Additions to the family Miroviaceae (Coniferae) from the Lower Cretaceous of West Greenland and Germany: *Mirovia groenlandica* n. sp., *Tritaenia crassa* (Seward) comb. nov., and *Tritaenia linkii* Mägdefrau et Rudolph emend.

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The genus *Tritaenia* with its type species *T. linkii* Mägdefrau et Rudolph emend. from the Wealden of Germany has been referred to the family Miroviaceae Bose et Manum, comprising Mesozoic and mostly Arctic conifer foliage with '*Sciadopitys*-like' stomatal distribution. Two other additions to the Miroviaceae, both from the Lower Cretaceous of West Greenland, are *Pityophyllum crassum* Seward, now attributed to *Tritaenia*, and *Mirovia groenlandica* n. sp., described on leafy stems and detached leaves. *Tritaenia* has distinct stomatal bands within the median stomatal zone. This and other stomatal distributions in the Miroviaceae and their implications for the interpretation of leaf venation are discussed with the conclusion that two veins are most likely indicated. Diagnostic characters and stratigraphic and geographic distribution of the presently known miroviaceous taxa are summarized.

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In a recent paper, Bose & Manum (1990) documented a large and distinctive complex of conifer leaves in the Lower Cretaceous of Spitsbergen, West Greenland and Baffin Island. These leaves share the distinctive character of having a median stomatal zone as in the monotypic extant genus *Sciadopitys* Siebold et Zuccarini. Four genera comprising a total of twelve species were recognized from these more or less co-eval Lower Cretaceous leaf-bearing beds of the Arctic. Another seven species previously described from Middle Jurassic to Upper Cretaceous formations elsewhere were also attributed to this complex, for which the family name Arctopityaceae was originally adopted. However, when that paper was at the final stage of printing, it was realized that the type genus *Arctopitys* (Bose & Manum 1990, p. 32) was a junior synonym of *Mirovia* Reymanówna (1985). In an addendum (Bose & Manum 1990, p. 64) the nomenclature was duely rectified and the family Miroviaceae introduced to replace Arctopityaceae.

Mirovia was interpreted by its author as having a ginkgoalean affinity. This interpretation highlighted the problem of interpretation of the venation in the '*Sciadopitys*-like' fossil leaves. This problem has been further emphasized by our recognition of the previously overlooked genus *Tritaenia* Mägdefrau et Rudolph as an additional member of the miroviaceous complex, since the type species of *Tritaenia*, like the type species of *Mirovia*, has stomata in bands within the stomatal zone.

Leafy stems from the Lower Cretaceous of West Greenland, which were briefly mentioned in Bose & Manum (1990, p. 15: *Arctopitys* sp.), are described as a new species of *Mirovia*, and *Pityophyllum crassum* Seward (1926), also from West Greenland, is attributed to *Tritaenia*. The main objectives of this paper are to complete our study of Early Cretaceous members of the Miroviaceae from West Greenland by documenting these additions to the family, and further to discuss the range of stomatal distributions within this group in terms of interpretation of venation. In connection with the revival of *Tritaenia*, the nomenclatural and taxonomic status of its type species, *T. linkii* sensu Mägdefrau et

Rudolph, is discussed, as well as the status of *T. crassa* (Seward) comb. nov. in relation to the taxa *Abietites linkii* (Roemer) Dunker (1846), *Pityophyllum*, and *Pseudotorellia heterophylla* Watson (1969).

All the material for the present study was derived from the Kome Formation of the Nugssuaq peninsula, West Greenland. The geology and stratigraphy of this formation was discussed by Bose & Manum (1990, pp. 10–11). The assemblage described in that paper corroborates the Barremian-Aptian age previously suggested by Rosenkrantz (1970). Two different lithologies and plant assemblages, both labelled 'Kome-lagene' (= the Kome Formation) are present in the collection from the Slibestensfjeld locality (between Ikorfat and Kûk) which is found in the Geological Museum, Copenhagen, and which was particularly studied for the present paper. One of these lithologies and plant assemblages is clearly different from and younger than that which we had described previously (Bose & Manum 1990) from the Kome Formation proper. It comprises a Late Cretaceous to Early Tertiary type of assemblage with angiosperms. This paper deals only with the older of the two which can be correlated with the assemblage which we had described earlier. In the material from Slibestensfjeld we have seen neither leaves nor pollen of angiosperms. The shale pieces show on their surfaces a dominance of *Sciadopityoides nathorstii* (Halle) Sveshnikova along with *Mirovia groenlandica* n. sp. and *Tritaenia crassa* (Fig. 1).

Fig. 1. Typical hand specimen from Slibestensfjeld showing leaf assemblage dominated by *Sciadopityoides nathorstii* (Halle) Sveshnikova (MGUH 20585, ×1).

Fig. 2. Nearly complete leaves of *Sciadopityoides nathorstii* (Halle) Sveshnikova from Slibestensfjeld (MGUH 20586, ×1.5).

Except for two denuded stems from Atanikerdluk, which belong to the Riksmuseum, Stockholm (slide number prefix S), all specimens

figured in this paper are stored in the Geological Museum, Copenhagen (slide number prefix MGUH).

Methods

We have applied the bulk maceration method described by Harris (1926) for isolation of cuticles from shale samples. Treatment with concentrated nitric acid (24 hrs or more) and subsequently alkali was carefully monitored to avoid destruction of the more delicate cuticles. Without this method, which proved extremely rewarding, the present study would not have been possible. It has yielded thousands of cuticles of single leaves and a few stems with and without attached leaves.

