Stem cross section, showing mycorrhizal cells (×160). (14) Gemmae (×385). [1–10, 13, from type, 66–0287a, Godhavn, Disko; 11–12, 14, 70–2675, Perdlertut; 1–7, drawn to 700 μ scale; 8–10, drawn to upper 100 μ scale; 13, drawn to lower 100 μ scale].

Subg. ***Buchiella*** SCHUST.

Scapania (*Buchiella*) *cuspiduligera* (NEES) K. MÜLL.

Distribution (Map 48)

1A: Behind Arctic Station (66–0150a, 66–0274, 66–0275, 66–0278, 66–0280, 66–0281b, 66–0298, 70–2020, 70–2026a, 70–2058). 1B: Lyngmarken (70–2023a). 1C: Blæsedalen (66–0302). 1D: Skarvefjeld (66–0306b, 66–0308a, 66–0309, 66–0318, 66–0320, 66–0321). 2: Fortunebay (66–0143a). 8: Kuánerssuit (70–2126a, 70–2153). 13: Jens Vahls Dal (70–2637, 70–2638a, 70–2644, 70–2647, 70–2651a, 70–2657, 70–2658). 14: Hareøen (70–2571, 70–2576, 70–2587, 70–2589, 70–2598, 70–2592, 70–2594, 70–2608, 70–2610). 31: Anap nunâ (70–2432). 38: Uvkusigssat (66–1388, 66–1392, 66–1396). 42: Magdlak (66–1356b, 66–1357b, 66–1367).

Additional collections:

1: Godhavn (LAGERKRANZ 1936?). 99: Sarqaq valley (K.J. 186). 145: Uligssat (K.J. 10.186c).

S. cuspiduligera is largely an Arctic species, basically circumarctic, occurring north to 82°30′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and, in North America, south to Vermont and Minnesota (SCHUSTER, 1974). In Eurasia from Spitsbergen, Novaya Zemlya, and Siberia southward to the Alps and Pyrenees and (in Asia) to Japan. In West Greenland not known from farther north than the preceding localities, in East Greenland to 79°08′N.(JENSEN, 1910).

The species is regionally frequent in basaltic areas, often found on creviced, moist, vertical basalt cliffs, sometimes in ravines cut through basalt; it is then associated with *Lophozia heterocolpos*, *L. quadriloba*, *Solenostoma pumilum*, *Blepharostoma trichophyllum brevirete*, *Sauteria alpina*, occasionally *S. invisa* or *S. gymnostomophila* (70–2153, 66–0309, 70–2023a, 66–0278, 66–0308a). Occasionally also over peaty ground over basalt, then sometimes with *S. brevicaulis*, *Plagiochila asplenioides*, *Cephaloziella uncinata* (66–0306b). In general it grows in humid or irrigated sites where never subject to drying out. In the Arctic, however, *S. cuspiduligera* acquires considerably distended ecological perimeters: it may occur as a prostrate, often fuscous dwarf form, on rapidly drying calcareous slopes, where it is confined to moist run-off crevices, associated with *L. heterocolpos harpanthoides* and *S. ligulifolia* [Hareøen (70–2608), Jens Vahls Dal (70–2637)], also together with *Distichium capillaceum*, *L. quadriloba*, *Tritomaria scitula*, *Arnellia fennica*, and *Blepharostoma trichophyllum brevirete*. Such prostrate, dwarfed phases may be quite atypical; the dorsal lobes may be only 0.55–0.65 the ventral in size, and lie loosely over the ventral lobes. The plants then acquire a facies approaching that of *S. ligulifolia*. At Hareøen it may occur as an exceptionally large, erect-growing, pale or whitish green phase, with only local fuscous pigmentation, to 2.7 mm wide × 20 mm tall, in tufts amidst *Drepanocladus*,

in a rich fen. In the latter type of site associated with *S. ligulifolia*, *L. grandiretis*, *L. heterocolpos*, and *L. gillmani.*

The smallest, most troublesome plants seen are those of 66–1388, mixed with *S. gymnostomophila* and *Odontoschisma macounii.* They are dwarfed, bear very unequally bifid leaves, often with the ventral lobe apiculate, and almost always with the dorsal lobe sharply acute. Such plants will be sought, surely, under subg. *Scapaniella*; they obviously grew in a very exposed site, as is clear from the yellow-brown coloration, the strongly differentiated hyaline border on some shoots, and the very coarse, often subconfluent trigones. Gemmae are brownish purple, 2-celled, and to 11–12×19–20 μ. The ventral leaf bases are formed of very thick-walled and hyaline cells, occasionally diagnostically elongated, but—unlike in *S. curta*—never vinaceous. Leaves are somewhat sheathing at the base, and the ill-defined keel is suberect basally but then gradually flares outward to an angle of ca. 45° (near its middle), increasing gradually to 65–85° (near its apex in the sinus). Critical for the plants are the leaf cells: on some the marginal cells, which are always strikingly thick-walled, are in part strongly tangentially elongated, as figured for *S. carinthiaca* by both SCHUSTER (1953, pl. 43:1) and MÜLLER (1951–58, fig. 330:b). In the "Artificial Key" to species of *Scapania* in SCHUSTER (1974), the species keys quite readily to *S. saxicola*, a close ally of the xylicolous-corticolous *S. glaucocephala.* It agrees with this in that some leaves, independent of gemma formation, may produce obscure lobe teeth; in gemma size and the dark color of the 2-celled gemmae; in the obvious leaf border. The stem, also, is only 10–11 cells high, has a yellow-brown, 1-stratose cortex, and shows, with age, mycorrhizal infestation—exactly as in *S. saxicola.* The plants differ from *S. saxicola*, however, in several ways: (1) ventral lobes often, dorsal lobes occasionally, may be blunt to rounded, even with gemma formation; (2) marginal cells are sporadically strongly tangentially elongated in the lobes; the lumen may, indeed, be 3–4:1 in some cases; (4) oil-bodies in lobe cells are large and 2–5 per cell; (5) leaf teeth, where distinct, are always formed by single projecting cells, except at lobe apices.

Such dwarf forms of *S. cuspiduligera* clearly demonstrate that *Buchiella* and *Scapaniella* are clearly allied—*Buchiella* being able to develop dwarf "throw-backs" which exactly mimic *Scapaniella.* The only way to recognize such phases is by noting the sporadically rectangularly elongated cells of the lobe margins, and the hyaline basal field of the ventral lobe, in which cells—sporadically at least—are always narrowly oblong.

S. cuspiduligera is almost always sterile in West Greenland, but is always abundantly provided with gemmae.

v. *diplophyllopsis* SCHUST.

Lobis ventralibus foliorum falcato-geniculatis lingulatis a var. *cuspiduligera* diversa. Lobi dorsales manifesto apiculati.

Distribution (Map 48)

1A: Behind Arctic Station (66–0150a, 66–0157a, 70–2049a).

Type: 1A: Behind Arctic Station (66–0157a). With *Blepharostoma trichophyllum* ssp. *brevirete* and *Lophozia quadriloba*.

Laxer-leaved shoots of this variant are strikingly like *Diplophyllum taxifolium* in aspect, with ventral lobes falcate-geniculate and lingulate, and only 0.55–0.6 × as wide as long. Dorsal lobes are typically only ca. 0.5–0.65 the area of the ventral lobes. In the type specimen the perianth mouth bears low and remote, but sharp teeth. Gemmiparous leaf lobes are not triangularly drawn out, unlike typical *S. cuspiduligera*, and non-gemmiparous leaf lobes are often faintly denticulate (much as in *Diplophyllum taxifolium*). Typical is the tendency for the dorsal lobes to be distinctly apiculate, sometimes with a 1-celled apiculum formed by a cell 2–2.5 × as long as wide.

Subg. ***Scapania***

Sectio *Brevicaules* SCHUST.

Scapania brevicaulis TAYL. (= *S. arnellii* BUCH)

Distribution (Map 49)

1A: Behind Arctic Station (66–0279, 66–0282). 1B: Lyngmarken (66–0342b). 1D: Skarvefjeld (66–0306, 66–0324). 8: Kuánerssuit (70–2127, 70–2129, 70–2133, 70–2134a, 70–2148). 22: Orpigsôq (70–3105). 53: Søndre Strømfjord (66–0066, 66–0072, 66–0073, 66–0075, 66–0079, 66–0080).

Additional collections:

1: Godhavn (LAGERKRANZ 1934). 92: Claushavn (S.B. Aug. 1870, publ. 1875 as *S. bartlingii*, type of *S. arnellii* BUCH). 136: Kangerdluarssûp qeqertâ (K.H. 16.141).

This rather rare species was described from "British North America"; the type of *S. arnellii* was from Claushavn, Greenland (typification by BUCH, 1928; the lectotypification, based on the plant from Amur Prov., Siberia, in FRYE & CLARK, 1937–44, p. 601, is illegal). Aside from two stations in Siberia, and the ambiguous type locality, the species is known only from Farmer Island, Hudson Bay, Northwest Territories (SCHUSTER, 1974), from British Columbia (MÜLLER, 1944), and from West Greenland, where locally rather frequent.

The ecology of *S. brevicaulis* is distinctive; the plant grows on damp, peaty ground, usually over basic (mostly basaltic) rocks—the same combination of features typical of the habitat of *Lophozia heterocolpos*. It often occurs in or near willow scrub areas, where irrigation from snow

melt is a constant feature, or on humus over seepage-moist rocks (then often with *S. cuspiduligera* and/or *S. gymnostomophila*); other frequent associates are *Cephaloziella uncinata*, *C. arctica*, *Plagiochila asplenioides*, *S. mucronata praetervisa*, *L. heterocolpos*, *L. quadriloba*, and, more occasionally, *Preissia*, *Sauteria*, and *Blepharostoma*. Occasionally it occurs over peat-covered rock crests, where usually as a prostrate, blackish, compact phenotype.

Plants often occur in rather extensive pure to deep green mats, with the deep brown gemma masses forming a strong contrast. Gemmae are always abundant; perianths are very rare (in 66–0342b only). Oil-bodies suggest an affinity to subg. *Kaalaasia*, as well as the green to deep green color, without trace of reddish pigmentation, and the deep brown color of the gemmae. The sinuate-crenulate to subentire or remotely denticulate perianth mouth, however, and the rather compressed perianth form are more suggestive of subg. *Scapania*.

Plants of 66–0066 are in part very well developed; they range to 2.25–2.4 mm wide or even more, and are then so large that they hardly have the aspect of the *Curtae*, and approach the *Irriguae* in size. Plants vary from rather dark brown—almost blackish when dry—to, in shaded, wet sites, green. The dark brown (never reddish brown) gemma masses are abundantly developed and recall those of, e.g., *S. cuspiduligera* and *S. gymnostomophila*. Leaves show rather broadly oblong-lingulate ventral lobes and narrowly ovate-oblong dorsal lobes; ventral lobes are 1120–1350 μ long×840–1025 μ wide (width 0.75–0.85 length, usually), have broad and rounded apices, entire or rarely with a few 1-celled teeth. Dorsal lobes are 880–1125 μ long×600–635 μ broad, average 0.65–0.75 the size of the ventral, are entire, rather broad at the apex and usually end in a weakly marked, 1-celled point. On lax green forms the dorsal lobes may be quite obliquely inserted and decurrent, otherwise both lobes are short-decurrent. Median cells bear (2)3–6 quite large oil-bodies of variable size, whitish, finely granulate, slightly rough-surfaced; they range to mostly broadly to narrowly ovoid or ellipsoidal and 5×7–10 to 6×7–12.5 to 7–8×10–11 μ, a few spherical and 5.5–6.5 μ. Gemmae are broadly ellipsoidal to subspherical, 11–12×12–14 μ to 11–14 ×16–17 μ; all are normally 1-celled. In some collections, however (70–3105, 66–0079), the gemmae are in very small part (always under 0.1 %) two-celled and then range to 14×24–26 μ and are somewhat more slenderly ellipsoidal. The greater part of the gemmae, however, is always unicellular at maturity and characteristically subspherical to very broadly ellipsoidal.

Sectio *Curtae* K. Müll., emend. Buch

The taxonomy of the Arctic *Curtae* is complex almost beyond comprehension. A recurrent problem is that the various taxa were all

established from non-Arctic phenotypes and the Arctic plants belong to evidently distinct genotypes. Also, much of the material is poorly developed and thus nearly unplaceable.

Scapania curta (MART.) DUMORT.

Distribution (Map 50)

1A: Behind Arctic Station (66–0146b, 66–0161c, 70–2047b, 70–2136). 1B: Lyngmarken (66–0557c trans ad *Sc. parvifolia*). 1D: Skarvefjeld (66–0311c). 6: Eqalúnguit (70–2229). 8: Kuánerssuit (70–2136). 9: Eqaluit (70–2558a). 14: Hareøen (70–2578, 70–2607). 25: Sarfaq (70–2334, 70–2336c, 70–2364, 70–2367a). 26: Pâkitsup ilordlia (70–2304a, 70–2308a).

Additional collections:

6: Eqalúnguit (M.P.P. 3321). 17: Tupilak (K.H. 16.995a). 60: Kugssuaq (M.P.P. 718).

S. curta s.l. occurs from the middle Arctic southward, in eastern North America as a Pleistocene disjunct within the gorges of central and western New York (SCHUSTER, 1949). It is not known from Spitsbergen, nor has it surely been found farther north than the above stations in Greenland [as reports from north Greenland (HESSELBO, 1923a) represent errors in determination (see ARNELL, 1960, pp. 3–4)].

This species is highly polymorphic in the Arctic. Broadly defined it includes: a typical variety, widespread in temperate-boreal sites, but extending into the Arctic; an Arctic variety (or perhaps subspecies) which occurs mostly in basaltic regions; a large-celled (polyploid?), thus far encountered only in areas with acidic rocks. All three extremes occur regionally; of these var. *curta* may be the least frequent. Indeed, it is possible that typical temperate-boreal var. *curta* hardly occurs this far north as wholly typical genotypes; we have left within var. *curta* an ensemble of plants which are small (mod. *parvifolia*), often ill-developed, often developed in exposed sites, associated with, e.g., *Gymnomitrion*. It is possible that some of these plants represent only depauperate phases of var. *isoloba*. For example, 70–2334, mostly a mod. *parvifolia*, has the generally sharp to blunt ventral lobes typical of var. *curta*—but on two or three of the largest individuals the ventral lobes were broadly rounded, suggesting that if the plants had grown in an optimal environment they might have grown "into" var. *isoloba*.

An additional complication is that ♂ plants are much more difficult to place accurately; they have, in any event, a marked tendency to form rounded lobes on leaves in the vicinity of androecia, and the dorsal lobes and keel tend to become, respectively, larger and longer. Pragmatically, we have left within *S. curta s. str.* those plants which seem to represent the typical variety, plus a few which could not be clearly referred to either var. *isoloba* or var. *grandiretis*.

The ecology of the variants of *S. curta* is not sharply enough defined to allow us to treat them separately. The known stations of the plants here assigned to var. *curta*, however, almost all lie in areas where gneiss or other acidic rocks occur. In the area near Godhavn, where both typical v. *curta* and v. *isoloba* occur, gneiss is found at lower elevations, basalt at higher elevations; in Disko Fjord there is the same combination of rocks, often closely juxtaposed. Regionally, the species, *s.l.*, is rather common but mostly occurs in admixture, often only as scattered plants. More or less typical phases may occur intermingled in mats of *Lophozia heterocolpos*, *Tritomaria quinquedentata*, *Solenostoma sphaerocarpum*, (66–0146b), over peaty soil, or over peaty soil on presumably weakly basic slopes, with *L. opacifolia* (70–2578) or *L. excisa* (70–2229) or *L. heterocolpos*, *L. polaris*, and *L. subapiculata* (70–2304a), or *L. quadriloba*, *L. hatcheri*, *L. wenzelii* (70–2558a); some of these taxa are at least weakly Ca-tolerant. Occurrences in strongly acidic sites are infrequent. Occurrences with other *Scapaniae* are frequent: *S. mucronata praetervisa* (70–2308a, 70–2558a), *S. curta grandiretis* (70–2308a), *S. irrigua rufescens*, and *S. lingulata* (70–2336c), *S. paradoxa* (70–2334); these often greatly complicate recognition of *S. curta* and we think that the various admixtures may not be clearly separable at times if only dead plants are at hand. (Our identifications always involved cytological study).

Plants clearly belonging to var. *isoloba* seem ecologically distinct; the variety seems limited to areas with basaltic rocks. Common associates, mostly over peaty rather than mineral soil, often along rills or small cascading brooks (then sometimes on thin, peaty soil over mineral soil or between rock fragments, sometimes very luxuriant and freely fruiting when in such sites, especially where kept moist by spray, as in 70–2157), are among the following: *L. heterocolpos*, *L. polaris*, *L. excisa* (less often *L. quadriloba*, *L. ventricosa rigida*, *Tritomaria scitula*, *Cephaloziella uncinata*, *Cephalozia pleniceps*, *Nardia geoscyphus*, *Blepharostoma t. brevirete*, *Solenostoma subellipticum*, *S. pumilum*, *Anthelia juratzkana*, *Scapania irrigua rufescens*, *S. cuspiduligera*, and *Sauteria alpina*). Association with *L. heterocolpos*, *L. excisa*, and *N. geoscyphus* is particularly frequent. Over permanently damp, broken soil along rills or around shallow pools, *Calypogeia integristipula*, *C. muelleriana*, *Cephalozia pleniceps*, *Pleuroclada*, *Diplophyllum taxifolium*, and *Solenostoma subellipticum* (70–2047b) may be associated.

S. curta curta and var. *isoloba* consistently have 2–5 oil-bodies in some or all cells. Occasional leptodermous phases (70–2158, 70–2771) may have only (1)2–4 or (1)2–4(5) oil-bodies per cell; they are not always relatively small. Not infrequently (e.g., 70–2304a) the leaf border is obsoletely developed, or (70–2585b) may be indistinct. Such plants, if not identified while with oil-bodies, and if lacking all pigments of cell

walls, may be indistinguishable. Sometimes red sun forms occur (70–2367 a) which are mixed with similar and juvenile modifications of *S. irrigua rufescens* (70–2367 a); these two taxa may then be very difficult to separate, but in the collection at hand, can be separated by the absence of a border in *S. irrigua.*

Occasionally we find variation towards *S. parvifolia*, and it is not impossible that the two species may represent the mere ends of a broadly intergrading spectrum. More than 95 % of pertinent collections, however, could very easily be placed into one or the other of these two taxa. In 70–2530, however, the perianth mouth is subentire, much as in *S. parvifolia;* in 66–0557 c we may have a more serious case of transition: the leaves are sometimes spinose-dentate and cells are (14.5)15.5–19.5 μ on the ventral leaf margin.

Capsules are produced (in the "warm springs" area of Disko Fjord; 70–2157) as early as July 10.

v. *isoloba* Schust.

Var. *curtae* similis praeter lobos dorsales circiter 0.65–0.75 ventralium longitudinis, carinam plus quam 0.6 lobi ventralis longitudinis, cellulas nonnullas solum 1–2 corpuscula oleifera cuique praebentes.

Similar to var. *curta*, but differing as follows: leaves (of mature shoots at least) almost equally bilobed, the dorsal lobes 0.75–0.85 the ventral [dorsal lobe 490–510 μ wide × 660 μ long (width 0.7–0.8 as wide as long); ventral lobe 470–500 μ wide × 780–810 μ long (width 0.58–0.65 as wide as long); keel 0.5–0.65 length of ventral lobe. On larger leaves both lobes become appreciably wider, and the keel longer]; ventral lobes often rather broadly obovate-lingulate, typically broadly rounded (even on leaves near gemmiparous areas); dorsal lobes from broadly acute to blunt with apiculum to, rarely, broadly rounded, a little shorter than ventral lobe, but often as broad or broader, usually ovate; leaf margins, except on gemmiparous leaves, consistently edentate (apiculum of dorsal lobe apex aside). Leaves not infrequently explanate; keel typically long, often 0.65–0.75 ventral lobe length. Marginal border of thick-walled cells is usually vestigial or even lacking above the postical basal sector; except for this last sector, where marginal cells lack oil-bodies, these are present in all but 2–8 % of marginal cells. Oil-bodies often relatively large, in isolated cells a single large oil-body (to ca. 7 × 13 μ). Perianth with mouth remotely and often obsoletely dentate, the teeth blunt to subacute, 1–3-celled only. Bracts with rounded, quite edentate lobes.

Type. Qasigíssat, mouth of Vesterdalen, W. side of Disko (70–2739), on steep, S. facing calcareous clay slopes, in a late snow area, with *Salix herbacea*, *Lophozia pellucida minor*, *Solenostoma pumilum polaris.*

Distribution (Map 50)

1A: Behind Arctic Station (66–0150a, 66–0283, 70–2022, 70–2026a, 70–2028, 70–2030). 1D: Skarvefjeld (66–0231a, 66–0232a). 2: Fortunebay (66–0214). 7: Angûjârtûtit (70–2149a, 70–2157, 70–2158, 70–2161a, 70–2176a). 8: Kuánerssuit (70–2149a). 9: Eqaluit (70–2527, 70–2528, 70–2530, 70–2545). 10: Enoks Havn (70–2771). 11: Qasigíssat (70–2726, 70–2730, 70–2739). 14: Hareøen (70–2585).

Additional collections:

16: Manîtsoq (W. & H. July 1884). 60: Kugssuaq (M.P.P. 725a). 64: Ingigigsoq (M.P.P. 3114). 72: Kuánit (L.H. Aug. 1932).

This variant is apt to be mistaken for the *S. obcordata* complex because of the frequent lack or vestigial presence of a leaf border. Gemmae, however, are at least normally greenish, even in sun forms (although a few are tardily reddish in 70–2030). Typical is the invariable presence of a minority of cells with single oil-bodies and, on mature leaves, of oil-bodies in virtually all marginal leaf cells, even distally in the lobes. The subisolobous leaves, always edentate, even near gemmiparous regions, are equally diagnostic.

In the type plants terminal-basiscopic, *Radula*-type branching is very frequent; often two, nearly opposed, branches of this type occur closely juxtaposed, accompanied by frequent lateral-intercalary branches from near the ventral angle of the leaf. Exactly such a mélange of branching types is diagnostic of *Jensenia*.

v. *grandiretis* Schust.

Var. *curtae* similis praeter cellulas multo majores, marginalibus circiter 25–28μm magnis, medianis loborum 23–28 (31)×25–30μm, corpuscula oleifera cuique cellulae (4)5–9(10–11), perianthium sinuatum ostio subintegerrimo.

Distribution (Map 50)

6: Eqalúnguit (70–2208, 70–2226). 23: Kangersuneq (70–3141, 70–3148b). 25: Sarfaq (70–2340a). 26: Pâkitsup ilordlia (70–2308a).

Similar to var. *curta* in size, the often pinkish color of the much thickened cell walls at the ventral leaf base, in the thickened cell border, in the pale green, narrow, elliptical 2-celled greenish gemmae, and in leaf form. Differing as follows: cells larger, thick-walled marginal cells (of ventral lobe) averaging 23–28 μ where subquadrate but often strikingly, if locally, elongated tangentially and then ca. 42×18–20 μ; median cells of lobes 23–28(31)×25–30 μ, with thin walls and distinct to conspicuous but not bulging trigones; oil-bodies of middle of lobes (4)5–9(10–11) per cell, absent from some or all marginal cells, 3.5–4×4.5–5 to 3.5–5×7 μ, a few to 4×10 μ, granular-botryoidal; gemmae pale green, large, the larger 16.5–19×28–33 μ, a few to 19–21×36–38 μ. Perianth (only one seen) sinuate and subentire at mouth with a few obscure, low, triangular 1-celled teeth.

Type. 6: Eqalúnguit (70–2208), Disko Fjord. The type was collected on exposed peaty ground along the braided and vegetated fenlike mouth of the river at the head of the fjord; associated was *Nardia geoscyphus* and *Anthelia juratzkana.*

A single plant of a second collection from Qissugssalik, Pâkitsup ilordlia (70–2038a), was found growing with *S. curta curta*, *S. mucronata praetervisa*, *L. opacifolia*, *L. polaris*, *L. heterocolpos*, *L. ventricosa*, etc., along a rill.

This variant occupies an analogous position, *vis à vis* var. *curta* as do *L. wenzelii lapponica* and *L. ventricosa rigida vis à vis* vars. *wenzelii* and *ventricosa.* Not externally distinct from var. *curta*, and, like exposed-growing phenotypes of this, with pinkish color of some ventral leaf bases but yellowish brown to brownish coloration of distal portions of leaves. As in var. *curta* the keel is rather long (over 0.5 ventral lobe length), the rounded ventral lobes may bear a 1-celled apical tooth and, occasionally, vestigial 1-celled teeth in addition; the dorsal lobe is usually pointed and, especially associated with gemma formation, may bear several additional small teeth.

We would also refer here, with few reservations, slender, attenuated plants from Sarfaq (70–2340a), mixed with deceptively similar plants of *S. irrigua rufescens*, as well as *Anthelia juratzkana*, *Marsupella revoluta*, and *Cephaloziella*, on a moist cliff wall. These plants represent a mod. *angustifolia-parvifolia-laxifolia-colorata* (the intermingled plants of the *S. irrigua rufescens* occur in a similar modification and size), with golden to yellow-brown leaf lobes and strong vinaceous pigmentation of leaf bases at shoot tips. Ventral lobes average under 0.45 as wide as long and there are only (5)6–8(9–10) oil-bodies per cell. Cell size is typical of var. *grandiretis* and the border is well marked.

The critical plants of 70–3148b grew with *Solenostoma pyriflorum innovatum*, *Nardia geoscyphus*, and *Prasanthus* on fine, silty, exposed ground around a shallow lake; some have the vinaceous to purplish pigmentation typical of *S. curta*, the remainder of the plant being pale green. They also have a rather distinct margin of thick-walled cells, from some of which oil-bodies are lacking. Marginal cells average over 20 μ, and oil-bodies are 5–9(10) per median lobe cell, as in var. *grandiretis.* As in many gemmiparous forms of *S. curta*, dorsal lobes often bear several strong teeth. Unfortunately, the combination of some strong but 1-celled teeth of the leaves, large cells, and a little vinaceous pigmentation of the ventral leaf bases is exactly typical of *S. lingulata* var. *microphylla*, and, in general, the present plants almost match the type of this taxon, except for the rather distinct leaf border. We assume that *S. curta grandiretis* bears an identical relationship to *S. curta curta* as does *S.*

lingulata to *S. mucronata:* the large-celled "end members", bearing more numerous oil-bodies per cell, may be almost inseparable.

Scapania parvifolia WARNST.

Distribution (Map 53)

1A: Behind Arctic Station (66–0102c). 6: Eqalúnguit (70–2220, 70–2243b, 70–2244). 16: Manîtsoq (70–3008b). 19: Nûk (70–2869c). 21: Umiasugssûp (70–2948d). 32: Qôrorssuaq (70–2447a, 70–2448h).

Additional collections:

6: Eqalúnguit (M.P.P. 2063a). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932).

Though presumably imperfectly circumboreal-circumarctic this species is known from so few stations that the range can hardly be sharply defined. Aside from a few stations in Fennoscandia and Scotland, it is reported from Spitsbergen (ARNELL & MÅRTENSSON, 1959), Siberia (type), northernmost Japan (AMAKAWA, 1968), Quebec (SCHUSTER, 1951) and several sites in Greenland (aside from the above stations in West Greenland, known from 65°39′N., in East Greenland, KD 69–308). The regional stations are the northernmost ones known in the New World.

S. parvifolia in our area seems quite distinct from *S. curta* in its ecology, occurring only in gneissic areas, most often on fine-grained mineral soil, but also on rocks, often where strongly subject to desiccation. Very typical of heaved, broken soil of stone polygons, where with *Gymnomitrion corallioides*, *Prasanthus*, *Marsupella ustulata*, *Nardia geoscyphus*, *Lophozia excisa*, *L. alboviridis*, *Anastrophyllum minutum*, and *Diplophyllum obtusifolium.* In such sites the plants are strongly xeromorphic in structure (bulging trigones are often developed); the cuticle is quite rough and leaves are intensely brown-pigmented, with red leaf bases.

A mod. *viridis-mesoderma*, however, with feeble (and vinaceous) pigmentation of only the ventral leaf bases, also occurs in shaded recesses and crevices of igneous cliffs, associated with *Nardia geoscyphus*, *Calypogeia muelleriana*, *Pleuroclada*, and *Cephalozia pleniceps* or (70–2869c) on permanently damp, peaty soil around acidic tarns, with *L. ventricosa silvicola*, *Blepharostoma* and *Odontoschisma macounii.* Such phenotypes retain the "normal" constellation of features that separate the species and are hardly subject to confusion with *S. curta;* they retain the relatively large oil-bodies of this species (as contrasted to *S. curta*), and, unlike *S. curta*, have (1)2–4 oil-bodies in all marginal cells in the leaf lobes.

In at least some phenotypes of *S. parvifolia* the perianth is rather inflated, hardly dorsiventrally compressed, and longly sulcate dorsally;

the innermost bracts may also be relatively small and erect to appressed to the perianth base. These features suggest *Jensenia*—and again emphasize that the latter is a very weak subgenus.

The Greenland plant seems quite typical; many plants show rose-red coloration of the postical leaf bases and those which have pigmentation of the distal parts of the leaves usually show a combination of brownish and reddish pigments. The keel in this species is supposedly shorter (often 0.3–0.4 the leaf length) than in *S. curta*, and the dorsal lobe is supposedly erect and points towards the stem apex. These two criteria are expressed to varying degrees only—most clearly on juvenile or weak stems. On robust individuals the keel is longer, to 0.45 the ventral lobe length and the lobe is then obliquely spreading. Such vigorous plants demonstrate an admitted approach to *S. curta*. Marginal leaf cells, away from isolated zones of tangentially elongated cells, average only 13–16 μ long—smaller than in *S. curta*. Oil-bodies are larger than in *S. curta* and often, away from leaf margins, obscure almost all the lumen; (2)3–5 oil-bodies occur in median cells and these range from 4.5–4.8×6–8.5 to 5–6×7–9 μ, rarely to 7×9 μ.

The pale green gemmae are produced in some quantity; gemmiparous leaf lobes are drawn out into strongly elongated, hornlike lobes formed of elongated cells.

Scapania lingulata BUCH[1])

Distribution (Map 51)

1A: Behind Arctic Station (70–2017c, 70–2029, 70–2058, 70–2035, 70–2053c). 1D: Skarvefjeld (66–0322a). 11: Qasigissat (70–2722). 15: Kronprinsens Ejland (70–2061a, 70–2106, 70–2108a). 21: Umiasugssûp (70–2947). 24: Jakobshavn (66–0240). 25: Sarfaq (70–2336, 70–2364). 26: Pâkitsup ilordlia (70–2255, 70–2392a). 29: Ritenbenk (66–0269). 30: Eqe (66–0322a). 53: Søndre Strømfjord (66–0071).

Additional collections:

45: Sagdliaruseq (K.H. 13.147). 65: Ûnartuarssuk (M.P.P. 652a).

This species (*s.l.* including *S. microphylla*) is probably circumboreal to low-Arctic in range; it is known from Fennoscandia and south to Scotland, Germany, France, east to the USSR, westward to Iceland and Greenland [where apparently not known from farther north than the above stations, as the report of plants cited as "probably" *S. lingulata* from Bjørlings Ø (HARMSEN & SEIDENFADEN, 1932) is based on a specimen of *S. mucronata praetervisa*], and southward to Vermont, Massachusetts, and Minnesota. No stations from western North America and

[1]) We have been informed that, orthographically, "*ligulata*" and "*lingulata*" are not identical; on that basis, *S. lingulata* BUCH is not an orthographic variant of *S. ligulata* Steph.

Asia are, so far, known. The Greenland distribution is poorly understood; the above reports are the only ones of the species.

The ecology of *S. lingulata* is still inadequately known. Our collections are all from areas where igneous (gneissic) rocks are present, often from rather xeric sites, on thin soil over rocks, or in rock crevices or chasms, associated with *L. hatcheri*, *Cephalozia bicuspidata*, *Cephaloziella arctica;* when on exposed soil over moist rocks associated with *S. curta curta*, *S. irrigua rufescens*, *Cephaloziella cf. grimsulana*, *Nardia geoscyphus* (70–2336) or *Cephaloziella arctica* and *Marsupella boeckii* (70–2061a), sometimes also with *L. wenzelii lapponica* and *Blepharostoma trich. trichophyllum*, on damp soil over and amidst acidic rocks (70–2947). The species sometimes occurs as a deviant mod. *viridis-dentata* (with unusually coarse teeth, and often sharp ventral lobes) in unduly moist sites, as, e.g., on a moist rock face in deep shade (70–2722), or (70–2255) in wet, sandy depressions near the shore of an acidic lake. [These plants are puzzling and diverge far from var. *lingulata* of temperate-boreal regions: ventral lobes are nonlingulate, sharply and triangularly pointed and, with gemma formation, bear strong, often oblique, 1–2-celled teeth—the dorsal (and sometimes ventral) lobes being serrate. Although the lobe form and dentition seem foreign to *S. lingulata*, the (5)6–9 rather large oil-bodies per cell and the marginal cell size (20–23 μ, tangentially measured) place these plants within *S. lingulata*, *s.l.* The tendency towards formation of strong teeth + a sharp, nonlingulate ventral lobe also occurs in Vahl 93, from Ameralik.] Exceptionally over low, flat, damp ground between rocks and around shallow pools in gneissic rocks, when found with *S. mucronata praetervisa*, *Marsupella ustulata*, and *Diplophyllum taxifolium* (70–2053b). At the opposite extreme sometimes with *Gymnomitrion concinnatum* and *L. hatcheri*, on soil over exposed rocks (70–2108a), then as a mod. *parvifolia-angustifolia*, with the ventral lobe almost always sharp-pointed or mucronate and very atypical in the rather longer keel and somewhat larger dorsal lobes, as well as in the presence of both lateral-intercalary and *Radula*-type branches.

S. lingulata is a controversial and difficult species; it is subject to confusion, on one hand, with the *S. obcordata-perssonii* complex (with forms of which it agrees in the large cell size, larger gemmae, and many oil-bodies, and the rounded ventral lobes). On the other hand, it may be confused with *S. mucronata* (with which it agrees in the strongly dentate perianth mouth, the rather large oil-bodies, the usually strong collenchyma, and gemma form and color range). It differs from *S. mucronata* primarily in the larger cells and more numerous oil-bodies per cell. In many Arctic phenotypes (here united as var. *microphylla*) the customary distinctions cited in leaf form (ventral lobes lingulate, rounded, in *S. lingulata;* ± sharp to mucronate in *S. mucronata*) hardly exist. As a

consequence, the discrimination of *S. lingulata* is critical. Both taxa typically develop a rather fuscous brown pigmentation of (at least distal portions of) the leaves in sun forms, associated with which the gemmae remain greenish or become tardily pink to vinaceous; both taxa, as Buch (1928) emphasized, react similarly to light with regard to leaf form and internode length. We once believed that *S. lingulata* could be placed as a mere large-celled (?polyploid) variety or subspecies of *S. mucronata.* If the ssp. *praetervisa* of *S. mucronata* is *truly* identical at the species level with *S. mucronata*, however, then the identity of *S. mucronata* and *S. lingulata* becomes almost impossible to defend, since in 70–2053 both taxa grow side-by-side (although actually not admixed), associated with *Diplophyllum taxifolium.* In ssp. *praetervisa* the plants, with the prevailing illumination, are clear green but the gemmae already predominantly vinaceous, while in *S. lingulata* the upper leaves are often a light fuscous brown distally; gemmae, however, remain greenish, with a few exceptions. In ssp. *praetervisa* gemma formation fails to induce development of teeth and ventral lobes are sharp; in *S. lingulata*, dorsal lobes, with gemma formation, acquire some sharp and often jagged teeth and ventral lobes (in nongemmiparous zones) are broadly rounded, a 1-celled mucro, often present, excepted. As a consequence, if we maintain the identity of *S. mucronata* and *S. praetervisa*, it seems necessary to retain *S. lingulata* as a *bona fide* species.

In so far as perianths are present (e.g., 70–2106), the perianth mouths in our plants are typical: closely fimbriate. Oil-body number (per median lobe cell) is typical, ranging from 6–10 or 6–11 per cell (70–2722, 70–2392a, 70–2947) to (5)6–9(10) per cell (70–2255, 70–2061a, 70–2108a), or, occasionally, 6–12(13) per cell (70–2106). Gemmae range (upper maxima) from 15–16×26–29(31) μ (70–2061a) to 14–15×25–29 μ (70–2255) up to 14–15×32–38 μ (70–2947). Deviations from the original concept of the species lie largely in the: (a) occasional feeble, 1-cell wide border (70–2947); (b) occasional strong reduction in size of gemmiparous leaves (70–2106); (c) formation of strong, sometimes jagged teeth, associated with gemma development (66–0269, 70–2106, 70–2722, 70–2255); this often is limited to the mod. *viridis* in sheltered, damp sites. [The ability to form such sharp teeth, especially of dorsal lobes, as in 70–2255, is so striking that one must question the conspecificity of these plants with *S. lingulata;* yet, if they are not placed here, we do not know where to place them. Furthermore, such plants seem to grade into others (66–0269) with a much lower proclivity for tooth formation. In all such phenotypes ventral leaf lobes are often blunt to sharp.]

Plants tending to develop sharp teeth of the leaves should perhaps be regarded as the mod. *viridis* of the next variety. We have (perhaps arbitrarily), however, placed all plants that lack any trace of vinaceous

pigmentation of the ventral leaf bases as var. *lingulata*. By contrast, all phenotypes with reddish coloration of the ventral leaf bases are placed in var. *microphylla*. Some collections, placed under the latter, show only limited, occasionally incipient, reddish pigment formation. Clearly a minimal level of insolation seems necessary to induce red pigment formation in var. *microphylla;* by contrast, in var. *lingulata* we may find strong brownish pigmentation—the plants may even be "deep brownish to blackish" (SCHUSTER, 1953, p. 463)—without trace of reddish pigmentation of ventral leaf bases—although gemmae may become slightly reddish.

A critical and almost unplaceable specimen is HOLMEN 13.147 (Qioqe Pen.); the plants are somewhat smaller than is often the case in *S. lingulata* and approach *S. mucronata* in size. They disagree, however, in (a) the very preponderantly rounded and lingulate ventral lobes; (b) a feeble tendency for the collenchymatous marginal 1(2) cell rows to develop thickened intervening walls so that a weak margin is distinct; (c) the strongly, closely papillose cuticle, which is typical of many forms of *S. lingulata;* (d) marginal cells along ventral margin average 19–21 μ. The last are small for *S. lingulata* but too large for *S. mucronata*. Gemmae are rather pink to vinaceous-red at maturity; they range 13–16×22.5–28.5 μ—are thus large for *S. mucronata* ssp. *mucronata* (also somewhat smaller than normal for *S. lingulata*; the pink color, coarse trigones, and very rough cuticle, however, suggest growth in a xeric site; in such sites cell size, of both leaf cells and gemmae, tend to be at the lower limits given for *S. lingulata*). The perianth mouth is rather spinose-dentate, with rigid, tapered, close teeth (1)2–4 cells long and often 2 cells wide at base; they are smaller than normal for *S. mucronata* but not quite as slender as is normal in *S. lingulata*. On balance, especially because of the ventral lobe shape, disposition at the perimeter of *S. lingulata* seems best. The leaf lobes, however, are usually essentially edentate; this may be related to the fact that the plant is a mod. *pachyderma-parvifolia*, from, evidently, a rather xeric site.

v. *microphylla* (WARNST.) SCHUST.

S. lingulata BUCH (nec. *S. ligulata* STEPH.) has been generally placed as a synonym of *S. microphylla*, or vice versa. MÜLLER (1944, 1951–58) stated that both he and BUCH had seen the type of *S. microphylla* and agreed it belonged with *S. lingulata* BUCH.

Basionym: *S. microphylla* WARNST., HEDWIGIA 63:75, 1921.

Similar to var. *lingulata* (and not surely distinct from this when in the mod. *viridis*), differing as follows: leaves, at least near shoot apices, with reddish pigmentation at or near juncture with the stem; leaves with

ventral lobes rarely perceptibly lingulate, mostly narrowly oblong-ovate, occasionally obovate, often pointed at the apex; dorsal lobes ca. 0.6–0.65 ventral in area, usually sharp, often (associated with gemma production) coarsely and irregularly dentate and somewhat malformed. Cells often smooth or almost so, sometimes rather larger than in var. *lingulata:* marginal cells 24–28 μ, median lobe cells 24–32 × 25–35 μ, basal often very large, 25–28 × 38–48 to 35 × 50 or 30–32 × 60–72 μ; basal cells of ventral lobe typically slightly vinaceous and of ± thick-walled cells, the cells not strongly elongated.

Type. "Grønland leg. VAHL n. 114" as "*Scap.* ?*curta*".

The type was not destroyed in World War II, as MÜLLER (1951–58) states, but a duplicate of this exact collection number in the Copenhagen Herbarium must be considered part of the type. A part of WARNSTORF's type still exists in Berlin. We have checked both specimens; the Berlin and Copenhagen plants are identical and clearly part of the same gathering, but we could find no reddish color in the Berlin plants (a few of the Copenhagen plants showed vestiges of color). VAHL's numbers before 114 (e.g., 113) and after 114 (e.g. 115–117) were collected at Ameralik in Aug.–Sept. 1830; it is thus almost certain that no. 114 is also from Ameralik. No. 114 bears an annotation by BUCH ("IV. 1922") of "*Sc. curta*, forma" which is surely incorrect; this must represent an early identification, prior to the "hardening" of his species concepts with regard to *Scapania*.

MÜLLER (1944) states that the type at Berlin had smooth and large cells, while *S. lingulata s. str.* always has the cells distinctly papillose; in the material of VAHL 114 (Berlin; Copenhagen) we have studied, the cuticle is smooth or locally finely papillose. In the type material the dorsal lobe is ca. 0.6–0.65 the ventral in size and is usually sharp; ventral lobes are normally sharp-pointed, or, infrequently ± rounded at the apex; they are not lingulate but are narrowly oblong-ovate to obovate. Cells are hyaline and unusually large; the marginal cells average, tangentially measured, to 24–28 μ, the median ones are usually diagnostically subquadrate and 24–30(32) × 25–35 μ; basal cells are very variable in size and often quite large, from 25–28 × 38–48 μ or even up to 35–38 × 50 to 30–32 × 60–72 μ in extreme cases. A feature neither MÜLLER nor BUCH noted is critical: basal cells of the ventral lobe are often slightly vinaceous and are ± thick-walled, contrasted to the warm yellow-brown to subhyaline, thin-walled and collenchymatous remainder of the leaf.

Distribution (Map 51).

1A: Behind Arctic Station (66–0174, 70–2018, 70–2050, 70–2054). 2: Fortune-bay (66–0129, 66–0131). 10: Enoks Havn (70–2767, 70–2770). 15: Kronprinsens Ejland (70–2077, 70–2091). 24: Jakobshavn (66–0229, 66–0226a). 25: Sarfaq (70–2364).

26: Pâkitsup ilordlia (70–2291a, 70–2304a). 30: Eqe (66–0322c, 66–0323). 32: Qôrorssuaq (70–2447b).

Additional collections:

54: Holsteinsborg (J.V. Aug. 1832). 90: Tasiussaq (S.B. July 1870).

This variety (or perhaps subspecies) is, on one hand, very difficult to separate from *S. l. lingulata* (when the reddish pigmentation of the ventral leaf bases is vagrant or absent; in shade forms), and on the other hand, from plants here placed in *S. perssonii.* Plants of 70–2256a and 70–2273a, placed here in *S. perssonii*, could conceivably represent *S. l. microphylla;* they show rather strong violet-red to purplish pigmentation and tend to have the dorsal lobes and keel longer than "normal" for *S. lingulata.* In particular, in 70–2273a, we have seen identical, vertical, hollow, essentially unkeeled leaves typical of exposed forms of *S. perssonii;* both collections show the pinkish or violet pigmentation spreading from ventral lobe bases to the dorsal lobes and, on upper leaves, suffusing the leaves (but blending on leaf lobes with light brownish pigments). Pigmentation, although less intense than in the Kânâk (type) material of *S. perssonii*, is qualitatively identical. Furthermore, in 70–2256a, unfertilized gynoecia with, admittedly, rather poorly developed perianths are present; these have a repand-sinuate to subentire mouth. Perianths of *S. l. microphylla* have been seen only once: they bear sharp teeth, 2–5 cells long (with elongated terminal cells, often 2–2.5:1). On that basis perianth-bearing plants of *S. perssonii* and *S. l. microphylla* are clearly distinct.

It is not impossible, however, that *S. perssonii* will be found to represent an extreme, high Arctic subspecies allied to *S. l. microphylla;* in that event it is almost certain that we will then have to admit *S. microphylla* as an independent species. Our current, but not fully firm, concept of the differences follow:

Key to *S. obcordata-lingulata-perssonii* Complex

1. Able to develop pink, violet or purplish to red pigments (at least of postical leaf bases) 2
   2. Leaves with ventral lobes consistently rounded to blunt; both lobes entire (exc. on gemmiparous leaves), without "normal" teeth. Oil-bodies (2)3–5(7) per cell. Perianth mouth subentire or with 1–3-celled remote teeth. *S. obcordata*
   2. Leaves with ventral lobes all or largely apiculate, triangularly pointed, or mucronate, often ± dentate; dorsal lobes, especially, tending to be dentate. Oil-bodies (5)6–10(12–13) per cell..... 3
      3. Red coloration usually extensive (mostly spreading to leaf lobes); gemma production associated with strong reduction of

leaves, the lobes ± aborted, triangular, of large, elongated cells, but without conspicuous dentition. Perianth mouth subentire to dentate, with close, 1–3(4)-celled teeth (terminal cells 1–2:1), never ciliate. *S. perssonii*

3. Red coloration usually limited (mostly at ventral lobe bases); gemma production not strongly reducing leaf lobes, but leaf lobes often ± strongly dentate. Perianth mouth ciliate to ciliate-dentate with crowded teeth, often rather coarse, 2–5 cells long, 1–3 cells wide at base, terminal cells often 2–2.5:1. *S. lingulata* v. *microphylla*

1. Unable to form reddish leaf pigments; sun forms with leaf lobes brown (often strongly so). Perianth closely, strongly ciliate-fimbriate with teeth to 3–8 cells long or more. (Ventral lobes typically lingulate, rounded but often with 1-several minute, 1-celled teeth). *S. lingulata* v. *lingulata*

We have attempted to find differences in keel form between the above taxa. In all of them (including larger, *Scapanioid* phases of *S. obcordata*) the basal sector of the keel is a little sheathing and, above the juncture with stem, for some distance polystratose; medially it normally becomes unistratose (although in *S. l. microphylla* it may remain somewhat more folded and locally 2-layered); distally it may become quite sharp. Although more prolonged study may reveal significant differences, variation between weak and strong individuals within the population is at least as great as that from taxon to taxon.

We had, variously, at one time considered *S. microphylla* as an entirely independent species, as wholly identical with *S. lingulata*, or as identical with the plant here described as *S. perssonii;* on another occasion we were convinced that all three taxa had to be united. A partial solution to this problem came through study of the plants—a mod. *viridis*—from Sarfaq (70–2364), in which the most mature shoot sectors, from nongemmiparous areas, had the obovate-lingulate, rounded ventral lobes typical of *S. lingulata*—yet, with prolonged search, a single plant with feebly vinaceous, red ventral leaf bases was found. This plant was identical cytologically with plants lacking this pigment. The obvious conclusion was that a population at the environmental threshold for pigment production was at hand. Identical in almost all respects are plants from Jakobshavn (66–0226), but here the vinaceous pigmentation is slightly more widespread. In both phenotypes there is a marked tendency, *vis à vis* plants from non-Arctic sites, for coarser dentition to be associated with gemma production.

As a consequence we are convinced a situation parallel to that of *S. irrigua* is at hand: in the latter, the "ordinary" brown sun phenotype

is replaced, chiefly under Arctic conditions, by a phenotype which produces red pigments (ssp. *rufescens*). It thus seems appropriate to distinguish a parallel Arctic variety of *S. lingulata* in which, tardily at least, vinaceous pigmentation of the leaf bases may develop.

Extremes of var. *microphylla* may prove essentially inseparable from the equally large-celled *S. perssonii*. In this last, however, we find the following distinctive ensemble of features that fail to recur in *S. lingulata* (incl. var. *microphylla*): (1) leaves, in larger forms, become broader, with ventral lobes 0.85–0.95 × as wide as long; (2) dorsal lobes tend to be larger, often 0.75 the ventral in size, with associated elongation of the keel; (3) pigmentation of the distal part of the leaves tends to be warm yellow to light chestnut brown, never fuscous; (4) gemmae, which attain an even larger maximal size, often become pinkish, even in phases with limited leaf pigmentation; (5) the perianth mouth is subentire to short-dentate. If it were not for this last criterion we would be inclined to regard *S. perssonii* as a mere high Arctic variety of *S. lingulata*.

Scapania mucronata Buch

Distribution (Map 52)

2: Fortunebay (66–0128b). 11: Qasigíssat (70–2734a). 17: Tupilak (66–0032c). 22: Orpigsôq (70–3107). 53: Søndre Strømfjord (66–0067, 66–0074, 66–0089a, 66–0083, 66–0088a, 66–0084).

S. mucronata is a plastic holarctic species, with a wide range (in North America south to North Carolina and Colorado; see Schuster, 1974; in Europe south to Central Europe); and is perhaps the most common and widely dispersed of the species of the *Curtae*. It occurs (as admittedly atypical phenotypes, regarded as a var. *polaris* Schust.) north to Peary Land and to northernmost Ellesmere Island.

Regionally *S. mucronata* usually occurs as the ssp. *praetervisa* (separately treated below), but also (more rarely) as plants we cannot separate from the ssp. *mucronata*. The above stations include specimens which seem to be typical ssp. *mucronata* or which verge on this (66–0089a, 70–2734a, 70–3107), as well as a few whose morphology is ambiguous and which cannot safely be attributed to either subspecies.

The ssp. *mucronata* seems rare this far north and is only exceptionally typically developed. Regional plants seem to be most frequent in areas with acidic rocks. Thus 70–3107 occurs on gneiss hills; 66–0089a near a lake shore in *Salix*-moss-tundra, under acidic conditions. Associates are few: *Cephaloziella* spp. (sometimes *C. grimsulana*) and *Blepharostoma trichophyllum* ssp. *trichophyllum*.

This subspecies differs from ssp. *praetervisa* chiefly in the smaller dorsal lobes (ca. 0.5–0.55 the ventral in area), the shorter keel (ca. 0.5

length of ventral lobe), the mostly smaller gemmae [ca. 10–14×20–25(27–29) μ]. Gemma size is typical in the plants referred here; in 70–2734a, for example, gemmae range to 14×26 μ in size. Oil-bodies are as in ssp. *praetervisa:* large and ca. (2)3–5(6) per free lobe cell.

ssp. *praetervisa* (MEYL.) SCHUST.

Distribution (Map 52)

1A: Behind Arctic Station (66–0187, 70–2048, 70–2053, 70–2057). 1B: Lyngmarken (66–0342). 6: Eqalúnguit (70–2220b, 70–2240, 70–2242, 70–2243a, 70–2244a, 70–2247a, 70–2254). 8: Kuánerssuit (70–2129, 70–2134, 70–2154). 9: Eqaluit (70–2558). 12: Perdlertut (70–2695). 14: Hareøen (70–2601, 70–2616). 18: Grønne Ejland (70–2811). 21: Umiasugssûp (70–2945b). 23: Kangersuneq (70–3149a). 25: Sarfaq (70–2339, 70–2352, 70–2355, 70–2358, 70–2359, 70–2365b, 70–2374a). 26: Pâkitsup ilordlia (70–2256, 70–2273, 70–2275, 70–2284, 70–2306, 70–2308a, 70–2388, 70–2395). 29: Ritenbenk (66–0267). 30: Eqe (66–0251, 66–0339a). 31: Anap nunâ (70–2405a, 70–2409, 70–2410, 70–2424). 36: Umanak (66–1561). 37: Agpat (66–1467d, 70–1469). 38: Uvkusigssat (66–1393). 42: Magdlak (66–1375a). 43: Kangerdlugssuakavsak (66–1280a, 66–1283c, 66–1287a). 44: Akuliarusikavsak (66–1320). 50: Simiútap kûa, valley (66–0866).

Additional collections:

1: Godhavn (LAGERKRANZ 1934, M.P.P. 357). 6: Eqalúnguit (M.P.P. 2642). 16: Manîtsoq (W. & H. July 1884). 17: Tupilak (K.H. June 1956). 24: Jakobshavn (S.B. Aug. 1870). 44: Akuliarusikavsak (K.H. 15.882, 16.690). 45: Sagdliaruseq (K.H. 16.933). 66: Gamle Qutdligssat (M.P.P. 2956). 88: Christianshåb (K.H. 16.630h). 95: Pâkitsoq (J.V. 166). 96: Qeqertaq (S.B. Aug. 1870). 129: Avatausaligssuaq (K.J. 914). 131a: Agpat, Qaqortuatsiaq (K.H. & G.M. 71–1693). 139: Qaqortukavsaq (K.H. 16.112). 141: Inukavsait qáqarssue (K.H. 16.286c).

This taxon, previously reported from the Alps and Scandinavia, is common in West Greenland—perhaps the most frequent member of the *Curtae.* It is most common in—but is not confined to—basaltic regions and may occur on gneissic rocks lying below basaltic cliffs (as at Eqalúnguit, 70–2242, 70–2243a, 70–2244a; then with the Ca-tolerant *Odontoschisma macounii*, *Cephalozia pleniceps*, and *Lophozia heterocolpos*, but also the Ca-intolerant *S. crassiretis*, *S. parvifolia*, and *Gymnomitrion concinnatum*) but is most frequent on humus or soil over basalt. When growing over rather rich, deep, moist humus, *S. brevicaulis* may be associated (70–2129, 70–2134). On relatively exposed, thinner soil over basalt, or in basalt crevices, it is typically found with *Peltolepis grandis*, *Athalamia hyalina*, *Tritomaria heterophylla*, *Solenostoma subellipticum* (70–2410, 70–2409). In moister, shaded sites, as in basaltic ravines, or on damp ledges or cliff walls, often with *S. gymnostomophila*, *T. heterophylla*, and *Solenostoma pumilum* (66–1280a, 66–1283c), sometimes also *T. scitula* and *T. quinquedentata* (66–1287a); on basalt dikes sometimes with *Lophozia heterocolpos*, *L. quadriloba* and *T. quinquedentata* (66–0339a).

Although usually stated to occur only over basic substrates (Buch, 1928), ssp. *praetervisa* may also occur under rather exposed and noncalcareous conditions; thus on soil over gneissic, damp rocks it may be associated with *Marsupella ustulata*, *Diplophyllum taxifolium*, and *S. lingulata* (70–2053); over noncalcareous rocks with *Cephaloziella byssacea*, *L. hatcheri*, and *L. excisa* (66–1469). Exposed phenotypes with reddish, mature gemmae are also found in gneissic regions, with *Gymnomitrion corallioides*, *Nardia geoscyphus*, and *L. excisa* (70–2388). Similar phenotypes may occur with *L. hatcheri* and occasionally *L. alpestris* (70–2048, 70–2395).

In addition to the usual mesic occurrences of the species in both calcareous and acidic sites, ssp. *praetervisa* may undergo ecesis in very exposed sites and then occurs in hardly recognizable manifestations. Perhaps the most extreme site was on glacier-deposited rock meal along a shallow lake in a raised glacial valley where the species grew on exposed, broken, fine soil, associated with *Prasanthus suecicus*, *Anthelia juratzkana*, and *Nardia geoscyphus* (70–3149a). These plants were mostly dwarfed, very compactly dense-leaved, and had brilliant reddish masses of gemmae at the shoot tips; their microscopic characters, however, were clearly those of ssp. *praetervisa*. Oil-bodies were as usual (large, to 6–7 × 9 μ) and occurred 3–6(7) per lobe cell; the reddish gemmae ranged from 12×20 to 15–17×24 μ. The only point of major deviation was a single unfertilized perianth whose mouth bore remote, mostly 1–3-celled teeth, with only 1 or 2 broader-based, larger teeth.

The preceding discussion fails to exhaust the ecological extremes and consociates of ssp. *praetervisa*, but largely delimits the ecological perimeters. The plant is a critical taxon which differs from ssp. *mucronata* not only in the larger dorsal lobes (usually 0.55–0.65 ventral in area) and the longer keel (to 0.65 ventral lobe length), but also in the sporadic tendency to develop denticulations of nongemmiparous leaves (especially in areas adjacent to the gynoecium). Occasional collections are troublesome; thus plants from Disko Fjord (70–2240, 70–2243a), which are "typical" in cell size, absence of a border, lack of red pigmentation (aside from the older gemmae, which may be tardily reddish), and in the, usually, 3–6 very large oil-bodies per cell, are deviant in: (1) lack of any teeth of the leaves, even associated with gemma formation; (2) often obscure or obsolete mucro of the ventral lobe apices. Yet, isolated plants, from the same small locality (and with the same associates: *S. parvifolia*, *S. crassiretis*, *L. alpestris;* 70–2220b), not only have strong dentition associated with gemma formation, but (larger plants) develop leaves with rather concave ventral lobes (with raised edges on distal portions of the lobes) which are broadly rounded, denticulations aside, apically. The obovate to lingulate form of the ventral lobes is here clearly identical to

that typical of *S. lingulata*. Oil-body number (3–6 per lobe cell), marginal cell size (17–19 μ, average), and the often large dorsal lobes, however, are all typical of *S. mucronata praetervisa*. It is possible that the stimulus to tooth formation, associated with gemma formation, is more or less latent in ssp. *praetervisa* (and essentially suppressed in ssp. *mucronata*), but under conditions of difficulty in water uptake (as is suggested by the optimal development of coarse trigones, and locally, vestiges of thick walls on marginal cells) is expressed to its optimal extent. An approach to *S. lingulata* also occurs in extreme sun forms (as in 70–2424, Anap nunâ), in which blunt or exceptionally even rounded and rather lingulate ventral lobes may be found. Such plants differ from *S. lingulata* in the (a) fewer oil-bodies, usually 3–6 per cell; (b) much larger dorsal lobes and longer keel; (c) smaller cells of the ventral leaf margin, averaging below 17–19 μ. Such plants, however, may also approach *S. lingulata* in the perianth mouth: this is, then, closely ciliate-laciniate, with intermingled, crowded cilia and narrow laciniae (the latter 2–4 cells broad at base, often bearing 1–2 smaller basal teeth).

Dentition of the perianth mouth, however, is sometimes a distressingly variable feature within plants occupying a single, small patch. Thus in 70–2409 (Anap nunâ) many perianths bear coarse, closely crowded cilia and laciniae that are basally armed with 1–2 smaller teeth; others bear only small and more remote cilia 2–4 cells long, arising from a broader base, and, in extreme cases, the dentition is reduced to small, 1–2-celled, very remote teeth, the perianth apex being hardly lobulate and appearing subentire. No other taxon in the *Curtae* exhibits such drastic variation in perianth mouth dentition.

Although perianths (and ♂ plants) are common in ssp. *praetervisa*, capsules are rarely produced (as, e.g., in 70–2244a, July 11, and 70–2273, July 20). Gemmae are always common; although sometimes not larger than in ssp. *mucronata* (only 13–15×22–28 μ in 70–2240, to 14×25 μ in 70–2306), they range slightly larger than in this subspecies. Thus in 70–2284 they are mostly 13–16×22–25 μ, but a few are to 14×30 μ; in 70–2374a they range to 14–19×31 to 16×29 μ; in 70–2352 they are 12–16×22–29(31) μ.

Scapania scandica (ARN. & BUCH) MACV.

Distribution (Map 53)

17: Tupilak (66–0021a). 23: Kangersuneq (70–3144b, 70–3147, 70–3146 all as f. *argutedentata* BUCH). 39: Tasiussaq (66–1259). 49: Skalø (66–1012).

Additional collections:

83: Angnertussoq (L.H. Aug. 1932). 145: Uligssat (K.J. 10.188).

Locally *S. scandica* is a rare species; it is a boreal to low Arctic, predominantly oceanic, species, apparently absent or at least very rare

in the high Arctic. As is noted below, in the Arctic it tends to "blend" into other species recognized in the *Curtae*. There are a few collections of poor material from Inglefield Bredning (RMS) which may represent an extreme of this species. An earlier report of *S. scandica* from Pandora Harbour, Inglefield Land (HARMSEN & SEIDENFADEN, 1932) represents *S. mucronata s. l.* Southward the species occurs in the western hemisphere to Maine, Massachusetts, and New York; collections from the last two loci are also atypical. Indeed, with study of material from the perimeters of the range, the boundaries of *S. scandica* become much less precise than the work of BUCH (1928) would lead one to believe. In Greenland the species is previously recorded only from Gåseland, Scoresby Sd., and Frederikshåb, by BUCH (l.c., p. 77).

