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CONTRIBUTIONS TO THE FLORA AND PLANT GEOGRAPHY OF WEST GREENLAND

I.

SELAGINELLA RUPESTRIS AND *SISYRINCHIUM MONTANUM*

BY

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WITH 7 FIGURES IN THE TEXT AND 2 PLATES

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INTRODUCTION

The following work deals with two species of plants whose occurrence in Greenland, total range, and biological features are of particular interest.

Prior to the war, studies on the flora of Greenland had reached a phase of discussion and hypothesis. Certain curious distributions seemed to suggest that some species, even some southerly ones, had existed in Greenland for a very considerable time. They were either to be regarded as survivals of the postglacial warm period, demonstrated as far as Greenland is concerned by HARDER & ADOLF JENSEN 1910 and IVERSEN 1934, in which case there was a possibility of post-glacial immigration, or they must have survived the last Glacial Age in Greenland, so that their immigration might have been interglacial. Unfortunately, there is still a lack of adequate geological evidence to enable the questions of immigration to be answered satisfactorily.

Some new data will be submitted in the following, data which, among other things, in a striking manner once more raise the immigration problem and actualize the question of plant refuges during the course of the glacial periods in Greenland. The chief purpose of the work, however, is to describe the biology and distribution of the two species and, by that means, to enter upon some reflections of importance to the plant geography of West Greenland.

SELAGINELLA RUPESTRIS (L. PART.) UNDERW.

This new species to Greenland was discovered in the course of an excursion at Narssarssuaq (Kiagtût), near the head of the great Tunugdliarfik fiord in South Greenland, lat. 61°9′ N. The area forms a lateral valley to the main fiord and is 80 km from the open sea. During the war the United States established an air base in the bottom of this valley. The direction of the valley is NNE—SSW. On account of the short time available, the excursion could cover only certain parts of the east side of the valley. Here we found luxuriant thickets of *Betula subescens* sup to a height of 4 metres, and an interesting rocky ground with dry rock shelves, where there was too thin a layer of soil to permit of tree growth. There was a good deal of variation in the vegetation on these shelves, but it was distinctly separated from other vegetation by species such as *Woodsia ilvensis*, *Saxifraga aizoon* and *Juniperus communis* var. *montana*. It was on these shelves that *Selaginella rupestris* was observed.

I follow HIERONYMUS (1902) in calling the plant *S. rupestris* (L. part.) Underw., as it was UNDERWOOD (1898) who described the species in detail. In most publications SPRING (1848) is mentioned as the author, but SPRING separated a var. *borealis* and a var. *tropica* within his very copious *S. rupestris*, and neither his limitation of the main species nor the varieties correspond to the plant now under discussion. *S. rupestris* (L.) Underw. may be regarded as a species within a collective species which perhaps might be called *S. rupestris* (L.) Spring. UNDERWOOD, by the way, draws attention to the fact that *Lycopodium rupestre* was based by LINNÆUS on a figure by DILLENIUS representing an East American plant.

The Greenland material of *Selaginella rupestris* agrees very well with that from East America in the Botanical Museum, Copenhagen. The colour is grey-green, the shoots are 3 to 5 cm high and 1,5 to 2.5 mm wide, growing very closely together in small clusters, their branches rising from a common basal shoot which carries rhizophores and is sometimes somewhat creeping, but often is more or less vertical and seems to die away at the base. Nearly all shoots are fertile, and

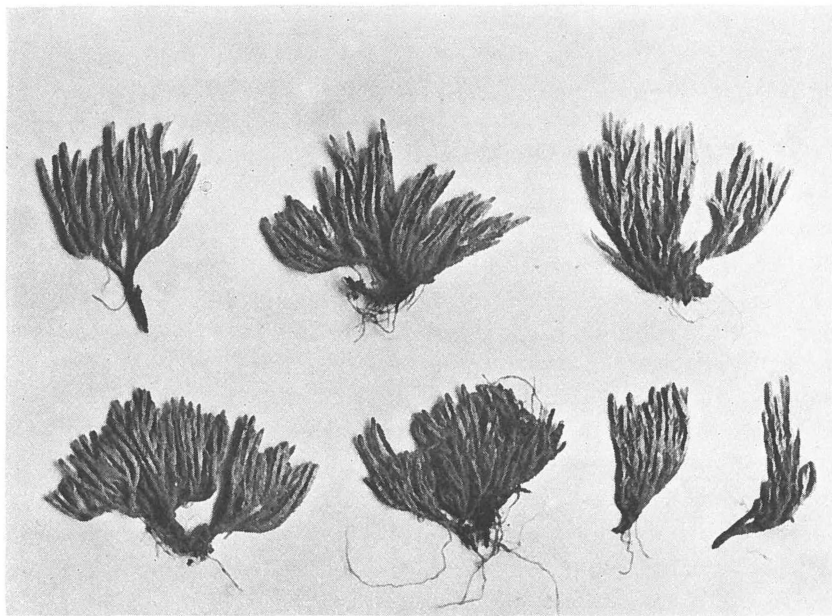

Fig. 1. *Selaginella rupestris* (L.) Underw. Material from Greenland. Most shoots with long cones; the specimen at the middle of the lower row alone consists of partly withered shoots and has only few and short cones. × 1/2. M. Køie phot.

the sporangia-bearing part is much the largest of the whole plant. The megaspores are pale yellow and coarsely reticulate. The diameter is 450—560 μ (mean of 10 measurements 507 μ). See fig. 1 and Plate 1.

Apomixis.

Whereas material of the closely related *Selaginella sibirica* (Milde) Hieron., which grows in Alaska and East Asia, had numbers of microsporangiae, it was impossible to find any in the Greenland and East American material of *S. rupestris*. In the Greenland material the megaspores are extremely large and do not occur in tetrads; only one megaspore is developed as a rule. This very remarkable circumstance demanded closer investigation, and therefore a series of transversal and longitudinal sections were cut through the cones on the microtome and stained with crystal violet or Feulgen's nucleal stain. The material was fixed in Greenland in Carnoy's fluid. A search was also made in the literature on the problem; it proved to be rather copious.

Hieronymus (1902, p. 660) writes that *S. rupestris* has no microspores and generally forms only one or two mature, unusually large megaspores in each sporangium; furthermore: "Es scheint mir wahrscheinlich, dass die Makrosporen Prothallien entwickeln, welche entweder

parthenogenetisch Embryonen in ihren Archegonien entwicheln oder solche, die direkt durch Sprossung, also apogam, junge Pflanzen erzeugen." HIERONYMUS at that time had not become acquainted with FL. M. LYON's fine investigations (1901), which most certainly suggested apomixis in *S. rupestris*. According to LYON, this species is almost purely megasporangiate. The megaspore mother cells might divide once or twice, so that two or four megaspores were formed; occasionally, however, the mother cell failed to divide and acted directly as a megaspore. Also, two mother cells might function and form eight megaspores. In any case, only one or two spores continued to grow later. No gametophytes were observed. Both LYON and later REEVE (1935) illustrated dumb-bell shaped double megaspores.

