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The Upper Triassic flora of Svalbard

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The Triassic plant fossils from the Svalbard archipelago are comprehensively reviewed. The poorly known flora is widespread and has been recovered from all Triassic exposures in the archipelago; 24 species are identified and one new species, viz. *Arberophyllum substrictum*, is described. The flora consists of sphenophytes, ferns, cycadophytes, and putative ginkgophytes and seed ferns. Ferns and Bennettitales are the dominant elements. The composition of the flora is strikingly similar to the Carnian flora of Lunz in Lower Austria, sharing an unexpectedly large number of taxa, and thus, it is proposed that most of the fossils derive from the De Geerdalen Formation, which is dated as Carnian. Key taxa in the Svalbard flora are *Asterotheca*, *Neocalamites*, *Pterophyllum*, and *Arberophyllum*. The floristic composition and sedimentology of the host strata suggests that the flora thrived in a coastal lagoonal/deltaic environment. The similarity of the Svalbard and Lunz floras argues that the North Atlantic floral sub-province hypothesised for the Rhaetian in this region was already established by the Carnian.

Key words: Bennettitales, *Asterotheca*, *Neocalamites*, *Pterophyllum*, *Paratatarina*, Carnian, Triassic, Lunz, Svalbard, Spitsbergen.

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Introduction

The Svalbard archipelago was subject to intensive geographical and geological studies during the late 19th and early 20th centuries, when several scholars travelled there for scientific exploration, mapping and prospecting for coal and mineral resources (Nathorst 1900). In Svalbard, Triassic strata are mainly exposed in the southern and eastern part of the archipelago (Fig. 1), and are well-known for their coal deposits. The coal has been mined for several centuries on Svalbard, mostly by Swedish and Russian companies, and this has encouraged economic and scientific interest in other aspects of the archipelago. Amongst the interested parties were geologists looking not only for natural resources but also collecting a vast amount of fossils from throughout the archipelago (see Nathorst 1900). Most plant fossils collected from Svalbard come from strata now known to be Cretaceous and younger. Some units previously interpreted as Jurassic (Heer 1876a; Nathorst 1897) have more recently been assigned younger (Cretaceous) ages (cf. Harland 1997a). A few publications on these floras derived from the early exploration of the archipelago and contributed to our knowledge of high latitude floras and temporal diversification in the Cretaceous and Paleogene periods (Heer 1874, 1876a, b; Nathorst 1897). However, only few palaeobotanical studies have been carried

out in more recent times (Vasilevskaya 1972, 1983, 1987; Dobruskina 1994; Strullu-Derrien et al. 2012).

Besides these Cretaceous/Cenozoic fossils, a small number of Triassic fossils were collected during the early exploration of the archipelago and in the 1960–70s. The latter material is stored in the collections of the A.P. Karpinsky Russian Geological Research Institute (VSEGEI) in St. Petersburg and has been described in Russian (Vasilevskaya 1972, 1983). However, these Russian publications were never widely distributed and, thus, not usually considered except by Russian palaeobotanists (Dobruskina 1994). The material stored in the Swedish Museum of Natural History (NRM) in Stockholm has never been subject to any previous study except for some permineralised axes and megaspores from Hopen (Selling 1944, 1945; Strullu-Derrien et al. 2012). A recent inventory of the NRM collections from the Arctic region revealed additional, almost forgotten, material, which was then included in the present study. In the original studies of the Russian material, Vasilevskaya (1972, 1983) was able to isolate cuticles. Attempts to prepare cuticles from the NRM specimens were unsuccessful; only very small fragments of badly preserved cuticle could be obtained, which could only be used to verify or reject hypotheses.

The central aim of this study is to assess whether the same species occur in the two geographically distant floras of Svalbard and Lunz or not. In addition, the plant fossils may



Fig. 1. Map of Svalbard with exposure of Carnian strata and NRM and VSEGEI localities; after the geological maps of Svalbard 1:100 000 provided by the Norwegian Polar Institute, Tromsø. Locality names are depicted in Table 1.

assist stratigraphic correlations during forthcoming geological mapping of eastern Svalbard (e.g., Edgeøya, Barentsøya), and help to interpret the floristic diversity and plant distribution during the Carnian in central Laurasia. In addition, ecological interpretations of the flora may provide insights into climatic and ecosystem reconstructions of landscapes and reveal evolutionary and dispersal patterns such as the

establishment of high-latitude refugia (e.g., McLoughlin et al. 2008, 2011).

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden; VSEGEI, A.P. Karpinsky Russian Geological Research Institute, St. Petersburg, Russian Federation.

Material and methods

Two hundred and forty five specimens have been considered in this study, whereof 227 yielded identifiable plant fossils. One hundred and forty seven are housed in NRM and 98 specimens are stored in the collections of VSEGEI. In addition, 25 specimens, reported by Vasilevskaya (1983) from an unidentified repository, were assessed from that author's descriptions and illustrations of these.

All studied fossils derive from the Svalbard archipelago and were collected on several expeditions from a total of 27 localities on the islands of Spitsbergen, Barentsøya, Edgeøya, and Hopen (Fig. 1). Since most of the material was collected more than a hundred years ago, determination of the source localities involved intensive studies of old and recent maps and excursion reports, because the naming of places on Svalbard underwent several major changes up to 1875, when Adolf E. Nordenskiöld attempted to clarify the geographic nomenclature (Nordenskiöld 1875). The most complete maps of Svalbard were published around 1923 (e.g., De Geer 1923), which was after most of the material under study here was collected. Here, modern names of the places are used following Hjelle (1970) and the Norsk Polarinstitutt (2003), and thus may differ from the names given on labels and in older publications (Table 1).

Specimens at NRM.—The collections at NRM hold 147 specimens, of which four are large rock slabs lacking any plant fossil. These have been excluded from the study. The remaining 143 specimens were collected on different expeditions of Swedish, Russian, and Monacan explorers between 1898 and 1916 during the geographical and geological exploration and field mapping of the Svalbard archipelago. The specimens have been collected at ten localities on Spitsbergen, Edgeøya, and Hopen (Fig. 1, Table 1) from strata assigned to the Upper Triassic based on information derived from geological maps and information accompanying specimens (see below). On 13 specimens, the fragmentary plant remains were unidentifiable, and one specimen was lacking. Additional 913 specimens were collected from Lower Cretaceous strata but they will be described in a separate paper.

Specimens at VSEGEI.—The 98 specimens come from Upper Triassic strata at eleven localities on Spitsbergen, Edgeøya, and Barentsøya (Fig. 1, Table 1). They were collected by Nina D. Vasilevskaya between 1962 and 1966 and most of this material has been published by Vasilevskaya (1972). Subsequently, a few brief accounts were published on additional material from the Russian expeditions, but were similarly poorly circulated (e.g., Vasilevskaya 1983). The 25 specimens investigated in Vasilevskaya's (1983) publication were studied for purposes of this report by using the illustrations and descriptions in that publication only (three of the specimens were not illustrated). The repository of most of this material remains unknown; however, two specimens were later incidentally identified among the collection studied

at VSEGEI. This suggests that the remainder may be stored in VSEGEI, but are misplaced in their collections; the specimens consequently have been marked '?VSEGEI' below. These specimens were collected on Hopen between 1966 and 1974 by various Russian collectors at six localities (Fig. 1, Table 1; Vasilevskaya 1983).

Photography.—Hand specimens were photographed in St. Petersburg and Stockholm using a NIKON D80 system camera with incident light from various angles to accentuate venation details. Polarising filters on camera lenses and light sources were used to enhance contrast.

Cuticles.—Very few of the NRM specimens bore organic material. Samples of these were processed in an attempt to extract cuticles. This was only successful in very few cases since the material is very old, was poorly stored over many years and, in several cases, is strongly oxidised, or the cuticles were just too thin and brittle to be properly isolated from the rock matrix. Cuticles were processed according to the standard procedure outlined by Pott and Kerp (2008) and Pott and McLoughlin (2009). Sediment was removed with c. 30% hydrofluoric acid (HF); cuticles were subsequently macerated in Schulze's reagent (30% HNO₃ with a few crystals of KClO₄) and coal remains were removed with 5% potassium hydroxide (KOH). Cuticles were dehydrated in glycerine and then mounted on permanent microscopic slides in Kaiser's glycerine jelly. All slides are stored in the palaeobotanical collections of the NRM. Sampling the VSEGEI specimens was not allowed by the authorities.

Geological setting

The Triassic strata are coal-rich and exposed mainly in the southern and eastern parts of the Svalbard archipelago (Fig. 1). Comparison of locality information from fossil labels and expedition reports with high resolution geological maps from Svalbard, provided by the Norsk Polarinstitutt, Tromsø, Norway, revealed that all the fossils under study most likely were derived from the De Geerdalen or Bravaisberget formations of the Kapp Toscana Group. Only in Fleur de Lyshamna and Midterhukfjellet on southern Spitsbergen (Fig. 1), it cannot be ruled out that some fossils may have been collected from the slightly older Sassendalen Group. The geology of Svalbard has been described in detail by Smith et al. (1975), Harland (1997b), and Dallmann (1999). All successions of the Kapp Toscana Group on Svalbard overlie the Sassendalen Group (Harland 1997c; Dallmann et al. 2001; Mørk et al. 2013). The Kapp Toscana Group is usually divided into the Tschermakfjellet Formation and the overlying De Geerdalen Formation. Both are assigned a Carnian age (e.g., Tozer and Parker 1968; Dobruskina 1994; Dallmann et al. 2001; Hounslow et al. 2007; Vigran et al. 2014), although the De Geerdalen Formation extends into the Norian (Dypvik et al. 1985). The latter is overlain by the Norian–Rhaetian Wil-

Table 1. Synopsis of place names, stratigraphy, age and collection details of the Svalbard fossil localities considered in the text. *Vasilevskaya (1987) described additional specimens collected in 1981 by Korchinski from the De Geerdalen Fm. at Flowerdalen at Botnehet Mountain at Sassenfjorden, which were not available for study and therefore are not included in this synopsis.

Island	Number on map (Fig. 1)	Modern locality name	Landscape area	Place names on old labels	Stratigraphy		Published	Collector	Year of collection	Specimens
Spitsbergen	1	Bertilryggen	Oscar II Land	Bertil's berg	Kapp Toscana Group	Upper Triassic–Late Jurassic	De Geerdalen and Wilhelmsøya Fm.	Högbom	1910	15
	2	Amadeusberget	Olav V Land	Kamelen			undiff. Fm.	De Geer	1899	2
	3	Edlundfjellet	Olav V Land	Edlunds berg			undiff. Fm.	De Geer	1899/1929	3
	4	Sassenfjorden*	Nordenskiöld Land	Sassen Bay/Advent Bay	Kapp Toscana or Sassenfjorden Group	Upper Triassic–Late Jurassic or Upper–Middle Triassic	De Geerdalen Fm. (most likely)	De Geer	1896	8
	5	Sassenfjorden/Trehøgden	Nordenskiöld Land	Sassenfjorden/Isfjorden			De Geerdalen Fm. (most likely)	unknown	1916	5
	6	Midterhukfjellet	Nathorst Land	Midterhuk/Belsund			De Geerdalen or Bravaisberget Fm.	Nathorst Polar Expedition 1898	1898	2
	7	Fleur de Lyshamna	Wedel Jarlsberg Land	Hvitfiskbukten, Van Keulen Bay	Kapp Toscana Group	Upper Triassic–Late Jurassic	De Geerdalen or Bravaisberget Fm.	Nathorst/Anderson, Polar Expedition 1898	1898	44
	11	Wimafjellet	Nordenskiöld Land				De Geerdalen Fm.	Vasilevskaya	1962	26
	12	Wichebukta	Sabine Land				undiff. Fm.	Vasilevskaya	1966	3
	13	Teistberget	Sabine Land		Kapp Toscana Group	Upper Triassic–Late Jurassic	undiff. Fm.	Vasilevskaya	1962	5
	14	Agardhbukta	Sabine Land				De Geerdalen Fm.	Vasilevskaya	1966	2
	15	Hymefjellet	Torrell Land				undiff. Fm.	Vasilevskaya	1965	25
Barentsøya	16	Vossebukta	Barentsøya		Kapp Toscana Group (same as Edlundfjellet/Wichebukta)	Upper Triassic–Late Jurassic	undiff. Fm.	Vasilevskaya	1963	6
	17	Schweinfurthberget	Barentsøya				Vasilevskaya 1972	Vasilevskaya	1963	4
	8	Kapp Lee	Edgeøya	Cap Lee			Vasilevskaya 1972	Russian expedition/De Geer	1899	54
	9	Kvalpynten	Edgeøya	Whales Point				Russian expedition/De Geer	1899–1901	3
	18/19	Kapp Pechuel Lösch/Lindemanberget	Edgeøya				Vasilevskaya 1972	Vasilevskaya	1962	7
	20	Kapp Lee	Edgeøya				Vasilevskaya 1972	Vasilevskaya	1962	17
	21	Negerpynten	Edgeøya				Vasilevskaya 1972	Vasilevskaya	1962	3
	10	Nørdstefjellet	Hopen				part in Høeg 1926	Prince Albert I. of Monaco	1899	11
	22	Lyngfjellet	Hopen				Vasilevskaya 1983	Korchinski	1974	1
	23	Blåfjell	Hopen				Vasilevskaya 1983	Korchinski	1974	2
Hopen	24	Kollerfjellet	Hopen		Kapp Toscana Group (same as Edlundfjellet/Wichebukta)	Upper Triassic–Late Jurassic	Vasilevskaya 1983	Pchelina/Korchinski	1971	13
	25	Husdalen	Hopen	Hopen Radio			Vasilevskaya 1983	Mirachov	1966/1972	1
	26	Werenskiöldfjellet	Hopen				Vasilevskaya 1983	Pchelina/Korchinski	1971	6
	27	Iversenfjellet	Hopen				Vasilevskaya 1983	Pchelina/Korchinski	1971	2

helmøya Subgroup (Smith 1975; Dypvik et al. 1985; Mørk et al. 1999; Hounslow et al. 2007). In some parts of Svalbard, the Kapp Toscana Group is not differentiated into constituent formations (cf. Dallmann et al. 2001; Hounslow et al. 2007). The plant fossils occur in two beds of the De Geerdalen Formation, layers dated as of late Carnian age based on palynology (Vigran et al. 2014), but possibly extending into the Norian (Dobruskina 1994). The correlated age agrees with an early Norian age for the overlying Flatsalen Formation as suggested by Korčinskaja (1982) based on ammonoids and bivalves. According to Dallmann et al. (2001), the grey shale, siltstone and sandstone beds of the Kapp Toscana Group were deposited in near-shore, deltaic environments (locally lagoonal) and are characterised by shallow marine and coastal fluvio-deltaic sediments.