Regional material is chiefly from areas with igneous rock. Associates are *Lophozia kunzeana* and *Blepharostoma trichophyllum brevirete* (66–0021 a), and *Cephalozia pleniceps*, *S. hyperborea*, *Pleuroclada albescens*, and *Nardia geoscyphus* (70–3144 b, 70–3146). Plants from the last locality occurred on thin, damp, exposed peaty soil over exposed "rock meal" deposited around a glacial lake; those of 70–3147 are from soil over ledges, associated with *Blepharostoma* and *S. paludicola rotundiloba.*

The distinction between *S. scandica* and *S. parvifolia* is often critical. Indeed, except for the leaf border, which is usually very conspicuous in the latter and absent or vestigial in the former, few convincing distinctions exist. Plants of 70–3144b and 70–3147 both differ from "normal" *S. scandica* in having the nearly erect dorsal lobes almost pointed towards the shoot apex (especially on weaker plants), much as in *S. parvifolia.* They differ from this last in the basically blunt, lingulate ventral lobes which are, however, reddish to purplish at the base, much as in *S. parvifolia.* As in *S. parvifolia*, leaf margins may bear cilia 2–4 cells long, especially of lobe apices associated with gemma formation. A feeble border is distinct, but this is also found in other phenotypes of *S. scandica* (as, e.g., in plants collected by RMS in Nova Scotia). The perianth mouth shows much variation in degree of dentition, although it is usually described as being entire to subentire. In the aforementioned plants, which belong to *f. argutedentata* (BUCH) SCHUST., there may be strong teeth present (70–3144b), or the teeth may be small, and the perianth mouth entire to subentire (70–3147). The strong dentition, lack of obvious border, blunt ventral lobes (when teeth are not present), small gemmae (averaging 8–10 × 16–20 μ) and small marginal cells (14–20, rarely to 22 μ, on ventral margin) suggest these collections must be referred to *S. scandica.* Also belonging here is 70–3146, which lacks a distinct margin; its gemmae are mostly 10–12 × 20–22 μ, a few larger, marginal cells 17–20 μ. In plants of 70–3146, as in the other collections from Kangersuneq, oil-bodies are 2–5(6) per lobe cell, closely matching those of *S. parvifolia.*

Plants of 70–3147 have been repeatedly studied—there are no wall pigments except that a few plants have a violet (rather than vinaceous) pigmentation of postical leaf bases. ♂ Plants often have very spinose-caudate dorsal lobe tips, associated with gemma formation, and often strikingly apiculate-acuminate ventral lobes, as well as some added sharp, scattered teeth—eliminating all but *S. scandica* f. *argutedentata* and *S. parvifolia*. The question, indeed, is which of these two taxa is at hand. Oil-bodies, typically (2)3–5(6–7) per lobe cell, are usually quite large and tend to occlude much of the lumen (unlike in *S. curta*), but on the few edentate plants are perceptibly smaller and *curta*-like. The leaf border in these plants is critical: sometimes present, sometimes not. Taking individual shoots through BUCH's key, for example, one comes to either *S. scandica* or *S. parvifolia*. An added complication are some shoots with larger than normal cells, and cells which in general are somewhat larger than normal for *S. parvifolia*. Keel length varies widely: all strongly dentate ♂ plants have a short keel and narrowly ovate, dorsal lobes, exactly as in *S. parvifolia* (but also like much of *S. scandica* f. *argutedentata*). The few ♀ plants seen have a longer keel and are more *curta*-like. The questions raised by these plants are many, e.g., (a) if they are one species, and belong to the *Marginatae*, sexual dimorphism between ♀ plants (more *curta*-like) and ♂ plants (more *parvifolia*-like) must be admitted; (b) is the distinction between *Marginatae* and *Immarginatae* raised by BUCH valid; often it is useful, but in actual fact, do not the present plants fall midway between? Also, plants of *S. scandica* var. *dimorpha* SCHUST. (from Nova Scotia), identified with *S. scandica* by S. ARNELL, may have a weak border formed by 1 cell row.

Not only do the plants from Kangersuneq raise major taxonomic problems *vis à vis* the distinction between *S. parvifolia* and *S. scandica*, but the single collection from Tupilak (66–0021) is a problem in other directions: it has marginal cells 15–20 μ and gemmae (which are restricted to lobe apices) 13–18×19–22 μ; ventral lobes are mostly blunt. The gemma size is rather too large for *S. scandica*, suggesting *S. lingulata* (to which the blunt ventral lobes also suggest an affinity). This last species, however, has much larger marginal cells.

We also refer to *S. scandica*, with some reservations, plants from Skalø (66–1012), of the mod. *viridis;* the leaves, which bear few or no gemmae, tend to have rounded and rather lingulate ventral lobes, and the cuticle is very closely roughened—both features suggesting *S. scandica*. Marginal cells (16–18, rarely to 20 μ) also agree with *S. scandica*, but the gemmae (up to an isolated maximum of 12–13×26–28 μ, although mostly smaller) seem too large for *S. scandica* and suggest *S. mucronata* or even *S. lingulata*. Even more critical is material of 66–1259 from Qaumarujuk; here we find, as in 66–1012, a mod. *viridis* (at most with

faint brownish pigments of the leaf lobes distally), with marginal cells 14–19 μ, and greenish gemmae 12×23–25 μ. The cells have rather coarse trigones and there is no trace of a border; the cuticle is rather strongly roughened. Most notable, ventral lobes are typically lingulate, broadly rounded at the apex, much as in *S. lingulata;* associated with slight gemma formation is virtual lack of dentition, although a very few obsolete 1-celled teeth can be found. Most important, bracts on the ♀ plants have diagnostically lingulate, broadly rounded ventral lobes—an unmistakable character of both *S. lingulata* and *S. scandica.* The perianth mouth, however, is "intermediate": it has crowded variable teeth, often 2–3 cells wide at base × 2–4 cells long (the longer teeth are uniseriate for 2–3 cells). The teeth are too short for *S. lingulata*, too short and narrow for *S. mucronata*—but too strong for "normal" *S. scandica*, in which the perianth mouth is subentire to toothed with, at best, 1–2(3)-celled teeth.

These observations on 66–0021, 66–1012, and 66–1259 suggest that boundaries between *S. scandica* and the *S. mucronata-lingulata* complex may be almost wholly bridged. Plants of this type never develop sharp marginal teeth associated with gemma formation such as occur in *S. scandica argutedentata*, or in *S. parvifolia.* It is not impossible that such seeming transitions may be the result of former hybridization or introgression of genes from one taxon to the next. Such a hypothesis, however, must be tested experimentally. In the meantime, we must continue to acknowledge the existence of marginal specimens, whose attribution is on the basis of approximation to recognized "species", rather than on the basis of total correspondence. In part this may reflect poor development of the species at its Arctic periphery.

Occasional collections of *S. curta isoloba* (as, e.g., 66–0163a) so closely approach *S. scandica* that they can be confused with it. Such plants may have the border weakly developed, only 1(2) cells broad, and have rounded to blunt ventral lobe apices. The perianth mouth is only denticulate to short-dentate—the plant thus being intermediate between "normal" *S. curta* and "normal" *S. scandica.* The marked tendency for dorsal lobes to be subequal to the ventral in size and often blunt at the tip suggests such plants, in spite of the weak border, must go into *S. curta isoloba.*

Sectio *Irriguae* K. Müll. emend. Buch

The *Irriguae* exhibit many of the same taxonomic problems in the Arctic as the closely related "*Immarginatae*" of the sect. *Curtae:* dentition, pigmentation and form of the leaf lobes (pointed vs. rounded) tend to show discrepancies *vis à vis* populations from temperate zones. We have adopted a more conservative taxonomic treatment here than Buch (1928) proposed in the *Curtae:* thus *S. irrigua rufescens* and *S. paludicola*

rotundiloba differ from their "parent" species to the same extent—and in similar features— as do "species" in the *Curtae*. It may prove necessary, in order to achieve a consistent taxonomy, to either reduce some of the species accepted by BUCH in the *Curtae*, or to raise some of the varieties we admit in the *Irriguae*. The problem, basically, is that there has been re-shuffling of the same limited "gene pool" in both groups: pigmentation, oil-body number + size, dentition, lobe apex form (sharp vs. rounded), keel length, and cuticle form. Superposed, perhaps, is polyploidy (thus *S. lingulata* appears to bear the same relationship to *S. mucronata* as *S. tundrae* does to *S. hyperborea*). It seems to us that the bewildering taxonomic situation now existing in the *Curtae* and *Irriguae* is likely to be resolved only with much modern experimental taxonomy, and that any solutions dictated by a nonexperimental approach may have only temporary value. The detailed observations on several of the *Irriguae*, which parallel those given for the *Curtae*, are intended to supplement the useful—but for Arctic taxa over-simple—account in BUCH l.c. That in MÜLLER (1951–58) is relatively static and perfunctory.

Scapania irrigua (NEES) DUMORT.

There are many reports of *S. irrigua* from Greenland, most of which must be viewed with suspicion; the species is reported as far north as Peary Land (ARNELL, 1960); these plants are all *S. gymnostomophila*. Collections from northern parts of East Greenland (e.g., Danmark Ø, Scoresby Sund, leg. HARTZ, 1892) that have been called *S. irrigua*, represent *S. obcordata*.

Although this species has been previously reported from several loci on the West Greenland coast, south of our region (Sukkertoppen; fjord S. of Frederikshåb; Agdluitsoq, Tasermiut Fjord; see LANGE & JENSEN, 1887), all collections studied from our area represent the following subspecies:

ssp. *rufescens* (LOESKE) SCHUST. (Figs. 16:1, 19:11–12)

Distribution (Map 54)

1A: Behind Arctic Station (66–0153a, 66–0154, 66–0155a, 66–0156, 66–0164, 66–0180). 1B: Lyngmarken (66–0562, 66–0569). 1C: Blæsedalen (66–1571). 2: Fortune-bay (66–0134, 66–0198). 9: Eqaluit (70–2523a, 70–2537). 14: Hareøen (70–2587). 21: Umiasugssûp (70–2937, 70–2940a, 70–2951b). 23: Kangersuneq (70–3127, 70–3129a, 70–3135, 70–3136a, 70–3137, 70–3138, 70–3139b, 70–3150, 70–3159a). 25: Sarfaq (70–2336a, 70–2340a, 70–2361, 70–2364, 70–2366, 70–2367a). 26: Pâkitsup ilordlia (70–2265, 70–2283, 70–2288, 70–2291a, 70–2386, 70–2389, 70–2390). 29: Ritenbenk (66–0259, 66–0262a).

Additional collections:

6: Eqalúnguit (M.P.P. 3849). 60: Kugssuaq (M.P.P. 716). 139: Qaqortukavsak (K.H. 16.082, 16.083).

This appears to be a largely Arctic subspecies, extending southward (usually as hardly typical phenotypes) to Minnesota and Quebec. The type, from the Harz Mts., Germany, is "more brownish red" than normal and is also not fully typical. The present reports appear to be the northernmost ones for the species *s. l.* from the western hemisphere, although there are reports from Jan Mayen and Spitsbergen.

The ssp. *rufescens* is basically similar to ssp. *irrigua* except that (a) leaf lobes are consistently edentate and rounded to (on weak shoots) blunt; (b) secondary reddish to vinaceous pigmentation is present in all but extreme shade forms; (c) gemmae are ovoid, somewhat shorter and broader, averaging (11)12–16×(18)19–22(27) μ (may range to 12–14× 22–24 μ, to 12×26–27 μ up to 14–16×20–23 μ). In ssp. *irrigua* gemmae are usually fully twice as long as wide, ellipsoidal to fusiform, and average 9–12×20–28 μ. Shade forms collected in early spring, prior to gemma initiation, may be difficult to identify since they lack reddish coloration, but even then, however, there are usually traces on the ventral leaf bases near the shoot tips. The consistently edentate and usually rounded leaf lobes are also distinctive but they may lead to confusion with *S. hyperborea.*

S. irrigua rufescens is often a species of rapidly flowing water in igneous regions. It is probably more common in the gneissic interior regions than the above reports suggest, and is there found on rocks or ledges adjoining rills and cascades, often on thin, sandy or silty, water-deposited soil, sometimes with *S. subalpina*, *S. lingulata*, *Anthelia*, *Cephalozia bicuspidata*, *Solenostoma pumilum s. l.*, *S. subellipticum*, and *Nardia geoscyphus* (70–3127). In similar but more exposed sites it may occur with *Marsupella arctica*, *S. pulcherrima*, *S. hyperborea*, *S. subalpina*, *Lophozia kunzeana*, *Solenostoma oblongifolium s. l.*, *Anthelia*, and *N. geoscyphus* (in 70–2951b). When somewhat farther from water, *Tritomaria quinquedentata* and sometimes *L. excisa* and/or *L. ventricosa rigida* may be consociated (70–3159a, 70–2361). Occasionally, however, *S. irrigua rufescens* is found on fine, water-deposited "rock-meal" on damp ground along lake shores with *Blasia pusilla* and *Cephaloziella grimsulana* (70–3150).

Exceptionally this taxon may occur under clearly basic conditions on calcareous, irrigated, damp slopes, then mixed with *S. cuspiduligera*, *Preissia*, *L. excisa*, *L. quadriloba*, *L. polaris*, and *T. quinquedentata* (70–2587), or with *T. polita polymorpha* and *N. geoscyphus* (70–2537). Frequently found over permanently damp, fine-textured silty soils or clays away from running water; then *N. geoscyphus* is almost always associated (70–2336a, 66–0154, 70–2283, 70–2288, 70–3138). In such loci *L. wenzelii* (both vars. *wenzelii* and *lapponica*) may also occur admixed (70–2523a, 66–0262a), very occasionally *S. hyperborea.* When the last

species is admixed, difficulties may arise in separating the two. Gemma color, however (greenish at maturity in *S. irrigua rufescens*, reddish in *S. hyperborea*), is usually enough to separate the two at a glance, although very early in the growing season, when gemma formation is just initiated, gemmae in *S. hyperborea* may be colorless. They are, however, usually more broadly ellipsoidal and—even early in the season—show a little pinkish wall pigment as they approach maturity.

Ssp. *rufescens* is moderately variable in West Greenland. Some plants (70–2265) may have, in part, almost semicircularly arched keels; they also may have relatively large oil-bodies, 2–4 per cell, occasionally attaining a size of $7 \times 10\ \mu$. Occasional collections (e.g., 66–0134) may have somewhat larger than normal dorsal lobes, approaching 0.75 the ventral in size—with the only feebly concave keel then ca. 0.6 the ventral lobe length. Such plants may be dififcult to separate from *S. hyperborea*.

Branching in at least some forms of this species (66–0134) may be exclusively or preponderantly terminal, basiscopic, of the *Radula* type. The branches then vary rather much in vigor, but, as in *Radula*, are always initially much inferior in vigor to the main axis. We have seen such terminal branching again only once, in *S. irrigua*, in a collection from Kap Ravn, East Greenland (cited by HARMSEN, 1933, as *S. hyperborea*). Normal branching is lateral-intercalary and axillary.

Occasional small forms of ssp. *rufescens* may cause difficulties. Thus, a mod. *parvifolia-angustifolia-colorata* from Sarfaq may be a problem. These plants occur, variously, on moist cliff walls with *S. curta grandiretis*, *Marsupella revoluta*, *Anthelia* (70–2340a), or on broken, stony soil, with *S. lingulata*, *S. curta curta*, *S. curta grandiretis*, *L. polaris*, *L. ventricosa confusa*, *Solenostoma subellipticum*, and *Prasanthus* (70–2364, 70–2366). They may be only 0.8–1.2 mm wide and, because of the narrow ventral lobes (ca. 0.5–0.85 wide as long) confused with the *Curtae*, where, on account of the reddish to purplish coloration, they may be sought under *S. scandica* or (because of the often blunt dorsal lobes, especially of ♂ shoots) under *S. helvetica*. The correct attribution of such juvenile phases almost depends on finding, in the same locality, more typical material of the taxon from which one can extrapolate to the juvenile phenotype. Such minute, hardly recognizable plants may furthermore produce androecia, leading to the assumption that the mature state of an independent (and undescribed) species is at hand. Until and unless perianths are found, however, and these show additional differential criteria, we see no point in considering such small, highly colored forms as more than dwarf manifestations of *S. irrigua rufescens*. Such small phases may also be confused with *S. obcordata*, but they are at once distinct in two features: some leaves, at least, have a concavely arched keel; the keel is at least sporadically ridged and often winged throughout its length.

When without gemmae, and as the mod. *viridis*, *S. irrigua rufescens* may be almost impossible to separate from *S. hyperborea*, since both have blunt to rounded and entire-margined ventral lobes. There is no doubt that two well-defined species are at hand, as is shown by 66–0262a, where we find admixed (a) pink-purple tinted or reddish ♂ plants, with green gemmae, of *S. irrigua rufescens;* (b) brownish pigmented, rather small plants, with a few tardily reddish gemmae, which are clearly a mod. *parvifolia* of *S. hyperborea.*

Several questionable specimens, especially 70–2950 (see also under *S. paludicola viridigemma*) and 70–2937 (see above under *S. irrigua rufescens*) need a separate discussion. They are of phenotypes with the ovate-oblong ventral lobes (width: length ca. 0.8–1:1) usually (but not always) rounded distally, typical of ssp. *rufescens;* both show the reddish color of that taxon; both have greenish gemmae, those of 70–2937 averaging 10–13×16–26 μ. These plants not infrequently (and in the case of 70–2950, often) possess strongly arcuate keels that become abbreviated in length—a *paludicola* character. We think it probable that these plants (and perhaps also 66–0313, from Disko, cited under *S. paludicola viridigemma*) may all represent phases of *S. irrigua rufescens* in which, perhaps, there has been introgression of some genes from *S. paludicola.*

These plants, all smaller than "normal" *S. paludicola*, grew at least in part under exposed but subaquatic conditions; in 70–2937 the plants were from insolated rock pools, with *Odontoschisma elongatum*, and are strongly brownish + reddish pigmented. Associated, perhaps, with the subaquatic growth, the subfloral innovations beneath the unfertilized gynoecia often show 1 or 2 smoothly originating, clearly terminal branches, sometimes one almost opposed to the other. These branches, owing to the malformation of the leaves which are juvenile in aspect, are difficult to interpret, but seem to be of the *Radula* type. At least no recognizable half-leaves are associated.

Scapania hyperborea Joerg. (Fig. 16:2–12, 18–19)

Distribution (Map 55)

1A: Behind Arctic Station (66–0155a, 66–0156, 66–0190a, 66–0191a, 66–0287, 70–2003a, 70–2013, 70–2014, 70–2015, 70–2033, 70–2041, 70–2044). 1B: Lyngmarken (66–0550a, 66–0552a trans. ad *Sc. kaurinii*). 1D: Skarvefjeld (66–0408, 66–0417, 66–0418). 2: Fortunebay (66–0145, 66–0214). 4: Flakkerhuk (66–0357). 6: Eqalúnguit (70–2216b, 70–2246). 9: Eqaluit (70–2520, 70–2533a, 70–2542, 70–2553a, 70–2557). 10: Enoks Havn (70–2757). 15: Kronprinsens Ejland (70–2062, 70–2082, 70–2085a, 70–2086a, 70–2087, 70–2089b, 70–2090, 70–2092, 70–2093, 70–2097, 70–2098, 70–2099, 70–2112, 70–2114, 70–2116a). 16: Manîtsoq (70–3012, 70–3018, 70–3024). 17: Tupilak (66–0009, 66–0022, 66–0027b, 66–0029a, 66–0034a, 66–0036). 17A: Egedesminde (66–0944, 66–0945, 66–0946). 19: Nûk (70–2836, 70–2839, 70–

2842, 70–2849a, 70–2869, 70–2876b, 70–2878a). 21: Umiasugssûp (70–2934a, 70–2936a, 70–2940a, 70–2942a, 70–2943a, 70–2946a, 70–2951b). 22: Orpigsôq (70–3108b). 23: Kangersuneq (70–3131b, 70–3134, 70–3135, 70–3140b, 70–3144, 70–3147, 70–3152, 70–3135b, 70–3156). 24: Jakobshavn (66–0218a, 66–0224, 66–0225, 66–0246a, 66–0247, 66–0248). 26: Pâkitsup ilordlia (70–2267, 70–2268, 70–2280, 70–2286, 70–2293, 70–2296, 70–2305, 70–2316a, 70–2319, 70–2382, 70–2387). 27: Arveprinsens Ejland (66–0489, 66–0492). 29: Ritenbenk (66–0252a, 66–0262a, 66–0268). 32: Qôrorssuaq (70–2442). 36: Umanak (66–1477, 66–1483, 66–1490, 66–1565). 37: Agpat (66–1426, 66–1468b). 45: Sagdliaruseq (66–1053).

Additional collections:

17: Tupilak (K.J. 1312). 24: Jakobshavn (K.H. 16.912). 29: Ritenbenk (S.B. Aug. 1870). 83: Angnertussoq (L.H. Aug. 1932). 86: Seqíneqârajutoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.631a). 92: Claushavn (S.B. 1870). 98: Sarqaq (K.H. 15.804, 15.805, 15.806, 16.717). 124: Tasíngortaq (K.H. 13.309). 136: Kangerdluarssûp qeqertâ (K.H. 16.138). 137: Esersiutilik (K.H. 13.986). 140: Small Island (K.H. 16.736).

S. hyperborea is an Arctic-alpine species of, basically, circumpolar range. In Greenland it extends north to Pandora Harbour (78°14′N., HARMSEN & SEIDENFADEN, 1932) and to Steensby Land, Nucluet (76°57′N., RMS, unpubl.). Southernmost stations in North America are in alpine sites in New Hampshire and Maine. The species is perhaps the most conspicuous and frequent *Scapania* in West Greenland; it is also perhaps the most plastic and difficult to comprehend. Two variants are separately described below (p. 257–58) since they appear to represent genotypically distinct entities. In addition there is a tremendous amount of phenetic variation which is largely, if not wholly, environmental in origin. For this reason we treat the species below in terms of "*helvetica*", "*kaurinii*", "*hyperborea*", and "*paludicola-degenii*" phenotypes. These, in part, are ecological responses; hence the ecology of the species is dealt with under each of these phenotypes. In general, *S. hyperborea* is best developed in fens and moors, frequently around rock-bordered tarns, often where it is likely to remain permanently moist, often where strongly exposed. The "normal" *hyperborea* phenotype always occurs in such sites. Although perhaps most common in areas with gneissic rocks, the species occasionally occurs in areas with basaltic rocks. Due to the complexity of the species, the extremes are dealt with separately, as below:

(a) *Hyperborea* Phenotype. This, the "normal" phase, is a medium-large to large plant, often 2.5–3.5 mm wide, strongly dorsiventrally compressed, with rather convex dorsal lobes that are blunt to bluntly pointed at the apex; the ventral lobes are at least 0.85 as wide as long and usually rounded at the apex, varying to (occasionally) blunt. No dentition is ever present (Fig. 16:8–12).

This phenotype is confined to permanently damp areas. It may occur on damp, silty or clayey soil ("rock-meal", water-deposited)

around lake margins, in areas with gneissic rocks (as, e.g., E. of Ivnarssuaq, 70–3135, 70–3144, 70–3156) or at Eqaluit (70–2553a), then with *Pleuroclada*, *Nardia geoscyphus*, *Lophozia wenzelii* (incl. var. *lapponica*), *L. kunzeana*, *Cephalozia bicuspidata*, *S. scandica* f. *argutedentata*, *Anthelia*. Occurrences, in such sites, with *N. geoscyphus* are almost constant (as, e.g., in 70–2942a; 70–2946a, at Umiasugssûp). More common, however, are occurrences around the margins of sunny rock pools (e.g., at Ritenbenk, 66–0252a; Manîtsoq, 70–3012; Nunarssuaq, 70–2114; Godhavn, 66–0191a; Jakobshavn, 66–0246a), then with *Cephaloziella arctica*, *Gymnocolea inflata*, *Marsupella arctica*, *S. paludicola s. l.*, *Odontoschisma elongatum*, *L. kunzeana*, *L. wenzelii*, *L. ventricosa s. l.* Similar, but ecologically more advanced, are sites in wet, rich fens developed around shallow tarns (as at Nûk, 70–2842, 70–2878a; also at Orpigsôq, 70–3108b; Jakobshavn, 66–0225; and Nunarssuaq, 70–2099). Then *O. elongatum*, *L. binsteadii*, *L. kunzeana*, *L. ventricosa confusa*, *Pleuroclada* may be associated, or, with development of rich, peaty vegetation, *Cephalozia pleniceps*, *C. bicuspidata*, *Calypogeia sphagnicola*, rarely also (70–2757, Enoks Havn) *L. excisa;* under very wet conditions *S. paludicola rotundiloba*, *L. ventricosa silvicola*, *O. macounii*, *S. parvifolia* (as in 70–2849a, 70–2869) or *Aneura pinguis* and *Cephaloziella byssacea* (70–2876b) may be associated, or (70–2092, Nunarssuaq) *Paludella squarrosa* and *Sphagnum*, especially when there seems to be feebly basic seepage.

Rather different ecologically are habitats over peaty soil along cascading rills (as at Qôrorssuaq, 70–2442), where mixed with *Marsupella boeckii*, *M. groenlandica*, and *Gymnocolea inflata*.

Oil-bodies are usually rather small and 3–5(6) per cell (70–2082), ranging to quite small and 5–7 to 7–10 per cell (70–2093), or variable within the same leaf from 2–4 to 7–9 per cell (70–2557).

(b) *Paludicola-degenii* Phenotype. This phase is found in rich fens and seems to be an optimal manifestation of the species. The keel may then become abnormally short, ca. 0.25–0.45 the ventral lobe in length and becomes strongly arched. Such bog forms, indeed, may be difficult to separate from *S. paludicola*, yet the latter and *S. hyperborea* occur intimately intermingled (as in a fen at Nûk) and remain completely distinct. Examples of this phenotype are 66–0944 (Egedesminde) and 70–2116a (Nunarssuaq), which occur with *L. kunzeana* and *Cephalozia bicuspidata*, respectively.

(c) *Helvetica* Phenotype. This represents a mod. *angustifolia-parvifolia* which, when gemma-free (as is often the case) is hardly identifiable. Ironically, plants of this type may not only bear androecia and perianths but may also bear capsules (e.g., 70–2015); the undescribed capsule has the wall 52–55 μ thick, 4-stratose, with epidermal cells 22–24 μ high,

inner cell strata each 8–9 μ thick. Larger plants of this phenotype may approach the "*kaurinii*" phenotype.

Plants of this phenotype typically occur on exposed, peaty ground where they grow closely prostrate, often with *Anthelia*, occasionally *Blepharostoma trichophyllum brevirete*, or small forms of *L. kunzeana*. Morphologically they appear to bridge the gap between *S. scandica* and *S. helvetica*. The greenish to brownish green plants seem to belong to the *Immarginatae* of the *Curtae*. The marginal cells are ca. 17–20 μ; gemmae are light green but reddish at maturity, 2-celled and up to 15×25 μ; oil-bodies are (2)3–6 per cell, thus eliminating *S. lingulata* and *S. perssonii*. Ventral lobes are rounded, eliminating *S. mucronata*. Only *S. scandica* and *S. helvetica* of the described species of the *Curtae* remain. Dorsal lobes of most plants, away from gemmiparous regions, are blunt to rounded—strongly suggesting *S. helvetica* rather than *S. scandica*.

In our opinion these small plants, which have the size and aspect of the *Curtae* and readily key to *S. helvetica* (in, e.g., BUCH, 1928), represent merely small, Arctic, impoverished prostrate phases of *S. hyperborea*, although they may be almost inseparable from *S. helvetica* [and we think that a report of the latter from West Greenland (Tasiussaq, BERGGREN, 1870; see H. W. ARNELL, 1922, p. 37) refers to such a phenocopy of *S. helvetica*]. We have seen a number of such collections of juvenile *S. hyperborea* which could be definitely identified only because more caespitose paludose phases of the species grew nearby, under more optimal conditions. Early in the season, prior to gemma initiation, such mods. *angustifolia-parvifolia* of *S. hyperborea* may be very troublesome. A single collection from South Greenland (Dyrnæs, N. of Narssaq [ELLITSGAARD, July, 1959], with a few juvenile perianths that have a sinuous,

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Fig. 16. *Scapania*, sect. *Irriguae*. (1) *S. irrigua* ssp. *rufescens;* median cells with oil-bodies (×835). (2) *S. hyperborea*, mod. *parvifolia-angustifolia:* ("*helvetica*-like phenotype"); median cells with oil-bodies (×700). (3) Same, similar modification, but mod. *mesoderma* ("*helvetica*-like phenotype"); median cells with oil-bodies (×760). (4) *Scapania hyperborea;* modification with many oil-bodies per cell, (3–4)5–9(11) per cell; median cells with oil-bodies (× ca. 835). (5) Gemmae of plant from fig. 4 (×340). (6) *Scapania hyperborea;* a fuscous modification approaching *S. degenii* v. *dubia;* median cells with oil-bodies (×870). (7) Gemmae of plant in fig. 6 (×320). (8–11) *S. hyperborea*, typical phase; shoot sectors and flattened leaves (×10). (12) Apex (at asterisk) of ventral lobe of fig. 11 (×148). (13) *S. degenii* v. *dubia*, flattened leaf (×10). (14) Ventral lobe apex of 70–2775 (×148). (15) Gemmae (×425). (16) *S. degenii;* lax extreme, mod. *viridis-leptoderma;* shoot apex (×10). (17) Median cells from plant in fig. 16 (×820). (18) *S. hyperborea* f. *subaequalis;* median cells (×760). (19) Gemmae from plant in fig. 18 (×375). [1,66–0154; 2, 70–2003a, 3, 70–2013, all from Godhavn; 4, 66–0218a, Jakobshavn; 6, 66–0357, Flakkerhuk, Disko; 8–11, 70–2757, 13–15, 70–2775; 16–17, 70–2761, all from Enoks Havn, Disko; 18–19, 70–3004, Manîtsoq; 8–11, 13, 16, drawn to 1.5 mm scale; 12, 14, drawn to 100 μ scale].

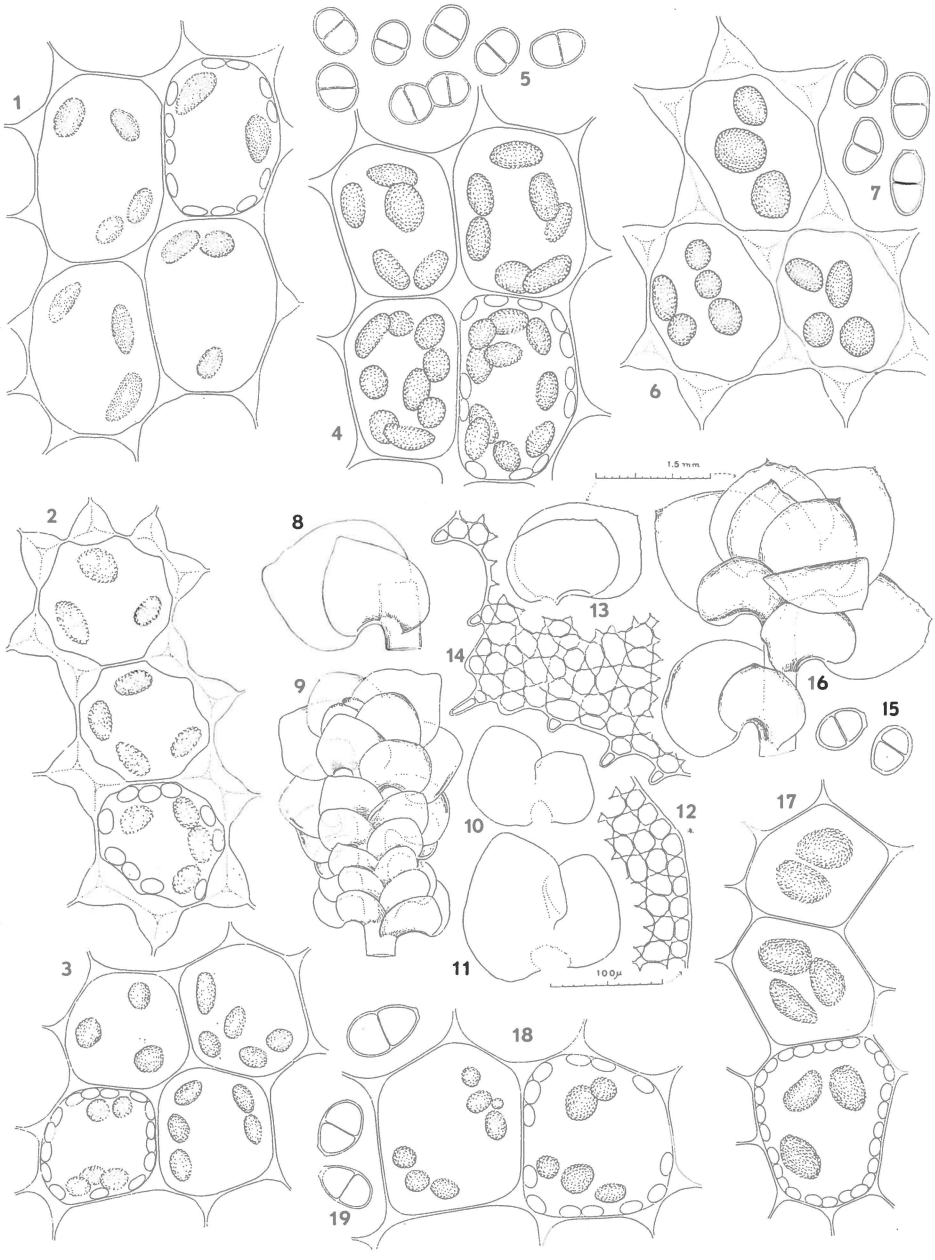


Fig. 16.

almost edentate mouth), although perhaps a juvenile phase of *S. hyperborea*, cannot be so easily dismissed. We would tend to refer these plants to *S. helvetica* if it were not for the fact that the dorsal lobe—exactly as in *S. hyperborea*—is ca. 0.65–0.7 the ventral in size.

Collections representing this phenotype are: 70–2936a, 70–2003a, 70–3153b, 70–2112, 70–2267, 70–2090, 70–2293, 70–2296, 70–2280, 70–2089b, 70–2015. Such phases, of exposed peaty to clayey soil, often occur with *Nardia geoscyphus*, *Anthelia*, *Cephaloziella arctica*, less often *L. ventricosa rigida*, *Anastrophyllum minutum*, *Cephalozia bicuspidata*, *Pleuroclada*, *Tritomaria quinquedentata*, and *S. curta* or *S. subalpina*.

(d) *Kaurinii* Phenotype. Of all extremes of *S. hyperborea* seen this has been the source of the greatest difficulty—going back to BUCH (1928) who reported *S. kaurinii* from Claushavn, Ritenbenk, and Upernavik. The Ritenbenk collection (BERGGREN, 1870) had previously been reported by both BERGGREN, 1875, and LANGE & JENSEN, 1887, as *S. nemorosa* [the Ritenbenk specimen is annotated by BUCH (1927) as being definitely *S. kaurinii* and only as "apparently" dioecious. However, the plants we refer to the *S. kaurinii* phenotypes of *S. hyperborea*—including the Ritenbenk specimen—are definitely dioecious and, in part, show vegetative transition to undoubted *S. hyperborea*]. In essence, a number of collections have been seen with upswept and sometimes antically connivent ventral and dorsal lobes, the lobes both becoming strongly concave (in antical aspect), with the shoot as a consequence strongly convex in ventral aspect or even subcylindrical. Typical of such plants is 66–0009 (Tupilak): it is clearly dioecious, and has shoots ca. 1.8–2.1 mm wide that are usually concave in dorsal aspect; dorsal lobes are often quite concave and rounded or blunt, to at most feebly pointed; ventral lobes are rounded to broadly obtuse; both lobes are quite entire-margined. The keel is ca. 0.3–0.55 the leaf length, mostly 1-stratose but locally 2-stratose. Dorsal lobes are ca. 0.65–0.75 (0.8) the ventral in size, transversely inserted. The ventral lobe is ca. 0.85–0.95 as wide as long, short-decurrent. Cells along leaf margins are collenchymatous like the others, 16–18 μ; cells of leaf middle have moderately strong trigones, 16–22 × 22–27 μ. The leaves, although quite variable, often show the strong antical arching of the outer margins of both dorsal and ventral lobes—so that the plant acquires the uniquely antically concave, postically convex aspect of *S. kaurinii*. This is often developed only very locally; when not expressed, the plant is nearly flat, with the dorsal lobe flat or convex and lying tightly over the slightly to somewhat larger, flat to weakly concave ventral lobe. The aspect, at times, is a little like that of *S. hyperborea* or *S. tundrae*, but the cells are much smaller than in the latter, and the oil-bodies fewer. Gemmae are pale green, varying to

pale reddish, broadly ovoid to subspherical, 2-celled when mature, 12–14×16–19 to 15×21 μ, to (66–0218a) 12–16×16–22 μ.

Such plants differ from true *S. kaurinii* as follows: constantly dioecious—only ♂ plants seen; leaf keel mostly 1-stratose, only locally 2-stratose; stems green to brownish, cortex relatively ill-demarcated, of 1–2 strata of flattened, moderately thick-walled cells with yellow-brown walls, the cortical cells only moderately smaller than the medullary cells; gemmae smaller and less ellipsoidal, often nearly rounded. It is probable that, at least in part, development of the "*kaurinii*" aspect is related to crowding of vigorous plants which are forced to grow erect rather than prostrate. The malleability of *S. hyperborea* can be gauged by study of 70–2033. In this, depending on the shoot sector examined, one can find sectors which correspond to normal *S. hyperborea* (in which the shoot is complanate and the leaf lobes horizontally spread), sectors which correspond with *S. degenii* (sector flat, with laterally patent leaves and a strongly arcuate keel), and sectors which closely simulate the monoecious *S. kaurinii* (leaves antically assurgent, the plants strongly convex ventrally, concave dorsally). In addition, there may be admixed small shoots with the dorsal lobes at most 0.65 the ventral in size; such shoot sectors are vegetatively almost inseparable from *S. helvetica*. Except for the latter plants, all these taxa have red-brown or reddish gemmae.

On shoot sectors corresponding most nearly to ordinary *S. hyperborea*, the keel is only 0.3–0.5 the length of the ventral lobe and is only weakly concave. In the sporadic shoot sectors that almost correspond to *S. degenii*, the keel may be only 0.2–0.3 the length of the ventral lobe and is then conspicuously arched. On both the *S. hyperborea* and *S. degenii* "sectors" the dorsal lobes are convex. Finally, on the sectors most nearly corresponding to *S. kaurinii*, the dorsal lobes become conspicuously concave, with the sides often recurved; they often become conspicuously larger and may be 0.8 the area of the ventral lobes which, *in situ*, they may nearly obscure. Associated with this, dorsal lobes undergo transformation from an almost reniform shape, with the width greater than the length, to an ovate form, with the length considerably greater than the width. With transformation to the *kaurinii* form, the dorsal lobes become nearly erect, diverging at an angle of only 10 to 25°. In the Godhavn area one may find intimately intermingled plants that show characteristics of all three of the enumerated extremes, as well as shoot sectors that almost simulate *S. helvetica*. All these plants agree in several cardinal features: (1) The leaf lobes, dorsal and ventral, lack all trace of dentition, even with gemma formation. (2) Although the leaf lobes are often angular at their apices, the ventral are never sharp-pointed and the dorsal are rarely so, being often blunt to rounded, like the ventral lobes. (3) Cells bear 3–5 or occasionally 6 relatively small oil-bodies from 4.5 to

4.8×5 to 6.5, rarely to 5×9 μ. All plants seen with perianths had the perianth mouth subentire, ranging to finely denticulate, with teeth formed of 1–3 cells. The dentition never extended to the ♀ bracts.

Of the various phenotypes of *S. hyperborea*, the two most obvious are the *S. kaurinii*–and the *S. helvetica*-like extremes. Induction of the first seems to occur chiefly under conditions of competition by other erect-growing plants, so that the individual shoots are often erect, crowded, and appear laterally compressed in extreme cases. Induction of the mod. *parvifolia-angustifolia*, which corresponds nearly in size and aspect to *S. helvetica*, seems to take place when plants are growing prostrate with other creeping taxa such as *Pleuroclada* and *O. elongatum* in exposed, peaty sites. The mod. *parvifolia* may be only 1.7 to 1.9 mm wide. It resembles a very small *S. irrigua* with dorsal lobes at most 0.5 the size of the ventral lobes. Under rather similar conditions a mod. *parvifolia-densifolia-latifolia* may be produced in which dorsal lobes are fully 0.65 the size of the ventral; in this phase, which is a very compact one of peaty soil, long snow-covered, superficial similarities may occur to the mod. *latifolia-densifolia* of *S. helvetica*. Confusion with this last is likely to occur because of the rounded to blunt leaf lobes and edentate leaf margins. Fortunately, reddish to purplish gemmae can usually be found. It is certain that, seen by themselves, such phases (which often occur in "difficult" sites, such as late snow areas, associated with depressed forms of *Anthelia juratzkana*; e.g. 70–2014, Godhavn) are quite indeterminable; only with an understanding of their ecology, plus a knowledge of the local amplitude of variation of *S. hyperborea*, can such phases be named with any certainty. On the basis of size, such small forms with relatively narrow ventral lobes approach the sect. *Curtae*. For example, in the mod. *parvifolia* ventral lobes may be only 635 μ wide but 800 μ long (0.79 as wide as long). On that basis the plants key without difficulty to sect. *Curtae* in BUCH (1928) and in that key come out easily to *S. helvetica*, in which BUCH states the ventral lobe width is 0.60–0.85 the length. Since such small, prostrate forms (e.g., 70–2015) may average less than 2 mm wide yet bear perianths, it is obvious that major taxonomic problems may be readily encountered. We know of only one reliable way in which this mod. *parvifolia* may be separated from *S. helvetica:* its dorsal lobe is rather consistently 0.65–0.75 the size of the ventral lobes. Also, if gemmae are present, these are always purplish to reddish at maturity. Furthermore, this mod. *parvifolia*, which seems to be confined to exposed peaty ground, almost always has coarse, yellowish trigones. In any event, any small *Scapania* keying out to the *Curtae*, but with both ventral and dorsal lobes blunt to rounded, should

not be referred to *S. helvetica* if all or most dorsal lobes are 2/3 to 3/4 the size of the ventral lobes.

The ecology of the "*kaurinii* phenotype" is not very different from that of "ordinary" *S. hyperborea:* both occur chiefly in moory or boggy, rich areas. The former, as noted, seems to be a phenotype associated with crowding and/or exposure; the latter usually grows prostrate or procumbent. In West Greenland this last phenotype is often found around shallow rock pools where there is often some basic seepage (associated may be *Odontoschisma macounii*, *Tritomaria polita*, *Aneura pinguis*, *Pleuroclada*, *Nardia scalaris botryoidea*, and mosses such as *Drepanocladus* and *Paludella squarrosa*). Other associates are *Lophozia binsteadii*, *L. kunzeana*, *L. wenzelii*, *Gymnocolea inflata*, *Cephalozia bicuspidata s. l.*, and *Anthelia juratzkana.* It is able to tolerate much direct sunlight and in very exposed sites it is often scorched. Some phenotypes (e.g. 66–0145) may have as many as (3)4–9(10–13) oil-bodies per cell.

Plants that approach or belong to the "*kaurinii*" phenotype include the following: 66–0034a, 66–0145, 66–0492, 66–0009, 66–0027b, 66–0552, 66–0550a, 70–2097 (Fig. 16:4)

Presumed Genetic Variation. In addition to the above phenetic variation assumed to be environmentally induced, two variants are not so easily dismissed:

f. *subaequalis* Schust. (Fig. 16:18–19)

A f. *hyperborea* carina saepe multo breviore (0.15–0.45 folii longitudinis), lobis foliorum gemmiferorum obtuse productis crenulato-denticulatis, gemmis fusco-purpureis diversa.

Distribution

16: Manîtsoq (70–3003, 70–3004).

Distinct in the often shorter keel (0.15–0.45 ventral lobe length), the bluntly, triangularly drawn out lobes of gemmiparous leaves which are crenulate-denticulate on the margins, and in the dull purplish to fuscous-purple mature gemmae. Gemmae are rarely formed.

This *forma*, which possibly may be worthy of a higher status, occurs under environmental conditions which seem quite distinct from those of any other phenotype of *S. hyperborea:* on cold, shaded, wet, often irrigated ledges—in sites more typical for *S. irrigua* or *S. subalpina.* Associated were *Lophozia ventricosa grandiretis*, *L. hatcheri*, *L. alpestris*, *Tritomaria quinquedentata*, *Pleuroclada*, and *Gymnomitrion concinnatum.* Plants are rather fleshy, intensely green with an overlay of brownish pigmentation on distal sectors of leaf lobes. The marked proclivity for development of distinct dentition, at least of the dorsal lobes, is unique within *S. hyperborea.*

f. *apiculata* SCHUST.

F. *hyperboreae* similis praeter bases posticas foliorum saepe rubellas, lobos ventrales rotundatos abrupte mucronatos vel apiculatos.

Distribution

19: Nûk (70–2874).

These golden to golden-brown plants have postical leaf bases somewhat reddish tinted (pigmentation which is very rarely present in other phenotypes of *S. hyperborea);* ventral lobes are rounded at the apex, with the contours suddenly broken by a mucro or apiculum; dorsal lobes range from bluntly pointed to frequently sharply apiculate or mucronate.

The type grew in a richly vegetated margin of a low-lying tarn, on acid, peaty, exposed soil, with *Anthelia*, *Gymnocolea*, and *Marsupella arctica*. The similarity in the golden brown color to *S. tundrae* is remarkable. However, the pink, 2-celled gemmae and the (2)3–5(6) oil-bodies per cell are typical for *S. hyperborea s. l.* We have seen no other populations of *S. hyperborea* with a proclivity for developing mucronate or apiculate leaf lobes: to date this has been one of the few "inviolable" criteria distinguishing this species.

Scapania kaurinii RYAN (Fig. 17)

Distribution (Map 56)

45: Sagdliaruseq (66–1055, 66–1059). 48: Amitsup (66–0813).

American plants, almost all from West Greenland, referred by MÜLLER (1905–16, 1951–58) and BUCH (1928) to *S. kaurinii*, remain a major taxonomic problem. As noted under *S. hyperborea*, we have collected many examples in the area near Ritenbenk and on Arveprinsens Ejland, at Tupilak near Egedesminde, at Jakobshavn, and elsewhere, in which some, many, or most shoots are vegetatively *S. kaurinii:* they key readily to this, on the basis of the upcurved ventral lobes (the plant thus very convex in ventral aspect), with erect, concave dorsal lobes, with both lobes rounded or broadly blunt at the somewhat narrowed tips. These plants, which bear 2-celled, usually broadly ellipsoidal, normally pink or reddish (rarely brownish or fuscous) gemmae, are always clearly dioecious (in 66–0492, Arveprinsens Ejland, both androecia and isolated perianth-bearing plants occur together; at Tupilak, 66–0009, 66–0027b, only ♂ plants were found). The perianths seen had rather remote, sharp, 1–2-celled teeth, not arising from a 2-celled base. Both perianth mouth (JØRGENSEN, 1934, emphasizes that the perianth mouth of true *S. kaurinii* is "folded in the upper part, contracted, with small and low, irregular, indistinct lobes and spreading, short cilia, formed of 5 cells in each row arising from a 2-celled foot."), color, and gemma shape (JØRGENSEN,

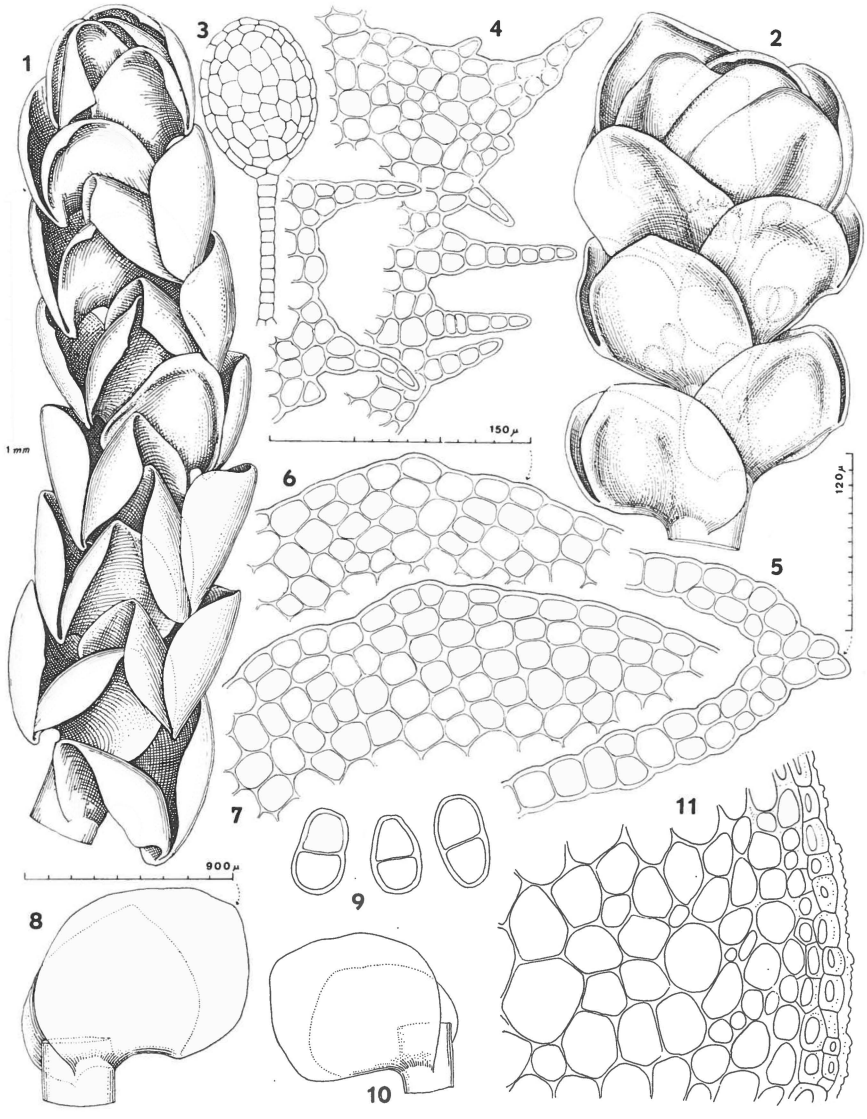


Fig. 17. *Scapania kaurinii*. (1) Sterile shoot (×31.5). (2) Paroecious shoot (×31.5). (3) Antheridium, from plant in fig. 2 (×105). (4) Two sectors of perianth mouth, from juvenile perianth from fig. 2 (×195). (5) Cross section through keel middle (×195). (6–7) Dorsal and ventral lobe apices, respectively (×228). (8) Leaf, ventral aspect, flattened (×30). (9) Gemmae (×405). (10) Leaf, postical aspect (×14). (11) Stem cross section (×360). [1–8, 66–0813, Amitsup; 9–11, from Buch (1928); 1–2, drawn to 1 mm scale; 4–5, drawn to 120 μ scale; 6–7, drawn to 150 μ scale; 8, drawn to 900 μ scale].

l. c., also states that the gemmae are "greenish, broadly ovate to egg-shaped, 21–28×14–20 μ, 2-celled" in *S. kaurinii*), as well as the wholly edentate and rounded to blunt leaf lobes, suggest *S. hyperborea.* Indeed, many plants have part or all of the shoot without the "*kaurinii*-like" upswept ventral lobe apices, and these plants all have the aspect of the Sect. *Irriguae.* It is our opinion that all of these dioecious plants with the broad, usually reddish gemmae of *S. hyperborea* are actually to be referred to that species.

The only plant seen which we are wholly convinced must be relegated to *S. kaurinii s. str.* is that from Amitsup (66–0813): a single, fertile plant, clearly paroecious, with diandrous ♂ bracts below the young perianth which was short-ciliate at the mouth. Linked with this is the usual "*kaurinii*" aspect, induced by the strongly upswept and abaxially convex ventral lobes and generally abaxially concave dorsal lobes. In contrast to *S. hyperborea*, in which similar phases occur, the dorsal lobes were somewhat larger: averaging 0.75–0.85, at the shoot tips 0.9–0.95, the ventral in size. This feature alone may be adequate to separate sterile *S. kaurinii.* In this collection a single, old, gemmiparous plant was seen with broad-oval, 1–2-celled gemmae which were, at maturity, dull purplish; in their color they differ from European plants, but otherwise no significant distinctions occur. A second collection, although sterile, from Sagdliaruseq (66–1059) is exactly like 66–0813 in the dull purplish gemmae, the "*kaurinii*" aspect of most plants, and, especially, the dorsal lobes mostly almost equal to the ventral in size and, in antical aspect, often nearly hiding them. Both collections have a high frequency of rather triangularly pointed ventral lobes, and these tend to be somewhat narrower than normal in *S. hyperborea.* On this basis we would admit, at this time, only these two collections as representing true *S. kaurinii.*

Scapania degenii SCHIFFN. (Fig. 16:13–17)

Distribution (Map 56)

1A: Behind Arctic Station (70–2051). 2: Fortunebay (66–0135, 66–0137, 66–0144). 30: Eqe (66–0288, 66–0294, 66–0296, 66–0330, 66–0340). 46: Qalatôq (66–1100b).

This predominantly Arctic-alpine species occurs, under subarctic conditions, in a few stations along the shores of Lake Superior (SCHUSTER, 1953, 1958) which represent the only stations from as far south as the United States. It is rather rare, and has a scattered, imperfectly circumarctic range, with isolated localities in Siberia, Scandinavia, Scotland, and England, the Alps; also on the north slope in Alaska (PERSSON & HOLMEN, 1961), in Manitoba, Quebec, and Labrador.

S. degenii is a variable entity, exhibiting phases with uniformly 1-celled gemmae (var. *degenii*) and phenotypes with them 2-celled at maturity, at least in large part (var. *dubia*). There is also variation in relative size of the dorsal lobe, which is typically rather small (under 0.65 the ventral in area) in var. *dubia*, while typical var. *degenii* has the dorsal lobe ca. 0.65–0.75 the ventral in area.

The species *s. l.* usually occurs in permanently moist areas, often in calcareous fens, in or around rills or (SCHUSTER, 1953) along the margins of rock pools. It is usually a species of basaltic regions, in the Great Lakes area usually associated with *Lophozia heterocolpos*, *L. gillmani*, *Tritomaria quinquedentata*, and other Ca-tolerant species. These also recur with it in West Greenland, as well as *L. quadriloba*, *Blepharostoma trichophyllum brevirete*, *Cephaloziella arctica*, etc. Typical var. *degenii*, when occasionally found on damp basaltic rocks, as, e.g., of a small dike in an area with igneous rocks (as at Eqe, 66–0288), may grow associated with *Anthelia*, *Odontoschisma macounii*, *L. quadriloba*, and *C. arctica*. Perianths are infrequent (and have been seen only in 66–0135). The species rarely occurs in areas away from basaltic dikes; thus is found along a rill at Qalatôq (66–1100b) with *Anastrophyllum assimile*, *A. minutum grandis*, and *Marsupella arctica*.

Var. *degenii* is usually readily distinct in the brownish, 1-celled gemmae, combined with the reniform dorsal lobes with strongly arcuate keel. The species, *s. str.*, may occasionally be mistaken for *S. hyperborea* (which sometimes produces "*degenii*-like phenotypes"). It differs from this in: (a) the often pointed and remotely finely dentate leaf lobes; (b) red-brown, ellipsoidal, and not very broad gemmae, averaging 11–13 μ wide×14–18 μ long, to 12×18 μ, all 1-celled at maturity. [The Fortunebay material is of interest in that it agrees with the type in the relatively large dorsal lobes, to 0.75 the ventral in area, in the rather strong dentition of the lobe apices, often associated, however, with gemma formation. The oil-bodies are large and as described for the preceding gathering. Gemmae, however, are not infrequently 2-celled and then are up to 14×21–24 μ, although most are 1-celled. Perianths have the mouth sinuate and remotely repand-denticulate to repand-dentate, as shown in SCHUSTER (1953, pl. 50:9), rather than being entire, as usually described. In addition to the usual lateral-intercalary branches, we have seen one terminal branch, at an acute angle to the axis, which was clearly of the *Frullania* type]; (c) oil-bodies (still well preserved in material several years after collection) mostly very large and few, mostly 2–4(5) per cell, ranging up to 9×10.5 to 7.5×11.5 μ in diam., and, in areas away from the leaf margin, virtually occluding the leaf cell-lumen in most cases. These features, as well as the distinctive facies (caused by the conspicuously convex, rather reniform-oblong, large

dorsal lobes, and the rather long and often rather strongly arched keel), are clearly indicative of *S. degenii*. Problems regarding the distinction of *S. degenii* and *S. hyperborea* are admittedly complex (see SCHUSTER, 1953).

v. *dubia* SCHUST.

Distribution (Map 56).

1A: Behind Arctic Station (70–2012e, 70–2017, 70–2040). 10: Enoks Havn (70–2761, 70–2775). 23: Kangersuneq (70–3132a).

This variant, distinguished by its predominantly 2-celled gemmae, is known to date only from the western hemisphere. PATON (1966) states that in Scotland *S. degenii*, although preponderantly provided with 1-celled gemmae, always has some 2-celled.

Var. *dubia* is perhaps less strictly bound to basic sites than is typical *S. degenii*. We have seen it from an irrigated, rich, rocky slope at Enoks Havn (70–2775) where it occurred with Ca-tolerant taxa such as *Lophozia quadriloba*, *Blepharostoma trichophyllum*, and *Tritomaria quinquedentata*. It also occurs on exposed soil over rocks, around rock pools in the gneiss zone at Godhavn, but where seepage from the overlying basalt may be significant; here (in 70–2012e) it is mixed with basiphytes such as *Odontoschisma macounii*, but also with usually more oxylophytic plants such as *Cephalozia bicuspidata*, *Gymnomitrion corallioides*, and *G. concinnatum*. Var. *dubia*, however, is occasionally found in distinctly acidic sites, as over peaty soil on fine, water-deposited silt in low, moory, moist areas around a lake (70–3132a, Kangersuneq), associated with oxylophytes like *O. elongatum* and *L. cavifolia*. In the gneiss zone at Godhavn it may also occur in irrigated areas with taxa that show little or no tolerance for basic conditions, e.g., *L. hatcheri*, *Solenostoma subellipticum*, *S. lingulata s. l.*, *L. kunzeana*. Perianths are not common but occur in 70–2775.

In this variant, as in typical *S. degenii*, we find 2–5(6) oil-bodies per cell [PATON, l. c., states that they are 2–8 per cell in Scottish plants. We have never seen more than 7 oil-bodies per cell. Mostly they are 2–4(5) per cell]; the largest of these range (in 70–3132a) up to $8 \times 13\ \mu$. Both oil-body size and number usually serve to separate this variant from *S. hyperborea* (compare Fig. 16).

Occasional extremes are met with; the two following are noteworthy:

(1) Plants of 70–2017 (Godhavn) represent one extreme: they show a high incidence of 2-celled gemmae when mature, but locally tend to have the dorsal lobes to 2/3 or even 3/4 the size of the ventral. Plants range to 4–4.4 mm wide (thus are even larger than the 3.5 mm upper

limit stated by Buch, 1928), are fuscous (as is usually the case with *S. degenii*), and have the reniform, convex dorsal lobes of typical *S. degenii*, with the apex obliquely patent. Cells have (2)3–5(6) large oil-bodies each. The larger, 2-celled gemmae are ca. 12–14×19–24 μ. Because of the brownish, 2-celled gemmae, this variant is likely to be sought under *S. hyperborea*, but differs in (a) the fuscous rather than warm brown color; (b) robust size; (c) the mostly strongly arched and often quite short keel of the leaves; (d) frequently dentate leaf margins and often distinct triangular tooth of the ventral lobe apex. These plants verge on *S. hyperborea* in the sporadically broadly rounded and quite edentate ventral lobes; the often very broad and short-ovoid gemmae; and—on some plants—the relatively small oil-bodies in some cells, not obscuring more than 40 % of the lumen. Size, color, and, in particular, the usually strongly arched keel, however, give these plants the aspect of *S. degenii.*

(2) Plants of 70–2761 (Enoks Havn) represent a mod. *viridis-leptoderma-laxifolia*, from wet sites, in a low river valley. They epitomize the problems sometimes faced in separating this phenotype from similar ones of the protean *S. hyperborea*, especially when gemmae are absent. The rather reniform dorsal lobes, the general presence of an obtuse to sharp point to the dorsal lobe, the occasionally sharp lobe apices, and the short and semicircular keel all suggest *S. degenii*, as does the presence in many cells of 2–4 large oil-bodies, from 4×6 to 5–6×8–9 μ. Mingled with these *S. degenii* criteria, however, are others suggestive of *S. hyperborea:* frequently to generally rounded ventral lobes; often 5–6(7) smaller oil-bodies per cell, averaging only 3.5–4.5(5)×5–6 μ. It is not impossible that the present plants represent a hybrid population although it is more likely that the smaller oil-bodies found in many cells represent a tendency found elsewhere in *Scapania* for reduction in oil-body size in subaquatic phenotypes (Fig. 16:17).

By contrast, in rich calcareous fens in the same area (70–2775), phenotypes occur which pose other taxonomic problems. These plants almost match the type plants in the coarse trigones and large oil-bodies (Fig. 16:13–14) and in the large dorsal lobes, which range, on all but weak shoots (where ca. 0.55–0.65 the ventral in size), up to 0.75–0.85 the ventral in area. These plants also show regular denticulation of the leaf lobes, usually at least indirectly associated with gemma formation. Two criteria set these plants apart: (1) gemmae average broadly ovoid (12.5–13×16–17 μ to 14×16.5 μ), to occasionally more elliptical and 12×18–19 μ; when mature they are more than 50 % bicellular, hence the plants belong to var. *dubia;* (2) many shoots, locally, have strongly upwardly arched ventral lobes, so that the almost equally large dorsal lobes also arch up on their outer edges and become rather concave; such shoots recall *S. kaurinii* in aspect.

Scapania tundrae (ARN.) BUCH (Fig. 18)

Distribution (Map 56)

26: Pâkitsup ilordlia (70–2309, 70–2310).

The range of this rare species is poorly known; it has been reported from Eurasia, from Tolstoinos, Siberia (70°10′N.; BUCH, 1928), Novaya Zemlya, Spitsbergen, northern Norway, and Sweden. From North America there is the sole, ambiguous reference in MÜLLER (1951–58, p. 961): "Kanada (TUOMIKOSKI) det. S. ARNELL". The above is the only definite station known from the western hemisphere.

Stated by both MÜLLER (l. c.) and ARNELL & MÅRTENSSON (1959) to be similar in its ecology to *S. hyperborea*. The Qissugssalik station is from the margins of a rivulet, emptying into a tarn, with *S. paludicola s. l.* and *Drepanocladus* associated.