Descriptions

Family Miroviaceae Bose et Manum (1990)

Genus *Sciadopityoides* Sveshnikova
1981 *Sciadopityoides* Sveshnikova, p. 1722
1990 *Sciadopityoides* Sveshnikova emend., Bose & Manum, p. 21

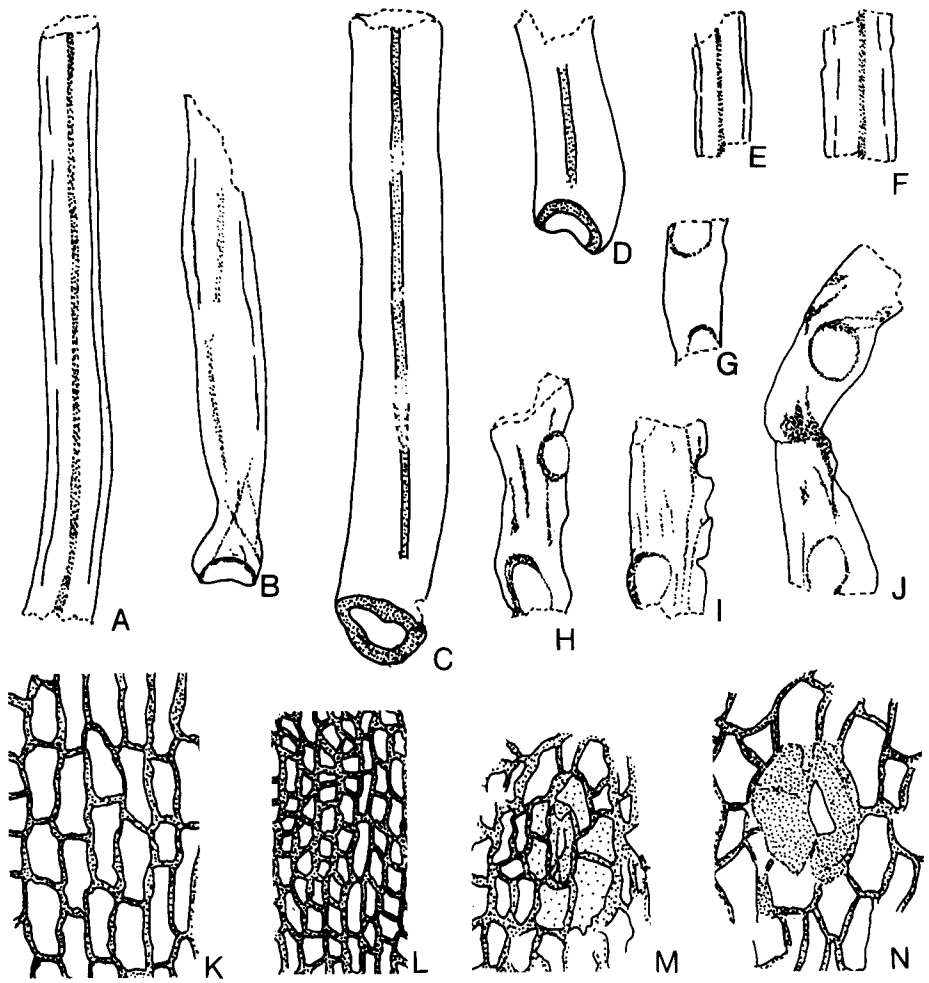


Fig. 3. A-F. *Sciadopityoides nathorstii* (Halle) Sveshnikova. B, D, leaf bases ×4; A, E, F, showing resin ducts, ×4. (Slide nos: A-MGUH 20587-1; B-MGUH 20588-1; C-MGUH 20589-1; D-MGUH 20589-2; E-MGUH 20590-1; F-MGUH 19457-2.) G, J, L, M. Denuded stem type 1. G, J, stem fragments with leaf scars, ×4; L, epidermal cells ×100; M, a stoma ×200. (Slide nos: S 20307, sub-nos: G, L-31: J, M-32). H, I, K, N. Denuded stem type 2. H, I, stem fragments showing leaf scars, ×4; K, epidermal cells ×100; N, a stoma ×200. (Slide nos: H, K-MGUH 20591-1; I, N-MGUH 20591-2).

Sciadopityoides nathorstii (Halle) Sveshnikova
Figs. 2 and 3A-F.
(For synonymy and emendation, see Bose & Manum 1990, p. 28)
The previous records of this species are from the localities Atanikerdluk and Kome. Bose & Manum (1990, pp. 10–11) discussed the stratigraphic position of these records, which is unverified, and considered them on palaeobotanical and palynological evidence to be coeval with the other Lower Cretaceous plant-bearing formations on the Nugssuaq peninsula, including the present record from the Slibestensfjeld locality. In the material from Atanikerdluk, *S. nathorstii* forms a monospecific mat on the shale surfaces. It still dominates at Slibestensfjeld, but there are also two other species (*Mirovia groenlandica* and *Tritaenia crassa*).

The leaves from Slibestensfjeld exceed 6 cm in length and are on the average somewhat wider than those from Atanikerdluk. Like the latter, leaf bases and apices are mostly missing, and leaf bases show a clear hole in the bottom (Fig. 3B-D). The present specimens have cuticles similar to those described previously, except that none of the ordinary cells within the stomatal groove has papillae, while some of the specimens from the type locality have a few papillate cells within the stomatal groove.

Occurrence. – Atanikerdluk, Kome, and Slibestensfjeld, Nugssuaq peninsula, West Greenland.