A Carnian (Late Triassic) age for the fossiliferous strata on Edgeøya and Barentsøya is favoured based on dating of likely correlative strata (the De Geerdalen Formation) in central Spitsbergen (Mørk et al. 1999, 2013; Dallmann et al. 2001; Hounslow et al. 2007; Krajewski 2008). This age is also well-supported by the plant fossils described here.

The NRM fossils from Hopen were collected by Prince Albert I of Monaco. According to logbook entries of his ship, the group landed at 9:50 in the morning of 1st August 1898, on the northern tip of Hopen (76°44' N, 23°30' E, based on the Paris meridian). Correspondence between the Prince and Alfred G. Nathorst, who was at that time head of the Palaeobotanical Department of the Swedish Museum of Natural History, dating from 1898/1899, revealed that the material was sent to him for study and for his opinion on the age of the rocks of Hopen (correspondence kindly provided by Jacqueline Carpine-Lancre, personal communication 2012; see also Carpine-Lancre and Barr 2008). The fossils were most likely collected on the beach according to the logbook 973 entry by Jules Richard (which reads “10h am–3h pm: Hope Island: different objects have been collected, ...”; Jacqueline Carpine-Lancre, personal communication 2012). Although Nathorst favoured a Jurassic age for the fossils (Albert I of Monaco 1899), Hopen is known to consist entirely of Upper Triassic (Carnian and Norian) rocks and the exposed succession comprises mostly claystone and sandstone beds of the De Geerdalen Formation (Smith et al. 1975; Mørk et al. 1999, 2013; Riis et al. 2008; Strullu-Derrien et al. 2012). Three specimens of the material belonging to the Prince Albert I of Monaco have been illustrated in a short note within an expedition report by Høeg (1926).

Systematic palaeontology

General remark.—For conciseness, synonymies or reference lists and generic descriptions have been kept as short as possible or omitted and only essential information has been included such as original descriptions, major changes in synonymy, works dealing with specimens from Svalbard and one or two very recent studies with detailed information

about the respective taxa including excellent figures enabling definitive identification. Since attempts to extract cuticles were virtually unsuccessful, descriptions, if given, follow Vasilevskaya (1972, 1983). Geographic and stratigraphic ranges are representing typical occurrence.

Pteridophyta

Order Equisetales de Candolle ex Berchtold and Presl, 1820

Family Equisetaceae Michaux ex de Candolle, 1804

Genus *Neocalamites* Halle, 1908

Type species: Neocalamites lehmannianus (Göppert, 1845) Weber, 1968 (see Pott and McLoughlin 2011); from the Rhaetian of Wilmsdorf, Landsberg, Silesia (today Gorzów Śląski, Poland).

Neocalamites merianii (Brongniart, 1828b) Halle, 1908

Fig. 2A–I.

1828 *Equisetum merianii*; Brongniart 1828b: 115, pl. 12: 13.

1908 *Neocalamites merianii* (Brongn.); Halle 1908: 6.

1926 Equisetaceous stems; Høeg 1926: 33, pl. 9: b3, 4.

1972 *Neocalamites merianii* (Brongn.) Halle; Vasilevskaya 1972: 32, pl. 1: 1–3.

1972 *Neocalamites* cf. *merianii* (Brongn.) Halle; Vasilevskaya 1972: 33, pl. 1: 4, 5, 8.

1972 *Neocalamites* sp.; Vasilevskaya 1972: 34, pl. 2: 1.

1983 *Neocalamites* sp.; Vasilevskaya 1983: 143, pl. 1: 1.

2008 *Neocalamites merianii* (Brongniart 1828) Halle 1908; Pott et al. 2008a: 188, pls. 3: 1–4; 4: 1–5.

Material.—Spitsbergen: Bertilryggen (NRM S080244–S080246, S080248–S080251, S080254, S080256, S080258); Fleur de Lyshamna (NRM S080071, S080072, S080088, S080105); Wimanfjellet (VSEGEI 10979-01, 10979-02); Trehøgden (NRM S151678, S151679); Teistberget (VSEGEI 10979-03, 10979-07); Amadeusberget (NRM S080259, S080260); Edlundfjellet (NRM S080261, S080262). Edgeøya: Kapp Lee (NRM S080202, S080203, S080226); Kvalpynten (NRM S080243); Kapp Pechuel Lösche/Lindemanberget (VSEGEI 10979-04–10979-06)]. Hopen: Nørdestfjellet (NRM S080264–S080269); Blåfjell (?VSEGEI 1/12163). Carnian (Upper Triassic).

Description.—*Neocalamites merianii* occurs at several of the localities as impressions and pith casts of two orders of axes (cf. Pott et al. 2008a). All specimens are incomplete; one of the longest shoot portions is 31.6 cm long (Fig. 2A); shoots of the first order (primary shoots) are 35–51 mm wide (e.g., Fig. 2B), those of the second order (lateral branches) are 22–24 mm or 10–13 mm wide in the middle of the internodes (e.g., Fig. 2B, E), the latter group may represent third order branches (cf. Pott et al. 2008a: text-fig. 3). Lengths of internodes are difficult to measure, since few are complete, but the longest in first order shoots exceed 145 mm in length whereas those of the other two categories are 54–118 mm long. The nodes are slightly wider than the internodes. The outer surface of the internodes is characterised by broad, almost imperceptible longitudinal striae, while the inner surface is marked by densely arranged prominent longitudinal

striae (depicting the positions of massive vascular bundles). Microphylls are not preserved attached to any shoots, but two specimens constitute incomplete rings of microphylls that are 2 mm wide and bear a prominent central single bundle (Fig. 2C, D). The number of microphylls per whorl may reach 65, since the preserved parts show up to 22 microphylls and are interpreted to represent c. one third to one half of the axis' circumference.

One specimen from Bertilryggen (NRM S080248; Fig. 2F) is here interpreted as a strobilus of *Neocalamites merianii*. A slender, 3–4 mm wide axis bears a small terminal strobilus, 42 mm long and 6–8 mm wide, consisting of small 2×3 mm wide scales (= sporangiophores), regularly arranged around a central axis. All scales bear thin, 2 mm long spines. The host axis bears spines (or leaf remnants) at intervals 7 mm apart (Fig. 2F).

Remarks.—*Neocalamites merianii* is a very common element in many Carnian–Rhaetian floras of central Europe and may have grown in large monotypic stands. A thorough revision of the species including the reconstruction of its growth habit and possible ecological requirements has recently been published based on a vast amount of excellently preserved specimens from the Carnian flora of Lunz in Lower Austria (Pott et al. 2008a). The Svalbard specimens match closely those from Lunz and are here considered conspecific. Vasilevskaya (1972, 1983) treated some of the specimens with caution and refrained from assigning them to *N. merianii*, but in my point of view, all belong to this species. The fertile specimen strongly resembles strobili assigned to *N. aff. carrerei* (Zeiller, 1903) Halle, 1908 by Vladimirovich (1958) or to *N. merianii* by Pott et al. (2008a). Additional evidence for this assignment comes from recently discovered *Neocalamites* specimens from the Upper Triassic of China with attached strobili that match very well in size, but the sporangiophores are smaller, have a different shape and the strobili were assigned to a different species, viz. *N. horridus* Zan, Axsmith, Escapa, Fraser, Liu, and Xing, 2012 (Zan et al. 2012).

Geographic and stratigraphic range.—Southern Germany, Switzerland, Austria, Svalbard; Ladinian–Carnian.

Neocalamites sp.

Fig. 2J.

Material.—Spitsbergen: Sassenfjorden (NRM S151685); Carnian (Upper Triassic).

Description.—One specimen from Sassenfjorden represents a *Neocalamites*-like stem, which has a circumference intermediate to the “categories” distinguished above (Fig. 2J). The width of the axis is 21 mm at the only node preserved and

decreases to 17 mm in the internode. The surface is covered with longitudinal striae, each less than 1 mm wide.

Remarks.—The specimen is similar to *Neocalamites merianii*, but does not fit in any of the size categories distinguished above for that species and is, therefore, kept separate, since it also comes from a different locality.

Genus *Equisetites* Sternberg, 1833

Type species: *Equisetites muensteri* Sternberg, 1833; from the Carnian of Abtswind, Bavaria, Germany.

Equisetites sp. cf. *Equisetites conicus* Sternberg, 1833

Fig. 2K.

1972 *Equisetites* cf. *glandulosus* Kräusel; Vasilevskaya 1972: 34, pl. 1: 6, 7.

Material.—Spitsbergen: Wimanfjellet (VSEGEI 10979-08, 10979-09); Carnian (Upper Triassic).

Description.—One specimen (part and counterpart) represents two shoot fragments, 116 mm long and up to 19 mm wide (Fig. 2K), characterised by a smooth surface that displays indistinct broad striae towards the nodes, each ending in an acute tip. These tips are up to 8 mm long and 6 mm wide and are interpreted as the apices of the leaf sheaths.

Remarks.—Vasilevskaya (1972) assigned these remains with some reservation to *Equisetites glandulosus* Kräusel and Leschik, 1959 described from the Carnian of Neuwelt, Switzerland, by Kräusel and Leschik (1959). The preservation of the fossils does not allow confident assignment to a species. The description of *E. glandulosus* by Kräusel and Leschik (1959) was based on three fragmentary specimens, which are barely distinguishable from *E. conicus* (cf. Pott et al. 2008a); moreover, the characters that separate these species in the original description are rather cryptic. Therefore, the autonomy of *E. glandulosus* is questioned, since it is very likely that the differences between the species mentioned by Kräusel and Leschik (1959) are taphonomically influenced, and the material from Wimanfjellet is transferred to *E. conicus* but with some reservation owing its fragmentary condition.

Geographic and stratigraphic range.—Southern Germany, Switzerland, Austria, Svalbard; Carnian.

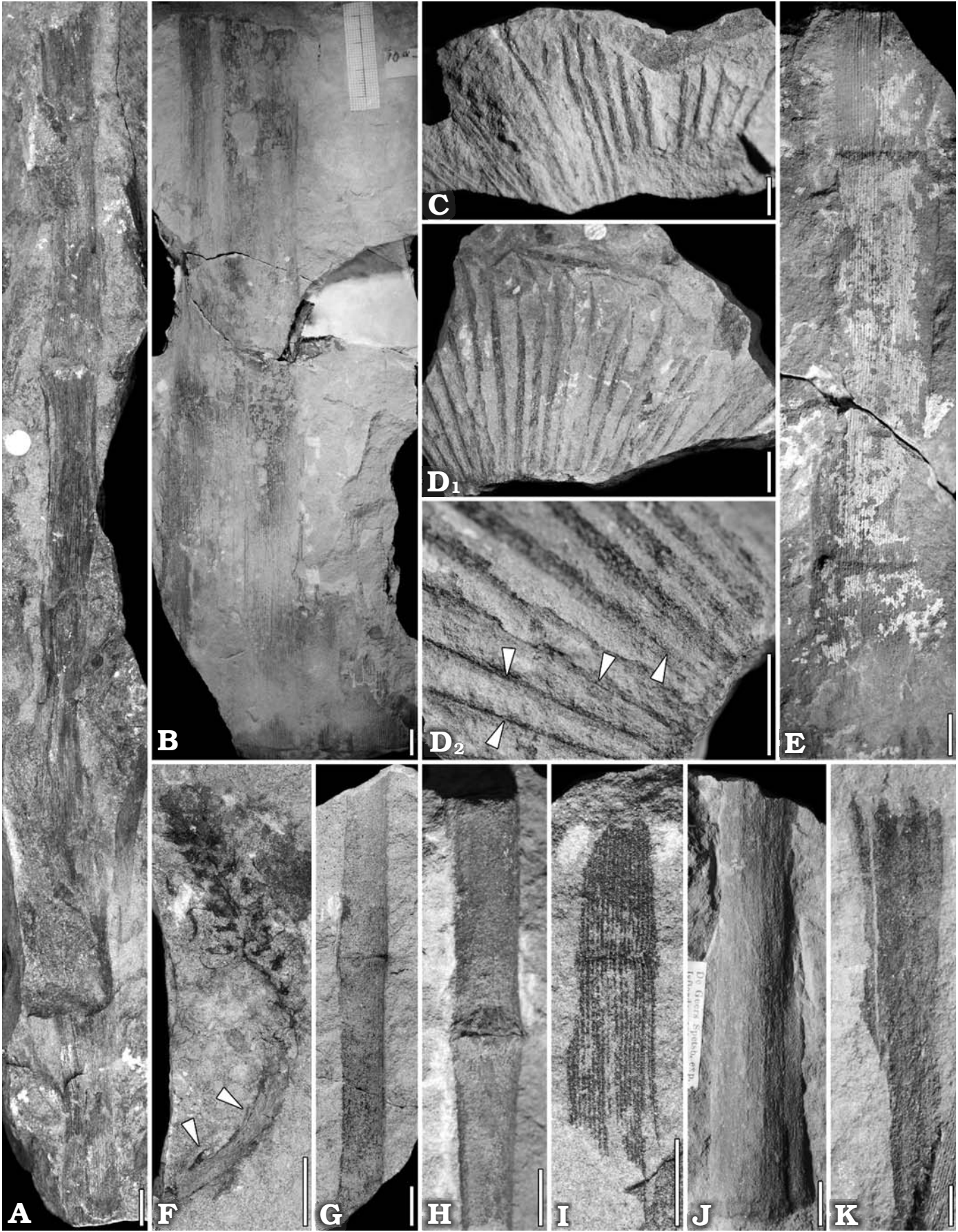
Order Marattiales Link, 1833

Family Marattiaceae Kaulfuß, 1824

Genus *Asterotheca* Presl ex Corda, 1845

Type species: *Asterotheca sternbergii* (Göppert, 1836) Presl ex Corda, 1845; from the Carboniferous of Saarbrücken, Saarland, Germany.