Oil-bodies in the present collection are rather small, obscuring no more than 0.2–0.35 the cell surface; they range from 4 to 4.5 μ to 3.5–4(5)×6 up to 4–5×6.–6.5 μ, and occur (6–7)8–14(15) per median lobe cell. In 70–2309, associated with free gemma production, the leaves tend to be rather freely and coarsely toothed in and adjoining gemmiparous zones; antical lobe bases may also have 1–2 sharp teeth. Free gemma formation in these plants is often linked with inhibition of leaf development, resulting in quite malformed leaves. The Greenland plants seem quite typical, except for the fact that gemmae become pink with maturation, not brown; in this they quite agree with Greenland phenotypes of *S. hyperborea*. Mature gemmae are 2-celled and ca. 17–19(21)× 24–28(33) μ.

Nothing in the present plants would preclude our considering them to have evolved by polyploidy from *S. hyperborea* (or perhaps by polyploidy, following a cross between *S. hyperborea*×*paludicola*). The often strongly arched keel suggests the presence of some *paludicola* genes.

Scapania pulcherrima SCHUST. (Fig. 19:1–10)

Planta valida, ad 3.5 mm lata, cellulis foliorum magnis, corpusculis oleiferis numerosis (6–12 in quaque cellula loborum) *S. tundrae* revocans, carinis foliorum brevissimis, saepe minus quam 0.15 folii longitudinem attingentibus, plerumque lunulatis, dentibus loborum validis crassis basi latis ab ea diversa.

Distribution (Map 54)

21: Umiasugssûp (70–2951).

The species is known only from the type collection, which occurred in small pools adjacent to a clear, acidic, cascading stream, admixed with *S. subalpina*, *S. irrigua rufescens*, *Marsupella arctica*, and *Solenostoma oblongifolium heteroicum*.

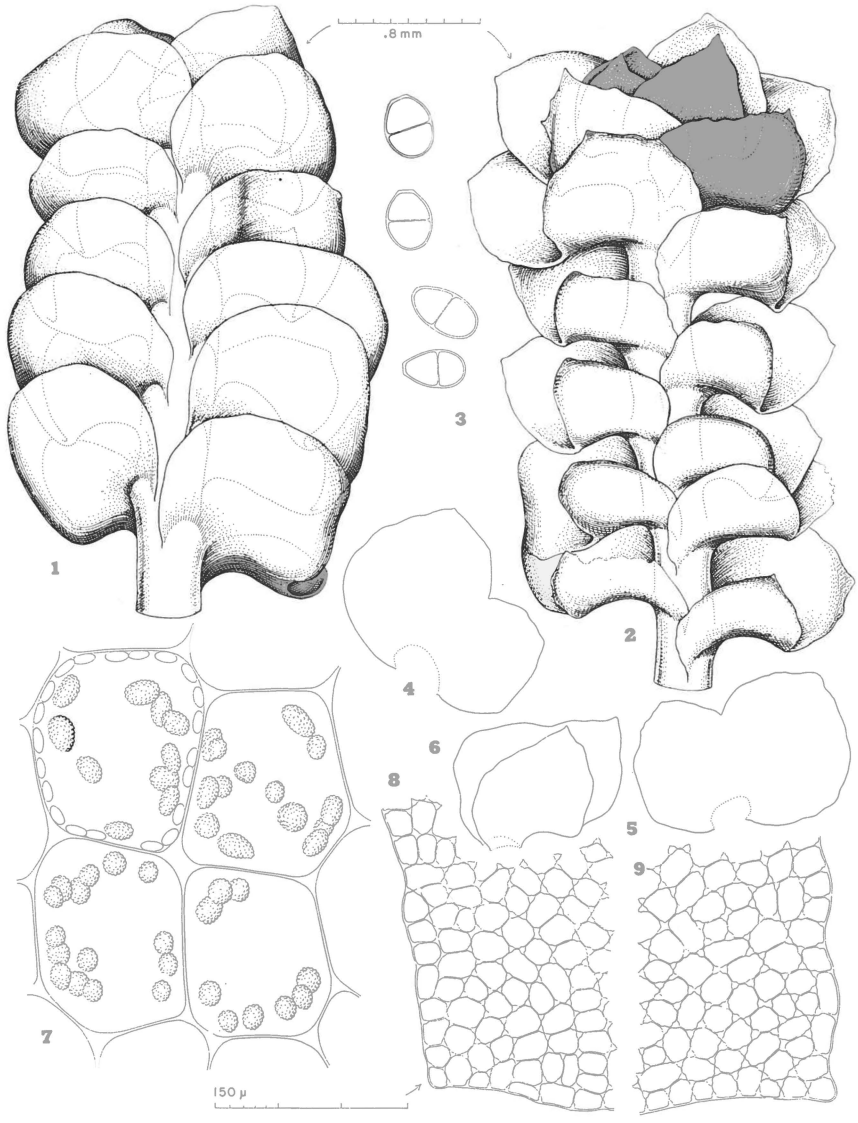


Fig. 18. *Scapania tundrae*. (1–2) Apices of plants, ventral and dorsal aspects (×23). (3) Gemmae (×282). (4–5) Leaves, flattened (×23). (6) Leaf (×23). (7) Cells with oil-bodies (×740). (8) Ventral lobe apex (×170). (9) Dorsal lobe apex (×170). [All drawn from 70–2310, Qissugssalik; 1–2; 4–6, drawn to 0.8 mm scale; 8–9, drawn to 150 μ scale].

S. pulcherrima is a more robust plant than *S. tundrae* but has the large cells and numerous oil-bodies of that species. It seems to have the same relationship to *S. degenii* as does *S. tundrae* to *S. hyperborea*, and differs in the same manner: the leaf is very deeply divided, with a very short, often almost circular keel that is diagnostically winged and often crispate; the dorsal lobe is strongly convex and arches across and often well beyond it. Oil-bodies are usually 6–8 to 9–12 per median lobe cell, much as in *S. tundrae*, but average rather larger: from 4.5–5.5 μ and spherical to 5–6×7, occasionally 6–7×8–9 μ. Gemmae, as in *S. tundrae*, are 2-celled and pink at maturity, ca. 16–18.5×(25)29–31 μ, not appreciably differing from those of *S. tundrae* in shape or size.

Distinctive for this species is the strong and coarse leaf dentition which is not clearly related to gemma production but may occur on gemma-free plants. We have not seen similar coarse, broad-based teeth in any other *Scapaniae*. Although the combination of short and strongly arched keel, and strongly convex dorsal lobes that cross the stem suggests *S. degenii*, the species differs from this in (a) lack of fuscous pigmentation, the plants being light golden brown, usually with very intensive vinaceous pigmentation of the leaf bases, even of otherwise greenish plants; (b) pinkish, 2-celled gemmae of superior size; (c) larger cells; (d) coarser dentition of the leaves; (e) smaller but many more oil-bodies per cell.

Scapania paludicola Loeske & K. Müll.

Distribution (Map 57)

15: Kronprinsens Ejland (70–2066c, 70–2109, 70–2115a). 18: Grønne Ejland (70–2815). 19: Nûk (70–2849, 70–2878). 21: Umiasugssûp (70–2940a). 25: Sarfaq (70–2547a). 26: Pâkitsup ilordlia (70–2303, 70–2310).

S. paludicola s. l. is a circumboreal-circumarctic species whose range in the western hemisphere extends southward merely to New England and New York, west to Minnesota. The species fails to occur northward in Greenland beyond the stations cited here, although it is known from as far north as Spitsbergen. In Disko Bugt the species is confined to the southern portions of the region; it is nearly restricted to areas with acidic rocks.

In the Arctic *S. paludicola* is a variable and complex entity which fails to correspond with the perimeters established for the central European type concept. In addition to typical var. *paludicola*, we distinguish a phase in which gemmae become tardily pink at maturity and in which ventral (and often dorsal) lobes tend to become broadly, evenly rounded at the apex (= *var. rotundiloba*), and a phase which is otherwise like var. *paludicola* in the pointed and often feebly dentate

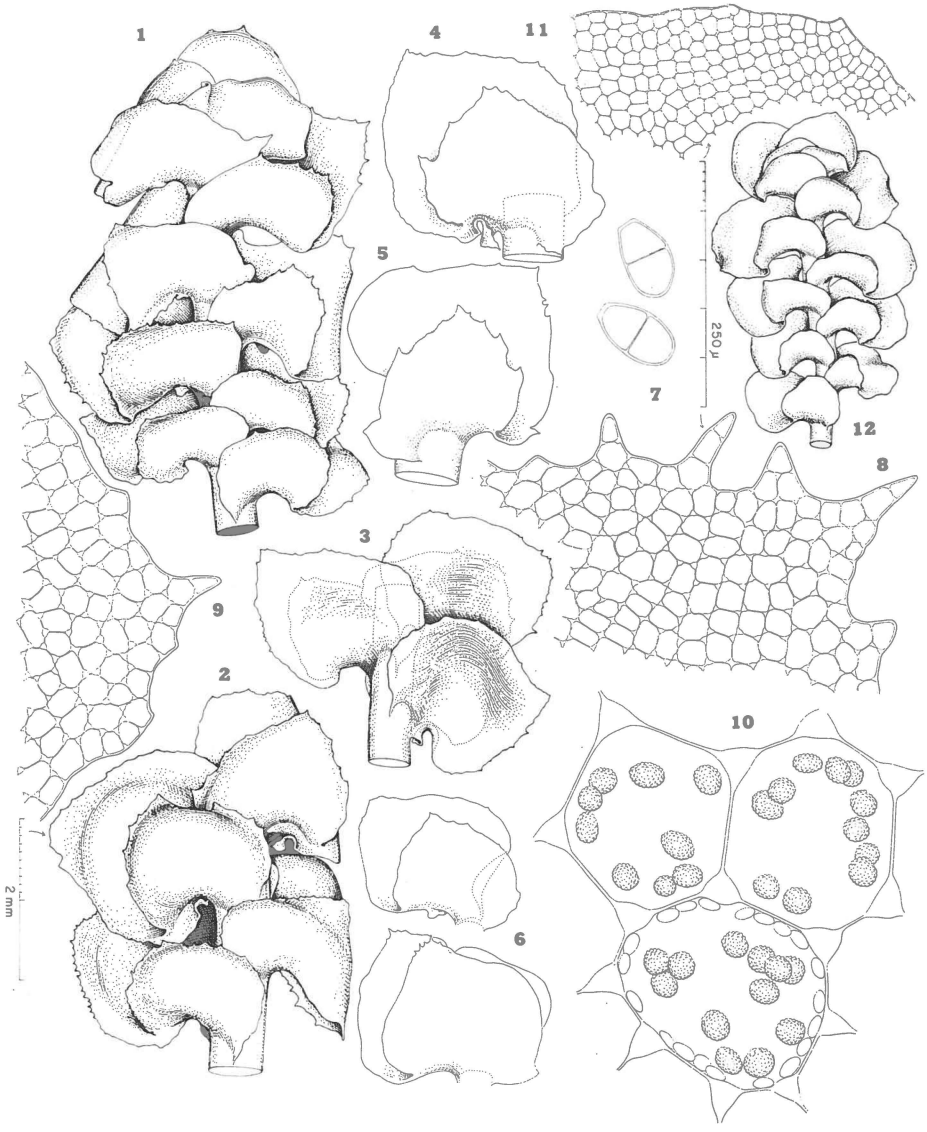


Fig. 19. *Scapania pulcherrima* (1–10) and *S. irrigua* ssp. *rufescens* (11–12). (1–2) Shoot sectors; note deflexed shoot and lobe apices (×10.5). (3) Shoot sector, ventral aspect (×10.5). (4–5) Leaves, *in situ* (×10.5). (6) Two leaves, dissected free (×10.5). (7) Gemmae (×355). (8) Dorsal lobe apex (×129). (9) Ventral lobe apex (×129). (10) Cells with oil-bodies (×830). (11) Ventral lobe apex (×129). (12) Shoot sector, dorsal aspect (×10.5). [All from 70–2951; 1–10, from type, the *S. irrigua* ssp.. *rufescens* a mod. *parvifolia-colorata;* 1–6, 12, drawn to 2 mm scale; 8–9, 11, drawn to 250 µ scale].

leaf lobes, but has gemmae that remain uniformly green until maturity (= var. *viridigemma*). There are other genetic divergences: we have not seen vinaceous pigmentation in plants from boreal regions, while some Arctic collections (70–2815, 70–2940) show such pigmentation of ventral leaf bases. It is not impossible that past hybridization with *S. irrigua* ssp. *rufescens* (which exhibits analogous differences from ssp. *irrigua:* leaf lobes become rounded and entire-margined, vinaceous coloration is developed) has introduced the genes for rounded, entire leaf lobes, plus the gene or genes for vinaceous pigment production. In any event, Arctic phenotypes of the *Irriguae* appear to show analogies that may very well be due to common interchange of genes that are absent from boreal-temperate zone populations. The expression of these genic differences is often imperfect: in *S. paludicola* the round, entire leaf lobes typical of var. *rotundiloba* are usually found only on mature shoots or shoot sectors, often only in nongemmiparous zones. Hence, sometimes (e.g., in 70–2878), depending on the vigor of the shoot studied, one could refer the plant either to var. *paludicola* or var. *rotundiloba.* Our placements in some cases are arbitrary and we have left "intermediates" in var. *paludicola.*

S. paludicola s. l. is sometimes frequent on irrigated, peaty slopes, associated with *Drepanocladus*, *Paludella squarrosa* (indicative of weakly basic seepage), *Pleuroclada albescens*, *Cephalozia bicuspidata ambigua*, *C. pleniceps*, etc. (70–2066c) or may occur almost submerged, with *Drepanocladus* (70–2109). It typically occurs in rich fens, often where there is some slightly basic seepage. In boggy areas it may be found (70–2815) with *Lophozia ventricosa longiflora*, *L. wenzelii wenzelii*, *Pleuroclada*, *Cephalozia pleniceps*, and occasionally (70–2115a) *Calypogeia sphagnicola.*

This large plant is almost always long, simple or subsimple, and relatively flaccid and lax; light brownish pigmentation is frequent, fuscous coloration almost never occurs. In insolated, irrigated areas the mod. *pachyderma*, with large bulging trigones, is found (70–2066c), which can develop weaker lateral-axillary innovations that closely simulate *S. hyperborea* in both size and in the weakly arched keel. The possibility exists, when the plant occurs as a mod. *pachyderma-parvifolia-angustifolia-integrifolia*, that it will be mistaken for *S. hyperborea.* The usually broader ventral lobes, at least occasionally pointed or apiculate, and the cordate dorsal lobes, mostly almost erect, together with the short and strongly arched keel, normally suffice to identify the species.

These criteria may fail with 70–2109; here vigorous shoot sectors typically have a very short and arched keel, no more than 0.2 the ventral lobe length; dorsal lobes are cordate, pointed and directed at an angle of 0–20° with the stem apex; the ventral lobe is very broadly rotundate-ovate, with a sharply pointed apex and, near gemmiparous zones, often

with a few small teeth. These are all characters of *S. paludicola*, as are the rather small trigones and lax, soft growth. Many or most shoots, however, have reniform-ovate convex dorsal lobes, often rather obliquely patent and blunt; ventral lobes are narrower, broadly rounded at the apex and edentate, though often triangularly narrowed to the blunt or rounded tip; the keel is weakly arched and over 0.35 the ventral lobe in length. These are all characters of *S. hyperborea.* Linked with them is the sparing production of gemmae, the few mature ones being short-ovoid and 13–14×19–24 μ and pink in color—the ovoid form with broadly rounded ends is typical of *S. hyperborea.* Since such plants occurred together with numerous phases of *S. hyperborea* with consistently rounded to blunt leaf lobes, with ventral lobes less broad, and the keel rarely as short and strongly arched, it seems best to regard this extreme as a hygromorphic form of *S. paludicola.* Depending on the shoot sector studied, however, disposition of the plants as either *S. paludicola* or *S. hyperborea* is possible. It is probably phenotypes like these that led Arnell (1922, pp. 45–46) to deny the existence of sharp distinctions between *S. paludicola* and *S. hyperborea* in the far north. Buch (1928, p. 98), who believes that these two taxa are closer to each other than the latter is to *S. irrigua*, does not recognize actual genotypic intergrades and, in essence, explains the *irrigua-hyperborea*-like extremes found in *S. paludicola* as weak and relatively juvenile phases developed under conditions of inadequate illumination. The position of such "*hyperborea*-type" plants within *S. paludicola* is quite clear, however, from a collection made close by to the last (70–2119) in which all vigorous plants, 3–3.6 mm wide, all show a perfect constellation of "*paludicola* characters" [broadly rotundate ventral lobes; very short keel, often under 0.2 length of ventral lobe; small and cordate, convex dorsal lobe that is rather obliquely inserted on the stem]. In such plants, however, ventral lobes are mostly perfectly rounded at the apex—which is supposedly a "*paludosa* character"; these plants represent the next variety, var. *rotundiloba.*

Normally var. *paludicola* has both dorsal and ventral lobes triangularly pointed and often apiculate; it also has reddish to brownish gemmae and otherwise lacks reddish pigmentation. We have not seen wholly typical material of the species from Greenland, but most plants here assigned to var. *paludicola* approach it. Some plants, however, (e.g. 70–2940) bear tardily light brown to pinkish brown gemmae; ventral lobes are narrower and more pointed, often bearing a few teeth; dorsal lobes are more reniform rather than ovate-cordate. Such plants seem to be a mod. *parvifolia* of var. *paludicola*, although, except for the strongly arched keel and the tardily pigmented gemmae, could almost be assigned to *S. irrigua.* They bear (70–2940) usually 2–5 oil-bodies per cell, mostly

rather small (3–3.5×4–5 to 4×6) to 5–6×8–10 μ. Diagnostic is the rather infuscated pigmentation, aside from the purplish red ventral leaf bases. These plants, on the collective basis of (a) only 2–5 oil-bodies per cell; (b) coloration; (c) somewhat narrower ventral lobes, strongly suggest *S. irrigua rufescens*. The ability to develop colored walls of the gemmae, however, strongly argues against such a disposition. Until more material of this phenotype is collected, it seems best to retain it within *S. paludicola*.

v. *rotundiloba* SCHUST.

Basibus foliorum ventre saepe rubellis, lobis ventralibus late suborbicularibus apice late rotundatis, dentibus in foliis omnino nullis, corpusculis oleiferis in quaque cellula plerumque 5–10 usque ad 10–13, gemmis late ellipticis a var. *paludicola* diversa.

Distribution (Map 57).

15: Kronprinsens Ejland (70–2119). 16: Manîtsoq (70–3012). 19: Nûk (70–2839, 70–2869a, 70–2878). 22: Orpigsôq (70–3113, 70–3119). 25: Sarfaq (70–2342, 70–2346, 70–2377). 29: Ritenbenk (66–0272, 66–0273).

Additional collections:

86: Seqíneqârajutoq (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.626)

Type: Disko Bugt: Nûk, east end of Alángup nunâ (70–2878, 70–2869a).

Known only from the above collections. This taxon, however, is probably more widespread in the Arctic; it seems to form a phase analogous to ssp. *rufescens* of *S. irrigua*, differing from typical *S. paludicola* in exactly the characters that separate ssp. *rufescens:* leaf lobes, especially the ventral, are typically rounded to obtuse (except on weak leaves or weak shoots); lobe margins are rather consistently entire. The ventral leaf bases normally do not always tend to develop reddish pigmentation, however.

The ecology of this taxon seems identical with that of plants here (provisionally) referred to var. *paludicola;* plants often occur in irrigated fens, often submerged with *Drepanocladus* and *Scapania hyperborea*, occasionally admixed with *Lophozia kunzeana*, *L. wenzelii*, *Gymnocolea inflata*, *Tritomaria quinquedentata*, and (where clearly emergent) *Calypogeia sphagnicola* f. *paludosa*.

The taxon is frequent in rich fens and there may occur with *L. binsteadii* and *L. excisa* over *Aulacomnium*.

We have referred certain collections to *S. paludicola s. l.* which, if better developed, probably could have been referred to var. *rotundiloba*. The unquestionable collections of the last tend to have rather more frequent oil-bodies per cell; in 70–2342 there are (2–4)5–8(9–11) oil-bodies per cell, and in 70–2839 usually 7–10 or even 12–13 oil-bodies per

cell. Gemmae, although always greenish when young, turn pink to red-brown on maturity, much as in *S. hyperborea* from West Greenland. Both taxa may occur intimately admixed (as in HOLMEN 16.626 and 70–2869); they show similar pigmentation responses as regards the gemmae.

Certain collections (e.g. 70–2839) strongly deviate because well-developed individuals exhibit superficial similarities to *S. kaurinii* in that the ventral lobes are upcurved and the dorsal lobes antically sulcate and concave. This is not true on weak shoots but may be marked on robust ones. The plants tardily develop pink gemmae and, associated with gemma formation, the leaf lobes become rather ciliate. Dorsal and ventral lobes are often blunt and the ventral lobe is occasionally pink at the base; median lobe cells have many oil-bodies, usually 7–10 or even 12–13.

v. *viridigemma* SCHUST.

Distribution (Map 57)

1D: Skarvefjeld (66–0313). 21: Umiasugssûp (70–2950).

This variant was first described from Hudson Bay (SCHUSTER, 1951). In it we combine a mod. *viridis* with gemmae that remain greenish to maturity, together with leaves whose keel is often arched as in *S. paludicola*, but sometimes (on weak shoots) longer and less arched, as in *S. irrigua*. The apparent inability to develop pigmented cell walls of the gemmae suggests *S. irrigua;* the keel and dorsal lobe form argue for *S. paludicola.*

Two collections, cited above, nearly approach this variety but, perhaps, represent a mere extreme of *S. irrigua rufescens* in which we find the keel on leaves of the larger plants shorter and abnormally highly arched. [It must be emphasized that in the *Irriguae* weak shoots of taxa like *S. pulcherrima*, *S. degenii*, and *S. paludicola*, in which a semi-circular keel is normal, simulate *S. irrigua* (or *S. hyperborea*) in the longer and less arched keel. For this reason all taxonomic conclusions must be based on the most mature plants that can be found]. An alternative explanation is that they represent phenotypes of *S. irrigua* ssp. *rufescens* in which there has been introgression of some *S. paludicola* criteria. The plants are both subaquatic phenotypes (70–2950 contains a few stems of *S. subalpina*, which is often aquatic or subaquatic in the Arctic) which have almost the aspect of *S. irrigua rufescens.* In both a small amount of reddish pigmentation at the ventral leaf bases is present; in both gemmae are green to maturity.

We provisionally refer these two collections here. It is, indeed, quite possible that the var. *viridigemma* is merely a hybrid population between *S. irrigua* and *S. paludicola.* The ovate ventral lobes, which never

approach the broadly rotundate aspect seen in normal forms of *S. paludicola*, strongly suggest a close affinity to *S. irrigua*. The oil-bodies are somewhat deviant in number: in 70–2950 there are only (1)2–5 small oil-bodies per cell; this may be related to the subaquatic habitat. *S. irrigua*, however, including ssp. *rufescens*, normally has 2–5 oil-bodies per cell; as few as 2 or 3 oil-bodies per cell are rare in any form of *S. paludicola s. l.* Plants of 70–2937, cited under *S. irrigua rufescens*, may also belong here.

Sectio *Undulatae* K. MÜLL.

The *Undulatae* are broadly treated herein, to include the sect. *Obscurae* BUCH (1928), for reasons given in SCHUSTER (1974).

Scapania uliginosa (SW.) DUMORT.

Distribution (Map 58)

81: Sarqardlîp nunâ, Tasiussaq (KORNERUP, 1879, W. & H. 1884).

We have not collected this species in West Greenland; it is evidently rare there. However, one of us (RMS) has collected it as far north as 77°30′N., at Kânâk, Inglefield Bredning; FREUCHEN (1917) also made a collection on Bjerrings Nunatak near Thule, 76°32′N. (which was published by HESSELBO, 1932, as *S. undulata*). The species is more abundant in South Greenland between 60° and 62°04′N.

S. uliginosa is strictly confined to areas with acidic rocks. Unquestionably the reason we have not collected the species in the Disko Bugt area is because our collecting was largely confined to regions with basaltic rocks. The species should be more widespread in and near rills and cascades in areas with gneissic rocks.

Scapania serrulata SCHUST.

Planta plerumque saturate vinacea vel atro-vinacea, gemmis bicellulis vinaceis. Lobi foliorum dentibus acutis e cellulis singulis (raro binis) longis hyalinis formatis serrulati, ventrales longe decurrentes, dorsales non decurrentes; cellulae magnae (juxta margines 20–28 μm diam.), corpuscula oleifera plerumque cuique 6–11 continentes.

Distribution (Map 58)

32: Qôrorssuaq (70–2438, 70–2476d, 70–2484). 42: Magdlak (66–1356). 45: Sagdliaruseq (66–1074). 46: Qalatôq (66–1139).

Additional collections:

32: Qôrorssuaq [S.B. 1870, publ. as *S. undulata* by BERGGREN (1875) and from Ritenbenk, probably mislabeled in the same way as *Sol. oblongifolium*]. 114: Eqaluit (K.J. 830a). 116: Puiagtukavsak (K.J. 679a). 122: South of Eqaluit (K.H. 13.315). 142: Niaqornánguaq (K.H. 15.771).

This rather rare taxon, described from Kânâk, Inglefield Bredning (RMS 45638) is known again from Pangnirtung, Baffin Island, and from the West Greenland stations cited above.

S. serrulata is a species of irrigated rills or intermittent drainage paths running through stone fields, of permanent rills threading through areas with acidic rocks, and of small, swift-running, cold streams draining ice fields. It occurs only in areas with acidic rocks. Typical are occurrences on silty soil at the edges of more or less intermittent rills, at Qôrorssuaq (70–2484, 70–2476d, 70–2438), associated with *S. subalpina*, *Lophozia wenzelii*, *L. opacifolia*, *Anastrophyllum assimile*, *Pleuroclada*, and *Solenostoma sphaerocarpum*. Other frequently associated taxa, elsewhere, are *S. crassiretis*, *S. spitzbergensis*, *A. assimile*, *A. minutum grandis*, *Marsupella arctica*, and *M. revoluta*. When clearly emergent, *Gymnomitrion concinnatum*, *Cephalozia pleniceps* and (rarely) *Odontoschisma macounii* may be associated. Exceptionally the species occurs in areas with basic rocks, as at Magdlak (66–1356); then *Anomomarsupella cephaloziella loides*, *Cephaloziella* sp., *S. cuspiduligera*, *L. gillmani*, *L. heterocolpos*, *Solenostoma sphaerocarpum*, *S. pumilum*, and *S. subellipticum* may be associated.

S. serrulata is characterized by the often intensive reddish to vinaceous color, the serrulate leaf lobe margins, and the vinaceous bicellular gemmae. The rounded ventral lobes are long-decurrent; the dorsal lobes are not. The species is probably allied to *S. obscura* and *S. uliginosa* with which it shares the nonmargined leaves and long-decurrent ventral leaf bases. The cells, however, are much larger, averaging 20–28 μ on lobe margins and bear conspicuous, often bulging, trigones. Oil-bodies are numerous, ranging from (5)6–11(12–13) per lobe cell. In plants of 70–2484 they may actually occur 9–15, rarely to 19 per cell and then are only 3.8–4.2×4.5–5.5 to 5–6×6–7 μ.

The plants often appear rather weather-beaten, owing to growth under at least intermittently submerged conditions. Holmen 13.315 seems typical: the combination of transverse dorsal and long-decurrent ventral lobes, serrulate leaf margins with oblique, 1-celled teeth, vinaceous pigmentation (both of younger leaves and mature gemmae), and nonmargined leaves is diagnostic. Marginal cells are 20–26(28) μ; gemmae range to 17–18×29–34 μ. The plants are a mod. *colorata-pachyderma*, with secondary brownish pigmentation on older leaves masking any purple pigmentation developed earlier. Trigones are often bulging and strongly developed and no trace of a border is distinct on such plants. Except for this, the facies of this taxon suggests *S. undulata*—particularly the convex, subreniform dorsal lobes.

Scapania obscura (ARN. & JENS.) SCHIFFN. (Fig. 20)

Distribution (Map 59)

32: Qôrorssuaq (70–2478c).

S. obscura is a poorly known plant, otherwise reported from northern Scandinavia, Switzerland, and Baffin Island, and from the Angmagssalik area of East Greenland. The critical plants of 70–2478 were initially relegated to the status of a mod. *colorata* of *S. subalpina*, a species found in the same site, in a rill (probably temporarily dry some summers), draining a steep acidic slope. (These plants suggest that MÜLLER, 1905–16, p. 471, was right in placing *S. obscura* immediately after *S. subalpina*, stating that it differs primarily in the "kleinere und zartere Gestalt ..., durch schwarze Farbe, abstehende, ganzrandige Blattlappen..." Leaf lobes, mutually spreading away from each other, with the dorsal sometimes nearly squarrose, however, recur again in *S. subalpina*). The plants are to 2 mm wide, mostly purplish tinted but brown pigmentation is present as well (hence the coloration is as in the allied *S. uliginosa*). Leaf form closely resembles that of *S. subalpina*. The cells—each with (2)3–6(8) rather small oil-bodies, from 4–5×4–5 to 5–6×5.5–6(7.5) μ, except for marginal cells which often lack oil-bodies—are exactly as in *S. subalpina*, as are the size, shape, and transverse insertion of the dorsal lobe, the long keel, and distinctly decurrent ventral lobe bases. However, these are also features diagnostic of *S. obscura*.

Other criteria unambiguously suggest *S. obscura;* leaf cells tend to be slightly larger (marginal cells, where not strongly tangentially elongated, are 18–24 μ in the lobes, vs. mostly 15–20 μ in *S. subalpina* from the same site); leaf dentition is lacking, even associated with gemma formation; leaf cells, typically of a mod. *mesoderma* with conspicuous but not bulging trigones, are normally everywhere similar, the marginal cells not being differentiated (on some plants, however, a feeble, 1-cell wide border of some leaves exists, even though neighboring leaves lack it); the stem has a 1–2-stratose cortex.

Still other criteria are ambiguous: the color, often more purplish than fuscous, is typical of neither species; the broadly oval, green to pinkish-purple gemmae are 2-celled and 16.5–19×19.5–24 μ [BUCH (1928) gives them as 15–18×25–33 μ for *S. subalpina* and its allies, 9–14×17–21 μ for *S. obscura;* for the latter he indicates them as brown in color. In Angmagssalik material of *S. obscura* gemmae are brownish and 17–20× 25–26 μ].

Ultimately the attribution of these plants to *S. obscura* rests on (a) lack of border of the leaves; (b) lack of all trace of dentition, even though the mod. *viridis-leptoderma* of *S. subalpina* growing nearby was

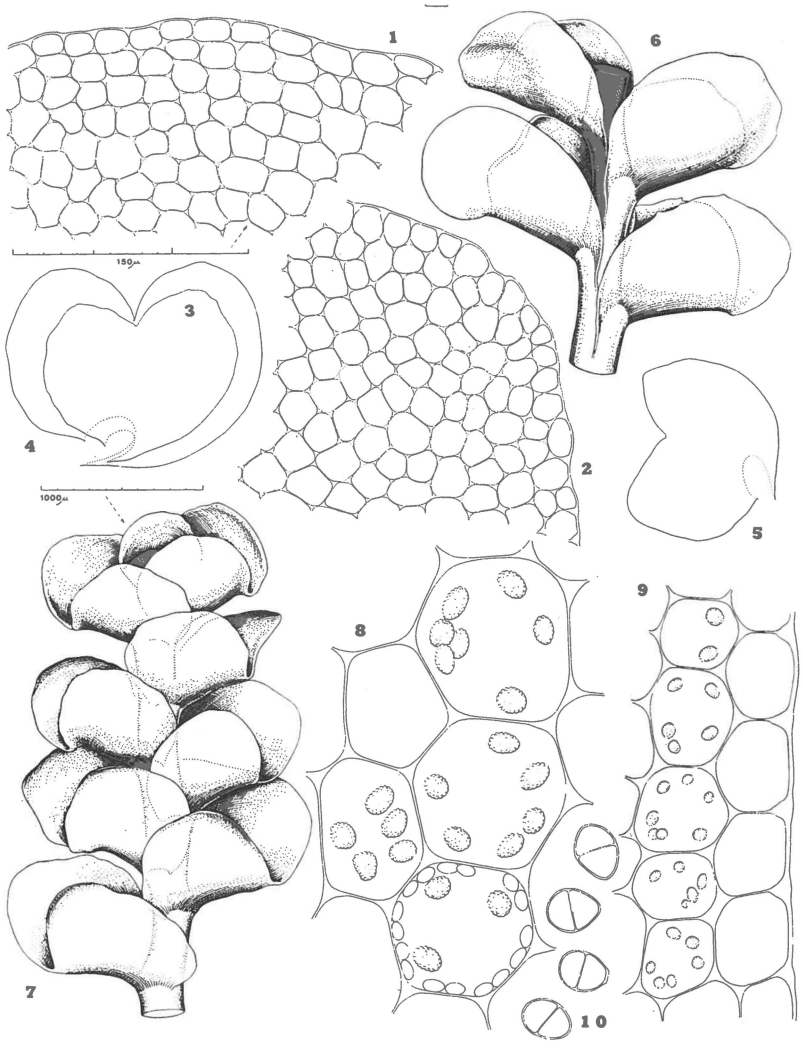


Fig. 20. *Scapania obscura*. (1) Cells along ventral leaf margin, near middle (×210). (2) Cells of dorsal lobe apex (×210). (3–5) Leaves (×22). (6) Shoot sector, postical aspect (×22). (7) Shoot, antical aspect (×22). (8) Cells of middle of lobe, mod. *colorata* (×695). (9) Cells along ventral leaf margin, showing absence of oil-bodies from marginal cells (×495). (10) Gemmae, greenish to pinkish (×310). [All from 70–2478, Qôrorssuaq; 1–2, drawn to 150 μ scale; 3–7, drawn to 1000 μ scale].

denticulate-leaved; (c) presence of a mixture of brown and red pigments, rather than only vinaceous pigmentation.

We remain sceptical of *S. obscura* as a species and suspect that, under exceptional environmental conditions, leaf border formation may be

suppressed in *S. subalpina*, even though collenchyma may form. Thus the Greenland plant, at least, may be a very deviant mod. *colorata-mesoderma-integriloba* of *S. subalpina*. It should be remembered that the differences in stem anatomy, which seem impressive, may be related to vigor. If there is a *S. obscura*, distinct from *S. subalpina*, the Greenland plant obviously has to be placed there. This holds for both the West Greenland material discussed above, and the East Greenland plant (Angmagssalik Ø: Mítivagkat 65°42′N., 37°55′W., FRISTRUP, Aug. 3. 1958). In both collections the leaf lobes have no trace of a border, but leaf bases, especially ventrally, may have somewhat thick-walled cells; in neither of them is there is any trace of leaf dentition.

Scapania subalpina (NEES) DUMORT.

Distribution (Map 58)

21: Umiasugssûp (70–2936c, 70–2950, 70–2951). 23: Kangersuneq (70–3127, 70–3129a, 70–3137). 32: Qôrorssuaq (70–2438, 70–2446, 70–2450). 42: Magdlak (66–1351).

Additional collection:

26: Pâkitsup ilordlia (S.B. Aug. 1870).

S. subalpina is circumsubarctic-alpine and subalpine, with limited penetration into Arctic regions. In Eurasia it occurs north to Siberia and southward extends to Madeira; in North America it fails to extend north of the localities cited above; southward it is more frequent in South and East Greenland, and extends to Maine, New Hampshire, and New York (where it is strictly alpine and subalpine).

In our area the species has an ecology identical to that of *S. serrulata* and *S. obscura:* it is confined chiefly to acidic rock areas with running water. Here it may be completely submerged in rapidly running rills (as at Qôrorssuaq; 70–2446) or may occur on thin, peaty soil over rocks at rill margins, associated with *Tritomaria quinquedentata*, *Lophozia cavifolia*, *L. ventricosa grandiretis*, *S. irrigua rufescens* (in 70–2450) or with *Solenostoma pumilum rivularis*, *Anthelia*, *Cephalozia pleniceps*, *Pleuroclada*, *S. irrigua rufescens*, and *Nardia geoscyphus* (70–3129a, 70–3137). The species is not common, as the paucity of reports indicates, but is probably not rare in and near cascades and rills in areas with gneissic rocks.

Regionally *S. subalpina* is usually quite typically developed. The only taxonomic problems offered by the regional materials are those of the Qôrorssuaq plants in which we find both plants with denticulate, margined leaves *(S. subalpina)* and similar, pigmented, emarginate plants with entire leaf margins corresponding to *S. obscura* and keying out to this

in Buch (1928). Whether or not *S. obscura* is a mere small, strongly pigmented phase of *S. subalpina* in which margin and teeth formation are suppressed cannot be answered by our collections.

Sectio *Nemorosae* K. Müll.

Scapania crassiretis Bryhn

Distribution (Map 59)

6: Eqalúnguit (70-2220a, 70–2242c, 70–2243, 70–2249b). 17: Tupilak (66–0032, 66–0109a). 21: Umiasugssûp (70–2925, 70–2927b).

Additional collections:

9: Eqalúnguit (M.P.P. 3859). 85: Sarpiussat (L.H. Aug. 1932). 141: Inukavsait qáqarssue (K.H. 16.286b).

S. crassiretis is a nearly strictly Arctic taxon, extending southward in Eurasia to northernmost Norway, Sweden, and Finland, with scattered alpine stations in Great Britain, Austria, Switzerland, and northern Italy; it is also found in Siberia. In North America reported from northern Quebec and from Greenland, where it is known northward from Inglefield Bredning (Kânâk and Kekertat; RMS) and from the above West Greenland stations.

The species is almost exclusively limited to areas with acidic rocks, usually occurring on seepage moist rocks, often in or near the edges of temporary rills, associated in such sites sometimes with *Odontoschisma elongatum* (66–0109a), at other times with *Anastrophyllum assimile* (70–2925, 70–2927b). Such forms are often juvenile, forming a mod. *parvifolia*, with very few teeth of the leaf margins and often with the ventral decurrence of the leaves unusually short—leading to potential taxonomic confusion. In such sites submersion and desiccation clearly alternate. Other associates in such niches are *Marsupella arctica*, *Gymnocolea inflata*, and *Cephaloziella* cf. *arctica*. Forms of this type often have enormous trigones, often so coarse in peripheral portions of the leaves that the plants seem to have hyaline, pale borders. No matter how poorly developed, the diagnostic cinnamon-brown, 1-celled gemmae are always abundantly developed.

Less often the species occurs in damp crevices of gneissic rocks, situated below basalt cliffs (hence a little basic seepage may be present); associated then may be (in 70–2220a, 70–2249b, 70–2243, 70–2242c) *S. mucronata praetervisa*, *S. parvifolia*, *Gymnomitrion concinnatum*, *Anastrophyllum minutum*, *Cephalozia pleniceps*, *O. macounii*, and *Lophozia heterocolpos*—the last two are suggestive of feebly Ca-enriched sites. Phenotypes from sheltered sites, between acidic rocks, may occur asso-

ciated with *S. spitzbergensis* and *L. hatcheri* (e.g. HOLMEN 16.286b). Such plants may be relatively pale, with only a little brown and purplish pigmentation; they may be very lax, have trigones no larger than in *S. nemorosa* and oblique, rather decurrent dorsal lobes. Such plants are almost inseparable from the temperate-zone *S. nemorosa*.

Sectio *Rufidulae* SCHUST.

Scapania spitzbergensis (LINDB.) K. MÜLL.

Distribution (Map 59)

16: Manîtsoq (70–3000, 70–3001b).

Additional collections:

29: Ritenbenk (S.B. Aug. 1870, publ. as *Sc. nemorosa*). 122: South of Eqaluit (K.H. 13.327). 141: Inukavsait qáqarssue (K.H. 16.286a, 16.259).

S. spitzbergensis has been the subject of detailed study (SCHUSTER, 1951 a), which showed that the species is paroecious—our only paroecious *Scapania* in Greenland except for the very different *S. kaurinii*.

The species occurs in northernmost Scandinavia to Spitsbergen, northern Alaska, the Hudson Bay area of Ontario, southward to Mt. Katahdin, Maine. In Greenland known from Kânâk, Inglefield Bredning (RMS), Nûgssuaq at Kraulshavn, 74°15′ N. (Cornell Party with the Peary Expedition, 1896), from Upernavik (ROSENVINGE), and from the above cited stations. A report (WARNSTORF, 1921) from Connecticut is based on *S. nemorosa*.

In West Greenland the species occurs both in clefts between rocks where apt to be intermittently desiccated, intermittently submersed (as in 70–3000, Manîtsoq, there with *Chandonanthus setiformis*, *Lophozia kunzeana*, *Ptilidium ciliare*, and *Gymnocolea inflata*), or in shallow, peaty depressions along the shores of tarns, where also periodically submerged or at least very wet (here associated, in 70–3001, with *Diplophyllum albicans*, *G. concinnatum*, *G. corallioides*, *Andreaea*, *Anthelia juratzkana*, *Cephalozia bicuspidata*, *L. alpestris*).

Even though the plant is demonstrably paroecious (as, e.g., in 70–3000), perianths are rare and sporophytes seem very rarely produced. Except in pigmented sun forms gemmae also seem only sporadically produced from the elongated teeth of the leaf margins—the teeth becoming truncated after gemma dehiscence. Occasional high Arctic extremes (e.g., HOLMEN 16.259; ROSENVINGE, 1886) may have the winged and arched keel generally edentate. Even on these phases some of the wings bear one or more jagged, spinous teeth.

Family ***Plagiochilaceae*** (JOERG.) K. MÜLL.

Plagiochila (DUMORT.) DUMORT.

Plagiochila asplenioides (L.) DUMORT.

(We do not accept the lectotypification of GROLLE, 1967, p. 280, which would necessitate substitution of *P. porelloides* for *P. asplenioides*).

Distribution (Map 60)

1A: Behind Arctic Station (66–0176, 70–2049). 1C: Blæsedalen (66–0305). 1D: Skarvefjeld (66–0306b, 66–0310). 2: Fortunebay (66–0128). 13: Jens Vahls Dal (70–2632, 70–2640, 70–2645, 70–2665). 14: Hareøen (70–2572, 70–2579, 70–2609). 35: Hollænderbugt (66–1506). 39: Tasiussaq (66–1234, 66–1262). 42: Magdlak (66–1357f, 66–1377). 43: Kangerdlugssuakavsak (66–1281). 51: Simiútap kûa, shore (66–0919). 52: Umîarfik, Qôrnoq (66–0966). 53: Søndre Strømfjord (66–0080a).

Additional collections:

1: Godhavn (S.B. 1870). 42: Magdlak (K.H. 12.915). 110: Ikorfat (K.H. 62–1574, 62–1576). 143: Kangerdlugssuaq (K.H. 16.385a, 16.388, 16.397a). 145: Uligssat (K.J. 10.186b).

This widespread plastic and malleable species is found principally under temperate-boreal to subarctic conditions in the northern hemisphere, except for east Asia, where replaced by the sibling species, *P. ovalifolia* Mitt.; it extends northward with a drastic decrease in frequency, to as far as 82°32′N in Ellesmere Island (SCHUSTER *et al.*, 1959) and to Svartenhuk Halvø in Greenland. Southward the species occurs to Alabama, Mississippi, and Georgia. Northernmost collections nearly all belong to or approach the phenotype recognized as var. *subarctica.*

P. asplenioides occurs regionally both as an explanate-leaved phenotype (typical, or var. *asplenioides*) and one that has strongly laterally appressed leaves, so that the shoots are laterally rather than antically compressed (var. *subarctica*). Plants here referred to var. *asplenioides* all belong to essentially edentate-leaved phenotypes; they are nearly all sterile (except for 66–0310), all more or less yellow-green, and all are rather poorly developed as contrasted to the various phenetic expressions found in temperate climates. Obviously in the Arctic the species is reduced to a very small suite of phenotypes which, however, can be at least superficially matched under "difficult" conditions in boreal-temperate loci.

The species is usually mesophytic, but avoids helophytic sites; it usually grows amidst other bryophytes over mineral to somewhat peaty soil in areas which are not too acid. Occurrences in areas with basic seepage, or on humus over basaltic rocks, or on steep, weathered basaltic slopes, are rather frequent. Common associates *(Lophozia heterocolpos*, *L. quadriloba*, *L. grandiretis*, *Scapania cuspiduligera*, *Anthelia*, *Anastrophyllum minutum*, and *Odontoschisma macounii)* are all either calciphytes or Ca-tolerant. Occasionally present on moist basaltic cliffs, on thin soil (Magdlak; 66–1357f), then with *L. badensis*, *Tritomaria scitula*, *S. cuspi-*

duligera, *S. gymnostomophila*, *Preissia*, *Athalamia*, *Sauteria*, *Mannia pilosa*, and *Solenostoma pumilum polaris*.

More rarely the species occurs on fast-drying, calcareous clay slopes, in a small impoverished phase; it may then be mixed (66–1506) with *Arnellia fennica*.

Cell size in *P. asplenioides s.str.* (after exclusion of the doubtfully specifically distinct *P. arctica*) is rather variable. As evident from Table I (pp. 114–116) in SCHUSTER (1959–60), Alaskan plants, and plants from northwestern North America in general, tend to have slightly larger cells on an average than those from temperate loci. In at least some Greenland populations cell size averages at the upper end known for *P. asplenioides* (e.g., in HOLMEN 12.915; here median cells are 29–36×28–39 μ; basal cells 34–44×34–54 μ); however, apical marginal cells, tangentially measured, are only 21–27 μ.

v. *subarctica* JOERG.

Distribution (Map 60)

1A: Behind Arctic Station (66–0165). 1B: Lyngmarken (66–0342f). 1C: Blæsedalen (66–0304). 14: Hareøen (70–2584). 42: Magdlak (66–1358b).

Additional collections:

34: Marrait kangigdlît (K.H. Sept. 1956). 129: Avataussaligssuaq (K.J. 944).

This doubtfully distinct phenotype, differing in the laterally compressed shoots, mimics *P. arctica* but is separated by the much smaller cells and fewer oil-bodies per cell (see SCHUSTER, 1959–60). It has exactly the ecology of *P. asplenioides s.str.* regionally, being confined to basaltic areas where it occurs with *Lophozia gillmani* and *L. heterocolpos* (66–1358b) or *L. quadriloba* and *L. heterocolpos* (66–0165). Known from Greenland up to 76°36′N. (Saunders Ø).

P. asplenioides subarctica may be merely an ecologically induced phenotype of very "difficult" sites. It should, however, be separated with care from *P. arctica*. The latter is known north to northern Ellesmere Island (SCHUSTER *et al.*, 1959) and has also been collected to our north at both Peary Land, 82°53′N. (HOLMEN 7011, WULFF, 1917) and Nucluet, 76°57′N. (RMS 46205), and Bowdoin Bugt, Inglefield Bredning, 77°33′N. (RMS 45787); it should occur in our area, but has not yet been found there.

Family ***Arnelliaceae*** NAKAI

Arnellia LINDB.

Arnellia fennica (GOTT.) LINDB.

Distribution (Map 61)

12: Perdlertut (70–2670, 70–2671b, 70–2685). 13: Jens Vahls Dal (70–2637b, 70–2646d, 70–2659). 35: Hollænderbugt (66–1504, 66–1505a, 66–1506). 40: Mârmorilik, head of the Fjord (66–1161, 66–1206, 66–1198, 66–1204). 47: Íngia (66–1031).

Additional collections:

39: Tasiussaq (K.H. 13.523). 50: Simiútap kûa, valley (K.H. 13.686). 106: Nûgssuaq (K.J. 97). 110: Ikorfat (K.J. 289a, K.H. 62–1567). 111: Kûtsiaq (K.J. 701).

This interesting Arctic species, which is found northward as far as there is available exposed land [to 82°32′ N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and to Peary Land (82°40′ N.) in Greenland], occurs southward to Ontario and, as a disjunct, in the Black Hills area of South Dakota; it is exceptionally rare south of the body of the Tundra, and has surely survived the Pleistocene in ice-free refugia in the Arctic.

A. fennica is a strict, apparently obligate, calcicole. It is able to tolerate very "difficult" sites and is, in our area, a typical species of steep, rapidly weathering, poorly consolidated shale slopes, where it often occurs with *Lophozia pellucida* (as on Ubekendt Ejland). On steep, exposed, weathered slopes it may also occur (70–2671b, 70–2646b, 70–2637b, 70–2685) with *Lophozia heterocolpos* (sometimes var. *harpanthoides*), *Scapania gymnostomophila*, *S. ligulifolia*, *Blepharostoma trichophyllum brevirete*, *Lophozia pellucida*, *L. quadriloba glareosa*, *L. polaris*, *L. gillmani*, *Tritomaria scitula*, and *S. cuspiduligera;* the last three taxa are usually associated in sites that are relatively moist with seepage. Most of these taxa also occur with *Arnellia* on fast-drying clay slopes (as at Hollænderbugt; 66–1504). *Arnellia* may also occur in calcareous, rich, low tundra, under moister conditions, associated with *Cryptocolea imbricata*, *T. scitula*, *L. quadriloba*, *L. heterocolpos* (66–1206a), or may actually occur in crevices of marble (Holmen 13.523). Regional specimens all seem to be sterile and we have seen no gemmae; by contrast, specimens from as far north as Alert, 82°32′N. (RMS 35633) may bear perianths and (RMS 35171) gemmae.

When dry, the species is characteristically dull-textured; it is the only regional taxon with opposite leaves and seems to be singularly unvariable and stenotypic.

Family ***Antheliaceae*** SCHUST.

Anthelia DUMORT.

Anthelia juratzkana (LIMPR.) TREV.

Distribution (Map 62)

1A: Behind Arctic Station (66–0153b, 66–0156, 66–0158, 66–0160, 66–0161b, 66–0172b, 66–0179, 66–0182, 66–0183, 66–0190, 70–2014, 70–2015, 70–2016, 70–2044a, 70–2045, 70–2050, 70–2055). 1B: Lyngmarken (66–0550). 2: Fortunebay (66–0138). 6: Eqalúnguit (70–2208, 70–2241). 8: Kuánerssuit (70–2140). 9: Eqaluit (70–2522, 70–2526c, 70–2533b, 70–2539a, 70–2542, 70–2543, 70–2544, 70–2546, 70–2547, 70–2552, 70–2554, 70–2556, 70–2559, 70–2766a, 70–2561). 10: Enoks Havn (70–2763d, 70–2769, 70–2770a, 70–2776a, 70–2778b). 12: Perdlertut (70–2963). 13:

Jens Vahls Dal (70–2630, 70–2662). 14: Hareøen (70–2572, 70–2574, 70–2581, 70–2613, 70–2622). 15: Kronprinsens Ejland (70–2077a, 70–2085, 70–2090a). 16: Manîtsoq (70–3001, 70–3007, 70–3010, 70–3015a). 17: Tupilak (66–0106a). 18: Grønne Ejland (70–2811). 19: Nûk (70–2874b, 70–2875a). 21: Umiasugssûp (70–2935, 70–2936b, 70–2951c). 22: Orpigsôq (70–3110a, 70–3118a). 23: Kangersuneq (70–3127b, 70–3129, 70–3130, 70–3140, 70–3145b, 70–3149, 70–3153a, 70–3145b). 25: Sarfaq (70–2320, 70–2322a, 70–2340a, 70–2364, 70–2367). 26: Pâkitsup ilordlia (70–2257a, 70–2263a, 70–2266b, 70–2314, 70–2319, 70–2392). 30: Eqe (66–0249d, 66–0250, 66–0288, 66–0289, 66–0322, 66–0323, 66–0331, 66–0336). 32: Qôrorssuaq (70–2440f, 70–2453, 70–2457, 70–2458, 70–2462, 70–2467, 70–2482, 70–2484a). 38: Uvkusigssat (66–1390). 39: Tasiussaq (66–1259). 42: Magdlak (66–1359). 43: Kangerdlugssuakavsak (66–1287c). 45: Sagdliaruseq (66–1054, 66–1074a). 46: Qalatôq (66–1101, 66–1138). 48: Amitsup (66–0780). 53: Søndre Strømfjord (66–0084, 66–0088).

Additional collections:

6: Eqalúnguit (M.P.P. 1662). 17: Tupilak (K.J. 1307, K.H. June 1956). 24: Jakobshavn (K.H. 15.958). 26: Pâkitsup ilordlia (S.B. Aug. 1870). 28: Atâ (LÆGAARD July 1962). 29: Ritenbenk (S.B. 1870). 32: Qôrorssuaq (K.J. 321). 34: Marrait kangigdlît (K.H. Sept. 1956). 52: Umîarfik, Qôrnoq (K.H. 16.366). 57: Nipisat (K.H. 14.369a). 67: Asuk (M.P.P. 135e). 83: Angnertussoq (L.H. Aug. 1932). 84: Qeqertasugssuk (L.H. Aug. 1932). 85: Sarpiussat (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN Aug. 1958). 88: Christianshåb (K.H. 16.621). 89: Marrait (S.B July 1870). 90: Tasiussaq (S.B. July 1870). 94: Rodebay (J.V. 172). 99: Sarqaq valley (K.J. 186a). 106: Nûgssuaq (K.H. July 1956). 110: Ikorfat (K.J. 334b). 112: Umiatorfik (K.J. 576, 631). 116: Puiagtukavsak (K.J. 679). 117: Sêrsínerssuaq (K.J. 612). 120: Itipilua qáqâ (K.J. 695b). 122: South of Eqaluit (K.H. 13.352). 123: Uigordleq (K.H. 12.891). 125: Sarqap taserssua (K.H. 17.113a). 128: Agatdalen (K.H. 13.863). 136: Kangerdluarssûp qeqertâ (K.H. 16. 167).137: Esersiutilik (K.H. 16.470). 139: Qaqortukavsaq (K.H. 16.079b). 141: Inukavsait qáqarssue (K.H. 13.604). 142: Niaqornánguaq (K.J. 14.988a). 144: Igdlorssuit (K.H. & W.C.S. 62.1632). 145: Uligssat (K.J. 10.176, 10.186g, 10.188b).

This abundant species is subcosmopolitan under Arctic and alpine conditions in the northern hemisphere and recurs as a rarity in cold parts of the southern hemisphere, where it is known from Tierra del Fuego and New Zealand (SCHUSTER, 1963, 1969a), from alpine sites of New Guinea (SCHUSTER, 1968) and from South Georgia and Livingston Island in the Antarctic (SCHUSTER, 1969a). It occurs everywhere on the coast of Greenland, north to at least 82°40′N. in Peary Land (ARNELL, 1960), and to 82°32′N. in Ellesmere Island (SCHUSTER *et al.*, 1959).

A. juratzkana is found almost everywhere in "difficult" sites in the Arctic; it often forms massive, light gray-green sheets in late snow areas, or in areas irrigated during periods of snow melt. It is as frequent, if not more so, in basaltic regions as in areas with igneous rocks. Associated with the easily demonstrated paroecious inflorescence is abundant sporophyte production extending locally from late June (rarely) or mid-July to mid-August.

The ecological range matches the abundance; typical occurrences are: (1) on soil over moist, gneissic cliffs, with *Anastrophyllum assimile*,

Marsupella arctica, *M. revoluta* (70–2322a); (2) on sandy to silty to somewhat peaty damp soil, often along irrigated sites or between damp rocks, then very often with *Nardia geoscyphus* (70–3140, 70–2539a, 70–2936b, 70–2766a, 70–2526c, 70–2045, etc.), and, less constantly, *Cephalozia bicuspidata*, *C. pleniceps*, *Cryptocolea imbricata*, *Calypogeia muelleriana*, *Lophozia pellucida minor*, *Scapania hyperborea*, *S. cf. obcordata* (rarely also *S. subalpina* in very moist loci), *Pleuroclada albescens*, etc.; (3) moist, sandy soil of river terrace margins, with *Salix herbacea*, *Cephalozia bicuspidata*, *C. pleniceps*, *S.* cf. *obcordata*, etc.; (4) moist, peaty soil over and between acidic rocks and boulders, edge of a rill, with *M. boeckii*, *Gymnomitrion concinnatum*, *L. opacifolia*, *L. ventricosa grandiretis*, *L. v. rigida*, *L. alpestris*, *Pleuroclada*, *Blepharostoma;* (5) moist, peaty soil over basaltic rocks, edge of a rill, with *Calypogeia muelleriana*, *L. grandiretis*, *C. pleniceps;* (6) irrigated, S. facing basaltic slopes, with *L. quadriloba*, *L. heterocolpos;* (7) insolated mucky, irrigated soil, temporary rill, with *S. hyperborea*, *M. arctica*, *Gymnocolea;* (8) damp soil over acidic ledges and cliffs, with *Diplophyllum taxifolium*, *Gymnomitrion concinnatum;* (9) low but intermittently dry, fine, water-deposited silty-sandy soil, river mouth, with *G. concinnatum*, *L. wenzelii lapponica;* (10) thin, damp soil, vertical wall, gneiss hills, with *G. corallioides*, *Prasanthus suecicus*, *Anastrophyllum minutum*, *Lophozia incisa;* (11) fine, silty-sandy, intermittently rather dry ground around a shallow lake, with *P. suecicus*, *Cephalozia bicuspidata*, *N. geoscyphus*, *Solenostoma pyriflorum*, *L. excisa*, *Riccardia sinuata*, *Tritomaria quinquedentata*, *A. minutum grandis.* Many other ecological niches are invaded and *A. juratzkana* must be classed as one of the most ubiquitous and tolerant of Arctic taxa, able to invade in arid as well as permanently moist, acid as well as circumneutral to basic loci.

We have checked numerous collections of *Anthelia* for sexuality. All in which we have found gynoecia could also be shown to have antheridia in the leaf axils of the bracts below the perichaetial ones. Also, in all of the sporophyte-bearing plants 2 or 3 narrow elater spirals were present. As a consequence, there is no doubt that all regional collections of *Anthelia* belong to this species; all earlier reports (including those of Berggren, 1875; Lange & Jensen, 1887) of plants of *A. julacea* from our area represent, in so far as we have checked them, *A. juratzkana.* We have seen a collection of sterile plants, perhaps correctly called *A. julacea*, from Upernavik (Vahl 141), which formed the basis for a report of *Hygrobiella laxifolia* from our region (Lange & Jensen, 1887). These are weak plants, with thin-walled cells; they are too poorly developed to name to species with any surety but are of much interest because on one plant we found a single terminal branch of the *Acromastigum* type.

Family ***Cephaloziaceae*** MIGULA

Broadly interpreted here to include *Pleuroclada* and *Hygrobiella* (the *Hygrobiellaceae* of MÜLLER, 1951–58) as well as the families *Odontoschismaceae* of MÜLLER (l.c.), *Cladomastigaceae* FULF., *Trabacellulaceae* FULF., and *Alobiellaceae* FULF. Reasons for this delimitation are given in SCHUSTER (1974).

Hygrobiella SPRUCE

Hygrobiella laxifolia (HOOK.) SPRUCE

Distribution (Map 62)

95: Pâkitsoq (K.H. & G.M. 71–1929).

Previously reported from Upernavik by LANGE & JENSEN (1887), but as is shown (see p. 283), this was based on weak material of *Anthelia* cf. *juratzkana*. There is also a report by EVANS (1915) from the Nûgssuaq, at Kraulshavn (74°15′N.) which we have not been able to verify. We have seen only one collection of this relatively southern and strictly oceanic species from our region; it is known in south Greenland and from the east coast northward from 60°06′N. to 65°36′N. (in Angmagssalik Fjord), Tûnok (65°53′N.) and Qingertívaq (66°06′N.).

The plants from Pâkitsoq (HOLMEN & MOGENSEN 71–1929) are sparing but quite typical in all respects; associated are *Marsupella emarginata* var. *aquatica* and *Solenostoma pumilum pumilum*. Although here restricted to the region with gneissic rocks, the *Hygrobiella* further southward is not restricted to acidic rocks (SCHUSTER, 1974), occurring at times with *Scapania cuspiduligera* and other Ca-tolerant taxa.

Pleuroclada SPRUCE

Pleuroclada albescens (HOOK.) SPRUCE (Table III)

Distribution (Map 63)

1A: Behind Arctic Station (66–0179, 66–0197, 70–2003, 70–2016, 70–2019, 70–2047d). 1B: Lyngmarken (66–0555, 66–0557a). 1D: Skarvefjeld (66–0311b). 2: Fortunebay (66–0199). 6: Eqalúnguit (70–2223b, 70–2227a, 70–2238). 9: Eqaluit (70–2522, 70–2529, 70–2532a, 70–2533, 70–2534, 70–2539a, 70–2540, 70–2541b, 70–2542, 70–2543, 70–2546, 70–2549, 70–2550, 70–2552, 70–2553, 70–2554). 10: Enoks Havn (70–2778a). 11: Qasigíssat (70–2720a). 14: Hareøen (70–2575, 70–2612). 15: Kronprinsens Ejland (70–2062a, 70–2063, 70–2066a, 70–2073, 70–2101, 70–2106, 70–2114). 16: Manîtsoq (70–3003, 70–3007c, 70–3008, 70–3009, 70–3013, 70–3015a, 70–3016, 70–3020). 17A: Egedesminde (66–0947). 18: Grønne Ejland (70–2814b, 70–2815b). 22: Orpigsôq (70–3108). 23: Kangersuneq (70–3126, 70–3129, 70–3135a, 3144c). 24: Jakobshavn (66–0234a). 25: Sarfaq (70–2344d, 70–2356a). 26: Pâkitsup ilordlia (70–2304, 70–2314, 70–2315, 70–2387). 28: Atâ (70–2512b). 29: Ritenbenk (66–0253, 66–0256, 66–0257, 66–0263a). 32: Qôrorssuaq (70–2438a, 70–2440e, 70–2453, 70–2462, 70–2466, 70–2469, 70–2470, 70–2473, 70–2476c, 70–2482). 37: Agpat (66–1468). 46: Qalatôq (66–1110). 48: Amitsup (66–0790b).