Genus *Mirovia* Reymanówna
1985 *Mirovia* Reymanówna, p. 4
1990 *Arctopitys* Bose et Manum, p. 32
1990 *Mirovia* Reymanówna emend., Bose & Manum, p. 64

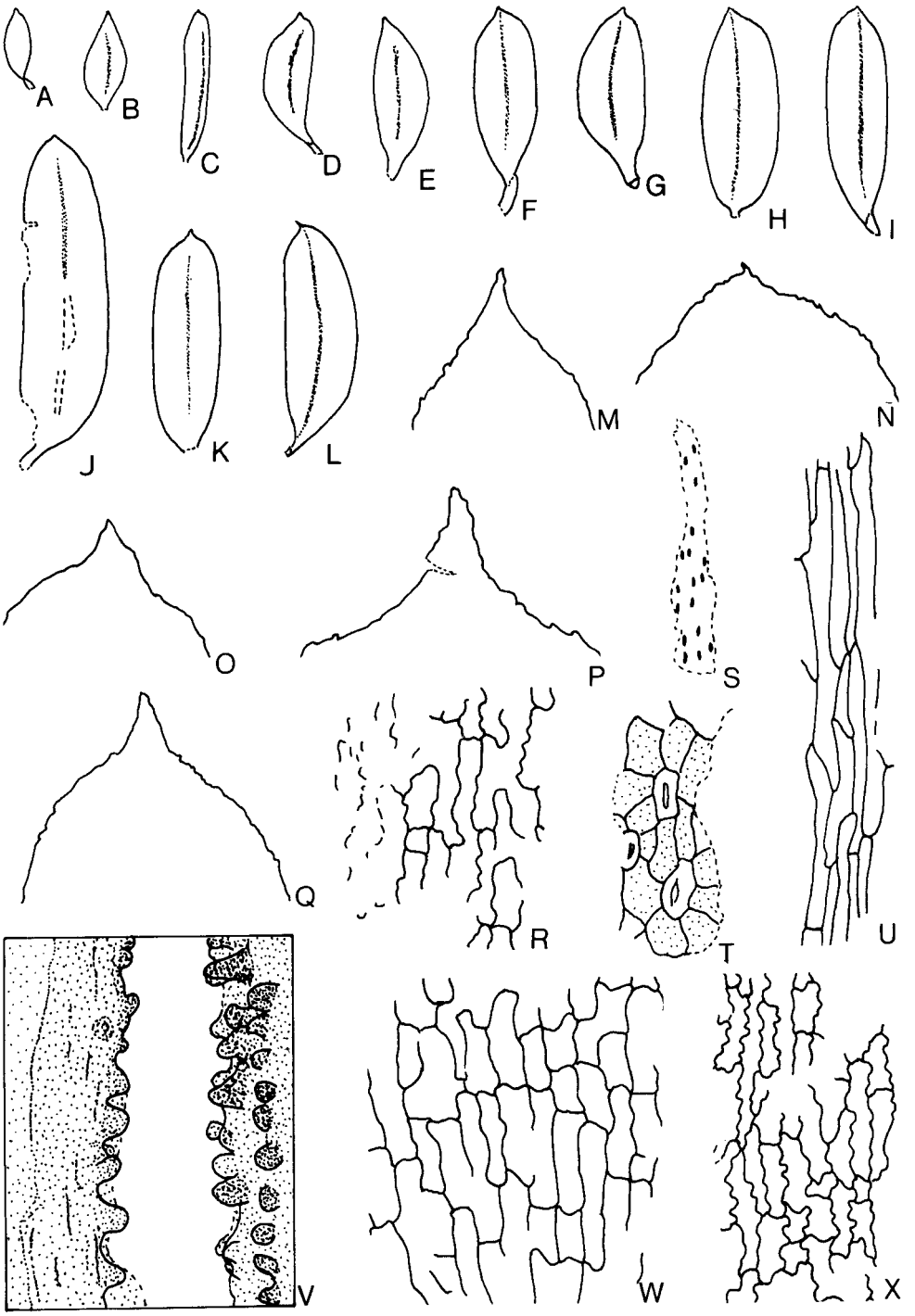
Mirovia groenlandica n. sp.
Figs. 4 and 5A-X
1990 *Arctopitys* sp.: Bose & Manum, p. 15, pl. 8, figs. 1–3

Diagnosis. – Leaves helically arranged and horizontally spreading. Average length 7–10 mm (noted range 3.2–12 mm), width 2–3 mm; base decurrent, twisted; apex acute or apiculate. Margin entire; near apical region mostly denticulate. Abaxial surface of leaf showing a distinct median groove, usually not reaching base and apex.

Except along lower median groove, cuticle of both surfaces of almost same thickness. Cells of

Fig. 4. Mirovia groenlandica n. sp., holotype, ×4.5 (from Bose & Manum, 1990, pl. 8, fig. 1; MGUH 19457).