Fig. 2. Sphenophytes from the Carnian (Upper Triassic) strata of Svalbard. **A–I.** *Neocalamites merianii* (Brongniart, 1828) Halle, 1908. **A.** NRM S080071, → from Fleur de Lyshamna. **B.** VSEGEI 10979-07, from Teistberget. **C.** VSEGEI 10979-05, from Kap Pechuel Lösche/Lindemanberget, microphylls. **D.** VSEGEI 10979-04, from Kap Pechuel Lösche/Lindemanberget, microphylls (D₁), enlargement (D₂), arrowheads showing central vein. **E.** VSEGEI 10979-01, from Wimanfjellet. **F.** NRM S080248, from Bertilryggen, putative strobilus, arrowheads indicating nodia. **G.** NRM S080245, from Bertilryggen. **H.** VSEGEI 10979-06, from Kap Pechuel Lösche/Lindemanberget. **I.** NRM S080265, from Nørdstefjellet. **J.** *Neocalamites* sp., NRM S151685, from Sassenfjorden. **K.** *Equisetites* sp. cf. *Equisetites conicus* Sternberg, 1833, VSEGEI 10979-08, from Wimanfjellet. Scale bars 10 mm.



Asterotheca merianii (Brongniart, 1828a) Stur, 1885

Fig. 3A–J.

1828 *Pecopteris merianii*; Brongniart 1828a: 57, 194.1834 *Pecopteris merianii*; Brongniart 1834: 289, pl. 91: 5.1885 *Asterotheca merianii* Bgt.; Stur 1885: 5.1972 *Asterotheca merianii* (Brongn.) Stur; Vasilevskaya 1972: 36, pls. 2: 4–9; 3: 1–17; 9: 6b; 17: 3b.2011 *Asterotheca merianii* (Brongniart) Stur 1885; Kustatscher and Van Konijnenburg-van Cittert 2011: 210, pl. 1: A–I, text-fig. 12A.

Material.—Spitsbergen: Bertilryggen (NRM S080247); Fleur de Lyshamna (NRM S080072, S080076, S080078, S080089, S080090, S080111); Wimanfjellet (VSEGEI 10979-08, 10979-12–10979-14); Trehøgdene (NRM S151681); Wichebukta (VSEGEI 10979-15, 10979-82, 10979-83). Barentsøya: Vossebukta (VSEGEI 10979-18–10979-21, 10979-80, 10979-81). Edgeøya: Kapp Lee (NRM S080188, S080189, S080191, S080193, S080197, S080204, S080205, S080209, S080211–S080215, S080221, S080223, S080240; VSEGEI 10979-16, 10979-17, 10979-24, 10979-25, 10979-44, 10979-53, 10979-84–10979-86); Kvalpynten (NRM S080241); Negerpynten (VSEGEI 10979-22, 10979-23, 10979-79). Carnian (Upper Triassic).

Description.—*Asterotheca merianii* is typically preserved as sterile (Fig. 3A–C, G, I) and fertile (Fig. 3D–F, H, J) isolated pinnae in the Svalbard assemblages. The longest fragment measures 108 mm. Pinnules are densely spaced, 8–14 mm long (decreasing in length apically), and inserted by their whole base lateral to the rachis. The basal width of pinnules is consistently 3–4 mm. Pinnules are inserted at 75° and have relatively parallel margins ending in bluntly rounded apices. The pinnae vascular bundle gives off first order veins at 75°, the latter giving off 4–6 pairs of secondary veins that usually bifurcate once close to the base. Additional bifurcations are not found in the preserved specimens. Fertile pinnules bear regularly arranged sori (on the abaxial side) that are arranged parallel to the midline of the pinnule; 4–8 pairs of sori are present on a pinnule (e.g., Fig. 3J), each consisting of four sporangia.

Remarks.—*Asterotheca merianii* is one of the most common ferns in Upper Triassic floras of Europe and Asia and it may represent a useful stratigraphic index fossil. The size of several *A. merianii* fossils argues for these plants having been quite tall tree-like ferns similar to modern *Dicksonia* species. Fertile and sterile pinnules were produced on different pinnae, and most likely on separate fronds. *Asterotheca merianii* is also one of the dominant elements of the Carnian flora of Lunz. This species is readily identified, but it is not strongly palaeoecologically informative. Vasilevskaya (1972) was able to isolate spores from the *A. merianii* specimens from Svalbard and these match perfectly with the

spores published by Bhardwaj and Singh (1957) from *A. merianii* specimens from the Lunz flora and by Kustatscher and Van Konijnenburg-van Cittert (2011) from *A. merianii* specimens from the Thale flora. These authors also provide a thorough discussion of this species, its history and a comparison with other species. *Asterotheca merianii* occurs widely among the fossil localities in Svalbard, and where it is one of the dominant taxa. At some localities, it is the only taxon found.

Geographic and stratigraphic range.—Europe, Asia; Ladinian–Carnian.

Genus *Danaeopsis* Heer ex Schimper, 1869

Type species: *Danaeopsis marantacea* (Presl in Sternberg, 1838) Schimper, 1869 (see Kustatscher and Van Konijnenburg-van Cittert 2011); from the Carnian of Stuttgart, Baden-Württemberg, Germany.

Danaeopsis sp. cf. *Danaeopsis marantacea* (Presl in Sternberg, 1838) Schimper, 1869

Fig. 3K–M.

1972 *Danaeopsis* cf. *marantacea* (Presl) Heer; Vasilevskaya 1972: 35, pl. 2: 2, 3.

Material.—Spitsbergen: Wimanfjellet (VSEGEI 10979-10, 10979-11). Edgeøya: Kapp Lee (NRM S080207, S080221, S080223, S080240). Carnian (Upper Triassic).

Description.—All specimens are isolated pinnae from compound fronds, the largest of which being 51 mm long; pinnae are 25–28 mm wide including a prominent central bundle 2.5–3.5 mm wide. The lamina margin is entire, the central vascular bundle gives off secondary veins at almost 90° and these typically bifurcate once close to the base (e.g., Fig. 3K, M). Secondary veins are regularly spaced (600–700 µm apart, or 12–15 veins per cm). Marginal anastomoses as mentioned by Kustatscher and Van Konijnenburg-van Cittert (2011) are visible in one specimen (Fig. 3M), but the density of veins is slightly higher. All specimens represent sterile foliage.

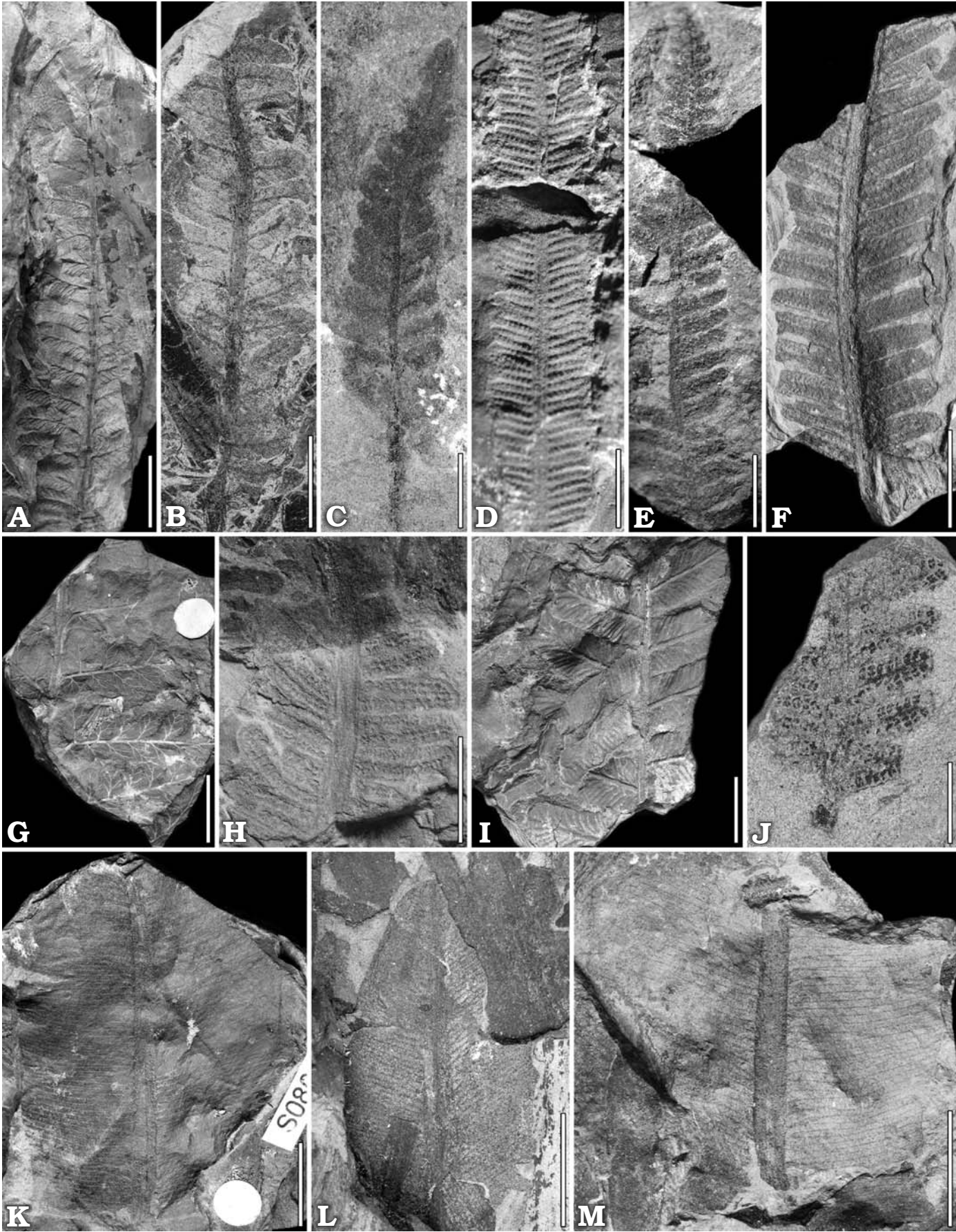
Remarks.—Six samples from two localities yield foliage that matches *Danaeopsis marantacea* from other Carnian floras (e.g., Schenk 1863–1864; Heer 1865; Kustatscher and Van Konijnenburg-van Cittert 2011). However, due to the fragmentary state, I assign them with some reservation to *D. marantacea*. Vasilevskaya (1972) also identified two specimens from Wimanfjellet as *D. marantacea* but with reservations.

Geographic and stratigraphic range.—Southern Germany, Switzerland, Austria, Svalbard; Ladinian–Carnian.

Order Gleicheniales Frank in Leunis, 1877

Family Dipteridaceae Seward and Dale, 1901

Fig. 3. Marattialean ferns from the Carnian (Upper Triassic) strata of Svalbard. **A–J.** *Asterotheca merianii* (Brongniart, 1828) Stur, 1885. **A.** NRM S080205-01, from Kapp Lee. **B.** NRM S080215, from Kapp Lee. **C.** NRM S080072-02, from Fleur de Lyshamna. **D.** VSEGEI 10979-24, from Kapp Lee. **E.** VSEGEI 10979-13, from Wimanfjellet. **F.** NRM S080223-01, from Kapp Lee. **G.** NRM S080212, from Kapp Lee. **H.** NRM S080215, from Kapp Lee. **I.** NRM S080189, from Kapp Lee. **J.** NRM S080247, from Bertilryggen. **K–M.** *Danaeopsis* sp. cf. *Danaeopsis marantacea* (Presl in Sternberg, 1838) Schimper, 1869. **K.** NRM S080207, from Kapp Lee. **L.** NRM S080240, from Kapp Lee. **M.** NRM S080223-02, from Kapp Lee. Scale bars 10 mm.



