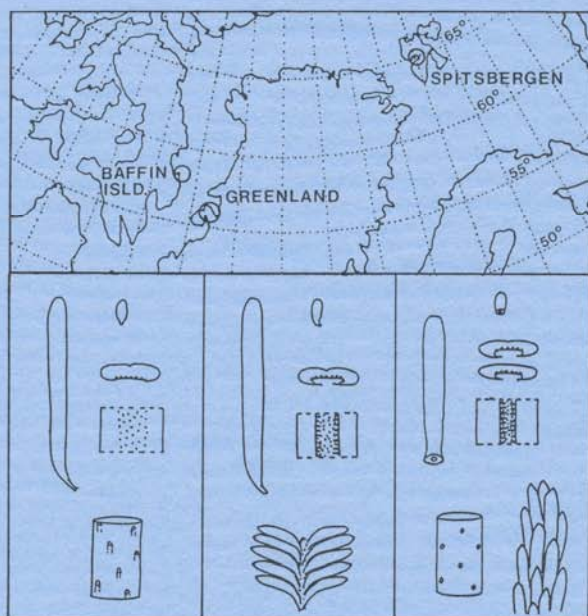




SKRIFTER NR. 192

M. N. Bose and S. B. Manum

Mesozoic conifer leaves
with '*Sciadopitys*-like' stomatal distribution.
A re-evaluation based on fossils from
Spitsbergen, Greenland and Baffin Island



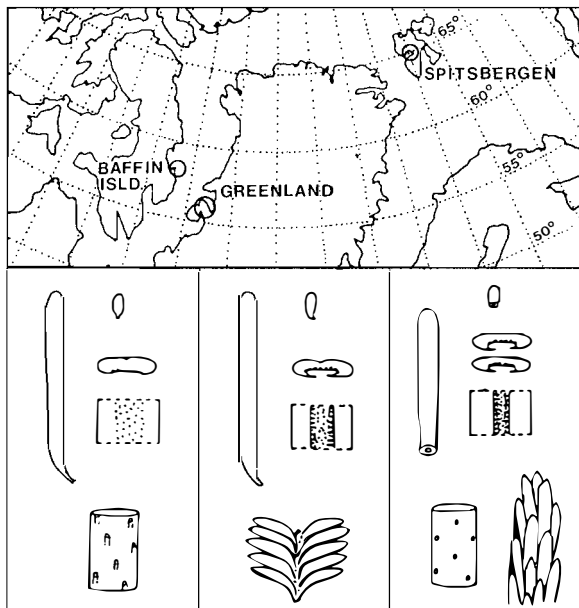
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Dedicated to our teacher and friend Professor emeritus Ove Arbo Høeg,
Oslo.

Abstract

Fossil conifer leaves possessing a median stomatal zone or groove as in the two-veined symphyllode peculiar to the extant *Sciadopitys verticillata* (Thunb.) Siebold et Zuccarini (family Sciadopityaceae) have long been regarded as related to the extant species, although their attachment and shoot morphology were unknown. From the Lower Cretaceous (Barremian) of Spitsbergen and more or less coeval formations in West Greenland and Baffin Island such 'Sciadopitys-like' leaves have been isolated in great abundance by bulk maceration. They show great diversity and demonstrate previously unknown or overlooked characters. Based on overall morphology, stomatal distribution and other epidermal characters, and shoot fragments, the entire group of such Mesozoic leaves has now been split into four genera: *Sciadopityoides* Sveshnikova emend. (7 species, one of which is new), *Oswaldheeria* n. gen. (4 sp., 2 new), *Arctopitys* n. gen. (7 sp., 4 new) and *Holkopitys* n. gen. (monotypic). The number of known species totals nineteen. *Oswaldheeria*, *Arctopitys* and *Holkopitys* had decurrent leaf bases, leaves were spirally arranged and horizontally spreading, while *Sciadopityoides* had spirally arranged and more or less forward pointing leaves with a well defined basal opening, indicating abscission (deciduousness). In most of the species described, leaf size dimorphism occurred. Spitsbergen and Baffin Island have five species in common, two of which also occur in West Greenland.

None of the Mesozoic 'Sciadopitys-like' taxa presently known shows the verticillate leaf arrangement of the extant species. Furthermore, leaves are dimorphic only with regard to size, not in venation and stomatal distribution as is the case in *S. verticillata*. Thus, they are now removed from the Sciadopityaceae and placed under the new family Arctopityaceae. These conifers with 'Sciadopitys-like' leaves formed a prominent element in the Lower Cretaceous floras in the Arctic region and to some extent in parts of Eurasia in contrast to coeval floras in western Europe. The affinity of conifers referred to Arctopityaceae is kept open until their cones are found. *Oswaldheeria (Sciadopityes) scotica* (Florin) comb. nov. from the Jurassic of Helmsdale, Scotland, has now been validated.

A few other gymnosperms from Spitsbergen are described, namely species of *Pseudotorellia* (Florin) emend. because they add to the known morphology of the genus, and species of *Marskea* Florin and *Torreya* Arnott, which extend the stratigraphic and geographic ranges of the genera. Bodies identified as *Burejosperrum* Krassilov, previously thought to be seeds of ginkgoalean affinity, are now considered non-vegetal.

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Preface

Initially, this work was intended merely to revise and document some vague records of leaves in the Lower Cretaceous flora of Spitsbergen which had been reported as '*Sciadopitys*-like' (Florin 1922; Manum 1987). In 1962 we had made collections to be used for this purpose, but not until August 1986 did circumstances permit our joint work on this material. By that time, new concepts concerning the '*Sciadopitys*-like' leaves had been developed through studies on Jurassic fossils from northern Norway (Manum 1987). That our study of the material from Spitsbergen would also result in new insight into this group of fossils was not anticipated, since our collection had appeared on preliminary inspection to be of a rather limited diversity. But bulk maceration produced quite unexpected results which completely changed the scope of our work. Entirely new morphological aspects of '*Sciadopitys*-like' leaves were discovered which showed them to be less like those of the assumed extant homologue than was previously thought. Completely new morphological and taxonomic concepts were required for this group of fossils. At an early stage it became clear that previously described taxa from Greenland and Baffin Island also occur in Spitsbergen and that a complete revision of these taxa was necessary. This led to exhaustive search in museum collections for types related to papers published since 1868. Our study resulted in the present monograph dealing with what has turned out to be a prominent group of conifers in three nearly contemporaneous Lower Cretaceous floras of the Arctic region. A detailed study of other plants in our material had to be deferred, but some other distinctive conifers and representatives of the genus *Pseudotsugites* found along with the '*Sciadopitys*-like' leaves in our material have been included.

We are dedicating this paper to Professor emeritus Ove Arbo Høeg of the University of Oslo, with whom we have enjoyed cooperation and friendship since 1950 (Manum, Oslo) and 1951 (Bose, Lucknow). He established the subject of palaeobotany in Norway, and he promoted palaeobotanical research in India as the first Director (1951–53) of the Birbal Sahni Institute of Palaeobotany, Lucknow.

Oslo, February 1990
M. N. Bose and S. B. Manum

Introduction

The principal subject of this paper is dispersed conifer leaves possessing a median stomatal zone (or groove or furrow) on the lower side as in the leaves of the extant *Sciadopitys verticillata* (Thunberg) Siebold et Zuccarini, including a discussion of their morphology, taxonomy and affinity. More than a dozen species of such leaves were previously known from Jurassic and Cretaceous strata. However, Manum (1987) pointed out that most of them were inadequately described. Our study of rich assemblages of such 'Sciadopitys-like' leaves from the Lower Cretaceous of Spitsbergen has provided new insight into the morphology and diversity of such leaves and it has formed the basis for new concepts regarding their taxonomy. A preliminary report has already been given by Manum & Bose (1988). We have now set out to document these interesting assemblages and discuss their taxonomy and affinities. Our study has forced us to make substantial descriptive and taxonomic revisions of previously described taxa of such fossils for which we have re-examined and made preparations from all the type material from West Greenland and Baffin Island.

Within the scope of the present paper, a treatment similar to that given to the 'Sciadopitys-like' leaves was not possible for the associated plants. Descriptions of a few noteworthy gymnosperms have been included, because they extend known morphology or distribution. Also, bodies identified as *Burejospermum* Krassilov have been recovered and their affinity is discussed.

Material

The material used for this study comes from more or less coeval Lower Cretaceous strata in localities which are all within the present Arctic zone: Spitsbergen, West Greenland and Baffin Island. In Early Cretaceous times these localities were situated closer to each other at lower latitudes, between 55 and 65 degrees north (Fig. 1).

The material from Spitsbergen was collected by us in 1962 and 1987. Comparative material from West Greenland was obtained from the Geological Museum, Copenhagen, the Swedish Museum of Natural History, Stockholm, British Museum (Natural History), London, and the

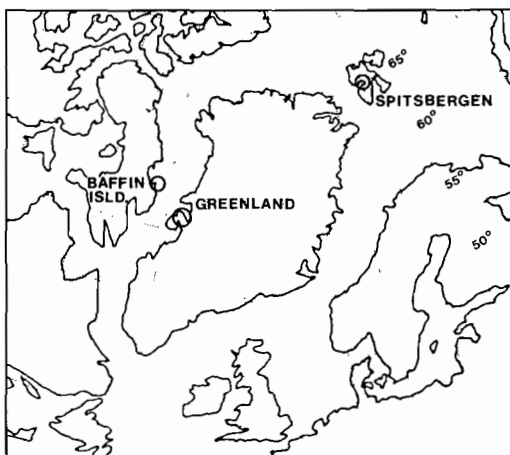


Fig. 1. The Lower Cretaceous localities on Spitsbergen. West Greenland and Baffin Island shown on a continental reconstruction at Hauterivian-Barremian times (after Firstbrook et al. 1975).

Palaeontological Museum, Oslo, while material from Baffin Island was supplied by the Geological Survey of Canada, Ottawa.

Spitsbergen

Most of our material has been collected from Bohemanflya (Loc. B, Fig. 2) and a minor collection comes from the northern side of Adventfjorden (Loc. A). Both localities belong to the Glitrefjellet Member of the Helvetiafjellet Formation (Table 1). This formation represents a continental sequence some 100 to 150 m thick in this part of Spitsbergen. The Glitrefjellet Member represents delta plain depositional environments with sandstones, shales that are usually carbonaceous and with plant remains, and thin coals showing rapid lateral facies changes (Steel 1977). The underlying Festningen Member is a massive fluvial sandstone.

The Helvetiafjellet Formation is indirectly dated as Barremian (to Aptian?) by evidence of ammonites in the underlying Rurikfjellet Formation (upper Hauterivian) and the overlying Carolinefjellet Formation (Aptian), respectively (Parker 1967; Major & Nagy 1972). Dinoflagellate cysts suggest that the top of the Rurikfjellet Formation may range into the Barremian (Grøsfjeld 1987).

Plant-bearing beds and coals of the lower part of the Glitrefjellet Member are exposed along the

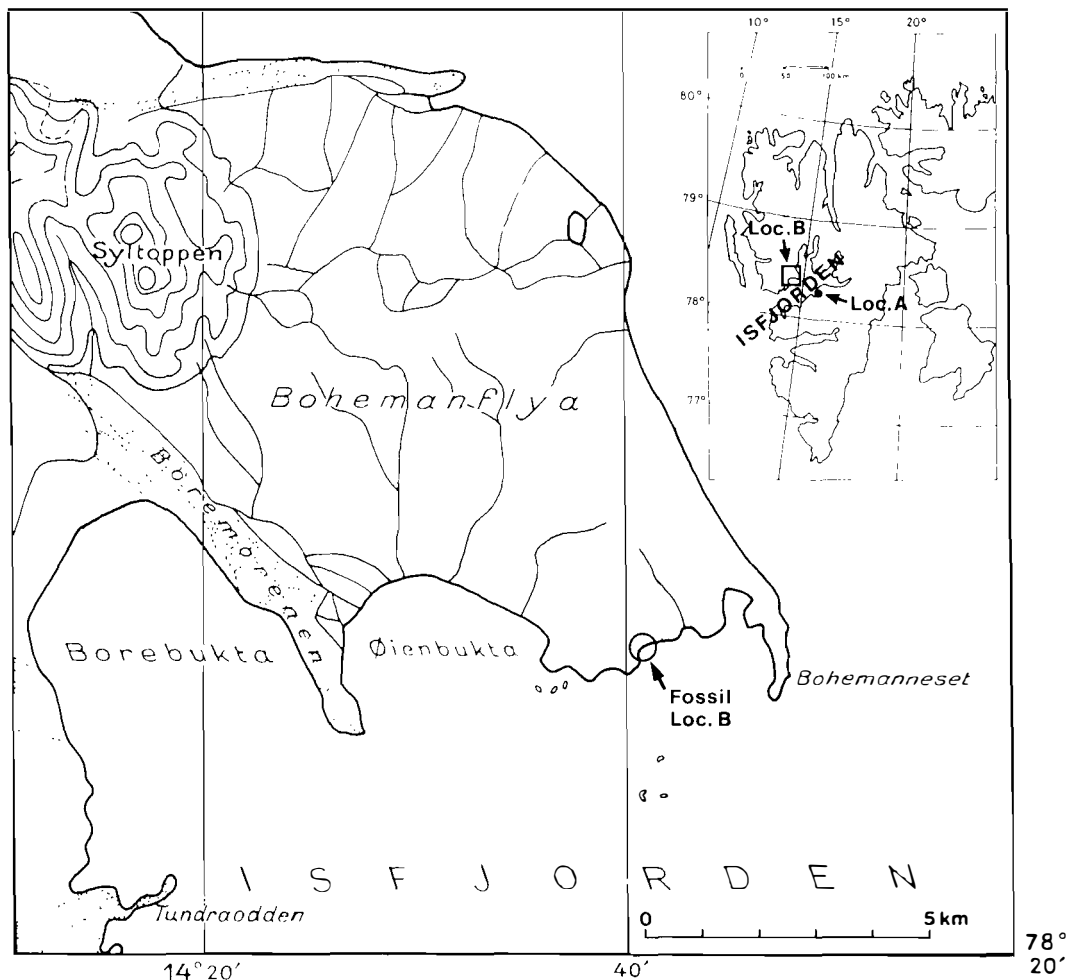
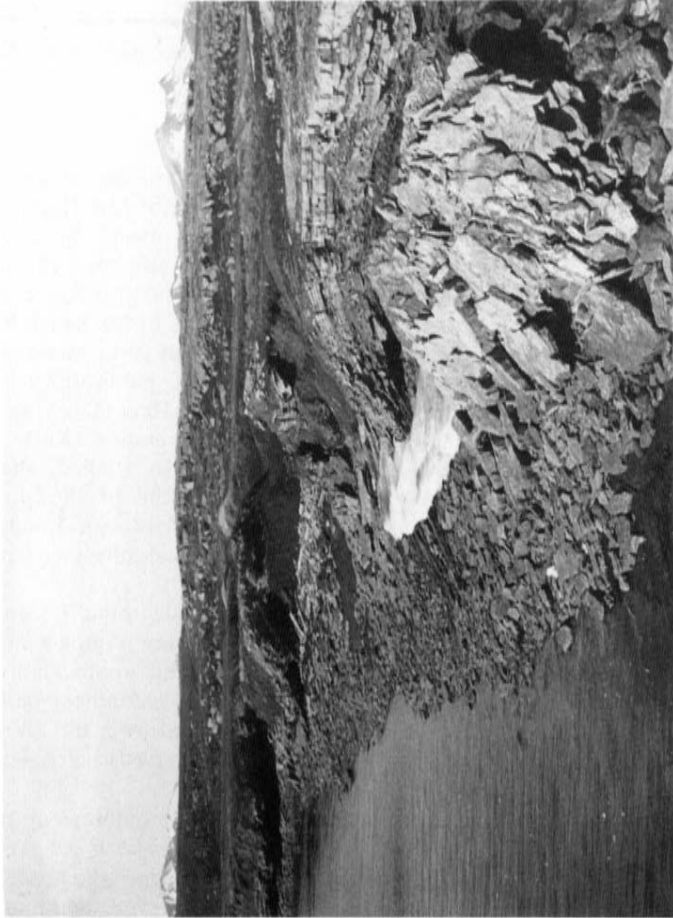


Fig. 2. Localities from where collections have been made on Spitsbergen. Loc. A: Advent City; Loc. B: Bohemanflya.

Table 1. Lower Cretaceous stratigraphy of Spitsbergen showing the position of the plant-bearing Glitrefjellet Member (after Flood, Nagy & Winsnes 1971).

STAGE	LITHOSTRATIGRAPHY	
Aptian-Albian	Carolinefjellet Formation	
Barremian	Helvetiafjellet Formation	Glitrefjellet Member
		Festningen Member
Valanginian-Hauterivian (-Barremian?)	Rurikfjellet Formation	

coast of Bohemanflya, a peninsula of low relief in Isfjorden (Loc. B, Fig. 2). The outcrops appear at several places for a distance of approximately 3 km westwards from Bohemanneset. Their exact correlation is difficult because of a number of faults and lateral changes in facies. We have analysed a large number of samples from these outcrops. The samples yielding the best preserved and richest assemblage were collected immediately west of the little brook outlet near the abandoned coal pit and huts at Bohemanflya. At this particular point a hard, fine-grained, red weathering sandstone, c. 0.5 m thick, is well exposed in the tidal zone. It contains some good plant



A



B

Fig. 3. Exposures of plant-bearing beds on Bohemanfya, Spitsbergen (Loc. B in Fig. 2). A: The deltaic formations with sandstones, shales and coals of the Giltrefjellet Member. B: Richest collecting site, at far left hand side of Fig. A; the person in the foreground is working on the horizon with *Pseudotoxarella*; the horizon rich in *Sciadopitys*-like leaves is at the bottom of the brink in the background. (Photo S.B.M., July 1962).

impressions dominated by *Ginkgo* and *Podozamites* (see Heer 1876). Our richest findings of ‘*Sciadopitys*-like’ leaves were obtained from a shale horizon occurring between 1.0 m and 1.4 m above this sandstone; another shale horizon, completely dominated by *Pseudotorellia*, occurs 0.3 m below the sandstone (Fig. 3).

On the north side of Adventfjorden, at the entrance to the abandoned Advent City coal mine (Loc. A, Fig. 2), shales with compressions were collected from just above the coals. Nathorst (1897, pp. 46–47) described another site with a fossil rich horizon (‘De Geer Schichten’) in a river bed which can be located in Louisdalen, approximately 900 m upstream from Revneset. This is the material from which Florin (1936) described the genus *Pseudotorellia*. In 1987 we made an attempt to relocate Nathorst’s site. Equivalent beds were observed, but evidently Nathorst’s plant horizon in the river bed had been washed away by 90 years of erosion. Both these sites represent the lower part of the Glitrefjellet Member.

West Greenland

Extensive collections from the Nûgssuaq peninsula north of Disko Bay (Fig. 4) made by 19th century expeditions exist in the Geological Museum, Copenhagen, the Swedish Museum of Natural History and British Museum. Cretaceous floras from these collections were first described by Heer (1868, 1874, 1883) who, however, did not recognize *Sciadopitys*-like leaves in them. Such leaves were first recognized by Schimper (in Schimper & Schenk 1890), and subsequently described by Halle (1915) and Florin (1922), based to a large extent on Heer’s taxa. We have made extensive searches for figured types and other relevant specimens from these previously described collections.

The collection from Kome (= Kûk) on the northern side of the Nûgssuaq peninsula which was described by Heer (1868) was available to us in the Geological Museum, Copenhagen. Heer (1868) provided no information regarding the collector of this material nor of the depository. From Seward (1926, p. 66) it would appear that it was collected by one or more British expeditions. We only discovered the depository for this collection when our manuscript was nearly finished. We therefore had to restrict our study of this material

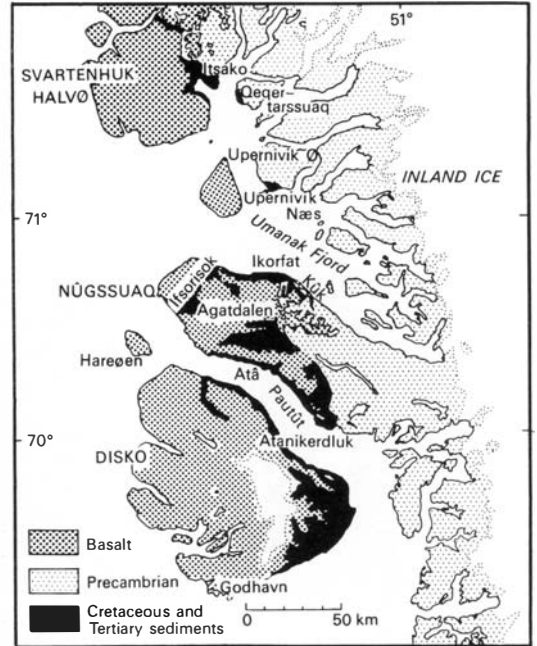


Fig. 4. Nûgssuaq peninsula, West Greenland (from Pedersen 1976).

in order to concentrate on taxonomic problems related to taxa described by Heer (1868).

The collections made by Nordenskiöld’s expedition in 1870, also from the north side of the Nûgssuaq peninsula (at Kome and Ikorfat), were available to us in the Swedish Museum of Natural History. This is the material for another of Heer’s classical publications (1874). This material and that for Heer (1868) are both derived from the Kome Formation (Koch 1964). From Kome we have also studied one sample of ‘Whymper’s collection’ of 1867 in the British Museum (Natural History), London. (For an account of the classical collecting expeditions, see Seward 1926.)

From the south side of the Nûgssuaq peninsula we have studied a few samples labelled Atanikerdluk, also available in Stockholm (Nathorst’s collection 1883). *Sciadopitytes nathorstii* Halle (1915) was described from this collection which according to Koch (1964) belongs to the Atane beds.

The floras of these outcrops on the Nûgssuaq peninsula have always been accepted as being of Cretaceous age ever since their description in the classical papers. However, their more precise age

and stratigraphic relationship are still problematic. Their association of angiosperms together with typical Lower Cretaceous gymnosperms and ferns poses a riddle. This association was first noted by Heer (1868, 1874, 1883) and later substantiated by Seward (1926) and Seward & Conway (1935a, 1935b); a useful summary of the floras was provided by Pedersen (1976).

Koch (1964) claimed that the angiosperms reported from the Kome Formation had either not been collected *in situ* or else had been misidentified. This claim serves to maintain Seward's (1926) conclusion that the flora has a 'Jurassic-Wealden' aspect. Pedersen (1968) also maintained an early Cretaceous age for the flora of the Kome beds, while at the same time reporting new findings of *in situ* angiosperms. The riddle posed by this unusual association of plants in the Kome flora and its implications for the age determination still remains.

Marine fossils from some of the formations on the Nûgssuaq peninsula were studied by Rosenkrantz (1970). This helped to date younger formations; for the Kome Formation, for which he proposed a Barremian-Aptian age, he had no direct fossil evidence. Our own view is that the overall composition of the flora from Kome indicates an Early Cretaceous age. The present study shows that it has a fair number of genera and species in common with the flora from the Barremian of Spitsbergen.

From the southern side of the Nûgssuaq peninsula Heer (1883) distinguished two floras from two laterally separated localities of uncertain stratigraphic relationship, Pautût and Atane, respectively; the Pautût flora being considered the younger by Heer. Seward (1926) and Seward & Conway (1935a), who re-examined these two floras, did not regard them as different. This view was also maintained by Koch (1964). The Pautût and Atane floras combined show a peculiar association of typical Lower Cretaceous plants along with angiosperms (Pedersen 1976) which one would normally consider to be younger. In the past this has formed the basis for speculations concerning angiosperm evolution and migration in this part of the world (Seward 1926).

Field observations led Koch (1964) to suggest higher stratigraphic positions for the plant-bearing beds as one moves eastward from Atane via Pautût to Atanikerdluk. However, he also warned that one should treat the various collections from this area with caution until their stratigraphy is

more satisfactorily understood. The Pautût beds have marine intercalations with molluscs indicating a Santonian-Campanian age (Rosenkrantz 1970). This is compatible with the angiosperm component of the flora.

No '*Sciadopitys*-like' leaves are known from Atane and Pautût, but Halle (1915) described *Sciadopitytes nathorstii* from Nathorst's collection labelled Atanikerdluk. The exact stratigraphic position of this material is unknown to us. If we follow Koch's (1964) interpretation that the plant beds become younger eastwards, the Atanikerdluk locality should be younger than the Pautût beds, i.e. Campanian or younger. Nathorst's Atanikerdluk samples studied by us have all yielded, besides *S. nathorstii*, a typical Lower Cretaceous assemblage of spores and pollen; no angiosperm pollen was observed. On this basis we find it problematic to accept a late Cretaceous age for this material from Atanikerdluk from which Halle (1915) obtained his specimens. This serves to stress Koch's (1964) warning concerning the stratigraphy of the various fossil collections from the composite Atane-Pautût-Atanikerdluk sequence of plant beds.

Baffin Island

Bose (1955) described *Sciadopitytes variabilis* in a sample from Padloping Island which is located off the north side of Cumberland Peninsula, Baffin Island. The sample consisted of a crumbly and coaly shale densely packed with small coniferous leaves, practically a 'leaf-coal'. It was collected on the Baffin Island Expedition, 1953, by D. J. Kidd of the then Arctic Institute of North America. Kidd (1953) referred to the sequence of interbedded basalts and sediments on Padloping Island as 'Tertiary-type rocks', as distinguished from the 'Precambrian-type rocks', tentatively correlating them with the Tertiary volcanic rocks extending from Scotland to East Greenland.

The sample used for Bose's paper (1955) was supplied by the Geological Survey of Canada and the age was then indicated as Lower Cretaceous; no further details concerning the locality and its stratigraphy were supplied. More recently, Langille (1987) has provided new information about the formations and their palynostratigraphy on Padloping Island and the adjacent Quqaluit Island and Durban Island. The most complete section is described from Padloping Island, consisting of about 112 m of sandstones with interbedded silt/

clay and eight coal seams. This sequence is overlain unconformably by volcanic ash and a few metres of silt/sand. Palynologically the coal seams in the section below the ash compare with Aptian-Albian assemblages from western and northern Canada, while the ash layers and the overlying sediments contain a completely different palynological assemblage representing angiosperms, for which Langille (1987) concluded a Palaeo-Eocene age. The entire sequence is continental; rare dinoflagellates found in the ash and overlying sediments were considered reworked.

The coaly samples which Bose (1955) studied are in all probability equivalent to one of the coal seams recorded by Langille (1987). We have for the present study re-examined a small residue from Bose's original material which was kept in Oslo. Besides *S. variabilis* Bose (1955), it contains five more 'Sciadopitys-like' species which are also found in the Barremian flora from Spitsbergen which we have described here (Table 3, p. 61). In addition, we have observed at least four other taxa shared between Padloping Island and Spitsbergen, but these have not been dealt with in this paper.

The close similarity between the floras of Spitsbergen and Padloping Island speaks for contemporaneousness. We therefore consider the prebasaltic sediments on Padloping Island containing the flora to be of Barremian(-Aptian?) age rather than Aptian-Albian as proposed by Langille (1987).

Depositories

Our own collections from Spitsbergen and the type specimens are curated in the Palaeontological Museum of the University of Oslo. Types and other material obtained from other institutions for re-examination came from British Museum (Natural History), London, the Geological Museum, Copenhagen, the Geological Survey of Canada, Ottawa, and the Swedish Museum of Natural History (Section of Palaeobotany), Stockholm ('Riksmuseet' for short in the following). Along with the figured specimens, some duplicate slides and specimens of most of the 'Sciadopitys-like' taxa have been deposited in all four museums.

Slide and specimen numbers referred to in the descriptions and explanations to figures and plates show the depositories by a letter preceding the

respective numbers thus:

V – British Museum (Natural History), London
MGUH and MMH – Geological Museum, Copenhagen

GSC – Geological Survey of Canada, Ottawa

PMO – Palaeontological Museum, Oslo (all PMO numbers cited are now curated under the new prefix PMO PA)

S – Riksmuseet, Stockholm

Method

This study is based literally on thousands of specimens which were isolated from shale samples, using the bulk maceration method of Harris (1926). Exposure to oxidation and alkali was carefully monitored in order to prevent destruction of delicate cutinized structures. In some samples from Spitsbergen a few leaves are visible on the surfaces of shales, but they never appear in mass accumulations like those known from most collections from West Greenland and Baffin Island. Only extensive bulk maceration has revealed the rich and diverse assemblages that we deal with in this paper.

Morphology and taxonomy of 'Sciadopitys-like' leaves

Generic concept

The concept of using a separate genus for fossil conifer leaves possessing a median stomatal groove in the lower epidermis was introduced by Halle (1915). In extant conifers this is a character restricted to *Sciadopitys verticillata*. This generic concept was further developed by Florin (1922) who described a number of new species and also presented the first review of the geological history of the family 'Sciadopitineae'.

Halle (1915), Florin (1922) and subsequent authors used the genus *Sciadopitytes* Goeppert et Menge (1883) to accommodate such fossil leaves (*Sciadopitys* has also been used). *Sciadopitytes* was first used for leaves preserved in amber which were thought to be like the extant *Sciadopitys*. They were later identified as being of ericaceous origin (Schimper & Schenk 1890, pp. 346 and 827) and the genus should clearly not have been used for leaves of conifers. Sveshnikova (1981) was the first to take the nomenclatural con-

sequences of this anomaly. She rejected the use of *Sciadopitytes* for conifer leaves with epidermal characters as in *Sciadopitys*, and instituted in its place the genus *Sciadopityoides* Sveshnikova. This change in nomenclature was supported by Manum (1987) who re-evaluated the Mesozoic 'Sciadopitys-like' leaves based on a study of Jurassic species from northern Norway. He pointed out that *Sciadopityoides* as conceived by Sveshnikova is a heterogeneous complex of species, and discussed taxonomically useful characters which had previously been overlooked in these fossils. Two species were shown by Manum (1987) to possess characters suggesting a closer affinity with the extant species; they were therefore transferred to *Sciadopitys* (*S. lagerheimii* and *S. macrophylla*). The remaining heterogeneous species referred to *Sciadopityoides* were left undifferentiated by Manum (1987), mainly because important characters were shown to be inadequately documented in most of them.

The present study of Lower Cretaceous fossils from Spitsbergen has revealed a much greater morphological diversity in *Sciadopitys*-like leaves than was previously known. We have confirmed this diversity also in previously described Mesozoic species whose type material we have re-examined. These include specimens of Halle (1915), Florin (1922), Bose (1955) and Manum (1987) from West Greenland, Baffin Island and northern Norway, respectively. Specimens of

species described by Russian workers have not been available to us, but their variation, too, can be recognized from their descriptions and figures.

We now recognize nineteen Mesozoic species of 'Sciadopitys-like' leaves which can be divided into four distinct genera. Seven species are described as new in this paper, in addition, one has yet to be formally described; for five existing species type material has been examined and revisions undertaken; the remainder have been reviewed on the basis of published documentation. Three of the genera are proposed as new, while *Sciadopityoides* Sveshnikova is retained for the fourth (Table 2). The new genera are named *Arctopitys*, *Oswaldheeria* and *Holkopitys*, respectively. The characters used to distinguish these genera are summarized as follows:

Sciadopityoides Sveshnikova emend.: Leaf base broad or expanded, with a well defined circular to oval opening; on lower surface a median stomatal groove with projecting margins having tuberculate or cylindrical papillae; upper surface with or without a median furrow. Seven species recognized.

Arctopitys n. gen.: Leaf base tapering or distinctly decurrent; median stomatal groove on the lower surface with margins which may or may not project, papillae along margins conical or cylindrical; upper surface with or without a median furrow. Seven species recognized (including one as yet undescribed).

Table 2. Diagrammatic presentation of leaf and shoot characters in *Sciadopitys verticillata* and the four extinct genera. I: long leaf (symphyllode in *S. verticillata*); II: short leaf (scale leaf in *S. verticillata*); III: cross section long leaf, stomata dotted; IV: lower side showing median stomatal zone or groove; V: shoot. (Modified from Manum & Bose 1988, fig. 4.)

SCIADOPITYS VERTICILLATA	OSWALDHEERIA	ARCTOPITYS	HOLKOPITYS	SCIADOPITYOIDES

Oswaldheeria n. gen.: Leaf base as in *Arctopitys*; median stomatal zone not forming a groove; upper surface with or without a median furrow. Four species recognized.