Fig. 5. Mirovia groenlandica n. sp. A-L, detached leaves – A, ×2, B-L, ×4; M-Q, apices, ×20; R, upper cuticle, ×100; S, stomatal distribution, ×50; T, stomata, ×200; U, marginal cells of lower cuticle, ×100; V, papillae along margin of a stomatal groove, ×100; W-X, lower cuticle showing cells of non-stomatal zones, ×100. (Slide nos: A-MGUH 19457-3; B, T-V, X-MGUH 20591, with sub-nos. B-3, T, V-4, U-5, X-6; C-MGUH 20587-2; D-MGUH 20587-3; E-MGUH 20587-4; F-MGUH 20592-1; G-I, L-O, Q, R-MGUH 20593, with sub-nos. G-1, H-2, I-3, L-4, M-5, N-6, O-7, Q-8, R-9; J, K-MGUH 20588-2/3; P-MGUH 20595-1; S-MGUH 19457-4; W-MGUH 20594-1).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adaxial surface somewhat serially arranged, mostly rectangular, sometimes trapezoidal; anticlinal walls undulate, periclinal wall smooth. Marginal cells (about 5–8 cells wide) much longer than broad, with straight anticlinal walls and smooth periclinal walls. Cells of non-stomatal zones of abaxial surface like those of adaxial surface. Cuticle of median groove slightly thinner than rest of lamina. Margins of groove protruding, often concealing considerable parts of groove; a few rows of cells along margins papillate; papillae conical or cylindrical, towards groove longer. Ordinary cells within groove polygonal, irregularly arranged; anticlinal walls straight, periclinal wall smooth. Stomata irregularly scattered within median groove, sparse, at places closely set, orientation longitudinal, rarely oblique. Subsidiary cells 5–7, rarely 8, non-papillate, sometimes shared between adjacent stomata, polar cells often distinct. Guard cells thinly cutinized, slightly sunken; stomatal aperture narrow, elliptical.

Holotype. – Specimen no. MGUH 19457, Figs. 4 and 5A, S.

Occurrence. – Slibestensfjeld Nugssuaq peninsula, West Greenland.

Remarks. – *Mirovia groenlandica* is the least common among the species from Slibestensfjeld recorded here. Most of the leaves are detached, but quite a few leafy shoots from 1 to 3 cm in length have also been found. In most leaves cells of the upper cuticle and of the lower median groove are obscure, and well-preserved stomata are also difficult to find. Resin ducts could not be detected. These leaves are often heavily infected with microthyriaceous fungal remains, unlike the two associated species dealt with here.

Comparison. – The characteristics of *M. groenlandica* are tabulated along with the previously known species of the genus in Table 1.

Table 1. Comparison of characters among known species of *Mirovia*.

CHARACTER \ TAXON	**Mirovia capbohemanensis** B. & M.	**Mirovia florinii** B. & M.	**Mirovia groenlandica** n.sp.	**Mirovia ineffecta** B. & M.	**Mirovia lagerheimii** (Joh.) B. & M.	**Mirovia persulcata** (Joh.) B. & M.	**Mirovia sibirica** (Sam.) B. & M.	**Mirovia szaferi** (Rm.) B. & M.
Length of leaf (mm)	8-15	7-15	7-10	10-12	10-15	50+	40+	10-14
Resin ducts	+	+	–	+	+	?	?	+
Groove margin papillate	+	+	+	+	–	+	–	?
Stomata orient. longit.		+	+	+		+	+	+
- - transverse	(+)							
- - oblique	+	(+)						
- - non-pref.					+			
Subs. cells papillate	–	+	–	+	+	+	+	–

Genus *Tritaenia* Mägdefrau et Rudolf
1969 *Tritaenia* Mägdefrau et Rudolf, p. 296

Emended diagnosis. – Leaves linear or elliptical; narrowing towards base with constriction slightly above ultimate base, apex obtuse or acute. Abaxial surface having a median stomatal zone with 3 (to 5) stomatal bands converging towards apex; subsidiary cells 4-8. Cuticle of stomatal zone much thinner than on rest of lamina.

Type species. – *Tritaenia linkii* sensu Mägdefrau & Rudolf (1969); *non: Abietites linkii* (Roemer) Dunker (1846). Type specimen of *T. linkii* M. et R.: Mägdefrau & Rudolf's fig. 1 (1969).

Type of Tritaenia: Abietites linkii versus Tritaenia linkii. – *Abietites linkii* was originally described as *Abies linkii* Roemer (1836) from the German Wealden and subsequently transferred to *Abietites* by Dunker (1846). Schenk (1871, pp. 39–40), commenting extensively on this species, found it peculiar and different from any modern conifer in contrast to what had been implied by referring it to *Abietites*, but he explicitly deferred referring it to a new genus until it could be more fully known. Mägdefrau & Rudolf (1969) made a detailed study of purported leaves of *A. linkii* other than the original specimens. Their difference from *Abies* and all other members of the Pinaceae was pointed out. They argued for a non-committal generic name and proposed *Tritaenia*, designating *A. linkii* the type. However, for reasons discussed below, it is doubtful whether *A. linkii* sensu Roemer and *T. linkii* sensu M. et R. are identical. Until and unless this can be proven, we hold them to be different.

The type species of the genus *Abietites* Hisinger (1837, p. 110) is *A. sternbergii* (Nilsson) from the

Rhaeto-Liassic of Scania. This species has a clear mid-vein. Dunker (1846, p. 19, pl. 9, fig. 11), when attributing *Abies linkii* Roemer to *Abietites*, explicitly stated and figured that species as having a distinct mid-vein, too. Unfortunately, the cuticles of the original specimens of *A. sternbergii* and *A. linkii* are not known. Benda (1961), who studied cuticles of purported *A. linkii* on material other than the original, also stated that the leaves had a more or less clear mid-vein, but he did not figure any specimen showing this. Michael (1936) and Mägdefrau & Rudolf (1969), on the other hand, when describing purported *A. linkii* and its cuticle in great detail, mentioned no mid-vein. Thus, whether or not *A. linkii* s. str. has a mid-vein remains to be settled; the original description and figures indicate a mid-vein, but subsequent authors who have studied the cuticles of purported *A. linkii* have not demonstrated a mid-vein. This ambiguity is the reason for the present nomenclatural treatment of *Tritaenia* and *T. linkii*.