Genus *Dictyophyllum* Lindley and Hutton, 1834

Type species: Dictyophyllum rugosum Lindley and Hutton, 1834; from the Bajocian of Gristhorpe, Yorkshire, UK.

Dictyophyllum exile (Brauns, 1862) Nathorst, 1878a

Fig. 4A.

1862 *Camptopteris exilis*; Brauns 1862: 54, pl. 13: 11.

1878 *Dictyophyllum exile* Brauns; Nathorst 1878a: 14, pl. 1: 9.

1878 *Dictyophyllum exile* Brauns; Nathorst 1878b: 39, pl. 5: 7.

2009 *Dictyophyllum exile* (Brauns 1862) Nathorst 1878; Schweitzer et al. 2009: 41, pl. 10: 1–3, text-fig. 7.

2011 *Dictyophyllum exile* (Brauns) Nathorst 1878; Pott and McLoughlin 2011: 1031, pl. 5: A–D.

Material.—Edgeøya: Kapp Lee (NRM S080220); Carnian (Upper Triassic).

Description.—The Svalbard specimen shows two fragmentary sterile pinnae, 21 and 30 mm long and 10 mm wide (Fig. 4A). The margins of the pinnae are strongly lobed; lobes are more arched and pointed than bluntly triangular. Each lobe has a prominent midvein that gives off a complex reticulum of subsidiary veins (Fig. 4A).

Remarks.—*Dictyophyllum exile* is represented by two pinnae and some lamina fragments on one slab from Kapp Lee on Edgeøya. The fragments are identical to material from Scania, southern Sweden, figured by Nathorst (1878a, b) and Pott and McLoughlin (2011). *Dictyophyllum exile* is a typical Rhaetian species (Pott and McLoughlin 2011) and it is possible that the specimen under study was collected ex situ on the beach and derives from a Rhaetian layer exposed higher on the cliffs. This taxon is readily confused with *D. nathorstii* Zeiller, 1903, which is distinguished mostly by its basally adnate pinnae as opposed to the completely free pinnae in *D. exile* (Schweitzer et al. 2009; Pott and McLoughlin 2011). However, this character is not useful if only isolated pinnae are preserved. Both species occur mainly in Rhaetian deposits and are commonly co-preserved.

Geographic and stratigraphic range.—Europe, Middle East; Norian–Middle Jurassic.

Dictyophyllum sp.

Fig. 4B.

1972 *Dictyophyllum* sp. 1; Vasilevskaya 1972: 38, pl. 5: 1–3a.

1972 *Dictyophyllum* sp. 2; Vasilevskaya 1972: 39, pl. 6: 1.

Material.—Spitsbergen: Wimanfjellet (VSEGEI 10979-08, 10979-29, 10979-30); Carnian (Upper Triassic).

Description.—Three samples from Wimanfjellet yield fragmentary sterile pinnae assignable to *Dictyophyllum*. The longest pinna fragment is 83 mm long and 23 mm wide; 12 pairs

of pinnules are incompletely preserved (Fig. 4B). Pinnules are 7–8 mm wide basally and up to 12 mm long with perfectly rounded apices. They are characterised by a thin central vein emerging at 70–80° from the midvein and extending to the pinna apex. The complex network of secondary veins typical of *Dictyophyllum* foliage is barely perceptible due to the poor preservation.

Remarks.—Like Vasilevskaya (1972), I refrain from assigning the isolated pinnae from Wimanfjellet to a formal species owing to their fragmentary state. The pinnae are quite similar to material reported by Yokoyama (1891, 1905) as *Dictyophyllum kochibei* Yokoyama, 1891 from the Rhaetian shales of Nagato, Japan. They match very well in pinna outline, margin shape and size ranges, however, more details of the venation are known from the Japanese material, whereas these are not visible in the Svalbard specimens. The central vein is straighter in the Svalbard material and marginal pinnae lobes are more rounded than the slightly acute lobes of *D. kochibei*. Consequently, I refrain from assigning the Svalbard specimens to *D. kochibei*. The specimens are readily distinguished from *D. exile* and *D. nathorstii* by their round (vs. pointed) pinnule apices and the straight (vs. curved) central vein (cf. Schweitzer et al. 2009; Pott and McLoughlin 2011).

Genus *Clathropteris* Brongniart, 1828a

Type species: Clathropteris meniscoides Brongniart, 1828a; from the Hettangian of Höör, Scania, Sweden.

Clathropteris sp. cf. *Clathropteris obovata* Ôishi, 1932

Fig. 4C–E.

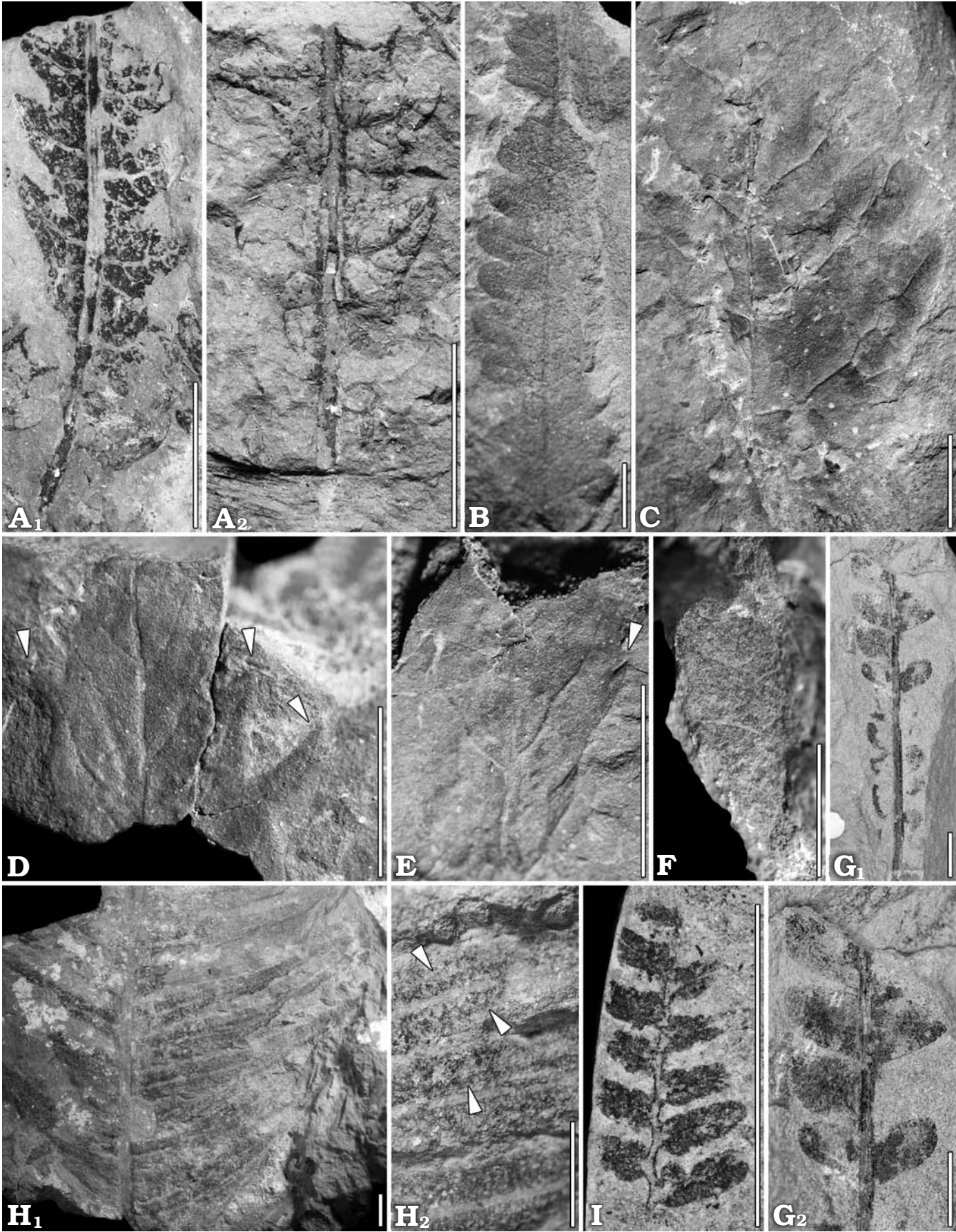
1972 *Clathropteris* sp.; Vasilevskaya 1972: 38, pls. 4: 1–3, 10: 1b.

1972 *Dipteridaceae* indet.; Vasilevskaya 1972: 41, pl. 5: 6.

Material.—Spitsbergen: Hyrnefjellet (VSEGEI 10979-26–10979-28, 10979-34); Carnian (Upper Triassic).

Description.—All specimens constitute middle and apical portions of sterile pinnae. The preserved parts are up to 58 mm long and 28 mm wide. Pinnae appear to have had a very thin lamina, the margin is lobate (Fig. 4C) with the rounded lobes becoming more acute (hook-like) and more arched towards the pinna apex (Fig. 4D–E). A central midvein (less than 1 mm wide) gives off lateral veins at regular intervals of 12–14 mm at an acute angle of 60°, each extending into the tip of a lobe. Lateral veins near the pinna apex are arranged at gradually more acute angles down to 40°. The lateral veins bear almost perpendicularly arranged, very thin subsidiary veins that are barely visible in some cases. These

Fig. 4. Dipteridaceous and matoniaceous ferns from the Carnian (Upper Triassic) strata of Svalbard. **A.** *Dictyophyllum exile* (Brauns, 1862) Nathorst, 1878, NRM S080220, from Kapp Lee, two different pinnae on the same specimen (A₁, A₂). **B.** *Dictyophyllum* sp., VSEGEI 10979-29, from Wimanfjellet. **C–E.** *Clathropteris* sp. cf. *Clathropteris obovata* Ôishi, 1932. **C.** VSEGEI 10979-26, from Hyrnefjellet. **D.** VSEGEI 10979-27, from Hyrnefjellet; note the shape of the lobes (arrowheads). **E.** VSEGEI 10979-28, from Hyrnefjellet; note the shape of the lobes (arrowhead). **F.** *Clathropteris* sp. VSEGEI 10979-12, from Wimanfjellet. **G.** cf. *Cladophlebis* sp., NRM S080258-02, from Bertilryggen (G₁), with close-up of distal portion (G₂). **H.** *Phlebopteris* sp. cf. *Phlebopteris muensteri* (Schenk, 1867) Hirmer and Hörhammer, 1936. VSEGEI 10979-31, from Wimanfjellet (H₁), enlargement (H₂), arrowheads indicate sori. **I.** cf. *Sphenopteris* sp., NRM S080263, from Edlundfjellet. Scale bars 10 mm.



connect the lateral veins and form the reticulate venation typical of *Clathropteris* species.

Remarks.—Schweitzer et al. (2009) stated that the discrimination between *Clathropteris obovata* and *C. meniscoides* (Brongniart, 1825) Brongniart, 1828 is difficult and based mainly on more distinct veins in *C. meniscoides*. This character is, thus, only utilitarian in a limited sense. However, following the figures of Schweitzer et al. (2009), foliage of *C. obovata* appears smoother (due to its less distinct veins) and less robust; in addition, the arrangement of the veins seems slightly different: veins of *C. obovata* appear to emerge at more acute angles from the midvein than those of *C. meniscoides*; and the mesh pattern looks much more regular “checkered” in *C. meniscoides* than in *C. obovata*. Considering these character tendencies and the excellent figures given by Schweitzer et al. (2009), the Svalbard material more strongly resembles *C. obovata* than *C. meniscoides*. However, even if the fossils match quite closely, I retain some reservation due to the fragmentary nature of the material and the very round and regularly shaped marginal lobes of at least two specimens (i.e., VSEGEI 2047-08 and 2047-28). The latter was identified as “Dipeteridaceae indet.” by Vasilevskaya (1972). All other specimens from Hyrnejfjellet were assigned to *Clathropteris* sp. by Vasilevskaya (1972). *Clathropteris* foliage in Svalbard has only been reported from Hyrnejfjellet in southern Spitsbergen (but see below).

Geographic and stratigraphic range.—Europe, Asia; Norian–Middle Jurassic.

Clathropteris sp.

Fig. 4F.

Material.—Spitsbergen: Wimanfjellet (VSEGEI 10979-12); Carnian (Upper Triassic).

Description.—One specimen from Wimanfjellet yields a very poorly preserved fern pinna portion (Fig. 4F) resembling *Clathropteris*-like foliage. The preserved part is 15×30 mm in size and has a few lateral veins 4–5 mm apart from each other. Perpendicular veins forming the characteristic *Clathropteris* meshes are partly visible.

Remarks.—The poor preservation of the specimen does not allow a totally reliable identification of the fossil, but it may be conspecific with the specimens assigned above to cf. *Clathropteris obovata*. Vasilevskaya (1972) did not mention this specimen.

Family Matoniaceae Presl, 1847

Genus *Phlebopteris* Brongniart, 1837

Type species: *Phlebopteris polypodioides* Brongniart, 1837; from the Bajocian of Scarborough, Yorkshire, UK.

Phlebopteris sp. cf. *Phlebopteris muensteri* (Schenk, 1867) Hirmer and Hörhammer, 1936

Fig. 4H.

1972 cf. *Thaumatopteris brauniana* Popp; Vasilevskaya 1972: 40, pls. 4: 4, 5; 5: 4, 5.

Material.—Spitsbergen: Bertilryggen (NRM S080257); Wimanfjellet (VSEGEI 10979-31–10979-33, 10979-87–10979-89); Carnian (Upper Triassic).