Holkopitys n.gen.: Leaf base as in *Arctopitys*; distinct median stomatal groove on the lower side with prominently projecting margins which lack papillae; stomata within groove arranged in two lateral bands, each lying protected below the projecting groove margins and separated by a median stomata-free zone. Presently monotypic.

All the four genera have a median stomatal zone, or more often a groove, on the lower side. *Sciadopitys verticillata* is the only extant conifer whose leaves possess this character which reflects the double vein peculiar to this species. To our knowledge, veins have not been directly demonstrated in Mesozoic leaves with stomatal distribution like that in *Sciadopitys*. Two veins in the fossil leaves are therefore only inferred from the well differentiated median stomatal zone. A furrow or median differentiation in the upper surface of the leaf as in *S. verticillata* is observed in some of the fossil leaves too.

Leaf dimorphism

The shoots of *S. verticillata* have two types of leaves: long, needle-shaped leaves which are arranged in a verticillate manner (actually condensed spirals) and scale leaves in spiral arrangement between the verticils; the scale leaves are partially adnate to the shoot. Scale leaves are also subtending the long leaves.

Associated with the 'long' leaves in most of the studied material, we have also found a large number of leaves which are distinctly shorter and which match the associated long leaves in gross morphology and epidermal characters including stomatal distribution (Fig. 5 gives an idea of the natural size of long and short leaves described here). From this association of two sizes of otherwise comparable leaves we conclude that they represent species which possessed leaf dimorphism. This type of leaf dimorphism is found in several of the species placed here under the genera *Sciadopityoides*, *Arctopitys* and *Oswaldheeria*, but so far not in *Holkopitys*. The relative frequency of short and long leaves is variable; mostly the long leaves are in majority but in places the short ones dominate.

Comparing this dimorphism with that in *S. verticillata*, we note one important difference.

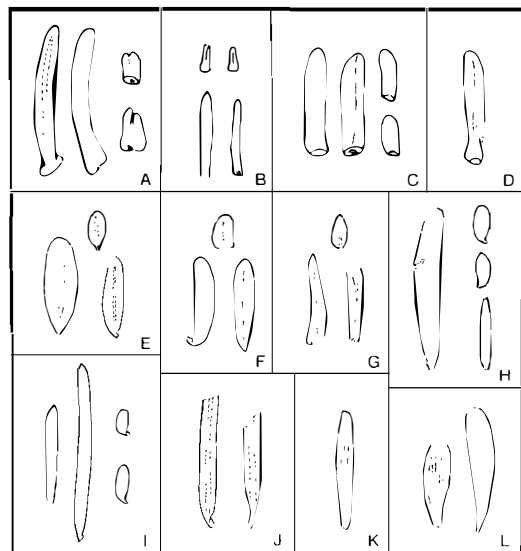


Fig. 5. Representative *Sciadopitys*-like leaf forms (A-J), eight of which are dimorphic, and two species of *Pseudotorellia* (K-L) described in this paper. (A: *S. microphylla*; B: *S. crameri*; C: *S. ikorfatensis*; D: *S. variabilis*; E: *A. florinii*; F: *A. cap-bohemanensis*; G: *A. ineffecta*; H: *O. hallei*; I: *O. arctica*; J: *H. hoegii*; K: *P. kordylina*; L: *P. retusa*.) C; $\times 1$.

The extant species has scale leaves with a single, poorly developed vein, the course of which is avoided by the stomata (Fig. 6); these are concentrated in two bands rather than one on the abaxial surface (and a few on the adaxial surface). Thus, while the fossil taxa show dimorphism with regard to size only, scale leaves and long leaves in *S. verticillata* have completely different types of venation and stomatal distribution. The scale leaves of *S. verticillata* would be placed in a different genus from the long leaves if found separately as fossils.

Shoots and leaf arrangement

In *S. verticillata* the needle-shaped, double-veined leaves of the verticils are subtended by scale leaves. The classical and most widely accepted interpretation of this structure is that the double-veined leaves represent symphyllodes formed by two needles (double-needle) borne on a dwarf shoot which in turn is subtended by a scale leaf (von Mohl 1871). Shoots that can be compared with the arrangement seen in the extant species have not been found in our material.

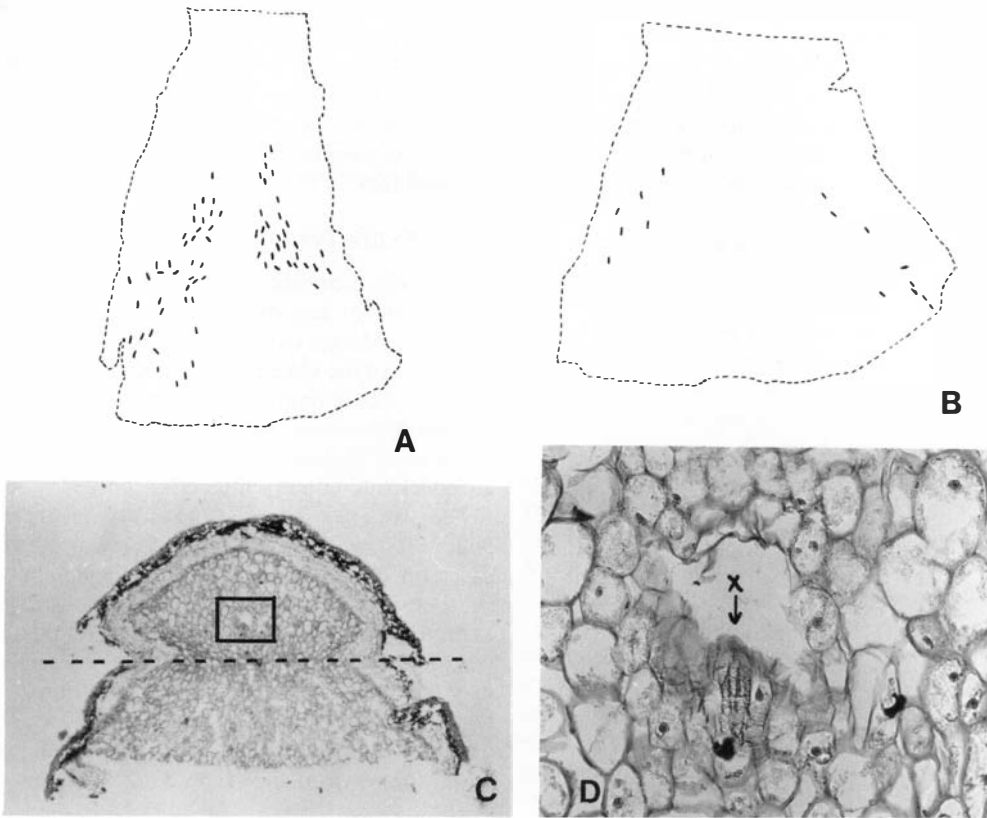


Fig. 6. *Sciadopitys verticillata*, scale leaves. A, B: Lower surface of leaves from two different trees showing distribution of stomata; $\times 15$. C: Transverse section near base of leaf, portion below broken line is part of stem; $\times 15$. D: Outlined area in C magnified to show xylem (x); $\times 100$. B and C are from a tree growing in the Botanical Garden of the University of Oslo; A is from the Botanical Garden of the University of Bergen.

Two types of fragmentary shoots without attached leaves have been found by bulk maceration of shales. They are associated with one species each of *Sciadopityoides* and *Oswaldheeria* (*S. crameri* and *O. hallei*), both of which show leaf dimorphism (Table 2; Pl. 1, fig. 6, Pl. 2, figs. 4–6). Both types of shoot show spirally arranged leaf scars. In that associated with *Sciadopityoides* the scars are circular to oval, whereas in that associated with *Oswaldheeria* the scars show remains of the decurrent leaf bases. The scars are simple, matching those of the associated leaves, and they lack any suggestion of a complex structure subtended by a short or scale leaf as in the extant species.

In addition to these shoots, we have found in the collections in the Geological Museum, Copenhagen, a few specimens of two different types of fragmentary twigs with attached 'Sciadopitys-like'

leaves. One type was found on the surface of hand specimens from Slibestensfjeld ('Kome-lagene') along with specimens which are labelled either '*Pinus eirikiana*' or '*P. crameri*' and shows horizontally spreading leaves; the other was found associated with leaves of *Sciadopityoides microphylla* (Heer) comb. nov. by bulk maceration of material from Kome, this type has spirally arranged, appressed leaves. Because these shoots were discovered during the final stage of preparation of our manuscript, it has not been possible to include a detailed description of them. Instead, we offer our preliminary observations below.

In the former type of shoot, with spirally arranged and spreading foliage, the leaves are 7–12 mm in length, with an acute or apiculate apex and a slightly decurrent base (*Arctopitys* sp., Pl. 8, figs. 1–3). On the lower leaf surface there is a median stomatal groove whose margins are papil-

late. Detached leaves with these characters have been described in this paper under the genus *Arctopitys* (p. 32), but the leafy twigs from Slibestensfjeld* belong to a different species of *Arctopitys* than those described from Spitsbergen and Baffin Island. Thus, they demonstrate the occurrence of this same genus in West Greenland, but with a different species.

In the latter type, having appressed foliage, the leaf cuticle corresponds to that of *Sciadopityoides microphylla*. One shoot is 9 mm long and has leaves that are up to 6 mm in length (Pl. 8, fig. 4), two others seem to be apical regions and here the leaves are 2–3 mm in length (Pl. 8, fig. 5). These leaves fall within the size range of the short leaves of *S. microphylla*.

Heer (1868, pl. 44, figs. 17 and 18) figured specimens of *P. crameri* with attached leaves. On re-examination none of them were found to be really attached, as earlier pointed out by Seward (1926).

The evidence from leaf bases and shoot fragments suggests the following foliage arrangements (Table 2): In *Sciadopityoides* the leaves were strictly spirally arranged and pointing upwards, or were more or less appressed to the shoot; in *Arctopitys* and *Oswaldheeria* the decurrent and more or less twisted leaf bases indicate a horizontal mode of spreading, as is documented for *Arctopitys* sp. from Slibestensfjeld, mentioned above. The same may apply to *Holkopitys*.

Short and long leaves might have been borne on different shoots or in different regions of the same shoot; another possible position for the short leaves were on cone-bearing shoots. The overall morphological similarities between short and long leaves together with the usually high relative abundance of the short leaves suggest that the latter formed part of the photosynthetic system more or less equivalent to the long leaves rather than having a more temporary function as, for instance, scales associated with buds or cones.

Deciduousness is strongly suggested by the clear abscission scar in *Sciadopityoides*, and an

originally cylindrical shape of the leaves is indicated by the variation shown in the position of the stomatal zone in the fossils. Leaf base characters in the three other genera suggest that they were persistent; they were dorsiventrally flat judging from the usually strict median position of the stomatal zone in the fossils.

Reproductive organs

Organically connected reproductive organs are not known for any of the species dealt with in this paper. Minute cone-like bodies are associated with some of the species of *Sciadopityoides* in our material. The scales of these 'cones' lack stomata (similar scales were also found in association with *S. variabilis* by Bose (1955)). Unfortunately, they have yielded neither pollen nor seeds.

The extant *Sciadopitys* has very distinctive pollen and we have therefore made a cursory check for dispersed *Sciadopitys*-like pollen in the leaf beds. Unfortunately, they have not proved to be very pollen-productive, but pollen that may be described as *Sciadopitys*-like does occur in our material. This pollen is infrequent and shows less taxonomic diversity than one would expect if it had been produced by the same species that produced the leaves.

Affinities

The affinity of fossil needle-shaped leaves possessing a median stomatal zone cannot be discussed without comparing them with *S. verticillata*, the only extant species which shows this same type of stomatal distribution. Normally stomata tend to avoid veins; their median concentration in the fossil leaves is taken to indicate two veins in the leaves as in *S. verticillata*. Palaeobotanists, including ourselves, who have studied leaves with this type of stomatal distribution have been biased by this comparison with the extant species. We show in this paper that the Mesozoic '*Sciadopitys*-like' leaves are less like those of *Sciadopitys* than previously thought, which makes it necessary to reconsider their affinities.

Extant *Sciadopitys* is often placed in a separate family, the *Sciadopityaceae*, rather than in a subfamily under the *Taxodiaceae*. This separation has been done on account of the peculiar leaf and shoot morphology and also some other characters, among them karyological ones (Schlarbaum & Tsuchiya 1985). Palaeobotanists have a long tradition for regarding the extant species and the

* The hand specimens are labelled 'Slibestensfjeld', a locality between Kome and Ikorfat, catalogued as 'Kome-lagene' (= Kome Formation). While the paper was in proof stage, we came across a dozen more specimens from the same locality which have an association of leaves not found in any other material studied for this paper, containing leafy twigs of *Arctopitys* together with a new type of *Sciadopitys*-like leaves (which for lack of base cannot be further identified) and *Pityophyllum crassum* Seward (1926).

fossil 'Sciadopitys-like' leaves as representatives of the Sciadopityaceae (e.g. Seward 1919; Florin 1922, 1963; Sveshnikova 1963).

S. verticillata is by all evidence a relic species of a pre-Tertiary lineage of conifers (cf. Schlarbaum & Tsuchiya 1985). Leaves and shoots of Palaeogene age show great resemblance to the extant species (Florin 1922, 1963; Christophel 1973). Pollen thought to represent species of *Sciadopitys* is well represented throughout the Tertiary in the temperate Northern Hemisphere (Zauer & Mchedlishvili 1966); particularly noteworthy are consistent records from the Palaeocene-Eocene in Arctic regions (Manum 1962; Florin 1963). Florin (1922) pointed out the great similarity between the geological history of *Sciadopitys* and *Ginkgo*. Both these genera are represented in the Tertiary with a few species which appear to be closely related to the respective single extant species, both of which survived the dramatic Plio-Pleistocene climatic oscillations as relics in East Asia.

Florin (1922, 1963) was the leading proponent for placing fossil leaves with stomatal distribution as in *Sciadopitys* along with the extant species in one family. The first review of the geological history of the family was produced by him (Florin 1922). He based this on species described by himself and those described previously by others (Heer 1868, 1874; Halle 1915; Johansson 1920). He drew particular attention to *Sciadopitytes macrophylla* Florin, from the Jurassic of northern Norway, which he showed to be remarkably like the leaves of *S. verticillata* in size, gross morphology and stomatal zone characters. Forty years later, in his comprehensive synthesis of fossil conifers, he again discussed leaves with this particular morphology, and considered the genus *Sciadopitys* to occupy a unique position (Florin 1963, p. 216), referring it to 'Taxodiaceae (including Sciadopityaceae)'.

On the basis of the characteristic median stomatal zone, Florin (1922, 1963) suggested a closer relationship between the Mesozoic leaves and extant *Sciadopitys*. Evidence of shoot characters which permitted comparison of the mode of leaf arrangement in Mesozoic forms with that in *Sciadopitys* was then lacking, but the arrangement was implicitly assumed to be similar. Our new evidence (see p. 14) shows that leaf arrangement in the Mesozoic species was different from the verticillate arrangement of symphyllodes or 'double needles' subtended by scale leaves found

in the extant species. Leaf size dimorphism has now been demonstrated in most of the species documented in this paper. Exceptions are *Sciadopityoides nathorstii* and *S. variabilis*. We have re-examined material of *Oswaldheeria (Sciadopitytes) macrophylla* (Florin) comb. nov., which was thought to be particularly resembling the extant species (Florin 1922; Manum 1987), but we have been unable to demonstrate short leaves in that species. The extent of this kind of leaf dimorphism was apparently variable. This size dimorphism is basically different from the dimorphism seen in *Sciadopitys* (p. 14). We find no evidence in our fossils for the kind of shoot morphology which can support the idea of symphyllodes or 'double needles' as in *Sciadopitys*. The differences in vegetative morphology demonstrated between the Mesozoic leaves and those of the extant species indicate more distant relationships than has been generally thought until now.

The range in morphological diversity seen in the Mesozoic 'Sciadopitys-like' leaves as presently known is illustrated by the genera *Oswaldheeria* and *Sciadopityoides*. They have completely different types of leaf bases (tapering/decurent versus broad with abscission mark) and different styles of stomatal zone margins. *Arctopitys* occupies an intermediate position, sharing leaf base character with *Oswaldheeria* and the style of stomatal zone characters with *Sciadopityoides*. The leaves had a horizontal mode of spreading in *Oswaldheeria* and *Arctopitys*, and they were probably persistent, while in *Sciadopityoides* they are interpreted as being spirally arranged and pointing more in a longitudinal direction. In all probability they were deciduous. *Holkopitys* is distinguished from the other genera in having the stomata arranged in lateral bands within the median stomatal groove. This distribution of stomata is interpreted as an extreme variation of the median distribution with tendency towards banding seen in other taxa (viz. *Oswaldheeria hallei*, Fig. 17 N and Q, and *Sciadopityoides variabilis* Bose 1955, Fig. 1 K and L).

In the absence of evidence from reproductive structures, we have no firm indications of closer affinities of these genera. Their leaf and shoot morphology place them securely among the conifers. The exceptional stomatal distribution which separates them from all other conifers merits, in our view, their assignment to a single group at the family level. They have other features in common, too. If we consider the two mor-

phologically most widely separated genera, viz. *Oswaldheeria* and *Sciadopityoides*, they share the characters of leaf size dimorphism and in some species a median differentiation in the upper epidermis. The stratigraphic and geographic distribution of these Mesozoic forms show a consistency which also lends support to the idea of taxonomic unity. They appear first in the Middle Jurassic, and show a diversity maximum in the Lower Cretaceous (Manum 1987; cf. p. 21, *Oswaldheeria macrophylla*). They were restricted to the Northern Hemisphere north of 40 degrees present latitude as was shown by Florin (1963) and Sveshnikova (1981). Our study has not altered this picture of their distribution in time and space.

The record of dispersed Mesozoic *Sciadopitys*-like pollen is ambiguous to establish affinities. Such pollen grains are present along with the leaves, but their frequency and diversity are much less than one would expect if they had been borne by the same plants as the leaf fossils. Zauer & Mchedlishvili (1966) discussed the stratigraphic and geographic distribution of *Sciadopitys*-like pollen based on a series of distribution maps. In our view, these maps require critical revision, mainly because of the doubtful taxonomy of many of the records included in them, particularly for the early Mesozoic. With these reservations the distribution of pollen is fairly compatible with that of the leaves.

In conclusion, we wish to emphasize that these leaves are not so like those of *Sciadopitys* as previously thought; their nature is different from that interpreted for the 'double needles' of the extant species. We would, therefore, not assign them to the *Sciadopityaceae* along with *Sciadopitys*. However, in spite of the diverse characters among these four extinct genera, we are inclined to maintain the importance previously given to that of the median stomatal zone, and we think that this merits their assignment to one family. For this family we propose the name *Arctopityaceae* with *Arctopitys* as the type genus, combining characters of both *Oswaldheeria* and *Sciadopityoides*. If further division is required, we would suggest two subfamilies: *Sciadopityoideae* including *Sciadopityoides* only, and *Arctopityoideae* including *Arctopitys*, *Oswaldheeria* and *Holkopitys*. If the stomatal distribution in *Holkopitys* is interpreted as separate bands avoiding a vein between them, then the genus will have to be excluded from *Arctopityaceae*.

Nomenclature of some species described by Heer

That some taxa described by Heer (1868, 1874) from West Greenland appear *Sciadopitys*-like was first recognized by Schimper (in Schimper & Schenk 1890, p. 293), who briefly described the cuticle of *Pinus crameri* as possessing this character, however, without making a nomenclatural transfer. Formal transfers were subsequently made by Halle (1915) for *Pinus crameri* Heer (1868) and by Florin (1922) for *P. eirikiana* and *P. olafiana* of Heer (1874), all three species being assigned to *Sciadopityes* based on cuticle characters.

Our re-examination and reprocessing of Heer's type material have shown that both Halle (1915) and Florin (1922) used other specimens than Heer's originals for their study of the cuticles of Heer's taxa. By doing so, they happened to deal with other species than those which they intended to describe. This has necessitated taxonomic and nomenclatural revisions. A summary of the nomenclatural status of those of Heer's species involved in this revision is given below:

West Greenland species:

Pinus crameri Heer 1868

Now: *Sciadopityoides crameri* (Heer) Sveshnikova 1981 emend.

Junior homonym: *Sciadopityes crameri* (Heer) Halle 1915

Pinus eirikiana Heer 1874

Reserved for Heer's figured specimens only

Rejected combinations: *Sciadopityes eirikiana* (Heer) Florin 1922; *Sciadopityoides eirikiana* (Heer) Sveshnikova 1981

Pinus olafiana Heer 1874

Reserved for Heer's figured specimens only

Rejected combinations: *Sciadopityes olafiana* (Heer) Florin 1922; *Sciadopityoides olafiana* (Heer) Sveshnikova 1981

Spitsbergen species:

Pinus microphylla Heer 1876

Now: *Sciadopityoides microphylla* (Heer) comb. nov.

Junior synonym: *Sciadopityes crameri* (Heer) Halle 1915

Pinus crameri was described by Heer (1868, p. 84, pl. 44, figs. 7–18) from Kome, West Green-

land. This species was again reported by Heer (1874) from Ikorfat and other nearby localities where it was stated to be very common. Along with this latter record of *P. crameri*, Heer (1874) also described *P. eirikiana*. On the basis of cuticle characters these two species were transferred to *Sciadopityes* by Halle (1915) and Florin (1922), respectively.

The actual sample and locality from which Halle (1915) obtained the cuticles for his description of *Sciadopityes crameri* (Heer) could not be established, as neither in his paper nor on the slide labels is there any reference to samples. We have now made cuticle preparations from a few leaves preserved in one of the original specimens of *P. crameri* figured by Heer (1868, pl. 44, fig. 9), and this cuticle is quite different from that described by Halle (1915). It is, on the other hand, identical to the cuticle described by Florin (1922) as *S. eirikiana* in material from Kome, according to the slide labels. Furthermore, Florin's two slides with *S. eirikiana* show leaves that are much shorter than those described for Heer's *P. eirikiana*. Their size matches leaves studied by us from various shale samples from Kome and Ikorfat with cuticles like the originals of *P. crameri*. Also, the gross morphology of these new specimens is in accordance with *P. crameri* as figured by Heer (1868), but different from *P. eirikiana*. While leaves with cuticle identical to that of the original *P. crameri* are quite common in various localities, which is in accordance with Heer's (1874) statement regarding the occurrence of that species, leaves with cuticle like that described as *S. crameri* by Halle (1915) are rare. We have found such leaves only in two samples from Ikorfat. From this we conclude that neither Halle (1915) nor Florin (1922) had studied the original specimens of Heer's species and that the names these authors applied to their respective specimens are erroneous. It appears that Halle made his preparations from a sample from Ikorfat. The correct epithet for Florin's specimens of '*eirikiana*' is '*crameri*'. Before we deal with the status of *P. eirikiana*, we shall give evidence regarding the correct name to be used for *S. crameri* Halle non Heer.

Florin (1922) reported *S. crameri* (Heer) Halle in material from Bohemanflya, Spitsbergen. Among the slides left by Florin in Riksmuseet we have found two which we presume to be the basis for this report. They are labelled 'Orig.: *Pinus microphylla* Hr. Spetsbergen, Cap Boheman' and

both also carry labels indicating that Florin had identified the cuticles as being identical with *S. crameri* of Halle. We can now confirm this identification. *P. microphylla* was first described by Heer (1876, pl. 9, fig. 9) from Bohemanflya. We were unable to locate this figured specimen or other specimens, but from the same collection we have got a few samples which have leaves with cuticle like that of *P. microphylla* of Florin's slides. Also, in our own material from Bohemanflya we have found hundreds of leaves which correspond to those in Florin's slides. With the presumption that Florin prepared his slides from original specimens of *P. microphylla* and the fact that the cuticle corresponds to that of Halle's *S. crameri*, we establish them as *Sciadopityoides microphylla* (Heer) comb. nov. (see p. 24).

The status of *P. eirikiana* Heer (1874) is more problematic. Only three of the figured specimens could be located (l.c. pl. 2, fig. 1; pl. 18, fig. 2b; pl. 23, fig. 16). Of these, the leaves shown in pl. 2, fig. 1, lying along with *Jeanpaulia lepida*, which are inaccurately drawn, have no cuticle preserved. There are impressions of other complete leaves on the same surface which are not shown in Heer's figure. These leaves are 12–17 mm long (mostly c. 15 mm) and less than 1.5 mm wide, with a slightly expanded base and an obtuse or acute apex. The reverse side of the slab also has quite a few similar leaves and from some of them it was possible to prepare the cuticle, which is identical to the cuticle of Heer's original *P. crameri*. The other two specimens of *P. eirikiana* figured in Heer (1874) are incomplete and doubtful forms which can not be assigned to a genus. The missing specimens appear from the figures to be incomplete and unsuitable for any identification. We consider that Heer's name of '*Pinus eirikiana*' should be reserved for his figured specimens only, with the exception of pl. 2, fig. 1, which we believe to be *Sciadopityoides crameri* (see p. 23).

In the collection of Heer's (1868) specimens preserved in the Geological Museum, Copenhagen, we found a few specimens labelled in Heer's own handwriting as '*Pinus eirikiana*'. Since that species first appeared in his 1874 paper, he probably returned to the 1868 collection before dispatching it to Copenhagen, or he worked on both collections more or less simultaneously. Some of these leaves exceed 4 cm in length (neither base nor apex is preserved). Their cuticle is different from any of the other species reported in this paper and they deserve a new name. These

leaves have a distinct median stomatal groove on their abaxial side. However, in the absence of a leaf base it is difficult to say whether they belong to *Sciadopityoides* or *Arctopitys*.

Pinus olafiana Heer (1874) was assigned to *Sciadopitytes* by Florin (1922). Under *Sciadopityoides ikorfatensis* (pp. 26–28) we have given the evidence for our conclusion that the cuticle studied by Florin could not have been derived from *P. olafiana*. Since the true nature of *P. olafiana* can hardly be understood, this name should also be reserved for Heer's figured specimens only. The cuticle of *Sciadopitytes olafiana* Florin is too badly preserved to form the basis for a new species, and since Florin did not illustrate it, we propose to reject the name.

Annotated list of valid species of *Sciadopitys*-like leaves

Genus *Sciadopityoides* Sveshnikova emended
New diagnosis: p. 21

Sciadopityoides crameri (Heer) Sveshnikova
Synonymy and description: p. 23

Age and occurrence. – Lower Cretaceous; Kome and Ikorfat, West Greenland.

Sciadopityoides ikorfatensis n. sp.
Synonymy and description: p. 26

Age and occurrence. – Lower Cretaceous; Ikorfat, West Greenland.

Sciadopityoides microphylla (Heer) comb. nov.
Synonymy and description: p. 24

Age and occurrence. – Lower Cretaceous; Ikorfat, West Greenland; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Sciadopityoides nathorstii (Halle) Sveshnikova
Synonymy and description: p. 28

Age and occurrence. – Lower Cretaceous; Atanikerdluk and Kome, West Greenland.

Sciadopityoides ukrainensis (Doludenko) Sveshnikova

1963 *Sciadopitytes ukrainensis* Doludenko, p. 123, pl. 12, figs. 1–13

1981 *Sciadopityoides ukrainensis* (Doludenko) Sveshnikova, p. 1726

1987 *Sciadopityoides ukrainensis* (Doludenko) Sveshnikova: Manum, p. 154

Age and occurrence. – Upper Jurassic; western Ukraine, U.S.S.R.

Sciadopityoides uralensis (Dorofeev et Sveshnikova) Sveshnikova (type species)

1959 *Sciadopitytes [sic] uralensis* Dorofeev et Sveshnikova, p. 1277, pl. 2, figs. 1–7

1963 *Sciadopitytes uralensis* Dorofeev et Sveshnikova: Sveshnikova, p. 221, pl. 2, figs. 5–12

1981 *Sciadopityoides uralensis* (Dorofeev et Sveshnikova) Sveshnikova, p. 1723, pl. 2, figs. 1–6

1987 *Sciadopityoides uralensis* (Dorofeev et Sveshnikova) Sveshnikova: Manum, p. 154

Age and occurrence. – Cenomanian-Turonian; Urals, U.S.S.R.

Sciadopityoides variabilis (Bose) Sveshnikova

Synonymy and description: p. 32

Age and occurrence. – Lower Cretaceous; Padloping Island, Arctic Canada.

Genus *Arctopitys* n. gen.

Diagnosis: p. 32

Arctopitys capbohemanensis n. sp.

Description: p. 37

Age and occurrence. – Lower Cretaceous; Bohemanflya, Spitsbergen.

Arctopitys florinii n. sp. (type species)

Description: p. 35

Age and occurrence. – Lower Cretaceous; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Arctopitys inefecta n. sp.

Description: p. 39

Age and occurrence. – Lower Cretaceous; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Arctopitys lagerheimii (Johansson) comb. nov.

1920 *Sciadopitytes lagerheimii* Johansson, p. 254, figs. 1g and l, 2d (non 1h)

1922 *Sciadopitytes lagerheimii* Johansson: Florin, p. 266

1981 *Sciadopityoides lagerheimii* (Johansson) Sveshnikova, p. 1725

1987 *Sciadopitytes lagerheimii* (Johansson) Manum, p. 155, pl. 3, figs. 1–6, text-figs. 3 A–D

Age and occurrence. – Middle Jurassic; Andøya, northern Norway (see *O. macrophylla* below).

Arctopitys persulcata (Johansson) comb. nov.

1920 *Sciadopitytes persulcata* Johansson, p. 255, figs. 1m-o, 2e

1922 *Sciadopitytes persulcata* Johansson: Florin, p. 266

1981 *Sciadopityoides persulcata* (Johansson) Sveshnikova, p. 1725

1987 *Sciadopityoides persulcata* (Johansson) Sveshnikova: Manum, p. 161, pl. 4, figs. 1–5
Age and occurrence. – Middle Jurassic; Andøya, northern Norway (see *O. macrophylla* below).

Arctopitys sibirica (Samylyna) comb. nov.

1963 *Sciadopitys sibirica* Samylyna, p. 111, pl. 36, figs. 1–5

1981 *Sciadopityoides samylynae* Sveshnikova, p. 1726

1987 *Sciadopityoides sibirica* (Samylyna) Manum, p. 154

Age and occurrence. – Lower Cretaceous; Lena Basin, Siberia, U.S.S.R.

Genus *Oswaldheeria* n. gen.

Diagnosis: p. 39

Oswaldheeria arctica n. sp.

Synonymy and description: p. 44

Age and occurrence. – Lower Cretaceous; Bohemanflya and Adventdalen, Spitsbergen; Padloping Island, Arctic Canada.

Oswaldheeria hallei (Florin) comb. nov. (type species)

Synonymy and description: p. 41

Age and occurrence. – Lower Cretaceous; Ikorfat, West Greenland; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Oswaldheeria macrophylla (Florin) comb. nov.

1922 *Sciadopityes macrophylla* Florin, p. 267, fig. 2b

1981 *Sciadopityoides macrophylla* (Florin) Sveshnikova, p. 1725

1987 *Sciadopitys macrophylla* (Florin) Manum, p. 157, pls. 2, 3, text-figs. 2 A, B, E, F

Age and occurrence. – Middle Jurassic; Andøya, northern Norway; ongoing studies indicate a Bajocian-Bathonian age rather than Upper Jurassic as proposed earlier (Manum 1987).

Oswaldheeria scotica (Florin) comb. nov.

Synonymy and description: p. 46

Age and occurrence. – Upper Jurassic; Helmsdale, Scotland.

Genus *Holkopitys* n. gen.

Diagnosis: p. 48

Holkopitys hoegii n. sp.

Description: p. 49

Age and occurrence. – Lower Cretaceous; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Other gymnosperms

Of the other gymnosperms we have described from Spitsbergen (pp. 49–69), *Marskea* and *Torreya* are new to the flora (*Torreya* had been recorded by Heer, 1876, based on very doubtful specimens). *Pseudotorellia* is not new to the flora, but the two new species we have described show characters which have led us to emend the generic diagnosis; in one of them we could confirm the presence of resin ducts running along the veins. Three species of *Elatocladus* have also been described. In West Greenland, too, we have seen leaves with cuticle like that of *Marskea* and *Torreya*, but specimens of better quality are needed in order to describe them.

Descriptions

Family ARCTOPITYACEAE n. fam.