We must maintain *Tritaenia* with *T. linkii* sensu Mägdefrau & Rudolf as its type (non: *A. linkii* Roemer sensu Dunker, which has been clearly stated to possess a mid-vein). The diagnosis of *Tritaenia* has been emended accordingly and Mägdefrau & Rudolf's (1969) fig. 1 is designated the type for *T. linkii* M. et R. The major characters of *Tritaenia linkii* sensu Mägdefrau & Rudolf (1969) are: (1) a thinly cutinized median stomatal zone flanked by more cutinized marginal zones, (2) absence of a mid-vein, and (3) the stomatal zone having three (to five) clearly defined stomatal bands. Specimens described below under *T. crassa* (Seward) comb. nov. differ from *T. linkii* only in minor characters separating them at the species level.

Comparison. – Mägdefrau & Rudolf (1969) considered *Tritaenia* to be a conifer without any extant generic or familial similarity. Among extinct groups, it falls naturally within the complex which we have referred to as the Miroviaceae and we regard it as an additional genus of that family. *Tritaenia* combines characters of both *Oswaldheeria* Bose et Manum (1990) and *Sciadopityoides* Sveshnikova emend. Bose et Manum (1990). It resembles most *Oswaldheeria* in having a median, thinly cutinized stomatal zone which is not developed into a groove with overhanging or otherwise clearly marked margins. *Oswaldheeria* differs in having stomata irregularly scattered within the stomatal zone and in having a decurrent leaf base. However, some rare leaves of *O. hallei* and *O. macrophylla* do have stomata arranged in 3–5 bands, but usually the stomata are either irregularly scattered or tend to form discontinuous files, a feature which is known in *Mirovia szaferi* Reymanówna (1985). In its leaf base, *Tritaenia* resembles *Sciadopityoides* Sveshnikova. *T. crassa* has a clear abscission scar. The base in *T. linkii* is also not decurrent, but an abscission scar has still to be ascertained.

Tritaenia crassa (Seward) comb. nov.
Fig. 6.
1926 *Pityophyllum crassum* Seward, p. 106, text-fig. 16
1988 *Pityophyllum crassum* Seward: Watson & Hall, p. 31 (name only)

Diagnosis. – Leaves 1–3 cm long, 2–4 mm wide, linear or elliptical in outline; leaf base twisted, having a clear circular to oval hole in bottom; apex obtuse or acute. Adaxial surface with or without a median furrow, sometimes visible along proximal half only. Abaxial surface with a distinct median zone flanked by more cutinized marginal zones, often thickened lateral margins slightly raised forming a sort of groove. Resin ducts 3–5.

Adaxial surface with cells arranged more or less serially, rectangular or trapezoidal; anticlinal walls thick, straight, periclinal wall smooth. Cells of abaxial surface outside non-stomatal zone similar to those of adaxial surface but more cutinized. Cuticle of stomatal zone much thinner; stomata longitudinally orientated, arranged in 3 bands, very rarely irregularly scattered; median band usually narrower, bands converging towards apex and ultimately often merging with each other. Subsidiary cells 4–6, rarely 7, non-papillate but more cutinized than ordinary epidermal cells, often polar subsidiary cells discernible. Guard cells slightly sunken in an oval pit, fairly well cutinized; aperture elliptical. Within stomatal bands the ordinary cells are rectangular, sometimes polygonal, slightly shorter and broader and less regularly arranged than cells among non-stomatal bands. In marginal non-stomatal zones, cells longer and narrower; anticlinal and periclinal walls same as in stomatal zone.

Lectotype. – Slide no. V. 19021a, The Natural History Museum, London; Seward 1926, text-fig. 16A i.