Later, in 1904, (p. 286—87) LYON demonstrates that apomixis is actually involved; in describing the development of the sporophyte in *S. rupestris* she writes: "It may be recalled that this is the form of Selaginella with a reduced number of functional megaspores (one or two) which are not shed until the embryo is fully equipped with leaves and root. In certain localities, the microspores are rarely produced and the embryos are frequently formed from the initial cell of the archegonium. Until the third or fourth division of this initial, it is impossible to determine whether a normal archegonium will result or an embryo."

Finally, GRAUSTEIN (1930) made a thorough study of *S. rupestris* and found that cones collected in seven widely separated regions showed that the species is almost wholly megasporangiate. From one station fifteen cones were cut, in which were only two microsporangia, and those were both in one cone. Of much importance is his observation that no typical (meiotic) prophases were seen in the megaspore mother cells. Many megaspore mother cells complete two divisions, which however are scarcely meiosis. In sixty-eight sporangia 44 per cent. contained two, 28 per cent. three, 25 per cent. four and 3 per cent. six megaspores. Regardless of the number of spores, only one or two grow. Many spores are dumb-bell or kidney-shaped, suggesting an uncompleted nuclear division. No gametophytic development was seen. The microspores too were often dumb-bell shaped, or might have bizarre forms. They always appeared in dyads. A very large number of the spores were sterile. The chromosome number is considered to be relatively high.

My own material, which was collected in Greenland, conforms closely to LYON's and GRAUSTEIN's descriptions. Only a single microsporangium was observed in sections through many cones, and in it all the spores were empty and shrunken. The majority of the megaspores were likewise shrunken or empty. As a rule two megaspores are formed, but generally only one continues to develop. No phase of meiosis was

observed, but in numerous degenerated spore mother cells it could be seen that the chromatin was lumped together in an abnormal manner. Neither spores sown on moist filter paper in a Petri dish nor spores sown in pots resulted in germination of the megaspores, which therefore must have been sterile.

Particularly on account of LYON's observations it must be regarded as an established fact that *Selaginella rupestris* propagates apomictically, and therefore it is probable that the polymorphism in *S. rupestris* coll., as in *Taraxacum* etc., is connected with this fact. However, it is by no means certain that all plants which, even today, are referred to *S. rupestris* s. str. propagate apomictically. For instance, it is noteworthy that R. T. CLAUSEN (1946) in his description of *S. rupestris* simply writes: "microspores deep yellow, 0.04—0.06 mm in diam., megaspores creamy white, 0.3—0.5 mm in diam., coarsely reticulate". His picture of the megaspores and the fairly small size of the latter might indicate that they grew in tetrads. His habitus figure shows a plant from Alabama that is much more creeping than the material of the species known to me. There is accordingly some probability that especially in the southern range of the species there are types which in time should be separated as independent species or sub-species (cf. the remark p. 11 on the sexual plants from Texas).

Other cases of apomixis in *Selaginella* are described by H. GEIGER 1935.

Ecology and Distribution.

The vegetation of which *Selaginella rupestris* forms a part in its station in South Greenland is a sub-arctic boreal rock community related to NORDHAGEN's *Saxifragion cotyledonis* in Scandinavia. According to NORDHAGEN (1943), vegetation of this kind is less typically developed in Scandinavia, because there are only very few exclusive rock plants. In Greenland there seem to be more typical rock communities. In a later paper I shall describe material of a *Dryopteris fragrans* sociation from the rocks in Søndre Strømfjord. At Narssarssuaq there were three types of this vegetation, one, dominated by *Selaginella rupestris*, attracting most attention. It was developed on very dry, sun-warmed rock shelves of Igaliko sandstone. The soil was sandy and rich in humus, the layer being very thin. At places where the soil was deeper, less warm and dry, there was low *Juniperus* heath or a mixed community of very different plants, among which special mention should be made of *Saxifraga aizoon*, *Sedum roseum*, *Chamaenerium angustifolium*, *Viscaria alpina*, *Thymus arcticus*, *Alchemilla alpina*, *Campanula rotundifolia*, *Potentilla tridentata*, *P. Crantzii*, *Draba aurea*, *D. incana*, *Sedum annuum*, *S. villosum*, *Luzula spicata*, *Botrychium lunaria* and *B. lanceolatum*.

Table 1.

Dry, almost flat rock shelf on south-exposed rock. Sandy soil rich in humus. The figures indicate the degree of covering by HULT-SERNANDER's scale. Size of quadrate 1. sq.m.

Selaginella rupestris	4	Poa glauca	+
Woodsia ilvensis	2	Deschampsia flexuosa	1
Potentilla tridentata	1—2		
Sedum annuum	1—2	Rhacomitrium canescens	3
— roseum	+	Polytrichum piliferum	2
Rumex acetosella	1—2	Hedwigia ciliata	1
Juniperus comm. var. montana	1	Stereocaulon alpinum	2
Thymus arcticus	1	Cladonia mitis	2
Cerastium alpinum	1	— coccifera	1
Festuca ovina	1	Cetraria crispa	1

In the *Selaginella* sociation, which was observed at three different places but which unfortunately I had time to analyze only at one, there are three true rock plants, viz. *Selaginella rupestris*, *Woodsia ilvensis* and *Potentilla tridentata*. Of these, however, only the species of *Selaginella* is an exclusive character species, to judge by all the signs; the others have a marked predilection for rocky ground. Species such as *Sedum annuum*, *S. roseum*, *Rumex acetosella* and *Juniperus communis* var. *montana* are also fond of rocks. Table 1 shows the analysis of the *Selaginella* sociation.

The total distribution of *Selaginella rupestris* (L.) Underw. appears from fig. 2, which in the main is based on a map by R. T. CLAUSEN (1946). What has been added is the Greenland find as well as another on the summit of Shobel's Mt. in Western Nova Scotia (FERNALD 1922 p. 160), finds at Lake Athabasca (RAUP 1936 p. 193) and Radville in Saskatchewan (DERICK 1919). In America it has a rather southerly distribution, at any rate compared with other American species which also occur in Greenland. It is quite distinctly associated with the deciduous forest region and part of the prairie region.