Additional collections:

6: Eqalúnguit (M.P.P. 2645). 17: Tupilak (K.J. 1305, 1306, 1309, 1323, 1450). 28: Atâ (LÆGAARD July 1962). 29: Ritenbenk (S.B. 1870). 124: Tasíngortaq (K.H. 13.308, 13.312b). 137: Esersiutilik (K.H. 15.886). 142: Niaqornánguaq (K.J. 14.996).

f. *islandica* (Nees) SCHUST.

Distribution (Map 63)

1A: Behind Arctic Station (66–0186, 70–2037). 16: Manîtsoq (70–3014c). 17: Tupilak (66–0027a). 26: Pâkitsup ilordlia (70–2258c). 32: Qôrorssuaq (70–2481).

This species, chiefly of subarctic-subalpine to low Arctic-alpine range is circumarctic to circumsubarctic in range. In North America it extends from southernmost Ellesmere Island (STEERE, 1941) and Baffin Island to Quebec (where southward, disjunctly, to the Gaspé); in Greenland known north to ca. 66° N. on the east coast; in West Greenland not known north of Upernavik (72°34′ N.).

P. albescens is a frequent plant, ecologically rather tolerant as regards pH, usually confined to relatively damp sites. It occurs mostly on fine-textured soils—clay, silt, and sand—or over peaty soil. It often occurs along small rills, or on peaty soil along the margins of insolated, rock-bordered tarns and pools, often where subject to occasional inundation. On such soft, mucky, organic substrata often forming large, yellow-green patches, often with *Anthelia juratzkana* (and other species tolerant of difficult sites). *P. albescens*, however, is rarely a component of the "Schneetälchen" vegetation in which *A. juratzkana* plays such an important ecological role. The plants are often fertile; capsules are frequent and produced from July 20 (70–2344d, 70–2315) to Aug. 8 (70–2532a) and Aug. 23 (70–3126). Gemmae, previously unknown in the genus *Pleuroclada*, rarely occur; they are present in 66–0234a and 70–3126. They occur on erect, leafy axes and may terminate the elongate, spicate androecial branches; they are found in small globose, intensely green heads formed of a pair of concave, malformed leaves surrounding a dense mass of 1-celled spherical to short-ellipsoidal, smooth, rather thin-walled gemmae; they average 12–14 to 13–14×16–18 μ.

Typical sites for *P. albescens* are: (a) Constantly damp to moist, peaty ground, often between rocks and boulders, near the edges of tarns and shallow lakes; here often associated with *Scapania hyperborea* (70–2062a, 70–3108, 70–2815b, 70–2553, etc.), more rarely *S. paludicola*, *Cephalozia pleniceps*, *C. bicuspidata*, *Lophozia ventricosa longiflora*, *L.v. confusa*, *L. wenzelii wenzelii* and *L. kunzeana*. (b) Similar sites and on better-drained but moist slopes, but on soils with a higher mineral content, often loamy or clayey; here are commonly associated *Nardia geoscyphus* (70–2073, 70–3135a, 70–3144c, 70–2016, 70–3015a, 66–0199, etc.), less often *Solenostoma subellipticum*, *Calypogeia muelleriana*, *C. inte-*

gristipula, *Diplophyllum taxifolium*, *Cephalozia pleniceps*, *C. bicuspidata*, *Scapania curta*, *Anthelia*, occasionally (when the ground is peatier) also *L. kunzeana* (in 70–3135a, 70–2073), *Anastrophyllum minutum grandis*, *S. scandica*, rarely *S. hyperborea* (70–3144c) or *S. hyperborea* and *S. irrigua* (70–3135a). (c) Wet, peaty ground at edges of insolated, acidic tarns; the species is rather rare in such helophytic acidic sites, but occurs (in 66–1468) with *Gymnocolea*, *Odontoschisma elongatum* and *S. hyperborea*. When growing in rich, low, damp moss-tundra, often near standing water, a wide array of other taxa may be associated, i.a., *Lophozia wenzelii lapponica*, *L. ventricosa rigida*, *L. v. confusa*, *L. v. longiflora*, *L. v. silvicola*, rarely (70–2720a) *L. heteromorpha*, or (70–2541b) *L. cavifolia*, or (70–2344d) *A. sphenoloboides*. The species may here occur with taxa of distinctly southern affinity, e.g., *Calypogeia neesiana*, *Cephalozia lunulifolia*, *C. leucantha*, *Mylia anomala*, as well as *A. sphenoloboides* and *Calypogeia sphagnicola* (70–2814b), or *Cephalozia leucantha* (66–0234a). (d) Occasionally along acidic, swift, cold rills, on peaty soil over and between stones (as in 70–2440e) then with *Marsupella boeckii*, *L. ventricosa grandiretis*, *L. v. rigida*, *L. alpestris*, *Anthelia*, and *Blepharostoma*. (e) In similar sites, but where subject to inundation (70–2438a), *S. serrulata*, *S. subalpina*, *L. alpestris*, and *Solenostoma sphaerocarpum* may be associated. (f) At the opposite extreme as a weak form, corresponding in part to *f. islandica*, on exposed, broken, rocky ground, over fine-textured mineral soil, associated with *Gymnomitrion concinnatum* and *G. apiculatum* (70–2481) or with these two taxa plus *Prasanthus* and *Tritomaria quinquedentata* (70–3014c). (g) Finally, when growing under feebly basic conditions, usually on irrigated slopes in basaltic areas, sometimes in rich, spongy tundra meadows traversed by small rills, a wide array of other taxa may be associated, often *Lophozia grandiretis* and *L. heterocolpos* (70–2227a, 70–2258c, 70–2512b, 70–2223b), less often *L. elongata* (70–2227a), *L. latifolia*, *L. ventricosa confusa*, *L. v. rigida*, *L. pellucida minor*, *L. cavifolia*, *Nardia geoscyphus*, *Anastrophyllum minutum*, *Riccardia sinuata*, *Solenostoma pusillum*, and *Cephalozia pleniceps*.

P. albescens has been traditionally held to include as a separate variety, *islandica* (Nees) Spr., which various workers, including Nees, Lindberg, and Pearson regarded as a distinct species. We have arbitrarily studied 10 collections (Table III), of which width of leaf cells at lobe bases and width of dorsal and dorsolateral cortical cells were measured. We believe the first three collections listed, on the basis of the slender aspect, correspond to "var. *islandica*". As Table III and Fig. 21 show, however, there is no observable discontinuity in our material. Perianth mouth cells also show little variation; they tend to be somewhat shorter and broader in the so-called var. *islandica*. Cortical cell width, ranging from 23–33 μ is rather less variable than leaf cell width, which shows

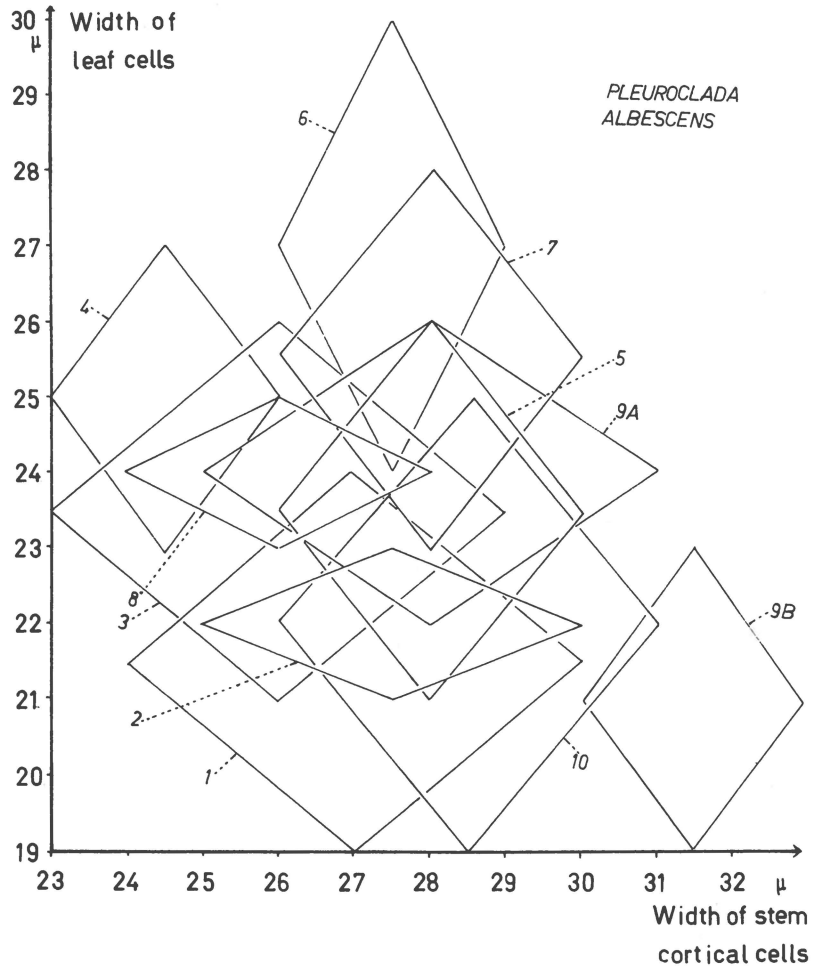


Fig. 21. See also Table III (p. 288).

variation from 19–30 μ. In general, leaf cells are broader in plants from richer, moister sites—but even here no good generalization seems possible. Thus in the two collections from most exposed sites, on broken soil over exposed rocks, with *Gymnomitrion concinnatum*, *G. apiculatum*, *Prasanthus suecicus* (70–3014c, 70–2481; nos. 9 and 10, respectively, in the accompanying Table and Fig., we find that there is no meaningful difference in cell size. Thus in 70–3014c we find lax- and small-leaved shoots, with narrow leaves whose width does not exceed the length, which correspond to "var. *islandica*"; and there (see 9b in Table III and Fig. 21) leaf cell size is admittedly minimal. Such plants, however, occur admixed with larger shoots (see 9a in Table III and Fig. 21) where leaf cell width is considerably larger and show the broad, strongly concave leaves of

Table III. *Pleuroclada* Cell Measurements.

	Width of leaf cells at base of lobes. μ	Width of stem cortical cells, dorsally. μ
1. Godhavn 66–0186	(17) 19–24 (26)	(22) 24–30 (31)
2. Godhavn 70–2037	(20) 21–23 (24)	(24) 25–30 (34)
3. Pâkitsup 70–2258c	(19) 21–26 (28)	(22) 23–29 (36)
4. Agpat 66–1468	(21) 23–27 (28)	(22) 23–26 (29)
5. Fortunebay 66–0199	(18) 21–26 (27)	(24) 26–30 (33)
6. Qasigíssat 70–2720a	(21) 24–30 (32)	(25) 26–29 (30)
7. Orpigsôq 70–3108	(22) 23–28 (30)	(23) 26–30 (31)
8. Jakobshavn 66–0234a	(22) 23–25 (26)	(23) 24–28 (31)
9. Manîtsoq 70–3014c		
(a)	(21) 22–26 (28)	(24) 25–31 (36)
(b)	(18) 19–23 (25)	(26) 30–33 (37)
10. Qôrorssuaq 70–2481	(17) 19–25 (26)	(25) 26–31 (33)

ordinary *albescens*. Furthermore, there is no necessary relationship between leaf cell width and cortical cell width, as these figures show. In 70–2481, in which a compact, julaceous form is present, mostly small-leaved and with leaves not broader than long or hardly so, we have basically "var. *islandica*". Yet these plants (no. 10 in the figure and table) have relatively wide cortical and leaf cells showing much variation in width, from leaf to leaf. We can only conclude that there is no meaningful basis for recognition of a var. *islandica*, at least in our region. At best one can rationalize the recognition of this plant as a mere forma.

Cephalozia DUMORT.

Cephalozia bicuspidata (L.) DUMORT. (Table IV)

Distribution (Map 64)

1A: Behind Arctic Station (70–2013, 70–2037, 70–2041, 70–2042). 1C: Blæsedalen (66–1570). 2: Fortunebay (66–0199a). 6: Eqalúnguit (70–2216, 70–2238, 70–2247). 9: Eqaluit (70–2525, 70–2532a, 70–2539, 70–2543, 70–2547, 70–2549b, 70–2561). 10: Enoks Havn (70–2757b, 70–2758b, 70–2763, 70–2766a, 70–2769, 70–2770d). 11: Qasigíssat (70–2721a, 70–2738). 15: Kronprinsens Ejland (70–2068a,

70–2082a, 70–2084, 70–2089, 70–2093a, 70–2096, 70–2101, 70–2106, 70–2116). 16: Manîtsoq (70–3001, 70–3007, 70–3008, 70–3012a, 70–3024c). 17: Tupilak (66–0009c, 66–0024a, 66–0025a). 17A: Egedesminde (66–0949). 18: Grønne Ejland (70–2810a). 19: Nûk (70–2835, 70–2870c, 70–2871, 70–2875c, 70–2877). 21: Umiasugssûp (70–2935c). 23: Kangersuneq (70–3125a, 70–3127a, 70–3131a, 70–3133, 70–3143, 70–3153, 70–3154a, 70–3156b). 24: Jakobshavn (66–0224, 66–0225a, 66–0230a). 25: Sarfaq (70–2320a, 70–2348). 26: Pâkitsup ilordlia (70–2260b, 70–2264, 70–2279, 70–2280a, 70–2294c, 70–2295, 70–2296, 70–2297b, 70–2316, 70–2320a, 70–2385, 70–2387, 70–2392). 29: Atâ (70–2512b). 29: Ritenbenk (66–0534). 30: Eqe (66–0249). 31: Anap nunâ (70–2425, 70–2435). 32: Qôrorssuaq (70–2448e, 70–2453, 70–2458, 70–2470). 45: Sagdliaruseq (66–1073, 66–1074a, 66–1091). 48: Amitsup (66–0789, 66–0817). 53: Søndre Strømfjord (66–0053, 66–0056, 66–0058a, 66–0062, 66–0088, 66–0090a, 66–0100).

Additional collections:

7: Angujârtûtit (M.P.P. 2548). 17: Tupilak (K.H. 16.993). 36: Umanak (K.H. 16.331a). 58: Itivneq kitdleq (M.P.P. 1937, 2353). 60: Kugssuaq (M.P.P. 725). 74: Kangerdluarssuk (M.P.P. 1766b). 82: Sarqardlîp nunâ (L.H. Aug. 1932). 83: Angnertussoq (L.H. Aug. 1932). 87: Kangersuneq (J.V. 109?). 88: Christianshåb (K.H. 16.616a). 90: Tasiussaq (S.B. July 1870). 92: Claushavn (S.B. Aug. 1870). 98: Sarqaq (K.H. 15.810a). 109: Kangilia (K.J. 446). 114: Eqaluit (K.J. 453, 508). 124: Tasíngortaq (K.H. 13.292, 13.312a). 126: west of Sarqap taserssua (K.H. 13.424). 131: Storø (A.R. July 1954). 140: Small Island (K.H. 16.738).

C. bicuspidata s.l. is a plastic and variable, holarctic species, occurring southward in eastern North America to North Carolina and Tennessee. It is here taken to include as (cytologically and partly geographically) distinct subspecies the taxa, *C. lammersiana*, *C. ambigua*, and *C. otaruensis* (Schuster, 1974). [The species also rarely occurs in New Zealand, hence is bipolar; the New Zealand plants, segregated as ssp. *australis* (Schuster, 1974), differ in ability to develop rather intense reddish, rather than brown or purplish brown, pigments, and in the larger cortical cells of the stem. Possibly an autonomous species is involved]. Only ssp. *bicuspidata* and ssp. *ambigua* occur regionally.

Broadly delimited *C. bicuspidata* is circumboreal to circumarctic and is seemingly absent only from the northernmost portions of the Arctic; it occurs to at least 77°30′N., in Inglefield Bredning, but seems absent from northern Ellesmere Island (Schuster *et al.*, 1959), although we have seen a collection made by Th. Wulff from Kap May, 82°27′N. in North Greenland.

ssp. *bicuspidata* (L.) Dumort.

C. bicuspidata ssp. *bicuspidata* is typically a widespread plant of acidic, often peaty sites, often around acidic, insolated tarns and fens (66–0090a, 66–0024a, 70–3131a, 70–3156b, 70–3024c, 70–2093a, etc.) with *Lophozia kunzeana*, *L. binsteadii*, *Calypogeia sphagnicola*, *Scapania hyperborea*, less often *Tritomaria quinquedentata*, *Pleuroclada*, *L. ventri-*

cosa s.l., occasionally (in very wet sites) *Gymnocolea inflata*. It may actually occur amidst or over *Sphagnum*, then sometimes with *L. binsteadii*, *Cephaloziella uncinata*, *Cephalozia pleniceps*, and *Calypogeia sphagnicola*, etc. (66–0053, 70–3125a, 66–0062) or (70–2758b, 70–2757b) with *L. excisa*, *S. hyperborea*, and *Cephaloziella byssacea;* or, alternatively, it may occur with or over *Aulacomnium*, then with (70–2870c), *L. polaris sphagnorum*, *L. excisa*, *Cephalozia pleniceps*, and *Calypogeia sphagnicola*.

The species, however, is not always in wet peaty loci, but may occur on circumneutral to weakly basic, moist slopes, forming reddish, compact forms (70–2770d, 70–2763), associated with *Cryptocolea*, *Nardia geoscyphus*, *Anthelia*, and *Cephalozia pleniceps*. Occurrences on fine-textured soils, with or without a high organic content, are frequent (70–3143, 70–3153, 66–0230a); then *N. geoscyphus* is almost always admixed, occasionally also *Solenostoma sphaerocarpum*, *Anthelia*, and *S. curta*.

At the opposite extreme are occurrences on (a) wet, acidic, exposed rocks, where there is seepage (as in 70–2068a), here associated with *Odontoschisma elongatum*, *Gymnocolea*, *Gymnomitrion apiculatum*, and *G. concinnatum*, or (b) exposed compact soil of stone polygons (as in 70–2448e), where occurring as an erect, julaceous, red-brown, dense-leaved phenotype, amidst *G. corallioides* and *Prasanthus*, with *L. alboviridis*, *L. excisa*, *N. geoscyphus*, *Anastrophyllum minutum*, *Diplophyllum obtusifolium*, *S. parvifolia* consociated. Occurrences analogous to the last are on fine, silty, fast-drying, heaved soils (70–2320a), with *Prasanthus*, *Anthelia*, *G. concinnatum;* on exposed peaty soil along a small rill (66–0249), with *Prasanthus*, *Cryptocolea*, *Anthelia*, *G. concinnatum*, *A. minutum*, etc.; or as a mod. *parvifolia-colorata* on water-deposited, fine sandy exposed soil near a lake edge (70–3133, 70–3154a), where with *Prasanthus* and *Anthelia*. The species is also found on fine, silty soil along streams, mixed with *Salix herbacea*, associated with *Anthelia*, *Scapania* cf. *perssonii*, *C. pleniceps*, *N. geoscyphus* (70–2763, 70–2935c), also as a mod. *colorata-parvifolia*. Small-leaved, pigmented phases also occur on fine, wind- or water-deposited, damp soils (as at the mouth of the river at Eqaluit; 70–2543, 70–2547), together with *N. geoscyphus*, *Anthelia*, and occasionally *Pleuroclada*.

Although seemingly almost exclusively restricted to acidic sites in temperate and boreal regions, *C. bicuspidata* seems to be more diverse ecologically in the Arctic. Here, for example, it may exceptionally grow on thin soil in crevices of ledges, in the contact region between basalt and gneiss, associated with calciphytes (e.g., in Disko Fjord, 70–2247, where with *Peltolepis grandis*, *Scapania mucronata praetervisa*, *Tritomaria scitula*, and *Lophozia heterocolpos*). It also grows in similarly locally Ca-rich sites on wet sand, in open depressions in moss-heath tundra around a lake (Qissugssalik; 70–2264, 70–2297b), associated with *L. rutheana*, *L. quadri-*

loba, *Blepharostoma tr. brevirete*, *Tritomaria polita polymorpha*, *Odontoschisma macounii*, and other Ca-tolerant taxa.

Perianths are abundantly produced; capsules are infrequent but have been seen from as early as June 23 (at Søndre Strømfjord; 66–0053) to July 20 (70–2387, 70–2295, 70–2316) to as late as Aug. 7 (70–2738). By contrast, gemmae seem to be rarely produced; we have seen them only in plants from Ivnarssuaq (70–3143).

ssp. *ambigua* (MASSAL.) SCHUST.

Distribution (Map 64)

1A: Behind Arctic Station (66–0156, 66–0161a, 66–0179, 70–2012b, 70–2045a, 70–2059b). 15: Kronprinsens Ejland (70–2066b). 21: Umiasugssûp (70–2936). 37: Agpat (66–1467a). 46: Qalatôq (66–1102b).

A purely Arctic-alpine race in which the chromosome number n=9 (in contrast to n=18 for ssp. *bicuspidata*) has been reported. In the absence of a chromosome count, cell size must be used to effect a separation. In view of the extreme phenetic variation within *C. bicuspidata*, associated with degree of exposure and available moisture, separation of ssp. *ambigua* on the sole basis of cell size is often a parlous undertaking. The above collections, referred to ssp. *ambigua* on the basis of cell size alone (see Table IV), show clear gradation to ssp. *bicuspidata* in some cases. Of the collections tabulated (Table IV) the first six are surely best attributed to ssp. *ambigua;* the next three probably so; the last two, in our opinion, are surely closer to ssp. *bicuspidata.*

The various collections of ssp. *ambigua* are not, seemingly, ecologically distinct from ssp. *bicuspidata.* Plants may occur in helophytic loci, with *Scapania hyperborea*, *S. irrigua rufescens* (66–0156), and other bog taxa, e.g., *S. paludicola*, *Pleuroclada* and *C. pleniceps* (70–2066b), or may occur with *Anthelia* and *Nardia geoscyphus* on damp peat over mineral soil; or with these taxa plus *S. hyperborea* and *S. subalpina* (70–2936). However, the plants may also occur on intermittently drier organic soils, over rocks, associated with *Gymnomitrion corallioides* (70–2059b, 70–2012b), less often *G. concinnatum*, *Nardia scalaris*, *Odontoschisma macounii*, *Blepharostoma*, and *S. degenii dubia.* These last loci are in areas with some basic seepage, on gneissic hills with basalt cliffs above. Occasionally, on clearly Ca-enriched soil (as in 66–0161a), then with *Calypogeia muelleriana*, *Cephalozia pleniceps*, *Anthelia*, *S. curta*, *Lophozia heterocolpos harpanthoides*, and *L. grandiretis.* The most common associates, in decreasing frequency of association, appear to be: *Anthelia juratzkana*, *C. pleniceps*, *G. corallioides*, *S. hyperborea*, *Pleuroclada albescens*, *L. heterocolpos harpanthoides*, and *Nardia geoscyphus.* The development of the *ambigua* phenotype does not seem to hinge on purely environmental causes. For example, in 70–2066b the *ambigua* phenotype is best expressed; here the

plants are provided with almost transverse leaves that are hardly broader than the stem; the leaves are somewhat appressed to the stem, much as in some *Cephaloziellae*, and the lobes are often incurved and formed of 1–2 superposed cells. In this phenotype, which grew under obviously helophytic conditions, with *S. paludicola*, *Pleuroclada*, and *C. pleniceps*, the cells of the leaf lobes base average only 19–22 μ wide.

Table IV: *Cephalozia bicuspidata* ssp. *bicuspidata* & ssp. *ambigua*

	Leaves divided	Leaf cells measured at lobe base. μ	Cortical stem cells dorsally measured. μ	Subspecies
Godhavn 66–0179	1/2	16–18×23–26	24–26×28–44	*ambigua*
Agpat 66–1467a	1/2	16–21×23–26	28–33×36–65	*ambigua*
Godhavn 66–0161a	1/2	15–20×26–31	28–34×42–47	*ambigua*
Kronprins. Ejl. 70–2066b	1/2	19–22×24–31	30–36×36–49	*ambigua*
Godhavn 66–0156	1/2	20–23×20–31	30–36×30–49	*ambigua*
Godhavn 70–2012b	1/2	22–24×29–36	34–39×66–85	*ambigua*
Godhavn 70–2045a	1/2	21–26×23–26	34–42×44–68	*ambigua*
Umiasugssûp 70–2936	1/2	23–25×23–31	28–31×34–40	*ambigua*
Godhavn 70–2059b	1/2	22–29×23–26	26–34×42–58	*ambigua*
Tupilak 66–0009c	1/2–2/3	23–26×21–26(42)	43–46×40–62	*bicuspidata*
Tupilak 66–0025a	2/3	26–31×39–48	36–40×44–59	*bicuspidata*

Cephalozia loitlesbergeri SCHIFFN.

Distribution

53: Søndre Strømfjord (66–0049).

This primarily boreal species is relatively infrequent in, principally, the Spruce-Fir regions of Europe and eastern North America, extending (as a rarity) west to Minnesota and south to New England. Not previously known from Greenland although we have seen a single collection from southwest Greenland. The above collection, although sterile, is clearly referable here. The rather decurrent leaves vary much in width, ranging

usually from 9–17 cells wide, are bifid almost or quite half their length, with the lobes long, often arched towards each other and—most diagnostically—with the slender tips often contiguous or actually slightly crossing. This feature is less evident on the largest leaves. Leaf tips most often end in 2 superposed elongated cells, more rarely in 1 elongated cell; on none have we seen acuminate tips formed by 3 cells. Only on very robust individuals with broader than normal leaves are the lobes less or not connivent, and less narrowly acute. Median cells are leptodermous, mostly 28–32×30–35 to 29–35(43–45)×38–47 μ. Branching is not exclusively ventral-intercalary; at least a single terminal, *Frullania*-type branch has been seen. No stolons are present, eliminating *C. pleniceps*. The stem consists in general of 15–17 rows of cortical cells, the dorsal cells being ca. (36)40–52×44–75 μ. Medullary cells are usually in 23–25 rows.

These plants have cells somewhat on the large side for *C. loitlesbergeri* (compare Table V). The only possible alternative placement, however, would be under *C. pleniceps*, a species always with much less sharp leaf lobes in which, furthermore, we usually find (a) even larger leaf cells; (b) conspicuous stolons.

Table V. *Cephalozia lunulifolia – C. loitlesbergeri*

	Stem cross section		Leaf cells at base of lobes. μ	Stem cortical cells dorsally measured. μ	Width of leaves measured in cells.
	outer cells	inner cells			
C. lunulifolia ... 70–2816b	9–14	11–16	(13)20–26(30)× 26–31(34)	26–36× 52–65	–
C. lunulifolia ... 70–2814f	10–14	17–21	21–36× 26–34(39)	26–36(47)× 41–60	9–13(15)
C. loitlesbergeri.. 66–0049.....	15–17	23–25	29–39(45)× 38–47	(36)40–52× 44–75	9–17

Cephalozia lunulifolia (Dumort.) Dumort. (Table V)

Distribution (Map 65)

18: Grønne Ejland (70–2814f, 70–2816b). 37: Agpat (66–1421).

C. lunulifolia is basically a temperate zone species, found relatively far south—with recent reports from as far south as northern Florida (Breil, 1970) in eastern North America. It is nearly lacking in the tundra. Earlier reports of *Cephaloziae* from Greenland (Kap Parry, Jensen, 1900, *C. media;* Danmark Ø, Hekla Havn, Gåseland, and elsewhere in Scoresby

Sd., JENSEN, 1897, *C. connivens* etc.) are all based on misidentifications—usually for *C. pleniceps*. We have seen only one other collection, from South Greenland (Kugssuaq 60°16′N., 44°43′W., PETERSEN 270c) that is true *C. lunulifolia*. The present reports are by far the most northern ones known. At Kugssuaq it grew among *C. pleniceps*, *C. leucantha*, *Calypogeia neesiana*, and *Mylia anomala*. It is remarkable that in the Disko Bugt site the plant occurs with all of these taxa, except for the *C. pleniceps*, in an acid, peaty, low, moory plain where snow lies late in spring (and, hence, where *Salix herbacea* grows); associated are many of the same moss genera found in more temperate sites *(Sphagnum*, *Polytrichum*, *Aulacomnium)* and some temperate-boreal hepatics *(Calypogeia sphagnicola*, *Lophozia ventricosa silvicola*, *Mylia anomala)* as well as the rare *Anastrophyllum sphenoloboides*.

The Grønne Ejland plant is definitely this species, not *C. pleniceps*, for the following reasons: (a) leaf cells average only ca. 25–32 μ medially (see Table V for range); (b) no stolons are present; (c) plants are unisexual; (d) branches are all intercalary; (e) the stem anatomy is much simpler. In cross section there are typically only about 9–12(14) rows of large cortical cells + ca. (11)16–18(21) rows of medullary cells of much inferior diam., with thicker walls; the cortical cells, dorsally, measure ca. 26–36(47)×41–65 μ. Leaves are often bistratose at the very base and 9–12 to 13–15 cells wide.

The second collection, from Agpat (66–1421), although sparing, can fall only here. It agrees with the Grønne Ejland material in points a–e above. The plants freely bear gynoecia—all unfertilized—but no androecia; cortical cells are very large and in 11–12 rows, with the thick-walled, much smaller medullary ones in 18–22 rows. Leaf cells show limited variation in size: from 20–27×26–27 μ up to 22–27×25–35 μ. Associates include *Lophozia binsteadii* and *Calypogeia neesiana*. This collection represents the northernmost station known for the species.

Cephalozia leucantha SPRUCE

Distribution (Map 65)

18: Grønne Ejland (70–2810a, 70–2814a, 70–2816). 24: Jakobshavn (66–0234).

This suboceanic, boreal-low-Arctic, imperfectly holarctic species has not heretofore been reported from Greenland, but seems to be relatively frequent in South Greenland, occurring at Frederikshåb (62° N.), Narssalik (61°40′N.), Nanortalik (60°07′N.), Agdluitsoq (60°33′N.).

Earliest collections were those of VAHL from Nanortalik and Tasermiut (1829), but these had not been correctly identified. *C. leucantha* is basically a weakly oceanic circumboreal species, most common in the

Spruce-Fir Forest regions; it barely penetrates into the Arctic and the four collections cited above are the only true Arctic collections known to us. It is notable that these are from "oceanic" loci and from the southern parts of the Disko Bugt region, an area in which other low Arctic plants occur. The occurrence of admixed *C. leucantha* and *C. lunulifolia* on Grønne Ejland is notable—the latter being almost exclusively non-Arctic in range.

In Greenland the species is found in peaty tundra; thus at Narssalik it occurs amidst *Sphagnum*, together with *Riccardia sinuata*, *Mylia anomala*, *Calypogeia sphagnicola*, *Nardia scalaris*, *Odontoschisma elongatum*, *Anastrophyllum minutum*, *Pleuroclada albescens*, and *Diplophyllum albicans*. At Nanortalik it is associated with the very rare *Lophozia obtusa* (at its single known Greenland station). The plants from Frederikshåb and from Sletten both occurred mixed with *Mylia anomala* and *Sphagnum*. The Disko Bugt plants are from mossy, peaty tundra, growing with *Cephalozia pleniceps*, *C. bicuspidata*, *C. lunulifolia*, *M. anomala*, *A. sphenoloboides*, *Calypogeia sphagnicola*, and *C. neesiana*. The Greenland localities are clearly from the "least Arctic" sites; the species is probably general in South Greenland.

Cephalozia pleniceps (Aust.) Lindb.

Distribution (Map 66)

1A: Behind Arctic Station (66–0161a, 66–0172a, 70–2007, 70–2018, 70–2026b, 70–2032, 70–2038, 70–2047c). 1B: Lyngmarken (66–0557a). 2: Fortunebay (66–0201). 6: Eqalúnguit (70–2217, 70–2223a, 70–2230a, 70–2238a, 70–2243c). 7: Angûjârtûtit (70–2169a, 70–2176a, 70–2181). 8: Kuánerssuit (70–2138). 9: Eqaluit (70–2522, 70–2524, 70–2526a, 70–2527, 70–2546d). 10: Enoks Havn (70–2763b, 70–2766b, 70–2770, 70–2778e). 11: Qasigíssat (70–2721a, 70–2729, 70–2738). 12: Perdlertut (70–2674, 70–2693a, 70–2694, 70–2703). 13: Jens Vahls Dal (70–2635, 70–2636, 70–2644b, 70–2659). 14: Hareøen (70–2574, 70–2579, 70–2583, 70–2584, 70–2590, 70–2593, 70–2609). 15: Kronprinsens Ejland (70–2066, 70–2072, 70–2074, 70–2083, 70–2102, 70–2104). 16: Manîtsoq (70–3008, 70–3009, 70–3015b, 70–3016). 17: Tupilak (66–0025). 17A: Egedesminde (66–0943). 18: Grønne Ejland (70–2810b, 70–2811, 70–2815b). 19: Nûk (70–2870c, 70–2871, 70–2877a, 70–2879b). 21: Umiasugssûp (70–2935). 23: Kangersuneq (70–3129, 70–3144a). 24: Jakobshavn (66–0224, 66–0225a, 66–0226, 66–0228a). 25: Sarfaq (70–2335a, 70–2344b, 70–2364, 70–2374b). 26: Pâkitsup ilordlia (70–2258c, 70–2259a, 70–2270b, 70–2272, 70–2279a, 70–2289, 70–2290b, 70–2316a, 70–2319, 70–2383a, 70–2385). 28: Atâ (70–2512). 29: Ritenbenk (66–0253a). 30: Eqe (66–0289, 66–0322b, 66–0325a, 66–0340). 31: Anap nunâ (70–2406a, 70–2412a, 70–2431, 70–2434). 36: Umanak (66–1474, 66–1482). 37: Agpat (66–1422b, 66–1438, 66–1461). 42: Magdlak (66–1359b). 44: Akuliarusikavsak (66–1320). 45: Sagdliaruseq (66–1065, 66–1081, 66–1091). 46: Qalatôq (66–1109). 48: Amitsup (66–0770, 66–0771, 66–0774, 66–0789, 66–0797, 66–0800, 66–0801, 66–0802, 66–0817). 49: Skalø (66–1006, 66–1007, 66–1010, 66–1012, 66–1016, 66–1019). 51: Simiútap kûa, shore (66–0826). 52: Umîarfik, Qôrnoq (66–0979). 53: Søndre Strømfjord (66–0054a, 66–0056, 66–0058a, 66–0061a, 66–0062).

Additional collections:

17: Tupilak (K.J. 1446). 34: Marrait kangigdlît (K.H. Sept. 1956). 60: Kugssuaq (M.P.P. 718b). 66: Gamle Qutdligssat (M.P.P. 120). 67: Asuk (M.P.P. 135c, 1051). 72: Kuánit (L.H. Aug. 1932). 88: Christianshåb (K.H. 16.616b). 106: Nûgssuaq (K.H. July 1956). 112: Umiartorfik (K.J. 604c). 124: Tasíngortaq (K.H. 13.311b). 126: west of Sarqap taserssua (K.H. 13.427). 128: Agatdalen (K.H. 13.968d). 129: Avataussaligssuaq (K.J. 914a).

This widely dispersed species is, next to *C. bicuspidata*, the only abundant *Cephalozia* in the Arctic. In areas with basic rocks, in fact, it may be the only frequent *Cephalozia*. In Greenland it occurs northward to Low Point (leg. TH. WULFF; 83°06′ N.) and the Inglefield Bredning region at ca. 77°30′ N. (RMS), but has not been reported from northern Ellesmere Island nor from Peary Land. Southward it is ubiquitous in Greenland and is found south to New England and New York (SCHUSTER, 1949) with disjunct stations, as a separate subspecies, at low elevations in the Southern Appalachians (SCHUSTER, 1974). *C. pleniceps* has been much misunderstood by students of the Greenland flora. It has frequently been cited from E. Greenland as *C. connivens* or *C. media (C. lunulifolia)*, as the several following citations show: Kangerdlugssuaq, ca. 68° N. (BÖCHER 904; reported by HARMSEN, 1933, p. 14, as *C. connivens*); Gåseland, Scoresby Sd., 70°15′ N., 26°30′ W. [HARTZ, July 1892; four collections, det. by JENSEN as *C. media* but published as *C. multiflora* (= *C. connivens*) and *C. multiflora* var. *elata*]; Hekla Havn, Scoresby Sd., 70°30′ N., ca. 26° W. (HARTZ, Apr. 1892; published by JENSEN, 1897, as *C. connivens*).

C. pleniceps is the most tolerant of the species of *Cephalozia* known to us. In a genus that consists principally of Ca-avoiding saxicoles and helophytes it is the only Ca-tolerant species. Commonly found in basaltic regions, in moist, irrigated, well-vegetated tundra slopes and around shallow tarns and ponds, usually on organic substrates; associated then are most commonly *Lophozia heterocolpos* (66–0161 a, 70–2635, 70–2176 a, 70–2223 a, 70–2693 a, 70–2674, etc.; associated in at least 12 collections), *L. grandiretis* (66–0161 a, 70–2635, 70–2176 a, 70–2877 a, 66–0172 a, 66–1359 b, 70–2644 b), less often *Blepharostoma*, *Calypogeia muelleriana*, *Scapania curta isoloba*, *C. bicuspidata*, *L. quadriloba*, *L. opacifolia*, *L. wenzelii*, *Odontoschisma macounii*, *Tritomaria quinquedentata*, *Anthelia juratzkana*, *Pleuroclada*, *Solenostoma pusillum*, *Plagiochila asplenioides*, and *Cryptocolea imbricata*, rarely *T. scitula* (when on damp or irrigated, basaltic slopes; 70–2644 b, 70–2138) or *T. polita polymorpha* (when on moist, peaty soil at edge of a "warm" spring; 70–2169 a). On damp basaltic slopes rarely (70–2644 b) with *Scapania cuspiduligera* associated.

The species may also occur on thin, moist soil over basalt dikes (66–0325 a), then with *Peltolepis grandis*, *L. quadriloba* f. *cephaloziellioides*,

etc. In areas with gneissic rocks, where there is some Ca-enriched seepage (as at Nûk; 70–2877 a), *C. pleniceps* may be associated with Ca-intolerant taxa such as *C. bicuspidata*, *Calypogeia sphagnicola*, *L. binsteadii*, *Mylia anomala*, and Ca-tolerant ones, such as *L. grandiretis* and *L. opacifolia*. Here the species occurs on rich, low peaty, helophytic slopes, at the edges of "pockets" filled with standing water.

C. pleniceps also is widespread in circumneutral to distinctly acidic sites. On thin, water-deposited mineral soil, varyingly enriched with peat, along streams, it may occur (70–2935) with *Nardia geoscyphus*, *Anthelia*, *Blepharostoma*, and *C. bicuspidata*, forming thin, green carpets. Occurrences on soil or soil-peat mixture with *N. geoscyphus* are common (70–3144 a, 70–2259 a, 70–2270 b, 70–2763 b, 70–2766 b). Along rivers, on water-deposited fine, silty soil we also find *Anthelia* and *C. bicuspidata* often associated (e.g., in 70–2763 a) in thin mats with *Salix herbacea*. On soil often also with *Solenostoma subellipticum* (70–2270 b, 70–2047 c), *L. pellucida minor* (70–2766 b), *Calypogeia muelleriana*, *C. integristipula*, *Scapania curta*, *Pleuroclada*, and *Diplophyllum taxifolium* (70–2047 c).

Under acidic conditions occasional in *Sphagnum* tussocks, sometimes with *Aneura pinguis* or *L. excisa* (66–0201, 66–0943); at other times, in low, irrigated areas, with *Dicranum* and other mosses, and *C. bicuspidata ambigua*, *Pleuroclada*, and *S. paludicola* (70–2066). Also, occasionally, on moist, sheltered, N. facing acidic cliffs, mixed with *S. crassiretis*, *S. mucronata praetervisa*, *S. parvifolia*, and *Anastrophyllum minutum* (70–2243 c). Under helophytic conditions frequently amidst *Sphagnum* and/or *Aulacomnium*, associated with *Calypogeia sphagnicola* (66–0228 a, 70–2230 a, 70–2290 b, 66–0056, 70–3016, 66–0225 a, 66–0061 a), and, less often, *S. hyperborea*, *L. excisa*, *L. polaris sphagnorum*, *L. kunzeana*, *Pleuroclada*, and *Cephaloziella uncinata* (70–2289). In low, wet, peaty areas also with (70–2810 b) *Mylia anomala*, *C. leucantha*, *C. lunulifolia*, *C. bicuspidata*, *L. ventricosa silvicola*, or (70–2279 a) *L. binsteadii* and *Cephaloziella arctica;* or (70–2344 b) *A. sphenoloboides;* or (70–2721 b; in crests of *Sphagnum* tussocks) *Cephaloziella subdentata.*

The above list of associates demonstrates the very wide range of loci invaded by this species. Only intermittently very dry, windswept sites are avoided, but exceptionally it may occur admixed even in thin mats of *Gymnomitrion corallioides*, *Anastrophyllum minutum*, and *Blepharostoma* on generally damp—but intermittently dry—gneissic rocks (70–2102). Such occurrences are very much exceptional.

Perianths and androecia are frequently present. Capsules are not rare and have been found from July 5 (70–2032), July 10 (70–2181), July 11 (70–2223 a), July 20 (70–2270 b) to Aug. 8 (70–2526 a); in northwest Greenland, at Nucluet (76°57′N.) the species has been collected with

capsules as late as Aug. 24 (RMS 46206b). Gemmae have not been seen in any Greenland populations.

C. pleniceps shows exceptional variability in the Arctic, associated with the wide range of sites invaded, hence has been the source of much taxonomic confusion. Arctic phenotypes are often deviant in various ways. Thus they often show free terminal branching (in i.a., the HOLMEN and WULFF collections from North Greenland; in material from Gåseland, Greenland [HARTZ, July 7, 8, 1892]; in 66–0061a, 70–2217, 70–2230a from Søndre Strømfjord and Disko Fjord). There appears to be some imperfect correlation in the Greenland populations studied between development of xeromorphic adaptations, e.g., copious stolons, concave and dense leaves, and suppression of terminal branching vs. hygromorphic structure, e.g., few or no stolons, larger cells, more remote and less concave leaves, and free development of terminal branches. Each of these terminal branches is subtended by an ovate-lanceolate leaf.

Lax Arctic phenotypes may also have leaves to 30 cells broad. Such plants, when fertile, also have perianths only 2 to, locally, 3 cells thick medially. In contrast, compact forms with concave, assurgent leaves that show copious stolon formation and suppression of terminal branching may have perianths with the wall 3–4(5)-stratose medially and to 125 μ thick. Cell size seems unusually variable in Arctic phenotypes. Thus exposed shoots with broad leaves, to 24 cells wide, may have cells only (24)26–30(35) × (24)26–35(38) μ; other shoots, with leaves only to 16 cells broad, have cells ca. 40–45 × 48–55 μ.

In critical cases sterile plants of marsh or bog forms are superficially close to similar forms of *C. lunulifolia* and may be almost impossible to separate. Stem anatomy of the two taxa is quite distinct. In *C. pleniceps* we usually find to 18–22 rows of cortical cells, with the dorsal cells much larger than the ventral, but in cross section not conspicuously tumid so that the stem is distinctly dorsoventrally differentiated; the numerous (usually 24–32) rows of medullary cells are somewhat smaller than the dorsal cortical cells in cross section, averaging 20–25 μ in diam. and are identical in diam. to the ca. 10 rows of cells that form the ventral cortex of the stem; these plants freely produce terminal branches. By contrast, in *C. lunulifolia*, there are only ca. 10–14 rows of cortical cells; the dorsal and lateral cells are very large and almost circular in cross section and very much larger in diam. (ca. 48–55, occasionally 60 μ laterally) than the more thick-walled medullary cells, which are only 12–18 μ in diam. and lie in at most 20–22 rows; the plants produce only ventral-intercalary branches.

At the opposite extreme are creeping, very fleshy, intensely green, vigorous and dense-leaved forms (e.g., 70–2047) to 650 μ wide, with orbicular, strongly concave, antically assurgent leaves whose lobes always end

in single cells. Such plants may have stems to 360 μ wide × 275 μ high, with cortical cells in 16–18(20) rows; medullary cells may be in up to 45–52 rows—an upper extreme not seen exceeded in the genus. Such compact forms seem to develop only ventral-intercalary branches.

Even with compact, intensely green phenotypes difficulty may arise in effecting a separation from *C. lunulifolia*. Some phases of *C. pleniceps* (e.g., 70–3015b) may be relatively small, dense-leaved, with antically assurgent, concave leaves. Such phases, of exposed peat (growing with *Anthelia juratzkana*, *Pleuroclada*, and *Diplophyllum taxifolium*), may have unusually small cells, sometimes as small as (24)26–30(32) × 25–36 μ medially. These plants would then tend to key to *C. lunulifolia*. Such small, compact phases, however, still retain the *C. pleniceps* stem anatomy, having 15–16 rows of cortical cells and 20–24 rows of medullary cells. Also, they are freely stoloniferous and have leaves to 18 cells wide or more.

Odontoschisma (Dumort.) Dumort.

Odontoschisma elongatum (Lindb.) Evs.

Distribution (Map 67)

1A: Behind Arctic Station (66–0190, 66–0191, 66–0196, 66–0197, 70–2007, 70–2009, 70–2037, 70–2046). 9: Eqaluit (70–2550). 15. Kronprinsens Ejland (70–2068a, 70–2071, 70–2072, 70–2083, 70–2099, 70–2112). 16: Manîtsoq (70–3012b, 70–3020). 17: Tupilak (66–0029, 66–0036, 66–0109). 19: Nûk (70–2872, 70–2875d). 21: Umiasugssûp (70–2937). 23: Kangersuneq (70–3132b). 26: Pâkitsup ilordlia (70–2319). 36: Umanak (66–1477). 37: Agpat (66–1468a, 66–1426).

Additional collections:

28: Atâ (Lægaard July 1962). 29: Ritenbenk (S.B. 1870, specimen not seen, but probably published 1875 by Berggren as *Sphagnocetis communis*). 98: Sarqaq (K.H. 15.810). 124: Tasíngortaq (K.H. 13.312). 126: west of Sarqap taserssua (K.H. 13.413).

A subarctic-subalpine and Arctic-alpine species, with the bulk of its range lying south of 65° N.; the present reports and those from Spitsbergen appear to be the northernmost ones of the species; in East Greenland it occurs north to Scoresby Sund (Kobberpynt, Jensen 1897). Southward *O. elongatum* occurs as a rarity to northern Michigan, Maine, and New Hampshire. It seems to be basically north Atlantic in range but chiefly western in range in Europe.

O. elongatum is a helophyte which tolerates intense illumination and both periodic inundation and periodic desiccation. It is a typical species of acidic tarns which partially dry out in the short Arctic summer, where it is commonly associated with that other scorched-appearing, plastic, and tolerant species, *Gymnocolea inflata* (as e.g., in 70–2009, 70–3012b), or with *Marsupella arctica* (in 70–3012b, 66–0036). In boggy, moory,

acidic areas around rock pools and in wet depressions in gneissic rocks, also with *Lophozia ventricosa rigida*, *L. wenzelii*, and *L. cavifolia* (70–3020), or rarely (66–0109) with *Scapania crassiretis;* where a large amount of peat has accumulated, *Scapania hyperborea* and *L. kunzeana* may be associated (66–0191), occasionally (66–0190) also *Anthelia juratzkana.* On acidic, damp, sandy-peaty undulating dunes near the mouths of rivers (as at Eqaluit; 70–2550) or along shallow lakes (Kangersuneq; 70–3132b) the *O. elongatum* may occur with *Blepharostoma*, *Pleuroclada*, *Gymnomitrion concinnatum*, and *L. ventricosa confusa* in thin, compact patches or (70–3132b) with *L. cavifolia* and *S. degenii.* In somewhat moister, peatier sites, *Cephalozia pleniceps* is often associated (in 70–2319, 70–2083, 70–2072), at times also with *L. kunzeana*, *Anastrophyllum minutum*, *Anthelia*, and *S. hyperborea.*

Exceptionally, when there may be minute amounts of Ca-enriched seepage, *O. elongatum* may occur on wet, irrigated, insolated thin peat on ledges, with *Odontoschisma macounii* (in 70–2071, 70–2872, 70–2857d), associated with *Blepharostoma tr. brevirete*, *Anthelia*, *C. bicuspidata*, and *G. concinnatum.* Occurrences with *O. macounii* are very exceptional.

In our area *O. elongatum* seems to be always sterile; we have not seen gemmae in regional plants, but they have possibly been overlooked. Plants are always brownish to scorched in color. They are singularly invariable.

Odontoschisma macounii (AUST.) UNDERW.

Distribution (Map 67)

1A: Behind Arctic Station (66–0196, 70–2005, 70–2006, 70–2012). 2: Fortune-bay (66–0142). 6: Eqalúnguit (70–2219, 70–2241, 70–2242, 70–2248a, 70–2251). 10: Enoks Havn (70–2778d). 12: Perdlertut (70–2705). 13: Jens Vahls Dal (70–2630, 70–2632, 70–2654, 70–2657, 70–2659, 70–2665). 14: Hareøen (70–2572, 70–2574, 70–2590a, 70–2593b). 15: Kronprinsens Ejland (70–2071, 70–2078, 70–2104). 17: Tupilak (66–0026a, 66–0032). 18: Grønne Ejland (70–2812a). 19: Nûk (70–2869b, 70–2872, 70–2875, 70–2879b). 26: Pâkitsup ilordlia (70–2269, 70–2272, 70–2297b, 70–2301, 70–2383a). 30: Eqe (66–0249b, 66–0288a, 66–0289d, 66–0292, 66–0296, 66–0340, 66–0341). 31: Anap nunâ (70–2406a, 70–2421). 36: Umanak (66–1474, 66–1479, 66–1480, 66–1481a, 66–1482, 66–1488, 66–1489, 66–1491). 37: Agpat (66–1461). 38: Uvkusigssat (66–1388, 66–1391). 40: Mârmorilik, head of the Fjord (66–1183). 43: Kangerdlugssuakavsak (66–1286). 44: Akuliarusikavsak (66–1320). 48: Amitsup (66–0770, 66–0771, 66–0788, 66–0801, 66–0802). 51: Simiútap kûa, shore (66–0914e, 66–0915, 66–0916, 66–0919).

Additional collections:

24: Jakobshavn (S.B. 1870). 34: Marrait kangigdlît (K.H. Sept. 1956). 45: Sagdliaruseq (K.H. 16.956a, 17.190). 52: Umîarfik, Qôrnoq (K.H. 13.065, 16.368, 16.369). 67: Asuk (M.P.P. 1066). 73: Igdlokasik (K.H. 14.497). 83: Angnertussoq (L.H. Aug. 1932). 95: Pâkitsoq (K.H. & G.M. 71–1930). 99: Sarqaq valley (K.J. 241a). 106: Nûgssuaq (K.H. July 1956). 110: Ikorfat (K.J. 289). 111: Kûtsiaq (K.J.

766). 126: west of Sarqap taserssua (K.H. 13.428). 127: Kangersôq (K.J. 1089). 128: Agatdalen (K.H. 13.970, 13.863b). 137: Esersiutilik (K.H. 13.995). 147: Amitsoq (K.H. 13.481, 14.642b).

O. macounii is principally Arctic in range, extending northward as far as there is land, to 82°53′ N. (Kap Emory) in Peary Land and 82°32′ N. in Ellesmere Island (SCHUSTER *et al.*, 1959). The species is basically circumarctic, and extends southwards only as far as Nova Scotia and the northern Great Lakes region (Michigan, Wisconsin, and Minnesota).

A highly distinctive species usually growing as subjulaceous, creeping to suberect, clear green shoots, with no secondary pigmentation even when growing under intense illumination. It is meso-hygrophytic and is almost exclusively restricted to areas with Ca-enriched seepage; hence regionally it is rare outside of the areas with basalt flows. Even when it occurs in an area with gneissic rocks (as at Nûk; 70–2872, 70–2879b), it is found in low, irrigated areas and around shallow tarns where there must be some basic seepage (as the adjoining occurrence of *Lophozia rutheana*, *Aneura pinguis*, *Cephalozia pleniceps*, *Tritomaria polita polymorpha*, and *L. grandiretis* attest).

Similarly, it occurs on intermittently moist, peaty ground around rock pools in gneissic areas near Godhavn (70–2006, 70–2012), in an area with overlying basalt cliffs, associated with *Gymnomitrion corallioides*, *G. concinnatum*, *C. bicuspidata*, *Marsupella arctica*, *Anastrophyllum minutum grandis*, and *Scapania degenii dubia*, the last almost wholly confined to areas with calcareous seepage. Rarely found (as at Nunarssuaq; 70–2078, 70–2104) on peaty ground around gneissic rock pools, associated with *M. arctica* and *A. minutum grandis*, where there is no obvious source of Ca-ions. Occasionally the species invades only very localized Ca-enriched areas, as damp sandy ground in depressions around a lake (at Qissugssalik; 70–2272, 70–2301), where with *Cryptocolea imbricata*, *Cephalozia pleniceps*, *A. minutum grandis*, and—nearby—*L. rutheana*, *Tritomaria polita polymorpha*, and *Pinguicula vulgaris*—the last taxa almost always indicators of calcareous sites.

Much more typical are occurrences under unambiguously basic conditions, in areas with marble (as near Mârmorilik), or with basalt. Sometimes only small basalt dikes occur, as at Eqe (66–0296, 66–0288a, 66–0289d), then associated with *Aneura pinguis*, *Anthelia*, *L. quadriloba*, *L. heterocolpos harpanthoides*, *T. heterophylla*, *Cryptocolea imbricata* (when on damp soil along a rill), or with *S. degenii*, *Cephaloziella arctica*, and *L. quadriloba*. In basaltic areas it is often frequent in rich, irrigated meadows or fens and around shallow lakes (at Simiûtap kûa; 66–0914e), where with *Cryptocolea*, *L. rutheana*, *L. heterocolpos*, *L. grandiretis*, *L. gillmani*, *L. quadriloba*, *Aneura pinguis*, and *Riccardia sinuata*. Some or most of these species, as well as *T. polita polymorpha*, are associated in

similar sites elsewhere, as on Hareøen, at Eqalúnguit, etc. Occasionally, on irrigated, steep, weathered, calcareous slopes (as at Jens Vahls Dal; 70–2657) with *S. cuspiduligera.*

The species also occasionally occurs on damp, peaty soil along rills (as at Eqe; 66–0249b), there as a small compact form with *Prasanthus, G. concinnatum, Anthelia, T. quinquedentata, T. heterophylla.* Isolated anomalous occurrences remain to be mentioned: rarely (at Umanak; 66–1479b), with *Anastrophyllum assimile, Marsupella revoluta* and *M. arctica*—taxa usually restricted to gneissic rocks; on soil in crevices or recesses of gneissic cliffs—but lying below basalt—with *S. crassiretis* (Eqalúnguit; 70–2242a), but also with the feebly Ca-bound *Lophozia heterocolpos* admixed; exceptionally on peaty irrigated soil near shallow tarns, with *O. elongatum*, as at Nûk (70–2875; with *Anthelia, G. concinnatum, C. bicuspidata*, etc.) and at Nunarssuaq (70–2071; with *T. quinquedentata, A. minutum, Blepharostoma t. brevirete*). Such occurrences with *O. elongatum* are exceedingly rare, the ecology of the two taxa being almost mutually exclusive.

The species regionally occasionally has gemmae; it very rarely has capsules (70–2272; Qissugssalik, July 20). It is noteworthy that the capsule wall, although stated always to be bistratose in *Odontoschisma*, is varyingly 2- or 3-layered. Spores are 14.5–16.5 μ and elaters 7–9 μ in diam.

Family *Cephaloziellaceae* DOUIN

Cephaloziella (SPR.) SCHIFFN.

The genus *Cephaloziella* remains a continuing source of taxonomic confusion, inherent in three problems: (a) the intrinsic difficulty of the group, because of the small size and, incident to general reduction, absence of adequate taxonomic criteria; (b) the high malleability of the taxa; (c) and—a purely extrinsic problem—the quality of prior taxonomic work, particularly that of DOUIN (1920). Until detailed comparative studies are made, and, in particular, growth experiments, any taxonomic verdicts remain of necessity tentative. The rather detailed notes here given are based on more intensive study of Arctic members of the group than has ever been previously undertaken, and include incorporation of much data gathered by the senior author on prior expeditions to Ellesmere Island (1955) and northwest Greenland (1960). In spite of this, we remain aware of the fact that in several cases our taxonomic judgements may be faulty. The problems are discussed in detail under the various species, of which we admit seven for the area.

Since cell size (width of leaf cells, measured at the base of the leaf lobes—near the sinus level; width of dorsal and dorsolateral cortical cells) is of such cardinal importance in separating taxa, in our current

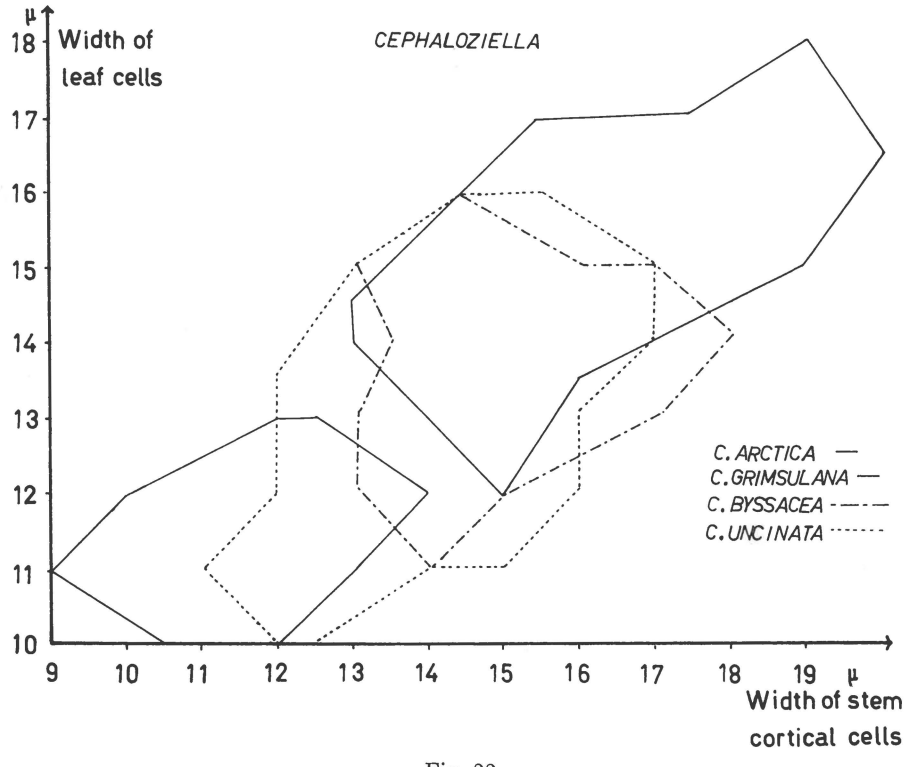


Fig. 22.

(mostly DOUIN-inspired) taxonomy, we diagrammed these dimensions for most taxa and gathered these diagrams (Fig. 22) into a construction which attempts to graphically show variation from species to species, in the four taxa which present most problems (*C. subdentata* is regionally stenotypic and affords no taxonomic problems). In each case a number of specimens were measured (*C. uncinata*, 10; *C. arctica*, 7; *C. grimsulana*, 10; *C. byssacea*, 10). The measurements show that there is a strong correlation between leaf cell and stem cortical cell width.

The diagrams taken together show that none of the four most frequent taxa coincide; they may have "areas" in common, but in no case is it possible to find total congruence. Most interesting is that *C. grimsulana* and *C. arctica* seem reasonably well separated, which may indicate that *C. grimsulana* is a true species and not a large-celled variety of *C. arctica*. *C. uncinata* seems to occupy an "area" between *C. arctica* and *C. grimsulana*, taxa from which *C. uncinata* can be separated at times only with difficulty. When perianths are present, the cells of the mouth typically separate *C. uncinata* from *C. arctica*, and the narrower stem cortical cells of *C. uncinata* should facilitate its separation from *C. grimsulana*. All three taxa are autoecious and are more nearly related to each other than

to *C. byssacea* or *C. rubella.* Further complicating the situation is the fact that *C. arctica* may be an Arctic and alpine "replacement" of the usually boreal-temperate *C. hampeana.* The latter, lacking ability to develop purplish-pigmentation and usually devoid of underleaves, seems to occur very rarely in our area.

The taxonomic problems in the group are greatly compounded by the fact that the phenotypic variability tends to "mask" the very limited genotypic diversity. Species concepts and limits, thus, must remain fluid.

Our concepts of the taxa are clear from the following key to regional species:

1. Dioecious; stems usually relatively stout; leaves often loosely folded; underleaves of sterile plants present; often with terminal branches. *C. byssacea* ..... 2.
   2. Abaxial leaf faces always smooth. v. *byssacea*
   2. Abaxial leaf faces tending to develop mammillae or cellular protrusions. v. *scabra*
1. Monoecious: ♂ and ♀ branches always occurring together (or androecia below gynoecia); stems usually slender; leaves not folded; terminal branches normally absent ..... 3.
   3. Autoecious (very rarely with single paroecious inflorescences), the ♂ and ♀ branches usually easily recognizable ..... 4.
      4. Leaves to 0.65 bifid, with relatively broadly triangular lobes usually 6–9 cells broad; ♂ and ♀ branches usually long, bearing many leaves below the androecium or gynoecium, the ♂ often remote from ♀ ones (plants then pseudo-dioecious); ♀ bracts broadly fused to bracteole, lacking sharp, recurved 1-celled teeth of lobe margins ..... 5.
         5. Mature nongemmiparous sterile shoots with underleaves (rarely strongly reduced); often with purplish or copper-purple pigmentation or scorched ..... 6.
            6. Leaf cells (9.5)10–13.5(14) μ wide at lobe bases; cortical cells (9)10–16(17) μ wide; gemmae (10)11–14(16) × 20–24 μ or smaller ..... 7.
               7. ♀ Bracts with margins strikingly dentate, lobes usually acuminate and ending in 1–2(3) elongated cells, forming a ± hooked apex. Perianth mouth fringed with strikingly long cells (usually 4–6:1), often free for 0.3–0.6, the free ends strongly pointed, the mouth ciliolate. ♂ Bracts conspicuously denticulate. Usually green to olive or dull brown, rarely purplish (green to olive phases with thick-walled cells, often with hooked leaf lobe tips). *C. uncinata*

7. ♀ Bracts with margins edentate to weakly toothed, lobes acute, not or rarely hooked. Perianth fringed with short (2–2.5:1) or a mixture of long (2.5–5:1) and short cells, not or little tapered, usually united to within 0.1–0.2 of apices, the mouth crenulate. ♂ Bracts entire or subentire usually. Usually ± purplish to scorched, the leaf lobe tips never strongly elongated and uncinate. *C. arctica*

6. Leaf cells (12)13–18(20) μ wide at lobe bases; cortical cells (12)13–20(21) μ wide; gemmae usually (12)13–18 × 18–26(29) μ. Plants usually strongly purplish. ♀ Bracts strongly dentate. Perianth mouth with long, narrow cells, free for 0.35 or more, the mouth ciliolate. Otherwise like *C. arctica*. *C. grimsulana*

5. Underleaves of sterile shoots absent or vestigial; green to ± brown, lacking purple pigmentation. ♀ Bracts sheathing, lobes nearly edentate. Leaf cells (11)12–14(15) μ wide. *C. hampeana*

4. Leaves 0.7–0.75 bifid, the lobes narrow-lanceolate, (2–3)4(5) cells wide at base; ♂ and ♀ branches often very short, juxtaposed (plants always obviously autoecious); ♀ bracts almost free from each other with slender, sharply serrate lobes, with sporadic recurved teeth. Only over *Sphagnum* heads. *C. subdentata*

3. Paroecious (but often with accessory, purely ♂ branches), the gynoecium with 2–3 large, pouched to concave, dentate ♂ bracts below the ♀ ones. Plants green, locally bright red-pigmented. *C. rubella* . . . . . 8.