Description.—The specimens assigned to *Phlebopteris* are all fragmentary and most are sterile portions from the middle of a large frond (Fig. 4H₁). The largest is 134 mm long with pinnules up to 77 mm long. The densely spaced pinnae are inserted laterally by their whole width to a prominent rachis that is typically 4 mm wide. Pinnules are 5–8 mm wide and taper gradually towards an acutely rounded apex. They are characterised by a prominent, 1 mm wide midrib emerging at an angle of 75–85° from the rachis; secondary veins are barely visible in the fossils. At least two specimens from Wimanfjellet appear to bear sori in a row along the midvein of the pinnules (Fig. 4H₂). The specimens from Bertilryggen probably constitute more apical portions; pinnules in these are inserted at angles of 50–55° and decrease in length towards the apex.

Remarks.—The fossils match closely specimens assigned to *Phlebopteris muensteri* (cf. Hirmer and Hörhammer 1936; Schweitzer et al. 2009; Pott and McLoughlin 2011). The secondary veins, including the mesh-like pattern crucial for a definite assignment, are barely visible in all specimens from Svalbard. However, some specimens bear an indistinct row of sporangia flanking the pinnule midvein, which is a characteristic feature of *Phlebopteris*. Sporangia in the very similar *Thaumatopteris brauniana* Popp, 1863 are distributed among the veins over the whole abaxial surface of the pinnules. The straight margin of the pinnules also favours assignment to *Phlebopteris* whereas pinnule margins in *Thaumatopteris* are usually undulate/lobate. The differences in venation separating these genera are not visible in the Svalbard specimens. Moreover, *Phlebopteris* is a typical fern of the Carnian, whereas *Thaumatopteris* becomes common only in the Rhaetian. Specimens identified by Vasilevskaya (1972) as cf. *Thaumatopteris brauniana* are here transferred to *Phlebopteris*. However, since venation details are absent from the Svalbard specimens, assignment to species level is with some reservation.

Geographic and stratigraphic range.—Europe, Middle East; Carnian–Lower Cretaceous.

Order Polypodiales Link, 1833 (“Filicales”)

Family incertae familiae

Genus *Cladophlebis* Brongniart in d’Orbigny, 1849.

Type species: Non designatus (see Farr and Zijlstra 1996).

Cladophlebis sp. cf. *Cladophlebis remota* (Presl in Sternberg, 1838) Zeiller, 1903.

For illustration see Vasilevskaya (1972: pl. 4: 2–4).

1972 *Cladophlebis* aff. *remota* (Presl) Zeiller; Vasilevskaya 1972: 41, pl. 4: 2–4.

Material.—Spitsbergen: Wimanfjellet (VSEGEI 10979-35, 10979-36); Carnian (Upper Triassic).

Description.—One specimen preserved as part and counter-part having affinities to *Cladophlebis remota* was described and figured by Vasilevskaya (1972). The specimen was not available for study because it was missing in the collection examined at VSEGEI in St. Petersburg. Thus, the description is necessarily based on Vasilevskaya's (1972) description and illustration. The preserved (= figured) part is 57 mm long and 22 mm wide showing a middle portion of a pinna with seven pinnule pairs preserved that are slightly sub-oppositely arranged on a 2 mm wide rachis. Pinnules expand to a width of 6–8 mm and a length of up to 10 mm, and are apically rounded and slightly contracted basally. All pinnules are of similar shape, the pinnule apex is slightly pointed or acute towards the pinna apex in some pinnules. Venation is neuropterid; the midvein extending to only one third of the pinnule length and then bifurcating into several secondary veins. They bifurcate once more, and part of them do so again close to the pinnule margin.

Remarks.—Vasilevskaya (1972) assigned this specimen to *Cladophlebis* aff. *remota*, which, in my opinion is warranted. *Cladophlebis remota* has a quite variable pinnule shape and venation pattern (cf. e.g., Schenk 1864; Schenk in Schönlein 1865; Van Konijnenburg-van Cittert et al. 2006), so the specimen from Svalbard appears to fit comfortably in *C. remota*, which is a typical Middle–Late Triassic fern. The latter authors were apparently not aware of the new combination proposed previously by Zeiller (1903).

Geographic and stratigraphic range.—Europe, Middle East; Ladinian–Carnian.

cf. *Cladophlebis* sp.

Fig. 4G.

Material.—Spitsbergen: Bertilryggen (NRM S080258); Carnian (Upper Triassic).

Description.—One specimen from Bertilryggen represents the basal part of a fern pinna/frond with nine pinnule pairs preserved that are oppositely positioned (Fig. 4G₁). Preservation is not very good and venation details are lacking. The preserved part is 85 mm long, the individual pinnules are 5–7 mm wide basally and the longest is 11 mm long. Pinnules are inserted laterally by their whole basal width on a 2–3 mm wide rachis (Fig. 4G₂).

Remarks.—Among the studied collections, only a single specimen was attributable to this taxon. Vasilevskaya (1972) did not mention or figure any comparable specimen. Specific assignment is uncertain due to the lack of venation details. The specimen closely resembles specimens assigned to *Phlebopteris muensteri* from the Rhaetian of Scania (Pott and McLoughlin 2011). *Phlebopteris muensteri* is a typical matoniaceous fern of Late Triassic–Early Jurassic floras and is common in several European floras (Schweitzer et al. 2009).

Order incerti ordinis

Family incertae familiae

Genus *Sphenopteris* (Brongniart, 1822) Sternberg, 1828

Type species: *Sphenopteris elegans* (Brongniart, 1822) Sternberg, 1828; from the Carboniferous of Waldenburg, Silesia (today Wałbrzych, Poland).

cf. *Sphenopteris* sp.

Fig. 4I.

Material.—Spitsbergen: Edlundfjellet (NRM S080263); Carnian (Upper Triassic).

Description.—One very small specimen from Edlundfjellet represents the apical part of a fern pinna/frond with 5–6 pinnule pairs that are sub-oppositely to alternately positioned (Fig. 4I). The preserved part is 10 mm long with individual pinnules 1.2–1.5 mm wide basally and reaching 3.1 mm long. Pinnules are inserted laterally by their whole basal width on a 0.3 mm wide rachis. A central vein is recognisable in each pinnule, but subsidiary veins are not distinct. Pinnule margins show some tendency towards lobation. The apical pinna is not preserved.

Remarks.—Among the studied collections, only this tiny specimen was found. Vasilevskaya (1972) did not mention or figure any comparable specimen. Assignment is equivocal due to its small size and incomplete venation details. Among the many *Sphenopteris* species, the typically Late Triassic *Sphenopteris schoenleiniana* (Brongniart, 1835) Presl in Sternberg, 1838 is very similar. The specimen from Edlundfjellet is among the lowest size range mentioned for this species by Kustatscher and Van Konijnenburg-van Cittert (2011), and is consequently interpreted as the tip of a pinna or, because the pinnae seem to show a tendency to dissect into third order pinnules, even a pinnule.

Pteridospermatophyta

Order ?Peltaspermales Taylor, 1981

Family incertae familiae

Genus *Paratatarina* Vasilevskaya, 1972

Type species: *Paratatarina ptchelinae* Vasilevskaya, 1972; from the Carnian of Edgeøya, Svalbard, Norway.

Remarks.—*Paratatarina* was introduced by Vasilevskaya (1972) for slender, linear to fusiform leaves with a central vein giving off secondary veins at acute angles. *Paratatarina* forms an isolated taxon that, similar to *Arberophyllum*, differs in various morphological traits from other Mesozoic foliage. Vasilevskaya (1972) classified it as a member of the pteridosperms following Meyen (1969) and erected *P. ptchelinae* Vasilevskaya, 1972 as the type species. *Paratatarina ptchelinae* was based on two fragmentary specimens yielding well-preserved cuticles. These are regarded here conspecific with *P. spetsbergensis* Vasilevskaya, 1972. Recommendations of the ICBN (McNeill et al. 2012) require the latter to be included in *P. ptchelinae*. The genus was established to

denote similarities to the Late Permian pteridosperm *Tatarina* introduced by Meyen (1969). *Tatarina* species appear strikingly similar to *Paratatarina*, not only in their macro-morphology but also their epidermal anatomy; and the separation of *Paratatarina* from *Tatarina* may be questioned on this basis. However, the 30–50 Ma separation suggests these similarities may be convergent. *Tatarina* was regarded a pteridosperm by Meyen (1969) and compared to the Jurassic *Zamiopteris*; however, the latter is today regarded a cycadophyte (e.g., Farr and Zijlstra 1996). The attribution of *Paratatarina* still remains questionable, but it is not a cycadalean. Based on epidermal characteristics, *Paratatarina* is similar to *Arberophyllum*. However, the systematic position of the latter is also unresolved, although it has generally been assigned to the ginkgophytes (Tralau 1968; Dobruskina 1998; Doweld 2000; Pott et al. 2007d). The more or less distinct midvein in *Paratatarina*, however, clearly separates the genus from ginkgophytes, which never have a midvein.

Paratatarina ptchelinae Vasilevskaya, 1972

Fig. 5A–O.

1972 *Paratatarina ptchelinae*; Vasilevskaya 1972: 44, pls. 6: 5–8; 7: 1–5; 8: 1–6.

1972 *Paratatarina spetsbergensis*; Vasilevskaya 1972: 44, pls. 9: 1a, 2–5, 6a, 7; 10: 1a, 2–9; 16: 2b; 17: 3c.

1972 *Paratatarina* sp.; Vasilevskaya 1972: 46, pl. 11: 1–7.

1983 *Paratatarina korchinskae*; Vasilevskaya 1983: 145, pls. 1: 3–5; 2: 1–3; 3: 1, 2.

Material.—Spitsbergen: Bertilryggen (NRM S080252, S080253); Fleur de Lyshamna (NRM S080080–S080085, S080095–S080102); Hyrnefjellet (VSEGEI 10979-26, 10979-28, 10979-40–10979-49, 10979-76, 10979-90, 10979-91); Wimanfjellet (VSEGEI 10979-12); Trehøgdene (NRM S151684); Teistberget (VSEGEI 10979-03). Barentsøya: Schweinfurthberget (VSEGEI 10979-54). Edgeøya: Kapp Lee (NRM S080187, S080188, S080191, S080193, S080197–S080199, S080202–S080206, S080208, S080210, S080212, S080216, S080218, S080223, S080229, S080232, S080235, S080236, S080238–S080240; VSEGEI 10979-24, 10979-25, 10979-50–10979-53, 10979-92, 10979-93); Kapp Pechuel Lösche/Lindemanberget (VSEGEI 10979-37–10979-39). Hopen: Kollerfjellet (?VSEGEI 3/12163–9/12163). Carnian (Upper Triassic).

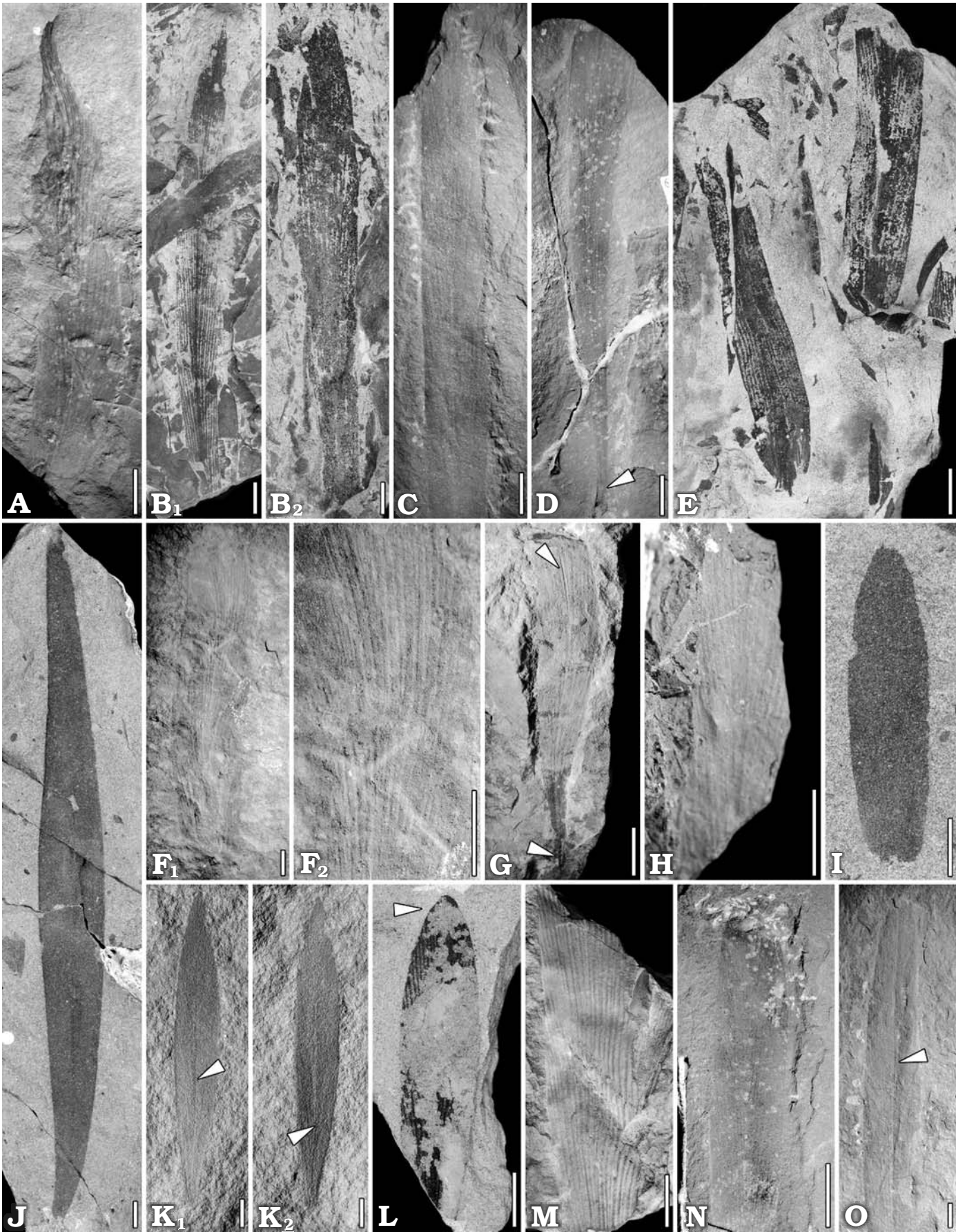
Description.—*Paratatarina ptchelinae* is characterised by long, slender, fusiform leaves (e.g., Fig. 5B₂, J–L) whose largest representative is 291 mm long and 28 mm wide, but typical leaves only reach 150–200 mm long and 20 mm wide. The lamina tapers straight towards the base and the apex