(For details, see p. 18)

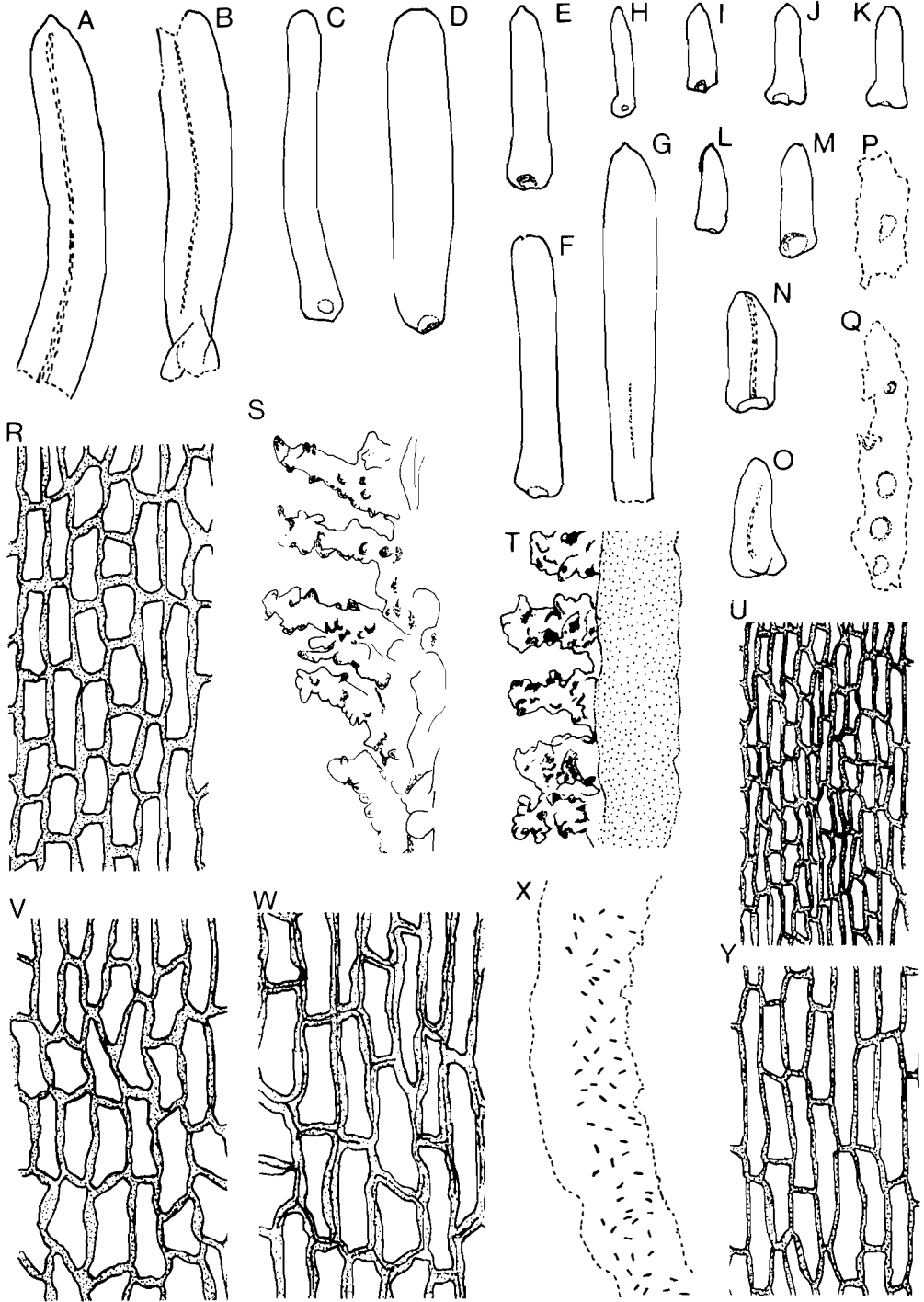
Genus *Sciadopityoides* Sveshnikova

Emended diagnosis. – Leaves dimorphic. Long leaves spirally arranged and directed upwards, linear, straight or slightly curved. Margins entire; base slightly expanded, showing a distinct abscission mark; apex obtuse, acute or acuminate. Upper surface with or without a median furrow; lower surface always with a median groove. Resin ducts may or may not be present.

Cells of upper cuticle and of lower cuticle outside median groove serially arranged; anticlinal walls straight or sometimes wavy, surface non-papillate. Stomata confined to lower surface within median groove; margins of groove projecting over stomatal zone; cells along margins of groove papillate, sometimes papillae present along slopes of groove; papillae mostly long and cylindrical with smooth or tuberculate surface. Stomata monocyclic, irregularly scattered, longitudinally, obliquely or transversely orientated. Subsidiary cells 4–8, may or may not be papillate. Guard cells semilunar or crescent-shaped, slightly sunken. Cells within stomatal zone polygonal, irregularly arranged, with smooth or papillate surface.

Short leaves, about 1/3–1/4 of long leaf; cuticle same as long leaf.

Type species. – *Sciadopityoides uralensis* (Dorofeev et Sveshnikova) Sveshnikova, 1981.



Sciadopityoides crameri (Heer) Sveshnikova
 Pl. 1, figs. 3, 5, 6; Pl. 8, fig. 6; Text-figs. 7 A–Q,
 U, Y, 9 A, B, D, Q–S, U
 1868 *Pinus crameri* Heer, p. 84, pl. 44, figs. 8b, 9
 (only leaves), 10–18 (only leaves). Non fig. 7
 1874 *Pinus crameri* Heer, p. 83, pl. 23, figs. 9, 12.
 Non figs. 11, 13–15
 1874 *Pinus eirikiana* Heer, p. 85 (in part), pl. 2,
 fig. 1 (excluding *Jeanpaulia lepida*)
 1882 *Pinus crameri* Heer, p. 17
 1922 *Sciadopityes eirikiana* (Heer) Florin, fig. 2a
 1926 *Sciadopityes crameri* (Heer): Seward, p. 105
 (name only)
 1981 *Sciadopityoides crameri* (Heer) Sveshnikova,
 p. 1724, pl. 2, figs. 7–11, pl. 3, figs. 1, 2
 Non: 1915 *Sciadopityes crameri* (Heer) Halle,
 jun. homonym

Emended diagnosis. – Long leaf linear, 7–18 mm
 long and 1.0–1.5 mm wide, rarely up to 2 mm
 wide, straight or slightly curved. Margins entire;
 base slightly expanded, bottom of leaf showing a
 broadly oval or circular opening; apex obtuse,
 sometimes acute, rarely apiculate. Lower surface
 with a median groove. Resin ducts 2, one on
 either side of median groove.

Stomata confined to lower surface within
 median groove, margins of median groove pro-
 jecting over stomatal zone. Within groove sto-
 mata irregularly scattered, closely set, orientation
 mostly transverse or oblique, rarely longitudinal.
 Subsidiary cells 6–7, rarely 5. Guard cells slightly
 sunken, semilunar; aperture narrow, elliptic or
 slit-like. Ordinary epidermal cells within groove
 polygonal, smaller than cells outside groove, anti-
 clinal walls thin; surface smooth, rarely papillate;
 papillae cylindrical, straight or curved. Cells along
 margins of stomatal groove mostly with long,
 cylindrical and hollow papillae. Two to four series
 of cells adjacent to marginal cells (towards lateral
 side) also commonly papillate; papillae solid,
 sometimes conical and hollow. Cuticle of stomatal
 groove slightly thinner than remaining surface.

Cells of upper cuticle and cells outside median
 groove on lower surface rectangular or elongated
 polygonal, arranged in longitudinal rows; anti-
 clinal walls thick, straight, rarely slightly wavy;
 periclinal wall unspecialized. Cells of lower sur-
 face sometimes slightly narrower than those of
 upper surface. Within stomatal groove irregularly
 arranged, thick-walled, polygonal cells present
 under the epidermis (hypodermal cells?).

Short leaves conical, 2.0–3.0 mm long and 1.0–
 1.5 mm wide, apex mostly obtuse, sometimes
 acute, rarely apiculate; base slightly expanded;
 bottom showing a circular or oval opening. Lower
 side having a median groove. Cuticle as in long
 leaves.

Lectotype. – *Pinus crameri* Heer, 1868, pl. 44, fig.
 9. (Specimen no. MMH6848.)

Occurrence. – Kome and Ikorfat, West Green-
 land.

Remarks. – Besides some of the figured specimens
 of Heer (1868) we had at our disposal several
 samples from Kome and Ikorfat from various
 collections labelled either as *Pinus crameri* or
Sciadopityes crameri. All these samples were
 extremely rich and even on the shale surfaces
 concentrated masses of leaves were visible.
 Leaves from different collections show some size
 variation. Three samples had leaves 7 to 15 mm in
 length, but mostly less than 10 mm. Their average
 width was between 1.0 and 1.5 mm, but some
 were 2 mm wide. From the remaining rock
 samples from Kome and Ikorfat they were on
 average less than 10 mm; here, the length was 6
 to 10 mm, in rare cases up to 12 mm. Their width
 was mostly about 1 mm, in exceptionally rare
 cases the width was 1.5 mm. Although there is a
 considerable size variation, they cannot be sep-
 arated on the basis of cuticle characters.

The samples with the smaller leaves behaved
 in a somewhat unusual manner. The leaves

Fig. 7. A–Q, U, Y—*Sciadopityoides crameri* (Heer) Sveshnikova. A–G, leaves (A, B, G: Ikorfat and C–F: Kome); ×5. H–O,
 short leaves (H, K–M, O: Ikorfat and I–J, N: Kome); ×5. P, Q, shoot showing leaf scars (Kome); ×5. U, lower cuticle showing
 cells outside median groove; ×125. X, showing distribution of stomata; ×50. Y, upper cuticle; ×125. (Slide and specimen nos.:
 A, S20303-1; B, S20303-2; C, PMO(A)27741-1; D, V1508-1; E, PMO(A)27741-4; F, PMO(A)27741-3; G, S20304-1; H, S20303-
 3; I, PMO(A)27741-4; J, PMO(A)27741-5; K, S20303-6; L, S20303-5A (consumed); M, S20303-5B; N, PMO(A)27741-6; O,
 S20303-4; P, PMO(A)22741-7; Q, PMO(A)27741-8; V, S20305; X, S20303-3; Y, S20305.)

R–T, V, W—*Sciadopityoides microphylla* comb. nov. R, cells of lower cuticle outside median groove of a long leaf; ×125. S,
 T, showing tuberculate papillae of long and short leaves, respectively; ×200. V, lower cuticle of a short leaf; ×125. W, upper
 cuticle of a short leaf; ×125. (Slide nos.: R, S20301; S, PMO4444-5; T, PMO4446-1; V, PMO4446-1; W, PMO4446-1.)

swelled in acid due to the formation of gas, and became extremely brittle and sensitive to even very weak alkali. The greater part of the lamina became slimy and the median groove coiled.

There are only two resin ducts, one on either side of the median groove. However, they are extremely difficult to observe, because they are not visible in unoxidized specimens and mostly disintegrate during oxidation.

In the upper surface of a few leaves a median narrow depression is visible, while in others an impression of the lower median groove can be seen. However, none of them shows any cell differentiation along these depressions or impressions.

Stomatal orientation is quite variable, between specimens as well as in different parts of the same specimen, being usually transverse or oblique, more rarely most of the stomata are longitudinally orientated.

The papillae along the margins and the slopes of the groove are mostly long, cylindrical and hollow with obtuse tips; rare papillae have bifurcating or somewhat tuberculate tips. Cells away from the groove margins have progressively smaller papillae and the cells in the lateral 2–3 rows have only solid papillae with circular base.

Comparison. – *Sciadopityoides crameri* usually has leaves with obtuse apices, whereas in *S. uralensis* the leaves have acute or apiculate apices. Both species have transversely or obliquely orientated stomata, but unlike *S. crameri* the latter has tuberculate papillae. *S. ukrainensis* has much longer leaves with pointed apices. Also, the papillae along the margins of the median groove are shorter than those of *S. crameri*.

Sciadopityoides microphylla (Heer) comb. nov.
Pl. 1, figs. 1, 2, 4, 7, 9; Pl. 2, fig. 9; Pl. 8, figs. 4, 5; Text-figs. 7 R–T, V, W, 8, 9 C

1876 *Pinus microphylla* Heer, p. 46, pl. 9, fig. 9
1915 *Sciadopityes crameri* (Heer) Halle, p. 509, pl. 13, figs. 1–13, jun. syn.

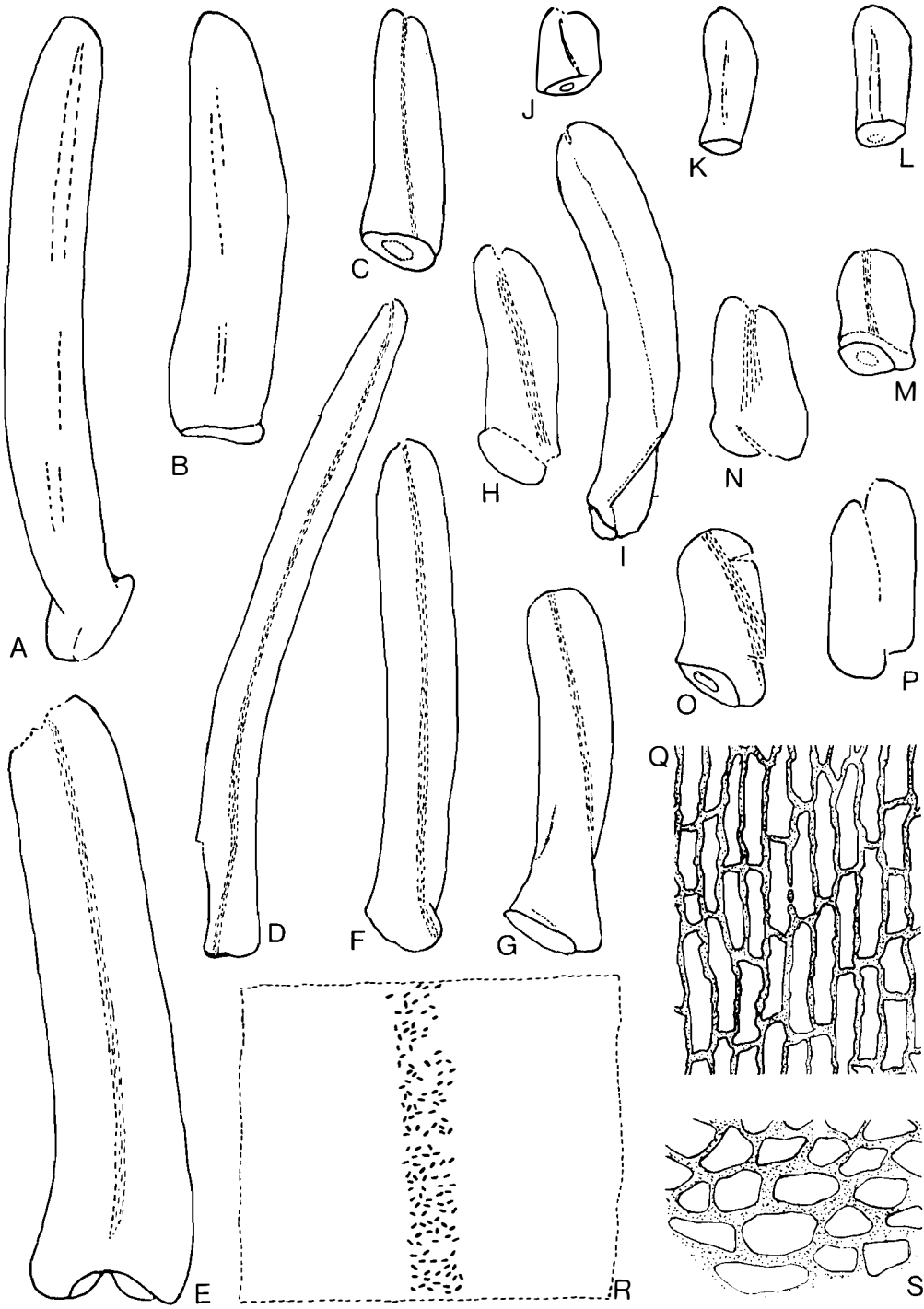
1922 *Pinus microphylla* Heer: Florin, p. 267 (name only)

Diagnosis. – Long leaf typically 10–14 mm long, 2.0–2.5 mm wide (range noted 10–20 mm long and 1.5–4.6 mm wide), straight or curved, substance of lamina thick and coriaceous; base slightly expanded, with clear circular or broadly oval hole in the bottom; apex obtuse, rarely acute; margins entire. Abaxial side has a prominent median groove; occupying middle of compressed leaf, sometimes running obliquely, mostly traversing almost entire leaf length.

Cuticle thick, almost of same thickness on both surfaces. On lower surface along median groove cuticle slightly thinner; stomata confined to median groove; margins projecting over groove. Cells of upper cuticle arranged in longitudinal rows, rectangular or trapezoidal, sometimes polygonal, usually 2–8 times longer than width; anticlinal walls thick, straight or at places wavy, rarely slightly sinuous or broken by pits; periclinal wall smooth. Cells of lower cuticle outside median groove like those of upper cuticle. Four to eight series of cells along margins of median groove papillate; cells of outermost series with solid thickening, sometimes with conical and hollow papillae, cells bordering marginal cells (up to 4 series or more) and occasionally along slopes of groove, with long papillae, mostly tuberculate, sometimes cylindrical with obtuse or forked apices. Papillae mostly crowded and overlapping, often papillae from either margin interfingering so as to conceal stomatal groove and stomata. Ordinary epidermal cells within stomatal groove polygonal with thin and straight anticlinal walls; periclinal wall smooth, very rarely having dome-shaped or conical papillae, or a mere cuticular thickening. Stomata crowded, subsidiary cells of adjoining stomata often abutting but never sharing a subsidiary cell, orientation oblique or transverse, rarely longitudinal. Subsidiary cells 5–8, mostly 6. Guard cells slightly sunken, crescent-shaped or semilunar, with thickened tangential walls. Aperture narrowly elliptical or slit-like.

Short leaf deltoid, 2–5 mm long and 2.0–2.5 mm wide. Base expanded, bottom having a circular or broadly oval hole; apex obtuse. Abaxial surface

Fig. 8. A–S—*Sciadopityoides microphylla* comb. nov. A–I, leaves (A, B: Ikorfat, C–G: Bohemanflya and H–I: Padloping Island); ×5, J–P, short leaves (J, M–P: Bohemanflya and K, L: Ikorfat). Q, lower cuticle showing cells outside median groove; ×125. R, showing distribution of stomata; ×20. S, thick-walled cells along median groove; ×200. (Slide nos.: A, S20302-1; B, S20302-4; C, PMO4444-7; D, PMO4444-1; E, PMO4445-1; F, PMO4444-3; G, PMO4444-2; H, GSC6702-29; I, GSC6702-28; J, PMO4444-8; K, S20302-2; L, S20302-3; M, PMO4444-9; N, PMO4444-10; O, PMO4444-11; P, PMO4444-12; Q, PMO4444-4; R, S20301; S, PMO4444-6.) Unless otherwise stated figures are of long leaves.



shows a median stomatal groove, running from base to apex. Cuticle same as long leaves.

Holotype. – Specimen figured by Halle 1915, pl. 13, fig. 2. (Slide no. S20301.)

Occurrence. – Ikorfat, West Greenland; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Description. – The largest and widest leaves (Figs. 8 D, E) are from Bohemanflya, measuring 20×1.5 mm and 17.5×4.6 mm, respectively. Often the apices are slightly cracked along the median groove. The leaf bases are mostly abruptly widening and a little above the base slightly constricted. In compressed state some are twisted at this place. Most of the leaves show flat upper surface, but some show an impression of the median groove. Rarely, in some partially macerated leaves, a median narrow 'furrow' is visible in the upper cuticle. When fully macerated, such 'furrows' disappear and the upper cuticle shows no median cell differentiation.

Tuberculation of the papillae along the margins of the stomatal groove shows some variation: leaves from Bohemanflya and Padloping Island nearly always have tuberculate papillae, whereas leaves from Ikorfat sometimes have smooth papillae. Within the stomatal groove a layer of thick-walled, more or less isodiametric polygonal cells (Fig. 8 S) are visible underneath the cuticle in many leaves, covering either the entire groove or being restricted to either side (4–6 cells wide) inside the margins (hypodermal cells?). These cells are like those present in *S. crameri*.

The short leaves are relatively more common at Bohemanflya than at the other two localities, but essentially their characters are similar. Ikorfat is the only locality where these leaves have been found in concentrated masses.

Comparison. – *Sciadopityoides microphylla* most resembles *S. uralensis* in overall shape and in the

characters of the cuticle. *S. uralensis*, however, differs in having leaves with acute or apiculate apices, a furrow in the upper surface and papillate subsidiary cells. The leaves of *S. ukrainensis* are much larger in size and they do not have tuberculate papillae (see Doludenko 1963). In *S. crameri* the leaves are less wide than *S. microphylla* and they usually have non-tuberculate papillae along the margins of the median stomatal groove.

Sciadopityoides ikorfatensis n. sp.

Pl. 1, fig. 8; Pl. 2, figs. 3, 10; Text-figs. 9 E–P, T, 10

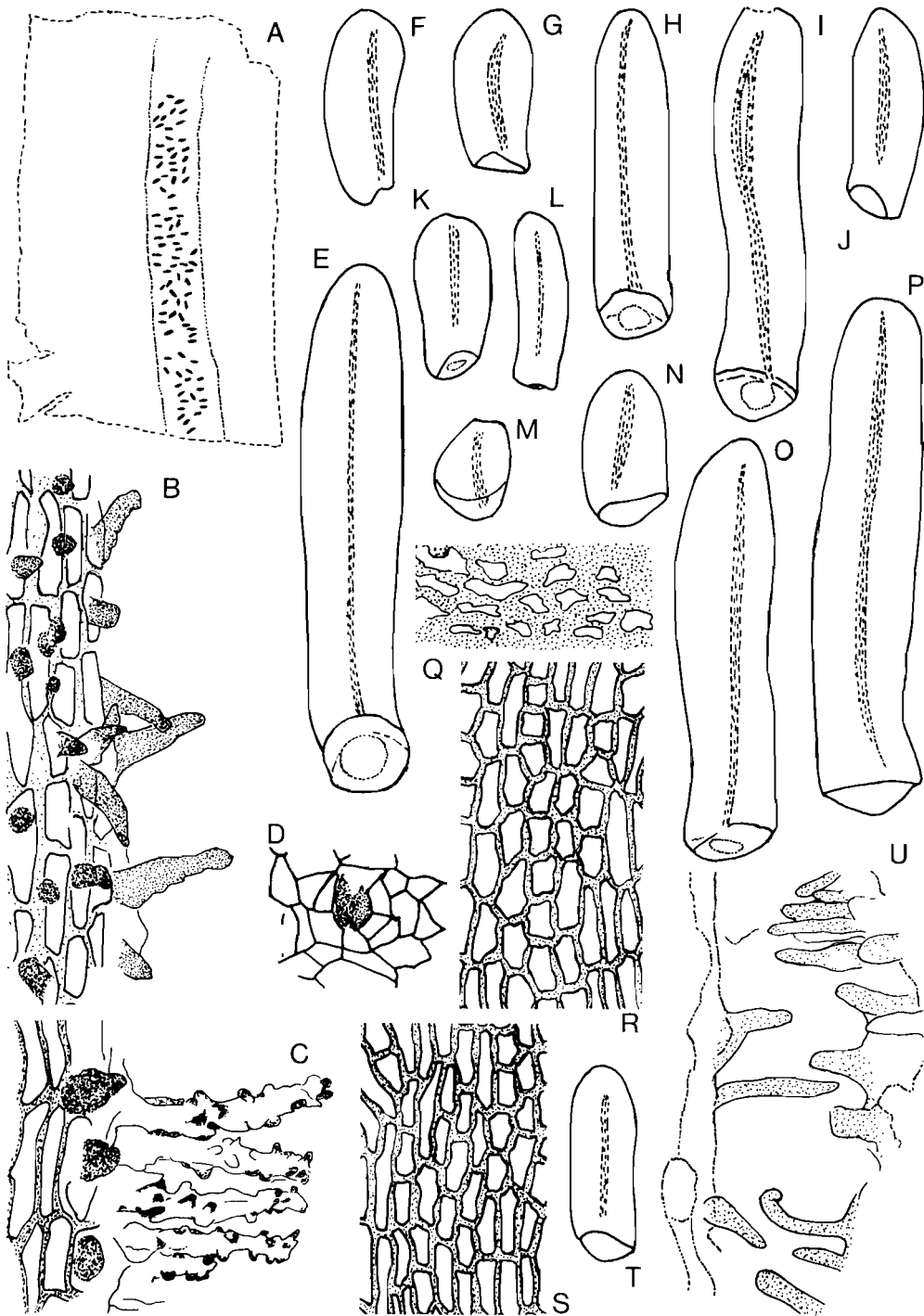
Diagnosis. – Long leaf linear, 13–18 mm long and 2–3 mm wide; margins entire; abaxial surface having a narrow median groove, both ends of groove terminating slightly away from base and apex. Base slightly swollen, bottom of leaf having circular hole; apex obtuse, sometimes acute.

Cuticle along median groove slightly thinner than cuticle of rest of lamina. Cells of adaxial surface serially arranged, rectangular or polygonal, sometimes more or less squarish; anticlinal walls thick, straight or slightly wavy; periclinal wall smooth or mottled. Cells of abaxial surface similar to those of adaxial surface, but cells within stomatal groove irregularly arranged, mostly polygonal in shape and smaller in size; anticlinal walls thinner and straight; periclinal wall smooth, rarely with a solid papilla. Stomata irregularly scattered within abaxial median groove; margins of groove projecting over stomatal surface. A few rows of cells along margins with long, tuberculate papillae; papillae crowded and overlapping. Some cells along slopes of groove also papillate. Outermost 1–3 (sometimes even more) rows of marginal cells along groove with solid papillae. Stomatal orientation mostly longitudinal but sometimes oblique or transverse. Subsidiary cells 6–7, rarely 5, often polar subsidiary cells distinct. Guard cells slightly sunken, spindle-shaped, well cutinized; aperture narrow, slit-like.

Fig. 9. A, B, D, Q–S. U—*Sciadopityoides crameri* (Heer) Sveshnikova. A, showing distribution of stomata on lower surface of leaf; $\times 20$. B, papillae along margin of groove; $\times 200$. D, a stoma; $\times 200$. Q, thick-walled cells along median groove; $\times 200$. R, upper cuticle of a short leaf; $\times 125$. S, cells of lower cuticle of a short leaf, outside median groove; $\times 125$. U, papillae along margins of groove of a short leaf. (Slide nos.: A, B, D, S20303-4; Q, V1509a-1; R–S, S20303-5B; U, S20303-6.) Unless otherwise stated figures are of long leaves.

C—*Sciadopityoides microphylla* comb. nov., tuberculate papillae along margin of groove of a long leaf; $\times 200$. (Slide no. PMO4444-4.)

E–P, T—*Sciadopityoides ikorfatensis* n. sp. E, H, I, O, P, long leaves; $\times 5$. F, G, J–N, T, short leaves; $\times 5$. (Slide nos.: E, S20306-1; F, S20306-2; G, S20306-3; H, S20306-4; I, S20306-5; J, S20306-6; K, S20306-7; L, S20306-8; M, S20306-9; N, S20306-10; O, S20306-11; P, S20306-12; T, S20306-13.)



Within the stomatal groove irregularly arranged, polygonal, thick-walled cells appear under the epidermis (hypodermal cells?).

Short leaf cylindrical or somewhat triangular in shape, slightly curved, usually 3–6 mm long, 1.5–2.5 mm wide. Apex mostly obtuse, rarely sub-acute; base slightly expanded, showing a distinct abscission mark. Abaxial surface having a median groove. Cuticle same as long leaves.

Holotype. – Slide no. S20306-12. Fig. 9 P.

Occurrence. – Ikorfat, West Greenland.

Remarks. – The diagnosis is based on hundreds of specimens isolated from a shale sample from Ikorfat. Besides a few stray pieces of leaves of some other conifers, the assemblage consists entirely of *Sciadopityoides ikorfatensis*, which in the mode of stomatal distribution resembles, more or less, the cuticle of *Sciadopityes olafiana* as described by Florin (1922). Florin had mentioned that in *S. olafiana* the stomata occur in longitudinal rows. In our specimens the stomata are longitudinally orientated, but they are irregularly scattered. In the collection of Riksmuseet we found a slide prepared by Florin (1922, p. 423) which is labelled as '*Pinus olafiana* Hr. = *Sciadopityes* sp.' from Ikorfat. The cuticle is badly preserved and only at places one can make out the stomatal distribution. It seems they are longitudinally orientated, but not in longitudinal rows. We have also had three hand specimens labelled as '*Pinus olafiana* Heer' from Ikorfat, one of which is Heer's (1874) specimen figured in his pl. 20, fig. 10. Portions from these specimens were macerated, but none of them yielded cuticles resembling Florin's preparation or on the whole cuticle which was *Sciadopitys*-like; on the contrary, some of them more resembled the cuticle of *Marskea* Florin and *Torreya* Arnott. In fact, Heer's description and figures do not suggest *Sciadopitys*-like leaves either.

The shale sample which yielded *S. ikorfatensis* also has some cone-like bodies (Figs. 10 L–N). They have, however, not yielded pollen or seed. The cone-scales(?) have no stomata.

Comparison. – *Sciadopityoides ikorfatensis* can be distinguished from *S. uralensis*, *S. crameri* and *S. microphylla* by the size of the leaf and the orientation of stomata. The average leaf of *S. ikorfatensis* is wider than the other three species and it has mostly longitudinally orientated stomata. *S. ukrainensis* has longer leaves with acute apices and its papillae, overhanging the stomatal groove, are non-tuberculate.