8. Leaf lobes 4–5(6–7) cells broad; underleaves lacking. v. *rubella*

8. Leaf lobes mostly (5)6–9 cells broad; underleaves of sterile stems locally large, sometimes bifid. v. *arctogena*

Cephaloziella byssacea (Roth) Warnst. (Fig. 24, Table VI)

We follow the usage of Evans regarding the nomenclature of this plant. Arguments that the earliest name (of Roth) is invalid because the type material was mixed, consisting of two *Cephaloziella* taxa, seem rather "thin" in view of the fact that the type of *C. divaricata* (Smith) Schiffn. is also mixed, as is, apparently, that of *C. starkei* (Funck) Schiffn. In effect, Warnstorf (1903) selected the unisexual element of the "mixed" *C. byssacea* as the type, and this emendation was accepted by Evans, Schuster, and others. If every name based on mixed collections were to be rejected, a large minority of *Hepaticae* would have to be renamed.

Distribution (Map 68)

10: Enoks Havn (70–2757c, 70–2758a, 70–2760 pro parte var. *scabra*). 12: Perdlertut (70–2686a). 15: Kronprinsens Ejland (70–2086). 16: Manîtsoq (70–3023a).

19: Nûk (70–2876a). 24: Jakobshavn (66–0227a, 66–0233, 66–0242, 66–0244). 25: Sarfaq (70–2336b). 32: Qôrorssuaq (70–2455, 70–2478b). 37: Agpat (66–1467b, 66–1469a). 53: Søndre Strømfjord (66–0046).

A widespread, probably circumboreal to circumarctic species which seems to become infrequent to rare in the higher Arctic; in North America it occurs southward at least to North Carolina. What appear to be at best distinct races occur sporadically in the cold Antipodes (see SCHUSTER, 1972a). The species is a *typus polymorphus*, with an enormous synonymy, contributed mostly by DOUIN (1920). Vigorous phenotypes often tend to have leaves armed abaxially (var. *scabra*) and, in extreme cases, may have the stem armed; this last phenotype is discussed below. The species is our sole unisexual *Cephaloziella*.

Regionally an infrequent species which seems sharply confined to areas with acidic rocks. (We have only one collection, seemingly this species, from Søndre Strømfjord, 66–0046, from sunny south-facing slopes, with *Rhododendron lapponicum*, *Lophozia excisa*, and a trace of *Scapania gymnostomophila;* the plants grew in sheltered crevices in a site subject to strong desiccation. These plants, from an area which clearly has Ca-enriched seepage, are not typical and their identity remains uncertain). Occurrences in low peaty areas over *Sphagnum* are not rare (Enoks Havn; 70–2757c, 70–2760, 70–2758a); then *Lophozia excisa*, in part var. *infuscata*, *Cephalozia bicuspidata* and *Scapania hyperborea* may be associated.

C. byssacea also occurs, perhaps more typically, in intermittently dry sites over gneissic rocks, away from seepage zones, associated with *L. rubrigemma*, *L. kunzeana*, *Ptilidium ciliare* (66–0227a), or *Cephaloziella hampeana* (66–0244). In similar sites it may occur (in 66–1469a) with *L. hatcheri*, *L. excisa*, and *S. mucronata praetervisa*, or (70–3023a) with the very xerophilous *Chandonanthus setiformis*, or (70–2086) with *S. hyperborea* in the xeromorphic mod. *parvifolia-angustifolia*. More rarely (as at Nûk; 70–2876a) it is found with *Aneura pinguis* and *S. hyperborea* in low, acid, moory sites around tarns. Finally, *C. byssacea* may occur over thin peaty soil, on and between rocks, along cascading acidic rills that (some summers) probably dry out; here (70–2455, 70–2478b) it may be associated with the often deceptively similar *Marsupella boeckii* and with *Gymnomitrion concinnatum*, *Gymnocolea inflata*, *S. obscura*, and *L. alpestris*.

Plants of 70–2686a (among *L. excisa*, *Tomenthypnum nitens*) represent an extraordinary, vigorous extreme, growing intertwined among coarser taxa, hence are shaded and mostly pale green (but with some local brown to dull purple pigments). Stems are 140–155 μ in diam., rather soft, straggly, lax; shoots are to 400–575 μ wide with the remote leaves included, depending on the vigor of the plant and the degree to which the leaves are patent. Leaves are mostly folded, at least in the sinus;

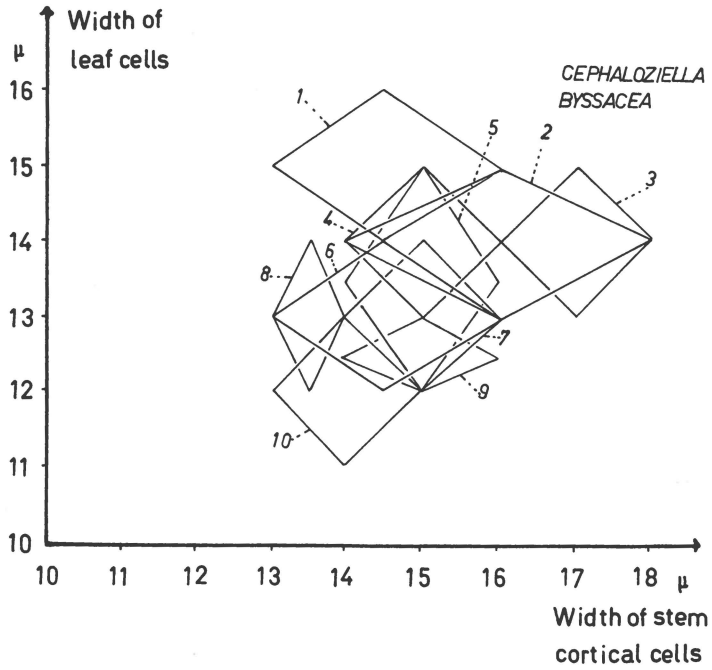


Fig. 23. See also p. 308, Table VI.

they are erect from a spreading base, or almost so, often with incurved lobes and range to 300–320 μ wide × 250–280 μ long; they are ca. 0.65–0.7 bifid, with lobes (7)8–12(13–15) cells broad. The leaf margins on almost all vigorous plants are strongly toothed, especially towards the base, but the abaxial faces are never mammillose. Cells are 11–13 to 13–15 μ wide, rather thick-walled, moderately verrucose; oil-bodies are (1–2)3–7(9) per cell and ca. 1.6–2×2–3 μ, a few to 2.5–3×3–3.6 μ. Underleaves, although usually small and rarely vestigial, are mostly distinct, often appressed to the stem; one atypical, isophyllous stem was seen with large, bifid underleaves. Branching, although usually lateral-intercalary, is exceptionally furcate, terminal.

It would be tempting to segregate these plants as a discrete variety, were it not for the fact that there are other similar phases regionally, e.g. 70–2757c, a vigorous but straggly plant, growing in a rich wet fen on a river terrace amidst *Sphagnum* and *Paludella squarrosa*, together with *S. hyperborea*, *L. excisa infuscata*, and *Cephalozia bicuspidata*. This phase is almost identical with that of 70–2686a, except for the fact that there is no proclivity present for formation of marginal teeth of the leaves. As is well known, the spectrum of phenetic variants produced by *C. byssacea* is seemingly endless, and to start taxonomic segregation of every variant, in the manner of Douin (1920) would be self-defeating if not taxonomically ridiculous.

Table VI. *Cephaloziella byssacea.*

	Width of leaf cells at base of lobes	Width of cortical cells on sterile stems
1. Manîtsoq 70–3023a	(13) 14–16 (17) μ	(12)13–16 (17) μ
2. Agpat 66–1469a	(12) 13–15 (16) μ	(12) 14–18 (19) μ
3. Jakobshavn 66–0227a	(12) 13–15 (16) μ	(15) 16–18 (19) μ
4. Søndre Strømfj. 66–0046	(12) 13–15 (16) μ	(13) 14–16 (18) μ
5. Nûk 70–2876a	(11) 12–15 (16) μ	(13) 14–16 (17) μ
6. Perdlertut 70–2686a	(11) 12–14 (15) μ	(12) 13–16 (17) μ
7. Qôrorssuaq 70–2478b	(11) 12–14 (16) μ	(12) 14–16 (18) μ
8. Enoks Havn 70–2760	(11) 12–14 (15) μ	(12) 13–14 (15) μ
9. Kronprinsens Ejland 70–2086	(11) 12–13 (14) μ	(13) 14–16 (18) μ
10. Qôrorssuaq 70–2455	(10) 11–13 (14) μ	(11) 13–15 (16) μ

In addition to the difficult pattern of variation from *C. byssacea* var. *byssacea* to var. *scabra* to *C. spinicaulis* (p. 309), there is (at least superficially) total intergradation between *C. byssacea* and *C. arctica.*

Typically, the larger stems of *C. byssacea* have a thicker axis (often to 150 μ in diam.), and stiff, remote, often loosely conduplicate leaves. Such leaves do not occur in any phases which we refer to *C. arctica* with any confidence. Some Arctic forms of *C. byssacea*, however, also fail to show such conduplicate leaves, or have them only obscurely and sporadically loosely folded; such plants, furthermore, approach many phases of *C. arctica* in having underleaves absent or vestigial on most axes, distinct only here and there (e.g., in 70–2086, Kronprinsens Ejland). These plants show mostly brownish pigmentation—typical of *C. byssacea*, but possess a little of the purplish pigmentation of *C. arctica.* They are definitely unisexual; the large patch of specimens examined is mostly sterile but scattered androecial axes are present—without a trace of gynoecia.

C. byssacea and its ally *C. spinicaulis* (and perhaps all members of the plastic *Byssaceae*) often show terminal branching—a primitive feature which is associated with another primitive feature—unisexuality. Such terminal branches have been seen in 70–2686a and 70–2455 (rarely!) and in 66–0227a. Gemmae are frequently present (e.g., in 66–0227a, 70–2455) and are ca. 12–14×20–24 to 17×24 μ; most collections are

sterile but occasional ones show androecia (70–2455, 70–2086, 66–1469a). We have seen no collections with well-developed perianths and, thus, no sporophytes. All collections placed here are either of large sterile plants that have vegetative characters of *C. byssacea* or of unisexual plants.

v. *scabra* (Howe) Schust. (Fig. 24:8–14)

Distribution (Map 68)

25: Sarfaq (70–2337, 70–2370c).

Occurring north to at least Siorapaluk, northwest Greenland (RMS). Apparently a rare, preponderantly sterile, plant in the Arctic, where it may occur, on moist, acid cliffs, growing amidst *Marsupella revoluta*, *M. arctica*, *Anastrophyllum assimile*, *Gymnomitrion concinnatum*, and *Tritomaria quinquedentata* var. *turgida*, as at Sarfaq (70–2370c). On the same cliff, growing in exposed patches of *Gymnomitrion concinnatum*, *G. corallioides*, and *Marsupella revoluta* (70–2337), was an extreme phase, showing transition to *C. spinicaulis* Douin (see below).

Arctic forms are almost always referred here with a slight element of hesitation. Thus 70–2370c is almost wholly sterile, a single, poorly developed androecium being seen. The more exposed plants are often purplish and almost inseparable from *C. arctica*, yet other plants show some olive to brownish coloration, have more folded and almost erect-sheathing leaves, often with incurved lobes, whose abaxial faces are coarsely papillose and, here and there, bear low cellular projections or mammillae. Such leaves can be found in only a small percentage of cases; their margins also often bear one or several teeth. Larger plants are basically more vigorous, with stouter stems (and correspondingly, often smaller-appearing leaves) than is the case in *C. arctica*.

Plants of 70–2337 are critical. Well-developed shoot apices show not only strongly abaxially armed leaf bases, but may have scattered cellular projections of the stem as well. In some cases the stem cells are gibbous and elevated in short lines rather than as individual spines or finger-like protrusions. These plants, technically, should "key" to *C. spinicaulis* Douin, a species known only from the Southern Appalachians northward to New England, which recurs in Japan ("*Cephaloziella echinata* Hattori"). That species, however, is gray-green, lacks any secondary wall pigments, has much more extensive and often sharper spines of the stem and more distinctly dentate leaf lobe margins. *C. spinicaulis* also rather freely produces terminal, *Frullania*-type branches, while the plants of 70–2337 bear only lateral- and ventral-intercalary, axillary branches.

Exceptionally we find rare abaxial cellular projections of the leaves in collections normally lacking them (e.g., in 66–0233, Jakobshavn). This proclivity also occurs in plants from temperate regions.

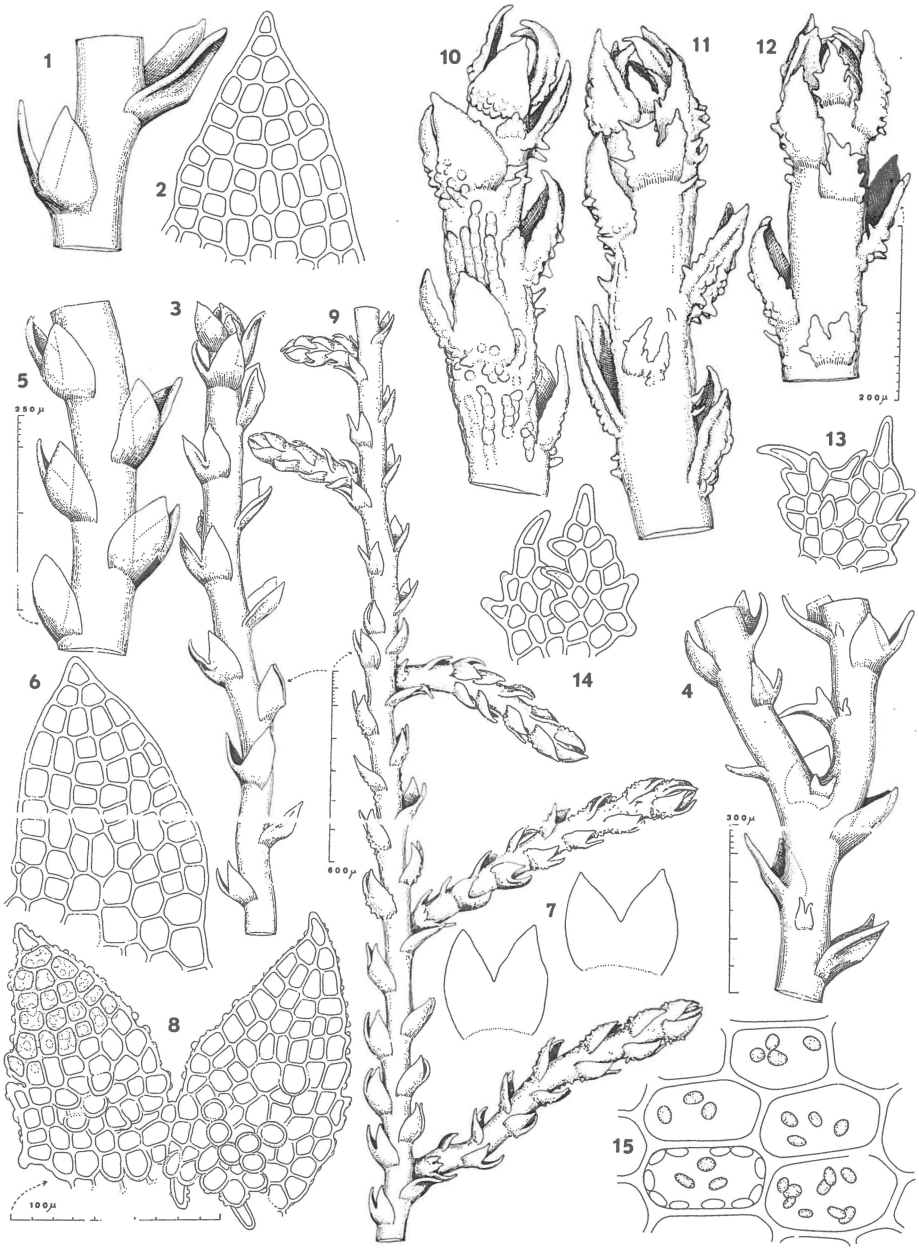


Fig. 24. *Cephaloziella byssacea*. (1) Shoot sector, robust shoot, antical aspect (×102). (2) Leaf lobe (×275). (3) Shoot apex, dorsal aspect (×42). (4) Shoot sector, postical aspect, showing *Frullania*-type branch; note underleaves (×73). (5) Shoot sector, antical aspect (×102). (6) Leaf lobe (×275). (7) Two leaves (×102). (8) Leaf, abaxial aspect (×275). (9) Shoot system, antical aspect, with 5 lateral-intercalary branches (×42). (10) Shoot apex, antical aspect; note sublamellate ridges of elevated cells (×115). (11–12) Same, postical aspect (×115). (13–14) Underleaves (×275). (15) Lobe base cells with oil-bodies and, lower left, chloroplasts (×840). [1–4, from v. *byssacea*, 66–1469; 5–7, v. *byssacea*, in part grading to v. *scabra*, 70–2370c; 8–14, Sarfaq, a phase showing gradation from v. *scabra* to *C. spinicaulis;* 15, 70–2686a, Perdlertut, a mod. *dentata* of optimal size; 1, 5, drawn to 250 μ scale; 2, 6, 8, 13, 14, drawn to 100 μ scale; 3, 9, drawn to 600 μ scale; 4, drawn to 300 μ scale; 10–12, drawn to 200 μ scale].

Cephaloziella subdentata WARNST. (Fig. 25:1–7)

Distribution (Map 69)

11: Qasigíssat (70–2721). 15: Kronprinsens Ejland (70–2117b). 19: Nûk (70–2871b, 70–2885c).

Additional collection:

85: Sarpiussat (GRØNTVED, Aug. 1932).

C. subdentata is a poorly understood plant whose range northward is in doubt. It seems to be at the north edge of its range in the Disko region and has not been found in the Inglefield Bredning area, although searched for there by the senior author. Southward in North America it extends as a rarity into the peat bogs lying in the contact zone between the deciduous and boreal forests (SCHUSTER, 1953), or exceptionally occurs as a relict in peat bogs in the deciduous forest (SCHUSTER, 1949).

The species always occurs in peaty areas, as in the crowns of *Sphagnum* plants, where often overlooked. It may be found in mere minute traces (as, e.g., in 70–2885c). Typically in moors, associated not only with *Sphagnum*, but also *Calypogeia sphagnicola*, *Riccardia sinuata*, *Cephalozia pleniceps*, *C. bicuspidata*, *Mylia anomala*, *Lophozia polaris sphagnorum*, *L. ventricosa silvicola*, and *L. opacifolia* (Nûk; 70–2885c, 70–2871b). The *Riccardia sinuata* and *Calypogeia sphagnicola* are also consociated at Nunarssuaq (70–2117b) and *Cephalozia pleniceps* and *C. bicuspidata* recur at Qasigíssat (70–2721).

The West Greenland plant (e.g. 70–2117b, 70–2885c) is the common phenotype, often creeping in *Sphagnum* heads, with exposed sectors, and especially androecia and gynoecia, copper or purplish red. It lacks the pure violet pigmentation of the larger-celled boreal forms which seem transitional to *C. elachista*. Cortical cells are very thick-walled, 12–14 × 26–31 μ; cells of leaf lobes are thick-walled, often greatly so, 10–12 × 14–18 to 11–13 × 16–25 μ at the lobe bases; leaf lobes are slenderly lanceolate, erect, and from (2–3)4(5) cells wide at the base, to (GRØNTVED, 321) 4–6 cells wide, usually ending in 2 superposed, often rather elongated cells; underleaves are distinct; leaf bases rarely, but demonstrably, bear a 1-celled tooth of one base or the other; the cuticle is mostly quite rough; plants are usually cladocarpous and androecia occur near the gynoecia; ♀ bracts have lanceolate, slender lobes and are sharply serrate to coarsely paucidentate below, with the teeth 1-celled and almost never recurved, although sporadic recurved or hooked teeth occur. These criteria all unambiguously speak for *C. subdentata*, as distinct from *C. elachista*.

The copious collection of 70–2721, from the surface of a (largely) decaying, dry *Sphagnum* polster, is of plants with *Cephalozia pleniceps* and *C. bicuspidata* intermingled. It is quite similar to the above phenotype except in one respect: gynoecia have the bracts, which are 2–3(4)-lobed,

with the lanceolate-acuminate lobes even more stiffly spinous-dentate, the teeth thick-walled, rigid, formed by a single, tapered cell that usually projects stiffly at right angles to the margin, but a small minority of these teeth are gently to abruptly recurved, thus betraying the close affinity to the boreal (but never Arctic) *C. elachista*. The spinous lateral teeth usually arise from an oblique cell that is relatively broad based, with the tapered, sharp apex arched so that it is situated at right angles to the margin. In extreme cases these cells may be as much as 40 μ long × only 7–8 μ wide. Plants of this collection bear sporophytes in abundance. Spores and elaters are both ca. 9–9.5 μ in diam.

The opposite extreme of this species is formed by the very sparse, but typically copper-red phase in 70–2885c (mixed with *Lophozia opacifolia*, *L. polaris sphagnorum*, *L. ventricosa silvicola*, *Cephalozia bicuspidata*, and *Calypogeia sphagnicola*). The gynoecia in these plants have the slenderly lanceolate-acuminate lobes only faintly denticulate, isolated teeth near the lobe bases excepted. In other respects the plants are quite typical.

A major deviation from the preceding, apparently uniformly autoecious phenotypes, is formed by GRØNTVED 321. The plants are clearly normally autoecious, with ♂ branches arising from near the ♀ ones, as is typical of *C. subdentata* (plants are never pseudodioecious); they have ♀ bracts with sharply serrulate margins; 1–2 of the lower teeth may be sharply recurved and uncinate; leaf cells are thick-walled and 10–12× 14–18 μ. It was possible to find at least one paroecious shoot in which the 1–2 pairs of bracts below the ♀ bracts were large, with serrulate lobes; these bracts each contained 1 or 2 antheridia. Paroecious inflorescences have not otherwise been seen in the *C. subdentata-elachista* complex. Diandrous ♂ bracts also have not been previously reported in the *Cephaloziellaceae* (thus MÜLLER, 1951–58, p. 1015, speaks of the antheridia as "einzeln" in the family as a whole).

C. subdentata has been reported several times from Greenland. All these reports are ambiguous and need confirmation, since determinations of *Cephaloziellae* from Greenland have more often than not been incorrect. In any event, the present reports are the northernmost ones known in the eastern Arctic.

The species is easily recognized by the criteria cited above. It is at once distinct in the dull texture (owing to the numerous, strong, cuticular papillae), the easily demonstrated autoecious inflorescence, with gynoecia and androecia usually closely juxtaposed, and the very deeply divided leaves (the sinus descending 0.75–0.8 the leaf length), with lanceolate lobes commonly at least twice as long as wide at base (actual measurements: 50–54 μ wide at base of "normal" lobes 4 cells wide × 100–210 μ long).

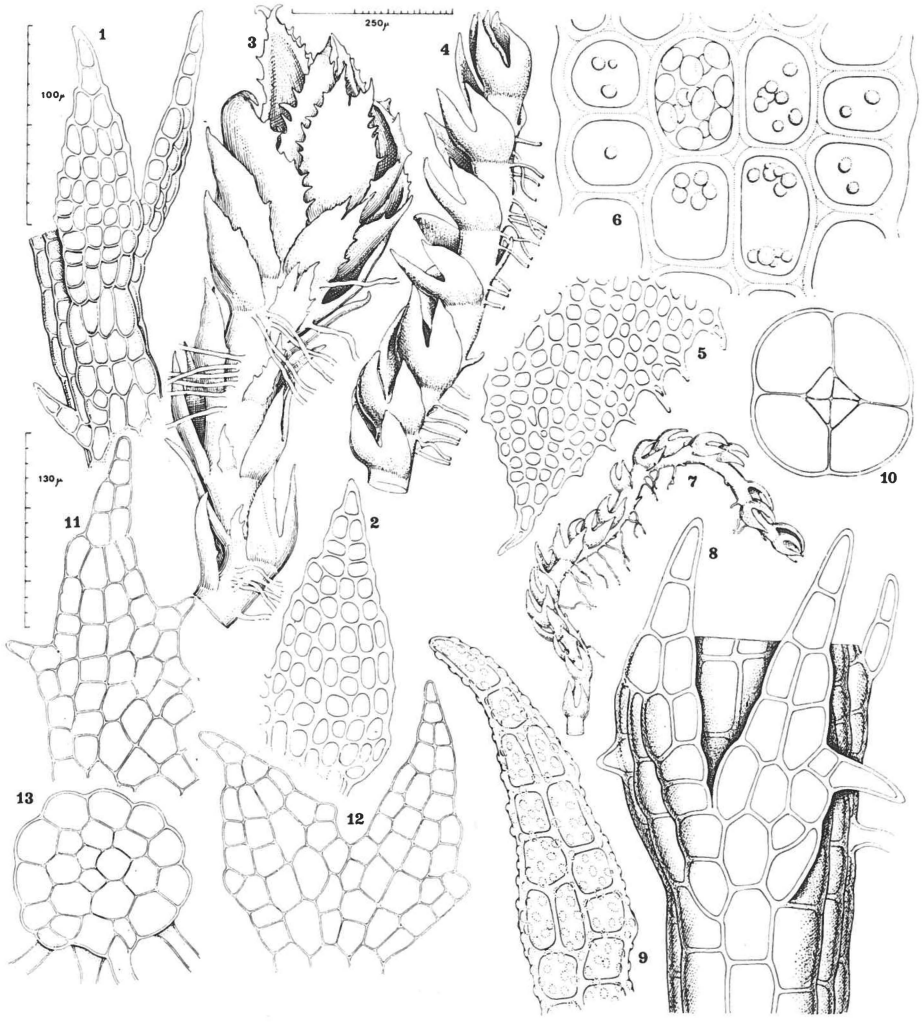


Fig. 25. *Cephaloziella subdentata* (1–7) and *C. elachista* (8–13), to show species distinctions. (1) Leaf and underleaf, *in situ* on stem (×260). (2) Lobe of large sterile leaf (×260). (3) Ventral aspect of gynoecial shoot apex (×85). (4) Lateral aspect of sterile shoot (×85). (5) Lobe of ♀ bract (×200). (6) Cells just above base of leaf lobe (×1100). (7) Sterile shoot, lateral aspect (× ca. 40). (8) Leaf and underleaf, *in situ*, of xeromorphic, low Arctic phase, but with cells at lobe base 13–16×20–25 μ (×365). (9) Leaf lobe, showing papillose extreme, of phenotype in fig. 8 (×365). (10) Seta cross section (×400). (11, 12) Lobe and whole leaf (×200). (13) Stem cross section (×260). [1–6, 70–2721, Qasigíssat, Disko; 7, RMS, s.n., Bergen Swamp, N.Y.; 8–9, Marr 661g, Hudson Bay; 10, RMS 61211, Cranberry Glades, W. Virginia; 11–13, RMS 68–164, Mass.].

Cephaloziella rubella (NEES) WARNST.

Distribution (Map 69)

32: Qôrorssuaq (70–2448).

C. rubella s.str. is essentially boreal-temperate in range; it has not been previously reported from so far north, nor are there, in fact, reliable prior reports of it from Greenland. The species is plastic, as here interpreted (to include *C. elegans* and *C. myriantha*, among others). The small amount of material found seems typical in the leaf lobes (4–5, more rarely 6–7 cells wide at base), and in the lack of distinct underleaves on the very few sterile stems seen. In addition to such plants attributable to var. *rubella*, more vigorous, underleaf-bearing plants are known from the same area (see below).

The sparing collection of 70–2448 is from heaved, exposed, intermittently desiccated soil, on a stony, frost-worked, gentle slope, in an acidic region (with *Ledum* in the more mature, less disturbed sites). Associated were a wide range of taxa typical of such sites (e.g., *Gymnomitrion corallioides*, *Prasanthus suecicus*, *Scapania parvifolia*, *Diplophyllum obtusifolium*, *Nardia geoscyphus*, *Lophozia excisa*, *L. alboviridis*, as well as a compact phase of *Cephalozia bicuspidata* and the ubiquitous *Anastrophyllum minutum*). Material extracted (all on one slide) was of paroecious, perianth-bearing plants, although (as is often the case with *C. rubella s.l.*) additional androecial branches also occurred. The plants were quite typical: ♀ bracts broadly united, with sharply serrulate margins; ♂ bracts below the ♀ bracts less but perceptibly serrulate; leaves broad, with ovate-lanceolate lobes often 4–5, occasionally 6–7, cells broad; cells very thick-walled, ca. 10–12 μ broad at the lobe bases. No deviant features were noted.

It is possible that this, the only paroecious *Cephaloziella* found in West Greenland, is more common than the sole collection suggests; the difficult and (for a bryologist) unattractive sites inhabited by the species perhaps account for the paucity of collections.

v. *arctogena* SCHUST. *var. nov.*

Planta paroica ut var. *rubella*, cellulis basalibus loborum circiter 9–12 μm diam., parietibus crassis; a var. *rubella* lobis foliorum basi (5)6–9 cellulas latis, foliis ventralibus manifestis, saepe magnis, interdum bifidis diversa.

Distribution (Map 69)

32: Qôrorssuaq (70–2456b).

This Arctic variety (or perhaps subspecies) of the basically temperate-boreal *C. rubella* is described (type locality) from Siorapaluk, northwest Greenland (RMS); otherwise known only from the above collection. The plants of 70–2456b grew among *Lophozia longidens* and *L. kunzeana*

in rather dry crevices on a rocky fellmark plateau. These copiously fertile plants can only be referred here; although normally paroecious, a few stems bear in addition intercalary androecia on vegetative branches. Cells are at the larger end of the variation exhibited by the type [mostly 8.5–11 μ wide up to (9)10–12(13) μ wide], and are, like the type, smooth but thick-walled. Oil-bodies are 10–16 per cell, ca. 1.8–2.2×2–2.8(3) μ. Leaf lobes vary greatly in width, but are mostly (5)6–9 cells broad. The perianth mouth cells are little elongated (usually 1.6–3.5:1; mostly ca. 2:1); ♀ bracts bear acutely triangular and sharply dentate lobes. Plants are green to, locally, bright reddish-pigmented. Sterile stems occasionally bear rather large and bifid underleaves. Cortical cells average (10)12–14(15) μ wide.

This anomalous variant may actually represent an Arctic subspecies of *C. rubella*, but, owing to the lack of any real knowledge of variation in the *Rubella* complex in the Arctic, the lesser status is opted for here. Presence of distinct underleaves throughout, usually very well developed, even on sterile axes, is linked with a paroecious inflorescence. Only *C. rubella* var. *elegans* exhibits this same linkage of features; it also tends to have similarly broad leaf lobes. However, var. *arctogena* differs in the (a) smooth cuticle; (b) larger cells, usually 8.5–12 μ broad at the lobe base; (c) leaf lobes in part from 6–9 or even 9–12 cells broad.

Cell size, identical to that of var. *rubella*, is here linked with var. *elegans* characters (such as broader leaf lobes, presence of underleaves). This seems to us adequate proof that placing *C. elegans* under *C. rubella* is correct, although MÜLLER (1951–58, p. 1027) regards var. *elegans* as an autonomous species. If so regarded, where would the present plant be placed?

Cephaloziella hampeana (NEES) SCHIFFN.

Distribution (Map 69)

17: Tupilak (66–0028a, 66–0029c). 24: Jakobshavn (66–0244).

This superficially holarctic species is essentially temperate-boreal in range and, to a large extent, replaced in the Arctic by the closely allied *C. arctica*. Indeed, there is some question as to whether these two taxa are always fully distinct. Insofar as they can be distinguished (*C. hampeana* lacks purplish pigmentation and is usually green to ± brownish, whereas *C. arctica* is usually copper-colored to purplish to scorched purplish-piceous; *C. hampeana* usually lacks underleaves of sterile stems, whereas *C. arctica* usually has them distinct on all but the feeblest sterile axes) the above plants seem to belong here rather than to *C. arctica*. They have very few underleaves of sterile stems and are autoecious. Gynoecial bracts are strongly sheathing, with nearly edentate lobes. The

perianth mouth is formed of a mixture of elongated and abbreviated cells, is in part crenulate (where all cells end at the same level), partly denticulate (where some longer cells project further). Neither ♀ bracts nor perianth mouth quite fit our concepts of *C. arctica* or *C. grimsulana*. The leaves are to $^2/_3$ bifid; leaf cells most often have thin walls and average (11)12–14(15) μ wide at the lobe base; cortical cells average (12)13–15(16) μ wide.

Cell measurements in this plant fail to quite correspond to those of *C. arctica* or *C. grimsulana* but reasonably agree with those of *C. uncinata* —a plant which is otherwise quite different.

The plant occurs admixed with an androecial phenotype of *C. byssacea*, sterile stems of which are distinct in the numerous underleaves.

Cephaloziella uncinata Schust. *sp. nov.* (Figs. 26–28, Table VII)

Planta autoica, gametangiis masculis a femineis longe separatis; folia ad 0.65 bifida, lobis plerumque 6–9 cellulas latis, apice saepe uncinato-incurvatis; folia ventralia nonnusquam saltem praesentia; bracteae femineae margine valde dentatae, apice saepe acuminatae uncinatae; masculae manifesto dentatae; ostium perianthii ciliolatum cellulis longis (plerumque 4–6:1).

Plants ± fleshy and compact to rather rigid and wiry, long and very slender, relatively large and often strongly elongated, sparingly branched, the branches erect or ascending, lateral-intercalary. Shoots light green to olive- to dull green or brownish (in drying leaves often whitish on older shoot sectors, when moist hyaline and decolorate), less often upper parts of leaf lobes and/or ♂ bracts and parts of ♀ bracts (and lower part of perianth) somewhat vinaceous or claret-red. Stems ca. 80–90 to 100–120 μ in diam. × 6–12 mm long, fleshy to wiry. Cortical cells (10–11)12–15(16–17) μ wide. Leaves remote, loosely folded or subcomplicate (as in *C. byssacea*) varying to concave (as in *C. arctica*), averaging 120–140 μ wide × 124–135 μ long to 260–290 μ wide × 200–240 μ long, usually bifid 0.65–0.7; the slender, sharply acute lobes (5)6–9(10) cells broad, lanceolate, very variable, usually suberect or obliquely patent, tips often formed by 1–2 thick-walled, hyaline, elongated (to 11×25–27 μ) cells that are diagnostically incurved (not or rarely so in xeromorphic extremes with very thick cell walls, there often nearly blunt) or hooked; basal parts of leaves occasionally armed with cellular processes and ventral (sometimes also dorsal) leaf margins with a subbasal tooth. Underleaves variably developed, usually very small (mere sessile or stalked slime papillae), but at tips of vigorous sterile shoots often small, bifid or lamellate structures 3–5(6–7) cells long. Cells varying from moderately thick-walled to very thick-walled (lumina then guttulate), with concave-sided trigones, closely and very coarsely papillose (mesic forms) to weakly or moderately so (xeromorphic phenotypes);

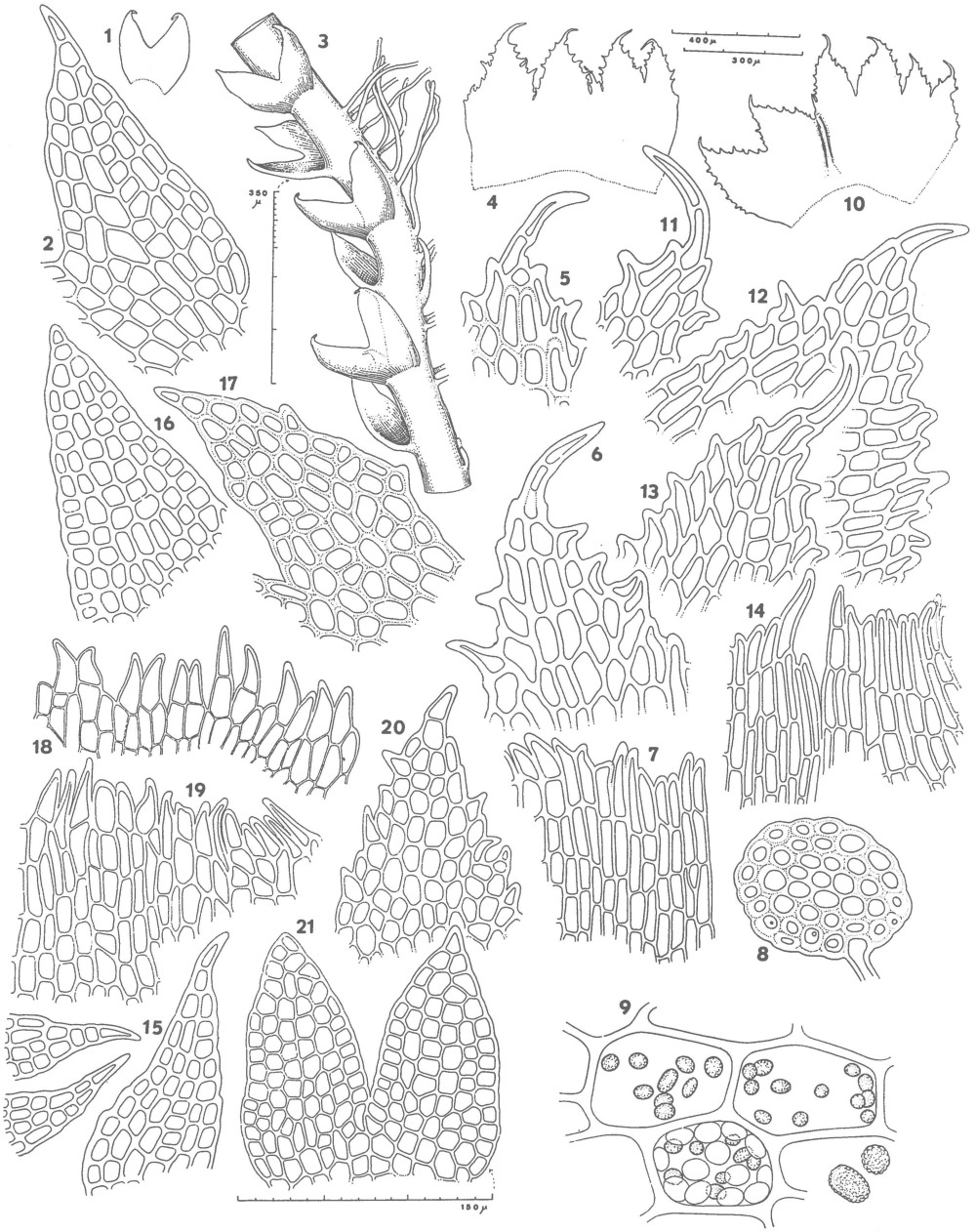


Fig. 26. *Cephaloziella uncinata* Schust. (1) Leaf (×53). (2) Leaf lobe (×230). (3) Shoot sector, lateral aspect (×75). (4) ♀ Bract and bracteole (×53). (5–6) Apices of lobes of ♀ bracts (×230). (7) Perianth mouth apex (×230). (8) Stem cross section (×230). (9) Cells of lobe base with oil-bodies and, below, chloroplasts (×800); at lower right, individual oil-bodies (×2000). (10) ♀ Bracts and, at right, bracteole (×43). (11–13) Apices of lobes of ♀ bracts (×230). (14) Perianth-mouth sectors (×230). (15) Leaf lobe and two lobe apices (×230). (16–17) Lobes of leaves from ♀ branches (×230). (18–19) Perianth-mouth sectors, the upper from a juvenile perianth (×230). (20) Lobe of ♀ bract (×230). (21) Leaf (×230). [1–9, v. *sphagnicola*, 70–2344; 10–21, v. *uncinata:* 10–17, 66–0054, Søndre Strømfjord; 18–21, 70–2128, Kuánerssuit, Disko Fjord; 1, 4, drawn to 300 µ scale; 2, 5–8, 11–21, drawn to 150 µ scale; 3, drawn to 350 µ scale; 10, drawn to 400 µ scale].

cells at lobe bases ca. (9.5–10)11–14(15) μ wide × 14–18 μ long; oil-bodies small, 2.8–3.2 × 2.8–4(5) μ, (2)3–7(8) per cell; leaf bases often locally bistratose. Asexual reproduction absent or rare: gemmae on ± brownish shoot tips, green to faintly brownish or vinaceous, 2-celled, (10)11–14(16) × 20–24 μ, ± beaked at both ends.

Autoecious. Androecia on long, ± leafy axes, often intercalary, compactly spicate, usually very long [often with (6)12–25 pairs of imbricate bracts]; bracts ventricose, green or often somewhat purplish, bilobed, the lobes normally serrulate to denticulate; normally monandrous. Gynoecia typically remote from androecia on rather short to very long lateral-intercalary branches or on leading axes, greenish (rarely locally reddish), with perianth mouth decolorate. Bracts ca. 0.2–0.45 fused with bracteole, bilobed ca. 0.35–0.4, the triangular lobes usually rather sharply but finely serrulate-dentate, usually decolorate on the margins and on the often slender, short-acuminate, often diagnostically hooked apex (not or rarely so on pigmented xeromorphic extremes). Perianth deeply 4-plicate, to within $^1/_3$ of base, locally 2-stratose in basal $^1/_3$, the decolorate apex of long, thick-walled cells, the mouth fringed with finger-like, narrow cells, mostly 8–9.5(12–13) × 52–72 μ grading down to 10–13 × (23–34)38–45 μ or 12–14 × 42–96 μ, the cells finger-like (usually averaging 4–7 : 1), often free for over 0.3 their length, mouth then ciliolate.

Capsules with seta 70 μ in diam., with the usual 4 very large epidermal cell rows opposed to 4 minute internal cell rows. Capsule wall 2-stratose, thin; valves ca. 150–170 × 375–395 μ. Epidermal cells in median region of valves often partly tiered, narrowly oblong, mostly 8–10(16–20 where a longitudinal wall is occasionally omitted) × 24–27 μ, with well-defined, rather strong nodular thickenings, mostly of longitudinal walls only, sporadically isolated ones on transverse walls. Inner cells less regular, mostly oblong and ca. 8–10(12) × 24–42 μ, in distal parts of valves less regular and mostly with narrow, complete to incomplete semiannular bands grading to nodular thickenings, in median and basal parts of valves almost all with nodular thickenings, sporadically extended as incomplete tangential bands. Spores (9.5)10–12 μ, brown, finely, sharply and rather closely asperulate-papillate to papillate-vermiculate through anastomosis of papillae. Elaters 7–9 × 72–125 μ, 2-spiral, spirals mostly ca. 2.4 μ.

Fig. 27. *Cephaloziella uncinata*. (1) Cells of perianth mouth (×230). (2) Leaf lobe (×230). (3) Leaf, *in situ* (×230). (4) Lobe tip of ♀ bract (×230). (5) Lobe of ♀ bract (×230). (6) ♀ Bracts and, at right, the bracteole (×38). (7) Sterile shoot tip (×40). (8) Autoecious plant; a second androecial branch, arising from main axis just below sector of main axis drawn, is omitted; note mammillate leaves of main stem (×40). (9) Seta cross section (×415). (10) Cells at lobe base, with oil-bodies and (lower left cell) chloroplasts; at lower right focus on surface to show papillae (×1200). (11) Gemmae (×740). (12) Perianth cross section (×87). [1–11 from 66–0306a, near Godhavn, Disko; 12, 66–0101, Head of Søndre Strømfjord; 1–5, drawn to 70 μ scale; 6, to 500 μ scale; 7–8, to 700 μ scale].



Fig. 27.

Type. Kânâk, Inglefield Bredning, NW. Greenland, near shore in a poorly drained sedge-grass meadow east of the village, 150–175 ft, among *Sphagnum* (RMS 45565).

Distribution (Map 70)

1A: Behind Arctic Station (66–0187a). 1D: Skarvefjeld (66–0299a, 66–0306a, 66–0313a). 6: Eqalúnguit (70–2246a). 7: Angûjârtûtit (70–2158a). 8: Kuánerssuit (70–2128). 26: Pâkitsup ilordlia (70–2281a, 70–2289a). 35: Hollænderbugt (66–1514). 43: Kangerdlugssuakavsak (66–1283c, 66–1284a, 66–1285a). 53: Søndre Strømfjord (66–0053a, 66–0054, 66–0058a, 66–0101).

Additional collection:

95: Pâkitsoq (J.V. 162).

This species seems widespread in both northwest and West Greenland and is clearly an Arctic species; its range elsewhere is not known.

Although exhibiting the usual variability encountered in the species of this genus, *C. uncinata* seems reasonably distinct in: (1) that all or most well-developed perianths are distally fringed by finger-like, often tapered, very strikingly elongated cells whose distal portions are free; (2) the usually serrulate-dentate lobes of the ♀ bracts whose tips are often strikingly acute to acuminate and hooked; (3) frequently hooked 1–2-celled tips of the leaf lobes; (4) firm, usually thick-walled cells which are larger than usual in *C. arctica*, smaller than usual in *C. grimsulana*— although overlap occurs with both taxa; (5) general lack of extensive purplish or vinaceous pigments; (6) autoecious inflorescences; (7) ♂ bracts usually clearly serrulate on lobes; (8) underleaves sporadically distinct on sterile stems, never large, often suppressed on many sterile shoots or vestigial.

C. uncinata is a puzzling taxon, frequently occurring on damp, basalt cliffs (as in 66–0306a), associated with mesophytic calciphiles such as *Scapania brevicaulis*, *S. cuspiduligera*, and *Plagiochila asplenioides*, or else (in 66–0299a) on thin soil over basalt ledges, on cliffs, associated with *Peltolepis grandis*. At times it occurs (70–2128) over irrigated, south-facing basalt slopes, or also on irrigated but rather peaty soil at the edge of a "warm spring" draining basaltic cliffs (70–2158a), associated with *S. curta*.

C. uncinata also occurs in more hygric but peaty sites (as in 70–2246a), mixed with *S. hyperborea*, *Lophozia kunzeana*, *Sphagnum*, etc. The species is also found growing between and over *Sphagnum* together with *Calypogeia sphagnicola*, *Cephalozia pleniceps*, and *C. bicuspidata*, or over *Aulacomnium palustre* and *Tomenthypnum nitens*, in a few cases under more exposed (dry?) conditions (e.g., 66–0187a, 66–1285a) together with *S. mucronata*, *Nardia geoscyphus*, and *Anomomarsupella*. Plants from such sites fall in the lower end of the cell-size diagrams of *C. uncinata* (see Table VII and fig. 28).

All plants with perianths (66–0053a, 66–0054, 66–0187a, 66–0306a, 66–1514, 70–2128) have the perianth mouth with the strongly elongated, distally free, finger-like cells typical of the species. The terminal cells are

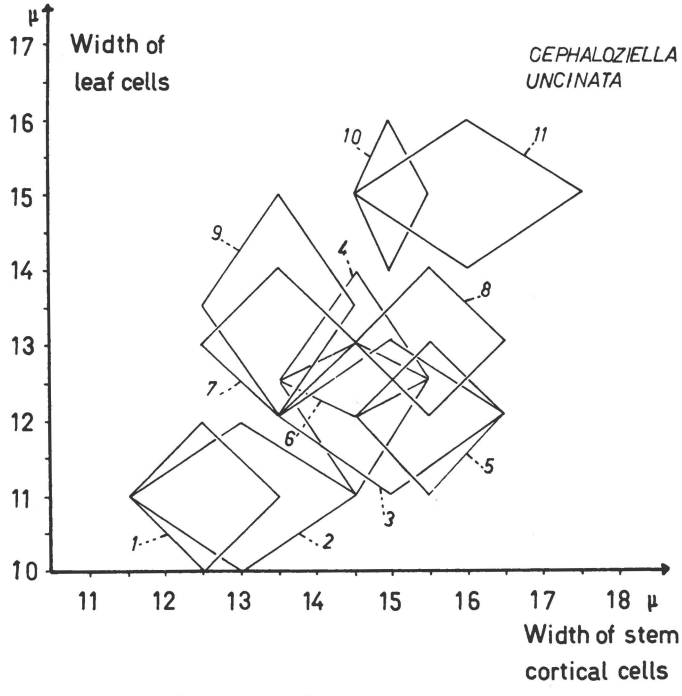


Fig. 28. See also p. 322, Table VII.

normally very long and protruding, but in at least one collection this character shows much variability. These plants, from Søndre Strømfjord (66–0054) may bear long and longly protruding cells of the perianth mouth but some plants have it crenulate. Bracts below the perianth also show a wide range of variation. One plant has strongly dentate bracts with hooked, spinose tips linked with a crenulate perianth mouth; another has bracts much more weakly dentate, without hooked lobe tips but the perianth mouth with strongly elongated, projecting cells. A third plant shows strongly dentate bracts with hooked tips and a perianth mouth with long, longly protruding cells. This variation in the ♀ bracts was also noted in other collections. Moderately dentate bracts occur in 66–0306a and 70–2128, while strong dentition is seen in 66–0053a and 66–0054. When ♀ bracts are strongly dentate, the leaves also tend to be dentate, while plants with weakly dentate ♀ bracts have leaves without or with very few teeth.

Deviating in two respects are the plants of Vahl 162: these have sporadic paroecious inflorescences and the perianth mouth, although with tapered cells free for 0.35–0.9 their length in most cases, bears less elongated cells at the mouth. ♀ Bracts, very sharply spinose-serrulate and with acuminate and often hooked 1–2-celled lobe apices, are typical; cells of the lobe tips are strikingly elongated and mostly 3–5:1.

Table VII. *Cephaloziella uncinata.*

	Width of leaf cells at base of lobes.	Width of stem cortical cells on sterile stems.	Terminal cells of perianth mouth.
1. Godhavn 66–0187a	(9) 10–12 (13) μ	(10) 11–13 (14) μ	11–13×29–65 μ
2. Kangerdlug. 66–1285a	(9) 10–12 (13) μ	(10) 11–14 (15) μ	
3. Skarvefjeld 66–0299b	(10) 11–13 (15) μ	(12) 13–16 (17) μ	
4. Søndre Strømfj. 66–0054	(10) 11–14 (15) μ	(12) 13–15 (17) μ	8–13×23–65 μ
5. Kuánerssuit 70–2128	(10) 11–13 (14) μ	(13) 14–16 (17) μ	7–8×21–42 μ
6. Eqalúnguit 70–2246	(10) 12–13 (14) μ	(12) 13–15 (16) μ	
7. Pâkitsup 70–2281	(11) 12–14 (15) μ	(11) 12–14 (15) μ	
8. Skarvefjeld 66–0306a	(11) 12–14 (15) μ	(13) 14–16 (17) μ	10–13×29–65 μ
9. Søndre Strømfj. 66–0053a	(11) 12–15 (16) μ	(11) 12–14 (15) μ	8–13×27–34 μ
10. Godhavn 66–0313a	(13) 14–16 (17) μ	(12) 14–15 (16) μ	
11. Sarfaq 70–2344	(13) 14–16 (18) μ	(13) 14–17 (18–20) μ	8–16×23–52 μ

Plants from Hollænderbugt (66–1514) are also atypical in some respects; they represent an xeromorphic extreme with papillose cuticle and thick-walled cells. Here the ♀ bracts bear, in part, 1-celled, oblique lateral teeth that are truncate and dilated at their free tips; the lobe apices, although often hooked, are not strongly acuminate. Perianth apices bear very thick-walled and exceedingly elongated terminal cells, free at their tapered ends for ca. 0.25–0.45 their length; the cells average from 14×42 μ up to 12–16×96 μ (then are 6–8:1).

The hooked leaf tips are not always present on each shoot. Adjoining the ♀ bracts they are often typically developed, even on plants from dry sites on which the vegetative leaves are often shorter and the lobe tips unhooked.

Admixed in 66–0313a is a *Cephaloziella* provisionally listed under *C. uncinata;* this collection is of interest because the few ♂ branches have nearly edentate bracts and at times 2 antheridia per bract. Dentition of the ♂ bracts is normally present in *C. uncinata.* The leaves are often strongly hooked, with longly acuminate leaf lobes ending in 2(1) superposed

single cells, and have bulging lateral margins, as if provided with incipient weak teeth. Only very young, seemingly edentate, ♀ bracts were seen. The edentate lobes of the ♀ bracts suggest that the collection is perhaps not correctly placed here, but we are unable to place it more satisfactorily elsewhere.

v. *sphagnicola* Schust. *var. nov.* (Fig. 26:1–9)

Habitu *C. hampeanae*, dentibus validis bractearum feminearum *C. uncinatae* similis. A var. *uncinata* cellulis corticis 14–17μm latis, folii lobo ventrali saepe dorsali minore, cellulis folii majoribus, ca. 15–18×18–24μm diam., cellulis ostii perianthii modo 2.5–4:1 diversa.

Distribution (Map 70)

25: Sarfaq (70–2344).

Plants relatively vigorous, shoots creeping, sinuous, green to pale brown, only androecia dull purplish to purplish brown. Stem with dorsal and lateral cortical cells oblong, little thick-walled, ca. (13)14–17(18–20) μ wide. Branching copious, all intercalary, mostly lateral and axillary. Leaves remote, obdeltoid to quadrate-rotundate when flattened, often somewhat asymmetric, with ventral lobe smaller and shorter; insertion transverse to moderately succubous; sinus descending 0.6–0.75 the dorsal lobe length, acute, the lobes suberect to moderately but never strongly patent, often arched and with incurved, sometimes almost hooked tips. Margins entire to occasionally (especially near fertile zones) obscurely crenulate, ventral base sporadically unidentate. Dorsal lobe lanceolate, 5–7(8) cells broad at base, ventral similar or smaller, 4–6(7) cells broad at base; lobe tips usually ending in 2, sometimes 1 cell(s), the cells not or rarely decolorate, not strikingly elongate. Cells firm, thick-walled with rounded angles, sometimes lumina almost guttulate, but smooth, large: at lobe bases usually averaging (13–14)15–18 μ wide on mature leaves × 18–24 μ long. Underleaves usually lacking (except near sex organs and at branch bases), at most a stalked slime papilla, occasionally rather distinct. No gemmae present.

Autoecious. ♂ and ♀ Branches usually both elongate, often arising from a common, vigorous sterile axis, never clustered, rarely closely juxtaposed. Androecia spicate, usually dull purple, bracts imbricate, with mutually appressed antical margins, with lobes crenulate to crenulate-serrulate, the marginal cells often diagnostically obliquely elongated and projecting; interior of lobes often of strikingly elongated, thick-walled cells. Bracts in 3–6 or more pairs, forming a distinct, compact, often smooth spike. Gynoecia with 1–2 pairs of ± denticulate subfloral leaves; bracts 2(3)-lobed, both united for ca. 0.3–0.45 to bracteole, lobes triangular and longly acute, sharply serrulate-denticulate with thick-

walled projections of cells usually extended at right angles; lobe apices longly acute or short-acuminate, ending in 1–2(3) superposed cells, the terminal cell elongate (occasionally strikingly so, to 60×12–14 μ), thick-walled, spinous, often hooked. Bracteole usually bifid, often shorter and smaller than bract. Perianth mouth crenulate-denticulate with the free, tapered tips of the terminal cells (whose distal 0.2–0.3 are free); terminal cells hyaline, not very thick-walled, ca. (8)9–11×24–32(38–40) μ (1:2.5–4) on immature perianths, 8–16 × 23–52 μ with maturity.

Type. 25: Sarfaq (70–2344), peaty area around tarns, high cliffs S. of narrows, between Pâkitsoq and Pâkitsup ilordlia. The type was associated with *Pleuroclada albescens*, *Lophozia kunzeana*, and *Anastrophyllum sphenoloboides*.

This plant and its status are problematic and (until much more adequate material comes to hand) will remain a problem. The plant keys to *C. hampeana* in ARNELL (1956), from which it differs most obviously as follows: cells thick-walled, larger; gynoecial bracts with conspicuous teeth of lobe apices; leaves erect-patent to erect, often with incurved lobes, with lobes usually narrower. MÜLLER (1951–58, p. 1034) has a helpful discussion of *C. hampeana* and would place here as variants two taxa described as species: *C. subtilis* (*C. curnowii* is a synonym), with cells 14–16 μ broad, and *C. gallica*, with cells 14–18 μ wide. From all the various described forms of *C. hampeana* the variety *sphagnicola* differs in the combination of large and very thick-walled cells and incurved, often unequal leaf lobes. We think it more likely the plant represents a large-celled extreme of *C. uncinata*.

Although the general lack of distinguishable underleaves at first led us to place this taxon as a variety of *C. hampeana*, some plants show rather distinct underleaves. Also, many leaves have hooked tips, often formed by 2 superposed elongated cells. ♂ Bracts are dentate, as in *C. uncinata;* ♀ bracts are strongly toothed and end in long, hooked teeth (sometimes formed by 2–3 superposed cells). The perianth mouth shows some variation: short cells, forming crenulate sectors, alternate with sections of more strongly elongated cells whose tips project like fingers. The perianth mouth, although similar to that of *C. rubella arctogena* (p. 315), lies within the range of variation we have seen in *C. uncinata*. The ♀ bracts and their dentition can also be readily matched in *C. uncinata*, but in var. *sphagnicola* some of the upper lobe laminar cells tend to develop projections from the abaxial surfaces, especially towards the tip.

On balance it seems best to regard this as a large-celled phenotype (possibly polyploid?) of *C. uncinata*. In 66–0054 (Søndre Strømfjord) we find normal *C. uncinata* with small cells, accompanied by at least a single stem with leaf cells (13)14–16(18) μ wide at lobe base, and cortical cells

(16)17–20 μ wide. Perhaps there is a mixture of normal (?haploid) *C. uncinata* here, together with the larger-celled var. *sphagnicola.*

Clearly this plant needs further study from more adequate collections.

Cephaloziella arctica Bryhn & Douin (Figs. 29, 31; Table VIII)

Distribution (Map 71)

1A: Behind Arctic Station (66–0279a, 70–2052, 70–2061b, 70–2183). 6: Eqalúnguit (70–2218). 12: Perdlertut (70–2678). 15: Kronprinsens Ejland (70–2061b, 70–2069, 70–2090b, 70–2099a, 70–2107). 17: Tupilak (66–0002, 66–0030, 66–0036b, 66–0106). 18: Grønne Ejland (70–2812b). 19: Nûk (70–2875a). 21: Umiasugssûp (70–2927c). 25: Sarfaq (70–2320c, 70–2366a). 26: Pâkitsup ilordlia (70–2271, 70–2279b, 70–2294a, 70–2392). 29: Ritenbenk (66–0252). 30: Eqe (66–0249, 66–0288b, 66–0290c, 66–0340, 66–0330a). 32: Qôrorssuaq (70–2472a). 45: Sagdliaruseq (66–1056). 46: Qalatôq (66–1100c). 48: Amitsup (66–0774). 53: Søndre Strømfjord (66–0063, 66–0069, 66–0070).

Additional collections:

1D: Skarvefjeld (Grøntved Aug. 1932). 16: Manîtsoq (W. & H. July 1884). 26: Pâkitsup ilordlia (S.B. 1870). 29: Ritenbenk (S.B. 1870). 45: Sagdliaruseq (K.H. 13.166, 17.191). 88: Christianshåb (K.H. 16.630a). 92: Claushavn (S.B. 1870). 93: Navdluarssuk (W. & H. July 1884). 112: Umiartorfik (K.J. 876e). 117: Sêrsínerssuaq (K.J. 644). 122: South of Eqaluit (K.H. 13.342). 125: Sarqap taserssua (K.H. 16.215). 137: Esersiutilik (K.H. 16.601). 139: Qaqortukavsaq (K.H. 16.121a). 140: Small Island (K.H. 16.732). 142: Niaqornánguaq (K.J. 15.408). 144: Igdlorssuit (K.H. & W.C.S. July 1962).