reaching its full width only in the middle fifth of the leaf (e.g., Fig. 5J). The leaf base is typically less than 4 mm wide (Fig. 5D, G). Leaf apices are acute and most are finely pointed (Fig. 5A, B₁, F₁, K); the lamina appears slightly frayed towards the leaf apex in most specimens. This may point to a very delicate lamina between the veins. Leaves are usually preserved with a slightly curved midvein and lamina (Fig. 5A, F₂, G). The central midvein (Fig. 5G, O) gives off fine secondary veins at regular intervals and at acute angles <15° (usually 4–10°), vein density is up to 20 veins/cm. Epidermal details are known from the type specimen (Vasilevskaya 1972) and from *P. korchinskae* Vasilevskaya, 1983 (Vasilevskaya 1983). The latter is here also regarded to be conspecific with *P. ptchelinae* (see Vasilevskaya 1972, 1983, for details).

A few specimens from the NRM collections provided cuticles serving at least for comparison and a rough description. Both abaxial and adaxial cuticles appear to be identical with one of both being slightly more strongly cutinised. Cuticles are robust; costal and intercostal fields are well distinguished; cells over the veins are elongate and slender, pointed, and arranged in rows parallel to the vein course; cells of intercostal fields are typically isodiametric or, in rare cases, slightly elongate, usually trapezoid and unordered, they are of similar shape to the subsidiary cells of the stomata but less cutinised; stomata are scattered at regular distances along one or two rows in the intercostal fields, surrounded by a ring of typically five (rarely four or six) trapezoid subsidiary cells that are more strongly cutinised than the surrounding epidermal cells. Each subsidiary cell cuticle is thickened towards the pit mouth and extends into a single solid papilla overarched the pit. Guard cells are deeply sunken but barely preserved. Anticlinal cell walls are straight with no ornamentation; in some specimens, periclinal cell walls show central cuticular thickenings (cf. Vasilevskaya 1972).

Remarks.—Some of the leaves here assigned to *Paratatarina ptchelinae* show almost parallel leaf margins as opposed to the tapering lamina in most specimens, and others have an acutely rounded apex as opposed to the pointed apex in most specimens. Attempts to sort the leaves into different “groups” based on lamina shape failed and thus, all are considered conspecific. No separation between leaves assigned to *Paratatarina ptchelinae*, *P. spetsbergensis* and *Paratatarina* sp. from Schweinfurthberget by Vasilevskaya (1972) could be achieved, and thus, the latter are here considered conspecific with *P. ptchelinae*. Vasilevskaya (1972) separated *P. ptchelinae* only by the presence of epidermal details from *P. spetsbergensis*. However, all specimens are macromorpho-

Fig. 5. Pteridosperm *Paratatarina ptchelinae* Vasilevskaya, 1972 from the Carnian (Upper Triassic) strata of Svalbard. **A.** VSEGEI 10979-45, from Hyrnefjellet. **B.** NRM S080239-01, from Kapp Lee, different leaves on same specimen (B₁, B₂). **C.** VSEGEI 10979-48, from Hyrnefjellet. **D.** VSEGEI 10979-28, from Hyrnefjellet, note the slender leaf base (arrowhead). **E.** NRM S080236-01, from Kapp Lee. **F.** VSEGEI 10979-42 from Hyrnefjellet (F₁), detail of venation (F₂). **G.** VSEGEI 4/12163, from Kollerfjellet, cf. Vasilevskaya (1983: pl. 1: 4), note slender leaf base and midvein (arrowheads). **H.** VSEGEI 10979-54, from Schweinfurthberget. **I.** NRM S080082, from Fleur de Lyshamna, below the *Pterophyllum* layer. **J.** NRM S080080, from Fleur de Lyshamna, below the *Pterophyllum* layer, two different light angles (K₁, K₂) to highlight venation (arrowheads). **L.** NRM S080253, from Bertilryggen, note the rounded apex (arrowhead). **M.** NRM S080205-01, from Kapp Lee. **N.** VSEGEI 10979-40, from Hyrnefjellet. **O.** VSEGEI 10979-49, from Hyrnefjellet, midvein arrowed. Scale bars 10 mm.



logically very similar and epidermal details documented for *P. spetsbergensis* reveal that the differences are minor and likely represent environmentally influenced variations. *Paratatarina ptchelinae* is comparatively common in the Upper Triassic flora from Svalbard and has been found at several localities. It is a very distinctive species and can only be mistaken for *Arberophyllum* species (see below). One specimen, identified as that illustrated in Vasilevskaya (1983: pl. 1: 4; *Paratatarina korchinskae*), has an epidermal anatomy very similar to leaves of *P. spetsbergensis*. Thus, *P. korchinskae* is here also regarded as conspecific with *P. ptchelinae*.

Leaves occurring in a separate layer that was termed “under *Pterophyllum*-lagret” [“below the *Pterophyllum* layer”] by Alfred G. Nathorst and Johan G. Andersson when they collected the specimens at Fleur de Lyshamna (e.g., Fig. 5I–K) are here also assigned to *Paratatarina ptchelinae* based on macromorphological agreement (specimens S080080–S080085, S080095–S080102).

Geographic and stratigraphic range.—Svalbard; Carnian.

Genus *Ptilozamites* Nathorst, 1878a

Type species: *Ptilozamites heeri* Nathorst, 1878b; from the Rhaetian of Bjuv, Scania, Sweden.

Ptilozamites sp. cf. *Ptilozamites nilssonii* Nathorst, 1878a

Fig. 6B.

1983 *Ptilozamites* sp.; Vasilevskaya 1983: 144, pl. 1: 2.

Material.—Hopen: Husdalen (?VSEGEI 2/12163); Carnian (Upper Triassic).

Description.—The specimen photographed (Fig. 6B₁) is lacking the lowermost part compared to the figure of Vasilevskaya (1983); it consists of a bifurcate segmented frond, 85.3 mm long. Leaflets are arched towards the frond apex, tongue-shaped with an acutely rounded apex, 18–20 mm long and basally up to 4–6 mm wide, densely spaced and inserted laterally at 35–40° to the rachis on both sides, even after the bifurcation. Leaflets have up to six parallel veins (Fig. 6B₂). The rachis is less than 2 mm thick and densely striate longitudinally. The angle of bifurcation is 30°.

Remarks.—Vasilevskaya (1983) briefly mentioned this specimen and figured it on plate 1. She described it deriving from Upper Triassic debris close to Hopen Radio in the southern part of the island (here called Husdalen). She questioned the Carnian age of this specimen, since the oldest *Ptilozamites* specimens were Rhaetian in age. However, records from older sediments have been published recently (Kustatscher and Van Konijnenburg-van Cittert 2007) and Hopen is considered to be consisting of entirely Carnian and Norian rocks (Smith et al. 1975; Mørk et al. 1999; Strullu-Derrien

et al. 2012). The specimen from Hopen can be assigned with confidence to the Carnian since it is co-preserved with *Pterophyllum filicoides*, a typical Carnian index fossil. The specimens match quite well with those of *Ptilozamites nilssonii* from the Rhaetian of Bjuv in Scania, southern Sweden (CP personal observation, May 2012; cf. also Kustatscher and Van Konijnenburg-van Cittert 2007). Unfortunately, the Hopen specimen does not provide any cuticle, which would be very useful for comparison. The discovery of *Ptilozamites* in Carnian strata of Svalbard confirms the older age range of the genus that was formerly deemed to be restricted to the Rhaeto-Liassic (Kustatscher and Van Konijnenburg-van Cittert 2007); the new record also extends the distribution of the genus northwards. The records from the Anisian–Carnian of the southern Alps require careful re-evaluation since the macromorphology of those leaves is distinct from typical *Ptilozamites* foliage, and one of those species has recently being transferred to the bennettitalean *Anomozamites triangularis* based on epidermal anatomy (Pott and McLoughlin 2009).

Geographic and stratigraphic range.—Europe, Middle East; Ladinian–Lower Jurassic.

Cycadophyta

Order Bennettitales Engler, 1892

Family Williamsoniaceae Carruthers, 1870

Genus *Pterophyllum* Brongniart, 1825

Type species: *Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906; from the Carnian of Neuwelt, Basel, Switzerland.

Pterophyllum filicoides (Schlotheim, 1822) Zeiller, 1906

Fig. 7A–H.

1822 *Algacites filicoides*; Schlotheim 1822: 47, pl. 4: 2.

1906 *Pterophyllum filicoides* Schlotheim; Zeiller 1906: 196, fig. A.

1970 *Pterophyllum filicoides* (Schlotheim) Thomas 1930; Barnard 1970: 7, fig. 2.

1972 *Pterophyllum jaegeri* Brongniart pro parte; Vasilevskaya 1972: 48, pls. 9: 6b; 12: 4; 13: 3; 14: 1, 2; 15: 1–3a.

1972 *Pterophyllum longifolium* Brongniart; Vasilevskaya 1972: 49, pls. 14: 4, 5; 15: 4.

1972 *Pterophyllum* sp.; Vasilevskaya 1972: 50, pl. 13: 4.

1983 *Pterophyllum jaegeri* Brongn.; Vasilevskaya 1983: 143, pl. 3: 3.

1983 *Pterophyllum* aff. *jaegeri* Brongn.; Vasilevskaya 1983: 143, pl. 4: 1.

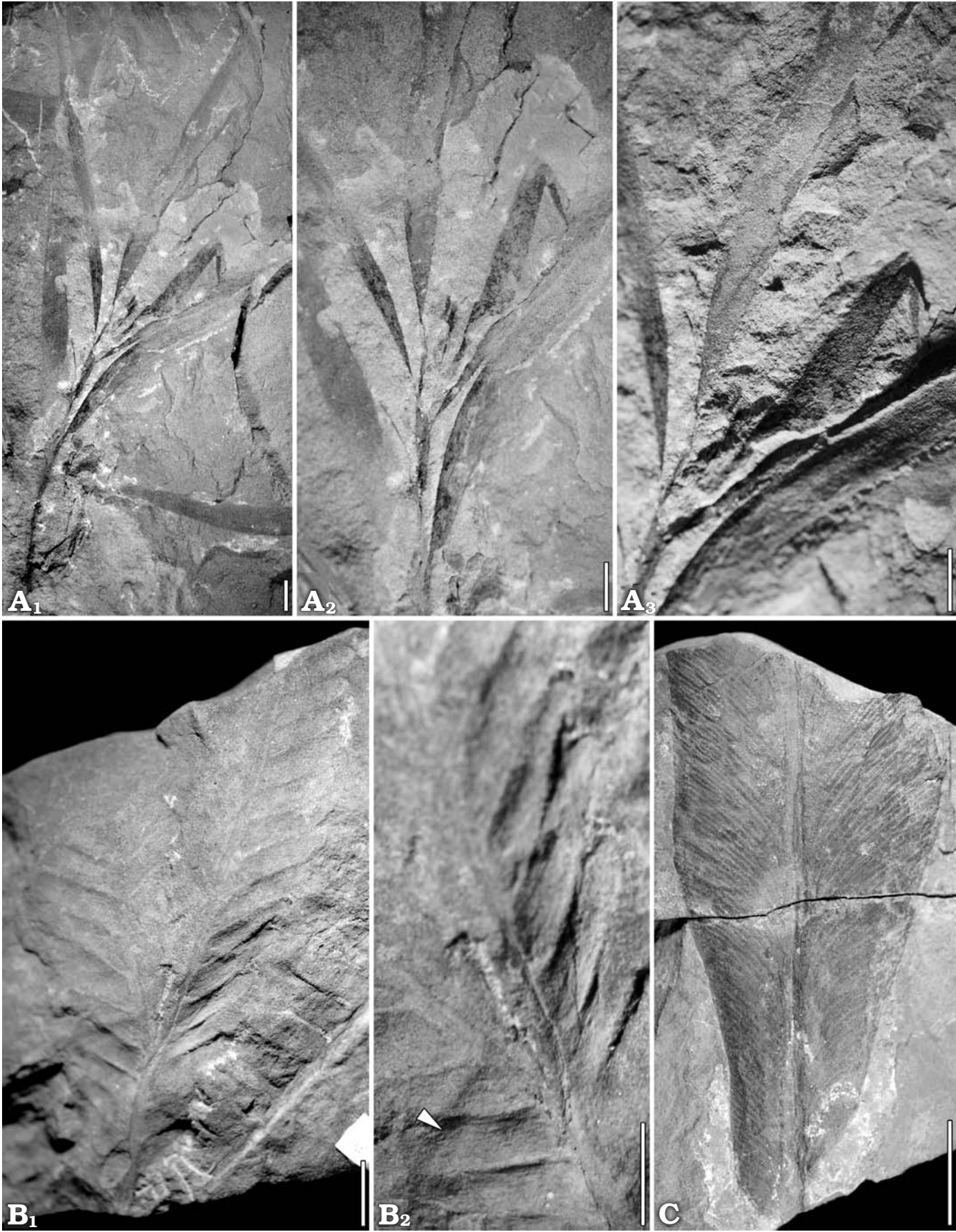
1983 *Pterophyllum*(?) sp. (*Pseudecten*(?) sp.); Vasilevskaya 1983: 143, pl. 4: 2.