Sciadopityoides nathorstii (Halle) Sveshnikova

Pl. 2, figs. 1, 2; Text-fig. 11

1915 *Sciadopityes nathorstii* Halle, p. 512, pl. 12, figs. 16–29

1922 *Sciadopityes nathorstii* Halle: Florin, p. 265

1926 *Sciadopityes nathorstii* Halle: Seward, p. 105

1981 *Sciadopityoides nathorstii* (Halle) Sveshnikova, p. 1725, pl. 3, fig. 4

Doubtful specimens:

1920 *Sciadopityes nathorstii* Halle: Johansson, p. 253, figs. 1d–f, 2a–c

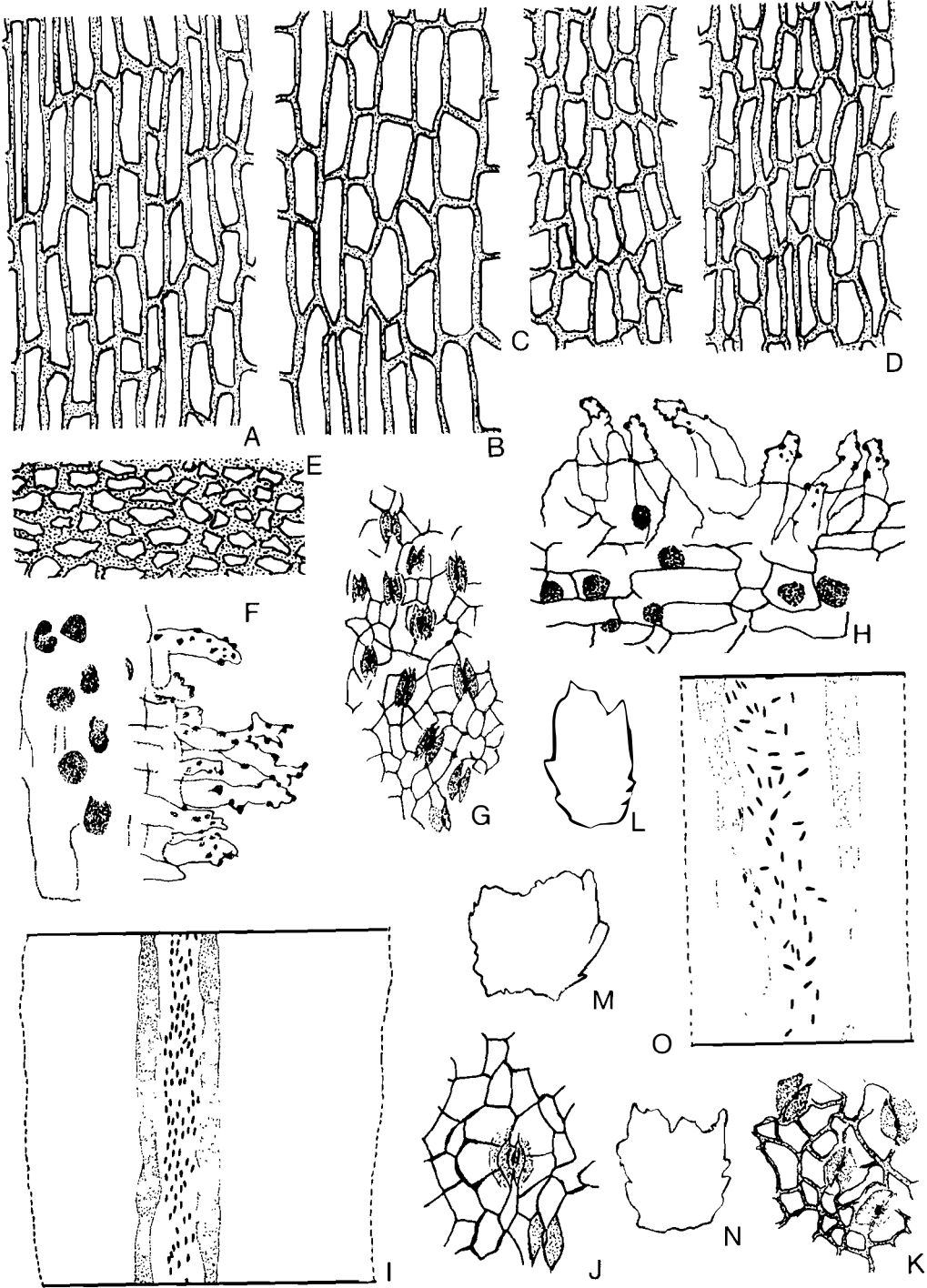
1987 *Sciadopityoides nathorstii* (Halle) Sveshnikova: Manum, p. 161, pl. 5, figs. 1–8

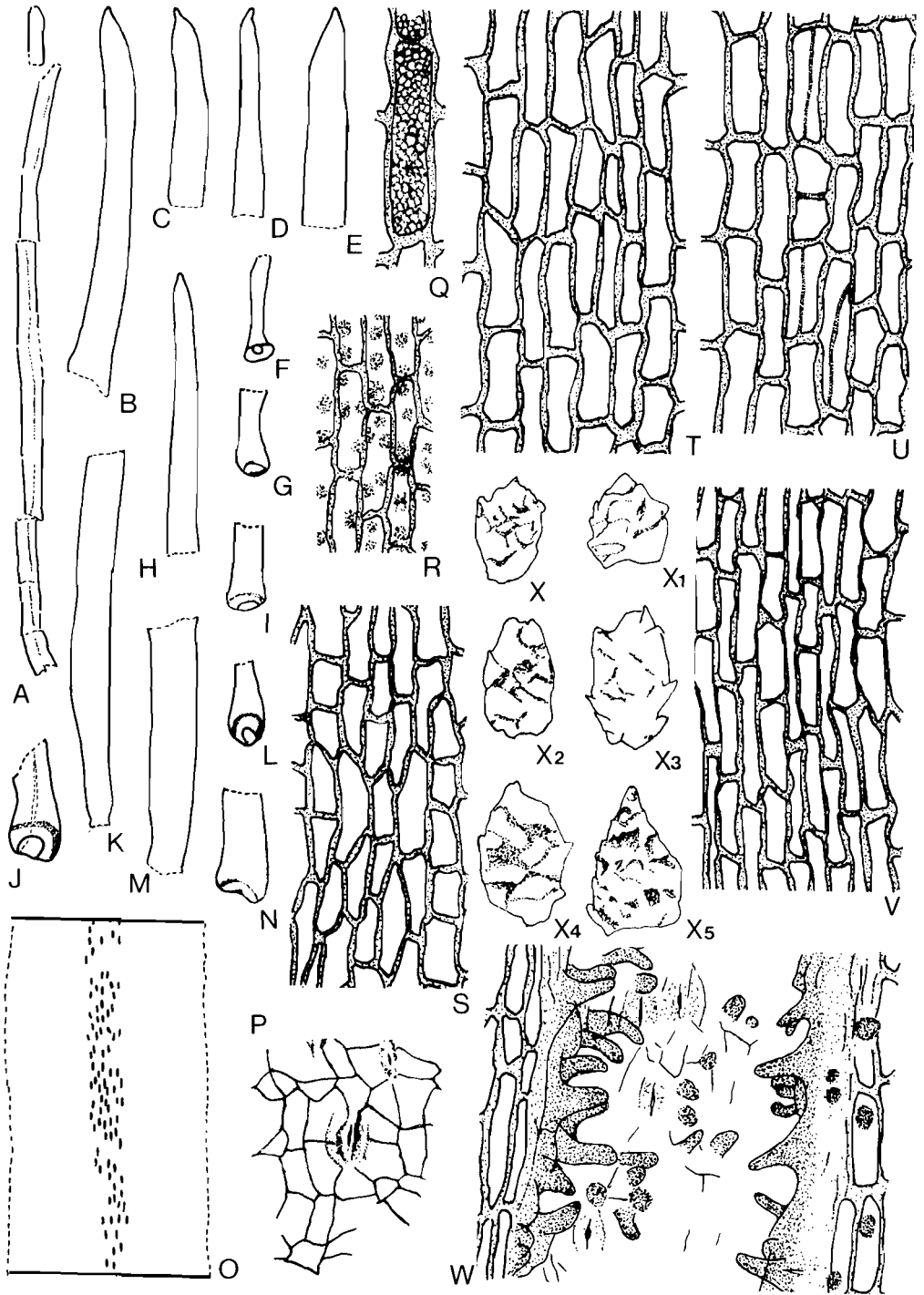
Non: 1969 *Sciadopityoides nathorstii* (Halle) Sveshnikova: Sveshnikova & Budantsev, p. 52

Emended diagnosis. – Leaf linear, substance of lamina thick, biconvex, about 4–5 cm long and 1.0–2.5 mm wide. Apex acute, sub-acute or apiculate, rarely obtuse; base slightly expanded, showing a hole in the bottom. Margins entire; dorsal surface with a narrow median groove. Resin ducts 2, lying on either side of median groove.

Cuticle of upper surface and that of non-stomatal regions on lower surface of almost same thickness, cuticle along median groove slightly thinner. Cells of upper surface serially arranged, rectangular or polygonal in shape; anticlinal walls unevenly thickened, straight or slightly undulate; periclinal wall smooth or mottled. Cells of non-stomatal regions of lower surface similar to those of upper surface. Margins of stomatal groove slightly projecting over stomatal surface. A few rows of cells along margins of groove papillate; rows of cells closer to margins with long conical

Fig. 10. A–O—*Sciadopityoides ikorfatensis* n. sp. A, lower cuticle showing cells outside median groove; $\times 125$. B, upper cuticle; $\times 125$. C, upper cuticle of a short leaf; $\times 125$. D, lower cuticle of a short leaf showing cells outside median groove; $\times 125$. E, thick-walled cells along median groove; $\times 125$. F, tuberculate papillae; $\times 200$. G, a few stomata; $\times 125$. H, tuberculate papillae of a short leaf; $\times 200$. I, showing distribution of stomata; $\times 20$. J, a stoma; $\times 200$. K, a few stomata of a short leaf; $\times 200$. L–N, cones(?); $\times 5$. O, showing distribution of stomata in a short leaf; $\times 50$. (Slide and specimen nos.: A, B, G, I, J, S20306-12; C, S20306-14; D, K, O, S20306-13; E, S20306-15; F, S20306-16; H, S20306-17; L, S20306-18; M, S20306-19; N, S20306-20.) Unless otherwise stated figures are of long leaves.





or cylindrical papillae, apices of papillae obtuse; outermost rows (1–3 cells wide) with solid papillae, sometimes with cutinized protuberances. Some cells within groove also papillate; papillae variable in shape and size, from long and cylindrical to conical or merely a circular thickening. Within groove cells smaller in size than those of non-stomatal regions, mostly polygonal. Stomata confined to median groove, crowded, orientation mostly longitudinal, rarely oblique. Subsidiary cells of adjoining stomata sometimes abutting, but never sharing a subsidiary cell, 6–7 in number, mostly 6, rarely 5; polar subsidiary cells marked, sometimes papillate. Guard cells slightly sunken, crescent-shaped; aperture narrow.

Lectotype. – Halle (1915), pl. 12, fig. 16. (Slide no. S20307-1.)

Occurrence. – Atanikerdluk and Kome, West Greenland.

Remarks. – *Sciadopityoides nathorstii* (Halle) Sveshnikova was first described by Halle (1915) from Atanikerdluk. Later, this species was recorded from the Jurassic of Andøya, northern Norway by Johansson (1920). The cuticle of Andøya specimens is rather poorly known (see Manum 1987) and the leaf-base is not known either. We therefore consider the record of this species from Andøya to be doubtful.

Florin (1922) had mentioned *S. nathorstii* from Kome, West Greenland. He did not figure any specimen and we have not been able to trace any of his specimens or slides in Riksmuseet. We have macerated several shale samples from Kome, but not from any of them could we get a single specimen of *S. nathorstii*.

Sveshnikova & Budantsev (1969) described *Sciadopityes nathorstii* from Bohemanflya, Spitsbergen. From their description and illustrations we consider their specimens to be distinct from *S. nathorstii*. They have obtuse apices and the stomata are obliquely orientated, whereas *S. nathorstii* from Atanikerdluk has apiculate or acute apices (Figs. 11 B–E) and the stomata are

longitudinally orientated. We think these specimens are more like *Arctopitys capbohemanensis* n. sp. (p. 37).

The original material of *S. nathorstii* was collected by Professor A. G. Nathorst from the 'Middle Cretaceous' beds of Atanikerdluk (see Halle 1915, p. 512). These beds were later assigned to the Atane Formation (Upper Cretaceous) by Koch (1964). The Atane Formation has been stated to be dominated by angiosperms (Pedersen 1976). We have macerated a shale sample from the original material collected by Nathorst, containing *S. nathorstii*, from Atanikerdluk for spores and pollen grains. The material was found to be rich in pteridophytic and gymnospermous spores and pollen grains, including a fair number of *Sciadopitys*-like pollen grains, but angiospermous pollen was not found.

Several specimens of cone-like bodies (Figs. 11 X to X₅) were obtained by bulk maceration of the material from Atanikerdluk, but none of them contained any pollen grain or seed. The 'conescales' have epidermal cells like those of the upper cuticle of *S. nathorstii*, but are devoid of stomata.

Description. – All the available leaves are incomplete, most of them are devoid of base and apex. Small pieces of basal and apical parts occur separately (Text-figs. 11 C–G). The largest leaf (Halle 1915, pl. 12, fig. 16) measures 5.0 cm in length and 1.2 mm in width. Mostly the leaves are less than 2.0 mm wide. The apex is mostly acute or apiculate. As compared to apical portions, bases of leaves are more rare. Such pieces are mostly less than 5 mm in length. The base is slightly swollen and the bottom has a circular or oval opening.

In most leaves cuticular characters are more or less uniform. However, a few leaves do show variations. In one leaf the cells of upper cuticle are rather small as compared to normal leaves. Cells of the non-stomatal regions of some of the specimens show a peculiar polygonal pattern (Fig. 11 Q) or circular thickenings (Fig. 11 R). Size and shape of the papillae along the margins of the

Fig. 11. A–X—*Sciadopityoides nathorstii* (Halle) Sveshnikova. A–N, leaves; A, ×2; B–N, ×5. O, showing distribution of stomata; ×20. P, a stoma; ×200. Q, a cell showing polygonal meshes; ×200. R, a few cells showing circular thickenings on their surfaces; ×200. S, lower cuticle of a cone scale(?); ×125. T, upper cuticle of leaf; ×125. U, upper cuticle showing a few abnormal cells; ×125. V, lower cuticle; ×125. W, papillae along margins of median groove; ×200. X–X₅, cones(?); ×5. (Slide and specimen nos.: A, S20307-1; B, S20307-2; C, S20307-3; D, S20307-4; E, S20307-5; F, S20307-6; G, S20307-7; H, S20307-8; I, S20307-9; J, S20307-10; K, S20307-11; L, S20307-12; M, S20307-13; N, S20307-14; O, S20307-15; P, S20307-16; Q, S20307-17; R, S20307-18; S, S20307-19; T, S20307-20; U, S20307-21; W, S20307-22; X, S20307-23; X₁, S20307-24; X₂, S20307-25; X₃, S20307-26; X₄, S20307-27; X₅, S20307-28. Note: Specimen nos.: S20307-12 and S20307-5 consumed.) Unless otherwise stated figures are of long leaves.

median stomatal groove and within the groove are rather variable, as has been indicated by Manum (1987).

Comparison. – *Sciadopityoides nathorstii* is more than double the size of all the other species described in this paper. *S. uralensis* and *S. microphylla* have tuberculate papillae along the margins of the median stomatal groove. In *S. nathorstii* the papillae are non-tuberculate. *S. nathorstii* resembles *S. ikorfatensis* in having longitudinally orientated stomata, but the latter species has tuberculate papillae along the margins of the median stomatal groove. In size and shape *S. ukrainensis* is more like *S. nathorstii*, but in *S. ukrainensis* the stomata do not have any preferred orientation and its epidermal cells within the stomatal zone are non-papillate.

Sciadopityoides variabilis (Bose) Sveshnikova
Pl. 2, figs. 7, 8; Text-fig. 12

1955 *Sciadopitytes variabilis* Bose, p. 53, pl. 1, figs. 2, 6, 7, text-figs. 1 A–I, K–N, 2 A, D, E, 3 A–D

1981 *Sciadopityoides variabilis* (Bose) Sveshnikova, p. 1726

Emended diagnosis. – Leaf linear, typically 12–15 mm long and 2.0–2.5 mm wide (range noted 6–24 mm long and 1–3 mm wide); apex acute or obtuse, base slightly expanded, sometimes twisted a little above base, bottom showing a circular or broadly oval opening. Margins entire, abaxial side having a median groove running along almost entire length, but mostly not touching base and apex.

On both surfaces cuticle about 6 µm thick, cuticle along lower median groove slightly thinner. Cells of adaxial surface more or less serially arranged, rectangular or trapezoidal in shape, sometimes polygonal; anticlinal walls thick, straight, sometimes slightly wavy; periclinal wall smooth, rarely mottled. Cells of abaxial surface like those of adaxial surface, sometimes cells (1–2 cells wide) on either side of median groove narrower and slightly more elongated; rarely periclinal wall of such cells with circular, solid papillae. Ordinary cells within median groove mostly polygonal; anticlinal walls thinner than those of cells lying outside groove; periclinal wall with or without papillae; papillae varying in shape and size, solid or elongated conical with obtuse apices. Papillae along margins and slopes of groove of variable frequency, sometimes even lacking. Sto-

mata restricted to median groove on abaxial surface, irregularly distributed or forming 2–4 bands, closely set, without any preferred orientation. Subsidiary cells mostly 5–6, rarely 4 or 7.

Sometimes polar subsidiary cells distinct, rarely papillate; papillae mostly solid and dome-shaped. Guard cells sunken, semi-lunar; aperture narrowly elliptical.

Holotype. – Slide no. GSC6702-1. Fig. 12 B.

Occurrence. – Padloping Island, Arctic Canada.

Remarks. – *Sciadopityoides variabilis* shows a good deal of variation in its median stomatal groove. Cells along the margins of the groove may or may not be papillate; when cells along the margins are papillate, they may be closely or distantly set. The shape and size of the papillae, too, vary between specimens or even within the same specimen. There is no fixed pattern of stomatal distribution. The stomata may be irregularly scattered or they may be forming 2–4 bands. When there are 3–4 bands, the marginal ones are narrower. There is no preferred orientation of stomata; mostly they are longitudinally or obliquely orientated, in some leaves they are mostly transversely and obliquely orientated. When in bands, the stomata are longitudinally or obliquely orientated. According to Manum (1987, p. 149), there are two resin ducts in *S. variabilis*, occupying the course earlier suggested by Bose (1955, pl. 1, fig. 6) to be veins.

Comparison. – Both in gross morphology and cuticular characters *Sciadopityoides variabilis* comes closest to *S. crameri*. The latter species, however, differs from *S. variabilis* in having mostly transversely orientated stomata. *S. variabilis* shows much variation in the pattern of stomatal distribution. *S. uralensis* Sveshnikova (1981), *S. microphylla* and *S. ikorfatensis* differ by having tuberculate papillae along the margins of the median stomatal groove.

Genus *Arctopitys* n. gen.*

Diagnosis. – Long leaves linear, helically arranged and horizontally spreading; base tapering or decurrent; apex obtuse, acute or apiculate. Upper surface with or without a median furrow; lower surface with a distinct median stomatal groove. Resin ducts 2–3.

Cells of upper cuticle arranged in longitudinal rows, rectangular, trapezoidal or polygonal; anticlinal walls straight, surface non-papillate. On

* Changed to *Mirovia* Reymańówna, sec Addendum, p. 64.



Fig. 12. A-K—*Sciadopityoides variabilis* (Bose) Sveshnikova. A-F, leaves; $\times 5$. G, showing distribution of stomata; $\times 20$. H, cells of lower cuticle outside median groove; $\times 125$. I, upper cuticle; $\times 125$. J, papillae along margin of median groove; $\times 200$. K, papillae along margins and within median groove; $\times 125$. (Slide nos.: A, GSC6702-8; B, GSC6702-1; C, GSC6702-10; D, GSC6702-9; E, F, GSC6702-13; G-I, GSC6702-22; J, GSC6702-23; K, GSC6702-27.)

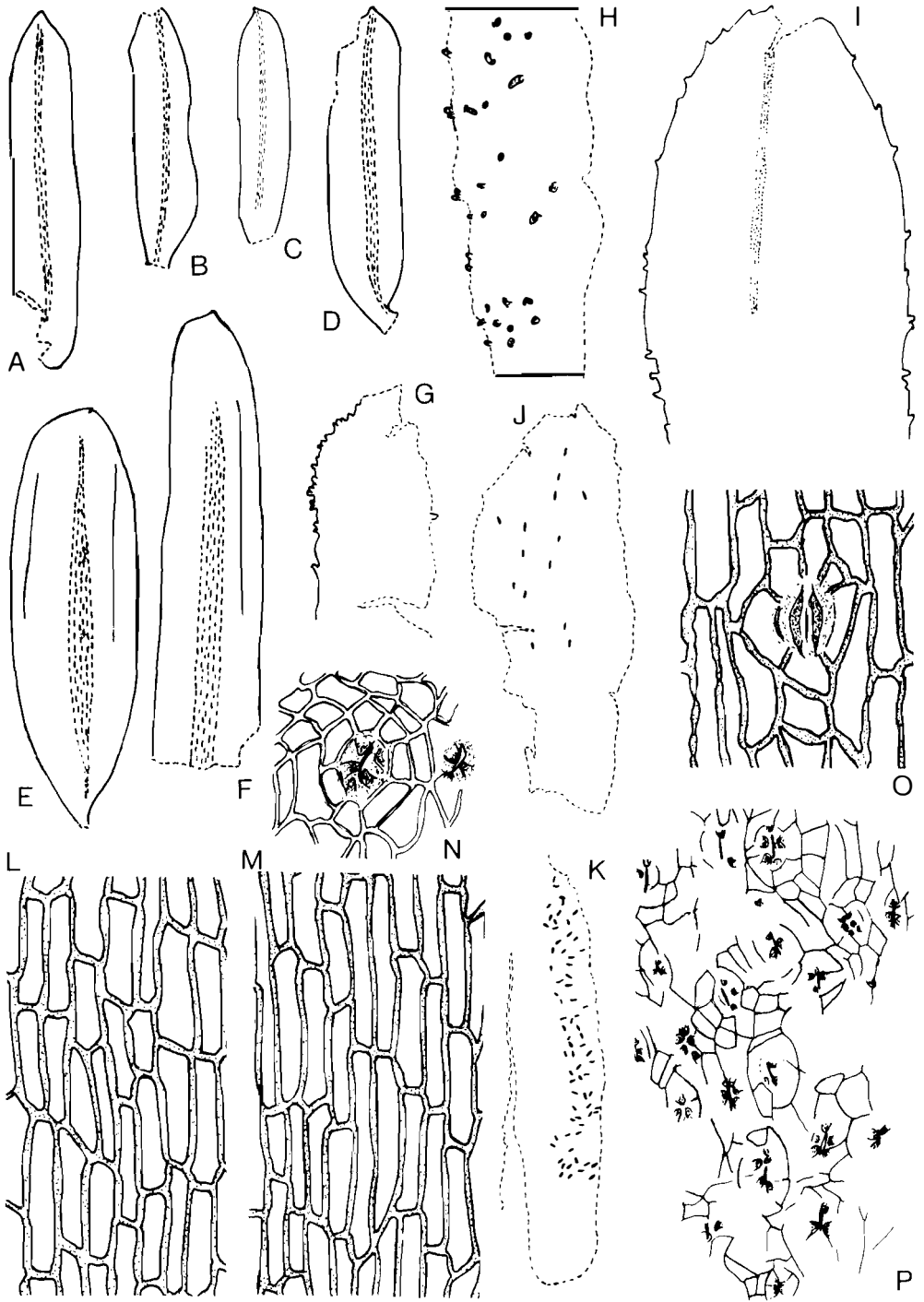
lower surface cells outside median groove like those of upper cuticle. Cells within median groove irregularly arranged, polygonal, shorter than cells outside groove; anticlinal walls straight; surface with or without papillae. Cells along margins of median groove mostly papillate; papillae varying in shape and size, surface non-tuberculate. Stomata confined to lower median groove, irregularly distributed, longitudinally or obliquely orien-

tated, rarely transverse. Subsidiary cells 5-8, papillate or non-papillate. Guard cells sunken, thinly cutinized.

Short leaves about $1/3$ - $1/4$ of long leaves; cuticle same as long leaf.

Derivation of name. - From Greek *arktos*, meaning north, and *pitys* for pine.

Type species. - *Arctopitys florinii*.



Arctopitys florinii n. sp.

Pl. 2, fig. 11, Pl. 3, fig. 3, Pl. 4, figs. 2, 3; Text-figs. 13, 14

Diagnosis. – Long leaf linear-lanceolate, sometimes oval, 7–15 mm long and 1.5–4.0 mm wide. Apex acute, sometimes obtuse; abruptly tapering towards base or decurrent, slightly above base lamina twisted. Margins entire; lower surface having a narrow median groove; mostly groove terminating slightly away from base and apex. Resin ducts 2, rarely 3.

Cuticle of abaxial median groove slightly thinner than cuticle of rest of lamina. Cells of adaxial surface arranged in longitudinal rows, rectangular or polygonal, 3–10 times longer than wide; lateral- and end-walls thick, straight or rarely slightly sinuous or broken by pits; surface non-papillate. Cells of non-stomatal zones of abaxial surface similar to those of adaxial surface. Cells within stomatal zone smaller than cells of non-stomatal zones, irregularly arranged, polygonal; lateral- and end-walls thin, straight, surface wall smooth, rarely with a solid, circular papilla. Margins of stomatal groove projecting inwards, often concealing major part of stomatal zone; 4–8 series of cells adjoining margins and slopes of projecting margins papillate. Along margins papillae long and cylindrical and closely set or overlapping; papillae of cells adjoining marginal cells (3–4 cell wide) sparse, shorter, or more often surface bulging. Cells along slopes of margins not so commonly papillate either. Stomata irregularly distributed, crowded, mostly longitudinally or obliquely orientated. Subsidiary cells mostly 6, sometimes 5, rarely 7 or 8, sometimes subsidiary cells of adjoining stomata abutting, but never sharing a subsidiary cell, papillate; papillae projecting over stomatal pit. Guard cells sunken, thinly cutinized; aperture narrow, elliptical.

Short leaf measuring 3.0–5.5 mm in length and 1.5–2.5 mm in width, oval or obovoid in shape. Margins entire; base abruptly tapering and slightly prolonged; prolonged portion twisted and bending downwards. Abaxial surface showing a median broadly elliptical groove; proximal and

distal ends of groove usually not reaching base and apex. Cuticle similar to that of long leaves, but margins of median groove fairly well cutinized, showing large distantly placed conical projections over groove, projections often nipple-shaped and with a broad base and a blunt or tapering apex, rarely apex forked.

Derivation of name. – After the Late Professor Rudolf Florin, Stockholm, who first reviewed the geological history of the *Sciadopityaceae*.

Holotype. – Slide no. PMO4444-16. Fig. 13 F.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

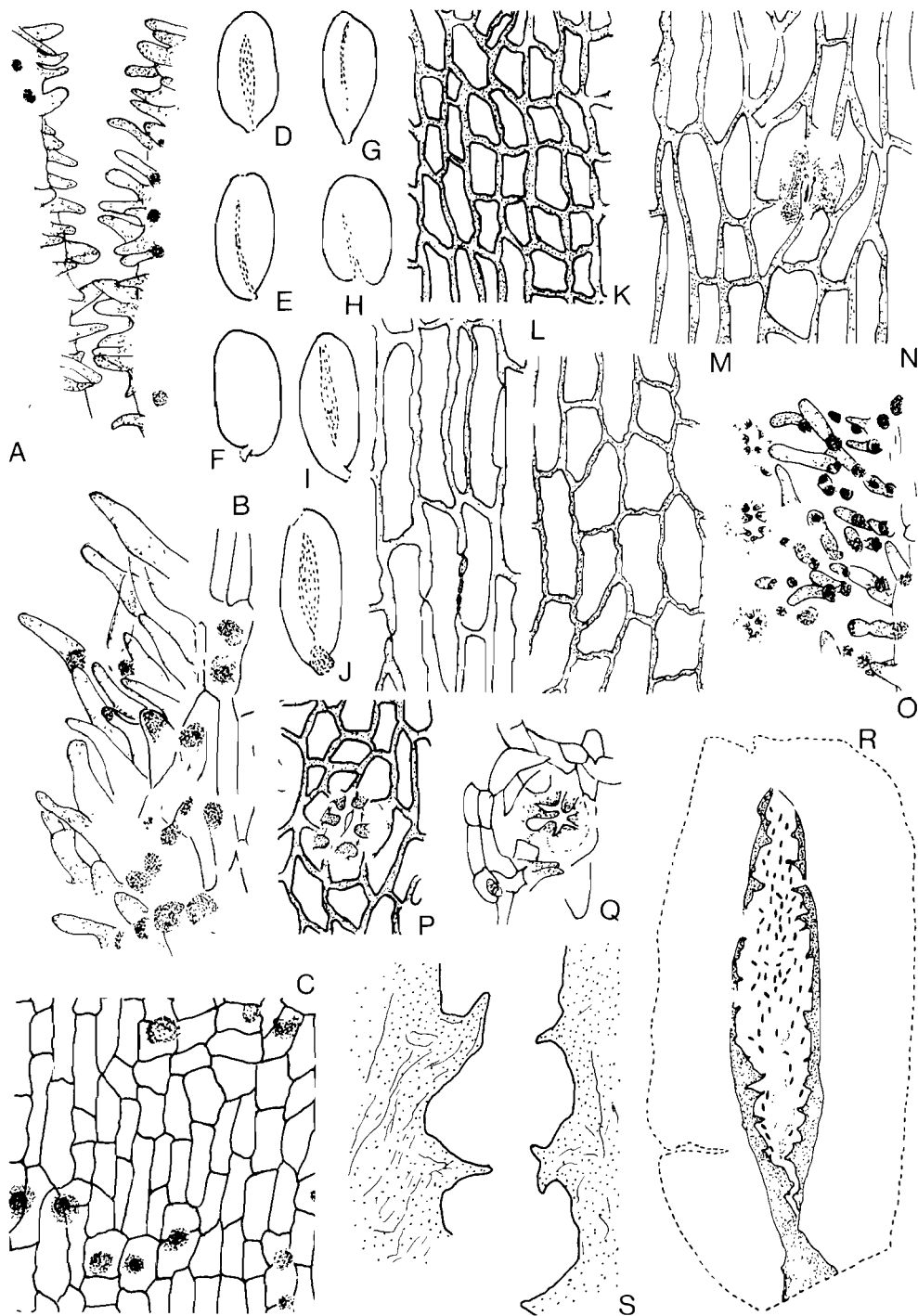
Description. – The largest leaf seems to have exceeded 20 mm in length. Most of the leaves have smooth surface and entire margins, but in three specimens the surface was found to be covered with sparsely distributed, unicellular trichomes (Fig. 13 H). Their margins were also microscopically dentate at places (Figs. 13 G, I).

In two specimens a few stomata are also present on the upper surface (Fig. 13 J). The stomata are irregularly scattered, usually longitudinally orientated, rarely oblique. The subsidiary cells are 5–8 in number, their walls facing the pit are more cutinized, but never papillate like the stomata on the lower surface (Fig. 13 O).

The short leaves have a distinctly decurrent base. Their abaxial surface has a median broadly elliptical groove. The margins of the groove are more cutinized than the remaining cells and they have distantly placed conical projections over the groove (Figs. 14 R, S).

Comparison. – Externally *Arctopitys florinii* looks like *A. lagerheimii*. Both have papillate subsidiary cells. *A. lagerheimii* differs in having a median furrow in the upper surface and in not having papillate cells along the margins of the median groove on the lower surface (Manum 1987). *A. persulcata* has much longer leaves. *A. sibirica*, too, has larger leaves which are also much wider (3–7 mm wide) and they have longitudinally orientated stomata.

Fig. 13. A–P—*Arctopitys florinii* n. sp. A–F, leaves (A, D: Padloping Island and B, C, E, F: Bohemanflya); $\times 5$. G–I, leaves with dentate margins and trichomes; $\times 20$. J, showing distribution of stomata on upper surface; $\times 20$. K, showing distribution of stomata within lower median groove; $\times 125$. L, cells of upper cuticle; $\times 125$. M, cells of lower cuticle outside median groove; $\times 125$. N, stomata; $\times 200$. O, a stoma; $\times 200$. P, a few stomata; $\times 125$. (Slide nos.: A, GSC6702-30; B, I, PMO4444-13; C, PMO4444-14; D, GSC6702-31; E, PMO4444-15; F, L–N, P, PMO4444-16; G, H, PMO4444-17; J, PMO4444-18; K, PMO4444-19; O, PMO4444-20.) Unless otherwise stated figures are of long leaves.



Arctopitys capbohemanensis n. sp.

Pl. 3, figs. 1, 2, 4, 5; Text-figs. 15, 16 K, P

Diagnosis. – Long leaf linear or lanceolate, 8–15 mm long and 1.5–3.0 mm wide. Base tapering, sometimes curving; apex obtuse or acute. Margins entire; lower surface having a narrow median groove; groove may or may not reach base and apex. Resin ducts 2, one on either side of median groove.

Cuticle of median stomatal zone slightly thinner than cuticle of rest of lamina. Margins of groove projecting, often covering most of stomatal zone, densely papillate; papillae also present on cells along slopes and adjoining cells (6–10 cells wide) of non-stomatal zones. Papillae on cells along margins and slopes long and finger-like, often crowded, in adjoining cells, papillae mostly dome-shaped, sometimes surface having merely circular cutinization. Stomata confined to median groove, closely set, irregularly scattered, obliquely or transversely orientated, subsidiary cells of adjoining stomata often abutting, but never sharing a subsidiary cell. Subsidiary cells 5–7, mostly 6, surface devoid of papilla. Guard cells sunken, well cutinized; aperture slit-like. Ordinary epidermal cells within stomatal groove polygonal, smaller than cells of rest of lamina, without any preferred arrangement; anticlinal walls thin, straight; periclinal wall flat, rarely with a dome-shaped papilla. Cells of non-stomatal zones rectangular, trapezoidal or polygonal, usually 3–10 times longer than broad; anticlinal walls thick, straight or wavy, rarely broken by pits; periclinal wall evenly thickened, rarely mottled. Cells of upper cuticle similar to those of cells of non-stomatal zones of lower cuticle.

Short leaf deltoid, 2.5–6.5 mm long and 2–3 mm wide; base expanded; apex obtuse, margins entire. Lamina thick; lower surface having a median groove; groove broadly elliptical or narrow, traversing entire length or terminating slightly away from base and apex. Cuticle same as long leaves. Cells along margins of stomatal groove may or may not be papillate; papillae

sparse, short and conical, projecting over median groove. Rarely cells adjoining marginal cells of groove slightly more cutinized.

Holotype. – Slide no. PMO4444-38. Figs. 15 M–R.

Occurrence. – Bohemanflya, Spitsbergen.