On the occurrence of *Selaginella rupestris* in America R. T. CLAUSEN reports that it grows on rocks mostly in exposed situations, rarely in sand. Further: "since it usually occurs on rocks, it is commonest in mountainous regions and on bluffs along streams in areas of slight relief. It seems rarest on the flat coastal plain". In Arkansas near the southern limit of the species it is found exclusively on dry sandstone. MOORE (1940) describes one locality as follows: "It is in the thin sandy soil on the edges and exposed surfaces above that *S. rupestris* occurs." Here it is usually associated with *Polytrichum* sp., *Cladonia* sp. and often with species of the genus *Talinum* (*Portulaccaceae*) and *Sedum*. At other places

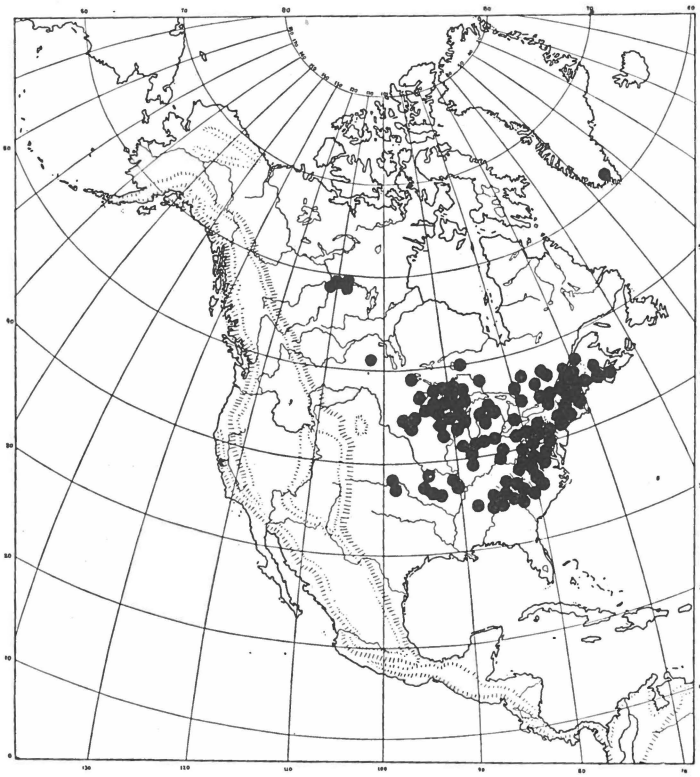

Fig. 2. Total range of *Selaginella rupestris* (L.) Underw.

apparently it grows on bare rock or in crevices between strata. These descriptions show that American localities bear a striking likeness to the Greenland locality. C. M. Derick (1919 p. 69) also mentions *S. rupestris* in an area in southern Saskatchewan with dry sandy soil, approximately four inches in depth, overlying a peculiar sticky clay. The flora includes *Polytrichum piliferum*, *Pulsatilla* and *Artemisia* species.

In his work on the vegetation on the inland sand deposits of Illinois Gleason (1910) also mentions *Selaginella rupestris* among the bunch-grass vegetation of the prairie, where it grows particularly in open places and is of importance in binding sand and, under certain conditions, has a prominent part in stabilizing blowing sand. It forms circular patches which are converted into rings by the death of the centre. It is also mentioned as the pioneer invader which starts the succession from open sand to bunch-grass vegetation. When the vegetation on windward slopes in blow-outs is undermined by the wind, whole mats of *Selaginella rupestris* slide down the slope but are able to persist at the bottom. Sampson (1921) gives the species as an important pioneer in various successional stages on sand. Gleason (p. 54) adds that "the megaspores

are produced in enormous quantities, but their successful growth must be rare".

LYON (1901) also discusses the ecology of the plant. She says that in New England the species is encountered on rocks wherever there has been enough weathering to ensure the deposition of a little soil in the hollows. "For six months a year they endure alternate drought and drenching, and the frequent and rapid changes of temperature, with no more protection than is afforded by their own structural adaptations.

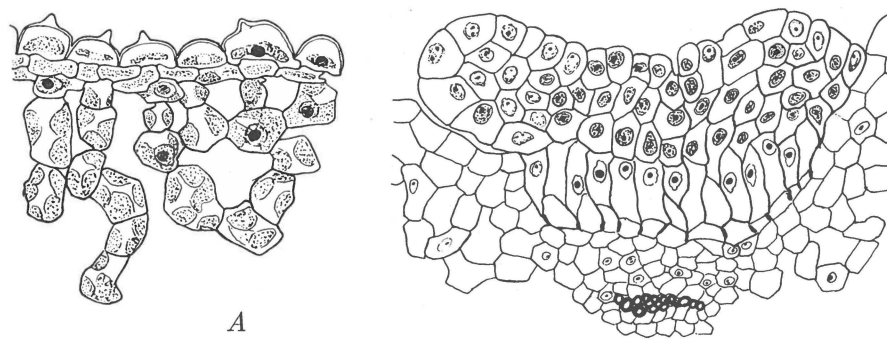

Fig. 3. *Selaginella rupestris*, material from Greenland. A: Cross section of very papillous epidermis on sporophyll. B: Cross section of ligula; at its base the elongated glossopodium cells and the sheath, of which the cells have Casparian strips. A×750, B×350.

The midsummer conditions are even more trying. The plants grew on bare rocks upon which the sun beats nearly all day from June to September." See also fig. 4 in MARIE-VICTORIN & MEILLEUR 1940. LYON examined the anatomy of the species too and places its pronouncedly xeromorphous structure in relation to its habitat. The anatomy of the leaves and the sporophylls was described by both HARVEY GIBSON (1897) and LYON. From the latter's work I take the following passage, which provides a good impression of the structure. "The closely overlapping sporophylls form four rows, in whose axils the sporangia have little space to develop. The growing apex is protected by at least twelve and frequently sixteen sporophylls which envelop it. The epidermis is two or three layers of cells thick on both surfaces of the sporophyll, except in a shallow groove running lengthwise along the middle of the ventral surface. In this groove are the comparatively large crowded stomata, which are protected by the next older overlapping sporophyll of the same row." To this description, which may also be applied to the Greenland material, I may add that the outermost epidermis cells on both sides of the stoma groove on the aligular side are very papillous. It is

these papillous areas that are particularly exposed to the light. The epidermis cells of the ligular side have thick, cutinized walls. On fig. 3 is a detail showing the papillous epidermis. The ligula, which must also be of importance to the water supply of the plant, consists of large-nuclear cells rich in plasma. It is demarcated from the leaf by a glossopodium of elongated, highly vacuolized cells and an endodermis-like sheath with Casparian strips (fig. 3 B).