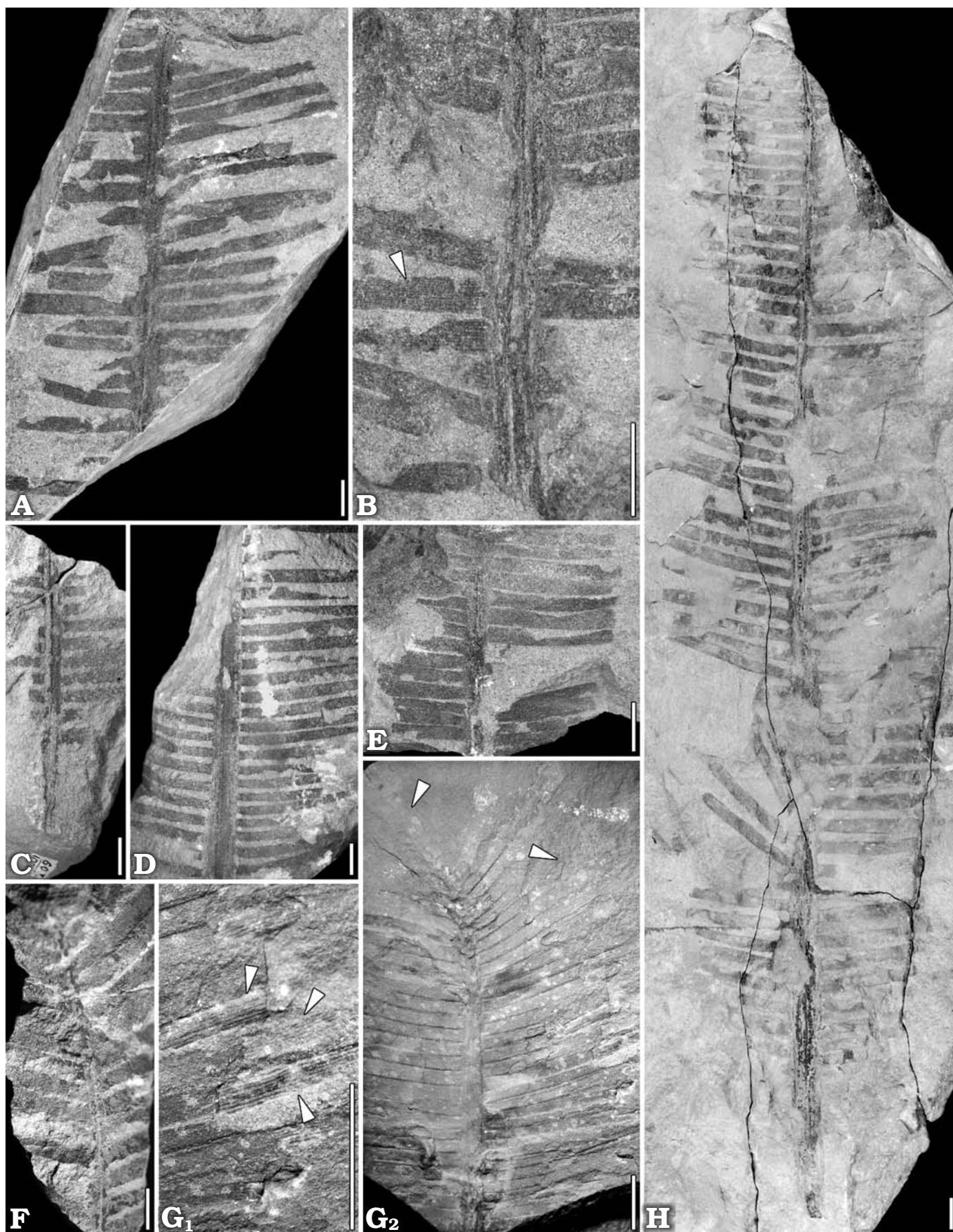
1983 *Pterophyllum* aff. *longifolium* Brongn.; Vasilevskaya 1983: 143, pl. 4: 3.

1983 *Pseudecten*(?) sp.; Vasilevskaya 1983: 143, pl. 5: 1–3.

2007 *Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906; Pott et al. 2007f: 7, pls. 1: 1–4; 2: 1–10; 3: 1–9; 4: 1–15; 8: 1, 4–5; 9: 1, 4–6.

Fig. 6. Ginkgophytes, pteridosperms, and caytoniales from the Carnian (Upper Triassic) strata of Svalbard. A. *Arberophyllum substrictum* sp. nov., → VSEGEI 10979-03, from Teistberget, seen from different angles and magnifications (A₁–A₃). B. *Ptilozamites* sp. cf. *Ptilozamites nilssonii* Nathorst, 1878, VSEGEI 2/12163, from Husdalen, cf. Vasilevskaya (1983: pl. 1: 2) (B₁), close-up showing venation details (B₂, arrowhead). C. *Sagenopteris* sp., VSEGEI 10979-78, from Hyrnejellet. Scale bars 10 mm.





Material.—Spitsbergen: Fleur de Lyshamna (NRM S080073, S080075–S080078, S080086, S080092–S080094, S080282, S080283); Hyrnefjellet (VSEGEI 10979-63, 10979-64); Wimanfjellet (VSEGEI 10979-67–10979-69); Agardhbukta (VSEGEI 10979-58, 10979-94). Barentsøya: Schweinfurthberget (VSEGEI 10979-60, 10979-61, 10979-70). Edgeøya: Kapp Lee (VSEGEI 10979-24, 10979-65); Kapp Pechuel Lösche/Lindemanberget (VSEGEI 10979-62). Hopen: Werenskioldfjellet (?VSEGEI 10/12163–12/12163, 14/12163–16/12163); Husdalen (?VSEGEI 2/12163); Blåfjell (?VSEGEI 13/12163). Carnian (Upper Triassic).

Description.—*Pterophyllum filicoides* is characterised by impari-segmented (Fig. 7G₂), petiolate leaves with a prominent rachis and parallel-sided, perpendicularly inserted leaflets (Fig. 7A, C–E, H). Leaflets are inserted laterally or almost laterally on the rachis (Fig. 7B, F). All preserved specimens are fragments from different portions of the leaves. The largest fragments are 382 mm long and 96 mm wide (Fig. 7H). The rachis is typically 6–8 mm wide, whereas leaflets range in width from 3–8 mm. Leaflets are parallel-sided and bluntly rounded apically; in only a very few specimens are they constricted basally, but none are expanded; longest leaflets exceed a length of 48 mm. One leaf is preserved with an apex; the apical leaflet (28 mm in length) is identical in shape to the lateral leaflets, the preceding two pairs are inserted at acute angles and arched towards the apex (Fig. 7F, G₂). Leaflets bear dense, parallel, fine veins (Fig. 7G₁). Cuticle could not be isolated from any specimen. Leaflets are densely spaced and almost touch each other except for a few specimens where gaps up to 2 mm wide are present. Such leaves have been interpreted to have grown under shady conditions (Pott et al. 2007f).

Remarks.—Pott et al. (2007f) recently investigated the identity of *Pterophyllum longifolium* and *P. jaegeri* and determined that the correct name of these conspecific species is *P. filicoides*, which has recently been accepted as the correct name for the type species of *Pterophyllum* (Pott et al. 2007e; Herendeen 2011). The material from different Svalbard localities, assigned to *P. longifolium* and *P. jaegeri* by Vasilevskaya (1972) together with additional material from the NRM collections, could confidently be identified as *P. filicoides*, even though epidermal details from the Svalbard material are unavailable. The specimens are identical to examples from the Carnian flora of Lunz (Pott et al. 2007f). *Pterophyllum filicoides* occurs with two other congeneric species in the Svalbard assemblages, i.e., *P. brevipenne*, which is also known from the Lunz flora, and *P. firmifolium*, which is known, e.g., from the Carnian of China and Kyrgyzstan (Wu et al. 1980; Moisan et al. 2011). Both are distinguished from *P. filicoides* by their shorter leaflets and, in *P. brevipenne*, the different shape of the apical leaflet. Epidermal details further

support separation of these species (Wu et al. 1980; Pott et al. 2007f), but are not known for the Svalbard material. Of the material published by Vasilevskaya (1972), I include all specimens published under *Pterophyllum jaegeri*, *P. longifolium*, and *Pterophyllum* sp. in *P. filicoides* except for one specimen that is transferred to *P. firmifolium* (see below).

The material reported by Vasilevskaya (1983) from Hopen as *Pterophyllum jaegeri* and *P. longifolium* is clearly conspecific with all other material from Svalbard assigned to *P. filicoides*. In addition, Vasilevskaya (1983) was able to isolate and figure cuticle from the Hopen specimens. The epidermal details match very well with the cuticles of *P. filicoides* reported from Lunz (Pott et al. 2007f) and thus support the identification made here. Vasilevskaya (1983) assigned two specimens that appear to be counterparts (i.e., ?VSEGEI 12/12163, 14/12163) with strong reservation to *Pterophyllum* or *Pseudoctenis* (?VSEGEI 12/12163) and to *Pseudoctenis* (?VSEGEI 14/12163), respectively. From the latter, cuticle was recovered. The cuticle, however, is almost identical to cuticle fragments figured for *Pterophyllum filicoides* from the Carnian of Neuwelt, Switzerland, by Pott et al. (2007f). In my opinion, assignment to *Pseudoctenis* is, therefore, not warranted and the specimens are here included in *Pterophyllum filicoides* as well. The cuticle of the only *Pseudoctenis* species thus far recorded from the Carnian, viz. *Pseudoctenis cornelii* Pott, Kerp, and Krings, 2007, has distinctly undulate anticlinal cell walls (Pott et al. 2007b) and strongly papillate stomata. Vasilevskaya (1983) mentioned two additional specimens from Iversenfjellet and Lyngfjellet on Hopen yielding *Pterophyllum* sp. foliage, but refrained from figuring them. No statement on these can thus be made.

Geographic and stratigraphic range.—Europe, Asia; Carnian.

Pterophyllum brevipenne Kurr ex Schenk, 1864

Fig. 8A–E.

- 1864 *Pterozamites brevipennis*; Kurr ex Schenk, 1864: 65, pl. 5: 1.
 1865 *Pterophyllum brevipenne* Kurr; Heer 1865: 52, pl. 3: 1.
 1972 *Pterophyllum brevipenne* Kurr; Vasilevskaya 1972: 47, pl. 12: 1–3.
 2007 *Pterophyllum brevipenne* Kurr ex Schenk, 1864; Pott et al. 2007f: 13, pls. 5: 1–8; 6: 1–8; 7: 1–12; 8: 2, 3, 6, 7; 9: 2, 3, 7–12.

Material.—Spitsbergen: Fleur de Lyshamna (NRM S080078, S080089, S080283); Wimanfjellet (VSEGEI 10979-55–10979-57); Carnian (Upper Triassic).

Description.—*Pterophyllum brevipenne* is preserved on five slabs; most of the preserved parts represent the lower middle portions of leaves (Fig. 8B–E). The typical tapering of the lamina is recognisable as are also the characteristic short leaflets (Fig. 8D). The preserved portions are up to 166 mm long (Fig. 8A). The leaflets are perpendicularly inserted lat-

← Fig. 7. Cycadophyte *Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906 from the Carnian (Upper Triassic) strata of Svalbard. **A.** NRM S080075, from Fleur de Lyshamna. **B.** NRM S080073, from Fleur de Lyshamna, with a few venation details visible (arrowhead). **C.** VSEGEI 10979-60, from Schweinfurthberget. **D.** VSEGEI 10979-58, from Agardhbukta. **E.** NRM S080094, from Fleur de Lyshamna. **F.** VSEGEI 10979-62, from Kapp Pechuel Lösche/Lindemanberget. **G.** VSEGEI 10979-63, from Hyrnefjellet; G₁, detail of leaflets showing venation details (arrowheads), G₂, long apical leaflets (arrowheads). **H.** NRM S080282, from Fleur de Lyshamna. Scale bars 10 mm.

erally to a prominent but only 3 mm wide rachis (Fig. 8A–D), 5–6 mm wide and up to 28 mm long; the shortest being 12–13 mm long. They are slightly contracted basally and, as far as visible, bluntly rounded to truncate apically. Leaf apices, petioles and cuticle are not preserved.