Remarks. – The short leaves differ in shape from the long leaves in being deltoid and having a swollen base and an obtuse apex; the bases are not tapering like the bases of long leaves. They look more like the short leaves of *Sciadopityoides microphylla*. In *S. microphylla* the short leaves have a distinct abscission mark. Here the abscission mark is absent.

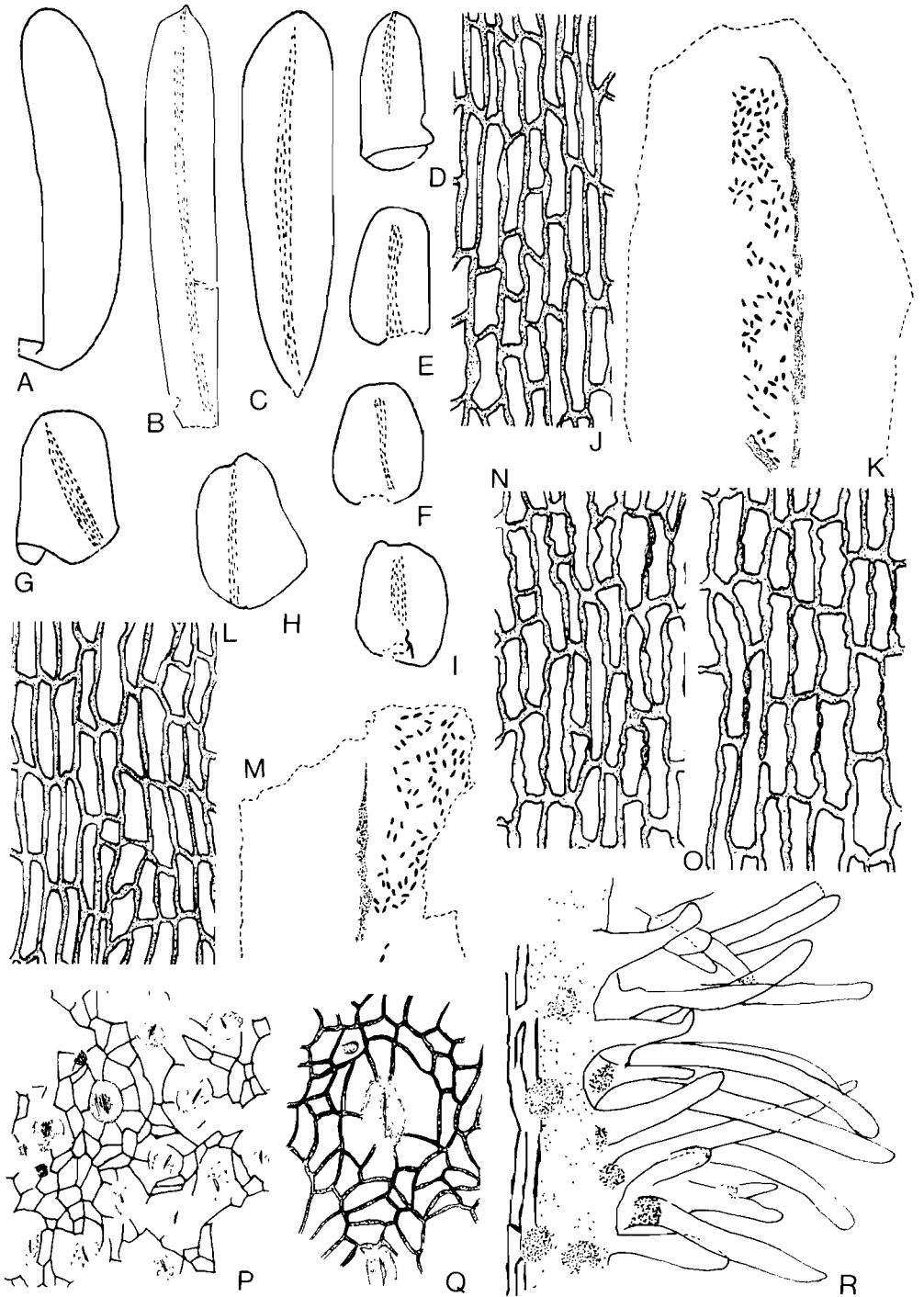
The cells along the median groove of *S. microphylla* have crowded tuberculate papillae. In *A. capbohemanensis* the papillae are short and conical.

The cuticle of the long and short leaves are similar. In both the stomata are closely set and they form a somewhat mosaic pattern. The marginal cells along the median stomatal groove in the long leaves have long cylindrical papillae, but the similar cells in the short leaves have short conical papillae.

Leaf apices and cuticle of specimens from Spitsbergen described by Sveshnikova & Budantsev (1969) as *Sciadopityes nathorstii* are in our opinion quite like specimens of *Arctopitys capbohemanensis*. However, in the absence of leaf base we prefer to leave the affinity of the former specimens open.

Comparison. – In gross features *Arctopitys florinii* and *A. capbohemanensis* look similar, but *A. florinii* differs in having papillate subsidiary cells. The short leaves of *A. florinii* have no papillae along the margins of the median groove, whereas the short leaves of *A. capbohemanensis* do have papillate cells along the margins of the median groove. *A. lagerheimii* (Johansson) differs in having a median furrow in upper surface and it does not have papillate cells along the margins of the median groove.

Fig. 14. A–S—*Arctopitys florinii* n. sp. A, B, papillae along margins of median groove; A $\times 125$, B $\times 200$. C, lower cuticle showing cells with trichome bases; $\times 125$. D–J, short leaves; $\times 5$. K, upper cuticle of a short leaf; $\times 125$. L, upper cuticle showing cells with wavy anticlinal walls and walls broken with pits; $\times 200$. M, upper cuticle with cells having slightly sinuous walls; $\times 200$. N, a stoma on upper surface; $\times 200$. O, papillae and stomata; $\times 125$. P, a stoma of a short leaf; $\times 200$. Q, a stoma; $\times 200$. R, showing distribution of stomata and conical projections from margins of median groove in a short leaf; $\times 20$. S, conical projections along margins of groove in a short leaf; $\times 125$. (Slide nos.: A, PMO4444-14; B, GSC6702-31; C, M, PMO4444-13; D, S, PMO4444-21; E, PMO4444-22; F, K, PMO4444-23; G, PMO4444-29; H, PMO4444-24; I, PMO4444-25; J, R, PMO4444-26; L, N, PMO4444-20; O, PMO4444-27; P, PMO4444-28; Q, PMO4444-15.) Unless otherwise stated figures are of long leaves.



Arctopitys ineffecta n. sp.

Pl. 3, fig. 6; Pl. 4, fig. 6; Text-figs. 16 A–J, L–O, Q, R

Diagnosis. – Long leaf linear, estimated length 10–20 mm, width 1.5–2.0 mm. Lower side having a narrow median groove. Base tapering; apex obtuse or acute; margins entire. Resin ducts 2–3.

Median stomatal groove with prominently projecting margins covering greater part of stomatal region; cells along margins papillate; papillae mostly distantly placed, short and conical, near apex papillae more closely set. Besides marginal cells, 2–4 rows of adjoining cells also papillate, outer rows mostly having thickened and bulging surface. Sometimes papillae also present along slopes of margins. Cuticle of groove slightly thinner than rest of lamina. Stomata confined to median groove, fairly closely set, longitudinally orientated, very rarely transversely placed. Subsidiary cells 5–8, mostly 6, rarely 8, polar subsidiary cells distinct, mostly papillate, when non-papillate, wall bordering pit more cutinized, both papillae and cutinized margins bulging over stomatal pit. Guard cells thinly cutinized; aperture narrow, elongated. Ordinary epidermal cells within median groove polygonal, irregularly arranged; anticlinal walls thin, straight; periclinal wall smooth. Cells of non-stomatal zones in longitudinal rows, rectangular or trapezoidal, sometimes elongated polygonal; anticlinal walls thick, straight, rarely wavy or slightly sinuous; periclinal wall smooth or mottled, occasionally showing a thinly cutinized median stripe. Cells of upper cuticle similar to those of non-stomatal zones of lower cuticle.

Short leaf more or less oval, 4.5 × 2.0 mm, margins entire; apex acute; base tapering. Lower surface having a narrow median groove. Cuticle same as long leaves.

Holotype. – Slide no. GSC6702-33. Fig. 16 C.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Description. – The specimens are all incomplete, so their exact length is unknown. They are gradu-

ally tapering towards the base, but as the ultimate base is unknown, it is not possible to decide whether it was decurrent or not. Resin ducts are persistent even after oxidation, and the three ducts seen in some specimens are taken to show the original number; they are often displaced from their original positions after maceration (Figs. 16 A–D). One specimen was observed with a single stoma on the upper surface as well. The stomatal apparatuses on the whole are broadly oval.

Comparison. – The distributional pattern of stomata and the sparsely placed, short papillae over cell walls along the margins of the groove distinguish *A. ineffecta* from *A. florinii* and *A. capbohemansensis*.

Among the two Jurassic species of *Arctopitys* from northern Norway, *A. lagerheimii* looks more like *A. ineffecta* but it differs in having a median furrow in the upper surface and having non-papillate cells along the margins of the median groove (see Manum 1987).

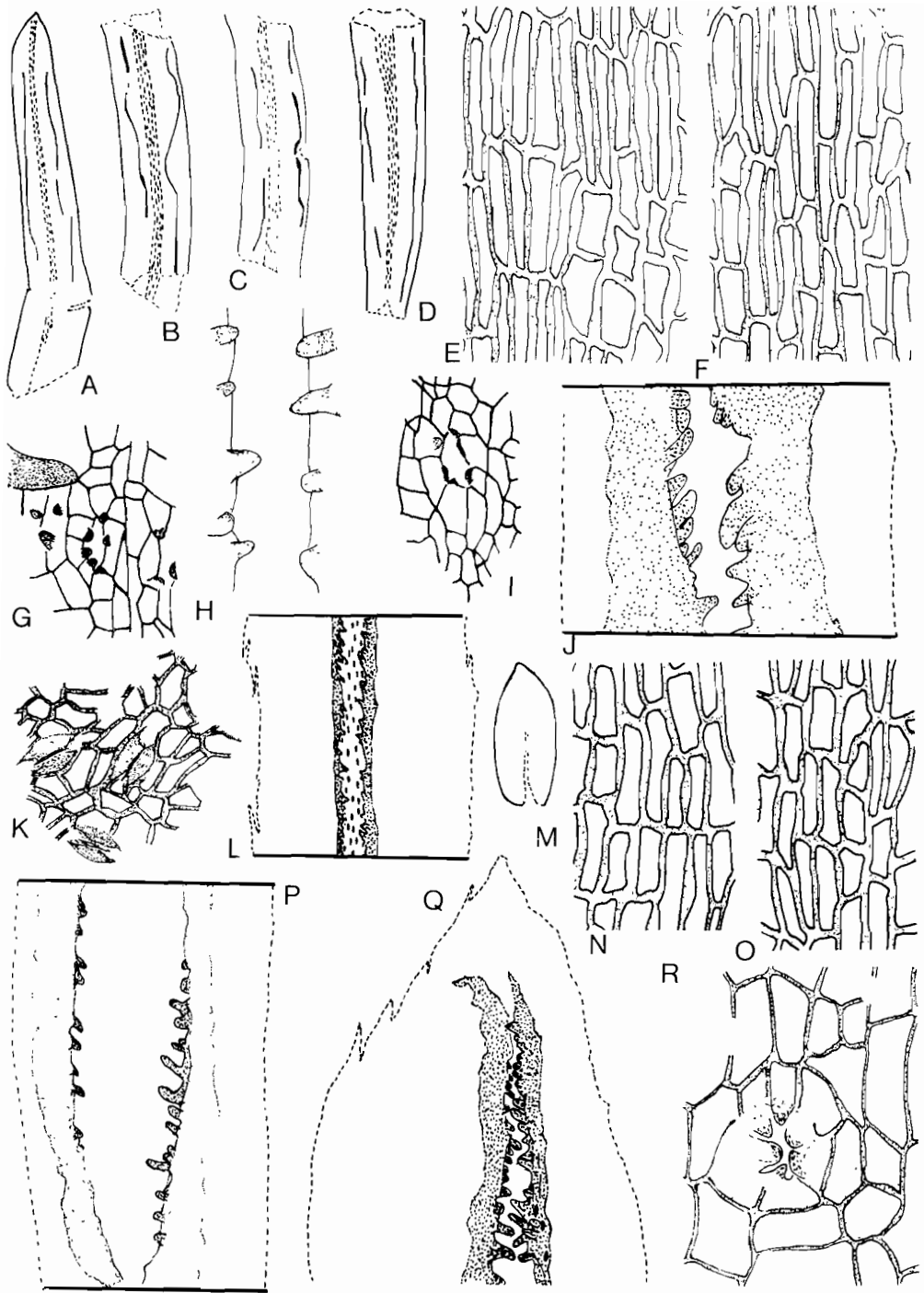
Genus *Oswaldheeria* n. gen.

Diagnosis. – Long leaves linear or lanceolate; tapering towards base or decurrent; apex obtuse, acute or apiculate. Resin ducts 2–5. Upper surface with or without median furrow; lower surface devoid of median groove, but with a clearly differentiated median stomatal zone. Cells of upper cuticle rectangular or elongated polygonal, arranged in longitudinal rows; anticlinal walls straight, rarely wavy; periclinal wall devoid of papillae. Stomata irregularly scattered within stomatal zone, occasionally tending to form discontinuous files; no preferred orientation. Subsidiary cells 4–8, commonly 5 or 6, papillate or non-papillate. Guard cells semilunar or crescent-shaped, slightly sunken. Ordinary epidermal cells within stomatal zone polygonal and irregularly arranged. Cells outside stomatal zone like those of upper cuticle.

Short leaves c. 1/3–1/5 of long leaves. Cuticle same as long leaves.

Derivation of name. – After the Swiss palaeo-

Fig. 15. A–R—*Arctopitys capbohemansensis* n.sp. A–C, leaves; ×5. D–I, short leaves; ×5. J, lower cuticle of a short leaf, showing cells outside median groove; ×125. K, short leaf, showing distribution of stomata; ×20. L, upper cuticle of a short leaf; ×125. M, showing distribution of stomata; ×20. N, lower cuticle showing cells outside median groove; ×125. O, upper cuticle; ×125. P, showing a few stomata; ×125. Q, a stoma; ×200. R, papillae along margin of median groove; ×200. (Slide nos.: A, PMO4444-30; B, PMO4444-31; C, PMO4444-32; D, J–L, PMO4444-39; E, PMO4444-33; F, PMO4444-34; G, PMO4444-35; H, PMO4444-36; I, PMO4444-37; M–R, PMO4444-38.) Unless otherwise stated figures are of long leaves.



botanist Professor Oswald Heer (1809–1883), whose pioneering work, *Flora Fossilis Arctica*, is still a major source of palaeobotanical information.

Type species. – *Oswaldheeria hallei* (Florin) comb. nov.

Note. – Under this genus we are also describing and validating *Oswaldheeria scotica* (Florin) comb. nov. from Helmsdale, Scotland, although the species falls outside the geographic and stratigraphic scope of the present paper (see p. 46).

Oswaldheeria hallei (Florin) comb. nov.

Pl. 2, figs. 4–6; Pl. 4, figs. 4, 5; Text-figs. 17, 18 O–Q, T–W

1922 *Sciadopitytes hallei* Florin, p. 265

1955 *Sciadopitytes variabilis* Bose (*partim*), pl. 1, fig. 8, text-fig. 1 J

1981 *Sciadopityoides* (?) *hallei* (Florin) Sveshnikova, p. 1725

1987 *Sciadopityoides* (?) *hallei* (Florin) Sveshnikova: Manum, p. 155

Diagnosis. – Long leaves linear–lanceolate, sometimes slightly curved, average length 10–20 mm, width 1.5–3.0 mm. Apex obtuse, sometimes acute or apiculate, abruptly tapering towards base, often base twisted, twisted part slightly prolonged; margins entire. Resin ducts 2–3. Adaxial surface sometimes slightly depressed or with a narrow furrow.

Upper cuticle slightly thicker than lower. Cells on adaxial surface mostly polygonal, sometimes rectangular or trapezoidal, serially or slightly irregularly arranged; anticlinal walls thick, straight, occasionally somewhat wavy, periclinal wall flat or evenly thickened, sometimes a few rows of cells along adaxial median furrow narrower than others. Abaxial surface with a broad median stomatal zone, its cuticle slightly thinner than that of lateral non-stomatal zones. Stomata irregularly scattered, closely or sparsely placed, longitudinally orientated, occasionally tending to

form discontinuous files, sometimes subsidiary cells of adjacent stomata abutting, but stomata never sharing a subsidiary cell.

Subsidiary cells 4–6, polar subsidiary cells distinct; anticlinal walls thick, surface smooth. Guard cells sunken, fairly well cutinized; aperture oval. Ordinary epidermal cells within stomatal zone slightly shorter than cells of non-stomatal regions, polygonal or rectangular in shape: anticlinal and periclinal walls like those of cells of upper surface. Cells of non-stomatal zones slightly longer than those of stomatal zone, more or less serially arranged, rectangular or polygonal in shape.

Short leaf ovate-lanceolate, 4–6 mm long and 1.5–2.5 mm wide. Margins entire; apex obtuse, rarely acute or apiculate; base tapering or bending downwards, curved portion narrower than rest of lamina. Resin ducts 2–3, rarely 5. Cuticle same as long leaf.

Holotype. – Slide no. S20309. Pl. 4, fig. 5; Figs. 17 S, T, 18 V.

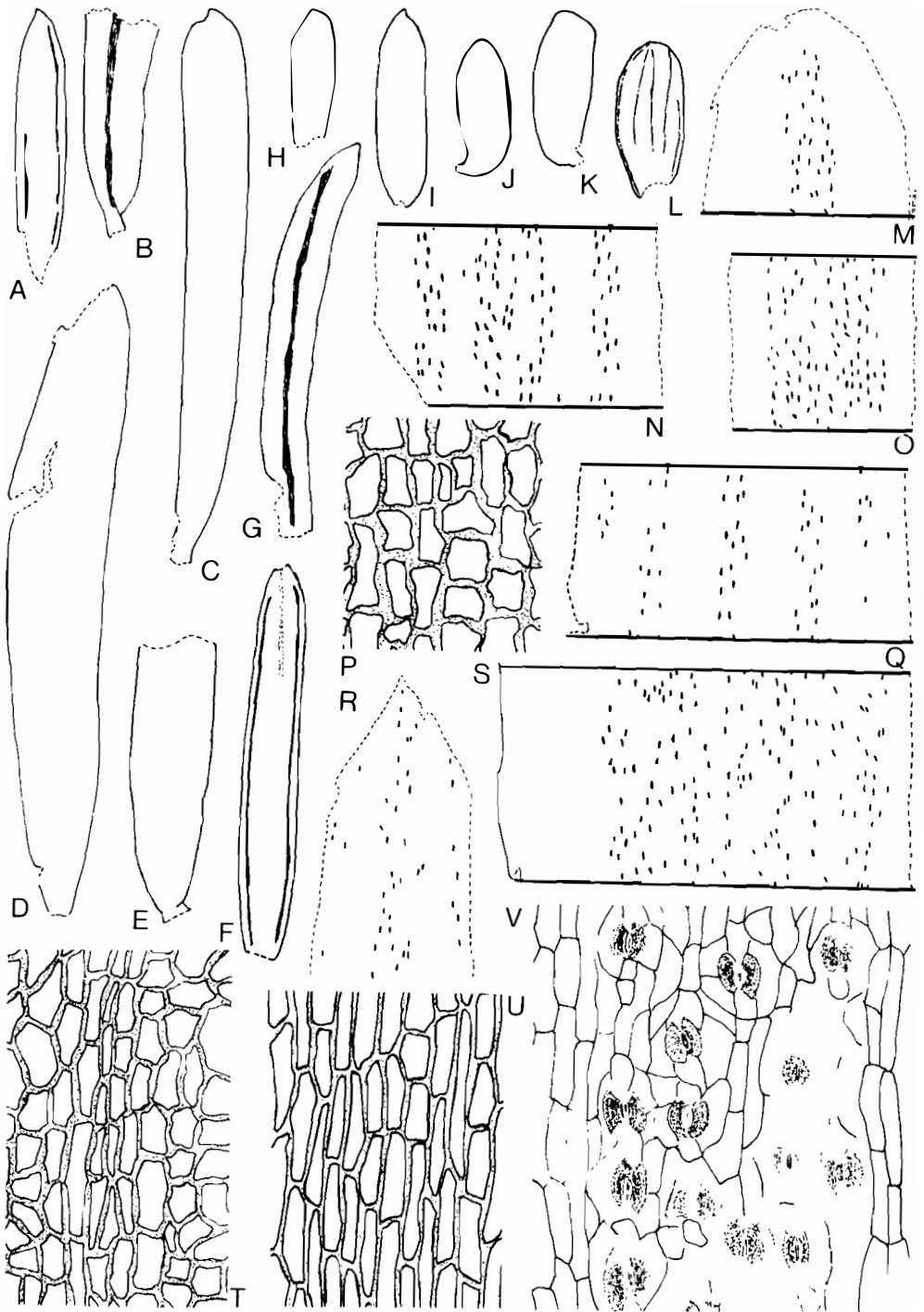
Occurrence. – Ikorfat, West Greenland; Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Remarks. – Manum (1987) considered this species to be invalidly published since Florin (1922) had given only a brief description, but no illustration. However, in Riksmuseet we were able to examine the original slide of *S. hallei* prepared by Florin (1922). Fortunately, the slide contains very well preserved cuticle fragments from both the upper and lower side. Furthermore, we have isolated a large number of specimens from a sample from Ikorfat. Florin had discovered his specimen of *S. hallei* from amongst leaves of *Sciadopitytes crameri* (Heer) Halle 1915 (not certain whether from amongst *Sciadopityoides microphylla* comb. nov. or *S. crameri* emend.), whereas the shale sample we have macerated is completely dominated by *Oswaldheeria hallei*.

Besides the leaves of *O. hallei*, there are a few

Fig. 16. A–J, L–O, Q–R—*Arctopitys ineffecta* n. sp. A–D, leaves (A, D: Bohemanflya and B, C: Padloping Island); $\times 5$. E, upper cuticle; $\times 125$. F, lower cuticle; $\times 125$. G, a stoma; $\times 200$. H, papillae along margins of groove; $\times 125$. I, a stoma; $\times 200$. J, papillae along margins of the groove in a short leaf; $\times 125$. L, showing distribution of stomata; $\times 20$. M, a short leaf; $\times 5$. N, upper cuticle of a short leaf; $\times 125$. O, lower cuticle of a short leaf, showing cells outside median groove; $\times 125$. O, papillae along margins; $\times 50$. R, a stoma; $\times 200$. (Slide nos.: A, PMO4444-40; B, GSC6702-32; C, GSC6702-33; D, PMO4444-41; E, F, PMO4444-42; G, PMO4444-43; H, PMO4444-44; I, PMO4444-45; J, M–O, PMO4444-46; O, PMO4444-47; R, PMO4444-48.) Unless otherwise stated figures are of long leaves.

K, P—*Arctopitys capbohemansensis* n. sp. K, 3 stomata of a short leaf; $\times 200$. P, papillate margins of groove of a short leaf; $\times 50$. (Slide nos.: K, PMO4444-39; P, PMO4444-37.)



fragmentary pieces of other conifers but not a single piece of *S. microphylla* or *S. crameri*. Most of our specimens are incomplete. The most complete ones measure 10–15 mm in length. Florin (1922) had recorded the dimensions of his specimens as c. 39 × 3.0 mm. We have not found such a large specimen, though the width of some of the specimens is c. 3.0 mm. The specimens from Spitsbergen and Padloping Island do not usually exceed 2 cm in length, and except for one specimen from Padloping Island (Fig. 17 D), most of the specimens are 1.5–2.5 mm wide.

Florin (1922, p. 265) had observed on the under side of his specimens a broad stomatal groove. None of our leaves shows such a groove. However, a few leaves from Ikorfat show a crease on their abaxial surface, on one side only, along the median line. Such folds originate a little above the base (Figs. 17 B, G), and terminate slightly away from the apex. Sometimes the folds are visible for a short distance either towards base or apex only. Quite likely such a folding took place during fossilization and compression, while the thicker cuticle of the non-stomatal zones got folded over the thinner surface of the stomatal zone. This could explain Florin's interpretation of a stomatal groove.

The median furrow in the upper surface in our material from Ikorfat is less distinct than was found by Florin (1922) in his specimens. However, in some of the specimens from Bohemanflya and Padloping Island this furrow is quite distinct and the lamina sometimes splits along it. Frequently, the upper median furrow is marked by a few rows of narrower cells, a feature also seen in Florin's slide.

The leaf bases are either narrowing abruptly or slightly twisted towards base. The basal twisted part is mostly 1.5–3.0 mm long. The leaves from Bohemanflya and Padloping Island, when partially oxidized, show one resin duct closer to either margin. Some of these ducts persist even when the leaves are fully oxidized. A median

resin duct is preserved, in addition to the two lateral ducts in some leaves. The specimens from Ikorfat usually lose the resin ducts while in acid and in none of them, so far, three ducts have been found.

The cells on the adaxial surface show a good deal of variation in size and shape. They are polygonal, rectangular or trapezoidal in shape. The specimens from Ikorfat even have occasional squarish cells at places. In general, the leaves from Ikorfat have shorter and broader cells which are mostly 1.5 to 2.5 times their width. Moreover, the cells are not so regularly arranged. The leaves from Bohemanflya and Padloping Island have cells arranged in longitudinal rows and they are mostly 2–5 times their width.

A good deal of variation is also observed with regard to the stomatal zone. The width of the zone in most leaves from Ikorfat exceeds half the width of the leaf. The cuticle is slightly thinner than in the non-stomatal zones. The stomata are longitudinally orientated and irregularly scattered but occasionally tend to form discontinuous files. They are, however, not in longitudinal rows as has been stated by Florin (1922). Also, his specimens lack distinct longitudinal rows of stomata, instead they are in discontinuous files.

Instead of scattered stomata within the stomatal zone there are in a few leaves three distinct bands of stomata (Fig. 17 N). In such leaves ordinary epidermal cells of the non-stomatal zones are slightly more elongated than those within the stomatal bands. One specimen from Padloping Island has as many as five stomatal bands (Fig. 17 Q). Specimens with three distinct stomatal bands have not been encountered in material from Bohemanflya. However, one leaf from Bohemanflya, having as usual a median stomatal zone, also has a few stomata arranged in single files outside the zone on either side, close to the margins (Fig. 17 R). This leaf is also exceptional in having in the upper surface one stoma, and its cells are broader and shorter than the cells of

Fig. 17. A–V—*Oswaldheeria hallei* comb. nov. A–G, leaves; A, F, leaves showing resin ducts (F, also showing apical median fold on lower surface) (A, C, F: Bohemanflya. B, E, G: Ikorfat and D: Padloping Island); ×5. H–L, short leaves; L, showing 5 resin ducts (all from Bohemanflya); ×5. M–O, Q–S, showing distribution of stomata (in M, O and S the stomata are confined to a median zone; in N and Q they are in bands and in R there is a median stomatal zone; outside it, on either side, there are a few stomata in files); ×20. P, cells of a shoot; ×125. T, upper cuticle showing cells along median furrow; ×125. U, lower cuticle; ×125. V, stomata and epidermal cells; ×125. (Slide nos.: A, PMO4444-2; B, S20308-1; C, PMO4444-49; D, Q, GSC6702-34; E, S20308-2; F, O, PMO4444-50; G, S20308-3; H, PMO4444-51; I, PMO4444-52; J, PMO4444-53; K, PMO4444-54; L, PMO4444-55; M, PMO4444-56; N, S20308-4; P, S20308-5; R, PMO4444-57; S, T, S20309; U, V, PMO4444-58.) Unless otherwise stated figures are of long leaves.

other leaves of *O. hallei* from Bohemanflya. The cells resemble more those of specimens from Ikorfat. Most specimens from Bohemanflya have a median stomatal zone like those of leaves from Ikorfat, but slightly less broad. However, in some leaves the median stomatal zone is narrow, occupying less than half the width of the leaf.

Despite the described variations in gross morphology as well as in cuticular features, the overall characters of the cuticle are essentially the same as in the specimens of Florin (1922) and we consider them conspecific. Since the original slide for Florin's invalidly published '*Sciadopitytes hallei*' is available, we have chosen to retain and validate the epithet with Florin's specimen as the holotype.

Shoots with leaf-scars. – Associated with the leaves of *O. hallei* from Ikorfat we have found a few fragmentary shoots (Pl. 2, figs. 4–6), measuring 4–18 mm in length and 1.5–4.0 mm in width. They have broadly oval leaf scars with prominently decurrent cushions in spiral arrangement. They also have a varying number of resin ducts, a maximum of eight was counted in one oxidized shoot. Characters of the cuticle and of the ordinary epidermal cells resemble *O. hallei*. All along the shoot there are a few sparsely placed stomata which are longitudinally orientated and the stomatal apparatuses also resemble those of *O. hallei*.

Considering the mono-specific assemblage of leaves with which these shoots have been found and the correspondence in available characters with *O. hallei*, we believe that the shoots bore leaves of *O. hallei*. Whether these leaves were the normal leaves or the small leaves cannot be ascertained; in any case they were spirally arranged. Many normal leaves of *O. hallei* are twisted at the base and have a narrow, curved portion representing the decurrent attachment. These conditions point strongly in favour of a spiral arrangement of leaves which were horizontally spreading.

Comparison. – The leaves of *Oswaldtheeria macrophylla* (Florin) described by Manum (1987) are much longer than *O. hallei* and they have papillate subsidiary cells. The subsidiary cells in *O. hallei* are non-papillate.

Oswaldtheeria arctica n. sp.

Pl. 5, figs. 2, 3, 5; Text-figs. 18 A–N, R, S, 19 F, G, J, K, M–P

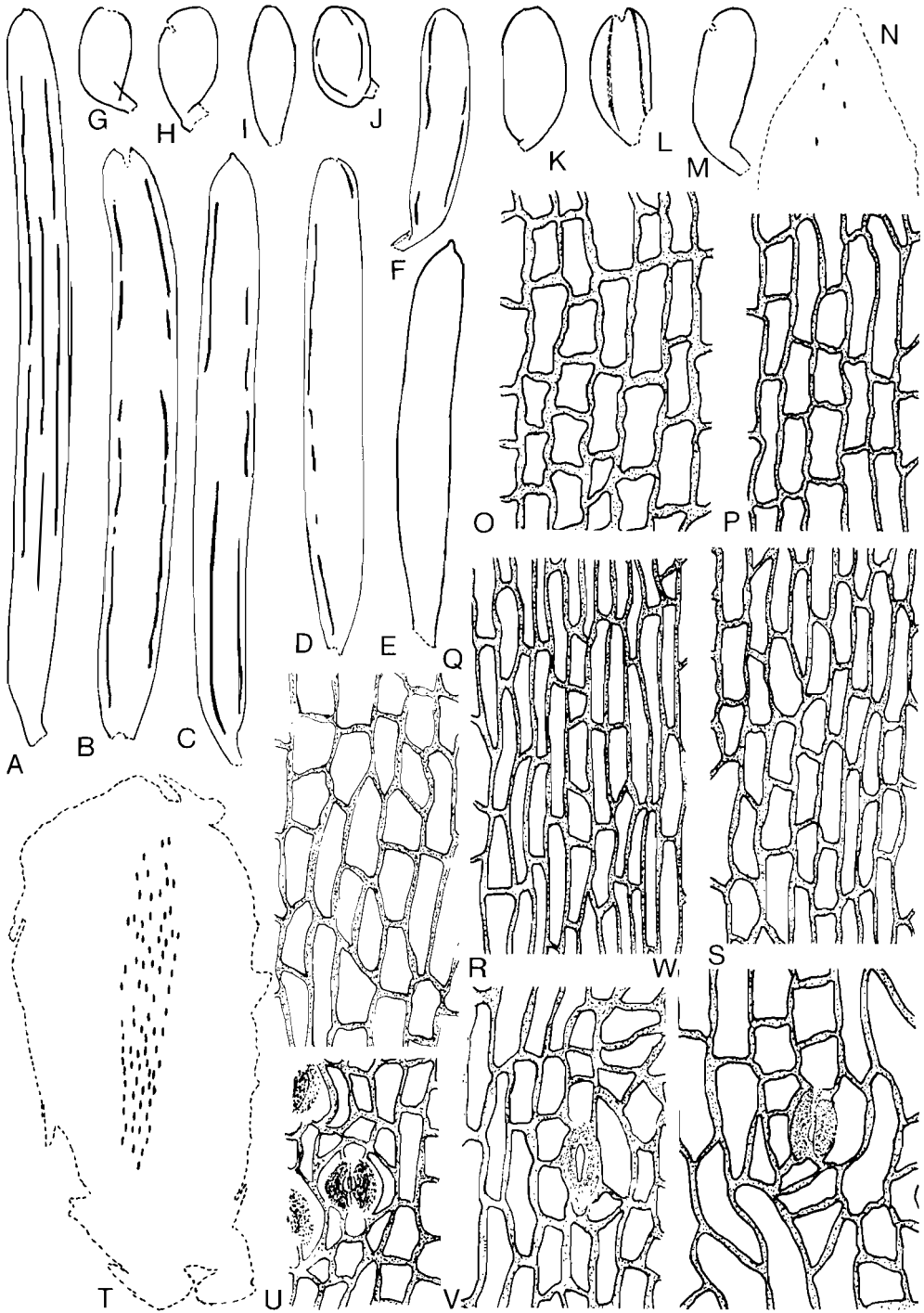
Diagnosis. – Leaves straight or slightly curved, linear, lanceolate, average length 8–15 mm, width 1.5–2.5 mm. Margins entire; apex obtuse or acute, sometimes mucronate; gradually tapering towards base or base curved and twisted; twisted portion of base 0.5–2.0 mm long. Resin ducts 2–3, rarely 5, lateral ducts converging towards apex. Sometimes upper surface showing a median depression.