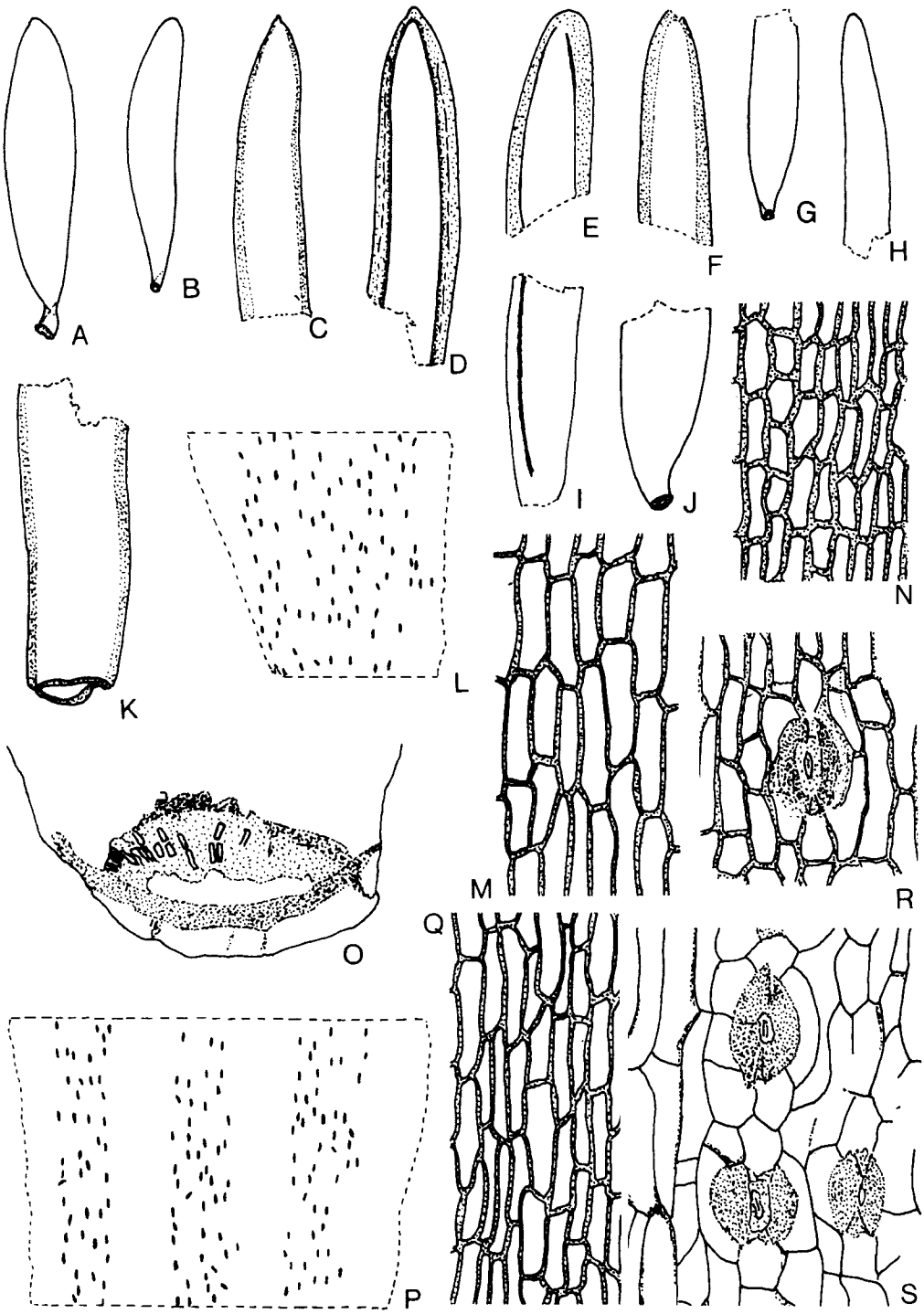

Fig. 6. Tritaenia crassa (Seward) comb. nov. A-K, detached leaves: C-K showing leaf bases and apices, thickened margin stippled-A-F, I-K ×4; G, H × 2; L, showing stomatal distribution in irregular manner, ×20; M, cells of non-stomatal zone on lower surface, ×100; O, base of leaf ×50; P, stomata in bands ×20; Q, marginal cells on lower surface ×100; R-S, stomata ×200. (Slide nos: A, B, J, O, R-MGUH 20593-10/11/12/13/14; C, F-MGUH 20588-4/5; D-MGUH 20589-3; E, G, I-MGUH 20587-5/6/7; H-MGUH 20594-2; K-MGUH 20592-2; L, M+N+Q, P, S-MGUH 20590-2/3/4/5.)

Occurrence. – Slibestensfjeld (incl. Angiarsuit), Nugssuaq peninsula, West Greenland.

Description. – *Tritaenia crassa* is fairly common in the material from Slibestensfjeld, but complete leaves are rare. Bases are slightly twisted or curved and always with a very clearly marked abscission scar like in *Sciadopityoides*; in some leaves the apical portion is slightly curved, but leaf as a whole is not falcate. Quite a few leaves have rather heavily cutinized lateral non-stomatal zones, which delineate a sort of groove, but never like the grooves of *Mirovia* and *Sciadopityoides*. Leaves with irregularly scattered stomata are rare.

Remarks. – The leaves of *Tritaenia crassa* from Slibestensfjeld have all the gross morphological and cuticular characters of *Pityophyllum crassum* described by Seward (1926) from Angiarsuit (this locality also belongs to Slibestensfjeld according to Steenstrup 1883, p. 57). They differ from *T. linkii* sensu Mägdefrau & Rudolf (1969) in lacking paillate subsidiary cells.

Seward compared the lower cuticle of his specimens of *P. crassum* with those of the juvenile leaves and cotyledons of *Sciadopitys verticillata* Siebold et Zuccarini. In juvenile leaves of *S. verticillata* the stomata are in two or three rows and there is no deep groove as in the 'double needles'. In the cotyledons the stomata occur in three to four ill-defined bands, but they are not situated inside a groove. Seward (1926, p. 107) stated: 'In the three forms of cuticle afforded by the different leaves of *Sciadopitys verticillata*, we have, as it were, a résumé of the features exhibited by the cuticular structure of the Greenland species of *Pityophyllum*'. Beyond this resemblance, *T. crassa* and *S. verticillata* are quite distinct. The leaf arrangement in *T. crassa* was most likely helical in a way similar to *Sciadopityoides* as inferred from associated denuded stems (see below: denuded stem type 2) and the type of leaf base. Leaf dimorphism is not known in *T. crassa*.

Watson & Hall (1988) considered *Abietites linkii* (Roemer), *Pityophyllum crassum* Seward and *Pseudotorellia heterophylla* Watson (1969) to be synonymous. The status of *A. linkii* has been discussed above. As for *Pityophyllum*, this name was first used by Nathorst (1897) when he described certain needle-like leaves as *Pinites (Pityophyllum) nordenskiöldi* Heer, *Pinites (Pityophyllum) microphyllum* Heer etc. Later, Nathorst (1899) described a few leaves from Franz Josef Land as *Pityophyllum* cf. *staratschini* Heer and *Pityophyllum* cf. *lindstrømi* Nathorst, but the genus *Pityophyllum* was never properly defined in any of these papers. The species assigned to *Pityophyllum* by Nathorst have a distinct mid-vein, but a mid-vein is lacking in Seward's (1926) specimens as well as in ours of *P. crassum*. We therefore consider *P. crassum* of Seward to be distinct from *Pityophyllum* as well as from *Abietites*, both of which possess a mid-vein. The cuticle of Nathorst's (1897, 1899) original specimens of *Pityophyllum* is not known. As for *Pseudotorellia heterophylla*, this species was commented on by Bose & Manum (1990). It has from two to eight dichotomizing veins which converge near the apex but end blindly. Like other species of *Pseudotorellia, P. heterophylla* has ordinary cells with a thickened ridge along the surface. *T. crassa* does not have such ridges. Moreover, the subsidiary cells in *P. heterophylla* are usually papillate, whereas in *T. crassa* they are non-papillate. Because of these differences we consider *P. heterophylla* to be quite distinct from *T. crassa*.