As to the spreading of the species, LYON writes that to a great extent this proceeds vegetatively by means of prostrate branches which attach themselves by rhizophores to the humus soil and subsequently lose connection with the parent plant. She found very few young plants that originated from spores, even though the soil may be thickly beset with spores that have been shed. "Bits of old plants that have been torn off by the action of the wind or rain are frequently caught in crevices along the precipices, and it is from these that new clumps are most frequently started." Later in her paper LYON points out that a rich development of seedlings may sometimes take place after rainy periods. However, part of her material seems to have come from Texas from sexual plants which, according to UNDERWOOD's classification, belong to a closely allied unnamed species. Consequently it is not clear whether it is the apomictic type that forms many seedlings. Finally, there is the possibility that some *S. rupestris* forms propagate exclusively in the manner described above. There is a good deal of investigation still to be done in this field.

SISYRINCHIUM MONTANUM GREENE

Synonym: *S. angustifolium* sensu Bicknell, see FERNALD 1946.

On the Botanical Expedition to West Greenland 1946 this species was discovered by the expedition bryologist, KJELD HOLMEN. It was found in quite a small area at the head of Søndre Strømfjord's northern arm in lat. 67° N. The locality was later examined by the present author with the assistance of HOLMEN.

Sisyrinchium montanum has been found in Greenland before, first by IVERSEN in 1935 at Nunatarssuaq at the head of Godthaabsfjord, later by IVERSEN and TROELS-SMITH in three other localities up the same fiord (see IVERSEN 1938). Thus we now have the species from five different places in West Greenland.

The material from Søndre Strømfjord was collected on August 27th. At this time the plants were ripening their fruits. They were between 17 and 27 cm tall with from one to three flowering shoots on each individual (see fig. 4). The capsules were 3.0—5.5 mm high, the leaves 1—2.5 mm and the stems 1—1.5 mm wide. Cultivated later in Copenhagen the leaves were 1.5—3 mm wide. Some of the individuals flowered, the flowers being pale blue, not violet blue as in the typical *S. montanum.* The dry specimens are rather dark and thus the material must be referred to *S. montanum* var. *crebrum* Fern. (see FERNALD 1946), perhaps to a special sub-variety with pale blue flowers.

There is no doubt that a modern taxonomical treatment of the species-group around *S. montanum* is called for. FERNALD's study (1946) on the identity of *S. angustifolium* sensu BICKNELL is a very valuable contribution to a monographic treatment. Various authors have drawn attention to the polymorphism of *S. montanum.* RAUP (1935) says that the species in the region southeast of Great Slave Lake presents considerable variation and may prove to contain more than one entity, and BICKNELL (1899) states that the species is something of an aggregate and will be found to include at least several geographical races. FERNALD's var. *crebrum* seems to be a variety with easterly distribution. The Greenland specimens from Søndre Strømfjord are very like plants from West Newfoundland (FERNALD) and Timagami Lake, Ontario (C. H. OSTENFELD) and several others in the collections of the Botanical Museum, Copenhagen.

Distribution.

American manuals give the range of *Sisyrinchium montanum* as being from Newfoundland to Virginia, westwards to British Columbia, Colorado and Utah. The northern limit on the east coast, however, must be put at 54°, Hamilton Inlet on the coast of Labrador (see WETMORE 1923).

Fig. 4. *Sisyrinchium montanum* Mill. Material from Søndre Strømfjord, West Greenland. Lat. 67° N. × 2/3. M. KØIE phot.

Northwards according to MACOUN (Catal. Canad. Pl.) the species ranges to Hudson Bay and, according to RAUP (1936), to Buffalo Park in the region between Great Slave Lake and Lake Athabaska and Upper Mackenzie River. From there the boundary must be drawn to the northern and eastern part of British Columbia, where the species was found on Columbia River (MACOUN). It is said to be missing in the state of Washington and in California, but in TIDESTROM's Flora of Utah and Nevada (1925) it is indicated "westward to British Columbia and California". To the south it does not reach beyond Colorado, where it is alpine; the southern boundary also runs through Nebraska, Iowa,

Illinois and northern Indiana to Virginia on the east coast. The American-Greenland range will be seen in fig. 5. The dots indicate herbarium specimens as well as the localities recorded by BICKNELL, WETMORE, RAUP and FERNALD. The hatched areas are where the species is mentioned in the literature. Naturally, the map merely shows the range of the species within its current limitations. The var. *crebrum* occurs in

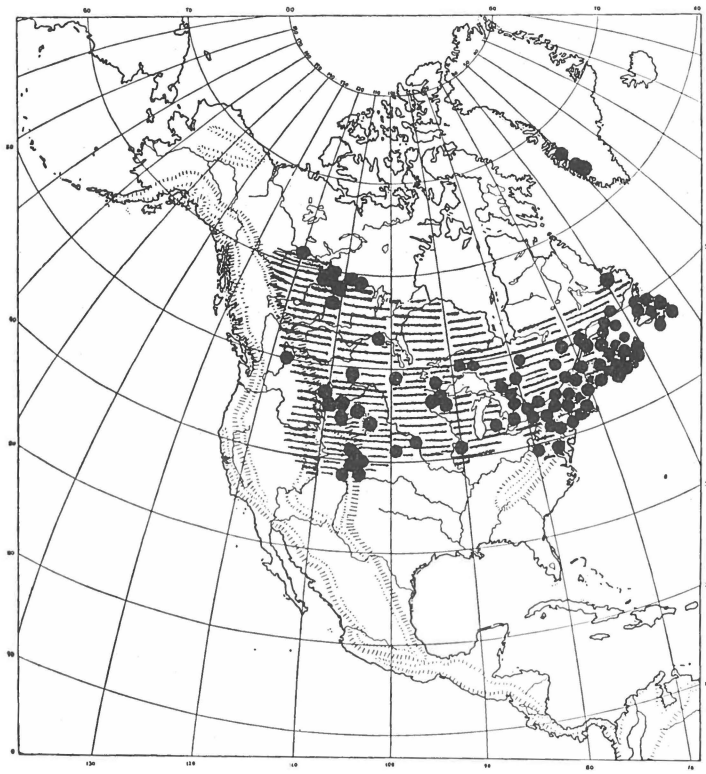

Fig. 5. American-Greenland range of *Sisyrinchium montanum* Greene.

Greenland, Newfoundland to Ontario, south to Nova Scotia, New England, Pennsylvania and the mountains of W. Virginia (FERNALD).

Outside of America, *Sisyrinchium montanum* has an area in western Ireland. PRAEGER (1934) and others believe it to be spontaneous there. Otherwise it has been found introduced in Europe, for example in the south of England and in Denmark, and, according to HEGI's flora, in many places in Central Europe. In the Carpathians at the sources of the river Pruth near Kolomea the species occurs in the wildest parts of the mountains up to about 1000 metres above the sea, and here it seems not impossible that it is a very ancient, pre-glacial relic and not introduced from North America (see WROBLEWSKI 1914 Kopern. Kosmos Roč. 49, pp. 26—32; LAUTERBORN 1927 Mitt. Bad. Landesver.