C. arctica s.l. (to include *C. verrucosa* Bryhn & Douin, *C. alpina* Douin, and *C. glacialis* Douin) is a widespread species in the Arctic, occurring northward as far as there is exposed land; it recurs southward in the New World as far as Minnesota, Michigan, and (perhaps) New England. Because of confusion of such proportions that its taxonomy is impossible to disentangle in these pages, geographic and taxonomic perimeters of this species today are almost impossible to decipher. For example, *C. lorenziana* Douin (type: Connecticut) was placed as a synonym of *C. arctica* by Müller (1947), but almost surely belongs elsewhere. Plants that appear indistinguishable from *C. arctica* occur in the Antarctic as well (Litchfield I., South coast of Anvers I.; RMS 69–137). Such Antarctic plants agree with the leptodermous phases ("var. *alpina*") of *C. arctica* in the thin-walled cells. They have the usual vinaceous pigmentation common to all exposed phases of the species, are clearly autoecious, have distinct underleaves; ♀ bracts have the entire-margined lobes sharp to rarely subobtuse; the apical cells of the perianth mouth are only 2–2.5× as long as wide. Only two features differentiate the Antarctic plants from ordinary *C. arctica:* underleaves are often larger and bifid and some shoots are almost subisophyllous; lobe margins of the ♀ bracts seem quite devoid of dentition. In view of the variability in the bracts found in

C. arctica s.l., this lack of dentition should not be overvalued as a criterion: also, in the Antarctic and subantarctic regions, various taxa tend to develop larger than normal underleaves. Hence at most, the Antarctic plant should be regarded as a geographical race of *C. arctica s.l.*

C. arctica s.l. is perhaps the commonest and most widespread *Cephaloziella* in Greenland and is one of the most abundant species of *Hepaticae* found there. It is commensurately variable, both in morphology and ecology, yet it seems impossible to recognize other than inconstant formas within the species, *s.l.* Often occurring in weakly basic sites (and as noted, in the "*alpina*" phase is a typical species of such sites southward; see SCHUSTER, 1953). In low, feebly basic, peaty moss-tundra, in peaty depressions, it is associated with *Odontoschisma macounii* and *Tritomaria polita polymorpha* (70–2812b), or with *Lophozia quadriloba* (66–0063); it may also occur on moist soil over basalt dikes, with *Scapania degenii*, *O. macounii*, *L. quadriloba*, and *Anthelia* (66–0288b). Occurrences under circumneutral to acidic conditions, however, are at least as frequent—the species being seemingly very tolerant as to pH and Ca concentration. Under more acidic conditions, *C. arctica* may occur on moist, peaty soil between rocks, or often forming large, scorched patches on moist, peaty muck around tarns and shallow rock pools. One then finds associated *S. hyperborea*, *O. elongatum* and (less often) *Anthelia*, *Blepharostoma trichophyllum brevirete*, *L. kunzeana*, *L. binsteadii*, *L. ventricosa confusa*, etc. (66–0252, 66–0036b, 70–2099a, 70–2090b). On thinly peat-covered, irrigated, wet, insolated acidic rocks it is often found with *Gymnocolea inflata*, less often also *L. alpestris*, *S. scandica*, *Anastrophyllum minutum* (66–0002, 70–2069, 70–2366a). Occasionally it is also found among *Sphagnum* or *Aulacomnium*, or *Cephalozia pleniceps*, in moory meadows, mixed with *L. binsteadii* (70–2279b, 70–2271), less often *L. ventricosa silvicola*, *A. sphenoloboides*, *Cephalozia bicuspidata*, *Calypogeia sphagnicola* (70–2294a), or *S. lingulata* (70–2392). The species also occurs along rills and streams, often on peaty, damp soil, or between or over rocks, associated with *Marsupella arctica*, *A. assimile*, *Gymnomitrion concinnatum* (66–1100c, 66–0030, 70–2927c), or on moist soil over cliffs, with *Anomomarsupella*, *M. revoluta*, *Solenostoma pumilum polaris* (66–0290c). At the opposite extreme, occasionally over and between rocks in acidic, rather dry sites, amidst *L. hatcheri* (70–2052, 70–2678), or on broken, exposed mineral soil where apt to dry out, mixed with *Prasanthus*, *Anthelia*, *Cephalozia bicuspidata*, and *Gymnomitrion concinnatum* (70–2320c). Under relatively arid conditions almost always with gemmae (as in 70–2320c), but also with gemmae, in sterile phases, from over silty soil on rocks, in depressions in acidic fell fields, where subject to both inundation and desiccation, associated with *G. apiculatum* and *G. concinnatum* (70–2472a); or over thin soil on exposed rocks, with *S. lingulata* and *M.*

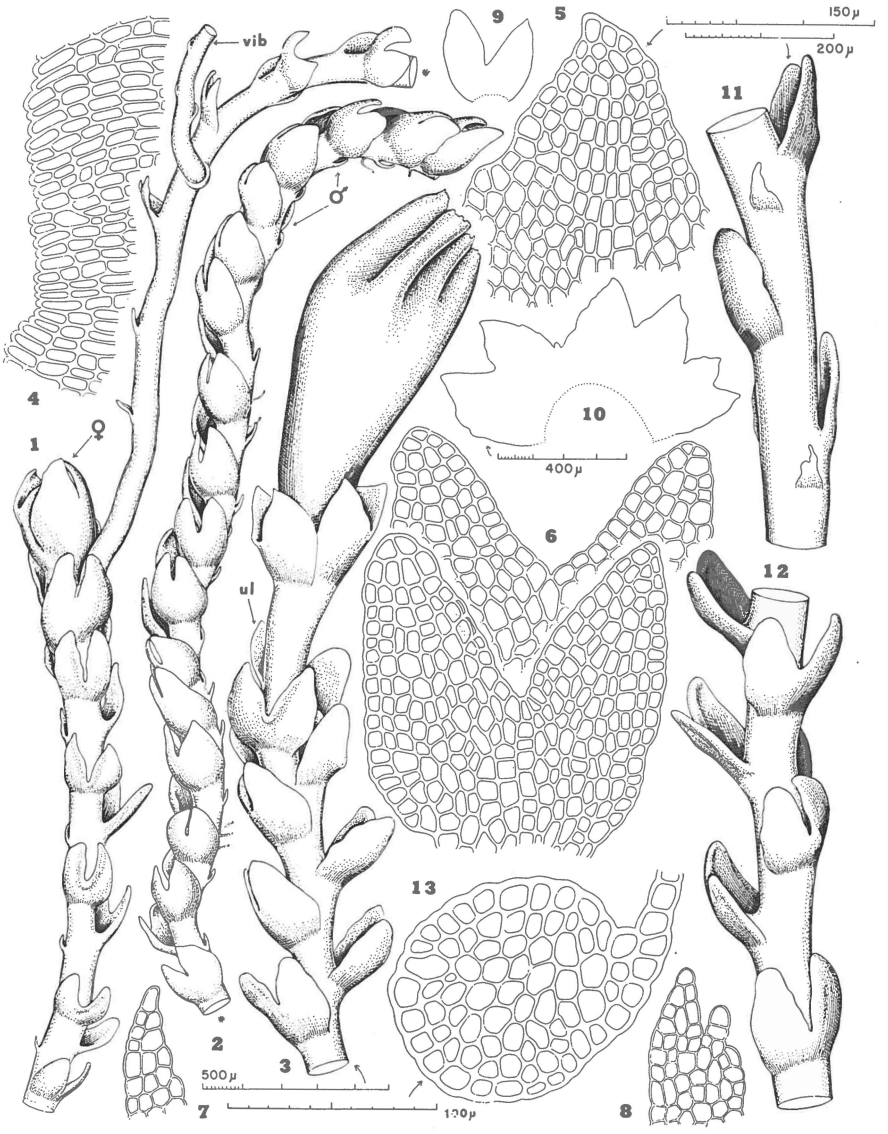


Fig. 29. *Cephaloziella arctica* var. *arctica*. (1, 2) Lower and upper portions of an autoecious plant; cut stem end indicated by asterisks; at vib a ventral-intercalary branch; at ♀ an unfertilized gynoecium (×49). (3) Perianth-bearing shoot tip (×49). (4) Perianth mouth cells (×180). (5) Lobe of ♀ bract shown in fig. 10 (×180). (6) Leaf, and distal portions of another (×180). (7–8) Large underleaves from sterile axis (×180). (9) Leaf (×49). (10) ♀ Bracts, and at right, bracteole (×42). (11–12) Ventral and dorsal aspects of shoot sectors (×100). (13) Stem cross section (×275). [All drawn from lectotype, from Framshavn, Ellesmere Island, Simmons; 1–3, 9, drawn to 500 μ scale; 4–8, to 150 μ scale; 10, to 400 μ scale; 11–12, to 200 μ scale; 13, to 100 μ scale. Note that in almost all Greenland phenotypes the leaf lobes are more consistently acute or subacute].

boeckii, in a gray-green phase of arid sites (70–2061 b). In dry sites also sometimes with *Tritomaria quinquedentata gracilis* (70–2218). Obviously the species is almost ubiquitous and the number of collections cited gives only an imperfect concept of its abundance, and its associates.

Reasons for the limited number of citations lie in the difficulty we found in making absolute identifications. Except for two of the last collections cited (70–2061 b, 70–2472 a), we have avoided naming specimens in which we could not definitely establish an autoecious inflorescence. Very often one sees long, leafy axes developing androecia, from which weak branches ("innovations") are produced, which are again androecial. Similarly, long, leafy, gynoecial axes produce subfloral innovations which are again gynoecial—sometimes this process may be repeated two or three times. In such cases one is likely to conclude that dioecious plants are present and that *C. byssacea* is at hand. Confusion with this species, indeed, is sometimes difficult to avoid. (Plants of 66–0002, from wet, sunny rocks around pools, epitomize this problem. They were initially named *C. byssacea* because of the seeming dioecious inflorescences; however, ± erect, *C. arctica*-like leaves were noted. The plants are a fuscous to black sun form and, like some such phases, essentially lack purplish or vinaceous pigments. Eventually a single, autoecious plant was found. The basic problem is that some populations of *C. arctica* tend to produce stems which, after developing sex organs, produce innovations which are of the same sex. With death and decay of the oldest parts of the plants, connections between the ♂ and ♀ branches are lost—so that the innovations, of the same sex, mislead one; the plants are then "pseudodioecious". If patches of plants are carefully dissected, one can, eventually always find physical connections between ♂ and ♀ branches. Frequently one finds a main axis which develops an androecium also developing gynoecial intercalary branches; it is equally common to find a gynoecial main stem with a subfloral innovation that is androecial. There seems to be no discernible pre-destined pattern).

In addition to the spatial variations in sex organ orientation, which, as we have seen, always represent deviations on the basic autoecious pattern, *C. arctica* is strikingly variable in other criteria as well. The lectotype of MÜLLER (1905–16) from Framshavn, Ellesmere Island, represents the pachydermous modification ("var. *arctica*") which has a very high incidence of blunt to narrowly rounded leaf lobe apices. These plants (Fig. 29) show ♀ bracts with the lobes moderately sharp to bluntly pointed—never acuminate or longly acute—and almost entire-margined; the crenulate perianth mouth is typical in having only the rounded tips of the nontapered cells free, the cells mostly 2–3× as long as wide. This phenotype is "pseudodioecious" and we succeeded, after much effort, in finding only one clearly autoecious plant—a gynoecial main shoot, with unfertil-

ized gynoecium bearing an androecial subfloral innovation. From this phase there is variation to the more common phenotypes in which we find (a) leaf lobes sharp; (b) cells usually much less extremely thick-walled; (c) lobes of ♀ bracts usually more sharp, sometimes longly so, and at least weakly denticulate. From this, the perhaps most common phase, we rather rarely find variations towards sharply denticulate margins of the ♀ bract lobes, sometimes linked with more strongly elongated cells of the perianth mouth. Then a seeming approach to *C. uncinata* occurs—an approach that is sometimes close enough so that for over ten years *C. uncinata* remained a "herbarium species" while one of us (RMS) tried to resolve whether or not it could be but a form of the malleable *C. arctica.*

As Tables VII & VIII show, cell dimensions of *C. arctica* and *C. uncinata* differ somewhat, suggesting that two taxa are at hand. Also, even though the normal *C. arctica* constellation of characters is not invariably present, deviations are usually in only one or two out of the whole ensemble of features. Thus in 70–2090b we find linked "typical" ♀ bracts with ± subentire and decolorate margins and perianth mouth cells that vary from the "*arctica*" extreme—2.5:1—to an "*uncinata*" extreme—5–6:1. In plants of 66–1056 and 70–2271 weakly dentate bract margins are linked with finger-like perianth mouth cells, usually 3–5:1 to 4–6.5:1. Even when these cells become strongly elongated, however, they are usually free only at the very tips, which are usually not distinctly pointed. This feature, we think, is critical in serving to separate *C. arctica* from both other allied taxa, *C. uncinata* and *C. grimsulana.* However, very rarely, even this criterion breaks down in part: in 66–1056 the perianth mouth cells, usually 3–5:1, are free for their distal 0.2–0.35, with the free tips pointed and ending in thick-walled "nipples". Here the merely acute lobes of ♀ bracts are sharply serrulate with the thickened projecting ends (or much elaborated walls only) of the marginal cells, and ♂ bracts are faintly denticulate. However, these plants show the strong purplish pigmentation of *C. arctica.*

C. arctica also occasionally occurs amidst *Dicranum*, *Lophozia hatcheri*, and other xerophytes, as erect, ramified stems largely hidden among these coarser species (as in 70–2678); it may then acquire the olive-brown color, with local purplish pigmentation (which may be lacking on the androecia) of *C. byssacea* and may have somewhat the same stringy aspect normal to that species. When found as such attenuated, remote-leaved phases, amidst xerophytic bryophytes, *C. arctica* may be very difficult to separate from extremes of *C. byssacea*, sharing with it the same dingy olive color, with localized dull purplish pigmentation, and the rather copious branching. The branches, although usually intercalary (and normally lateral) are exceptionally furcate and terminal in such cases—again a "*byssacea* character". Furthermore, underleaves may be large

and lanceolate, to 80–85 μ wide × 135 μ long, although usually much smaller. In the single gynoecium of this phenotype dissected and flattened bracts and bracteole are united only ca. 0.1–0.15 (again a "*byssacea* character"). ♂ Bracts may be quite large, olive-colored rather than purplish, and have dentate lobes (varying to obscurely denticulate). Such phenotypes, when pseudodioecious (as is 70–2678), will almost unquestionably be sought under *C. byssacea;* yet, in the collection involved, 3 or 4 unquestioned autoecious inflorescences could be located—after several hours of effort! A logical conclusion seems to be that if both sex organs occur admixed it is never safe to infer that *C. byssacea* is at hand until patches clearly of only a single sex can be located.

We have also seen a scorched, clearly autoecious phase of *C. arctica* (70–2183), in which branching was wholly anomalous. In addition to the more common intercalary branches, we could find furcate terminal branching, both lateral and postical. Terminal postical branching has not been seen again in *Cephaloziellaceae*, and in this case, may represent an environmentally-induced abnormality.

Gemmae are freely produced in this species, usually ca. 14×19 μ to 12–14×19–22 μ. Capsules are also common and produced from July 16 (70–2183) to July 19 (66–0252), July 20 (70–2279b, 70–2271, 70–2294a) to Aug. 24 (70–2812b).

Cephaloziella grimsulana (JACK) LACOUTURE (Fig. 30, Table VIII)

Distribution (Map 71)

14: Hareøen (70–2606). 15: Kronprinsens Ejland (70–2079a). 21: Umiasugssûp (70–2944). 23: Kangersuneq (70–3150b). 25: Sarfaq (70–2320c, 70–2336b). 26: Pâkitsup ilordlia (70–2314). 35: Hollænderbugt (66–1507a, 66–1512a). 53: Søndre Strømfjord (66–0089).

C. grimsulana is apparently a rare or infrequent and greatly misunderstood taxon, seemingly purely Arctic-alpine and cited from Norway (S. ARNELL, 1956; ARNELL states that collections so-named from Sweden are all *C. arctica*), Switzerland (type), France, the Caucasus, Greenland, and Ellesmere Island (SCHUSTER *et al.*, 1959). In addition to plants from the above localities, we have seen *C. grimsulana* again from the Inglefield Bredning region of northwest Greenland.

The ecology of the large-celled plants placed here seems to correspond rather closely with that of *C. arctica.* We have found plants from fine, fast-drying, steep, highly calcareous clayey-stony slopes, chiefly in runoff crevices, with *Tritomaria scitula*, *Solenostoma pumilum*, *Lophozia badensis*, and *L. pellucida* (66–1507a, 66–1512a); others occur on damp, rocky but richly vegetated clayey slopes with *L. quadriloba* (70–2606). The species also occurs in *Salix*-moss-tundra fields, with *Scapania mucronata* (66–0089), or on fine, silty mineral soils, either where deposited

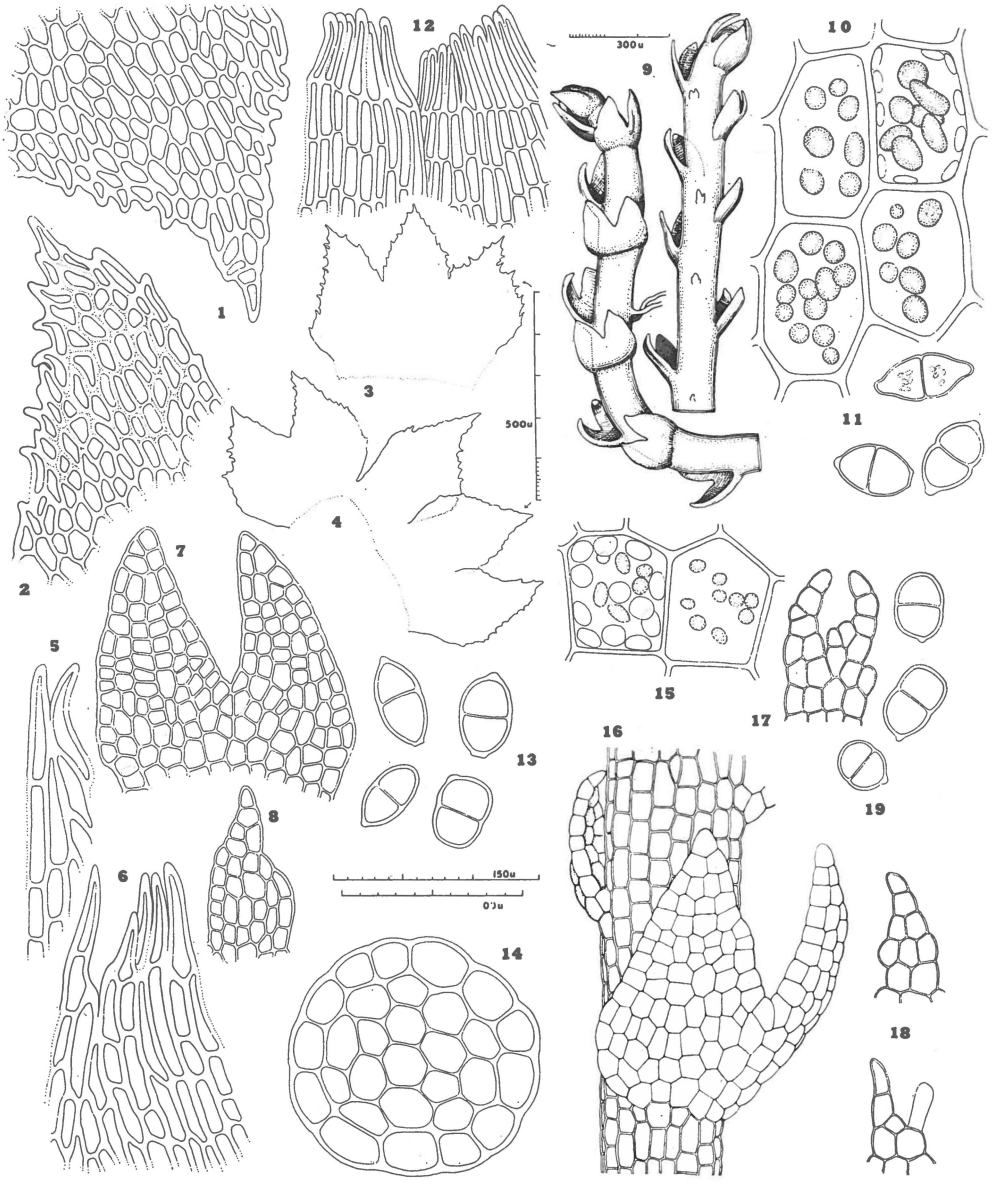


Fig. 30. *Cephaloziella grimsulana.* (1–2) Lobes of ♀ bracts (×180). (3–4) ♀ Bract and bracteole, and ♀ bracts + bracteole, respectively (×54). (5–6) Sectors of perianth-mouth (×240). (7–8) Leaf and adjoining underleaf (×180). (9) Lateral and postical aspects of shoot-tips (×43). (10) Cells of leaf lobe base, with oil-bodies and, upper right, chloroplasts (×850). (11) Gemmae (×380). (12) Cells of perianth mouth (×180). (13) Gemmae (×525). (14) Stem cross section (×370). (15) Cells of lobe base with oil-bodies and, left cell, chloroplasts (×750). (16) Leaf and underleaf, *in situ*, on stem (×168). (17–18) Underleaves (×215). (19) Gemmae (×400). [1–9 from 66–0089, Søndre Strømfjord; 10–11, 66–1507, Hollænderbugt, Nûgssuaq; 12, RMS 45551c, Kânâk, Inglefield Bredning; 13–14, RMS 35226a, and 15–19, RMS 35227, both Hilgard Bay near Alert, Ellesmere Island; 1–2, 7–8, 12, drawn to 150 μ scale; 3–4 to 500 μ scale; 5–6, to lowest 100 μ scale; 9, to 300 μ scale].

by run-off (in 70–2336b; with *S. lingulata*, *S. irrigua rufescens*, *S. curta*, and *Nardia geoscyphus*) or by dropping of lake levels (in 70–3150b; with *S. irrigua rufescens* and *Blasia pusilla*). Occasionally also over thin, wet, exposed, peaty soil in shallow depressions in richly vegetated meadows around lake edges (70–2314), associated with *Blepharostoma trichophyllum brevirete*, *Gymnocolea*, and *Anthelia*.

This "species" remains a dubious entity, separable from the plastic and variable *C. arctica* chiefly by the larger cells of leaves, stem cortex, and gemmae. ARNELL, 1956, states that *C. grimsulana* also has larger spores (9–12 μ) and broader elaters (10–12 μ) vs. spores 8–10 μ and elaters 6–8 μ wide in *C. arctica*. We have seen no capsules in the plants we attribute to *C. grimsulana* and perianths occur only in the plants from Søndre Strømfjord (66–0089). The frequency with which perianths (and capsules) occur in *C. arctica*, while the larger-celled plants attributed to *C. grimsulana* almost always have gemmae but rarely bear perianths—and in Greenland appear never to have capsules—may be significant.

ARNELL (l.c.) also tried to restrict *C. grimsulana* to plants with the lobe apices "rotundate obtuse" vs. "± subacute" in *C. arctica*. This criterion seems unreliable, the lectotype of *C. arctica* from Framshavn possessing obtuse to rounded leaf lobe apices. All our plants of *C. grimsulana* have ± sharp leaf lobes. The larger size of leaf-and stem cells is in no way related to growth under more favorable conditions since large-celled plants may occur in very difficult loci (as, e.g., in 70–2079a, whose plants occur as a scorched, rigid, sterile, gemmiparous phase mixed with *Gymnomitrion corallioides* and *G. concinnatum* in loose patches on thin, silty soil over exposed, gently sloping rock shelves, in full sun, where subject to long periods of drought). Cells are usually ca. 14–17 μ wide at the leaf lobe bases (as in 66–1507a). Gemmae range from 13–16×24–29 μ to 16.5–19×24–25 μ in extreme cases (in 66–1507a). In plants from the same locality (66–1512a) leaf lobe cells may be only 13–15 μ wide, and gemmae to 16.5×27–29 μ. On plants with the cell width of *C. grimsulana* (70–2079a; cells 14–16 μ wide at lobe bases) gemmae may be only 12–14× 21–24 μ, thus grade into those of *C. arctica* in size. Deviations in cell size of both leaf lobes and cortex are usually slight; the ranges—which are obviously higher than in *C. arctica*—are shown in Table VIII, p. 334.

This taxon is recorded from only ten specimens and eight localities. In some cases (as in 70–2079a, 70–2314, 70–2336b) it occurs mixed with plants that seem to be typical *C. arctica* and is then distinct in the wider cortical- and leaf cells. *C. grimsulana* shows the same variation in color as *C. arctica*, from greenish in wet, sheltered sites to ± vinaceous or brownish black plants from exposed places. Size of cortical stem and leaf cells should give a reasonably clear distinction between the two taxa (as shown

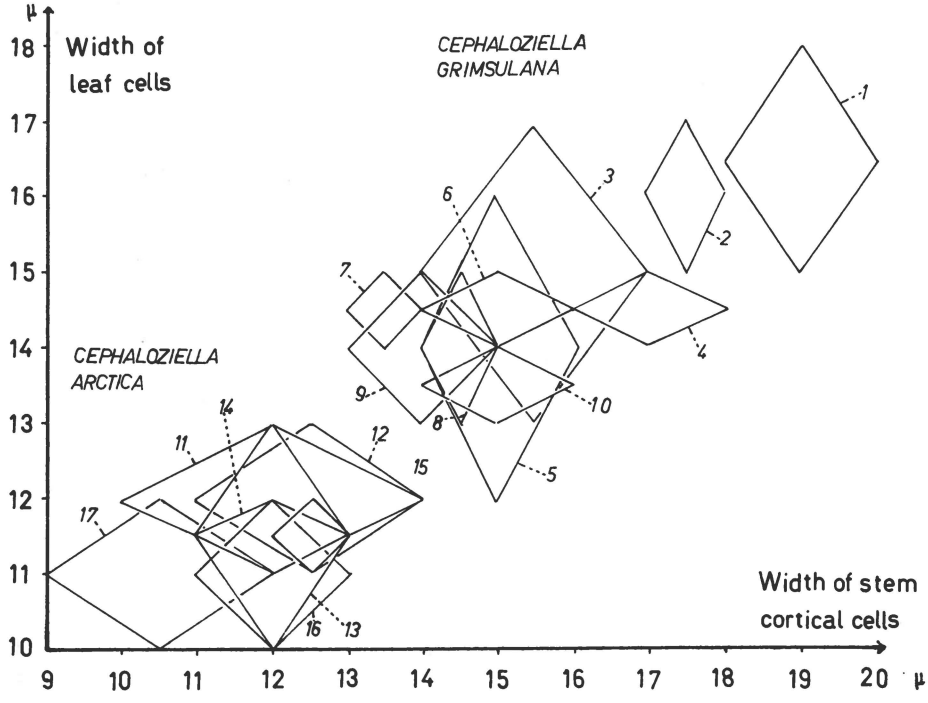


Fig. 31. See also p. 334, Table VIII.

in the diagram, Fig. 31). It seems possible, however, that *C. grimsulana* represents merely a polyploid variety of *C. arctica*.

Only in the Søndre Strømfjord plants of *C. grimsulana* (66–0089) were perianths common. ♀ Bracts show stronger dentition than is normal in *C. arctica*, often with some teeth recurved, and the perianth mouth with long, narrow cells, which, at their tips, are like finger-like protrusions. In *C. arctica* the bracts are often dentate but the dentition is not as strong and the teeth not as long as in 66–0089. The perianth mouth cells in *C. arctica* can be long and narrow, but they are connate to virtually their tips, forming a crenulate mouth. Perianths of *C. grimsulana* from the Thule area (RMS 45.551 c) show the same ciliolate mouth as the plants from Søndre Strømfjord, although the dentition of the ♀ bracts is not as strong.

The specimen from Hareøen (70–2606) falls under *C. grimsulana* on the basis of cell measurements, yet these lie at the lower end. The perianth mouth of this specimen shows transition between that of *C. grimsulana* and that of *C. arctica* in having a mixture of narrow cells which are free and protuberant at the ends, and shorter cells, which form merely crenulate mouth sectors. Bracts in this case are dentate, with rather strong teeth. In typical *C. arctica* the perianth mouth often consists of a mixture of narrow and wider cells. As the perianth becomes older and more mature

Table VIII: *Cephaloziella arctica* (11–17) and *C. grimsulana* (1–10)

	Width of leaf cells at base of lobes μ	Width of stem cortical cells on sterile stems μ	Terminal cells of perianth mouth μ	Gemmae size μ
1. Kangersuneq 70–3150b	(14) 15–18 (20)	(16) 18–20 (21)		
2. Sarfaq 70–2336b	(13) 15–17 (18)	(16) 17–18 (20)		10–18×15–23
3. Hollænderb. 66–1507a	(12) 13–17 (18)	(13) 14–17 (18)		18–26×26–31
4. Hollænderb. 66–1512a	(13) 14–15 (17)	(15) 16–18 (20)		17–18× 18–29*
5. Søndre Strømf. 66–0089	(11) 12–16 (17)	(13) 14–16 (17)	10–18×44–66	10–15×21–26
6. Kronpr. Ejl. 70–2079a	(13) 14–15 (16)	(13) 14–16 (18)		12–14× 21–24*
7. Umiasugssûp 70–2944	(13) 14–15 (16)	(12) 13–14 (15)		
8. Sarfaq 70–2320c	(12) 13–15 (16)	(13) 14–15 (16)		13–18×18–26
9. Hareøen 70–2606	(12) 13–15 (16)	(12) 13–15 (16)	11–13×23–39(42)	
10. Pâkitsup 70–2314	(12) 13–14 (15)	(12) 14–16 (17)		
11. Tupilak 66–0030	(10) 11–13 (14)	(9) 10–14 (15)	8–11×21–34	
12. Søndre Strømf. 66–0070	(10) 11–13 (14)	(10) 11–14 (15)	8–10×18–36	10–13×16–23
13. Godhavn 66–0279a	(8) 10–13 (14)	(10) 11–13 (14)	5–13×21–52	
14. Qôrorssuaq 70–2472a	(10) 11–12 (13)	(10) 11–13 (14)		
15. Perdlertut 70–2678	(10) 11–12 (14)	(11) 12–13 (14)		21–26×31–34
16. Eqe 66–0290c	(9) 10–12 (13)	(9) 11–13 (14)	5–10×20–36	
17. Pâkitsup 70–2271	(9) 10–12 (13)	(8) 9–12 (13)	8–11×20–42	

* measured from living plants.

the narrow cells especially become longer and narrower, to form the plicate sectors of the perianth mouth. The longest cells may, exceptionally, become 6–7× as long as wide, just as in *C. grimsulana*, but the mouth is never adorned with projecting, finger-like protuberances formed by the free ends of the long perianth mouth cells.

Order ***Metzgeriales***

The *Metzgeriales* are very poorly represented in Greenland, with only four species locally. *Moerckia blyttii* occurs in one locality at the extreme south of Greenland, and *M. hibernica* var. *flotowiana* has been reported from northern Ellesmere Island (SCHUSTER *et al.*, 1959); also plants that seem similar to *R. palmata* have been found in the Inglefield Bredning area (RMS); the taxonomic problems with these last plants are acute, however, and they are being reported on elsewhere. Finally, *Pellia neesiana* occurs in South Greenland.

Clearly the *Metzgeriales* are, by and large, not cold-adapted plants. They also are apparently always devoid of sporophytes regionally.

Family ***Blasiaceae*** DUMORT.

Blasia L.

Blasia pusilla L.

Distribution (Map 75)

23: Kangersuneq (70–3150a). 43: Kangerdlugssuakavsak (66–1281a, 66–1290, 66–1304). 46: Qalatôq (66–1101, 66–1124, 66–1142).

B. pusilla has a rather wide range in Europe and North America, but mostly under temperate to boreal conditions. The present reports are the northernmost ones of the species; it is distinctly rare locally, but found southward in North America to California and, in the east, as a rarity to northwest Florida. In temperate areas it very freely produces both sporophytes, in the spring, and, all season long, gemmae. Gemmae of both the ovoid type, formed in "flasks", and surface gemmae of the stellate type are known; we have seen only the latter type in our plants, which are all sterile.

Blasia occurs in West Greenland most often on fine, silty, water-deposited soils. It may occur on damp, silty-sandy "rock meal" exposed with the drop in water level of shallow lakes, then associated with *Cephaloziella grimsulana* and *Scapania irrigua rufescens* (70–3150a). Perhaps more often it occurs on damp, exposed soil along small rills, where sheltered and kept damp; then it may occur (66–1290) with *Cryptocolea imbricata*, *Nardia geoscyphus*, *Solenostoma pumilum*, and *S. sphaerocarpum*—all taxa which often are found on damp, fine-textured mineral soils low in organic content. The species not only grows in few localities, but seems distinctly rare even when found. At Ivnarssuaq, for example, it occurred as a mere trace.

Family ***Aneuraceae*** (NEES) KLINGGR.

Riccardia S. F. GRAY

Riccardia sinuata (DICKS.) TREV.

Distribution (Map 72)

6: Eqalúnguit (70–2227f, 70–2238c). 11: Qasigíssat (70–2742). 15: Kronprinsens Ejland (70–2074, 70–2117). 17: Tupilak (66–0104b). 19: Nûk (70–2871c, 70–2873, 70–2836a, 70–2877e, 70–2879a). 26: Pâkitsup ilordlia (70–2297, 70–2383a). 48: Amitsup (66–0798, 66–0802, 66–0816). 51: Simiútap kûa, shore (66–0914d).

Additional collections:

17: Tupilak (K.H. 16.989). 24: Jakobshavn (S.B. 1870). 57: Nipisat (K.H. 14.189b).

This species appears to have an extraordinarily wide range in the northern hemisphere, in both Europe and North America, going southward in North America as far as southwest Mississippi and Louisiana; it recurs in eastern Asia and (supposedly) Micronesia. It is rarely very common in temperate sectors of North America but appears to be quite frequent under helophytic conditions in Greenland, occurring from as far south as Tasermiut Fjord (60°05′N.) where it was collected by VAHL in August, 1829 (VAHL 205; this specimen published by LANGE & JENSEN, 1887 as *Aneura multifida*), north to the Inglefield Bredning area (ca. 77°30′N.). Sterile traces of what we regard as this species have also been seen in HOLMEN (6326 and 7472c) collections from Peary Land (81° 48′N.).

Plants we refer to *R. sinuata* regionally usually grow as helophytes, often amidst *Sphagnum* (or sometimes also *Aulacomnium*), usually in boggy fens or moory meadows which are interspersed with shallow pools or tarns; they usually occur at the edges of tarns. Associated are commonly *Calypogeia sphagnicola* (in 70–2117, 70–2873, 70–2871c, 66–0104b), *Lophozia kunzeana* (66–0104b, 70–2074), *L. excisa* (70–2074, 70–2836a), *Cephalozia pleniceps* (70–2074, 70–2871c), *Cephaloziella subdentata* (70–2871c) or rarely *L. opacifolia* and *Scapania hyperborea* (70–2836a).

The species also occurs, however, in gently sloping, richly vegetated areas, at times in sites irrigated with Ca-enriched flowing water, associated then with Ca-tolerant taxa such as *L. elongata*, *L. grandiretis*, *L. latifolia*, *L. ventricosa confusa*, *Pleuroclada albescens*, *Blepharostoma trichophyllum brevirete*, and *Anastrophyllum minutum* (70–2227f). It may also occur over damp, sandy-peaty depressions along lake shores, with *L. quadriloba*, *Odontoschisma macounii*, and *Cephalozia bicuspidata*, in weakly Ca-enriched sites, judging from the association with *Pinguicula vulgaris* (70–2297). In rich fens, with interspersed tarns and irrigation (from localized basalt dikes, in otherwise gneissic regions, as at Nûk), plants provisionally referred to *R. sinuata* occur amidst *Drepanocladus*, with an anomalous

admixture of Ca-tolerant or demanding taxa such as *O. macounii*, *C. pleniceps*, *L. grandiretis*, *L. rutheana*, *L. opacifolia*, and *Aneura pinguis*, and Ca-intolerant taxa such as *C. bicuspidata*, *L. binsteadii*, *Calypogeia sphagnicola*, *Mylia anomala*, and *Gymnocolea inflata* (70–2877e, 70–2879a); these plants may approach *R. latifrons* in lacking oil-bodies in all cells.

Finally, the species may occur on mucky, wet ground around shallow, calcareous lakes, as at Umiarfik Fjord (66–0914d), associated with *Cryptocolea*, *L. rutheana*, *L. heterocolpos*, *L. grandiretis*, *L. gillmani*, *L. quadriloba*, *O. macounii*, *A. pinguis*, and *Tritomaria quinquedentata*—all taxa that are either Ca-demanding or Ca-tolerant. *R. sinuata s.l.*, thus, is locally very much Ca-tolerant and thus seems to have a highly "expanded" ecological tolerance compared with populations from temperate regions. The species has been reported once from over calcareous shale in central New York (SCHUSTER, 1949).

R. sinuata s.l. is not only ecologically "different" in the Arctic, but also differs cytologically and morphologically. It occurs typically in West Greenland as light green, pigment-free, broad, closely once-pinnate (or pinnatifid—the "pinnae" are often so short they seem to be mere broad, dilated lobes on the margin of the thallus) phenotypes. In these one may look in vain for either epidermal or hypodermal oil-bodies (as, e.g., in 70–2879a and 70–2877), but other collections, seemingly morphologically identical, possess, in anywhere from 1–5% or more of epidermal cells, a grayish, granular oil-body of rather small size (ca. 7–7.5×8–10 μ); all hypodermal cells seem to have a single oil-body, similar but often a little larger (ca. 9×10–12 μ, up to 10×14 μ). Such phenotypes typically grow admist *Sphagnum*, usually associated with *Mylia anomala*, *Calypogeia sphagnicola*, *S. paludicola* and/or *S. hyperborea*, and *Cephalozia pleniceps*.

Similar phases may occur, however, in areas with a little basic seepage, on wet muck at tarn margins, associated with *O. macounii*, *L. rutheana*, *A. pinguis*, *C. pleniceps* (in 70–2879a). Then we may find: (1) The broad phenotype, contiguously pinnatifid with abbreviated "pinnae" that are broad, contiguous, irregular, and variable in length; the main axes of such plants are dilated, often concave antically, thin on the margins, ca. 800–1800 μ broad; no oil-bodies could be found in such phases. (2) Under more exposed conditions, adjacent, what seems to be the same plant (and what we think is a mere environmental phase) may be much more like "normal" *R. sinuata:* freely, rather remotely 1(2)-pinnate, with linear distant branches, and main axes flat or slightly convex, only 400–475 μ wide, blunt on the margins. Such phases have oil-bodies in a majority or almost all epidermal cells and, seemingly, in all hypodermal cells. Cell walls may be distinctly brown-pigmented.

The "broad phenotype", oil-body free even in shoot apices (as in 70–2877) may be so very variable as to defy description. Basically there

is a single, band-shaped, broad, main axis, quite flat usually both dorsally and ventrally, and with blunt, never unistratose margins. This axis bears close to juxtaposed lateral branches, or pinnae, many or most of which may remain very abbreviated, in which case we get the irregularly pinnatifid aspect alluded to earlier. Deviations from this type, however, are frequent: one or several lateral pinnae may grow out, broaden, and pinnatify. Also, we find two types of additional lateral branches: (a) narrow, colorless, rhizoid-bearing, geotropic lateral pinnae, elliptical in cross section, which form stolons; these rarely, if ever, branch; (b) sexual branches. Often the gynoecial branch is an almost sessile lateral projection, covered and fringed with filiform paraphyllia amidst which the several archegonia occur. Occasionally an archegonial branch is stalked, and, rarely, an elongated archegonial branch occurs which is fertile along the whole dorsal surface and which may bear 6–8 archegonia oriented roughly in two rows (thus simulating the antheridial branch, except that lateral paraphyses are present). Antheridial branches, which may arise from stoloniform lateral branches, or in pairs or even triads from the main axis, are usually narrow and of limited length; they may be sessile, or the fertile portion may be ± stalked. Antheridia are usually in 6–8 pairs, in 2 rows, seemingly sunken in the dorsal face of the branch. Rarely a pair of androecial, linear branches may occur with a gynoecial, almost sessile branch in the notch between them. We have, however, never seen synoecious inflorescences such as often occur in *Riccardia multifida.*

One other peculiarity of the "broad" phenotype deserves mention: near the apices of some shoots, lateral rhizoids, often ramified distally, may occur, arising from marginal cells. This was also noted for *Riccardia* cf. *multifida* (SCHUSTER, 1966, fig. 44:13, as *R. latifrons*).

A large specimen from Narsalik (leg. DAMSHOLT) is of the utmost interest in that it represents a form with relatively fleshy main axes and limited development of smaller secondary branches—perhaps an ecotype adapted for growth under Arctic conditions. Other specimens almost all show much the same type of branching—with an unusually broad and thick "trunk" and rather slight branching, much less regularly pinnate than in *R. sinuata* of temperate climates. The main "trunk", which is planoconvex or even concave dorsally may be 1300–1500 (1700) μ wide (with the whole plant, including the limited, short, blunt, lateral branches, only 3500 μ wide). The leptodermous epidermal cells are ca. 25–35 × 50–95 μ to (70–2297) only 18–25 × 50–65 μ. Yet, on all of the Greenland collections except one from S. Greenland (Amitsuarssuq) we could definitely find autoecious inflorescences; the thallus margins were never unistratose for more than 1–1.5 cells on the ultimate branches and these did not show the "*multifida*-type" crenulation. On that basis none of the Greenland plants seem referable to *R. multifida.*

We have tried to "wedge" our material into two or more species, but this seems impossible. If only oil-bodies are used as a criterion, our plants would key in part (e.g. 70–2879a, 70–2877e) to *R. latifrons* in the key in LITTLE (1968); others, on the basis of oil-bodies in under 5–10 % of epidermal cells would be sought under *R. multifida*, and still others, in which most or all epidermal and all hypodermal cells bear oil-bodies, would "key" to *R. sinuata* in the LITTLE key. It is possible that the plants which lack oil-bodies entirely and which represent the "broad phenotype", should all be cited under *R. latifrons*, but we suspect that, more likely, hygrophytic extremes of *R. sinuata* are at hand. In any event, it is impossible to equate the observations and key of LITTLE (1968) with the Arctic plants here reported. Furthermore, even when oil-bodies are present, they never appear to exceed $10 \times 14\ \mu$ in hypodermal and $7.5 \times 10\ \mu$ in epidermal cells, while LITTLE states they are as much as $8–15 \times 9–20(35)\ \mu$ in British plants of *R. sinuata*. The situation with regard to these taxa thus remains much more complex than LITTLE's account would indicate. He also points out that the chromosomal situation is more complex than previously assumed. Initially (MÜLLER, 1951–58) *R. sinuata* was separated by the chromosome number, n=30, from *R. multifida*, n=20. British plants of *R. sinuata*, however, have n=20.

There are no chromosome counts of our plants; a count of plants from Inglefield Bredning, which seem to correspond reasonably well with *R. palmata* (and are sterile), yielded n=10 (±1). Capsules are not known from any Greenland collection, nor have gemmae been seen. Under these conditions, placing all demonstrably monoecious plants without unistratose thallus margins in *R. sinuata* seems to be the only rational procedure at present.

Aneura (DUMORT.) DUMORT.

Aneura pinguis (L.) DUMORT.

Distribution (Map 72)

6: Eqalúnguit (70–2248). 7: Angûjârtûtit (70–2159, 70–2174a). 14: Hareøen (70–2593a, 70–2609). 17: Tupilak (66–0026, 66–0105, 66–0113). 17A: Egedesminde (66–0943). 19: Nûk (70–2876, 70–2879a). 30:Eqe (66–0289, 66–0294). 34: Marrait kangigdlît (66–0726). 36: Umanak (66–1488). 51: Simiútap kûa, shore (66–0916c, 66–0937).

Additional collections:

1B: Lyngmarken, Engelskmandens Havn (M.P.P. 1546). 17: Tupilak (K.J. 1455). 57: Nipisat (K.H. 14.189). 88: Christianshåb (K.H. 15.713). 91: Itivdliup ilua (S.B. July 1870). 92: Claushavn (S.B. July 1870). 106: Nûgssuaq (K.H. 15.636, 15.646). 126: west of Sarqap taserssua (K.H. 13.420). 147: Amitsoq (K.H. 14.649).

A. pinguis is one of very few almost cosmopolitan *Hepaticae*. It occurs as far north as Peary Land, 82°14′N. (HOLMEN 64536) and Alert, Ellesmere Island, 82°32′N. (SCHUSTER *et al.*, 1959) and southward to Campbell

Island (RMS) some 350 miles south of New Zealand; it also occurs in many or most temperate and tropical areas between, wherever moisture conditions are adequate. Biologically, a series of at least subspecies or ecospecies is surely involved, but the morphology of the plant is so highly simplified that no taxonomic recognition of infraspecific taxa is currently feasible. Furthermore, the diagnostic capsule wall anatomy seems uniform, at least judging from comparison of material from Europe, North America, and Taiwan.

As thus broadly delimited, *A. pinguis* is Ca-tolerant and often found in highly calcareous areas, it is usually rare or infrequent in strongly acidic sites (and we suspect that in many of the gneissic areas it exists because of local, Ca-enriched seepage from basalt dikes). Such an occurrence is that at Nûk (70–2879) where it is found in a rich, peaty fen, with interspersed shallow tarns, mixed with *Lophozia rutheana*, *Odontoschisma macounii*, and *Cephalozia pleniceps*—all Ca-tolerant or "demanding"—and *Gymnocolea inflata*, which is usually confined to oxylophytic sites. In the same locality, where subject to inundation on mucky, peaty soil, it grows with *Scapania hyperborea* and *Cephaloziella* cf. *byssacea* (70–2876). Analogous are occurrences on insolated ledges over thin, peaty soil, where irrigated, often partly submerged in rills and drainage channels; associated (Tupilak; 66–0105) may be *Tritomaria polita polymorpha* and *Gymnocolea*. More typically the species is found on moist, fine-textured, loamy or clayey soils along rills or streams in areas with basic seepage, associated with *L. quadriloba*, *T. heterophylla*, *O. macounii*, *Cryptocolea imbricata*, *L. heterocolpos harpanthoides*, *Anthelia*, *Blepharostoma*, and other species (66–0289), or on moist, irrigated, richly vegetated slopes (70–2248), with *O. macounii*, or (70–2609, 70–2593 a), with *L. heterocolpos*, *L. quadriloba*, *Cephalozia pleniceps*, *Anastrophyllum minutum grandis*, *Plagiochila asplenioides*, and *T. polita polymorpha*.

The plants from Eqe (66–0294) occurred as a compact, very fleshy phase with rounded, thick margins; associated was an unusual series of Ca-tolerant taxa: *L. quadriloba*, *Anomomarsupella cephaloziellioides*, *S. degenii*, *Cephaloziella arctica*, as well as *Marsupella revoluta*. The species, however, also occurs in igneous rock areas in the Arctic (as, e.g., at Egedesminde; 66–0943), among *Sphagnum* at the edges of acidic tarns, associated with *Cephalozia pleniceps*. Even here, however, there may be traces of Ca from neighboring basaltic dikes. Similar phenotypes occur at Eqalúnguit (70–2248), with narrow thalli and tumid margins. The species, however, is also found regionally as a broader form, with the thallus 15–16 cells high in the middle, but the margins thin and unistratose for a width of 4–5 cells (70–2159; Angûjârtûtit, edge of a "warm spring").

Arctic phases are often rather different from "normal" temperate-zone phenotypes. ♂ Plants (as e.g., in the Tupilak plant) may have very

short androecia, with sharp, erect, or even slightly antically connivent "flanks"; the androecia are also usually single (rarely a pair from a common base, never in groups of three, and never linear), the thalli seemingly pinnulate with these very short, compact androecial branches.

We have seen ♂ plants and (questionable) young gynoecial plants, but never any evidence of sporophyte production in the West Greenland plants; all agree in possessing numerous, very small oil-bodies per cell, ranging mostly from 2.2–3.5 μ; they are almost homogeneous but (under oil-immersion) are faintly to clearly papillose-botryoidal and occur mostly 12–40 per cell. Some cells, however, appear to have only 8–11 oil-bodies each. We have seen no material with the oil-bodies "4–6(9) μ" in diameter, as described by LITTLE (1968) for British plants.

Cryptothallus MALMBORG

Cryptothallus mirabilis MALMBORG

Distribution (Map 72)

1B: Lyngmarken, Engelskmandens Havn (P. MILAN PETERSEN, 1971).

This remarkable taxon, the only echlorophyllose bryophyte known, has been previously known only from northern (and? central) Europe: Britain, Denmark, Sweden, Norway, and (doubtfully) Austria. The above is the only station known from the western hemisphere and the only station known from the Arctic. *C. mirabilis* typically grows in moist heaths or mires, often under mats of *Mnium* or *Sphagnum*, usually occurring as individual plants or in small, gregarious colonies. Owing to the fact that the spore tetrads do not separate, or do so only tardily, ♂ and ♀ gametophytes are usually found together, much as in *Sphaerocarpos* spp. The fleshy, brittle, and often irregularly pinnate ♀ thalli may have the pinnae mostly remaining very short and the thallus is then merely pinnatifid in aspect; ♂ plants are much smaller and typically much more clearly pinnate, with slenderer, longer pinnae.

The distribution of this plant in Greenland remains conjectural; because of its subterranean growth most bryologists (ourselves included) have not made the systematic search needed to find the species; it is no accident that the sole collection reported above (see PETERSEN, 1972) was made by a mycologist.

Order ***Marchantiales***

The *Marchantiales* are—considering the high latitude—surprisingly well represented in West Greenland, with 12 species known. This, to a large extent, reflects the high incidence of calcareous or basaltic habitats. Even in areas with acidic rocks, as at Eqe, basalt dikes are frequently

found. By contrast, in the northwest Greenland flora, from 75–78° N., there are only two taxa present *(Marchantia alpestris*, *Riccia sorocarpa)*, reflecting the presence of prevailingly noncalcareous rocks (SCHUSTER, in prep.).

Although the *Marchantiales* are seemingly rather well known, we find that most statements in the literature derive from a copying and recopying of data found in MÜLLER (1905–16) and MASSALONGO (1916); there has been relatively little attempt to study copious living material, especially as regards the patterns of variation, and the perimeters of variability. For this reason detailed notes are given under most of the species, based in almost all cases on study of fresh material.

Family *Aytoniaceae* CAVERS

Mannia CORDA

Mannia fragrans (BALB.) FRYE & CLARK (Table X)

Distribution (Map 73)

31: Anap nunâ (70–2413, 70–2426). 44: Akuliarusikavsak (66–1326). 53: Søndre Strømfjord (66–0038, 66–0040, 66–0042, 66–0047, 70–3200, 70–3201, 70–3202, 70–3203, 70–3204).

Additional collections:

53: Søndre Strømfjord (K.H. 4406, 4453c).

A species of strikingly southern affinity, occurring in North America southward to Georgia, Alabama, and Texas; the southernmost station appears to be in Big Bend Park, Texas (RMS, *s. n.*), on the Mexican border. Northward it is distinctly rare, found in Quebec at a single station along the Vermont border (RMS, *s. n.*) and is not at all known from maritime Canada or Maine (the distribution map in SCHUSTER, 1958; fig. 40, does not include the recent collections from southwest Texas, Quebec, or West Greenland). It then reappears as a total disjunct in East Greenland, the Scoresby Sd. area, and in an equally limited area in West Greenland. The range is from 66°50′ to ca. 71°00′ N. The presence of a heliophilic xerothermophyte like *M. fragrans* as a disjunct in Greenland raises many phytogeographic questions. Is the species a Tertiary relict there, or is it a post-Pleistocene migrant? It seems probable that the latter must be the case; the occurrence in areas like Søndre Strømfjord of taxa like *Sisyrinchium*—temperate American genera that could not conceivably have survived the Pleistocene in Greenland—suggests that the *Mannia* is also a recent migrant.

M. fragrans is limited to relatively continental sites; in West Greenland it is known from three stations, all lying within ca. 10–12 miles of the Inland Ice, in regions with an unusually high incidence of sunlight. Here the plants occur strictly on exposed, warm, south-facing slopes

which get maximal insolation. The plants are subject to frequent desiccation and we may have overlooked them for this reason. Dry patches are usually readily recognized because of the conspicuous tuft of white *paleae* at the thallus apices—at least at the tips of potentially fertile segments. The species usually occurs in clearly basic sites. At Søndre Strømfjord it was abundant on a steep, south-facing slope, on soil over exposed ledges along a temporary rill, associated with *Saxifraga aizoides*, *Rhododendron lapponicum* and other taxa of basic sites. It is often found in pure patches, but may occur with *Peltolepis*, *Athalamia*, and/or *M. pilosa*.

The Greenland plants from both west and east coasts show some points of divergence vis à vis plants from temperate to warm-temperate regions. The collection of HOLMEN 4453c is of interest on several counts. Firstly, the apical "beard" of hyaline scale appendages, although quite distinct, is less marked than in non-Arctic phenotypes. Secondly, the dorsal epidermis has extraordinarily thick-walled cells, with large, confluent trigones—so that the lumina are droplike. Thirdly, the only antheridia seen occurred below a fork in a thallus and were diffuse (as figured for the species in SCHUSTER, 1953), but each antheridium lay beneath an almost finger-like ostiole. Such ostioles—much lower than, but reminiscent of those of *Athalamia*—have not been seen in any other *Mannia* collection. Future study may show that taxonomic recognition of the Greenland phenotypes is necessary.

The collection of HARTZ (1892, from Hekla Havn), however, has the "beard" magnificently developed, much as in plants from temperate climates. It has the very high cross section, with very high and narrow, almost canal-like air chambers figured for var. *alpina* MEYL. by MÜLLER (1951–58, fig. 60, c), and the exceedingly thick-walled epidermal cells of that variety (also as figured by MÜLLER, *l.c.*, fig. 60, h–i). JENSEN (1897, p. 368) referred this plant to *Grimaldia fragrans* (as occurring with *Desmatodon leucostoma*, *Bryum argenteum*, *Pohlia nutans* forma). It would appear that var. *alpina* Meyl., if representing a genotypically distinguishable form, must be a synonym of var. *convoluta* Nees. The other collection from Kobberpynten, Scoresby Sd., is, we think, quite identical. It also has only "diffuse" androecia—consisting of several scattered antheridial chambers with low, pigmented ostioles in a line along the thallus midline. A single carpocephalum was found, of quite typical form, with a conspicuous apical "beard" at the summit of the stalk. In all Scoresby Sund collections thallus margins are strongly ascending and the thallus cross section forms a pronounced V. This is particularly true of plants from Gåsefjord, in which the thallus forms a very narrow and sharp V and is provided with a prominent, acute keel below—typical of the var. *convoluta* NEES (=*alpina* of MEYLAN).

Sterile *M. fragrans* is rarely difficult to separate from *M. pilosa*. The former is usually at once distinct in the more intensely red-pigmented ventral scales which bear many oil-cells each (usually 7–20 per scale; individual scales rarely with fewer oil-cells), and in the wider, 5–7 mm broad thalli. *M. fragrans* also has smaller spores, usually 62–73 μ in maximal diam. Occasional specimens may present problems because of the form and position of the androecia. Thus in 70–3200 a leading thallus with an apical gynoecium bore short lateral branches, one of which developed a normal, discoid androecium distally—but the other had diffuse antheridial ostioles—the antheridia not being united into a receptacle. Also, at times, such plants with lateral antheridial branches and terminal gynoecia of the main thallus may bear subfloral innovations—and these may bear paired and almost juxtaposed subreniform antheridial disks. The species thus is considerably more variable in both form and position of androecia than the literature suggests (although the "diffuse" type of androecium in Minnesota material is discussed and illustrated in SCHUSTER, 1953).

Mannia pilosa (HORNM.) FRYE & CLARK (Tables IX & X)

Distribution (Map 73)

31: Anap nunâ (70–2404, 70–2423). 34: Marrait kangigdlît (66–0740, 66–0767). 38: Uvkusigssat (66–1384). 39: Tasiussaq (66–1247). 40: Mârmorilik, head of the Fjord (66–1162, 66–1200). 42: Magdlak (66–1357). 43: Kangerdlugssuakavsak (66–1288, 66–1295). 49: Skalø (66–1002). 50: Simiútap kûa, valley (66–0863). 53: Søndre Strømfjord (66–0041, 66–0045, 66–0047, 70–2002).

Additional collection:

44: Akuliarusikavsak (K.H. 16.787).

M. pilosa is infrequent but not rare in West Greenland. A low Arctic and subarctic species, found southward to northern Vermont, and (in the Great Lakes region) to southernmost Minnesota, where it occurs as a Pleistocene relict in deciduous forest. Except for scattered sites in Alaska-Yukon, the Cordillera along the Alberta-British Columbia border, and southern Ellesmere Island, known only from stations in East and West Greenland where it extends north only to ca. 70–72° N. Limitation to distinctly basic sites obviously restricts the areas which are "open" to the species.

M. pilosa, being bound to Ca-enriched loci, usually occurs on thin soil over calcareous ledges, at times on south-facing, steep slopes, where subject to strong desiccation, along temporary rills, and then with *M. fragrans* (Søndre Strømfjord; 66–0047, 70–2002); such phenotypes may approach "*Mannia sibirica*". Or, at the same site (66–0041), it may grow on vertical faces of ledges where partly sheltered and less subject to desiccation, then mixed with *Solenostoma pumilum polaris*. At the oppo-

site pole are occurrences adjoining waterfalls, on small, soil-covered "shelves" on rock walls, associated with a series of calciphilous mesophytes such as *Lophozia badensis*, *Scapania gymnostomophila*, *S. cuspiduligera*, *Preissia quadrata*, *Tritomaria scitula*, *Plagiochila asplenioides*, *Solenostoma pumilum polaris*, *Athalamia hyalina*, and *Sauteria alpina* (Magdlak; 66–1357). Such phenotypes have essentially leptodermous cells of the dorsal epidermis and constitute "typical" *M. pilosa.*

The more leptodermous phases, without strikingly thick-walled epidermal cells and with large spores (75–85 μ, rarely larger) normally either lack oil-cells in the ventral scales (66–0041, 66–0047, 66–1357, 70–2404) or occasionally have 1–2 oil-cells in some ventral scales, none in others (66–0045, 70–2423). These plants, which constitute "typical" *M. pilosa*, have relatively loosely organized photosynthetic tissue, with large air chambers only slightly and partially subdivided by secondary plates or teeth; the air chambers occupy ca. 0.6–0.7 the height of the thallus along the ventral keel and the thallus is usually not sharply costate ventrally [exactly identical to such plants, especially in spore size, "75–85 μ in diam." is *Neesiella carnica* (Mass.) Schiffn. *(Grimaldia carnica* Mass.*);* see Massalongo, 1916, p. 727, pl. XV]. "Typical" *M. pilosa* is perhaps nothing more than a phase of the species *s.l.*, of less exposed sites. We have seen several other Greenland collections that fall within this general phenotype. Three Greenland collections illustrate the perimeters involved:

(1) Holmen 16.787 seems nearly typical; thalli in cross section have low ventral tissue and large, open air chambers not or feebly subdivided; the ventral tissue is only ca. 0.3–0.35 the height of the thallus or even less, epidermal cells are essentially leptodermous. Ventral scales, each with 1–2 appendages, usually lack oil-cells, but occasional ones have 1–2 per scale, very rarely have we seen scales with 7 and 11 oil-cells each. Median cells of the ventral scales are 24–34 × 95–168 μ, and are thus typical; the spores are very large, 73–84 μ in diam.—and thus typical.

(2) Holmen 18.075b represents a mesophytic extreme, with very large and high aerenchyma tissue, the air chambers empty and hardly subdivided. Associated with this are unusually large ventral scale cells and ventral scales which normally lack oil-cells, although single ones sometimes occur. The Hartz collection from Kobberpynten resembles that of Holmen 18.075b: epidermal cells are soft and leptodermous, the aerenchyma is high and consists of large chambers which lack accessory walls or lamellae; the ventral tissue is poorly developed and often only 0.2 the height of the thallus medially. Ventral scales lack oil-cells and in the middle are of large cells, ca. 24–35 × 68–90(132) μ.

(3) Plants from Røde Ø (Hartz, 1892) are unique. Thalli are sometimes linear and sterile, sometimes repeatedly gynoecial at the tip, with a cuneiform and soon again fertile apical innovation. Some plants show

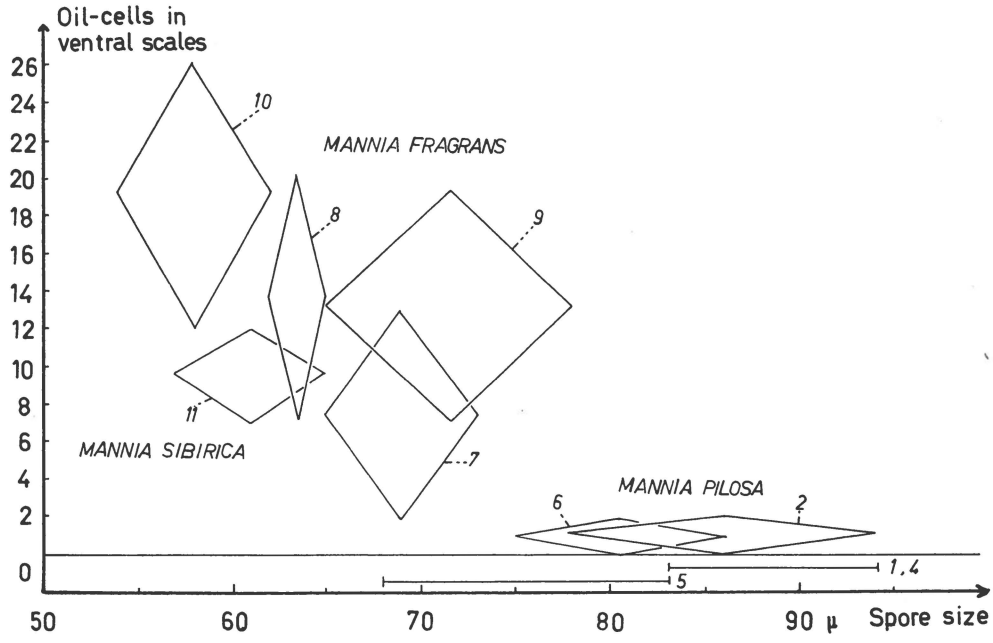


Fig. 32. [*M. pilosa*, 1–2, 4–6; *M. fragrans*, 7–9; *M. sibirica*, 10–11].

such repeated innovation that, as in *Plagiochasma cuneatum*, a series of short, wedge-shaped segments results, from the sides of which many small ventral ♂ branches are produced. The segments are narrow, high, with the aerenchyma laterally compressed so that the air chambers are unusually high and narrow. The thallus surface is often decolorate, as are the margins—so that dry plants are chalk white. With age the delicate epidermis often ruptures, much as in *M. rupestris*. In the lack of free, dichotomous branching, the decolorate thalli, and the hyaline-tipped ventral scales, these plants are very unusual. Carpocephala are lacking; yet even without them it seems impossible to place the plants elsewhere. The ventral tissue is remarkably well developed, forming a rounded ventral keel, and may be as high as the aerenchyma—suggesting *M. sibirica*. Yet the leptodermous and often hardly persistent epidermis argues against this. So do the ventral scales, which lack oil-cells and have median cells (21)22–25×80–120 μ in size.