Denuded stems

Type 1 (Fig. 3G, J, L, M). – Associated with the leaf mats of *S. nathorstii* from Atanikerdluk we have found two fragmentary denuded stems, both showing spirally arranged leaf scars. The larger piece is 1.2 cm long and about 2 mm wide. Overall cuticular features of these stems match the leaves in *S. nathorstii*.

Type 2 (Fig. 3H, I, K, N). – Associated with *S. nathorstii, M. groenlandica*, and *T. crassa* in the material from Slibestensfjeld were a few stems. These have cuticular features which are different from type 1 and resemble more *T. crassa*.

Concluding remarks

The family Miroviaceae is as yet known from foliage only; reproductive structures are unknown. The main and distinctive feature shared by all the taxa in this complex is a median, thinly-cutinized stomatal groove or zone, as in the extant genus *Sciadopitys*. Leaf dimorphism is documented in many species, but unlike *Sciadopitys*, where the dimorphism involves size as well as distribution of stomata, dimorphism in the Miroviaceae involves size only. Some species in three of the five genera also have a median furrow

in the upper surface similar to *Sciadopitys*. The distribution of the most distinctive characters in known taxa is summarized in Table 2.

Mirovia was assigned a ginkgoalean affinity by its author, who especially compared the type species, *M. szaferi* Reymanówna (1985), with *Pseudotorellia*. But *Mirovia* is quite distinct from *Pseudotorellia* or any other ginkgoalean genus in having a median stomatal zone well-protected in a groove with overhanging margins. Moreover, dichotomizing veins, a distinctive character in ginkgoalean leaves, cannot be demonstrated in *Mirovia*. *Mirovia* also lacks the cutinized ridges usually present on the surfaces of ordinary epidermal cells in *Pseudotorellia*. Within the stomatal zone, *Mirovia szaferi* has stomata in

Table 2. Main characters and stratigraphic and geographic occurrences of known taxa of the Miroviaceae; data from Manum (1987), Bose & Manum (1990), Manum et al. (1991), and the present study. Abbreviations of authors' names: B. & M.: Bose & Manum (1990); Dol.: Doludenko (1963); Dor. & Sv.: Dorofeev & Sveshnikova (1959); Fl.: Florin (1922); Hl.: Halle (1915); Hr.: Heer (1868, 1876); Joh.: Johansson (1920); Rm.: Reymanówna (1985); Sam.: Samylina (1963); Sew.: Seward (1926); Sv.: Sveshnikova (1981).

CHARACTERS \ TAXON	**Mirovia capbohemanensis** B. & M.	**M. florinii** B. & M.	**M. groenlandica** n.sp.	**M. ineffecta** B. & M.	**M. lagerheimii** (Joh.) B. & M.	**M. persulcata** (Joh.) B. & M.	**M. sibirica** (Sam.) B. & M.	**M. szaferi** (Rm.) B. & M.	**Oswaldheeria arctica** B. & M.	**O. hallei** (FL.) B. & M.	**O. macrophylla** (Fl.) B. & M.	**O. scotica** (Fl.) B. & M.	**Holkopitys hoegii** B. & M.	**Tritaenia crassa** (Sew.) comb.nov.	**T. linkii** sensu M. & R.	**Sciadopityoides crameri** (Hr.) Sv.	**S. ikorfatensis** B. & M.	**S. microphylla** (Hr.) B. & M.	**S. nathorstii** (Hl.) Sv.	**S. ukrainensis** (Dol.) Sv.	**S. uralensis** (Dor. & Sv.) Sv.	**S. variabilis** (B.) Sv.
Decurrent leaf base	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	·	·	·	·	·	·	·
Hole in bottom of leaf	·	·	·	·	·	·	·	·	·	·	·	·	·	+	?	+	+	+	+	+	+	+
Stomatal zone in groove	+	+	+	+	+	+	+	+	·	·	·	·	+	·	·	+	+	+	+	+	+	+
Stomatal zone not in groove	·	·	·	·	·	·	·	·	+	+	+	+	·	+	+	·	·	·	·	·	·	·
Stomata irregularly arranged	+	+	+	+	+	+	+	·	+	+	+	+	·	·	·	+	+	+	+	+	+	+
Stomata in files or bands	·	·	·	·	·	·	·	+	·	(+)	(+)	·	+	+	+	·	·	·	·	·	·	(+)
Furrow in upper surface	–	–	–	–	+	?	?	+	+	+	+	–	–	–	–	+	–	+	–	?	?	–
Leaf dimorphism documented	+	+	·	+	·	·	·	·	+	+	·	·	·	·	·	+	+	+	·	·	·	·
Stems, denuded (D) or leafy (L)			L							D				D		D		L	D			
OCCURRENCES																						
Cretaceous Up. — U.S.S.R.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Cretaceous Lower — West Greenland	·	·	+	·	·	·	·	·	·	+	·	·	·	+	·	+	+	+	+	·	·	·
Cretaceous Lower — Baffin Island	·	·	·	+	·	·	·	·	+	+	·	·	+	·	·	·	·	+	·	·	·	+
Cretaceous Lower — Spitsbergen	+	+	·	+	·	·	·	·	+	+	·	·	+	·	·	·	·	+	·	·	·	·
Cretaceous Lower — Germany	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·
Cretaceous Lower — U.S.S.R.	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Jurassic Upper — N. Norway	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Jurassic Upper — Scotland	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Jurassic Middle — U.S.S.R.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·
Jurassic Middle — Poland	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Jurassic Middle — N. Norway	·	·	·	·	·	·	·	·	·	(cf.)	+	·	·	·	·	·	·	·	·	·	·	·