Fig. 6. The station of *Sisyrinchium montanum* at the head of Søndre Strømfjord. *Kobresia myosuroides* sociation. In the background *Salix glauca* scrub and the fiord. T. W. B. phot.

f. Naturk. N. F. Vol. 2, p. 84). It is remarkable that in other places in the East Carpathians the species also occurs indigenously. DOMIN & KRAJINA's Flora Čechoslovenica exsiccata No. 328 comes from Rossia Subcarpatica "In pratis montanis species haec originis boreali-americanae impressionem plantae indigenae praebet". It has also been found in Upper Tatra (see GYÖRFFY 1934). It is anthropochorous in Mauritius, Australia and New Zealand (MARIE-VICTORIN 1929 p. 140).

The Station at the Head of Søndre Strømfjord.

The vegetation in the systems of valleys that continue Søndre Strømfjord in to the ice cap is very stabilized. In the low land there are particularly four ground-covering types of vegetation. One of these is associated with slopes with a northern exposure and is characterized by dwarf shrub heath of *Betula nana-Ledum decumbens* with *Aulacomnium turgidum* at the bottom. Flat land is dominated by scrub of *Salix glauca* or *Kobresia myosuroides* steppe, though these two communities

are also met with on southern exposures where the soil moisture does not fall too low. At the dryest places on the sunny slopes there is especially a *Carex supina* steppe community.

Generally speaking, the meadow-like herb-field rich in species is totally absent, due to the very severe desiccation. The herb-field requires a constant covering of snow in winter, a constantly high atmospheric humidity and thorough percolation of the soil, and preferably a southern exposure in order to develop typically. No such combination of conditions is to be found in the interior Søndre Strømfjord area. Only rarely is a kind of rudimentary herb-field community met with. Wherever the conditions change in one way or another in the direction of those which favour the formation of herb-fields, there appear different types of vegetation comprising a number of species that are rare or very selective in the region.

Sisyrinchium montanum was in fact growing in a community which in several ways had an ecology approximating that of the herb-field. These communities were found on a small part of the southern mountain slope that rises above the USA air base built during the war at the head of the Strømfjord. Behind the upper ridge of the slope at a height of about 400 metres is a ravine with an elongated and very narrow lake which has an outlet down over the southern fell side. Here we find a gully through which a little water runs in spring or after showers, and on both sides of it some areas where the ground occasionally is soaked with water. Here the soil lies in a rather thin deposit on the solid rock, which forces the water to the surface. The vegetation at these places is remarkable in being distinctly steppe-like and yet containing species requiring rather more moisture. We found various sociations containing *Sisyrinchium*, first and foremost a *Kobresia myosuroides-Carex scirpoidea* sociation rich in species and a ditto *Carex supina* sociation. In these sociations we found from eight to fifteen *Sisyrinchium* individuals per square metre, whereas in sociations dominated by *Festuca ovina* (coll.) or *Calamagrostis purpurascens* there were at the most one or two individuals. It made its best display in the *Kobresia* sociation, where the *Kobresia* tussocks were slightly scattered (fig. 6). It was characteristic that *Carex scirpoidea*, which ecologically approaches herb-field plants, here attains to dominance together with *Kobresia*. The *Carex supina* sociation rich in species was remarkable in that it included quantities of both of Greenland's rare Gentian species, *Gentiana detonsa* and *G. aurea*, as well as *Euphrasia frigida* in large numbers too. Only quite occasionally was *Sisyrinchium* seen together with *Festuca ovina*. This grass increases at the same time as *Woodsia glabella* and several kinds of mosses appear, which indicates rather more moisture. In communities that are a little wetter still (*Carex scirpoidea* sociations or *Juncus castaneus* sociations), *Sisyrinchium* is totally absent. The same is the

case where desiccation becomes too severe and we get the dense *Kobresia*-steppe or a *Carex supina*-steppe with naked or partly lichen-grown soil between the stems. In all we counted 60 individuals of *Sisyrinchium* on the spot; there can hardly be more than a hundred in this locality. Some quadrate analyses of various patches with *Sisyrinchium* will be described in a later paper together with the other analyses of the vegetation in the region. At present we shall confine us self to publish a frequency analysis and an analysis of the degree of covering of the *Carex supina* sociation on a patch of 2 sq.metres which contained 19 individuals of *Sisyrinchium* (Table 2). On Plate 2 fig. 1 is an individual of *Sisyrinchium* together with *Gentiana aurea* just in front of a bush of *Salix glauca*. Fig. 6 shows the locality looking west and Plate 2 fig. 2 looking east. In both pictures a stretch of the bare rock can be seen exposed. After a shower this rock is wet with water which wells up from the vegetation-covered soil. The stick is standing at a spot with several vigorous *Sisyrinchium* plants.

Table 2.

Southern slope, inclination 35°; rather thin Loess layer over occasionally wet rock. *p*H 7.3. The figures indicate the degree of covering according to HULT-SERNANDER's scale (first column) and the shoot density (frequency) in the second column. The principal figure in this column is the number of occurrences of the species within 10 circles $^1/_{10}$ sq.metre in size, whereas the small figures appended to the main figures show the number of occurrences within 10 circles 0.006 sq.metre in size (see BÖCHER 1935).

Carex supina	3—4	10_{10}	Draba sp.	+	3_0
Potentilla nivea.....	+ — 2	9_2	Campanula rotundifolia ..	+	1_0
Artemisia borealis	+	9_2	Trisetum spicatum	+	4_0
Calamagrostis purpurascens	+	8_2	Poa glauca	+	+
Kobresia myosuroides....	1	1_0	Festuca ovina.....	+	1_0
Melandrium triflorum....	+	1_0			
Sisyrinchium montanum .	1	4_0	Ceratodon purpureus	+	10_6
Gentiana aurea	+ — 1	10_7	Tortella fragilis	1	4_0
— detonsa.....	1	9_2	Hypnum revolutum	+	1_0
Euphrasia frigida.....	+ — 1	10_9	Cladonia pyxidata.....	+ — 1	10_6
Salix glauca (seedlings) ..	+	9_3	Physcia muscigena	1	10_3
Cerastium alpinum	+	7_1	Cornicularia aculeata	+	1_0

Ecology.

Its occurrence in Søndre Strømfjord suggests that *Sisyrinchium montanum* here has little ecological amplitude, for it seems to be very selective as regards station. This is what happens to a great many species near their area limits. Outside of Greenland *Sisyrinchium* is less exclusive, but all the same we find a fair measure of agreement between

the occurrence in Greenland and elsewhere. One circumstance makes comparison difficult: the polymorphism of the species. It is very probable that the species consists of races with different ecology.