Lower surface having a median stomatal zone. Cuticle of upper surface and non-stomatal zones of lower surface of almost same thickness; cuticle of stomatal zone slightly thinner. Cells of upper surface more or less serially arranged, mostly rectangular, sometimes polygonal, rarely trapezoidal; lateral and end-walls thick, straight, sometimes wavy, more rare slightly sinuous; surface wall smooth. Cells of lateral non-stomatal zones same as cells of upper surface. Median stomatal zone in level with non-stomatal zones, cells within this zone irregularly arranged, shorter than cells of non-stomatal zones, mostly polygonal. Stomata irregularly scattered, sometimes abutting but never sharing a subsidiary cell, longitudinally orientated, sometimes slightly obliquely placed. Subsidiary cells 4–6, rarely 7, polar ones mostly differentiated in longitudinally orientated stomata. Subsidiary cells with papillae overhanging stomatal pit. Guard cells sunken, semi-lunar, well cutinized. Aperture slit-like.

Short leaves broadly oval or obovate, 3–5 mm long and 1.0–2.5 mm wide. Base mostly twisted or curving on one side with a prolonged base;

Fig. 18. A–N, R, S—*Oswaldtheeria arctica*. A–F, leaves (A–D, F: Bohemanflya and E: Padloping Island), except E, rest showing resin ducts; $\times 5$. G–M, short leaves, J and L showing resin ducts; $\times 5$. N, showing distribution of stomata on upper surface; $\times 20$. R, cells of lower cuticle outside median groove; $\times 125$. S, upper cuticle. (Slide nos.: A, PMO4444-60; B, PMO4444-61; C, PMO4444-62; D, PMO4444-63; E, GSC6702-35; F, PMO4444-64; G, PMO4444-65; H, PMO4444-66; I, PMO4444-67; J, PMO4444-68; K, PMO4444-69; L, PMO4444-70; M, PMO4444-71; R, PMO4444-72; S, PMO4444-73.) Unless otherwise stated figures are of long leaves.

O–Q, T–W—*Oswaldtheeria hallei* comb. nov. O, upper cuticle of a short leaf; $\times 125$. P, lower cuticle of a short leaf showing cells outside median groove; $\times 125$. Q, upper cuticle of a leaf; $\times 125$. T, showing distribution of stomata in a short leaf; $\times 20$. U, a few stomata; $\times 200$. V, a stoma; $\times 200$. W, a stoma of a short leaf; $\times 200$. (Slide nos.: O, T, W, PMO4444-53; P, PMO4444-54; Q, PMO4444-49; U, PMO4444-59; V, S20309.) Unless otherwise stated figures are of long leaves.



apex obtuse; margins entire. Resin ducts 2–3. Cuticle same as long leaves.

Holotype. – Slide no. PMO4444-60. Fig. 18 A.

Occurrence. – Bohemanfya and Adventdalen, Spitsbergen; Padloping Island, Arctic Canada.

Description. – Largest leaf measures 22 × 2 mm. In most leaves the apical ends are entire. However, in some the apices are slightly torn and in one leaf on one side the margin is torn in a zig-zag pattern (Fig. 19 P). This was perhaps caused by insect nibbling.

Upper surface sometimes shows a narrow median depression along which the lamina often splits. The crack is visible either along the entire length or only partly (Fig. 18 B). There is no median groove in the lower surface. The resin ducts sometimes persist even in fully oxidized leaves, but they are often slightly displaced from their original position (Figs. 18 A–D).

The stomatal apparatuses on the abaxial surface show slight variation in overall shape, from broadly oval to somewhat circular. In the latter case differentiation between polar and lateral subsidiary cells is weak. Very rarely a few stomata are present on the adaxial surface as well (Fig. 18 N). They are irregularly distributed, longitudinally orientated, and are away from margins; their subsidiary cells are non-papillate.

The upper cuticle of short leaves has slightly broader epidermal cells than that of long leaves.

Comparison. – In gross features *Oswaldheeria arctica* resembles *O. hallei* (Florin), but differs in possessing papillate subsidiary cells. *O. macrophylla* (Florin), which also has papillate subsidiary cells, is more than twice as long as *O. arctica* (see Manum 1987).

Validation of Sciadopitytes scotica Florin from the Jurassic of Scotland. – *Sciadopitytes scotica* was described by Florin (1922) from the Upper Jurassic of Helmsdale (Scotland), without giving

any illustration. This species was referred to *Sciadopityoides* by Sveshnikova (1981), while Manum (1987), because of lack of illustrations, considered it to be an invalidly published species. We have been able to trace Florin's original specimen (Pl. 5, fig. 4) and a slide. It is referable to *Oswaldheeria*, and we therefore validate the species under the new combination *O. scotica*.

Oswaldheeria scotica (Florin) comb. nov.

Pl. 4, fig. 1; Pl. 5, figs. 1, 4; Text-fig. 20 D–F

1922 *Sciadopitytes scotica* Florin, p. 266

1981 *Sciadopityoides scotica* (Florin) Sveshnikova, p. 1726

1987 *Sciadopityoides scotica* (Florin) Sveshnikova: Manum, p. 155

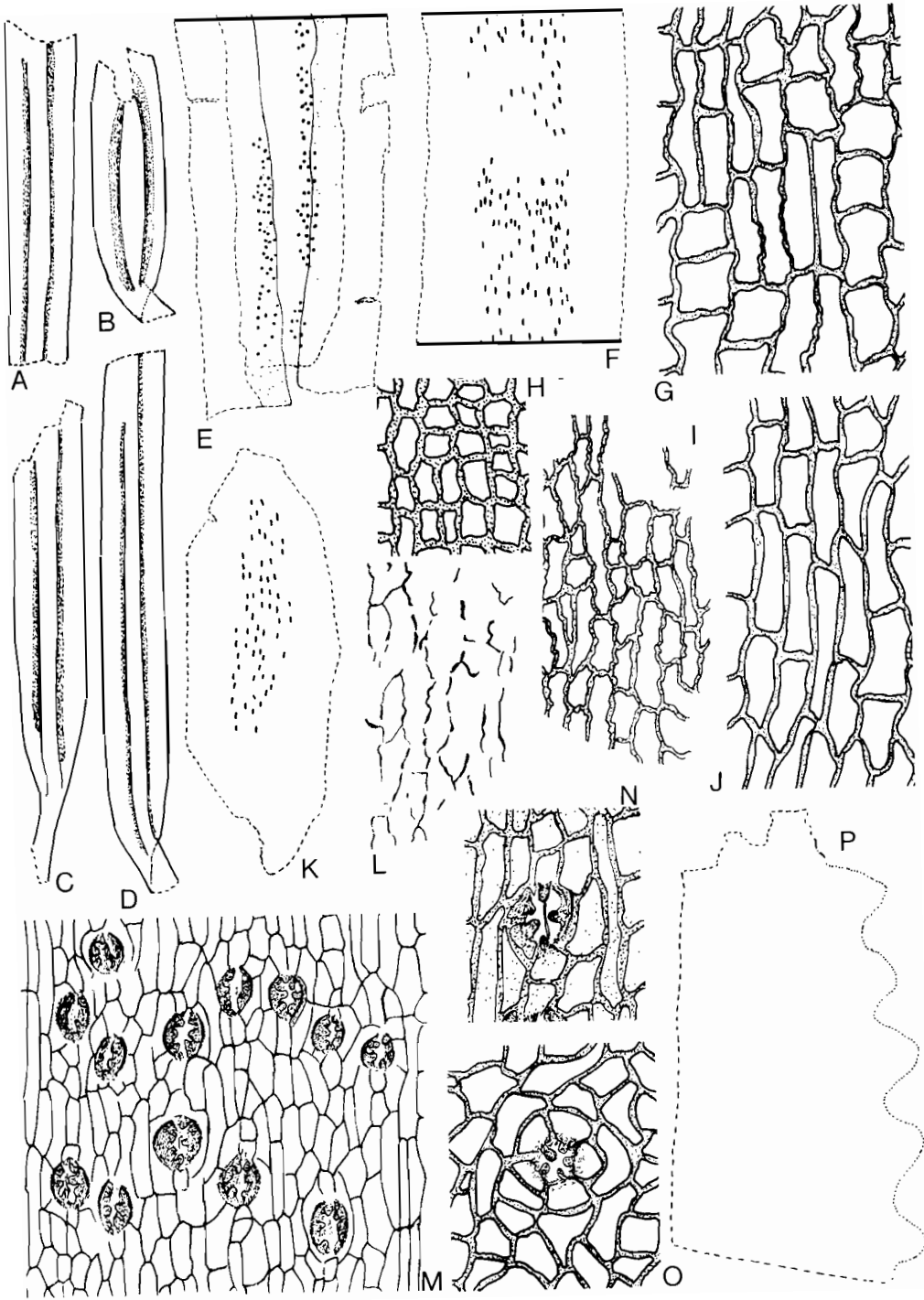
Diagnosis. – Leaves linear, c. 9.0 cm long and 1.5–2.0 mm wide. Margins entire. Resin ducts 2, one on either side of median stomatal zone. Both upper and lower surfaces devoid of median furrow or groove.

Cuticle of same thickness on both sides; stomata confined to lower surface in a broad median zone. Cells of upper cuticle more or less arranged in longitudinal rows; generally much longer than broad, rectangular or trapezoidal, rarely polygonal; anticlinal walls thick, straight; periclinal wall smooth or mottled. Cells of lower cuticle outside stomatal zone like those of upper cuticle. Epidermal cells within stomatal zone much shorter and broader than cells outside stomatal zone; irregularly arranged, polygonal; anticlinal walls thick, straight; periclinal wall unspecialized. Within stomatal zone stomata tending to form discontinuous files. Stomata longitudinally orientated, distantly or at places closely placed, sometimes subsidiary cells of adjacent stomata abutting. Subsidiary cells commonly 4 or 5, rarely 6 or 7 (2 polar and 2–5 lateral). Guard cells sunken, thinly cutinized; aperture elliptic or slit-like.

Holotype. – Specimen no. S431. Pl. 5, fig. 4.

Fig. 19. A–E, H, I, L—*Holkopitys hoegii* n. sp. A–D, leaves; projecting margins over lower median groove indicated by stippling (A, B: Bohemanfya and C, D: Padloping Island); ×5. E, portion of leaf magnified, the stomata are hidden under stippled areas and the bold dots are papillae; ×20. H, cells of lower cuticle near base, lying outside median zone; ×125. I, lower cuticle showing cells closer to margin; ×125. L, upper cuticle; ×125. (Slide nos.: A, I, PMO4444-77; B, PMO4444-78; C, GSC6702-35; D, E, GSC6702-38; H–L, PMO4444-79.)

F, G, J, K, M–P—*Oswaldheeria arctica* n. sp. F, showing distribution of stomata; ×20. G, upper cuticle of a short leaf; ×125. K, showing distribution of stomata in a short leaf; ×20. M, a few stomata showing orientation; ×125. N, a stoma; ×200. O, a stoma of a short leaf; ×200. P, margin of a leaf which has been nibbled in a zig-zag manner; ×20. (Slide nos.: F, PMO4444-60; G, J, O, PMO4444-68; K, PMO4444-74; M, PMO4444-75; N, PMO4444-76; P, GSC6702-36.) Unless otherwise stated figures are of long leaves.



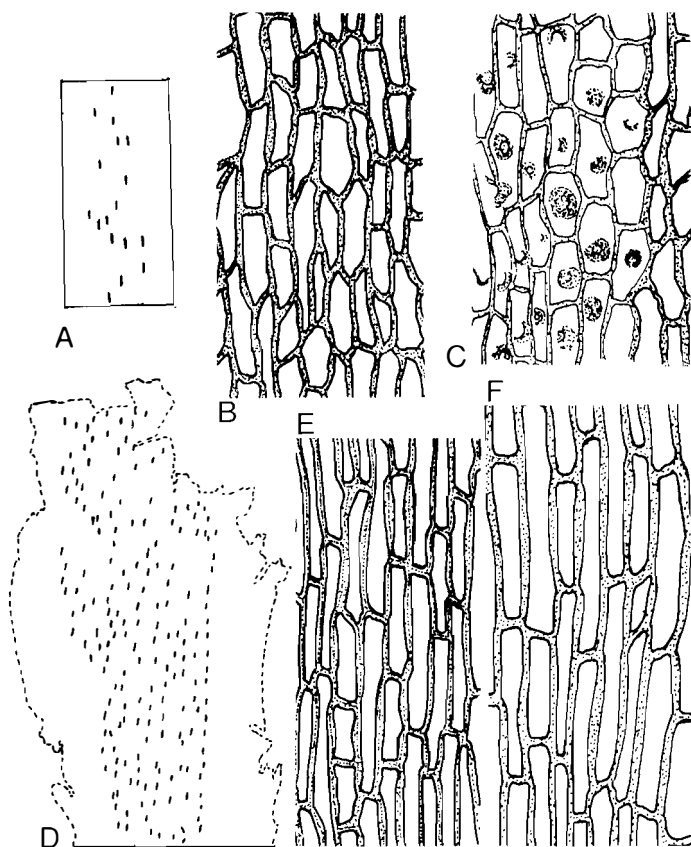


Fig. 20. A-C—*Holkopitys hoegii* n. sp. A, showing distribution of stomata within a band; $\times 20$. B, cells of median zone within the groove; $\times 125$. C, papillate cells of the zone flanking the median zone of non-papillate cells; $\times 125$. (Slide nos.: A, GSC6702-37; B, C, PMO4444-80.)

D-F—*Oswaldtheeria scotica* comb. nov. D, showing distribution of stomata; $\times 20$. E, lower cuticle showing cells of a non-stomatal zone; $\times 125$. F, upper cuticle; $\times 125$. (Slide no.: D-F, S431-1.)

Age and occurrence. – Upper Jurassic; Helmsdale, Scotland.

Remarks. – Florin (1922) had suggested that the leaves in this species were probably arranged in a verticillate manner. The specimen shows only fragments of leaves (Pl. 5, fig. 4) lying crowded together, from which it is not possible to make out their arrangement. Neither base nor apex is clearly visible in any leaf. Re-examination of the leaves did not show a median groove on the lower surface, nor do they have a furrow on the upper surface. When a few fragments were oxidized, the leaves showed two resin ducts, running close to margins. The measurements of leaves given in the diagnosis are after Florin (1922).

Comparison. – The cuticle of *Oswaldtheeria scotica* is like *O. hallei* (Florin), but *O. scotica* has much longer leaves, and it is almost twice as long as *O. macrophylla* (Florin) as described by Manum (1987), but the leaves of *O. macrophylla* are usually wider. Also the subsidiary cells of *O.*

macrophylla are papillate. Similarly, *O. arctica* differs from *O. scotica* in having papillate subsidiary cells.

Genus Holkopitys n. gen.

Diagnosis. – Leaf linear, straight or slightly curved, margins entire; base decurrent; apex obtuse or acute. Lower surface with a median groove.

Stomata confined to median groove in lower surface. Cells of upper cuticle and of lower cuticle outside median groove serially arranged, rectangular or trapezoidal; anticlinal walls undulated, surface non-papillate.

Margins of median groove deeply involute, cells along margins non-papillate. Cuticle within groove differentiated into five zones. Stomata confined to thinly cutinized outermost zones covered by involute margins; between these and the median zone with non-papillate cells lies on either side a zone with papillate cells. Stomata irregularly scattered, longitudinally orientated;

subsidiary cells 5–7. Guard cells slightly sunken, aperture slit-like.

Derivation of name. – From Greek *holkos* = track, referring to the stomatal bands, and *pitys* = pine.

Type species. – *Holkopitys hoegii* n. sp.

Holkopitys hoegii n. sp.

Pl. 6, figs. 5–7; Text-figs. 19 A–E, H–I, L, 20 A–C

Diagnosis. – Leaves linear, estimated length 1.5–2.0 cm, width 2–3 mm, slightly curved. Margins entire, abruptly tapering towards proximal end or base decurrent; apex obtuse or acute. Lower surface having a prominent median groove with deeply involute margins. Substance of lamina thick.

Upper cuticle uniformly thick; cells of upper cuticle more or less in longitudinal rows, rectangular or trapezoidal; anticlinal walls undulated, at times broken by pits; periclinal wall unspecialized. Lower cuticle showing five zones within median groove. Stomata confined to lateral zones having non-papillate subsidiary cells and ordinary epidermal cells; each of these zones followed by a zone having papillate cells flanking a median zone having non-papillate cells. Cuticle of median zone within groove and outside groove of lower side of almost same thickness as upper cuticle, remaining cuticle inside groove slightly thinner. Cells outside median groove like those of upper surface. Within groove, cells of median non-stomatal region rectangular or rhomboidal; anticlinal walls thick and straight, periclinal wall smooth. Cells of papillate zone rectangular, shorter, with anticlinal walls straight and thinner than those of median zone; periclinal wall with a prominent solid papilla. Stomatal zones always concealed by projecting margins of groove. Stomata irregularly scattered, longitudinally orientated; subsidiary cells 5–7, mostly 5 or 6, sometimes polar subsidiary cells distinct. Guard cells thinly cutinized; aperture slit-like. Ordinary cells within stomatal zone rectangular or polygonal with thin and straight anticlinal walls; periclinal wall smooth.

Derivation of name. – After Professor emeritus Ove Arbo Høeg, Oslo.

Holotype. – Slide no. PMO4444-77. Fig. 19 A.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Remarks. – The diagnosis is based on ten fragmentary specimens, the largest of which is from Padloping Island. The stomatal zones are concealed under the projecting margins of the median groove, and are usually appressed to it so that they are not easily separated.

Comparison. – *Holkopitys hoegii* shares with *Arctopitys* and *Sciadopityoides* the distinctive median stomatal groove on the lower side. However, the type of zonal differentiation of cells within the groove possessed by this species is not known in any other conifer. Stomata in bands within the groove occur in some specimens of *Sciadopityoides variabilis*, but otherwise the characters are quite different from *H. hoegii*. Some specimens of *Oswaldheeria hallei*, too, have stomata concentrated in bands (three) within the stomatal zone.

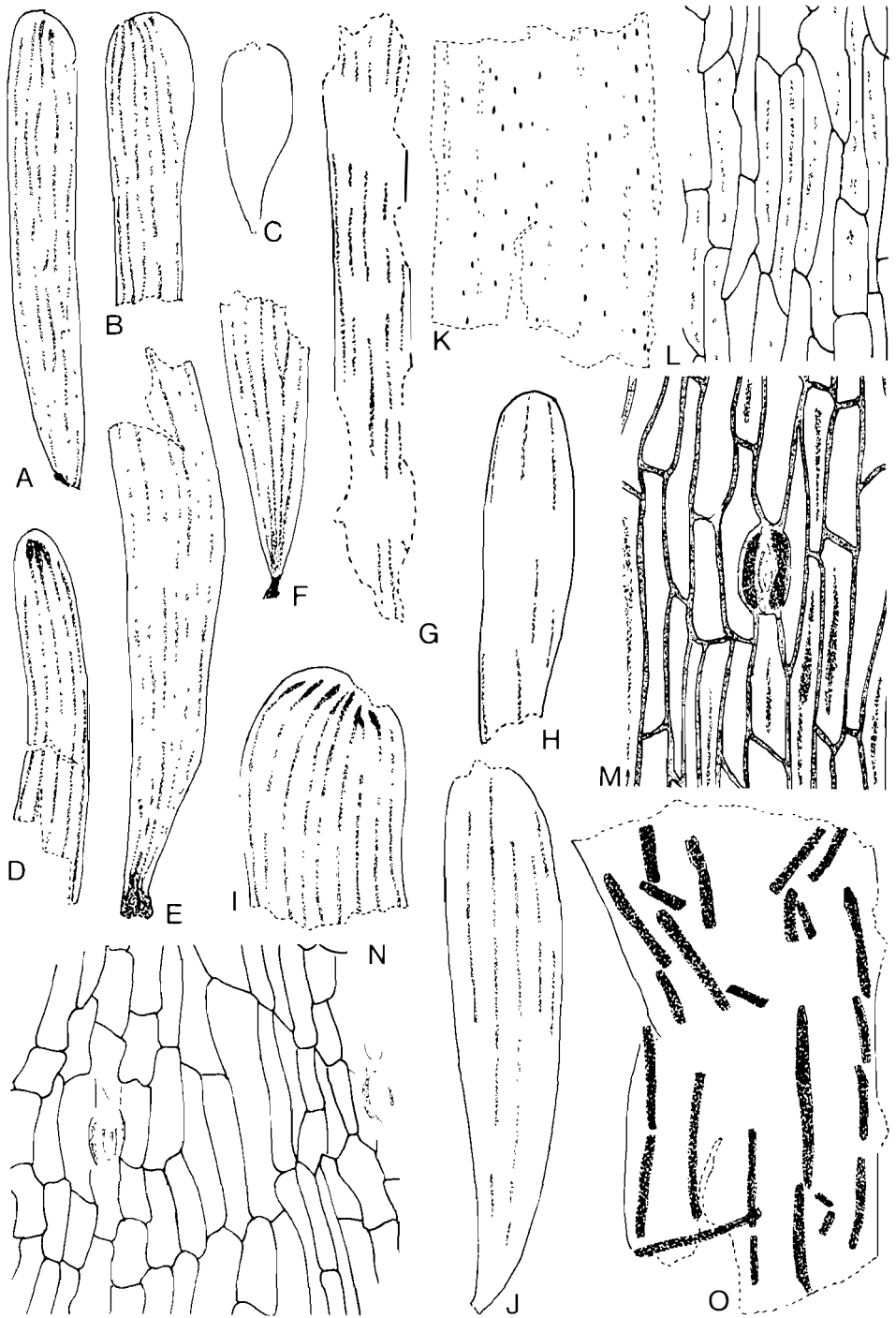
GINKGOALES

Genus *Pseudotorellia* Florin

Emended diagnosis. – Leaves coriaceous, entire or microscopically dentate, almost linear to narrowly tongue-shaped or obovate, straight or slightly falcate, with their maximum width in the middle region or more apically; apex obtuse; gradually narrowing towards base, hardly forming a petiole. Veins moderate in number, dichotomizing chiefly in basal part, ending separately at, or just below apical margin. Lamina with or without resin ducts.

Stomata confined to lower side in stomatal strips between narrower, non-stomatal longitudinal zones. Within strips stomata in short longitudinal rows or irregularly scattered, sparse or crowded, always longitudinally orientated. Guard cells sunken, next to the slit showing a more or less strongly cutinized ridge ('Vorhofleiste'; Florin 1922) and side wall facing lateral subsidiary cells also strongly cutinized. Subsidiary cells 4–6. Epidermal cells with slightly sinuous to straight outlines, surface of one or both sides having a median longitudinal ridge.

Type species. – *Pseudotorellia nordenskjöldii* (Nathorst) Florin (1936, p. 142). (The epithet *nordenskjöldii* was given by Nathorst (1897) in honour of the Swedish explorer, A. E. Nordenskiöld. However, by the original as well as many subsequent authors it has been variously



spelt, viz. *nordenskjöldi*, *nordensköldi* and *nordenskiöldi*. As Lundblad (1968, p. 190) pointed out, the correct latin spelling is *nordenskjoeldii*.)

Discussion. – The diagnosis of *Pseudotorellia* has been emended so as to include certain characters not originally mentioned by Florin (1936). The present diagnosis basically follows Lundblad's (1957) English translation of Florin's (1936) original with the addition of the following two characters: the veins ending separately at, or just below, the apical margin and the presence of resin ducts or bodies. Also, the character of cuticular ridges on epidermal cell surfaces is clarified, in line with Florin's (1936) original description and observations by subsequent authors.

Harris and Millington (in Harris et al. 1974) pointed out the venation character, however, without including it in the original version of the diagnosis which they just cited from Lundblad's (1957) translation. Harris and Millington (l.c.) also stated that *Pseudotorellia* did not possess resin bodies, although this had been observed by Manum (1968, in *P. heeri*) and by Krassilov (1970, 1972, in *P. angustifolia* Doludenko and in *P. sp.*). We now believe that resin ducts or bodies may well be an overlooked character which may be revealed in many species by more careful observation during the process of macerating the leaves. Watson (1969) gave an emended diagnosis for the genus, which was aimed at being broader and more simplified than the original in order to accommodate a new species from the English Wealden (*P. heterophylla*). This species has subsequently been synonymized with *Abietites linkii* (Roemer) and *Pityophyllum crassum* Seward (Watson & Hall 1988). On the basis of this, and its distribution of stomata which is unlike any other species, we consider the inclusion of this species in *Pseudotorellia* very doubtful. Therefore, we have not taken Watson's emendation into consideration.

Pseudotorellia kordylina n. sp.

Pl. 6, fig. 2; Text-figs. 21 A, B, D–I, K–O

Diagnosis. – Leaves somewhat club shaped, slightly curved, 1.0–1.3 cm long, 1.0–1.5 mm wide, maximum width slightly below apex, gradually tapering towards base, not forming a definite petiole; apex obtuse, sometimes with a depression, very rarely acute; margins entire. Mostly 5 (rarely 3 or 4) veins arising from base, 5–9 veins ending separately slightly away from apical margin, mostly unforked, sometimes bifurcating at different levels. Resin ducts running along veins from base to apex, terminating slightly away from apex; apical end of each duct slightly swollen.

Cuticle fairly thick and almost equal on both surfaces; stomata confined to lower surface. Cells on upper surface much longer than broad, elongated polygonal or rectangular, cells along veins narrower and more elongated; anticlinal walls thin, mostly straight, sometimes slightly wavy; periclinal wall having a median longitudinal thickening. Ordinary cells of lower surface like those of upper surface, cells along veins more distinct than intervenal cells, arranged in longitudinal rows. Non-stomatal zones narrower than stomatal zones. Within stomatal zones stomata sparsely and irregularly distributed, longitudinally orientated; strips between stomatal zones rarely with stomata. Stomata monocyclic, rarely incompletely dicyclic; subsidiary cells mostly 4, sometimes 5, rarely 6. Guard cells slightly sunken, mostly poles overhanging, aperture slit-like, flanked by well cutinized ridges, also side walls of guard cells as well as proximal walls of lateral subsidiary cells strongly cutinized.

Derivation of name. – From Greek *kordylinos* = clublike.

Holotype. – Specimen no. PMO44447-1. Fig. 21 A.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Remarks. – All the specimens of *Pseudotorellia kordylina* were obtained by bulk maceration of shale samples. In one horizon at locality B, Bohemanflya (Fig. 2), the assemblage is almost

Fig. 21. A, B, D–I, K–O—*Pseudotorellia kordylina* n. sp. A, B, D–I, leaves: resin ducts indicated by stippling (A, B, D–F, I: Bohemanflya and G, H: Padloping Island); A, B, D, F, H; $\times 5$. E, $\times 12.5$. I, $\times 10$. K, showing distribution of stomata: $\times 20$. L, upper cuticle: $\times 200$. M, a stoma: $\times 200$. N, showing two stomata: $\times 125$. O, disintegrated resin ducts lying between upper and lower cuticles of an oxidized leaf: $\times 20$. (Slide and specimen nos.: A, PMO4447-1; B, PMO4447-2; D, PMO4447-3; E, PMO4447-4; F, PMO4447-5; G, GSC6702-39; H, GSC6702-40; I, PMO4447-6; K, PMO4447-7; L, PMO4447-8; M, PMO4444-81; N, PMO4447-9; O, PMO4444-82.)

C, J—*Pseudotorellia retusa* n. sp. C, J, leaves; in J position of veins indicated by stippling; $\times 5$. (Slide nos.: C, PMO4444-83; J, PMO4444-84.)

entirely composed of *P. kordylina*, whereas at other horizons it is not so frequent. Complete leaves are rare. The most complete specimen measures 1.3 cm in length. From Padloping Island no complete specimen was obtained, but two of the specimens recovered seem to have exceeded 1.3 cm in length. In some of the specimens from Bohemanflya the extreme base is slightly twisted and the cuticle of the base is slightly thicker than the rest of the lamina.

In *P. kordylina* the resin ducts are clearly visible in partially macerated leaves; some also withstand complete maceration as long, thick threads or as disintegrated pieces (Fig. 21 O). These resin ducts are different from the 'dark strands' described by Harris (1952) and Harris and Miller (in Harris et al. 1974, figs. 25 A–C) in *Solenites vimineus* (Phillips) Harris.

Comparison. – *Pseudotorellia kordylina* can be readily distinguished from all the known species of the genus by its small size alone. The largest leaf is almost half the size of *P. minuta* Lundblad (1957), which was considered to be the smallest amongst the rest of the species (Lundblad 1968, p. 193). Moreover, *P. minuta* differs in having papillate subsidiary cells. Likewise, *P. ephela* (Harris) Florin (1936), *P. vachrameevii* Gomitzy (1965), *P. heeri* Manum (1968) and *P. tibia* Harris et Millington (1974) are also different from *P. kordylina*, because in all these species the subsidiary cells are papillate. *P. heeri*, however, resembles *P. kordylina* in having resin ducts, but unlike the latter species *P. heeri* has resin ducts between two veins. The stomatal apparatuses of *P. kordylina* are more like *P. nordenskjöldii*. The latter species, besides having larger leaves than *P. kordylina*, has epidermal cells which have sinuous anticlinal walls.

Pseudotorellia retusa n. sp.

Pl. 6, fig. 1; Text-figs. 21 C, J, 22

Diagnosis. – Leaves obovate, measuring 1.0–1.9 cm in length and 3–5 mm in width at the widest part (slightly below apex); abruptly or gradually narrowing towards base; apex retuse (asymmetrical, showing a depression on one side), rarely obtuse. Margins entire, rarely microscopically dentate except along apical region. Five veins radiating from base (actual number emerging from base not known), majority unforked,

mostly in each leaf one vein forking only slightly away from base, otherwise forking at different levels, mostly 6 (rarely 7) veins ending separately a little below apical margin.

Cuticle almost of same thickness on both surfaces, stomata confined to lower surface; on upper surface ill-marked vein strips. Cells of upper cuticle irregularly arranged, polygonal, near apex shorter and broader; anticlinal walls thin, straight or slightly wavy at places; periclinal wall having a median longitudinal thickening almost running from one end wall to the other, cells near apex having 2 such thickenings, rarely 3. Cells along veins tending to be seriatly arranged, mostly rectangular, much longer than wide, sometimes elongated polygonal. Lower cuticle showing distinct non-stomatal and stomatal zones, cells along veins seriatly arranged. Stomata irregularly scattered, also rarely occurring along veins, longitudinally orientated, rarely two adjacent stomata sharing a subsidiary cell. Stomata monocyclic, rarely incompletely amphicyclic. Subsidiary cells 4–6, commonly 5, proximal wall thickened. Guard cells slightly sunken, aperture slit-like, on both sides having a thickened ridge, also distal side of guard cells more cutinized. Ordinary epidermal cells within stomatal zones polygonal, with straight or wavy anticlinal walls; periclinal wall with a longitudinal median ridge, sometimes median ridge indistinct.