The collections cited above and the East Greenland collections, studied for comparative purposes, seem to establish the fact that there is a distinction between *M. pilosa* and the next taxon, *M. sibirica*, whereas "*Grimaldia carnica*" represents merely the mesic extreme of *M. pilosa*. The accompanying table (Table IX) compares these two taxa, including the type of *M. sibirica*.

Table IX. *Mannia pilosa* and *M. sibirica.*

	Ventral scales: Oil-cells	Ventral scales: Median cells	Spores
M. pilosa: Norway: Tromsö Amt, Nordreisen (Aug. 18, 1891, W. H. ARNELL)	Absent	24–32×60–130 μ	86–92(96) μ
Norway: Nordlands Amt, Salten, Sörfolden Dypirksfjeldet (HAGEN, Aug. 22, 1893)	Absent	25–33×65–135 μ	69–84 μ
E. Greenland: Scoresby Land, Mesters Vig (HOLMEN 18.075b)	Absent (rarely!)	(23)24–35×(75) 80–125 μ	(absent)
Sweden: Torne Lappmark Tjasinnjaska tjåkko (SAMMUELSSON, Aug.1916)	Absent	(23)24–32(33)× 84–130 μ	84–88 μ[1]) (only 4 seen)
W. Greenland: Akuliarusikavsak (HOLMEN 16.787)	Absent, to 1–2, rarely 7–11 per scale	24–35×95–168 μ	73–84 μ
M. sibirica: Norway: Lilleby, 60° N. (N. BRYHN, June, 1898)[1])	10–14(18) per scale	(12)13–18×(35) 45–65(84)μ	(52)55–60(62) μ
Type: (Siberia, Jenisei R.)	(3)8–14 per scale	14–18(19)×50–90 (100–110) μ	(60)62–70(72) μ
E. Greenland: Ella Ø (HOLMEN 18.840)	7–10 per scale	(12)13–17×(38) 48–72(75) μ	55–62 μ
W. Greenland: Søndre Strømfj. (M. LANGE 4448)	(2–4)7–12 per scale	15–21×45–72(80) μ	(48)57–62(65) μ
W. Greenland: Akuliarusikavsak (66–1326)	12–26	16–19×38–48 to 20–23×47–65 μ	54–62 μ
S. E. Minnesota	3–8 (or more)	13–17×32–60 μ	57–65 μ

[1]) Epidermal cells thin-walled!

Mannia sibirica (K. MÜLL.) FRYE & CLARK (Tables IX & X)

Distribution (Map 73)

44: Akuliarusikavsak (66–1326). 53: Søndre Strømfjord (LANGE 4448).

This controversial plant, retained as a species distinct from *M. pilosa* with many reservations (see detailed discussion in SCHUSTER, 1953) is known from a few stations in Scandinavia, Siberia, disjunctly in southeast

Minnesota, ?Alaska, and from East and West Greenland. LANGE 4448 is from the most continental part of Greenland. The plants are a xeromorphic form, with the epidermis atypical in that the cells are not only thick-walled (as is true of the type, and of the Minnesota material cited and figured in SCHUSTER, 1953) but bear prominent trigones at the angles —thus corresponding in this feature with the so-called *M. fragrans* var. *alpina* of MÜLLER. The plants are much smaller than in *M. fragrans*, however, are freely and relatively closely furcate, have the small discoid androecia of small ventro-lateral branches of the *M. pilosa-sibirica* complex, and lack the hyaline "beard" of ventral scales at the base of the gynoecial stalk, from the thallus apex. In cross section the aerenchyma is rather compact and the ventral keel angularly produced; at the deepest point the ventral tissue is fully as high as the aerenchyma layer. Spores are typical in size: 57–65 μ. As in *M. sibirica* (*fide* MÜLLER, 1951–58 and *fide* SCHUSTER, 1953) the deep purplish ventral scales bear conspicuous oil-cells which occur (2–4)7–12 per scale. Median cells of ventral scales are also quite small [15–21 × 45–72(80) μ]; these dimensions closely correspond with the type of the species.

The plants from Akuliarusikavsak (66–1326) grew on steep south- and southwest-facing, relatively insolated, warm ledges, with *Mannia fragrans* (also associated at Søndre Strømfjord and in Minnesota—although usually not immediately consociated; see SCHUSTER, 1953, who reports

Table X. *Mannia:* Species criteria.

	Thickening of epidermal cells ±	Ventral scales Oil-cells	Spore size (incl. wings)	Lateral ♂ branches
Collection				
1. 66–0041	–	0	83–91 μ	+
2. 66–0045	–	0–2	78–94	
3. 66–0047	–	0		
4. 66–1357	–	0	83–91	+
5. 70–2404	–	0	68–83	+
6. 70–2423	–	0–2	75–86	
7. 70–2002	+	2–13	65–73	–
8. 70–3200	+	7–20 (24)	62–65 (73)	–(+)[2]
9. 70–3204	+	7–19 (25)	65–78	–
10. 66–1326	+	12–26	54–62[1]	+
11. Lange 4448 .	+	(2–4) 7–12	57–65	+

[1]) Perhaps slightly immature, but sculpture complete and elaters mature.

[2]) Plus rare diffuse androecia of thallus surface.

1–6 *M. pilosa*, 7–9 *M. fragrans*, 10–11 *M. sibirica*

the two taxa admixed at Wacouta, Minn.); other associates were *Asterella ludwigii* and *Peltolepis grandis*. These plants (our observations are all taken from a single spore-bearing plant, in order to avoid possible confusion with admixed *M. fragrans* and *A. ludwigii!*) have a leathery dorsal epidermis, with thick-walled and strongly collenchymatous cells which average 17–19×17–24 μ; the ventral scales have median cells ca. 16–19× 38–45 up to 20–23×47–65 μ (but in the appendages cells are clearly wider, subisodiametric); ventral scales have up to 12–26 oil-cells each; spores (yellow, perhaps still slightly immature, although tetrads disjoined and elaters with spirals distinct) 54–62 μ. These criteria speak unambiguously for *M. sibirica*—especially the many oil-cells per ventral scale. Epidermal cells are firmer, with stronger collenchyma than in LANGE 4448 (here epidermal cells average 16–20×26–31 μ and are less thick-walled but with equally strong trigones, cell lumina being rounded), and oil-cells are more freely developed in the ventral scales. These observations give some—although surely not sufficient—support for the position of those (e.g., MÜLLER, 1951–58) who insist that *M. sibirica* is distinct from *M. pilosa*. By contrast, SCHUSTER (1953, p. 609) is sceptical, considering *M. sibirica* as probably a "xeromorphic modification".

These collections and the one from East Greenland (Ella Ø, Solitærbugt, 72°52′N., 25°10′W., HOLMEN 18.840) are the only Greenland collections we have seen that represent *M. sibirica*. As the associated table shows, these collections cannot be placed in *M. pilosa* if a distinction between *M. pilosa* and *M. sibirica* is to be maintained. Both LANGE 4448 and HOLMEN 18.840 have the typical *M. sibirica* thallus cross sections with high ventral tissue, a keeled thallus, and the aerenchyma tissue much subdivided and compact; in both the epidermal cells are thick-walled; in both the linkage of small spores (48–62 μ) and small cells of the ventral scales [13–21×(38)45–72(80) μ] occur, and the ventral scales have colorless, small, scattered oil-cells (Table X, and Fig. 32). These plants agree in all essentials with the type (and have been compared with it), possessing even smaller spores than syntypes of *M. sibirica* we have seen (Copenhagen). The only obvious "intergradation" appears to occur with HOLMEN 16.787 in which—depending on ventral scale studied—no oil-cells, 1–2 oil-cells, or rarely, 7–12 oil-cells may be found. Here, however, median cells of ventral scales and spore size, as well as the epidermal cells and the high aerenchyma tissue, all suggest we deal with "normal" *M. pilosa*. The linkage of the five species criteria is, thus, reasonably perfect (HOLMEN 16.787 shows this linkage except for variation in oil-cell number per ventral scale) over the range of more than a score of specimens studied. However, there is no absolute way in which we can separate *M. sibirica* from *M. pilosa* in the field.



Fig. 33. *Asterella saccata*. (1) Fertile plant, in dorsolateral profile (× ca. 5). (2–7) Ventral scales (× ca. 20). (8) Appendage apex of ventral scale (×95). (9) Cells, from marginal and intramarginal portion of basal half of scale (×95). [8, 9, drawn to 400 μ scale; all from material from Søndre Strømfjord, leg. LANGE].

Asterella BEAUV.

Asterella saccata (WAHL.) EVANS (Fig. 33)

Distribution

53: Søndre Strømfjord (LANGE 4077).

This species, of southern affinity, is not known from any other station in Greenland, and we have looked for it without success at the locality where LANGE found it, on at least three separate occasions. *A. saccata* has a peculiar distribution, mapped for North America in SCHUSTER (1958a, fig. 76; the Søndre Strømfjord locality was not then known).

The range is basically montane and Cordilleran, with a single relict station (in deciduous forest) in southeastern Minnesota. The existing range probably reflects a massive Pleistocene extinction of populations.

At the single Greenland station it is found with (and evidently growing under similar environmental conditions as) *Mannia fragrans*, *M. pilosa*, *Athalamia hyalina*, and *Peltolepis grandis*—and in the same general area (one of the few known stations in Greenland) where *Sisyrinchium* occurs.

The single Greenland collection is fertile and quite typical in the high conical carpocephala and the long, projecting ventral scales. When sterile, or with unfertilized gynoecia, very likely to be mistaken for *M. fragrans*. The LANGE collection is atypical in only one feature: antheridia occur in a poorly defined sessile group some distance behind the carpocephalum and are hardly defined—except for the high and conspicuous, tubular ostioles.

Asterella ludwigii (SCHWAEGR.) UNDERW.

Distribution (Map 74)

1A: Behind Arctic Station (70–2182). 1B: Lyngmarken (66–0560). 1D: Skarvefjeld (66–0297, 66–0315). 8: Kuánerssuit (70–2135). 9: Eqaluit (70–2789). 12: Perdlertut (70–2692). 31: Anap nunâ (70–2411). 34: Marrait kangigdlît (66–0745). 36: Umanak (66–1499). 37: Agpat (66–1420). 38: Uvkusigssat (66–1383). 39: Tasiussaq (66–1261). 43: Kangerdlugssuakavsak (66–1284). 44: Akuliarusikavsak (66–1327). 45: Sagdliaruseq (66–1067). 46: Qalatôq (66–1135). 48: Amitsup (66–1550). 49: Skalø (66–1001). 50: Simiútap kûa, valley (66–0861). 52: Umîarfik, Qôrnoq (66–0963).

Additional collections:

1B: Lyngmarken (J.V. Sept. 1834, L.K.R. July 1886, C.K. July 1897, K.H. & W.C.S. June 1962). 17A: Egedesminde (S.B. July 1870). 38: Uvkusigssat (K.H. & W.C.S. 62–1578). 44: Akuliarusikavsak (K.H. 16.787). 53: Søndre Strømfjord (LANGE 4169). 61: Taserârsuk (L.H. July 1932). 98: Sarqaq (J.V. 50). 106: Nûgssuaq (K.J. 69).

An almost strictly Arctic-alpine species, occurring in the New World south to northernmost Labrador and, as a gross disjunct, in the Lake

Superior region in Ontario, Minnesota, and Michigan, at a very few localities; it is much more common in montane sites in the west and has been regarded as a montane or alpine Cordilleran species (see map, fig. 58 in SCHUSTER, 1958a; the dubious Quebec occurrence, noted with a question mark, has been shown to be based on an old error). *A. ludwigii* is known north to Prøven (72°23′N.) in Greenland and north to Pond Inlet, Baffin Island in Canada.

A. ludwigii is a calciphyte and its range is conditioned by this. The species is most common on basalt cliffs, often on thin, soil-covered shelves or broken basalt detritus, but also occurs frequently on soil on rocky, calcareous slopes—often between boulders. It is most frequent in open, insolated sites which undergo periodic desiccation. Often growing without associated hepatics, it may, under unusually mesic conditions (as at Godhavn; 70–2182) grow mixed with *Tritomaria scitula* and *Scapania gymnostomophila.* In somewhat less sheltered sites it may be associated with *Peltolepis grandis*, *Sauteria alpina*, *Athalamia hyalina*, and *Preissia quadrata.*

Depending on degree of exposure, *A. ludwigii* shows much variation with regard to thallus characters and pigmentation. Plants are usually relatively compact and have broad purple margins and deep purple ventral scales. Associated with this, the small and often ill- or hardly-defined androecia—or scattered antheridial ostioles—behind the gynoecial stalk are deep purplish tinged as is the small circlet of small scales at the base of the carpocephalum stalk. In phases of exposed sites the carpocephala themselves may bear some purplish pigmentation; the pseudoperianth is usually bleached but occasionally weakly purplish tinted.

Thalli tend to be freely branched; each segment is short and distally rather copiously dilated; apical and sometimes ventral innovations are frequent. At least in Arctic plants fertile thalli, by the time spores are mature (late July-early August at the latitude of Disko), show much disintegration and fissuring of the dorsal epidermis; this appears to be the result of the severe winters. The pseudoperianth segments may then be shriveled and, in part, caducous; thus superficial examination results in confusion with *Mannia* (particularly *M. pilosa*), but *Asterella* lacks the small beard at the summit of the carpocephalum stalk and is paroecious rather than autoecious.

The plants of LANGE 4169 represent a deviant phenotype with wider than normal, strongly dilated thalli. Occasional gynoecial receptacles lack androecial papillae behind their point of insertion; the androecial papillae are isolated, never in disks or groups. The thalli are cuneately expanded distally and much thinner and wider than is normal, with very low but extensive, wholly empty and unsubdivided air chambers. Ventral

scales have little purplish pigmentation but are otherwise normal; they bear single, ill-demarcated tapering appendages; cells in the appendages are variable, irregularly quadrate to diamond-shaped, 36–40 × 40–60(80) μ; cells of the intermediate zone of the body are similar, 36–44 × 40–60 μ; cells of main portion of the body irregularly oblong, (24)25–32 × (52)60–105 μ. These plants are unusual in that unfertilized gynoecial receptacles, which remain sessile, become dorsal through the development of apical innovations which are relatively broadly continuous with the thallus.

Family ***Sauteriaceae*** EVANS

With the current version of the International Code of Nomenclature, the old, well-established family name *Cleveaceae* becomes suddenly invalid, since the type genus, *Clevea*, has been placed as a synonym of *Athalamia*.

Athalamia FALC.

Athalamia hyalina (SOMMERF.) HATT.

Distribution (Map 75)

1D: Skarvefjeld (66–0298, 66–0317). 8: Kuánerssuit (70–2146, 70–2152). 12: Perdlertut (70–2692, 70–2699). 31: Anap nunâ (70–2410a, 70–2418, 70–2433). 34: Marrait kangigdlît (66–0732, 66–0765). 38: Uvkusigssat (66–1382). 39: Tasiussaq (66–1247). 40: Mârmorilik, head of the Fjord (66–1160, 66–1200). 42: Magdlak (66–1357d). 50: Simiútap kûa, valley (66–0868). 49: Skalø (66–1005). 51: Simiútap kûa, shore (66–0827b). 53: Søndre Strømfjord (66–0038, 70–2001, 70–3207, 70–3205, 70–3208, 70–3209).

Additional collections:

1A: Behind Arctic Station (L.H. July 1932). 40: Mârmorilik, head of the Fjord (K.H. 14.605a). 59: Kvannit (K.H. & W.C.S. 62–156a). 98: Sarqaq (J.V. Aug. 1835). 108: Niaqornat (L.V. July 1834). 128: Agatdalen (K.H. 13.861). 129: Avataussaligssuaq (K.J. 928). 143: Kangerdlugssuaq (K.H. 16.397).

A. hyalina is a rather frequent to common species of calcareous sites, principally of Europe and North America. It occurs in the New World north to 82°32′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and to 82°10′N. in Peary Land (ARNELL, 1960). As REIMERS (1940) and SCHUSTER (1953) have emphasized, *A. hyalina* is an amphizonal species with its major range in Arctic and alpine regions, but also recurring under xerothermophytic conditions in the warm lowlands (in Europe associated with *Riccia ciliifera*, *Corsinia*, *Targionia*, and other xerothermophytes). In North America the species occurs southward to northern Vermont and, as a clear relict, on deciduous-forested bluffs in southeastern Minnesota and northeastern Iowa (Schuster, l. c.).

A. hyalina is rather common in the basaltic region of West Greenland, often occurring as isolated plants or small gregarious colonies—never in extensive patches—over Ca-rich soils on the weathered detritus

of basalt cliffs. Under mesic conditions (66–0317, 66–0298) it may occur with *Scapania ligulifolia* and *S. gymnostomophila*, on small shelves of basalt cliffs, near waterfalls, mixed with *Mannia pilosa*, *Sauteria alpina*, *Preissia quadrata*, *Tritomaria scitula*, *Scapania cuspiduligera*, *Solenostoma pumilum polaris*, *Lophozia badensis* and *Blepharostoma* (66–1357d). Common on south-facing, insolated but irrigated basalt slopes (70–2146; here with *Sauteria alpina*) and on exposed, insolated, steep slopes (Søndre Strømfjord) on thin soil adjoining temporary rills; here it may occur mixed with *Peltolepis* (70–3205), *Mannia fragrans* (66–0038), or *Riccia beyrichiana* (70–3209)—in all cases in strongly exposed sites, with maximal insolation, in "continental" areas with long, warm and dry summers.

A. hyalina is singularly stenotypic and easily recognized. The only significant variations are in the numbers of lobes (hence, potentially sporophytes) per carpocephalum, which range from 2–4(5), and in the presence vs. absence of reddish pigmentation of the dorsum of the thallus and of the carpocephalum surface. ♂ and ♀ Plants usually occur in the same area and spores are freely produced. Capsules have been seen from July 10 (70–2146), July 21 (70–2418) to Aug. 7 (70–2699).

In 70–2001 the pores are often strongly elevated, especially near the depressed gynoecial receptacles; here the penultimate ring of cells is strongly elongated radially, so that the ring of strongly thick-walled innermost cells is situated at the summit of a distinct tube. We have never observed such pores in other *Marchantiales*.

Peltolepis LINDB.

Peltolepis grandis (LINDB.) LINDB.

Distribution (Map 76)

1B: Lyngmarken (66–0342f, 66–0556). 1D: Skarvefjeld (66–0299, 66–0316). 2: Fortunebay (66–0368, 66–0147). 6: Eqalúnguit (70–2247, 70–2250). 25: Sarfaq (70–2359). 30: Eqe (66–0261, 66–0322, 66–0325a). 31: Anap nunâ (70–2409a, 70–2410a). 37: Agpat (66–1428). 38: Uvkusigssat (66–1380). 39: Tasiussaq (66–1225, 66–1247). 42: Magdlak (66–1369). 43: Kangerdlugssuakavsak (66–1292). 44: Akuliarusikavsak (66–1324, 66–1325, 66–1332). 46: Qalatôq (66–1136). 48: Amitsup (66–0772). 49: Skalø (66–1004). 50: Simiútap kûa, valley (66–0865). 51: Simiútap kûa, shore (66–0832). 52: Umîarfik, Qôrnoq (66–0962). 53: Søndre Strømfjord (66–0039, 66–0044, 70–3205).

Additional collections:

1: Godhavn (L.H. Aug.–Sept. 1932). 1B: Lyngmarken (L.K.R. July 1886). 42: Magdlak (K.H. 15.756). 43: Kangerdlugssuakavsak (K.H. 14.824). 44: Akuliarusikavsak (K.H. 16.687, 15.884). 45: Sagdliaruseq (K.H. 13.146, 16.012, 16.925, 17.171, 17.173). 52: Umîarfik, Qôrnoq (K.H. 16.367). 53: Søndre Strømfjord (K.H. 4195, 4451). Aulatsivik Fjord (Iliverquvik? S.B. July 1870). 61: Taserârsuk (L.H. July 1932). 84: Qeqertasugssuk (L.H. Aug. 1932). 87: Kangersuneq (K. HANSEN

Aug. 1958). 95: Pâkitsoq (K.H. & G.M. 71–1930). 98: Sarqaq (J.V. Aug. 1832). 131a: Agpat, Qaqortuatsiaq (K.H. & G.M. 71–1695). 139: Qaqortukavsaq (K.H. 16.112). 141: Inukavsait qâqarssue (K.H. 16.286). 142: Niaqornánguaq (K.H. 16.753).

P. grandis, is rather frequent regionally and is probably the most frequent of the three Greenland members of the *Sauteriaceae;* it is found north at least to 81°51′N., on Mt. Christie, near Lake Hazen, Ellesmere Island (Powell, 1958, ver. RMS). In Greenland it is general north to ca. 70°N., where basic substrates occur, and on the east coast it attains 72°44′N. on Geographical Society Ø (Holmen 18.148); from there it extends south to Dyrnæs near Narssaq, at 60°57′N. (Holmen, July 1963).

Peltolepis, like *Athalamia* and *Sauteria*, is often restricted to basic substrates, but often occurs in feebly calcareous areas, as near dikes, in igneous sites. It may occur on exposed soil over basic cliffs in rather arid, continental sites (as at Søndre Strømfjord; 70–3205), and may then be mixed with *Athalamia hyalina* and *Mannia pilosa;* similar occurrences are with *Athalamia* on sunny ledges, on thin, exposed soil, at Anap nunâ (70–2410a), and with *Scapania mucronata praetervisa* also admixed. *Peltolepis*, however, is usually more mesophytic than *Athalamia* and more often grows on thin soil layers over sheltered ledges—sometimes in recesses, or where shaded by *Salix glauca*, sometimes in ravines and recesses of craggs—even on peaty, Ca-enriched soil along small rills (66–0261). Very frequently it is found on moist coastal basalt cliffs, as on Disko, in sheltered niches, associated with *S. ligulifolia*, *S. gymnostomophila* (66–0316) or *Cephaloziella uncinata* (66–0299), or *Lophozia heterocolpos* (66–0147). On damp soil over or between basic rocks it may also occur with *S. mucronata praetervisa*, *Solenostoma subellipticum*, *L. heterocolpos*, *Tritomaria heterophylla*, or *T. scitula* (70–2247, 70–2409a). Occasionally in areas without an obvious source of Ca (as at Sarfaq; 70–2359), on damp cliffs, associated with *S. mucronata praetervisa* and *Anastrophyllum minutum.* At Eqe (66–0322) it occurs adjoining a small basalt dike, on thin, moist soil, with *Solenostoma subellipticum*, *Cephalozia pleniceps*, *Scapania lingulata*, *S. ?obcordata* and *S. polaris.*

P. grandis is a rather variable, monoecious species. The sessile androecial disk is always elevated above the thallus surface, with only short-conoidal, antheridial ostioles (in contrast to the cylindrical, slender, typically scattered ostioles of *Sauteria* and *Athalamia*); peripheral to the disk are only very short and relatively blunt scales forming an obscure ring. The gynoecium, when still young, however, is surrounded by a more conspicuous ring of acute and slender scales which are usually purplish tinged, except in shade forms (in sharp contrast to *Athalamia hyalina* in which they are always decolorate and bleached). Except for this, the young gynoecial and mature androecial receptacles can be confused. Gynoecial receptacles are normally situated in an apical notch of the

thallus, in contrast to those of *Athalamia*. There is, however, some variation in this. Thus in HOLMEN 16.753 (Upernivik Ø) the carpocephala are in part unquestionably dorsal, as in *Athalamia*. The carpocephalum stalk normally has two well-defined rhizoid furrows, but in at least one specimen seen (HOLMEN 18.140, from East Greenland) one of the two rhizoid furrows is (at least at the loci where sections were cut) completely internal and reduced in diameter.

Peltolepis usually shows a zigzag mode of growth, typically involving initial formation of a dorsal androecial disk (sometimes 2–3 androecia may be formed in acropetal succession before a gynoecium is laid down; occasionally two androecia may be laid down, side-by-side on either side of the thallus midline). After formation of an androecium (or androecia) a gynoecium develops, situated in a terminal notch. One of the two thallus lobes, that overtops the gynoecial branch, ceases further growth, the other elongates (and then laterally displaces the gynoecium); this overtopping thallus lobe again forms an androecium and then a gynoecium, followed again by overtopping of one of the two thallus lobes, the other lobe ceasing growth; and so on, *ad infinitum*. There may be rather regular alternation in inhibition vs. development of left-hand and right-hand thallus lobes, so that progression may be regularly zigzag; this is most obvious on plants in which fertilization has not occurred. On vigorous plants both overtopping lobes, on each side of the gynoecium, may develop equally, and soon after initiation, develop 1–3 nearly juxtaposed androecia.

Various other deviations can be observed when abundant materials are studied. Capsules have been observed as early as July 27 (66–0316), but in plants from South Greenland may be mature by July 14 (HOLMEN, July 1963).

Sauteria NEES

Sauteria alpina (NEES) NEES

Distribution (Map 77)

1A: Behind Arctic Station (66–0168, 66–0178). 1B: Lyngmarken (70–2023). 1D: Skarvefjeld (66–0231, 66–0307, 66–0308a, 66–0319). 8: Kuánerssuit (70–2146a, 70–2148, 70–2150). 10: Enoks Havn (70–2756). 12: Perdlertut (70–2709). 13: Jens Vahls Dal (70–2643). 14: Hareøen (70–2577, 70–2619). 30: Eqe (66–0323, 66–0327). 34: Marrait kangigdlît (66–0742, 66–0766). 38: Uvkusigssat (66–1381). 40: Mârmorilik, head of the Fjord (66–1187a). 42: Magdlak (66–1357a, 66–1369a). 47: Íngia (66–1041). 48: Amitsup (66–0819). 49: Skalø (66–1009). 50: Simiútap kûa, valley (66–0864). 51: Simiútap kûa, shore (66–0824, 66–1642).

Additional collections:

1: Godhavn (L.H. July 1932). 29: Ritenbenk (S.B. 1870). 34: Marrait kangigdlît (K.H. Sept. 1956). 42: Magdlak (K.H. 15.756). 59: Kvannit (K.H. & W.C.S. 62–156b). 70: Sarqardlît (M.P.P. 637). 106: Nûgssuaq (K.H. 62–931). 108: Niaqornat (J.V. July 1834). 110: Ikorfat (K.J. 292, SØRENSEN Aug. 1947). 128: Agatdalen (K.H. 15.489).

In West Greenland locally the most common member of the *Sauteriaceae*, particularly on moist, clayey slopes, extending north as far as 82°32′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and to 82°17′N. in Peary Land (TROELSEN 9052), southward as a disjunct to Mt. Albert, Gaspé, Quebec (where it was collected [RMS] in late snow areas, on damp soil between rocks, with *Anthelia juratzkana*). Unlike *Athalamia*, *S. alpina* is not known from xerothermophytic loci, and generally avoids sites where desiccation is apt to occur.

S. alpina is an obligate calciphile, with its distribution strongly restricted by this fact. Like *Peltolepis*, it often occurs on nearly permanently damp sites and may occur with this species, *Lophozia gillmani*, and *L. collaris* (in HOLMEN 15.756, Magdlak). On damp, calcareous slopes it may be found with *L. quadriloba*, *Tritomaria scitula*, *Solenostoma sphaerocarpum*, and *S. pumilum polaris* (70–2643, 70–2619); also present in areas with gneissic rocks, wherever basalt dikes occur, as at Eqe (where on moist, almost vertical exposures, associated with *L. quadriloba*, *L. polaris*, and *Anthelia juratzkana*).

Even when sterile or fragmentary, *S. alpina* is usually readily identified by the light green color with margins often bleached, and the tumid, inflated air chambers. Its inability to form pink to vinaceous secondary pigments—even when exposed to full sun—is diagnostic in separating it from the two other genera of *Sauteriaceae*. Plants are monoecious, with the high antheridial ostioles of *Athalamia;* however, pseudodioecism is frequent. With casual examination, plants may be regarded as unisexual, and then attributed to *A. hyalina*. [This, perhaps, misled ARNELL, who reported *Sauteria* from many Peary Land stations; all reports but three represent *Athalamia*].

Family ***Marchantiaceae*** DUMORT.

Preissia CORDA

Preissia quadrata (SCOP.) NEES

Distribution (Map 78)

1A: Behind Arctic Station (66–0167, 66–0280a). 1D: Skarvefjeld (66–0318). 8: Kuánerssuit (70–2148, 70–2150, 70–2154, 70–2156). 10: Enoks Havn (70–2756). 13: Jens Vahls Dal (70–2634, 70–2656, 70–2666). 14: Hareøen (70–2587). 30: Eqe (66–0295a). 34: Marrait kangigdlît (66–0743, 66–0748, 66–0763). 35: Hollænderbugt (66–1508). 40: Mârmorilik, head of the Fjord (66–1187). 42: Magdlak (66–1357e, 66–1365, 66–1369a). 45: Sagdliaruseq (66–1085). 49: Skalø (66–1003). 50: Simiútap kûa, valley (66–0866a). 51: Simiútap kûa, shore (66–0827a). 53: Søndre Strømfjord (70–3206).

Additional collections:

1: Godhavn (L.H. July–Aug. 1932). 1C: Blæsedalen (M.P.P. 376). 34: Marrait kangigdlît (K.J. 1052, A.R. Aug. 1954). 42: Magdlak (K.H. 12.919). 51: Simiútap

kûa, shore (K.J. 17.202). 53: Søndre Strømfjord (K.H. 4228). 103: Qapiortoq kitdleq (K.J. 1052a). 108: Niaqornat (J.V. July 1834). 110: Ikorfat (K.J. 335, 336, SØRENSEN Aug. 1947).

A widespread, subcosmopolitan calcicole that extends northward as far as 82°32′N. in Ellesmere Island (SCHUSTER *et al.*, 1959) and southward in North America to Virginia and, at high elevations, to Arizona and Mexico. In Greenland it is probably general on ice-free land, wherever strongly basic conditions prevail (but for this reason not yet found in the Inglefield Bredning area of northwest Greenland or in Peary Land). Thus the northernmost station on the west coast of Greenland is 51: Simiútap kûa, 71°59′ N., (Umîarfik), and on the east coast Danmarkshavn in Dove Bugt 76°49′N. (JENSEN, 1910).

P. quadrata is strictly confined to basic sites, often to Ca-enriched mineral soils over basaltic ledges, where it may occur (as on Disko; 66–0280a, 66–0318) with *Scapania cuspiduligera* or (66–0280a) with *Solenostoma pumilum* or (70–2156, 70–2150) with *Lophozia heterocolpos* or *Sauteria*. Also on steep, calcareous, clay-shale slopes, often in run-off crevices where hardly subject to desiccation (at Hollænderbugt; 66–1508), then with *L. gillmani* or *Scapania gymnostomophila*. The species also occurs on peaty-gravelly terraces along beaches, sometimes forming a matrix for *Equisetum variegatum* (at Jens Vahls Dal; 70–2634), or mixed with *L. quadriloba*. Occurrences on steep sides of basalt dikes are frequent (as at Eqe; 66–0295a, there with *S. gymnostomophila*); the species also grows on basaltic rock walls adjoining waterfalls (as at Magdlak; 66–1357 e), with *Sauteria*, *Athalamia*, *Mannia pilosa*, *L. badensis*, *Tritomaria scitula*, *Solenostoma pumilum polaris*, *Scapania gymnostomophila*, *Plagiochila asplenioides* and other calciphiles associated. Capsules have been observed as late as August 10 (66–1508). (In northern Elsemere Island they may form as early as July 5—from receptacles formed the previous year).

Thallus segments innovate soon after a terminal receptacle is formed, the innovation being strictly terminal rather than formed by a thallus lobe on one side or the other of the receptacle; these innovations are soon again fertile and the corresponding segments cease to grow vegetatively. Four or five such, sometimes apparently annually produced, segments can often be found—one after the other. Often a segment that has produced an archegoniophore develops a very short terminal innovation that almost immediately thereafter produces an antheridiophore. In other cases an archegoniophore-bearing segment is succeeded by 3–4 longer innovations, produced sequentially, each of which terminates in an antheridiophore. Also, archegoniophore-bearing segments may be succeeded by innovations that again produce archegoniophores. Although pseudodioecious thalli can be found—which result when innovations are

produced, sequentially, bearing receptacles of the same sex—it seems clear that, sooner or later, the Arctic plants have the genetic ability to develop innovations or segments that produce receptacles of the opposite sex. An Ellesmere Island specimen, indeed, produced receptacles that were in part gynandromorphs (SCHUSTER *et al.*, 1959).

Plants in West Greenland, as elsewhere in the Arctic, thus seem to be always, or at least normally, autoecious, with both archegoniophores and antheridiophores arising from a single plant. By contrast, plants from boreal to temperate sectors of North America are, so far as they have been seen, all clearly dioecious.

The unisexual-bisexual problem with regard to *Preissia* is an old and still unresolved one (MÜLLER, 1905–06, states simply "Ein- und zweihäusig", while in, 1951–58, he states "Gemischtgeschlechtig. Mitunter scheinbar getrenntgeschlechtig"). ARNELL (1928, p. 27) states (translation): that the main form, which he calls *P. quadrata*, is more often autoecious, larger, purer green, with broader thalli, more plane, and with the four elevated radii of the archegoniophore strongly convex; fewer, often only 2–4 sporophytes are produced, and the spores are smaller. By contrast, var. *commutata* (LINDENB.) LINDB. (LINDB., 1882, p. 4) is mostly dioecious, smaller, more or less brownish red, with narrower thalli, with the carpocephalum more elevated or convex; more numerous sporophytes are produced per carpocephalum (up to 10), and the spores are larger. ARNELL states that, according to most hepaticologists, these two forms "go over" into each other.

JENSEN (1915, p. 42) also distinguishes a species *Chomocarpon quadratus*, as distinct from a dioecious (very seldom autoecious) *C. commutatus*, on the basis of its autoecious inflorescence (rarely dioecious), larger size, with thalli 1–1.5 cm broad and often greener; the carpocephalum is red-brown, less convex, with the four radii obviously and sharply elevated; sporophytes are fewer, 2–4 per "head", and smaller; spores are a little smaller and with lower reticulations. The dioecious plant is widespread in Denmark; the autoecious one is reported from the Faroes only.

Neither author mentions the crucial antheridiophore which is clearly different in the bisexual Arctic phenotypes (see SCHUSTER *et al.*, 1959, p. 71), being provided with a polished, hyaline, thin, chartaceous, wide wing around the periphery of the receptacle.

We are of the tentative opinion that the collective species *P. quadrata* consists of a predominantly or exclusively monoecious Arctic and subarctic population, and of a dioecious population of boreal and temperate regions. In any event, the Greenland and the Ellesmere Island plants seen are all monoecious and have "Arctic phenotype" antheridiophores.

Marchantia L.

Marchantia alpestris (NEES) BURGEFF

Distribution (Map 79)

1A: Behind Arctic Station (66–0151). 1B: Lyngmarken (66–0565). 2: Fortunebay (66–0210, 66–0211). 3: Sinigfik (66–0452). 5: Qeqertaq (66–1525). 6: Eqalúnguit (70–2252). 7: Angûjârtûtit (70–2163, 70–2170, 70–2174). 11: Qasigíssat (70–2733). 14: Hareøen (70–2586). 28: Atâ (70–2488). 49: Skalø (66–1000).

Additional collections:

1: Godhavn (GRØNTVED July 1932). 1A: Behind Arctic Station (M.P.P. July 1934, L.H. July 1932). 1B: Lyngmarken (S.B. Sept. 1870, W. & H. July 1884, C.K. July 1897, M.P.P. June 1898 & July 1940). Engelskmandens Havn (G. SEIDENFADEN July 1928, M.P.P. Aug. 1898). 1C: Blæsedalen (L.H. June 1932). 2: Fortunebay (K.H. & W.C.S. 62.050). 3: Sinigfik (M.P.P. 3393). 8: Kuánerssuit (GELTING Aug. 1949). 17a: Egedesminde (P. SØRENSEN July 1893). 34: Marrait kangigdlît (K.H. 12.214, 13.749, A.R. 8010). 41: Mârmorilik, south of the Fjord (K.H. 13.726). 59: Kvannit (K.H. & W.C.S. 62–147). 61: Taserârsuk (L.H. July 1932). 65: Ûnartuarssuk (M.P.P. 105). 72: Kuánit (GRØNTVED Aug. 1932, L.H. Aug. 1932). 73: Igdlokasik (K.H. 14.083). 70: Sarqardlît (M.P.P. 702). 102: Atâ (L.H. July 1932). 129: Agatdalen (K.H. 13.976 burn-patch). 144: Igdlorssuit (S. HANSEN July 1888).

This northern, boreal to Arctic-alpine taxon, regarded by BURGEFF (1943) as a "good" species and one of the "parents" of *M. polymorpha* L., has a still largely undefined range, extending through much of northern Europe but recurring supposedly in Madeira; MÅRTENSSON (1955) states that it occurs throughout "the Scandes" and is "generally more or less common in the subalpine and low-alpine belt"; it is also reported from Jan Mayen. In North America it is found westward from Greenland to Alaska; it is apparently the only *Marchantia* known from Greenland (although *M. aquatica* may very well occur in South Greenland), where it occurs as far north at least as Agpat, Saunders Ø (HESSELBO, 1923; as *M. polymorpha* var. *arctica*). In N. America it recurs southward at least to Percé, in the Gaspé (RMS 44015), but the southern limit of its range is uncertain owing to its prior confusion with *M. polymorpha*. Westward reported from Southampton Island and Victoria Island by PERSSON & HOLMEN (1961).

M. alpestris, though a much less "weedy" taxon than *M. polymorpha*, is unquestionably still a nitrophile that, particularly in the Arctic, often follows man. Thus at Fortunebay it occurs over soil amidst vertebrae of long-dead whales, on the site of a long-abandoned whaling station. On Skalø near the mouth of Umîarfik it occurs along a small stream, in a site with old Eskimo houses. The accumulation of nitrogenous materials around old Eskimo dwellings is too well known a fact to need elaboration here. Since away from such sites Arctic soils are often highly deficient in nitrogen, the distribution of *M. alpestris* in Greenland seems at least in part bound up with the present or former

influence of man. The species usually occurs along streams or rills, often with mosses, sometimes with *Equisetum variegatum* (rarely *E. scirpoides*). It is much more frequent in sites where former settlements occur than the stations enumerated above suggest, since to a large extent, the sites where it is apt to occur are rather devoid of other *Hepaticae*, and we have not systematically sampled such niches.

Family ***Ricciaceae*** REICHENB.

Riccia L.

Riccia beyrichiana HAMPE

Distribution (Map 80)

44: Akuliarusikavsak (66–1329). 53: Søndre Strømfjord (66–0043, 70–3209, 70–3210, 70–3211, 70–3212, 70–3213, 70–3214).

Additional collections:

44: Akuliarusikavsak (K.H. 15.883, 16.752). 53: Søndre Strømfjord (T.W.B. Aug. 1946).

A species of southern affinity, found southward in North America to at least Texas and the outer coastal plain of the southeastern United States; northward it has been previously reported only to British Columbia, in the west, and Massachusetts, in the east. The present reports thus mark a very major northward extension in range. It is also found in Europe, there hardly entering the subalpine and subarctic belts.

R. beyrichiana occurs in only two localities in West Greenland and is abundant at only one (Søndre Strømfjord) where massive quantities occur on thin (in part sandy) soil over ledges which are alternately irrigated and baked dry. The species is clearly confined to the most continental parts of Greenland and occurs at Søndre Strømfjord together with *R. sorocarpa*, *Salix glauca*, *Saxifraga aizoides*, and not far from the type of *Sisyrinchium groenlandicum*.

The Greenland material seems quite typical. The plants vary much in size but often form handsome rosettes. The tumid thallus margins, broadly channeled thallus apex, and superior size distinguish it at a glance, in the field, from *R. sorocarpa*.

R. beyrichiana, together with *R. sorocarpa*, *Mannia fragrans*, and *Asterella saccata* form the only xerothermophilous communities of *Hepaticae* in Greenland. The presence of all of these taxa as far north as Søndre Strømfjord strongly suggests that winter minima are not the critical factor in governing their dispersal northward but, rather, summer maxima and amount of insolation (these last two factors are obviously related). It is likely that on the steep, south-facing slopes—in "continental" areas—to which *R. beyrichiana* is confined, the amount of radiant energy available during the short Arctic summer is extremely high and

probably equals or exceeds that available in, e.g., Massachusetts. It probably also equals the amount available in e.g., the cultivated field environment which is often frequent southward—where the species is a "winter annual", with growth in fallow fields chiefly from fall to spring.

Rosettes of both *R. beyrichiana* and *R. sorocarpa*, in thrifty condition, can be found in West Greenland as early as June 23, within 4–6 weeks of the time snow cover is gone. It is certain that the plants are perennial in such sites (much as in Massachusetts, where *R. beyrichiana* is spring-fruiting).

Riccia sorocarpa BISCH. (Table XI)

Distribution (Map 80)

22: Orpigsôq (70–3104). 31: Anap nunâ (70–2413). 37: Agpat (66–1420). 53: Søndre Strømfjord (70–3215).

One of the most widespread species of *Riccia* in the northern hemisphere, found throughout most of Europe into North Africa, and in North America known from Mexico northward to Washington, in the west, and Massachusetts, in the east. It then recurs in the Scoresby Sd. region of East Greenland, from where it was reported by JENSEN (1897), at Dyrnæs in South Greenland (HOLMEN 62–903), and at the four stations cited above in West Greenland; it has been collected (RMS, 1960) from one station at Inglefield Bredning, at Kangerdlugssuaq, 77°23′N., 67°W. (RMS 45831), which marks the northernmost point at which any member of the family has been found. In much of its area *R. sorocarpa* is a "weed" associated with man; it may be very abundant in continuously disturbed sites such as garden paths (as, e.g., in Seville and Granada, Spain) or in cultivated fields.

R. sorocarpa typically occurs in West Greenland on south-facing, warm, insolated, intermittently desiccated soil, usually on steep, rocky banks or slopes. It may be associated (as at Orpigsôq; 70–3104) with the relatively southern *Sedum roseum*. At Søndre Strømfjord it occurs on sandy soil over ledges along a small, intermittent, steep rill, associated with *R. beyrichiana* and (nearby) *Mannia fragrans*. The latter is also associated with *R. sorocarpa* at Anap nunâ (70–2413). On Agpat, in contrast, *Asterella ludwigii* is admixed (66–1420). The species, southward in North America, is not at all Ca-demanding, occurring as far as Louisiana and Mississippi in old cotton and corn fields on acidic soils. The West Greenland stations, however, are mostly from sites with Ca-enriched soil, as the frequent association with *M. fragrans* (and occasional association with *Asterella ludwigii*) shows. The main limiting factor regionally seems to be the need for long periods of strong sunlight and associated warmth; hence the species is lacking from all of the

oceanic or suboceanic sites in our region. At Inglefield Bredning, also, it was found only in the interior parts.

R. sorocarpa is easily recognized in the field; it lacks reddish pigmentation and is small, green at least in the median sectors of the thallus—although the diagnostically sharp thallus margins are usually bleached and decolorate; the segments are linear and narrow and sharply furrowed dorsally—as if impressed with a sharp knife—towards the segment apices.

There are striking differences in spore structure between some of the Greenland populations (including those from Inglefield Bredning) and plants from temperate loci. All populations from temperate sites appear to have a distinct and complete wing margin, but in several Greenland populations no wing margin, or mere vestiges of one, interrupt the contours between the inner and outer faces. It is likely that the populations with spores of the last type are purely Arctic in range and should be segregated as a distinct subspecies (they have been so segregated in Mss. by the senior author). In the present paper, however, we are maintaining *R. sorocarpa* in the broad sense. Judging from the occurrence of the species to 77°23'N., one must admit the possibility that some populations may have survived the Pleistocene in the Arctic and represent a distinct Arctic segregate. As the accompanying table (Table

Table XI. *Riccia sorocarpa*

	Diameter (without event. wing-margin)	Areoles across the convex face	Aver. diam. of areoles	Spore inner face		
				areolate	vermiculate	granulate to smooth
1. Hekla Havn ..... E. Greenland	68–83	10–12	7.4–10.2μ	+	–	–
2. Inglefield RMS(45831)	68–91	9–11	7.4–10.2μ	–	+	–
3. Orpigsôq (70–3104).....	65–86	7–10	8.3–11.0μ	–	+	–
4. Agpat (66–1420).....	62–83	10–12	4.8–6.2μ	–	+	–
5. Sdr. Strømfj. (70–3215).....	65–91	8–9	8.6–10.2μ	–	–	+
6. Anap nunâ (70–2413).....	65–83	8–9	7.1–8.3μ	–	–	+
7. Dyrnæs S. Greenland..... (K.H.62.903)	57–81	8–9	7.4–9.4μ	–	(+)	–

XI) shows, the Greenland populations exhibit other differences in spore characteristics. The inner spore faces, in particular, tend to be areolate to vermiculate in populations with mostly 9–12 *areolae* across the diameter of the external spore face. In populations with only 8–9 *areolae* across the spore face, the inner spore faces are granulate to almost smooth, rarely feebly vermiculate-marked. Variation, however, tends to be rather discordant; thus the plants from Agpat (66–1420) stand apart because of the small *areolae*, averaging only 5–6 μ across, while in other populations they average 7–10 or even 9–11 μ in diameter.

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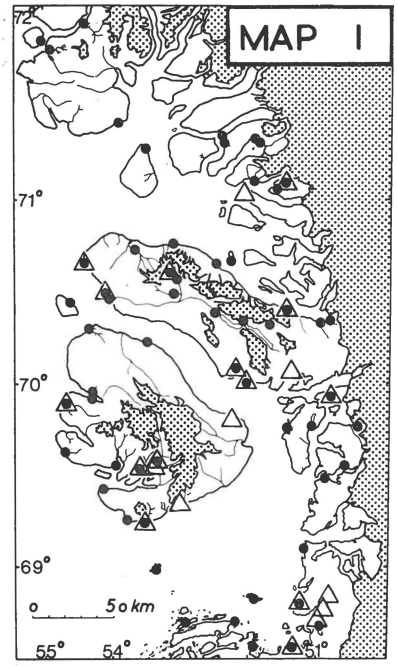
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— *subellipticum*	180
Tritomaria exsectiformis ssp. *arctica*	142
— *heterophylla*	144
— *polita*	148
— — ssp. *polita*	149
— — ssp. *polymorpha*	150
— *quinquedentata*	145
— — v. *grandiretis*	148
— — f. *gracilis*	147
— — v. *turgida*	148
— *scitula*	142

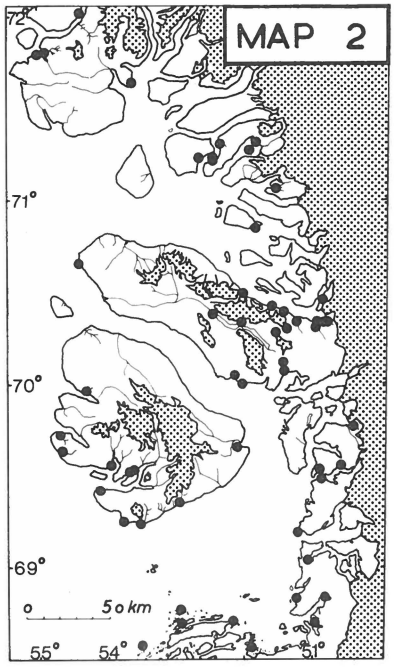
Færdig fra trykkeriet den 15. oktober 1974

MAPS

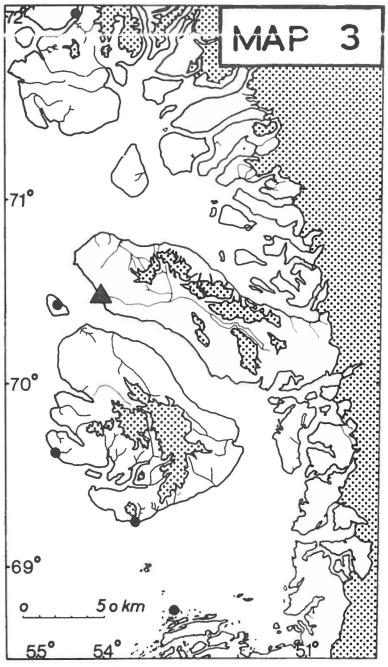


Blepharostoma trichophyllum ssp. trichophyllum △

ssp. brevirete ●

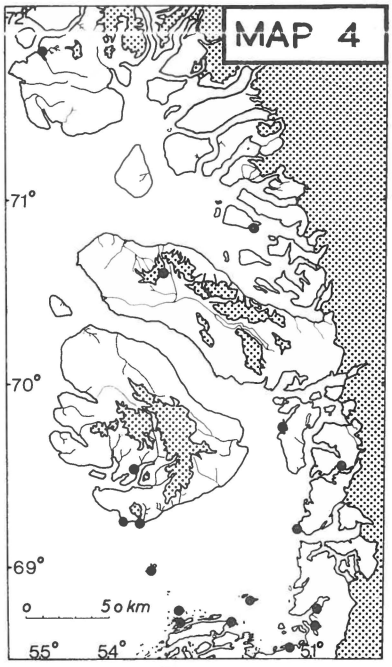


Ptilidium ciliare ●

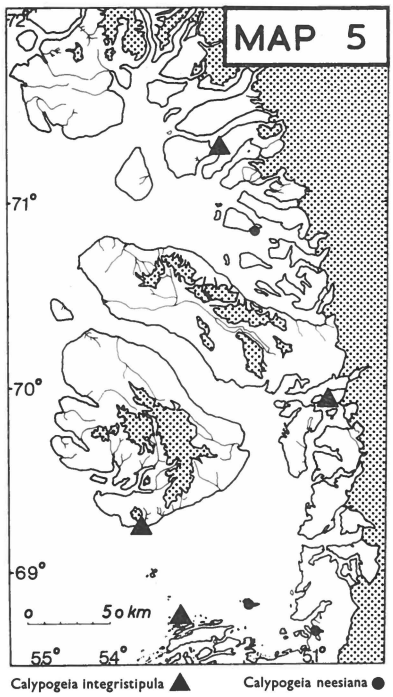


Calypogeia muelleriana ●

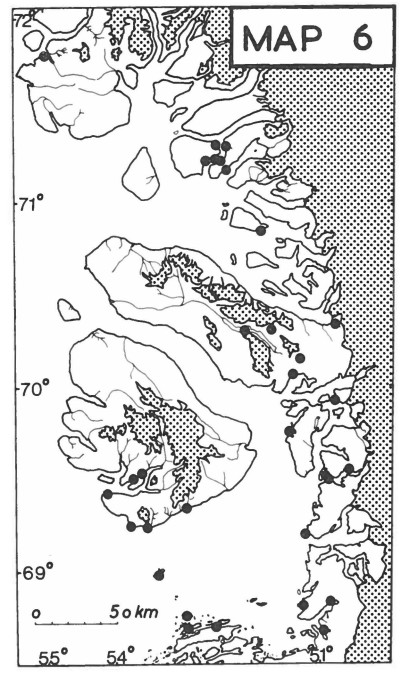
Metacalypogeia schusterana ▲



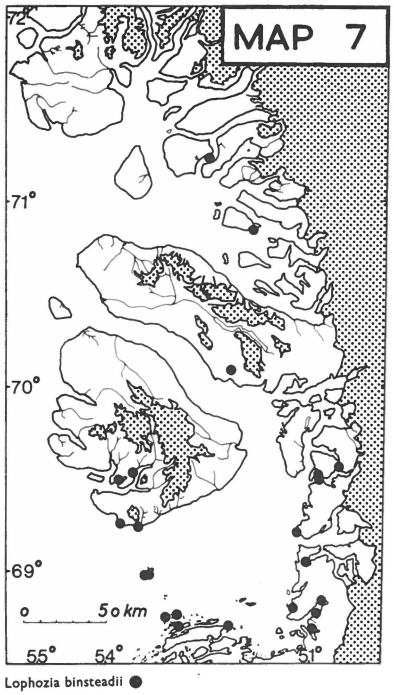
Calypogeia sphagnicola ●



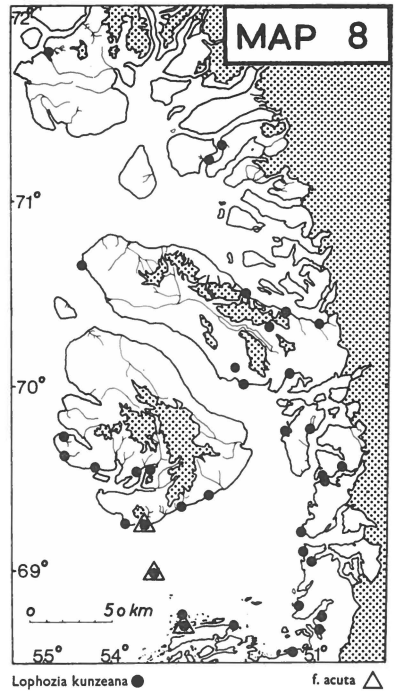
Calypogeia integristipula ▲ Calypogeia neesiana ●



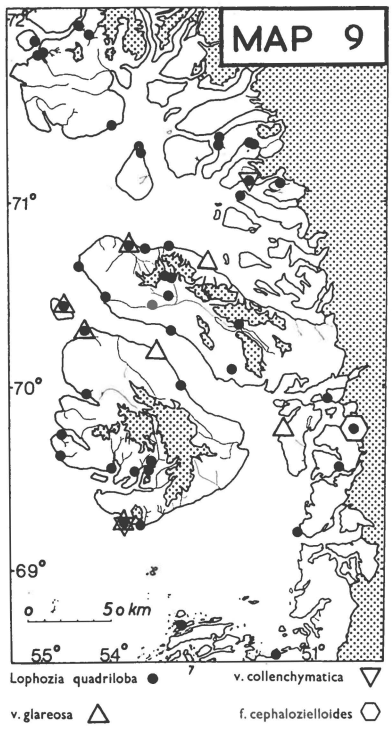
Chandonanthus setiformis ●

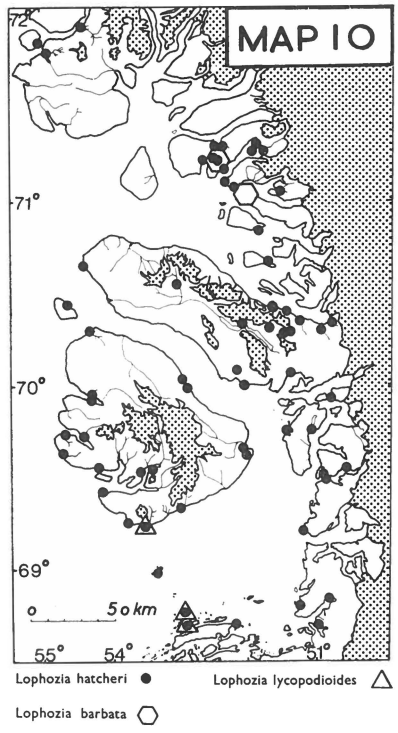


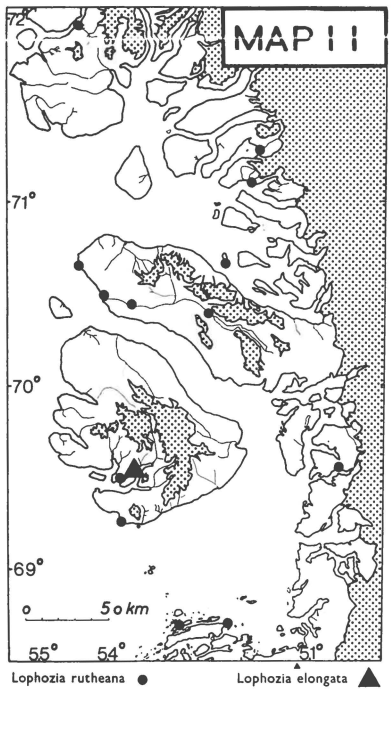
Lophozia binsteadii ●

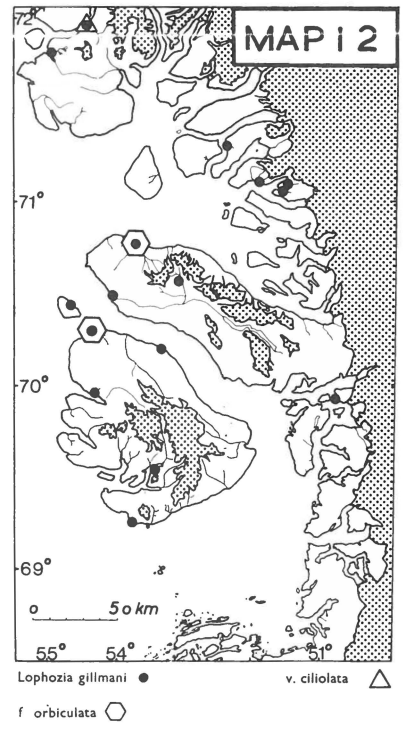


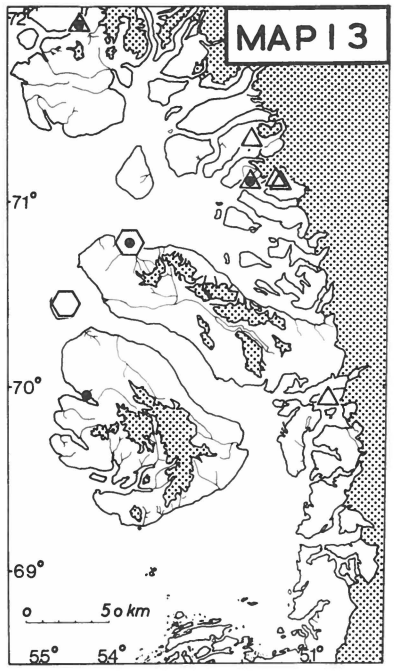
Lophozia kunzeana ● f. acuta △


MAP 9
71°
70°
69°
0 50 km
55° 54° 51°
Lophozia quadriloba
v. collenchymatica
v. glareosa
f. cephalozielloides


MAP 10
71°
70°
69°
0 50 km
55° 54° 51°
Lophozia hatcheri
Lophozia lycopodioides
Lophozia barbata

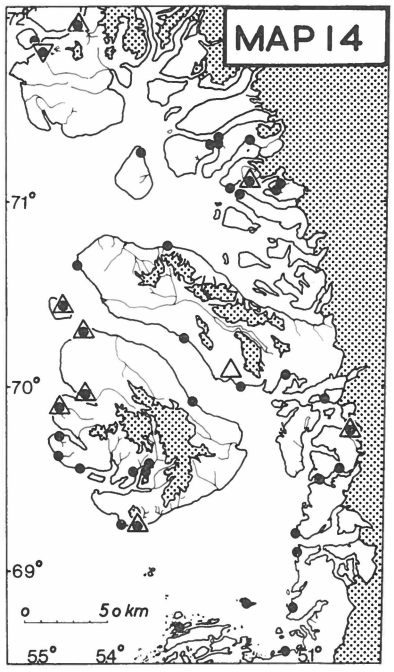

MAP 11
71°
70°
69°
0 50 km
55° 54° 51°
Lophozia rutheana
Lophozia elongata


MAP 12
71°
70°
69°
0 50 km
55° 54° 51°
Lophozia gillmani
v. ciliolata
f orbiculata