There is some contradiction between the mode of its occurrence in various parts of its area. In America, for instance in the Chicago region, it is recorded from dry prairie knolls and grassy banks; at other places, Quebec for example, from meadows, and (Nova Scotia) from peat bogs; ROUSSEAU (1938) indeed mentions it from "turbières, sur le littoral en compagnie de l'Empetrum nigrum ou du Juniperus horizontalis, et sur les plages graveleuses". The occurrence in peat bogs recalls the stations in Ireland, where PRAEGER mentions it in old marshy meadows and gravelly stream beds. It would be interesting to have ascertained whether the Irish stock belongs to an Atlantic race or an ecotype found also in Atlantic North America, whereas more continental ecotypes occurred in Central America and perhaps in Greenland (see the writer's theory (1938) on biotype elimination through plant migrations across the North Atlantic). In any case, continental American stations are very reminiscent of the Greenland station. According to RAUP, southeast of Great Slave Lake *Sisyrinchium* is common in prairie openings throughout the upland districts. In dry sandy sink-holes it becomes very abundant and makes up a large part of the herbaceous cover. There are two types of prairie, a very dry *Stipa-Koeleria* steppe and a less dry one, dominated by *Agropyrum trachycaulon*. It is the latter that contains *Sisyrinchium*. The less dry prairie closely recalls the vegetation in the dry sink-holes, where *Sisyrinchium* grows together with *Potentilla anserina*, *P. norvegica*, *Oxytropis splendens*, *Anemone canadensis* and several others besides *Agropyrum trachycaulon*. As in Greenland, this is actually a semi-dry steppe community, conditioned by alternating soil moisture. SAMPSON (1921) refers to the occurrence of *Sisyrinchium* on the prairie in Illinois at the southern border of its range. In the succession from swamp to prairie it grows in the two last and driest communities, the *Panicum virgatum* and *Andropogon furcatus* associations. Both communities consist of tall grasses and perennials and are sometimes invaded by woodland.

One factor of interest for the occurrence of the species in Greenland is its vertical range. In Colorado it rises to over 3,000 metres above sea level (9—11,000 feet in the Sangre d. Christo range), and it is stated to be a prominent species in the *Populus tremuloides* belt at 2,600 metres (F. E. and E. S. CLEMENTS). Thus it extends well up into the sub-alpine region, the upper limit of which according to Cox (1933) lies at 11,000 feet, which conforms well with the fact that it grows in the deep West Greenland fiords where the vegetation is more sub-arctic than arctic. In Ireland *Sisyrinchium* grows in valleys and on the skirts of the mountains on the Ben Bulben plateau, but not on the very tops of the mountains (PRAEGER).

DISCUSSION

The distribution of these two species presents several features of much interest. In both cases they are very southern plants in the flora of Greenland. The *Sisyrinchium* species has a sub-arctic temperate, and the *Selaginella* species a temperate range and southwards approaches sub-tropical regions. In both cases the Greenland localities are separated from the nearest East American ones by a distance of 13 degrees of latitude. IVERSEN (1938) has pointed out the difficulty of imagining a post-glacial immigration of *Sisyrinchium* to Greenland by natural means, without the instrumentality of man, and considers that the species was probably carried to Greenland by the Norsemen during their voyages to Vinland (Gulf of St. Lawrence). He thinks there is no chance of *Sisyrinchium* being an inter-glacial survival as it is "a distinctly thermophilous plant" incapable of living through the climatic depression of the last glaciation. It is obvious that IVERSEN's theory can also be applied to *Selaginella rupestris*, as it has an exactly similar range and also grows at a place where Norsemen once lived. On the other hand, the finding of *Sisyrinchium* in Søndre Strømfjord, where no Norse settlement has been found, detracts from the theory but does not exclude the possibility that *Sisyrinchium* may have come to Greenland with the Norsemen. It may perhaps have been transported to the fiord from Godthaabsfjord, where it grows in the region where the Norsemen lived, on their voyages northwards; for it is less probable that it was twice brought into Greenland, once to a place where there is no definite evidence of Norse habitation.

In actual fact there are two main problems: that of ecology and that of immigration history. The former may be set out as follows: To what degree are the distributions in question unique or deviating?, the latter: Which immigration history is the more probable for these species when all the data are considered?

An examination of plant distributions round about the North Atlantic will show that a whole number of species reach a remarkably long way up towards the north in Greenland. It is particularly striking when America and Greenland are compared. FERNALD (1925) has an

excellent survey of the position, and we may extract the following from his work: In FERNALD's Table II there are about 80 arctic species whose northern limit in America lies between 48° and 83°, the mean being at 69°. In Greenland the northern limit of these species lies between 68° and 83°, with 73° as the mean. Here we find a difference of four degrees of latitude in the mean values. In Table I FERNALD has a similar number of slightly southerly arctic species. In America their northern limits lie between 44° and 85° (mean 65°) and in Greenland between 61° and 85° (mean 73°), the difference here being eight degrees. Finally, there are 13 boreal species in his Table III that are common to Greenland and America. In America their northern limit is between 49° and 60° (mean 54) and in Greenland between 61° and 68° (mean 64°), which gives a difference of ten degrees. Taking the species separately, the northern limits are always more to the north in Greenland, varying from 2° to 18° more than in America. Thus there is close agreement between these boreal species and *Sisyrinchium montanum* and *Selaginella rupestris*, where the difference amounts to 13 degrees of latitude. However, the 13 boreal species in FERNALD's Table III comprise nothing like all more or less southerly species that make the great leap from the Newfoundland region to Greenland. On page 320 FERNALD writes that 75 species occurring in Greenland (18 per cent. of its flora) reach their northernmost limit of range in North America at or near the straits of Belle Isle, their northern limits varying from 48° to 54°. In addition to the species on the maps (see fig. 7) these include e. g. *Polystichum lonchitis*, *Orchis rotundifolia*, *Ranunculus reptans*, *Coptis trifolia*, *Arabis Holboellii* and *Menyanthes trifoliata*. The curious fact is that among the many species making the leap there are both those with an oceanic distribution (*Subularia*, *Cornus suecica*) and those with a continental distribution (*Orchis rotundifolia*, *Carex pratensis*, *Calamagrostis purpurascens*).

There cannot be any doubt that the distribution of the *Sisyrinchium* and *Selaginella* species is nothing unique; on the contrary, it agrees with that of a large number of other southern plants. For this reason we should now prefer to formulate the problem thus: Is there reason for supposing that the Vinland voyages of the Norsemen led to the introduction of all the southerly and westerly species into the flora of Greenland which in America do not grow north of 54°?