discontinuous files, but this is not a specifically ginkgoalean character. On the other hand, *Mirovia szaferi* shows all the characters distinctive of the genus which we had originally named *Arctopitys* and subsequently realized to be a junior synonym of *Mirovia* (Bose & Manum 1990, pp. 32, 64). This genus has spirally attached and horizontally spreading leaves as documented in the leafy shoots of *M. groenlandica* and inferred from bases of detached leaves. These characters clearly indicate a coniferous affinity.

The members of the Miroviaceae seemingly resemble the extant *Sciadopitys* in the distribution of stomata and the presence in many species of a furrow in the upper side of the leaves. Evidence from denuded stems, leafy twigs, and the character of the leaf bases in detached leaves confirms that none of the taxa had their leaves in verticillate arrangement. There is no evidence which suggests that small leaves (scale leaves) subtended large leaves (needles) as in the extant species.

The two-veined leaves in *S. verticillata* have been interpreted as symphyllodes (double needles, see Bose & Manum 1990, pp. 12–18). Venation has not been observed directly in any member of the Miroviaceae and can only be inferred from the stomatal distribution. Stomatal zones or bands are as a rule interpreted as intervenal, since stomata concentrations avoid veins. A good example is provided by *S. verticillata* (Fig. 7). The two-veined needles have a distinct intervenal stomatal zone, while the single-veined scale leaves have two stomatal zones which avoid the poorly developed mid-vein, as shown by Bose & Manum (1990, fig. 6).

Members of the Miroviaceae all have a well-developed median stomatal zone which strongly indicates two veins (Fig. 7, alternative I). The median furrow in the upper epidermis in some species, as in the two-veined *Sciadopitys*, is also noteworthy and suggestive of a dual venation. In *Holkopitys* and *Tritaenia*, and in rare leaves of *Sciadopityoides variabilis*, *Oswaldheeria hallei* and *O. macrophylla*, the stomata are arranged in bands within the stomatal zone. If these bands were to be interpreted as intervenal, then the venation in these taxa would be as indicated in Figure 7, alternative II. The number of veins would also vary since the number of stomatal bands is not constant within the species. We consider it unlikely that the banded arrangement of stomata within the stomatal zone in these taxa in any way reflects the courses of veins. In conclusion, we consider it most likely that the leaves had two veins (Fig. 7, I). As stated earlier (Bose & Manum 1990), the Miroviaceae represents an important group of conifers in high latitudes of the northern hemisphere in the Early Cretaceous. The family as a whole is known from the Middle Jurassic to the Late Cretaceous (Table 2). It is to be hoped that fertile organs of this group of conifers will soon turn up so that their affinities can be better known.

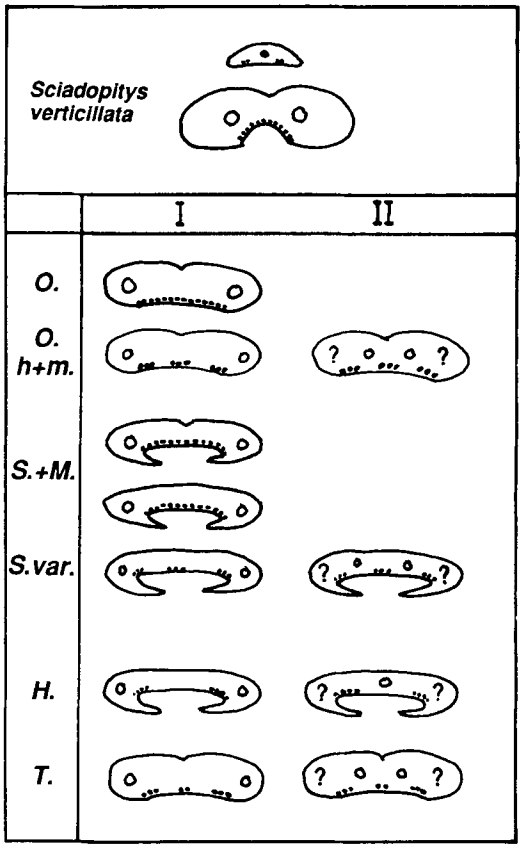

Fig. 7. Venation in *Sciadopitys verticillata* and miroviaceous taxa. Idealised cross-sections (alternatives I and II), stomatal distribution (dots) and possible venation (rings, ?) compared with scale leaf and double-needle in *Sciadopitys verticillata*. – O.: *Oswaldheeria*; O.h+m.: *O. hallei* and *O. macrophylla*, rare leaves; S. + M.: *Sciadopityoides* and *Mirovia*; S. var.: *S. variabilis*, rare leaves; H.: *Holkopitys*; T.: *Tritaenia*.

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