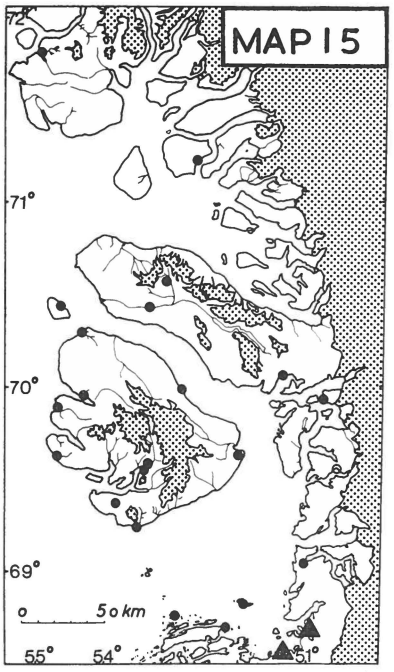
Lophozia badensis ● v. apiculata ⬡

Lophozia collaris △

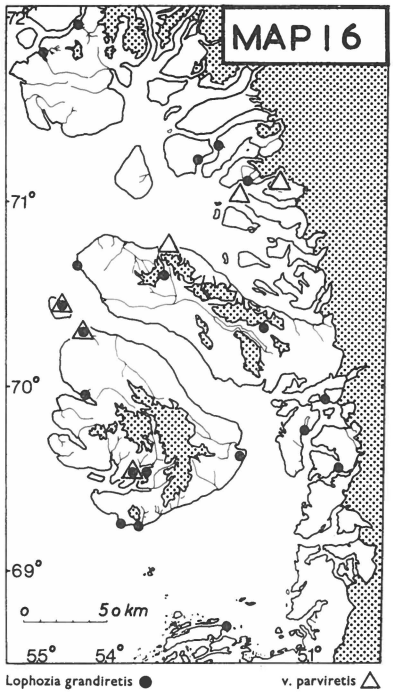


Lophozia heterocolpos ● v. harpanthoides △

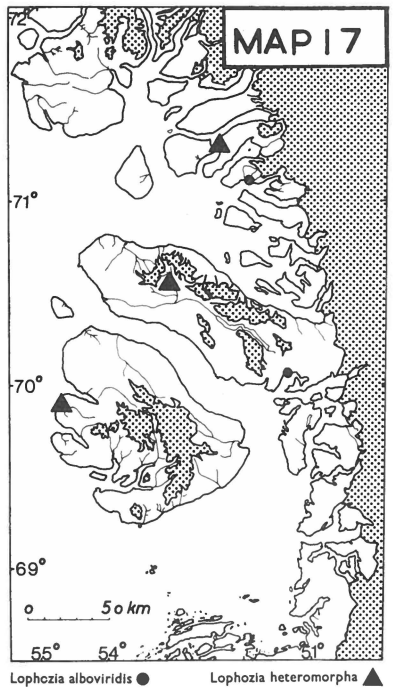
v. arctica ▽

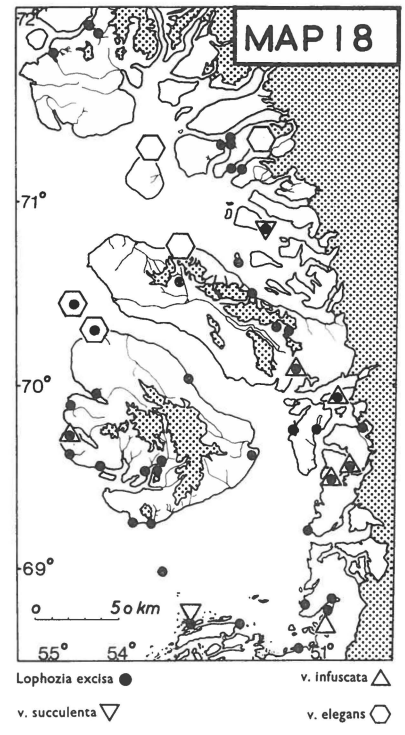


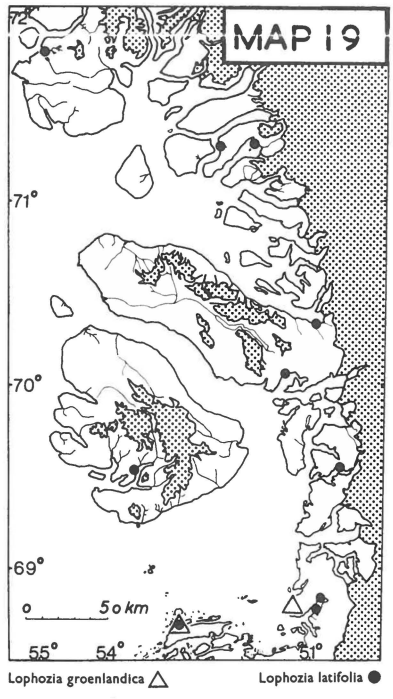
Lophozia opacifolia ● Lophozia incisa ▲

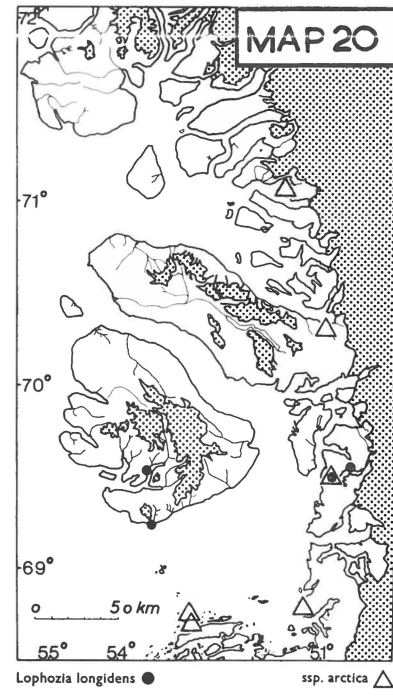


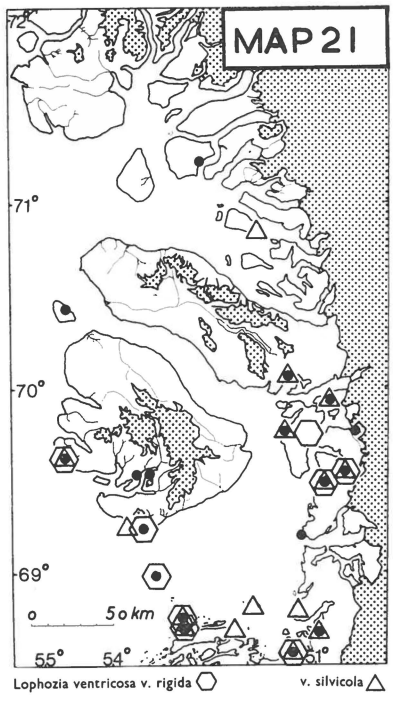
Lophozia grandiretis ● v. parviretis △

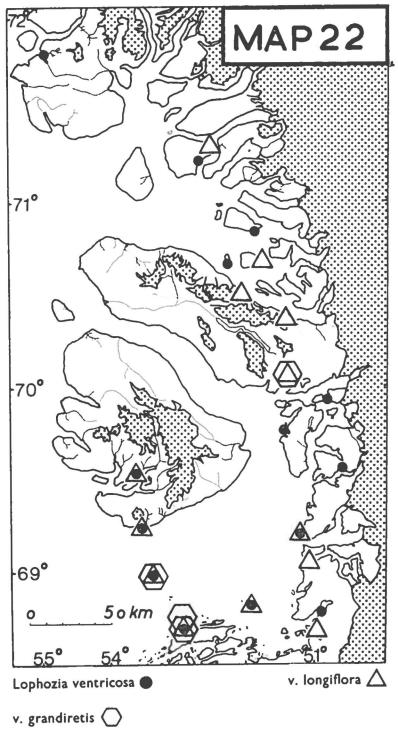

MAP 17
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia alboviridis
Lophozia heteromorpha

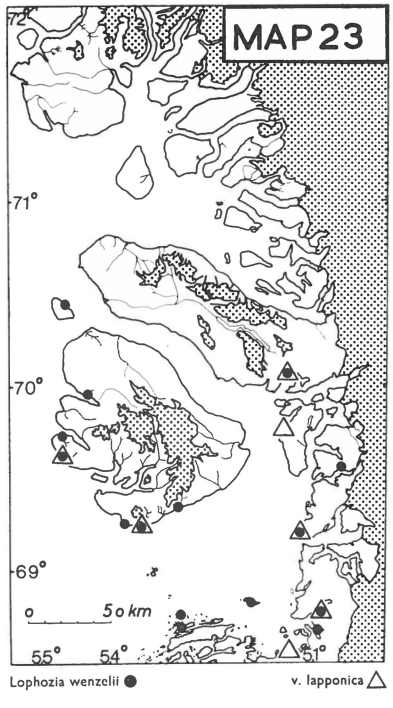

MAP 18
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia excisa
v. infuscata
v. succulenta
v. elegans

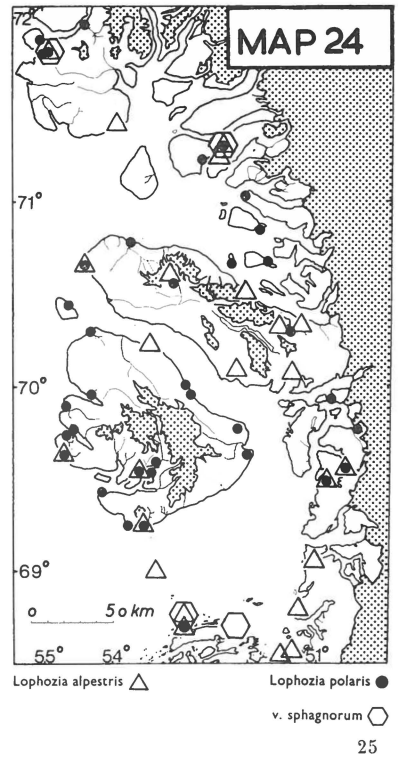

MAP 19
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia groenlandica
Lophozia latifolia

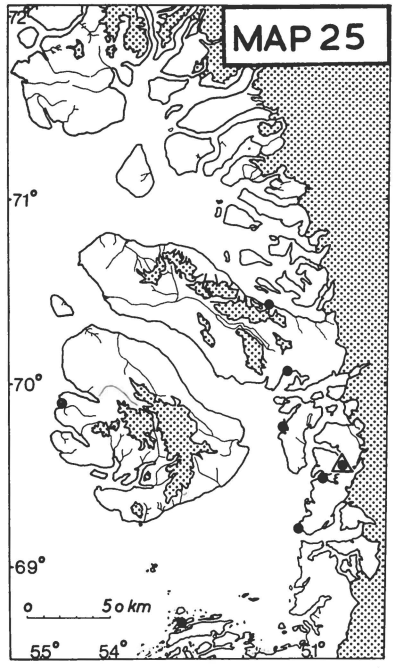

MAP 20
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia longidens
ssp. arctica


MAP 21
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia ventricosa v. rigida
v. silvicola
v. confusa

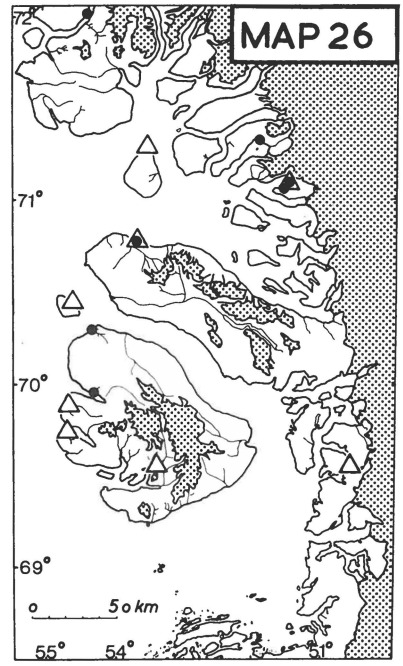

MAP 22
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia ventricosa
v. longiflora
v. grandiretis


MAP 23
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia wenzelii
v. lapponica

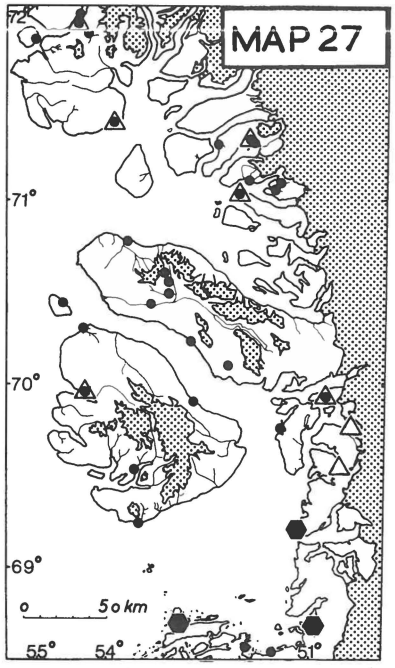

MAP 24
72°
71°
70°
69°
0 50 km
55°
54°
51°
Lophozia alpestris
Lophozia polaris
v. sphagnorum



Lophozia rubrigemma ● Lophozia subapiculata △

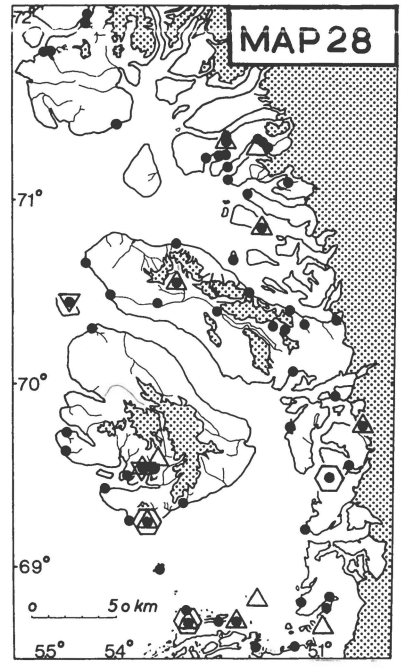


Lophozia pellucida ● v. minor △



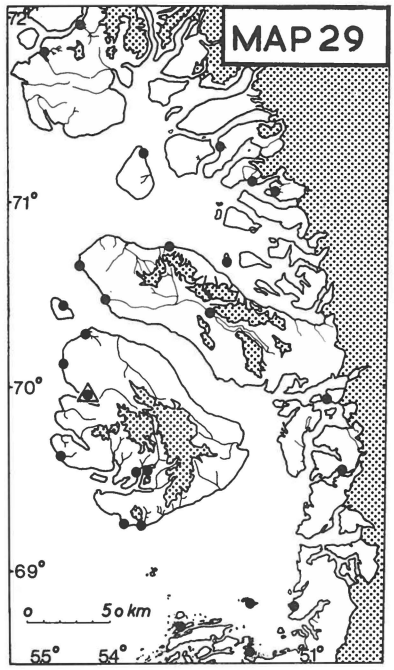
Tritomaria scitula ● Tritomaria heterophylla △

Tritomaria exsectiformis ssp. arctica ⬢

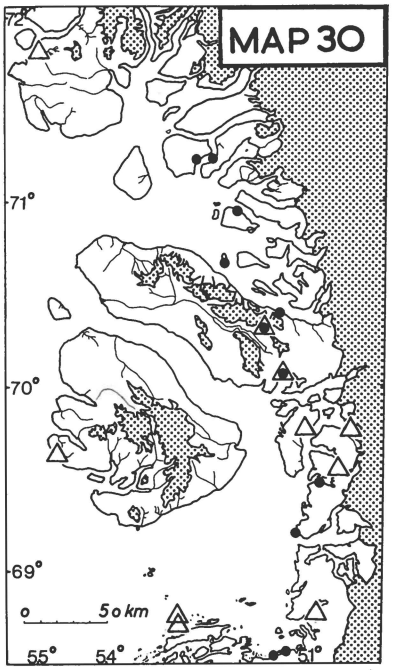


Tritomaria quinquedentata ● v. turgida ▽

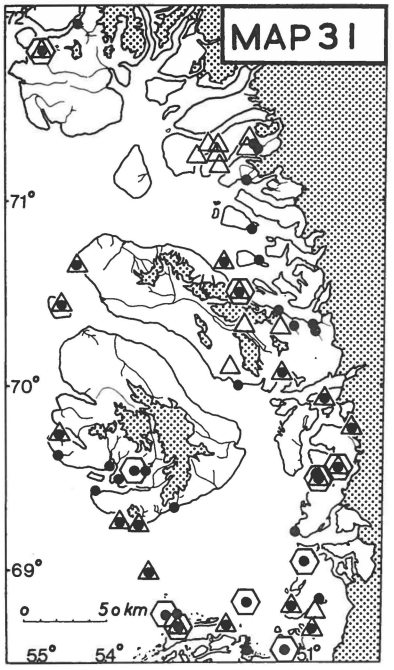
v. grandiretis ⬡ f. gracilis △



Tritomaria polita ssp. polymorpha ● ssp. polita △

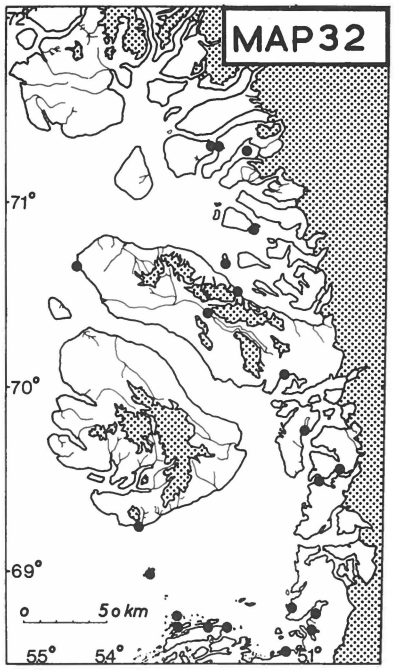


Anastrophyllum assimile ● Lophozia cavifolia △

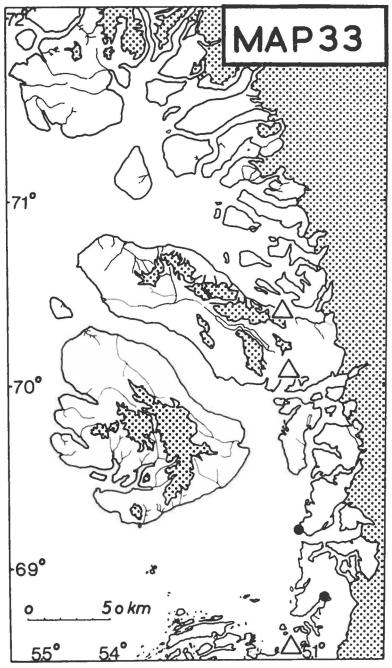


Anastrophyllum minutum ● v. grandis △

Anastrophyllum sphenoloboides ⬡

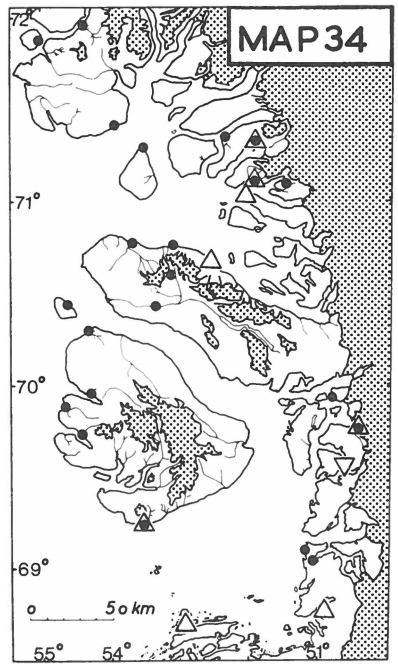


Gymnocolea inflata ●



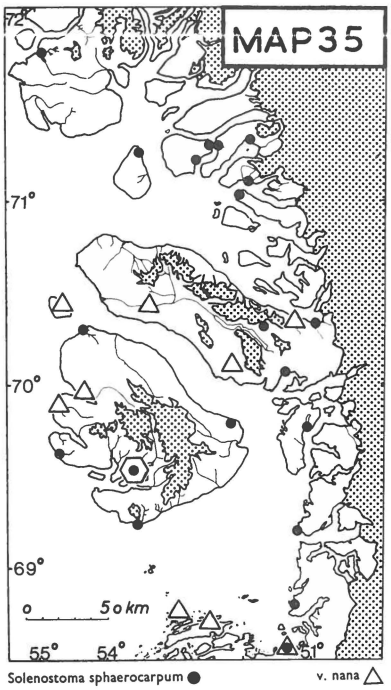
Jamesoniella undulifolia ●

Solenostoma oblongifolium △



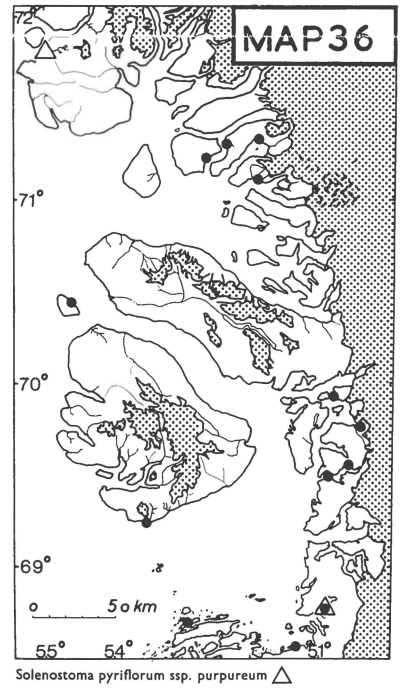
Solenostoma pumilum △ ssp. polaris ●

ssp. anomalum ▽



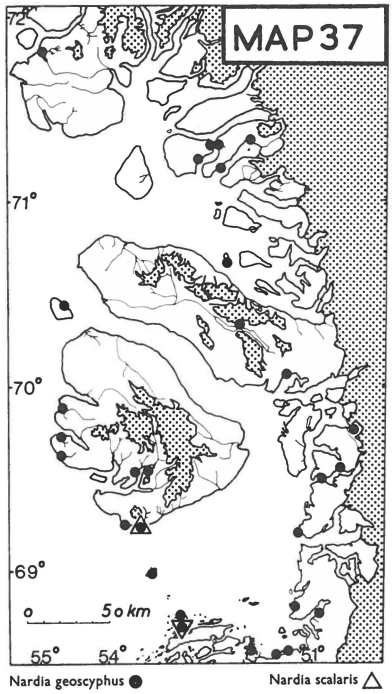
Solenostoma sphaerocarpum ● v. nana △

Solenostoma pusillum ⬡

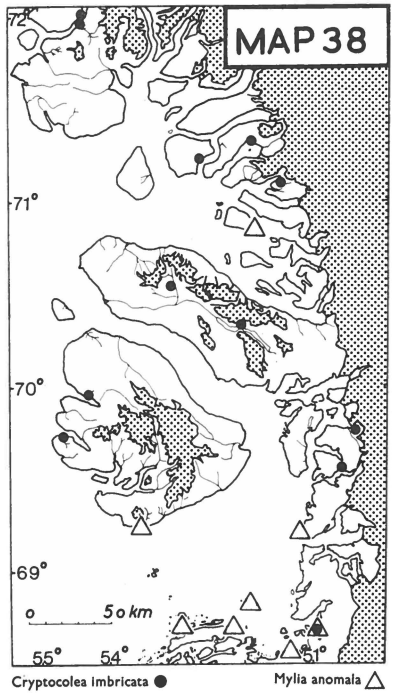


Solenostoma pyriflorum ssp. purpureum △

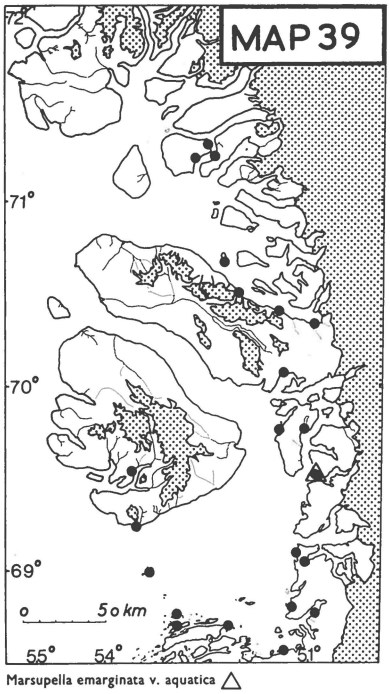
Solenostoma subellipticum ●



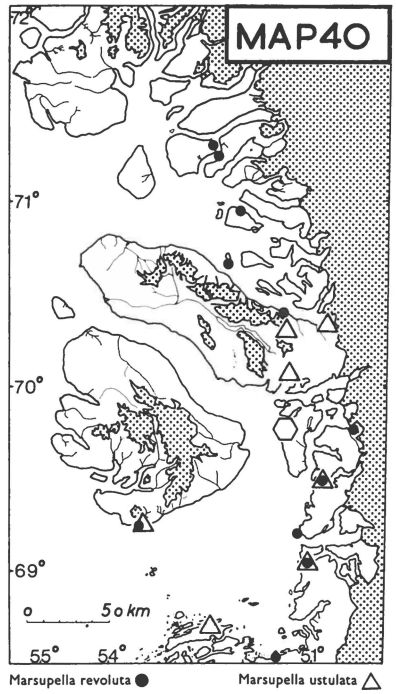
Nardia geoscyphus ●
Nardia scalaris △
ssp. botryoidea ▽



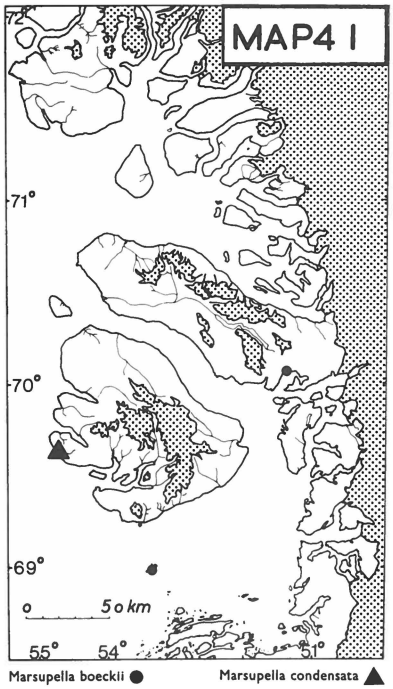
Cryptocolea imbricata ●
Mylia anomala △



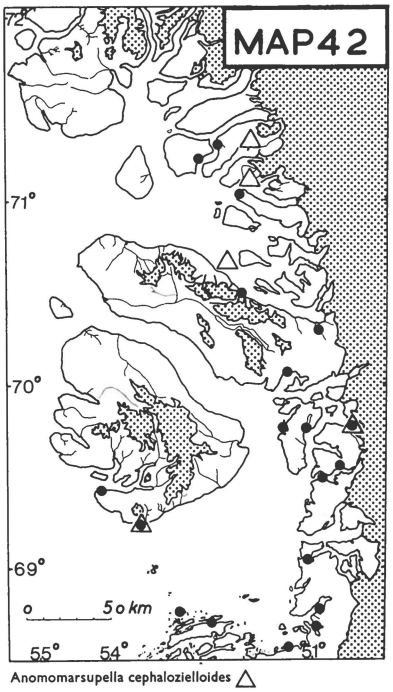
Marsupella emarginata v. aquatica △
Marsupella arctica ●



Marsupella revoluta ●
Marsupella ustulata △
Marsupella sparcifolia ⬡

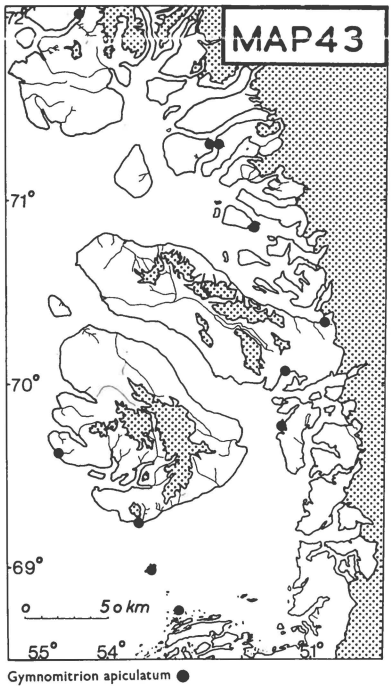


Marsupella boeckii ● Marsupella condensata ▲

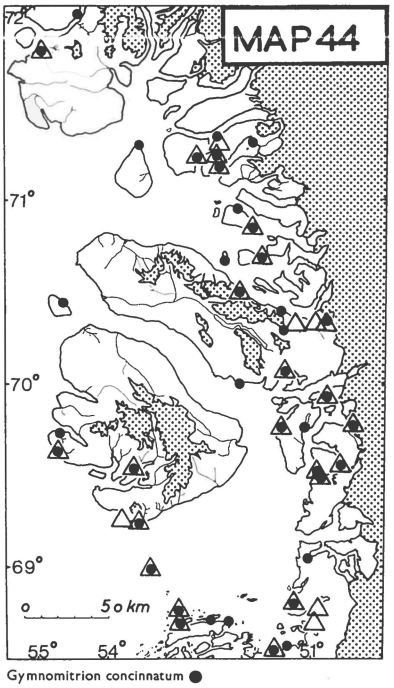


Anomomarsupella cephaloziellioides △

Prasanthus suecicus ●

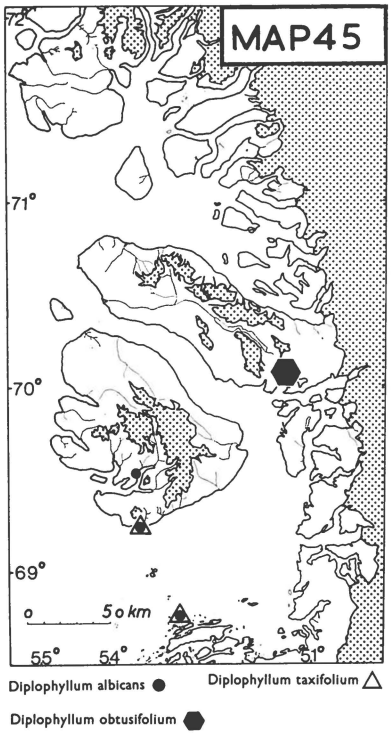


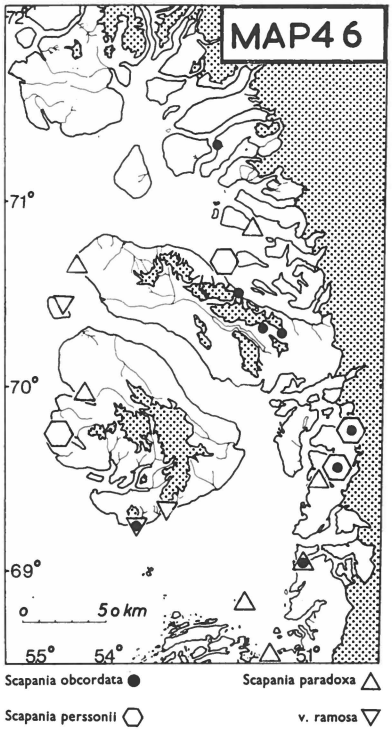
Gymnomitrion apiculatum ●

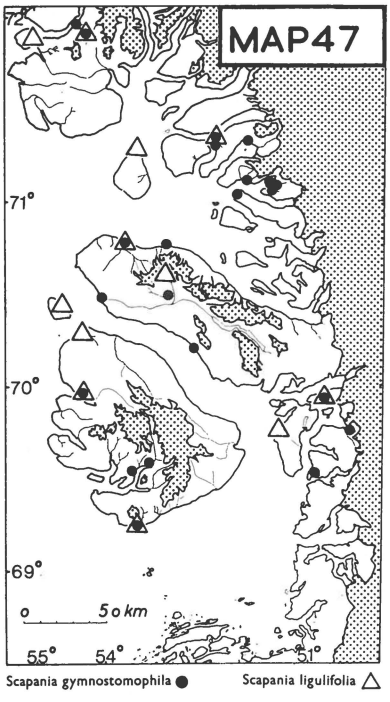


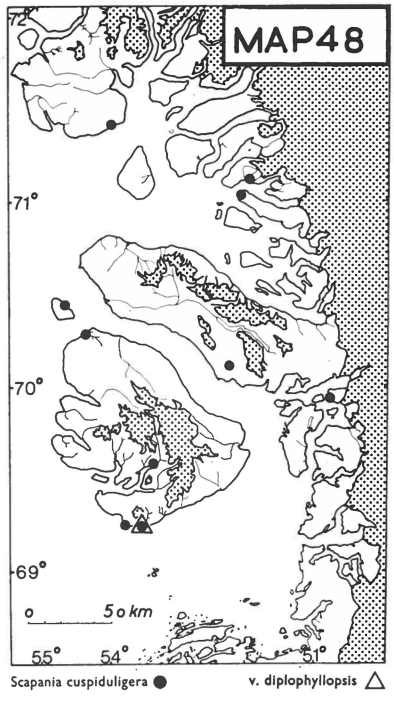
Gymnomitrion concinnatum ●

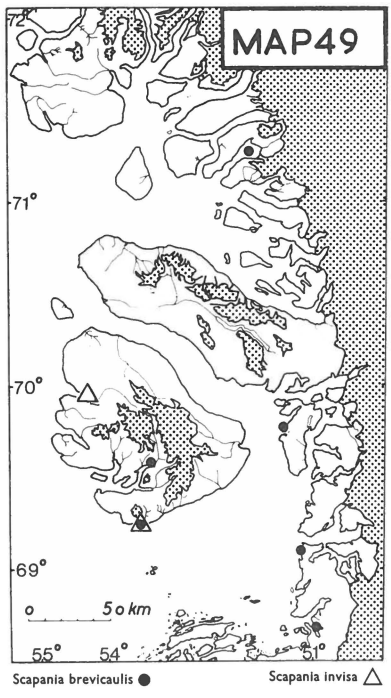
Gymnomitrion corallioides △

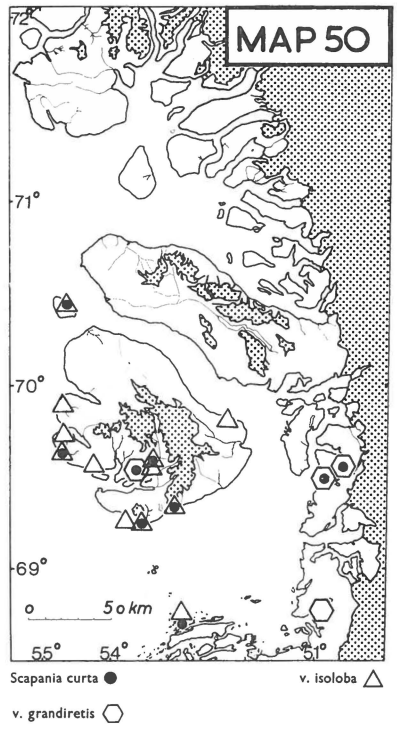

MAP45
72°
71°
70°
69°
0 50 km
55°
54°
51°
Diplophyllum albicans
Diplophyllum taxifolium
Diplophyllum obtusifolium

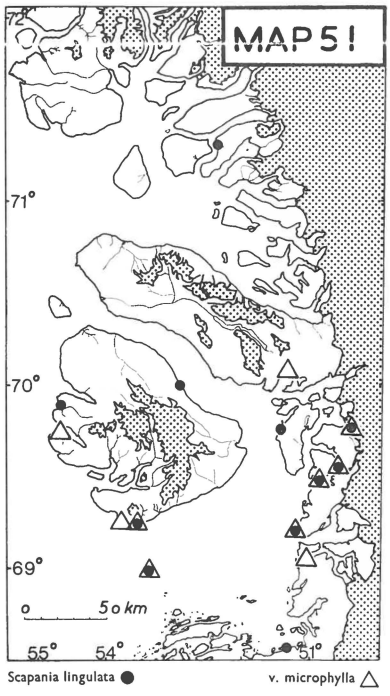

MAP46
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania obcordata
Scapania paradoxa
Scapania perssonii
v. ramosa

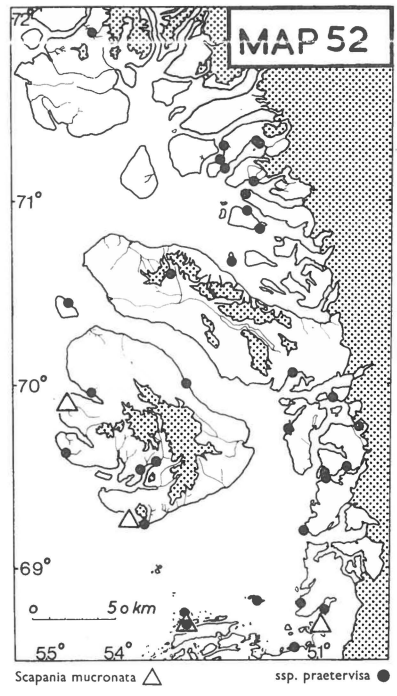

MAP47
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania gymnostomophila
Scapania ligulifolia

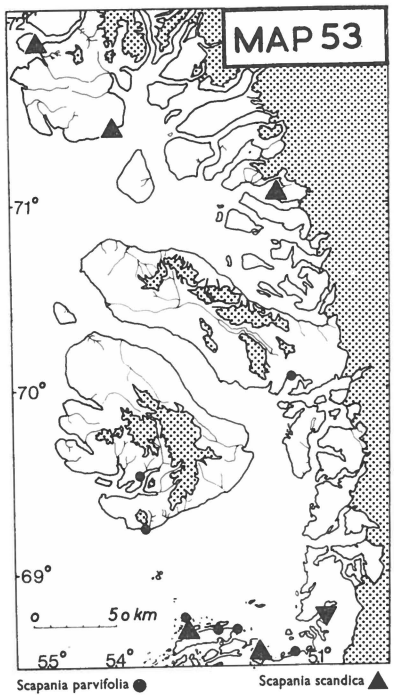

MAP48
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania cuspiduligera
v. diplophyllopsis

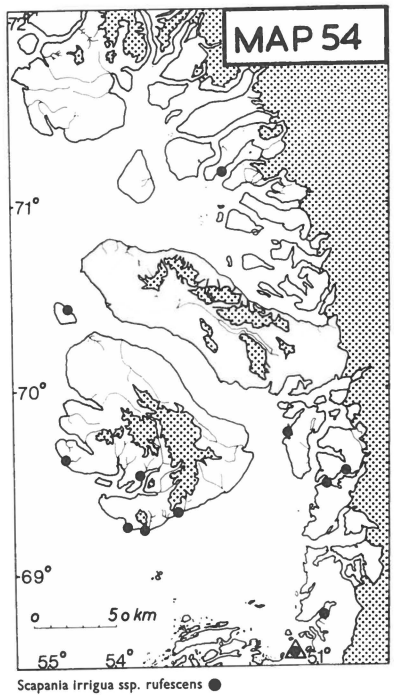

MAP49
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania brevicaulis
Scapania invisa

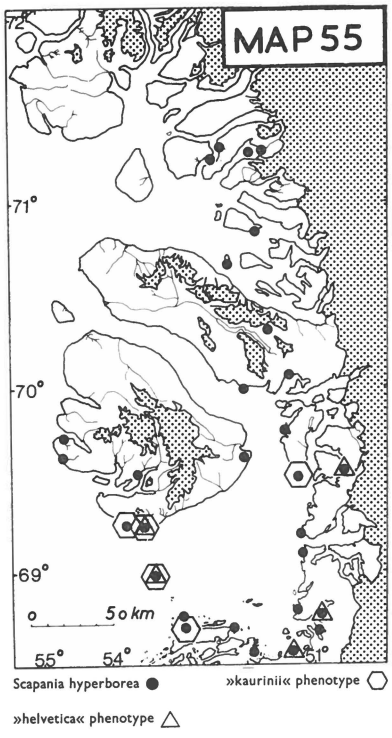

MAP 50
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania curta
v. isoloba
v. grandiretis

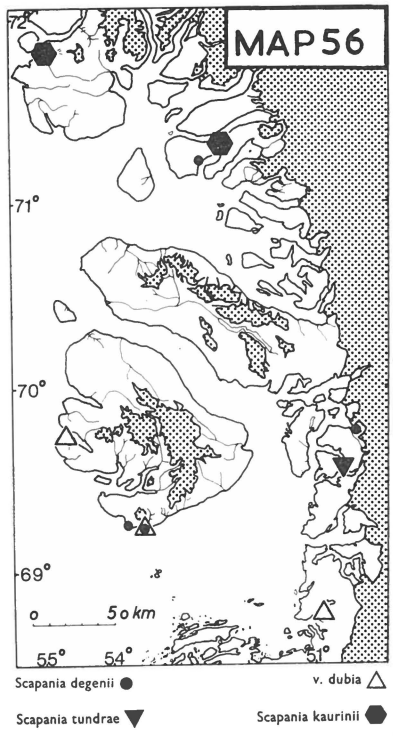

MAP 51
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania lingulata
v. microphylla

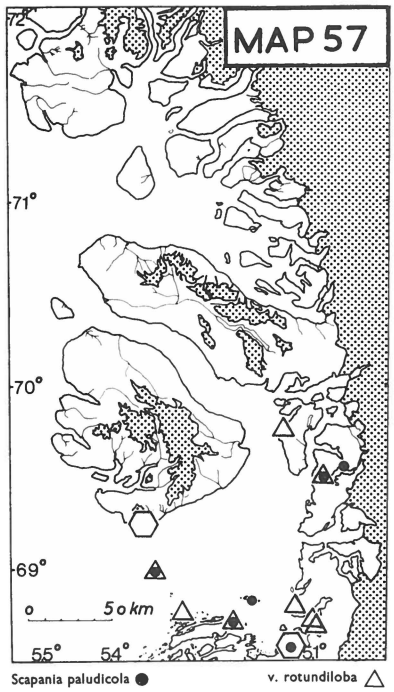

MAP 52
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania mucronata
ssp. praetervisa

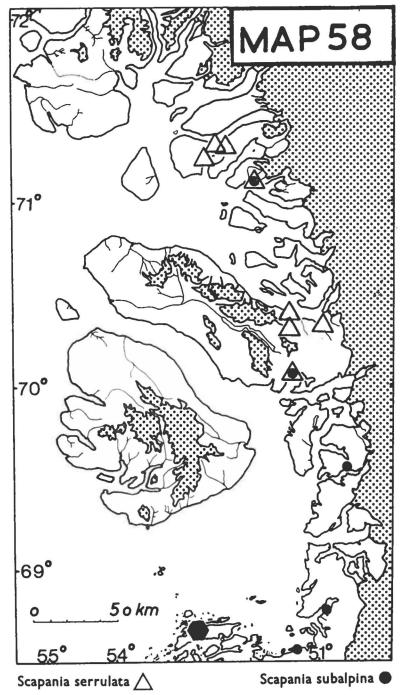

MAP 53
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania parvifolia
Scapania scandica
f. argutedentata

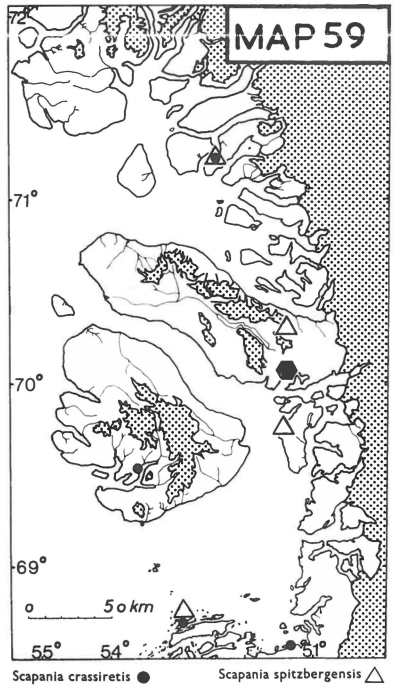

MAP 54
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania irrigua ssp. rufescens
Scapania pulcherrima

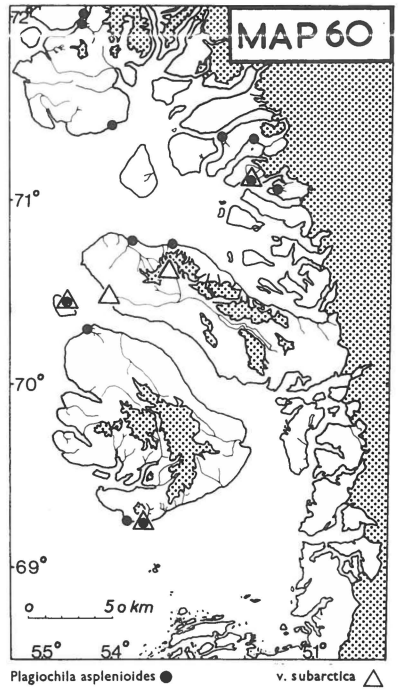

MAP 55
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania hyperborea
»kaurinii« phenotype
»helvetica« phenotype

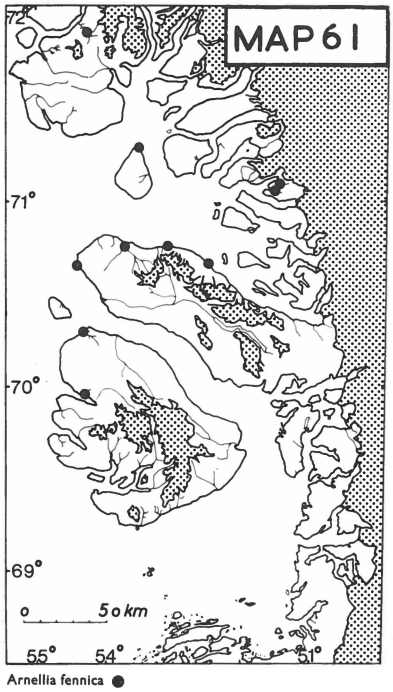

MAP 56
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania degenii
v. dubia
Scapania tundrae
Scapania kaurinii


MAP 57
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania paludicola
v. rotundiloba
v. viridigemma

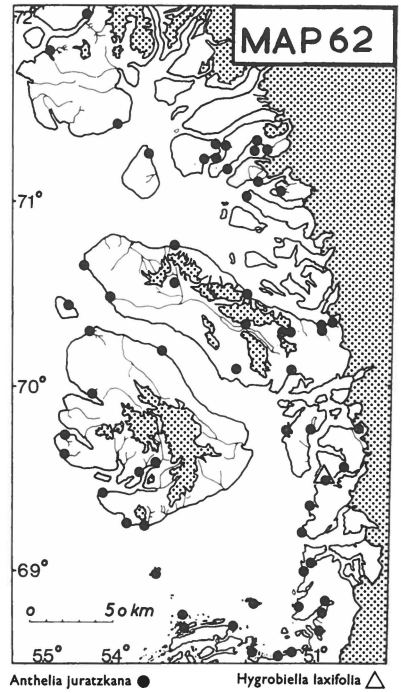

MAP 58
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania serrulata
Scapania subalpina
Scapania uliginosa


MAP 59
72°
71°
70°
69°
0 50 km
55°
54°
51°
Scapania crassiretis
Scapania spitzbergensis
Scapania obscura

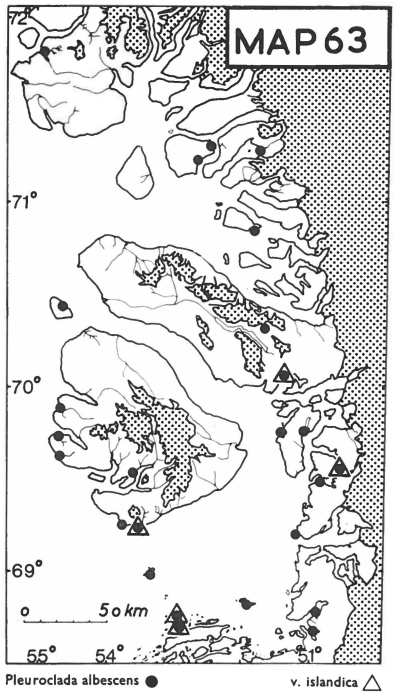

MAP 60
72°
71°
70°
69°
0 50 km
55°
54°
51°
Plagiochila asplenioides
v. subarctica



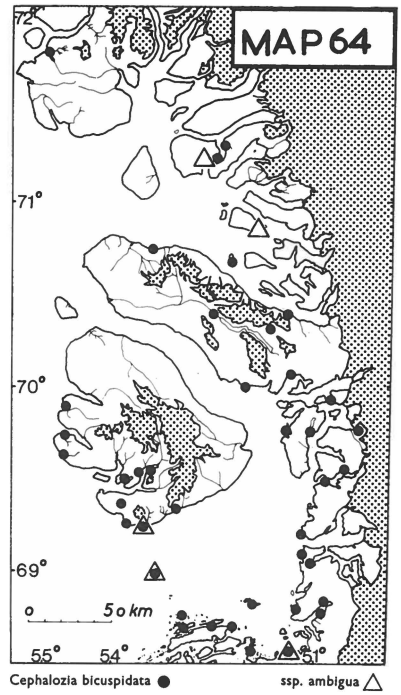
Arnellia fennica ●



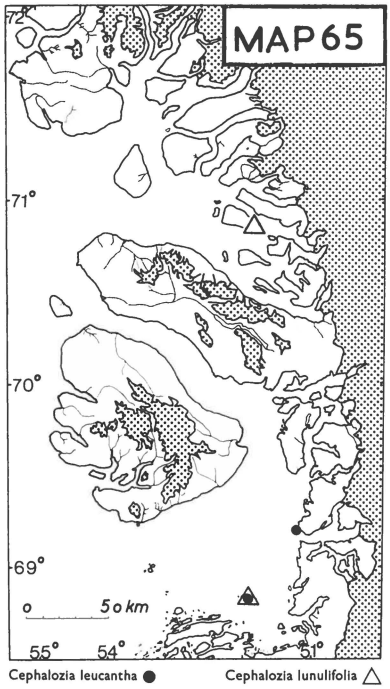
Anthelia juratzkana ● Hygrobiella laxifolia △



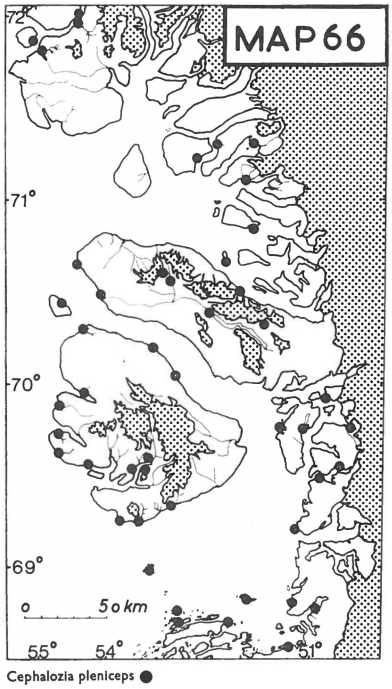
Pleuroclada albescens ● v. islandica △



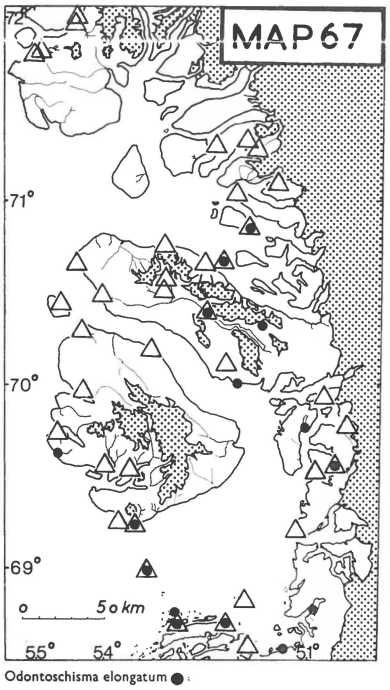
Cephalozia bicuspidata ● ssp. ambigua △



Cephalozia leucantha ● Cephalozia lunulifolia △

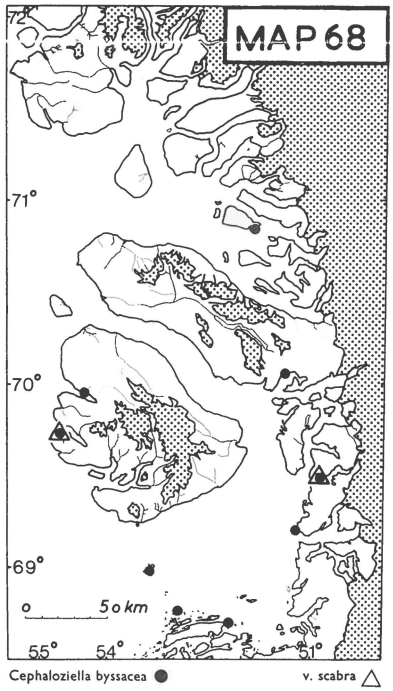


Cephalozia pleniceps ●

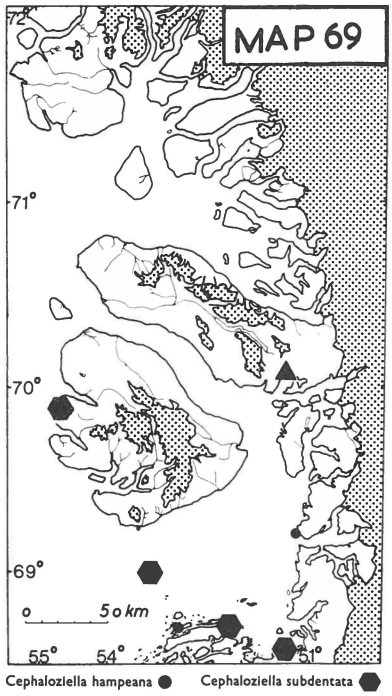


Odontoschisma elongatum ●

Odontoschisma macounii △

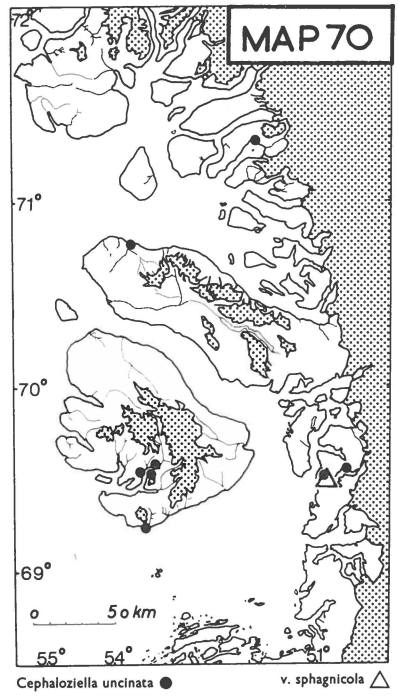


Cephaloziella byssacea ● v. scabra △

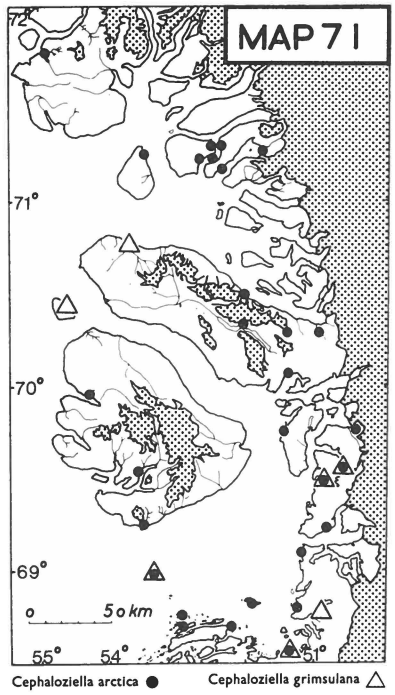


Cephaloziella hampeana ● Cephaloziella subdentata ⬢

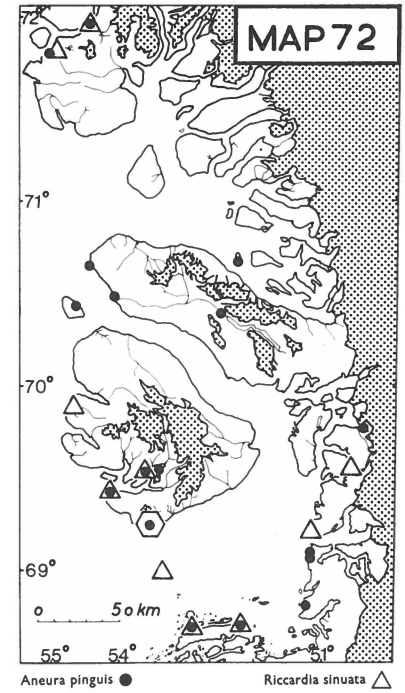
Cephaloziella rubella v. arctogena ▲



Cephaloziella uncinata ● v. sphagnicola △

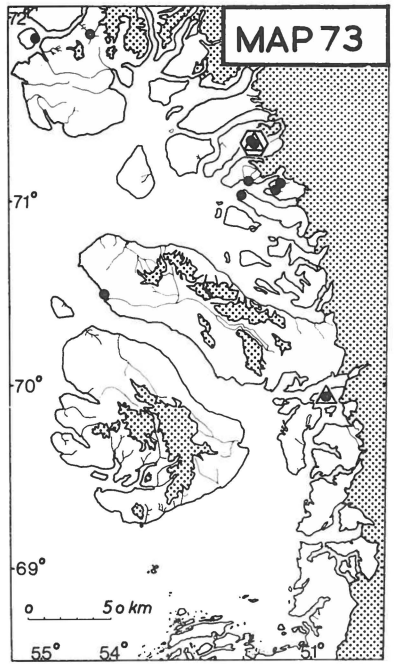


Cephaloziella arctica ● Cephaloziella grimsulana △



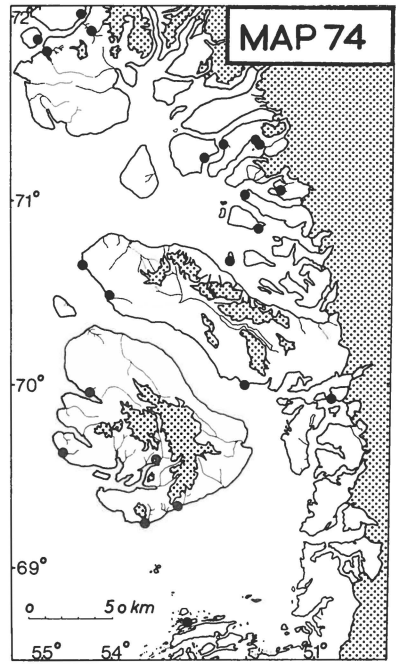
Aneura pinguis ● Riccardia sinuata △

Cryptothallus mirabilis ⬡

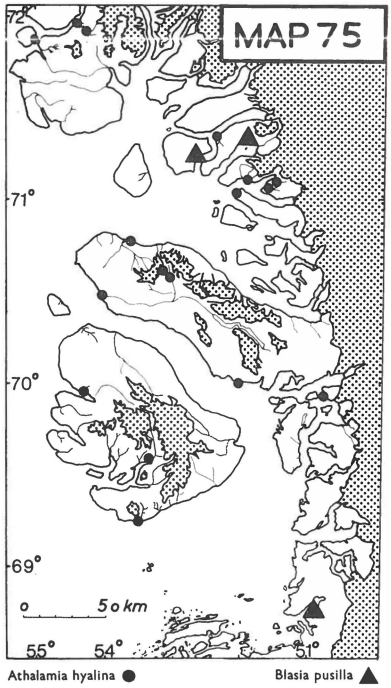


Mannia fragrans △ Mannia pilosa ●

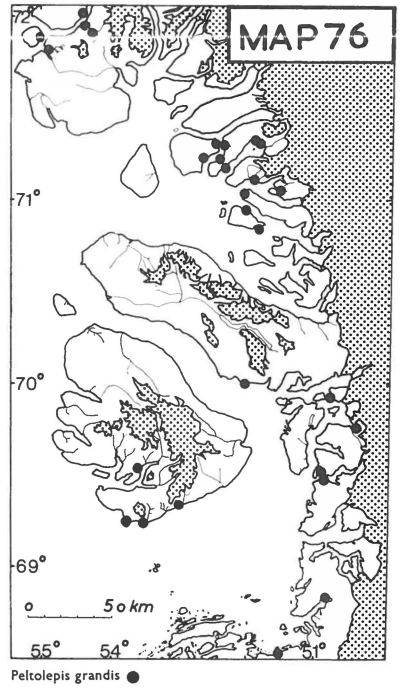
Mannia sibirica ⬡



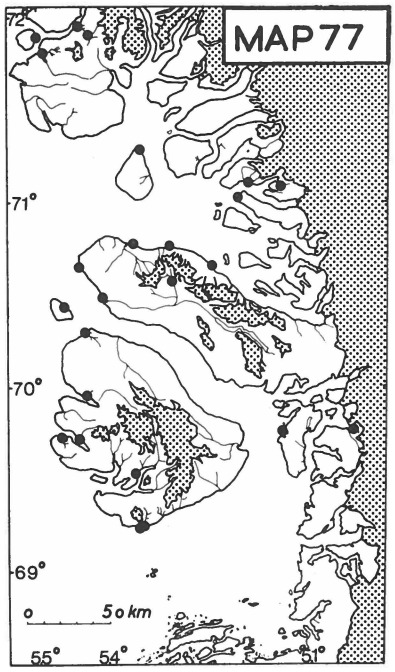
Asterella ludwigii ●



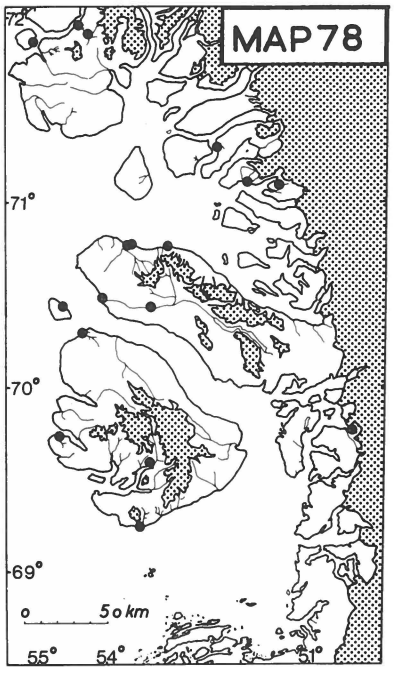
Athalamia hyalina ● Blasia pusilla ▲



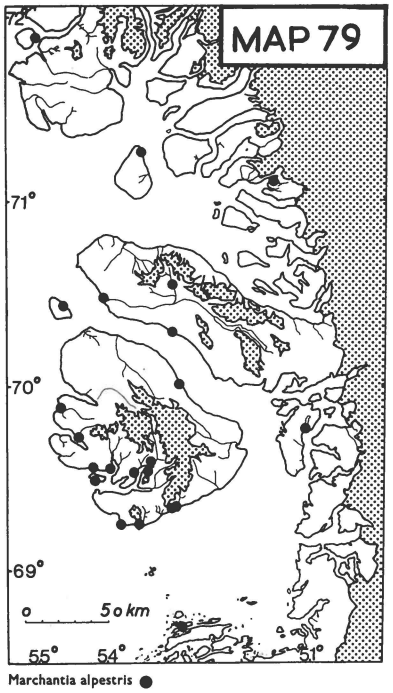
Peltolepis grandis ●



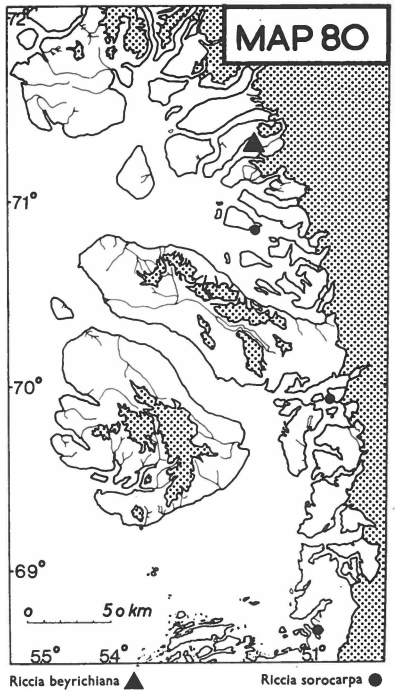
Sauteria alpina ●



Preissia quadrata ●



Marchantia alpestris ●



Riccia beyrichiana ▲ Riccia sorocarpa ●