Before going further into the matter, let us see whether there are climatic factors capable of explaining these peculiar distributions. Fig. 5 in my paper of 1938 gives curves for the thermic continentality. All these curves leave Greenland and bend southwards, reaching eastern America 10 degrees farther south. Almost the same holds good of the isohyets. We see that the agreement with the plant distributions is particularly close, and it is fairly easy to see an ecological explanation

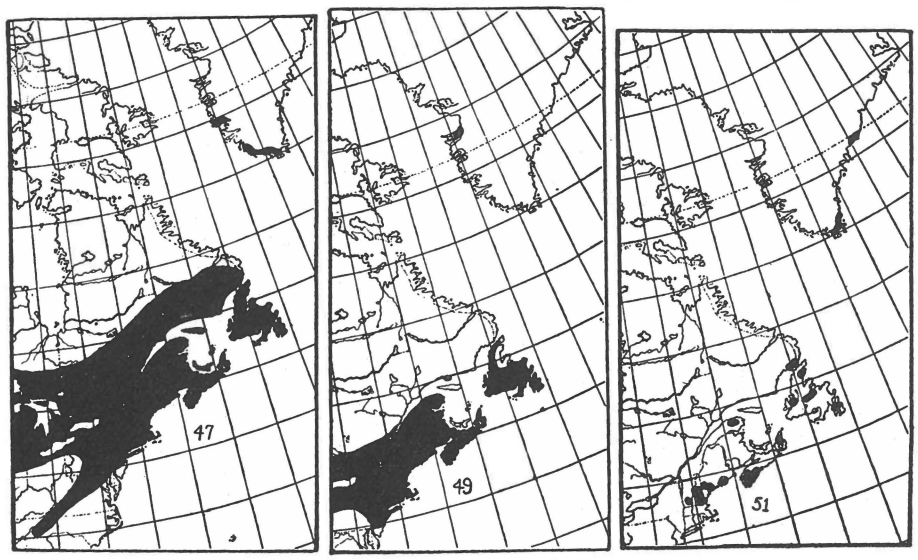

Fig. 7. Three species with a distribution rather similar to that of *Selaginella rupestris* and *Sisyrinchium montanum*. 47: *Galium triflorum* Michx. 49: *Utricularia intermedia* Hayne. 51: *Subularia aquatica* L., after FERNALD 1925.

of the distribution of the oceanic species (see *Subularia* fig. 7). As regards the other species, we must remember that we are concerned with relatively southern kinds. The 10°-July isotherm, which roughly coincides with the northern boundary of the sub-arctic region, in fact intersects the northern part of the coast of Labrador and turns inwards across the mainland right over Hudson Bay. In Greenland this isotherm cannot be plotted with certainty at present, but there are weighty reasons for believing that several places in the deep West Greenland fiords reach a July mean of 10°[1]). Thus as far as some of the species are concerned the aforesaid gap in the distribution can be explained with the aid of the summer temperature. In this connection, however, we must not forget the hygric conditions, for they will doubtless play a more or less decisive rôle for a species like *Selaginella rupestris*. According to the find in Greenland, the northern limit of this species can scarcely be governed by the summer temperature. In America the northern boundary runs almost parallel with an 16°-July isotherm, whereas in South Greenland it would be unsafe to reckon with more than 10° in July. For a genuine xerophyte like *Selaginella rupestris* the greater humidity of the climate in the northern part of eastern America may very well have a limiting effect. A map of the ratio of rainfall to evaporation (see SAMPSON p. 524)

[1]) According to American measurements in the years 1941—45 Narssarssuaq in South Greenland has a July mean of 10.6 and the head of Søndre Strömfjord 10.1° C.

shows that this ratio is strikingly low throughout the greater part of the American range of the *Selaginella* species. Unfortunately we do not know the rainfall-evaporation ratios of Greenland, but it is not impossible that in the interior of South Greenland we may reach values similar to those in Nova Scotia, where the northern limit of the species lies. Thus it may be possible to explain the aforesaid plant distributions by deductions from the climate. On the other hand it is quite possible that other factors, especially historical, have some causal relation to their distribution. FERNALD (l. c.) has shown that the region around the mouth of the St. Lawrence is in fact the home of isolated occurrences of a number of species, for which reason he reckons with glacial-epoch refuges in this area. Therefore if certain species have a northern limit in a relatively southerly position in America, the reason may be that after the glacial period these species were unable to spread very far from the refuges. Actually, it is only the great distance between the Greenland and the American areas that causes speculation and leads to theories of immigration by human agency.

However, as it is not a matter of one species alone, but of a fairly large part of Greenland's flora, the theory of the agency of the Norsemen in this immigration has lost much of its attractiveness. Among the species mentioned there are no distinctly anthropochorous plants, as the *Sisyrinchium* species for the most part is a stray from cultivation in gardens, though HEGI also refers to the possibility of dispersal by birds or perhaps "durch Frachtverkehr". All in all, however, there can hardly be much reason for imagining that *Sisyrinchium* differs from the other southern and western species, which most probably came to Greenland by their own means.

The question now is whether the species are able to spread over such great distances or whether the explanation is that during warmer climatic periods the southerly species reached Greenland along a broad front and thereafter returned to the present "bicentric" or "polycentric" distribution. Although dispersal over long distances is certainly possible for several species, it is not very probable that an entire flora element, the southerly, boreal element, should immigrate by dispersion over so great a distance and succeed in establishing itself in a number of suitable localities in Greenland. Perhaps the latter explanation therefore is the more probable one, especially for those species which have large, heavy dispersal units such as *Utricularia* species (see PORSILD 1935 pp. 30—34 and fig. 7). But then comes the question of whether the favourable juncture was the post-glacial warm period or the last inter-glacial era. Here I think we must stop, or at any rate emphasize very strongly that we are getting far into the world of theory. But one or two other points induce me to continue the discussion for a little while yet:

Among the species that have crossed the great gap from the Gulf of St. Lawrence to Greenland is *Arabis Holboellii*, which has a surprising distribution in America, having been found only on the Gaspé peninsula and in the region of St. Lawrence, thereafter in Central Canada and in a region among the mountains of Western America. MARIE-VICTORIN (1935) considers it to be a typical pre-glacial relic found only in territories which must be assumed to have been ice-free during the last glacial age. My studies of the ecology of this species at its stations in Søndre Strømfjord indicate a distinctly warmth and drought-loving steppe plant. Its Greenland distribution too is curiously disrupted, almost "polycentric" (BÖCHER 1938 fig. 49).

Another species, *Galium triflorum* (fig. 7) should be mentioned. This markedly sub-arctic plant may either have spread in post-glacial time to Greenland, Scandinavia, the Urals and the Alps without touching Iceland, where it is missing, or it spread to these regions at a much earlier time, survived a glaciation in refuges there and afterwards spread from them to some extent. Either it did not reach Iceland or it was unable to find suitable refuges there and died off. In the latter case the refuge theory seems much more acceptable than a post-glacial dispersal over such enormous distances.