Remarks. – The leaves show a good deal of variation in size, the smallest measuring about 2 mm in length and width. Only a few leaves have dentate margins; dentations are distantly placed and the apical depressed portion is free of dentations.

Holotype. – Slide no. PMO4444-85. Fig. 22 A.

Occurrence. – Bohemanflya, Spitsbergen.

Comparison. – The leaves of *Pseudotorellia retusa* are slightly larger and wider than *P. kordylina* and they are obovate in shape. In *P. retusa* 6 veins are ending near the apex and there are no resin ducts, whereas in *P. kordylina* the number of veins varies from 5 to 9 and resin ducts occur. In *P. retusa* the stomata are more crowded and have 5 subsidiary cells. Otherwise it differs from the remaining species of *Pseudotorellia* in the same way as *P. kordylina*.

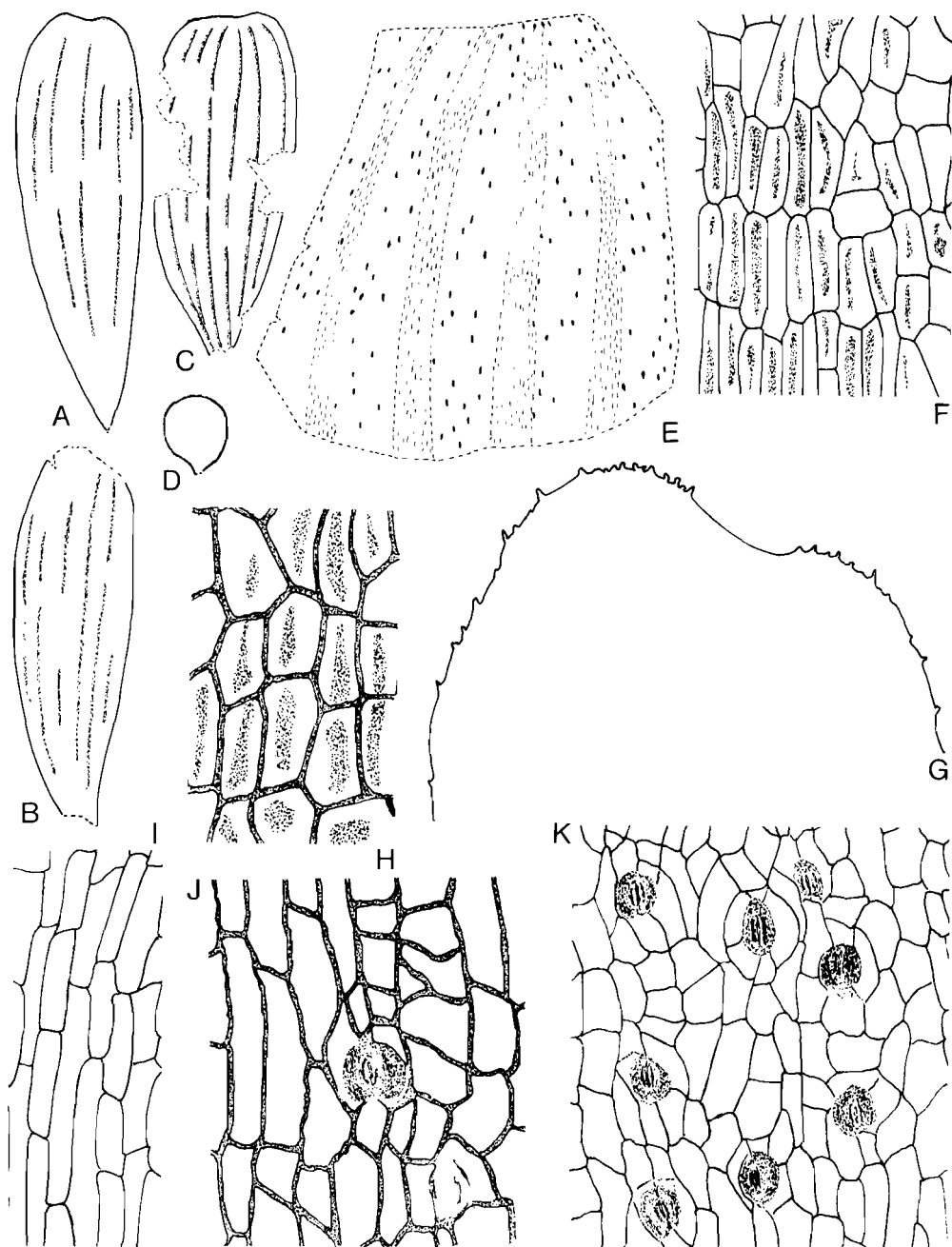


Fig. 22. A-K—*Pseudotorellia retusa* n. sp. A-D, leaves (stippled lines indicate position of veins); $\times 5$. Showing distribution of stomata between veins; $\times 20$. F, upper cuticle; $\times 125$. G, showing dentate margin near apical portion of a leaf; $\times 20$. H, upper cuticle; $\times 200$. I, lower cuticle; $\times 125$. J, a stoma; $\times 200$. K, a few stomata; $\times 125$. (Slide and specimen nos.: A, PMO4444-85; B, PMO4444-86; C, PMO4444-87; D, PMO4444-88; E, PMO4444-89; F, PMO4444-90; G, PMO4444-91; H, PMO4444-92; I, K, PMO4444-93; J, PMO4444-94.)

DIVERSE CONIFERS

Genus *Marskea* Florin

Marskea spitsbergensis n. sp.

Pl. 7, figs. 3, 4; Text-figs. 23 A, B, F–I, N, P

Diagnosis. – Leaves detached, lanceolate, widest part slightly away from point of attachment, 7–9 mm long, 1.7–2.0 mm wide at its widest portion. Margins entire; abruptly tapering towards base; apex acute. Median vein running from base to apex.

Cuticle moderately thick on both surfaces. On upper surface cells elongate–rectangular or polygonal, along midrib cells slightly narrower; anticlinal walls slightly wavy or straight; end walls sometimes rounded; periclinal wall smooth or mottled. Cells of lower surface more or less like upper surface in shape and size, but anticlinal walls more prominently wavy and periclinal wall mostly having a number of circular or oval thickenings often joined by narrow ridges. Stomata confined to two distinct stomatal bands on lower surface, median non-stomatal zone broader than marginal non-stomatal zones. Within stomatal bands ordinary epidermal cells and subsidiary cells slightly more cutinized than cells of non-stomatal zones; moreover, ordinary epidermal cells mostly polygonal and shorter than cells of non-stomatal zones, their surface wall mostly having 1–3 papillae. Stomata arranged in 3–5 ill-marked files; longitudinally orientated, unevenly spaced, sometimes closely set, even sharing polar subsidiary cell. Subsidiary cells 4–6, forming a broadly oval or circular ring, polar subsidiary cells distinct, subsidiary cells slightly more cutinized than ordinary epidermal cells and with a solid papilla; papillae of adjacent subsidiary cells united to form a rampart-like structure around stomatal pit, sometimes distal part of subsidiary cells bearing 1–3 papillae in addition to papillae bordering stomatal pit. Stomatal pit of varied shape, more often polygonal. Guard cells sunken, thinly cutinized.

Holotype. – Slide no. PMO4444-95. Fig. 23 A.

Occurrence. – Bohemanflya, Spitsbergen.

Comparison. – Other species of *Marskea* and the genus itself are based on leafy shoots, while our material consists of dispersed leaves only; thus, the phyllotaxy of *Marskea spitsbergensis* is not known. However, the cuticle has the same distinctive characters as other species of the genus *Marskea*, i.e. its epidermal cells have undulated walls, on the lower side there are papillate cells, the stomata are in ill-marked files within two papillose stomatal bands and the subsidiary cells form ramparts around the stomatal pits. *M. jurassica* (Florin) Harris (1979) differs in having leaves which are almost twice the length of the leaves of *M. spitsbergensis* and its stomata are less closely set than in the latter species. The leaves of *M. laticosta* Reymanówna (1963) are also longer and wider than *M. spitsbergensis*. It has 5–7 subsidiary cells, each with one papilla only. The upper epidermis of *Taxus bornholmiensis* Florin (1958), another species with distinctive *Marskea* characters but not yet formally transferred to that genus, has cells which have a fissure along the median lines of their surfaces and minute crystal cavities.

Marskea fragilis n. sp.

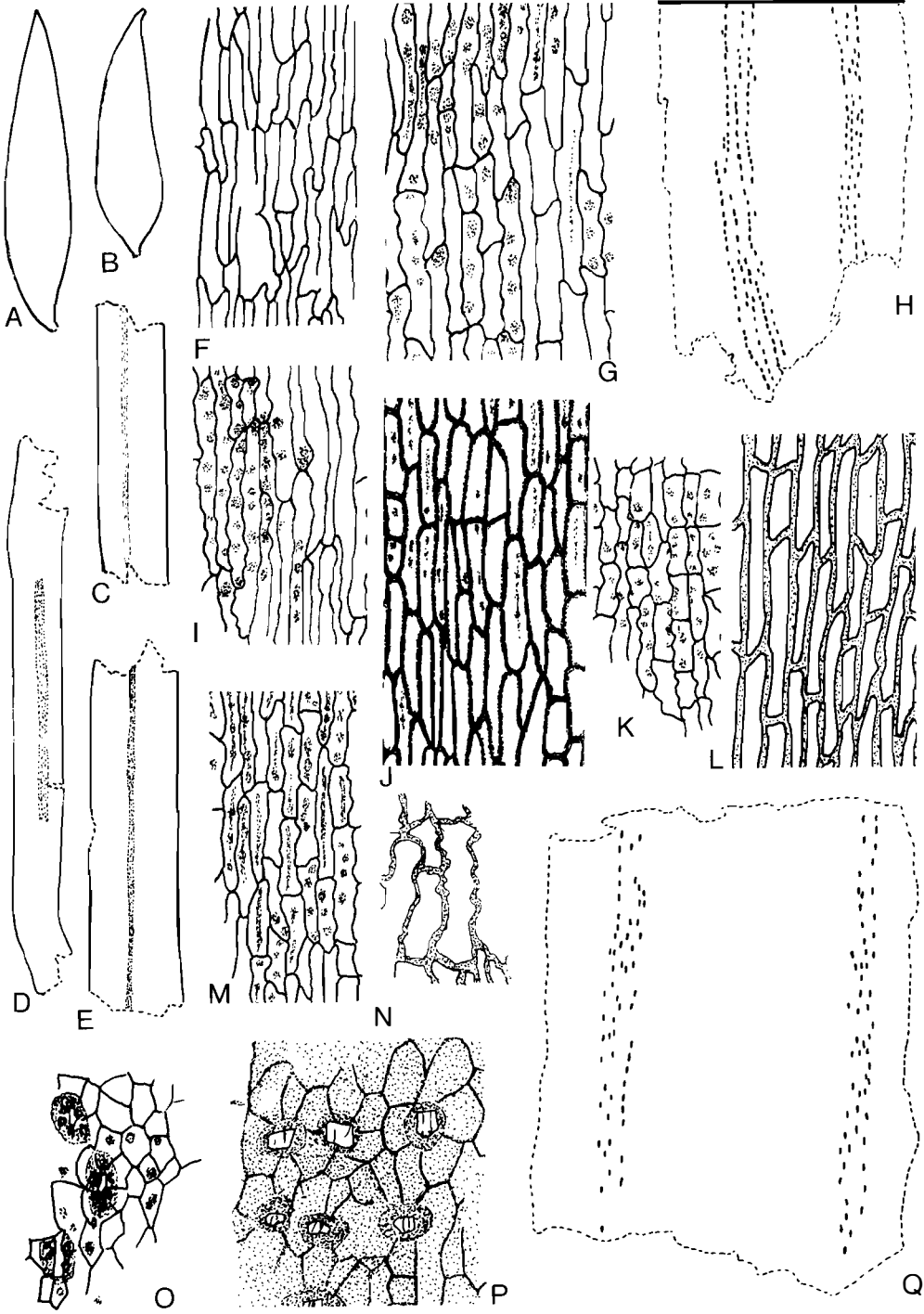
Pl. 7, figs. 1, 2; Text-figs. 23 C–E, J–M, O, Q

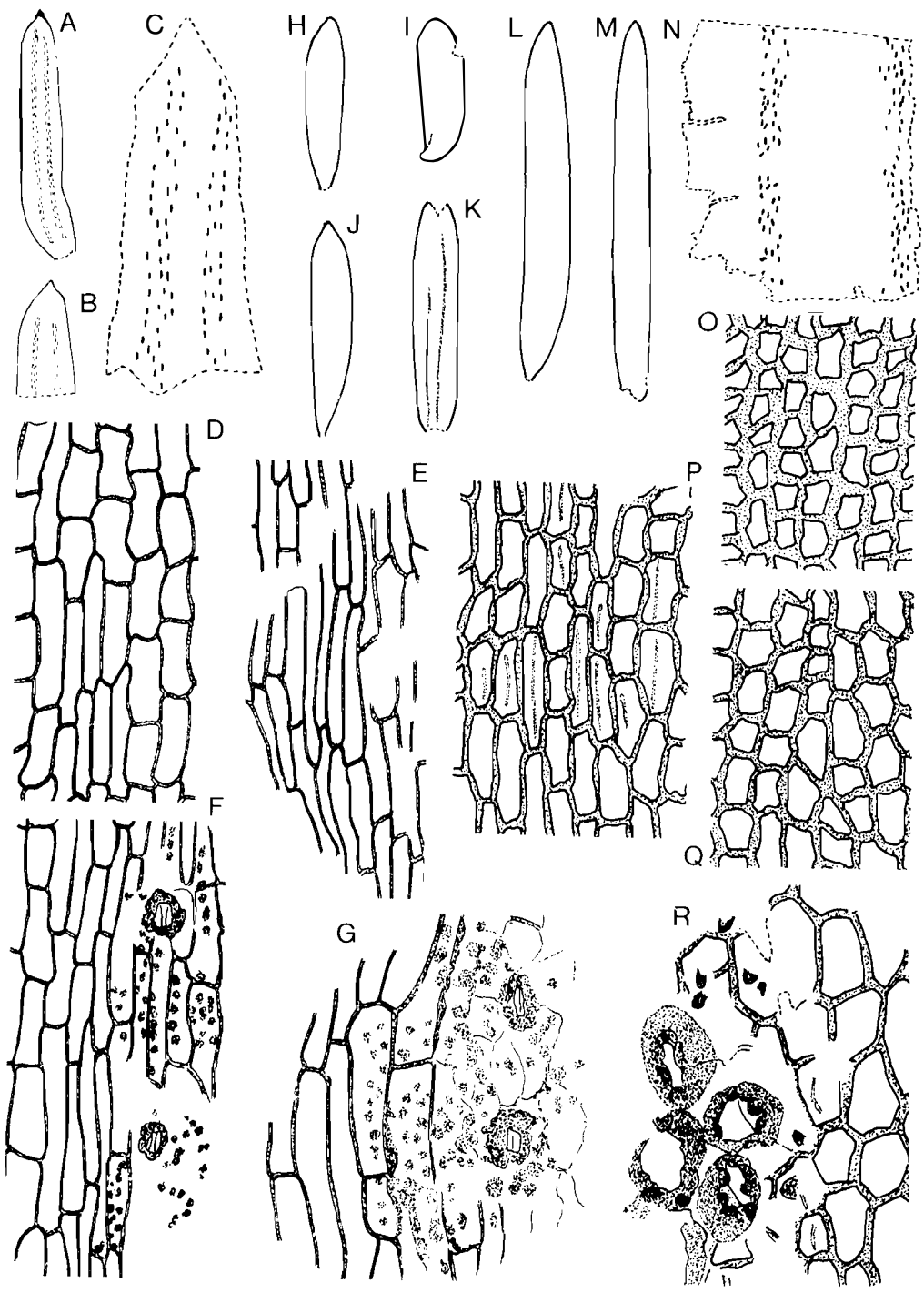
Diagnosis. – Leaves detached, exceeding 13 mm in length (only incomplete ones known), width 1.5–3.0 mm. Lamina showing transverse wrinkles on both sides of midrib. Margins entire. Midrib prominent on lower side, fairly wide.

Upper cuticle devoid of stomata, moderately thick, almost of same thickness as lower cuticle. Cells of upper cuticle along midrib rectangular or elongated polygonal; anticlinal walls thick, straight, sometimes irregularly thickened; periclinal wall mottled, often with a thickened longitudinal ridge, sometimes ridges breaking into small circular thickenings. Cells closer to margins like those along midrib but mostly devoid of

Fig. 23. A, B, F–I, N, P—*Marskea spitsbergensis* n. sp. A, B, leaves; $\times 5$. F, upper cuticle; $\times 125$. G, lower cuticle, showing cells along median region; $\times 125$. H, showing distribution of stomata; $\times 20$. I, lower cuticle, showing marginal cells; $\times 125$. N, upper cuticle, showing marginal cells; $\times 125$. P, a few stomata within a stomatal band; $\times 20$. (Slide nos.: A, F, I, N, P, PMO4444-95; B, PMO4444-96.)

C–E, J–M, O, Q—*Marskea fragilis* n. sp. C–E, leaves; $\times 5$. J, upper cuticle, showing cells along median region; $\times 125$. K, upper cuticle, showing marginal cells; $\times 125$. L, lower cuticle, showing cells along median region; $\times 125$. M, lower cuticle, showing marginal cells; $\times 125$. O, a few stomata; $\times 125$. Q, showing distribution of stomata; $\times 20$. (Slide nos.: C, PMO4444-3; D, PMO4444-4; E, PMO4444-97; J–L, PMO4444-98; M, O, Q, PMO4444-99.)





median thickening or papillae. Cells over rest of surface mostly rectangular, sometimes polygonal or trapezoidal; anticlinal walls straight or undulate; periclinal wall mostly with small circular thickenings, rarely having a thickened longitudinal ridge. Cells of lower cuticle like those of upper cuticle but within stomatal bands much smaller and mostly polygonal, surface smooth or slightly thickened, thickenings forming one or two circular bulges. Stomata confined to two stomatal bands, within bands stomata in 3–4 ill-defined files, longitudinally orientated, mostly distantly placed, sometimes touching each other but never sharing a subsidiary cell. Subsidiary cells 6–10, mostly 8, rarely 10; surface with a solid papilla close to stomatal pit, papillae united to form oval rampart-like structure. Stomatal pit oval. Guard cells thinly cutinized, sunken; aperture slit-like.

Holotype. – Slide no. PMO4444-98. Figs. 23 J–L.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Remarks. – None of the leaves seen so far has either apex or base preserved. In partially oxidized leaves the lamina shows transverse wrinkles on either side of the midrib. The midrib is often thick and represented by a prominent ridge on the lower side. Within stomatal bands the stomata are either in ill-defined or discontinuous files.

Comparison. – The leaves of *Marskea fragilis* are longer than *M. spitsbergensis*, and have more distantly placed stomata which have 6–10 subsidiary cells in contrast to 4–6 in *M. spitsbergensis*. In *M. jurassica* (Florin) Harris (1979) and *M. laticosta* Reymanówna (1963) too, the number of subsidiary cells are less than in *M. fragilis*.

Genus *Torreya* Arnott

Torreya arctica n. sp.

Pl. 6, figs. 3, 4; Text-figs. 24 A–G

Diagnosis. – Leaves detached, largest leaf 12 × 1.5 mm. Margins entire; apex acute. Lower side showing a median vein.

Cuticle on both surfaces of almost same thickness, stomata confined to lower surface. Cells of upper surface rectangular or elongated polygonal, serially arranged; anticlinal walls thin, straight or slightly wavy at places; periclinal wall mottled. Lower surface showing two distinct stomatal bands with papillate cells and three non-stomatal zones – two marginal and one median. Cells of median zone arranged in longitudinal rows, rectangular, much longer than broad; anticlinal walls thin and straight, end walls straight or oblique; periclinal wall mottled. Cells of marginal zones slightly shorter and wider than cells of median zone, generally with smooth or mottled surface, sometimes cells (1–3 cells wide) adjacent to stomatal bands with a number of circular thickenings. Ordinary epidermal cells within stomatal bands shorter than cells of marginal and median zones, irregularly arranged, polygonal; anticlinal walls thin and straight; periclinal wall having a number of circular, oval or irregularly shaped thickenings. Within stomatal bands stomata commonly separated from one another, irregularly scattered, longitudinally orientated. Subsidiary cells 6–8, forming an oval deep pit; papillate; papillae situated close to pit, sometimes bulging over pit. Guard cells sunken, thinly cutinized.

Holotype. – Slide no. PMO4444-100. Fig. 24 A.

Occurrence. – Bohemanflya, Spitsbergen.

Remarks. – The above diagnosis is based on a few detached leaves. In none of them is the base preserved.

Comparison. – The leaves of *Torreya arctica* are slightly smaller than *T. gracilis* Florin (1958) but have almost the same width (see Harris 1979, fig. 52A). *T. gracilis* has specialized marginal epidermal cells along the stomatal bands, such cells are not present in *T. arctica*. Leaves of *T. valida* Florin (1958) are broader than those of *T. arctica*, and have stomata with 5–10 subsidiary cells. *T. moelleri* Florin (1958) has much larger leaves.

Fig. 24. A–G—*Torreya arctica* n. sp. A, B, leaves (broken lines indicate the position of stomatal bands); ×5. C, showing distribution of stomata; ×20. D, upper cuticle; ×125. E, marginal cells of lower cuticle; ×125. F, showing two stomata and cells of median zone; ×125. G, two stomata; ×200. (Slide nos.: A, C–G, PMO4444-100; B, PMO4444-101.)

H–R—*Elatocladus* sp. A. H–M, leaves (K, showing stomatal bands. H, I, K, M: Bohemanflya and J, L: Padloping Island); ×5. N, showing distribution of stomata; ×20. O, upper cuticle; ×125. P, lower cuticle, showing cells along median region; ×125. Q, lower cuticle, showing marginal cells; ×125. R, a few stomata; ×200. (Slide nos.: H, PMO4444-102; I, PMO4444-103; J, GSC6702-41; K, PMO4444-104; L, GSC6702-42; M, PMO4446-5; N, P–R, PMO4444-105; O, PMO4444-106.)

Genus *Elatocladus* Halle

Elatocladus sp. A

Pl. 6, fig. 8; Pl. 7, fig. 5; Text-figs. 24 H–R

Description. – Leaf commonly measuring 5–10 mm in length (range noted 2–12 mm) and 1.0–1.5 mm in width, linear or lanceolate; margins entire. Abruptly narrowing towards base, sometimes base slightly constricted; apex acute or apiculate, rarely obtuse.

Upper and lower cuticles moderately thick; stomata confined to lower surface in two distinct bands. Cells of upper cuticle irregularly arranged, along median region tending to be more uniformly arranged. Cells polygonal; anticlinal walls thick, mostly straight; periclinal wall mottled, sometimes with median, narrow longitudinal stripes. Cells of lower cuticle like those of upper cuticle, but between stomatal bands cells more elongated and tending to be arranged in longitudinal rows. Ordinary epidermal cells within stomatal bands irregularly arranged, polygonal; anticlinal walls thinner than in non-stomatal bands, periclinal wall often with a dome-shaped or conical papilla. Stomata irregularly scattered within stomatal bands, closely set, sometimes sharing a subsidiary cell, orientation mostly longitudinal, sometimes oblique, rarely transverse. Subsidiary cells 6–8, surface thicker than ordinary cells, forming a circular or broadly oval ring, mostly papillate, papillae more commonly overhanging stomatal pit. Stomatal pit oval, circular or polygonal. Guard cells sunken, thinly cutinized.

Occurrence. – Bohemanflya, Spitsbergen; Padloping Island, Arctic Canada.

Remarks. – *Elatocladus* sp. A is almost as common as *Sciadopityoides microphylla* and *Oswaldheeria arctica* at Bohemanflya. Even in partially oxidized leaves the stomatal bands are clearly visible, whereas the midrib is not discernible.

Elatocladus sp. B

Pl. 7, fig. 6; Text-figs. 25 A, B, F, G, I

Description. – Leaf incomplete, available length 7 mm, width about 1 mm. Margins entire, parallel; apex sub-acute.

On both surfaces cuticle of same thickness, hypostomatic. Cells of upper surface arranged in longitudinal rows, mostly rectangular, towards base and apex somewhat polygonal; anticlinal walls thick, straight; periclinal wall mottled. Cells

of lower surface like those of upper surface. On lower surface stomata forming two ill-defined zones close to margins, leaving a broad, median non-stomatal zone; stomatal zones converging towards apex. Stomata irregularly scattered, sparse, sometimes 2 or 3 stomata lying close to each other, rarely a few stomata lying outside stomatal zone, always longitudinally orientated. Subsidiary cells 4–6, mostly 6, polar subsidiary cells distinct. Subsidiary cells slightly more cutinized than ordinary epidermal cells, forming a ring, pit broadly oval or rectangular. Guard cells sunken within pit, thinly cutinized; aperture oval. Encircling cells may or may not be distinct.

Occurrence. – Bohemanflya, Spitsbergen.

Remarks. – The description is based on a single specimen, whose extreme base is not preserved, but otherwise its cuticle is very well preserved. At one place one stomatal pit has two pairs of guard cells (Pl. 7, fig. 6). The lower cuticle is reminiscent of the lower cuticle of *Elatocladus setosus* (Phillips) Harris (1979). *E. setosus* differs in being amphistomatic.

Elatocladus sp. C

Pl. 7, fig. 7; Text-figs. 25 C–E, H, J, K

Description. – Leaf measuring 4.2×1.2 mm. Apex obtuse; base slightly expanded; margins entire.

Cuticle moderately thick on both surfaces, amphistomatic; stomata on both surfaces forming two ill-defined zones; stomatal zones lying closer to margins. On both surfaces median non-stomatal zone broader than stomatal zones and marginal non-stomatal zones; on one surface (?lower) cells within median zone slightly more elongated than cells on remaining surface, also more regularly arranged in longitudinal rows; arrangement of cells outside median zone not so regular. On both surfaces cells polygonal; anticlinal walls thick, straight; periclinal wall mottled. Stomata dicyclic, irregularly scattered within stomatal zones, more often distantly placed, majority longitudinally orientated. Subsidiary cells 6–7, rarely 8, surface slightly more cutinized than ordinary epidermal cells, but lacking papilla, often showing a thin stripe closer to stomatal pit. Guard cells sunken, thinly cutinized. Encircling cells like those of ordinary epidermal cells.

Occurrence. – Bohemanflya, Spitsbergen.

Remarks. – The description is based on a single specimen whose cuticle is very well preserved.

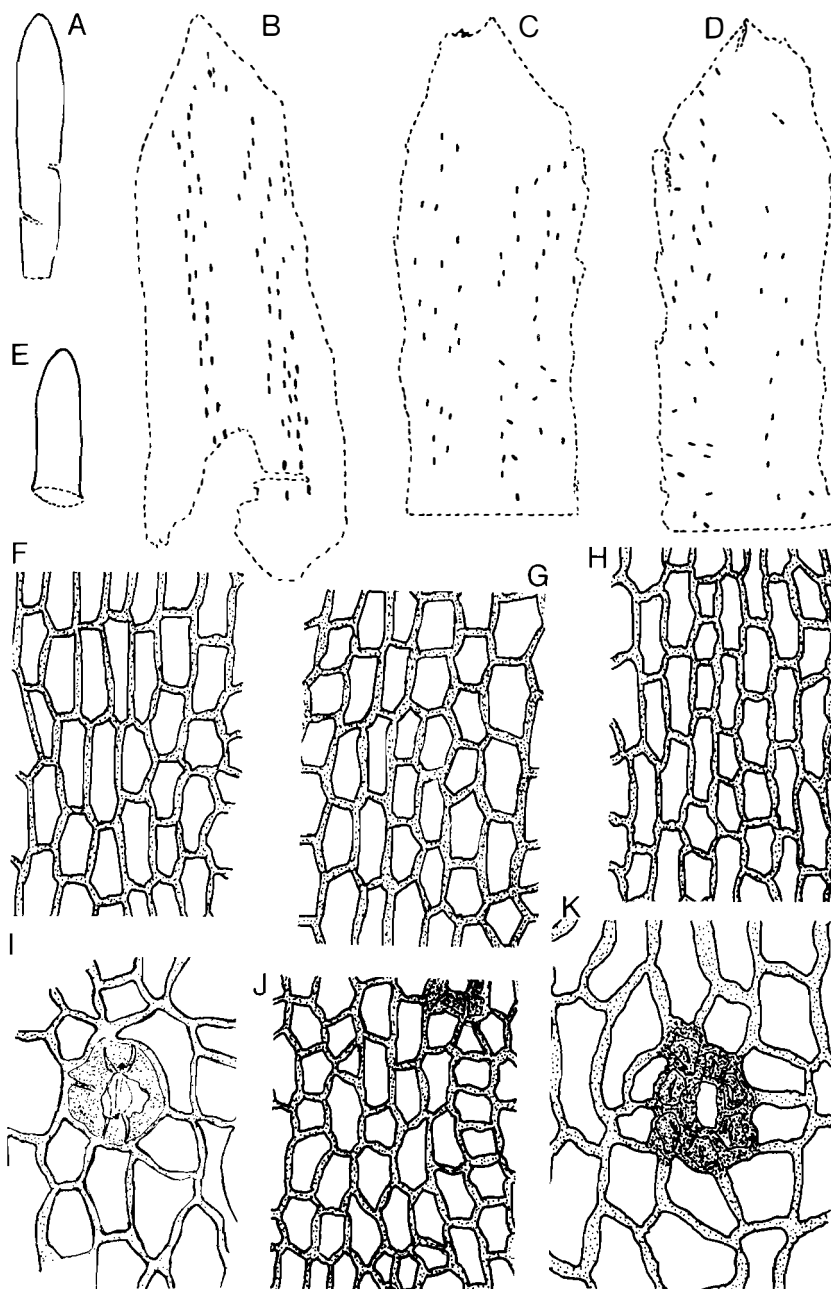


Fig. 25. A, B, F, G, I—*Elatocladus* sp. B. A, leaf; $\times 5$. B, showing distribution of stomata; $\times 20$. F, lower cuticle; $\times 125$. G, upper cuticle; $\times 125$. I, a stoma; $\times 200$. (Slide no.: PMO4444-107.)

C–E, H, J, K—*Elatocladus* sp. C. C, upper cuticle, showing distribution of stomata; $\times 20$. D, lower cuticle, showing distribution of stomata; $\times 20$. E, leaf; $\times 5$. H, lower cuticle, showing cells of median region; $\times 125$. J, upper cuticle; $\times 125$. K, lower cuticle, showing a stoma; $\times 200$. (Slide no.: PMO4444-108.)

Burejospermum Krassilov: clitellate cocoons?

Associated with the leaves from Spitsbergen, Greenland and Padloping Island are oval sack-like bodies which are indistinguishable from *Burejospermum* Krassilov (1972, p. 65, pl. 22, figs. 1–4, 9–14) from the Upper Jurassic of the Bureya Region, USSR. They are approximately 2 to 10 mm long (Pl. 8, figs. 7, 9). Complete specimens show no indication of a micropyle or point of attachment. They have a characteristic net-like structure, adhering to a continuous, more or less amorphous inner layer. The net-like structure has no resemblance to any acid resistant plant cells or tissue that we are aware of. Inside the wall are tube-like structures showing annular markings.

The substance of these bodies is more lustrous and brittle than cuticle, reminding more of chitinous material. This, together with the absence of any cellular structure that we know from plants lead us to conclude that they are not of plant origin.

Krassilov (1972) interpreted such bodies as seeds with ginkgoalean affinity, though he was unable to demonstrate the chalazal or micropylar end in any of them. The outer wall layer was considered as the cuticle of the integument and the inner as that of the nucellus; the net-like structure was taken as cells. Krassilov (l.c. pl. 22, figs. 10, 14) interpreted elongated dark structures observed inside the 'seeds' as resin ducts. Identical, tube-like structures observed by us are in fact embedded in the wall on its inner face and remain in position even after prolonged acid and alkali treatment, quite unlike resin ducts which become displaced and usually disintegrate after such treatment.

In the absence of proven seed-like or any other vegetal structure in these bodies we consider that *Burejospermum* is of animal origin, and that they represent some sort of cocoons of organisms related to clitellates (Phylum Annelida). Besides the form described above, there is another showing only a web after prolonged acid and alkali treatment (Pl. 8, figs. 8, 10). However, in some partially oxidized specimens a thin inner membrane is visible. This type of net-like bodies has been referred to *Dictyothylakos* Horst (1954).