In conclusion, *Alchemilla filicaulis* deserves mention. This easterly species has reached Greenland and eastern America, where its northern limit lies at 52°. It is very doubtful whether this species is capable of spreading across Danmark Strait or the waters between Greenland and Newfoundland and reaching its present distribution in the time since the last glaciation. It was among the flora found about the hot springs on the Blosseville coast (BÖCHER 1933 p.12), a region which may well have contained ice-free mountain areas during the last glaciation by reason of its topography and its springs.

With these additions, which show that the theory of the persistence of southerly species in Greenland during the last ice period is not sheer speculation, we must leave the discussion to the geologists, who must try to find out what the conditions were in Greenland during the last glaciation; in particular we wish to know what the climate was like on ice-free southern slopes in favourable situations. For we must look for the refuges there.

As regards a species so southerly as *Selaginella rupestris* I have my doubts about its having persisted in Greenland. Perhaps in its case it were easier to imagine that one of its few fertile megaspores was carried to Greenland by the wind or—as a very faint possibility—in the clothing of one of the Norsemen. It is fortunate that this species was discovered so soon after the establishment of the U.S. base in the valley below the locality, otherwise it would in future have been regarded as

having been brought in by the Americans. This possibility can be ignored, for as already stated the plant was present in large numbers in wholly stabilized natural communities which were observed in several places and surrounded by virgin vegetation. The same applies to the finding of *Sisyrinchium* in Søndre Strømfjord. It was discovered in wholly untouched vegetation at a place where a large number of other rare species were growing, including several which in that region occurred only at the *Sisyrinchium* station. It may also be stated that in spite of most careful botanizing at the American air-base the expedition found only a single fungus that may have been imported by the Americans. The vascular flora of the base consisted exclusively of Greenland species.

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Færdig fra Trykkeriet den 6. Juli 1948.

PLATES

Plate 1.

Selaginella rupestris (L.) Underw. Material from Greenland.

Fig. 1. Part of a large clump showing the typical very dense habitus of the Greenland material and most of the northeast American. × $^3/_2$. M. Køie phot.

— 2. Tips of fertile shoots showing the groove on the aligular side and the bristle at the end. × 5. M. Køie phot.

— 3. Central part of the cone. When the megaspores are ripe the sporophylls spread so that the megaspores, which mostly are clear of the sporangia, become exposed. In most places only one megaspore is seen, but almost at the middle of the picture there are two together. × 5. M. Køie phot.

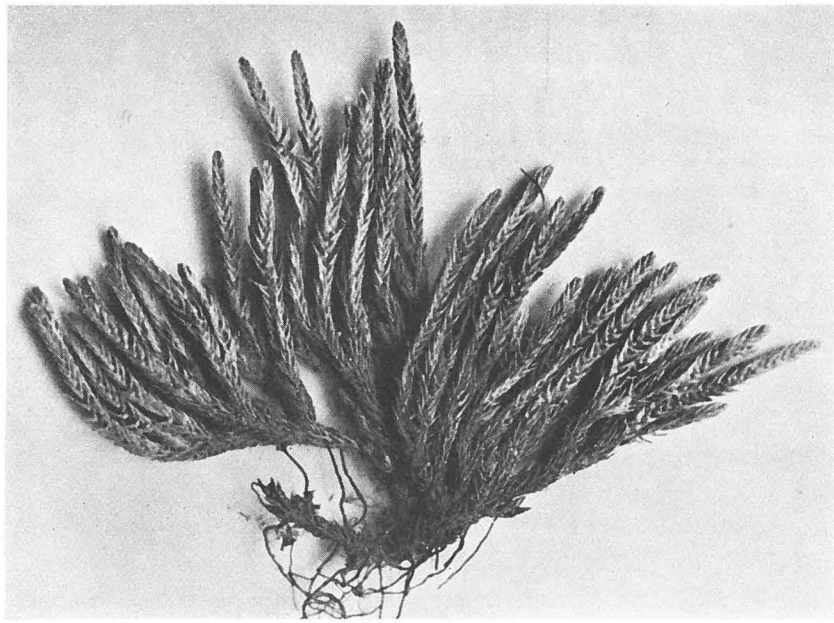

Fig. 1.

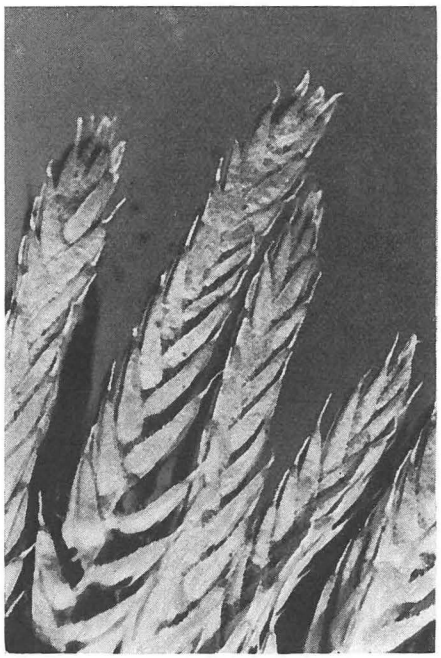

Fig. 2.

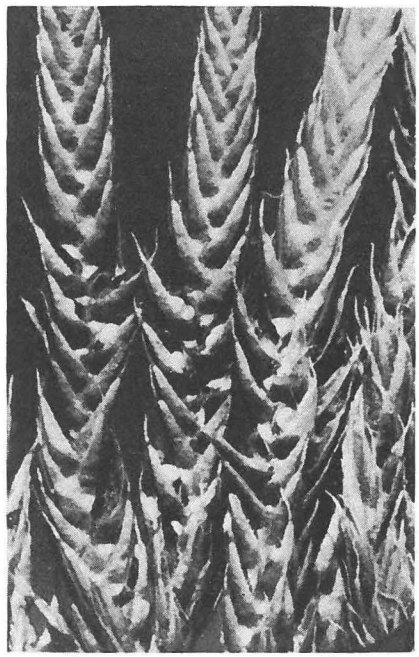

Fig. 3.

Plate 2.

Sisyrinchium montanum Mill. on its station in Søndre Strømfjord, Greenland.

Fig. 1. A very vigorous individual of *Sisyrinchium* standing in dry *Carex supina* vegetation together with *Gentiana aurea* (left). In the background *Salix glauca*. T. W. B. phot. 27th Aug. 1946.

— 2. The *Sisyrinchium* locality from the west. *Salix glauca* round about. In the background large areas of dry *Carex supina* steppe with solitary willow bushes. T. W. B. phot. 27th Aug. 1946.

Fig. 1.

Fig. 2.