A fuller report of these and related netted bodies will be published elsewhere (Manum, Bose & Sawyer in press).

Insect nibbling. – Some leaves appear to have lost

their apex by nibbling (cf. also Harris 1952, p. 379; Manum 1987, p. 158, pl. 3, figs. 2–5). In some other leaves the margins appear to have been nibbled in a zig-zag manner (Fig. 19 P).

Conclusion

The early and until now most comprehensive studies on the Lower Cretaceous flora of Spitsbergen (Heer 1876; Nathorst 1897) contained no records of 'Sciadopitys-like' fossils. These classical papers, which were based mostly on impression fossils, show a flora dominated by *Ginkgo*, *Elatides*, *Podozamites* and *Pinites* (*Pityocladus*), with fragmentary remains of pteridophytes and very rare cycadophytes. These early works are in great need of critical revision, particularly with the aid of modern methods applied to compression fossils. The present work, concentrating on a particular group of fossils only, has demonstrated the potential of bulk maceration of samples containing compressions.

A more recent contribution to the knowledge of the flora from Spitsbergen was made by Sveshnikova & Budantsev (1969) from a locality about 1 km west of our collecting site on Bohemanflya (Fig. 2). At this locality *Elatides curvifolia* dominates, followed by ginkgoalean and bennettitalean remains. There are also 'Sciadopitys-like' remains but cuticles prepared by us from this locality are poorly preserved.

Hitherto the flora from West Greenland was the richest in 'Sciadopitys-like' taxa of Lower Cretaceous age from the arctic region. When cuticles of 'Sciadopitys-like' leaves were first described from this flora (Halle 1915; Florin 1922), there was no indication of the morphological and taxonomic diversity that we have now found in all the three areas. The classical studies of the West Greenland flora (Heer 1868, 1874, 1883) were partly revised and extended by Seward (1926) and Seward & Conway (1935a, b). Like the flora from Spitsbergen, this flora is also in need of re-investigation; for instance, conifers having horizontally spreading leaves should be re-examined in view of our findings of leafy twigs of *Arctopitys*. We have also observed many plants new to that flora in our preparations but their treatment is outside the scope of this paper.

We have studied carbonaceous shales which show leaves preserved as compressions on the

surface of hand specimens. Sometimes they have been pure leaf-coals (X-ray diffraction shows no silica). These deposits represent swampy or lacustrine conditions and they contain grossly equivalent fossil associations on Spitsbergen, West Greenland and Baffin Island in terms of the plant groups present. They also have some 'Sciadopitys-like' taxa in common; Spitsbergen and Baffin Island share five species, while two of them are also present on West Greenland (Table 3).

The method of bulk maceration used in this study has been rewarding far beyond our expectations. It has in most cases produced more diverse assemblages than is seen on the surfaces of hand specimens. But for this method, it would not have been possible to demonstrate leaf dimorphism and the mode of leaf arrangement in the 'Sciadopitys-like' genera. We found shoots with leaf scars which helped us to interpret the leaf arrangement before we were fortunate enough to find a few leafy twigs which confirmed our interpretations.

We have demonstrated important differences in terms of vegetative morphology between the 'Sciadopitys-like' fossils and the extant species. They are now considered to be more distinct from the extant species than previously thought, and we have accommodated the fossils in a separate family, the Arctopityaceae. Clearly, a great deal still remains to be learnt about these plants, particularly their fertile organs, before their affinities can be firmly established.

Until now, these Mesozoic fossils were considered to be the only candidates for the ancestry of *Sciadopitys verticillata*. We are no longer so sure that they remain candidates, and are therefore posed with the question as to where to look for the pre-Tertiary ancestors of *Sciadopitys*. Unlike the Mesozoic fossils, the Tertiary ones show closer affinity with the extant species. Clearly, Mesozoic 'Sciadopitys-like' fossils will have to be studied with a fresh outlook. Leafy shoots and reproductive structures would be particularly rewarding objects. Detailed pollen

Table 3. Stratigraphic and geographic distribution of presently known Mesozoic taxa of *Sciadopitys*-like leaves. (*S. nathorstii* is here assigned a Lower Cretaceous age, see discussion p. 31.). While this paper was at proof stage, we learnt from J. O. Vigran that on palynological evidence the strata in northern Norway containing *O. macrophylla* should now be considered to be Middle Jurassic.

TAXON		<u>SCIADOPITYOIDES</u>										<u>ARCTOPITYS</u> n.gen.	<u>OSWALD- HEERIA</u> n.gen.		<u>HOLKO- PITYS</u> n.gen.	Total number of species						
		<u>S. crameri</u>	<u>S. ikorfatensis</u> n.sp.	<u>S. macrophylla</u> comb.nov.	<u>S. nathorstii</u>	<u>S. ukrainensis</u>	<u>S. uralensis</u>	<u>S. variabilis</u>	<u>A. capbohemansensis</u> n.sp.	<u>A. florinii</u> n.sp.	<u>A. ineffecta</u> n.sp.	<u>A. lagerheimii</u> comb.nov.	<u>A. persulcata</u> comb.nov.	<u>A. sibirica</u> comb.nov.	<u>A. sp.</u>		<u>O. arctica</u> n.sp.	<u>O. hallei</u> n.sp.	<u>O. macrophylla</u> comb.nov.	<u>O. scotica</u> comb.nov.	<u>H. hoegii</u> n.sp.	
Cretaceous	Upper	U.S.S.R.	+	1
		West Greenland	+	+	+	+	+	.	+	6
	Lower	Baffin Island	.	.	+	.	.	.	+	.	.	+	.	.	.	+	+	.	.	.	+	6
		Spitsbergen	.	.	+	+	+	+	.	.	.	+	+	.	.	.	+	7
		U.S.S.R.	+	1
Upper Jurassic		U.S.S.R.	+	1
		N. Norway	+	+	+	.	.	.	3
		Scotland	+	.	.	1

studies of leaf-bearing strata might show the relationships between leaf and pollen assemblages and might also provide evidence for affinities.

The conifers that we have described and now referred to the Arctopityaceae appear to have formed a prominent and in certain environments dominant element of the forests around 55–65 degrees northern latitude in the Lower Cretaceous. They formed nearly monospecific communities under certain conditions, as indicated by pure leaf-coals. Their distribution extended to eastern parts of Eurasia (Table 3), in contrast to western Europe and Great Britain where they appear to have been absent in the Early Cretaceous. It seems that they first appeared in the Middle Jurassic and attained their acme during the Early Cretaceous; there is only a single record from the Upper Cretaceous. Our records of other gymnosperms, namely *Marskea* and *Torreya* on both Spitsbergen and West Greenland, represent extensions of the known stratigraphic and geographic ranges of these genera into the Lower Cretaceous of the arctic region. The genus *Pseudotorellia* has been emended on the basis of new species described from Spitsbergen.

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Addendum

While this paper was at page proof stage, we received from Dr. Maria Reymanówna, Kraków, a paper which makes *Arctopitys* n. gen. (pp. 13, 32) redundant, being a synonym of the monotypic genus *Mirovia* Reymanówna (1985). Reymanówna interpreted the type species (*M. szaferi*) as ginkgoalean, but we consider it beyond doubt that its affinity is with the coniferous leaves which we have described herein under *Arctopitys*. The purpose of this addendum is to substantiate this conclusion and to formalize its nomenclatural implications. Wherever in the preceding pages the names *Arctopitys*, *Arctopityaceae* and *Arctopityoideae* appear, they should be replaced by *Mirovia*, *Miroviaceae* and *Mirovioideae*, respectively.

Mirovia szaferi Reymanówna (l.c.) has leaves 10–14 mm long and about 2 mm wide with a single median stomatal zone, a character used herein to distinguish the *Arctopityaceae* (p. 18). Moreover, the stomatal zone is frequently hidden by the protruding zone margins, as shown for the holotype (pl. 1, fig. 6); this, too, is a characteristic feature of the *Arctopityaceae*, except for the genus *Oswaldheeria* where the stomatal zone is not protected in a groove. Finally, *M. szaferi* has tapering and twisted leaf base as described by us for *Arctopitys*; also compatible with *Arctopitys* is the presence of a median furrow in the upper leaf surface and of resin ducts. *Mirovia szaferi* differs from all the species referred in the preceding pages to *Arctopitys* in having stomata in files within the stomatal groove. *M. szaferi* has been described as polymorphic with stomatal zone being lateral in some specimens (e.g. figs. 1 A, D, L). This is a normal mode of preservation in originally near-cylindrical leaves which we have also observed in our material. The 'abscission scar' described by Reymanówna is quite different from the distinctive scar typical of *Sciadopityoides* (pp. 13, 21).

The generic diagnosis of *Mirovia* easily accommodates all our species of *Arctopitys*, provided it is altered with regard to distribution of stomata thus: 'stomata arranged in files or irregularly distributed'. However, since Reymanówna's diagnosis is very brief compared with that of ours for *Arctopitys*, we prefer the latter with a corresponding change with regard to stomatal dis-

tribution as the emended diagnosis for *Mirovia* (see below).

Reymanówna (1985, p. 10) considered *Mirovia* to belong to the Ginkgoales, based mainly on comparison with species of *Pseudotorellia*, 'although the typical dichotomous venation of the *Ginkgoales* was not observed in *Mirovia*'. The absence of this important ginkgoalean character and the presence of a median stomatal groove are in our opinion incompatible with a ginkgoalean affinity (for our discussion of affinity, see pp. 16–18).

The occurrence of *Mirovia* in the Middle Jurassic of Poland is within known stratigraphic and geographic ranges of this group of conifers as shown in Table 3 (p. 61).

Mirovia Reymanówna, 1985

Emended diagnosis.—As per diagnosis of *Arctopitys* (p. 32), with the following change in the last sentence p. 33, first column: 'Stomata confined to lower median groove; irregularly distributed or arranged in files'.

Type species.—*Mirovia szaferi* Reymanówna, 1985, p. 6.

List of valid species and nomenclatural transfers from *Arctopitys* (cf. Annotated list p. 20):

Mirovia szaferi Reymanówna (*partim*; including only leaves with protruding stomatal groove margins as in the holotype; Reymanówna's figures suggest absence of protruding margins over the stomatal groove in some specimens, thus we suspect these to belong to *Oswaldheeria*)

Mirovia capboheanensis (Bose et Manum) comb. nov.

Mirovia florinii (Bose et Manum) comb. nov.

Mirovia inefecta (Bose et Manum) comb. nov.

Mirovia lagerheimii (Johansson) comb. nov.

Mirovia persulcata (Johansson) comb. nov.

Mirovia sibirica (Samylina) comb. nov.

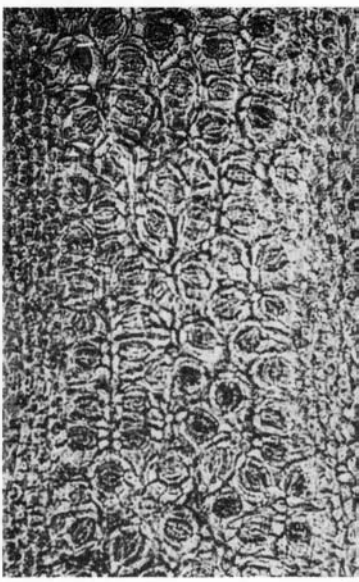
Reference.—Reymanówna, M. 1985: *Mirovia szaferi* gen. et sp. nov. (Ginkgoales) from the Jurassic of the Kraków region, Poland. *Acta Palaeobot.* 25, 3–12.

Plates 1–8

[Note: Unless otherwise stated figures in Plates 1–5 are of long leaves.]

Plate 1

- Fig. 1. Sciadopityoides microphylla* comb. nov. showing distribution and orientation of stomata; $\times 80$. Slide no. S20301.
- Fig. 2. S. microphylla* comb. nov. showing a few stomata of a short leaf; $\times 200$. Slide no. PMO4446-6.
- Fig. 3. S. crameri* (Heer) Sveshnikova showing orientation of stomata; $\times 200$. Slide no. S20303-4.
- Fig. 4. S. microphylla* comb. nov. showing stomata; $\times 200$. Slide no. S20301.
- Fig. 5. S. crameri* (Heer) Sveshnikova, a few stomata enlarged; $\times 400$. Slide no. S20303-4.
- Fig. 6. S. crameri* (Heer) Sveshnikova, a fragmentary shoot; $\times 3$. Slide no. PMO(A)27741-8.
- Fig. 7. S. microphylla* comb. nov. showing tuberculate papillae of a short leaf; $\times 200$. Slide no. PMO4444-11.
- Fig. 8. S. ikorfatensis* n. sp. showing a few stomata; $\times 200$. Slide no. S20306-12.
- Fig. 9. S. microphylla* comb. nov. showing tuberculate papillae; $\times 400$. Slide no. PMO4444-6.



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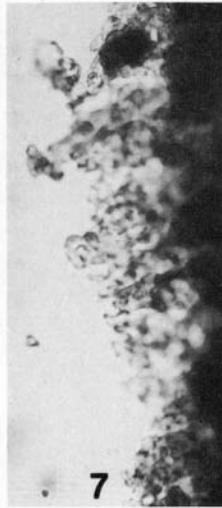
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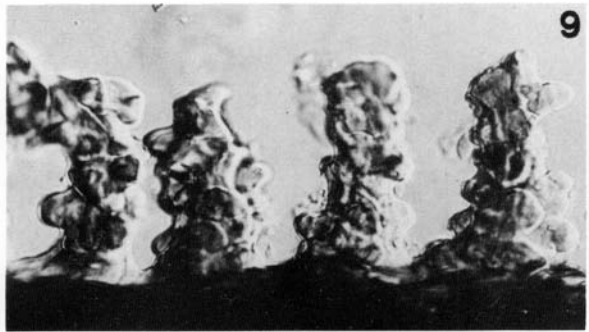
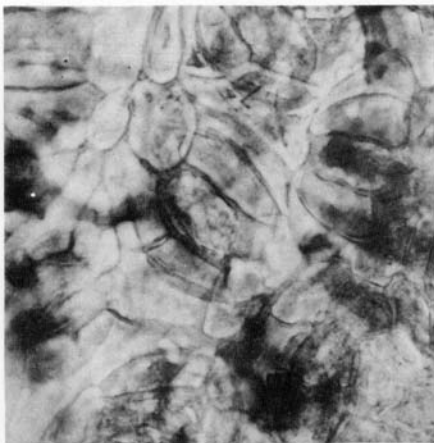
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Plate 2

Figs. 1–2. Sciadopityoides nathorstii (Halle) Sveshnikova. 1: Stomata; $\times 200$. 2: A few stomata magnified; $\times 400$. Slide no. S20307-29.

Fig. 3. S. ikorfatensis n. sp. showing stomata; $\times 400$. Slide no. S20306-12.

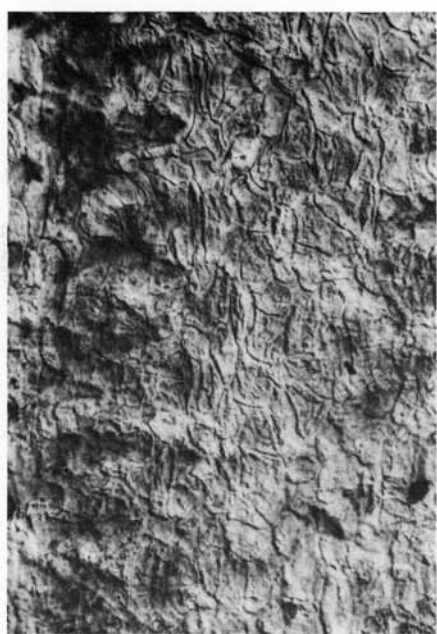
Figs. 4–6. Oswaldheeria hallei comb. nov., fragmentary shoots; $\times 3$. Slide nos. S20308-7, S20308-5 and S20308-6, respectively.

Figs. 7–8. Sciadopityoides variabilis (Bose) Sveshnikova. 7: Stomata; $\times 200$. 8: A stoma enlarged; $\times 400$. Slide no. GSC6702-18.

Fig. 9. S. microphylla comb. nov. showing stomata; $\times 400$. Slide no. S20301.

Fig. 10. S. ikorfatensis n. sp. showing stomata of a short leaf; $\times 400$. Slide no. S20306-13.

Fig. 11. Arctopitys florinii n. sp. showing stomata; $\times 200$. Slide no. GSC6702-31.



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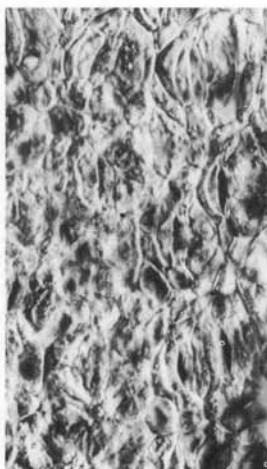
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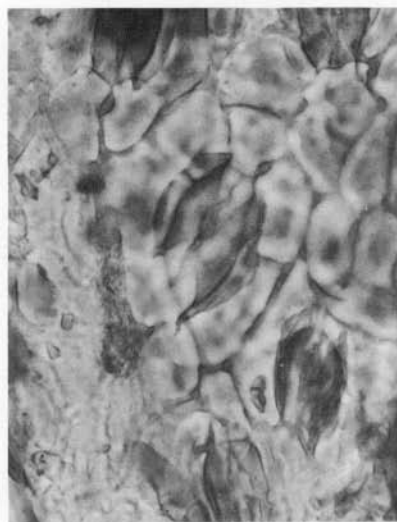


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Plate 3

Fig. 1. Arctopitys capbohemanensis n. sp. showing a stoma; ×400. Slide no. PMO4444-38.

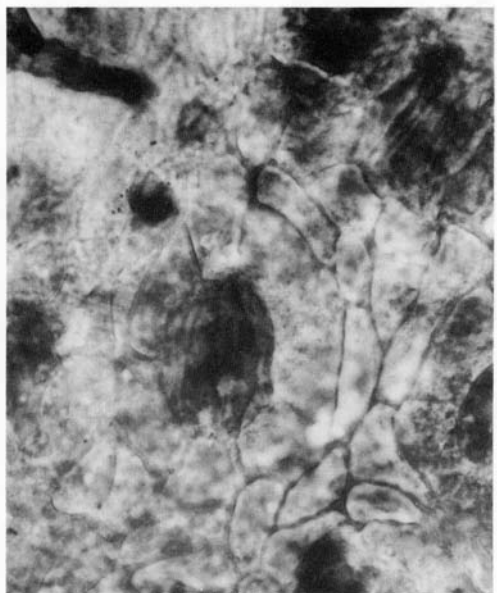
Fig. 2. A. capbohemanensis n. sp. stomata of a short leaf; ×400. Slide no. PMO4444-39.

Fig. 3. A. florinii n. sp. showing a few stomata; ×400. Slide no. GSC6702-31.

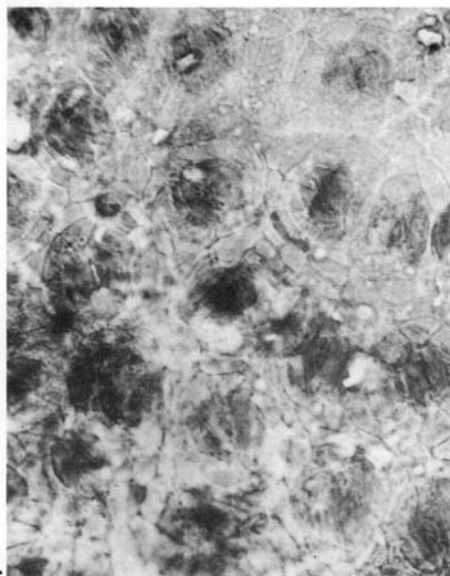
Fig. 4. A. capbohemanensis n. sp. showing distribution of stomata; ×200. Slide no. PMO4444-38.

Fig. 5. A. capbohemanensis n. sp. showing distribution of stomata in a short leaf; ×200. Slide no. PMO4444-39.

Fig. 6. A. ineffecta n. sp. showing distribution of stomata; ×200. Slide no. PMO4444-46.



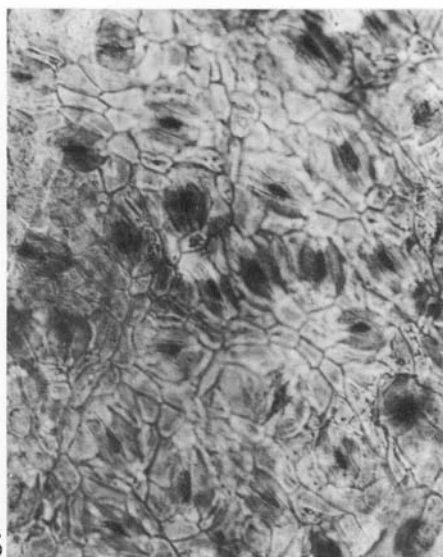
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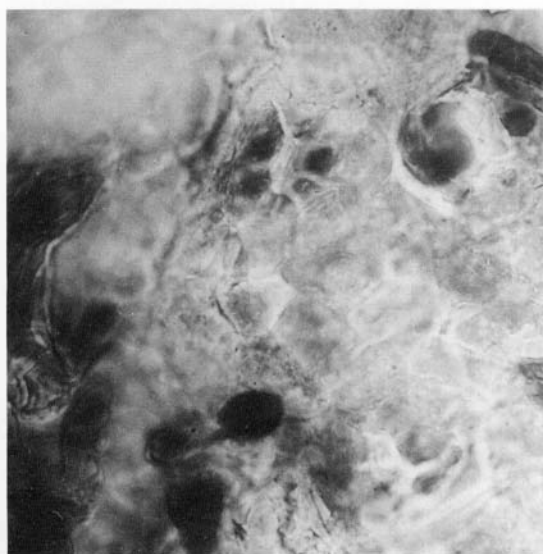
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Plate 4

Fig. 1. Oswaldheeria scotica comb. nov. showing distribution of stomata; $\times 200$. Slide no. S431-1.

Figs. 2–3. Arctopitys florinii n. sp. 2: Distribution of stomata in a short leaf; $\times 200$. 3: Margins of the lower median groove with conical projections; $\times 80$. Slide no. PMO4444-109.

Fig. 4. O. hallei comb. nov., a few stomata of a short leaf; $\times 200$. Slide no. PMO4444-53.

Fig. 5. O. hallei comb. nov. showing orientation of stomata; $\times 200$. Slide no. S20309 (holotype).

Fig. 6. A. ineffecta n. sp. showing a few stomata; $\times 400$. Slide no. PMO4444-42.



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Plate 5

Fig. 1. Oswaldheeria scotica comb. nov. showing a stoma; $\times 400$. Slide no. S20310.

Fig. 2. O. arctica n. sp., a stoma of a short leaf; $\times 400$. Slide no. PMO4444-68.

Fig. 3. O. arctica n. sp., a stoma; $\times 400$. Slide no. PMO4444-110.

Fig. 4. O. scotica comb. nov.; $\times 0.8$. Holotype no. S431.

Fig. 5. O. arctica n. sp. showing orientation of stomata; $\times 200$. Slide no. PMO4444-110.

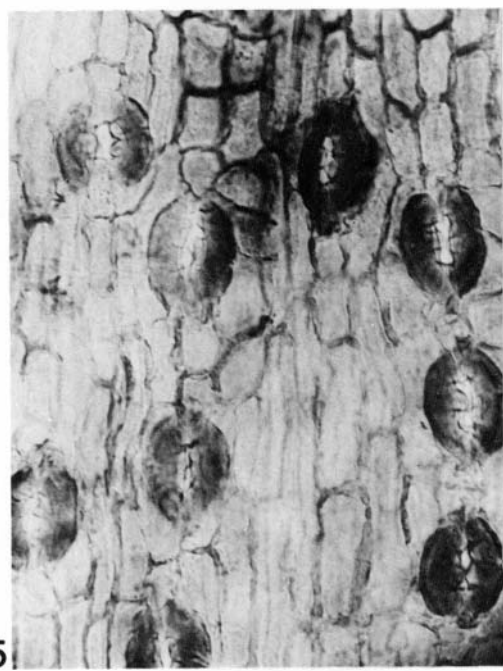
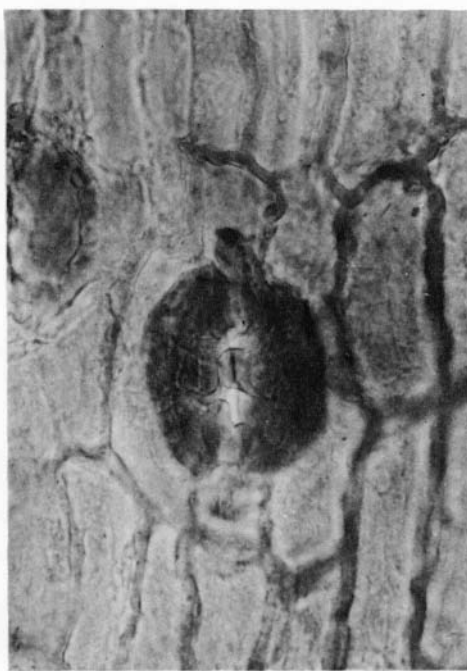


Plate 6

Fig. 1. *Pseudotorellia retusa* n. sp. showing a stoma; $\times 200$. Slide no. PMO4444-93.

Fig. 2. *P. kordylina* n. sp. showing a stoma; $\times 200$. Slide no. PMO4444-81.

Figs. 3-4. *Torreya arctica* n. sp. 3: Stomatal bands; $\times 80$. 4: Two stomata; $\times 400$. Slide no. PMO4444-100.

Figs. 5-7. *Holkopitys hoegii* n. sp. 5: Non-stomatal zones within median groove; $\times 80$. 6: A few stomata; $\times 200$. 7: Enlarged from fig. 6; $\times 400$. Slide no. GSC6702-37.

Fig. 8. *Elaeocladus* sp. A showing a stomatal band; $\times 80$. Slide no. PMO4444-105.

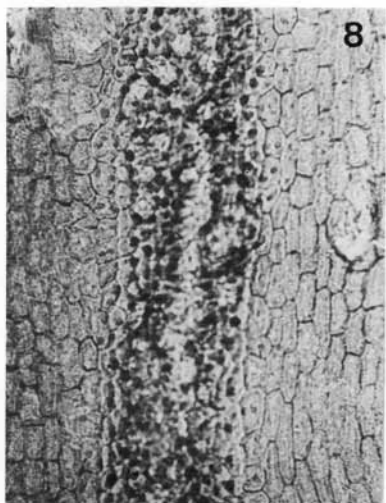
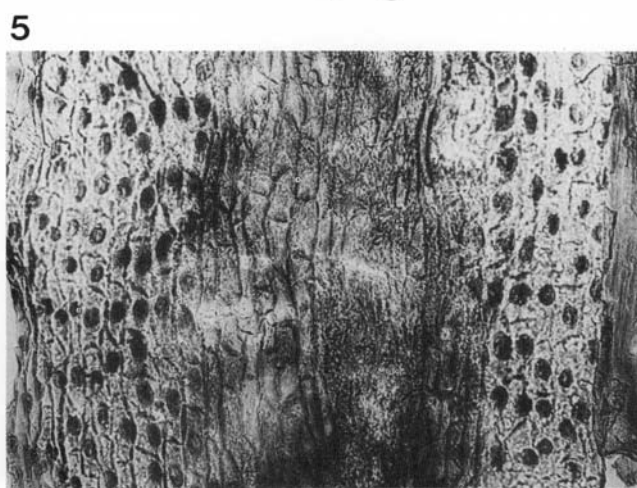
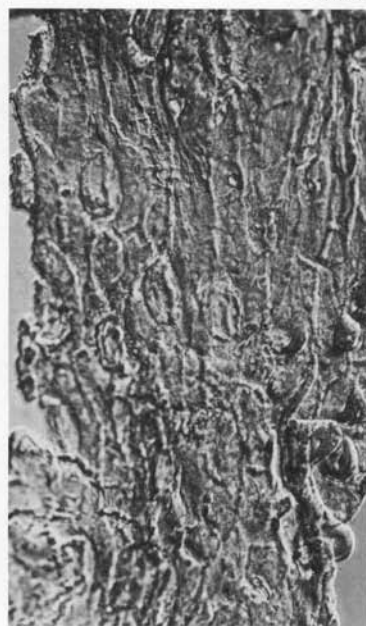
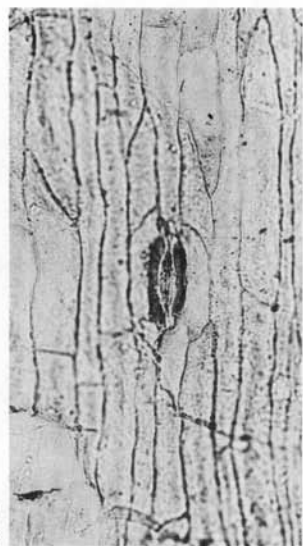
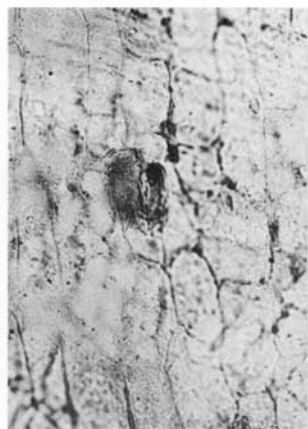


Plate 7

- Figs. 1–2. Marskea fragilis* n. sp. 1: Part of a stomatal band; $\times 200$. 2: A few stomata; $\times 400$. Slide no. PMO4444-98.
Figs. 3–4. Marskea spitsbergensis n. sp. 3: A stomatal band; $\times 200$. 4: Stomata; $\times 400$. Slide no. PMO4444-96.
Fig. 5. Elatocladus sp. A showing stomata; $\times 400$. Slide no. PMO4444-105.
Fig. 6. Elatocladus sp. B showing stomata; $\times 400$. Slide no. PMO4444-107.
Fig. 7. Elatocladus sp. C showing two closely set stomata; $\times 400$. Slide no. PMO4444-108.

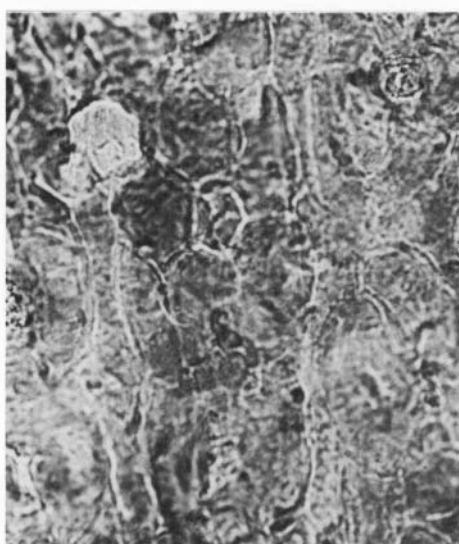
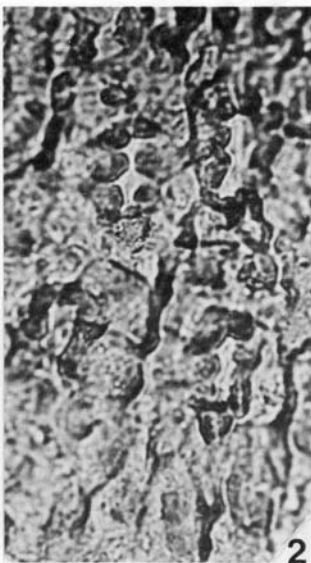


Plate 8

Figs. 1–3. Arctopitys sp. 1.3: Leafy twigs showing horizontally spreading leaves; $\times 3$. 2: A detached leaf showing the median stomatal groove; $\times 9$. Specimen nos. MGUH19457, MGUH19457A-1 (mounted on a slide) and MGUH19458, respectively. All from Slibestensfjeld.

Figs. 4–5. Sciadopityoides microphylla comb. nov. fragmentary leafy twigs showing spirally arranged appressed leaves (?short leaves); $\times 9$. Specimen nos. MGUH19459 and MGUH19460, respectively. Both from Kome.

Fig. 6. Sciadopityoides crameri (Heer) Sveshnikova showing a few dispersed leaves; $\times 1.5$. Holotype no. MMH16848 (Heer 1868, pl. 44, fig. 9).

Figs. 7, 9. Burejospermum Krassilov; $\times 7$. Specimen nos. PMO4444-111 (fig. 7) and PMO4444-112 (fig. 9).

Figs. 8, 10. Dictyothylakos Horst. 8: An almost complete specimen; $\times 7$. 10: A magnified portion from fig. 8; $\times 200$. Specimen no. PMO4444-113.