Remarks.—These specimens are identical to and easily identified with *Pterophyllum brevipenne* from, e.g., the Carnian flora of Lunz in Lower Austria (Pott et al. 2007f). They match exactly in size, shape and outline of the lamina and leaflets. The very characteristic apical leaflet that differs from the lateral examples is not preserved. The material identified by Vasilevskaya (1972) as *P. brevipenne* is confirmed, however, the specimens have, unfortunately, been figured upside-down. *Pterophyllum brevipenne* is less common and less widely distributed on Svalbard than *P. filicoides* and occurs only in the southern part of Spitsbergen.

Geographic and stratigraphic range.—Europe, Asia; Carnian.

Pterophyllum sp. cf. *Pterophyllum firmifolium* Ye ex Wu, Ye, and Li, 1980

Fig. 8F–I.

1926 *Pterophyllum*; Høeg 1926: 32, pl. 9: b2.

1972 *Pterophyllum jaegeri* Brongniart pro parte; Vasilevskaya 1972: 48, pl. 13: 2.

1972 *Pterophyllum* aff. *jaegeri* Brongniart; Vasilevskaya 1972: 49, pls. 13: 1; 14: 3a.

Material.—Spitsbergen: Teistberget (VSEGEI 10979-03, 10979-59, 10979-66). Probably Edgeøya: Kapp Lee (NRM S080203). Hopen: Nørdstefjellet (NRM S080273). Carnian (Upper Triassic).

Description.—The present material consists of three poorly preserved specimens that were recovered exclusively from Teistberget. The largest preserved leaf portion is 345 mm long and c. 60 mm wide (Fig. 8I). The rachis is prominent and up to 4 mm wide (Fig. 8F). The laterally and perpendicularly inserted leaflets are 2.8–3.8 mm wide and up to 23 mm long (Fig. 8G, H), parallel-sided and bluntly rounded to truncate apically. They are densely spaced and touch each other (Fig. 8H, I). Leaflets increase in length in the proximal two thirds of the leaf and then decrease in length towards the apex. Apices and venation details are not preserved.

Remarks.—The specimens are different from those found elsewhere on Svalbard and have only been found at Teistberget. They are not assignable to either *Pterophyllum filicoides* or *P. brevipenne*. Leaflet width and length in combination with gross lamina shape are more similar to *P. firmifolium*, which has been described from Late Triassic (?Carnian) Hsiangchi Coal Series in Western Hubei, China (Wu et al. 1980; Moisan et al. 2011). Although the leaves from

Svalbard exceed those from China in length, the width and length of the leaflets and the gross lamina shape match very well; the acute angles in the latter might be a taphonomic artifact. One other species, i.e., *Pterophyllum ptilum* Harris, 1932, from Rhaetian deposits of Scania and Greenland (cf. Pott and McLoughlin 2009) is similar but even smaller, and has leaflets arranged at acute angles. However, since the material is scarce in Svalbard and the epidermal anatomy remains unknown, I assign the specimens with reservation to *P. firmifolium* until additional material becomes available. One *Pterophyllum* specimen found at Nørdstefjellet on Hopen (Fig. 8F) and one from Kapp Lee on Edgeøya may also belong in this species. In those specimens, the leaflets are separated by 2-mm-wide gaps, but have venation that is, nevertheless, strikingly similar to *P. firmifolium*, and similar gaps also occur in some of the specimens from China (Wu et al. 1980) and Madyen (Moisan et al. 2011).

Geographic and stratigraphic range.—Europe, Asia; Carnian–Norian.

Pterophyllum sp.

Fig. 8J, K.

Material.—Spitsbergen: Sassenfjorden (NRM S080284, S151682, S151683); Carnian (Upper Triassic).

Description.—Three specimens from Sassenfjorden are isolated leaf segments with fine, narrow parallel venation (Fig. 8J, K) and have margins that gently taper slightly to what is interpreted as the apex of the leaflets. The fragments are 16–21 mm long and 6–8 mm wide, with up to 23 veins.

Remarks.—The isolated leaflets are difficult to assign to any species. From their shape and venation details, they likely belong to a species of *Pterophyllum*. *Nilssoniopteris* and other cycadophyte leaves may have similar veins, but have not yet been found on Svalbard.

Genus *Nilssoniopteris* Nathorst, 1909

Type species: *Nilssoniopteris tenuinervis* Nathorst, 1909 (see Cleal et al. 2006); from the Bajocian of Cloughton Wyke, Yorkshire, UK.

Nilssoniopteris angustior (Stur ex Krasser, 1909) Pott, Krings, and Kerp, 2007c.

Fig. 9A–D.

1885 *Taeniopteris angustior* nom. nud.; Stur 1885: 97.

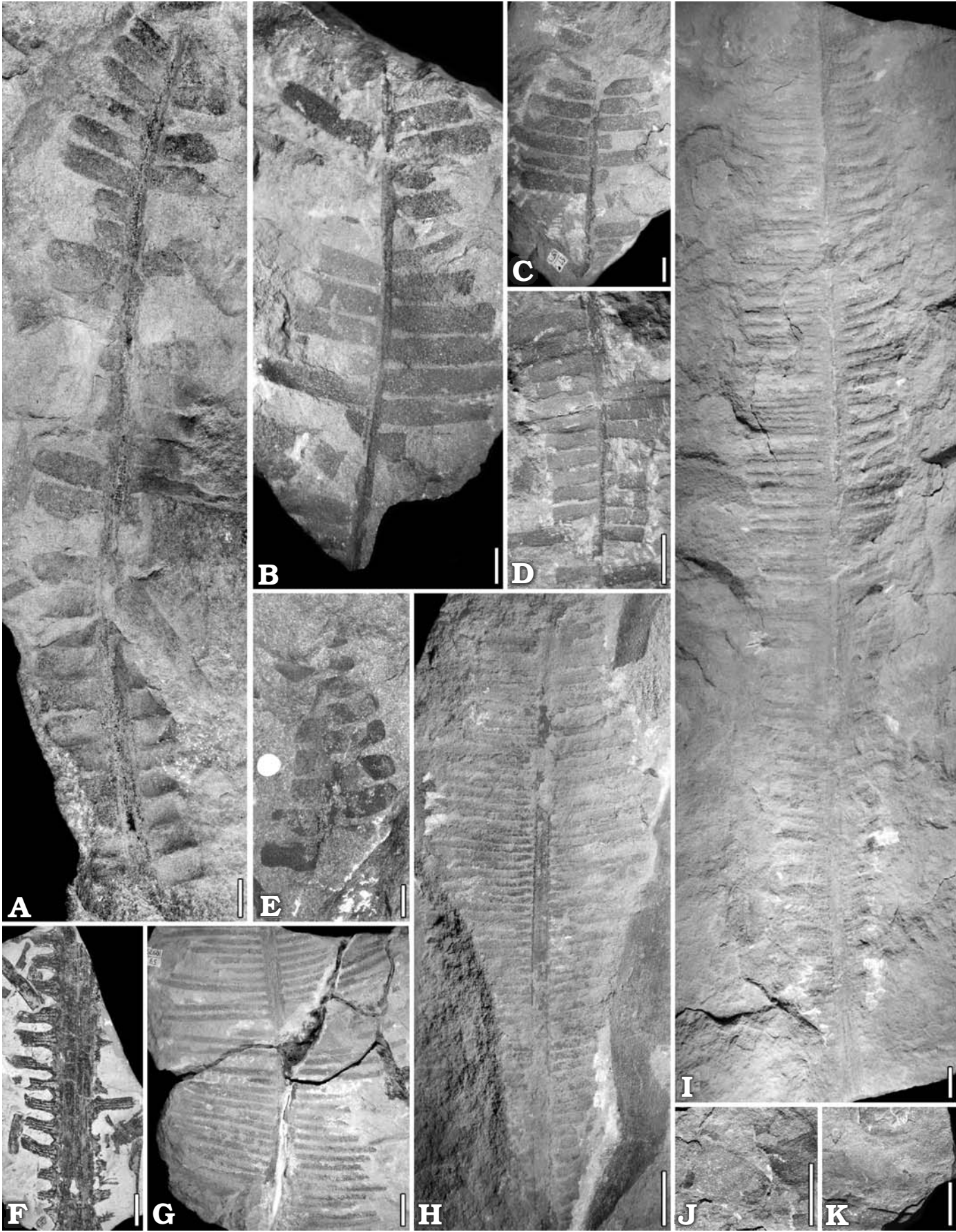
1909 *Macrotaeniopteris angustior*; Krasser 1909: 39.

1972 *Taeniopteris* sp.; Vasilevskaya 1972: 51, pls. 15: 3b; 16: 1–2a, 3–5.

1983 *Taeniopteris* sp.; Vasilevskaya 1983: 143, pl. 6: 2–4.

2007 *Nilssoniopteris angustior* (Stur ex Krasser, 1909); Pott et al. 2007c: 1306, pls. 3: 1–7; 4: 1–9.

Fig. 8. Cycadophytes from the Carnian (Upper Triassic) strata of Svalbard. A–E. *Pterophyllum brevipenne* Kurr ex Schenk, 1864. A. NRM S080283, → from Fleur de Lyshamna. B. VSEGEI 10979-56, from Wimanfjellet. C. VSEGEI 10979-57, from Wimanfjellet. D. VSEGEI 10979-55, from Wimanfjellet. E. NRM S080078-01, from Fleur de Lyshamna. F–I. *Pterophyllum* sp. cf. *Pterophyllum firmifolium* Ye ex Wu, Ye, and Li, 1980. F. NRM S080273, from Nørdstefjellet. G. VSEGEI 10979-59, from Teistberget. H. VSEGEI 10979-66, from Teistberget. I. VSEGEI 10979-03, from Teistberget. J, K. *Pterophyllum* sp. J. NRM S151683, from Sassenfjorden. K. NRM S151682, from Sassenfjorden. Scale bars 10 mm.



Material.—Spitsbergen: Fleur de Lyshamna (NRMS080078); Trehøgdene (NRM S151680). Edgeøya: Kapp Lee (NRM S080191–S080197, S080205, S080221, S080234–S080236; VSEGEI 10979-24, 10979-25, 10979-52, 10979-65, 10979-71). Hopen: Kollerfjellet (?VSEGEI 18/12163–20/12163). Carnian (Upper Triassic).

Description.—Several incomplete specimens of *Nilssoniopteris* foliage, found at Kapp Lee, are 144.2 mm long and 69.5 mm wide. The narrow and lanceolate leaves are apparently entire-margined and characterised by a prominent rachis up to 3.2 mm wide. The lamina is laterally inserted on the rachis and tapers slightly towards the base; apices are bluntly rounded (Fig. 9B). A petiole is not preserved in the specimens. Numerous parallel, densely arranged veins depart from the rachis at 80–90° (Fig. 9A, C, D), enter the lamina and bifurcate one or two times close to the rachis. Vein density is 15–19 veins/cm. In the distal portion of the leaves, veins are slightly curved towards the apex. The lamina is not subdivided into segments, but local growth aberrations of the leaf margin resemble weak lobations or the lamina is locally lacerated, as in extant *Musa* leaves (Fig. 9A, D). Epidermal details remain unknown because no organic material could be isolated from any fossil.

Remarks.—Pott et al. (2007c) described *Nilssoniopteris angustior* in detail from the Carnian flora of Lunz in Lower Austria and demonstrated the bennettitalean nature of these leaves that were originally described as marattialean ferns. Although epidermal details are unavailable from the Svalbard specimens, the fossils match exactly with the leaves described from Lunz, hence, assignment to *N. angustior* is justified. Epidermal details have been published in detail by Pott et al. (2007c) from specimens from Lunz. *Nilssoniopteris angustior* is found mainly at Kapp Lee on Edgeøya, but also occurs at Fleur de Lyshamna on Spitsbergen. Vasilevskaya (1972, 1983) described leaves with some reservation as *Taeniopteris* sp. from Trehøgdene and Kollerfjellet of Hopen that are slender, but fit comfortably in the range from the specimens from Lunz assigned to *N. angustior* (Pott et al. 2007c). The Lunz material, originally described as *Taeniopteris* (Stur 1885) and *Macrotaeniopteris* (Krasser 1909) was unknown to Vasilevskaya since it was not figured until 2007.

Geographic and stratigraphic range.—Europe; Carnian.

Ginkgophyta

Order Ginkgoales Gorozhankin, 1904

Family incertae familiae

Genus *Arberophyllum* Doweld, 2000

Type species: *Arberophyllum florinii* (Kräusel, 1943) Doweld, 2000; from the Carnian of Lunz, Lower Austria, Austria.

Remarks.—*Arberophyllum* forms an isolated taxon that differs in various morphological traits from other members of the Mesozoic ginkgophytes (Tralau 1968; Dobruskina 1998; Pott et al. 2007d). The most characteristic features of *Arberophyllum* are the strap-shaped leaf and absence of a petiole. The generic name is a substitute for *Glossophyllum* Kräusel, 1943, which is preoccupied by a genus of extant mosses (for details, see Farr and Zijlstra 1996; Doweld 2000).

Arberophyllum spetsbergensis (Vasilevskaya, 1972) Doweld, 2000

Fig. 9E–G, O.

1972 *Glossophyllum*(?) *spetsbergense*; Vasilevskaya 1972: 52, pls. 5: 3b; 9: 1b; 14: 3b; 16: 6–8; 17: 1–3a.

1983 *Desmiophyllum* sp. 1; Vasilevskaya 1983: 143, pl. 6: 5.

1983 *Desmiophyllum* sp. 2; Vasilevskaya 1983: 143, pl. 6: 6.

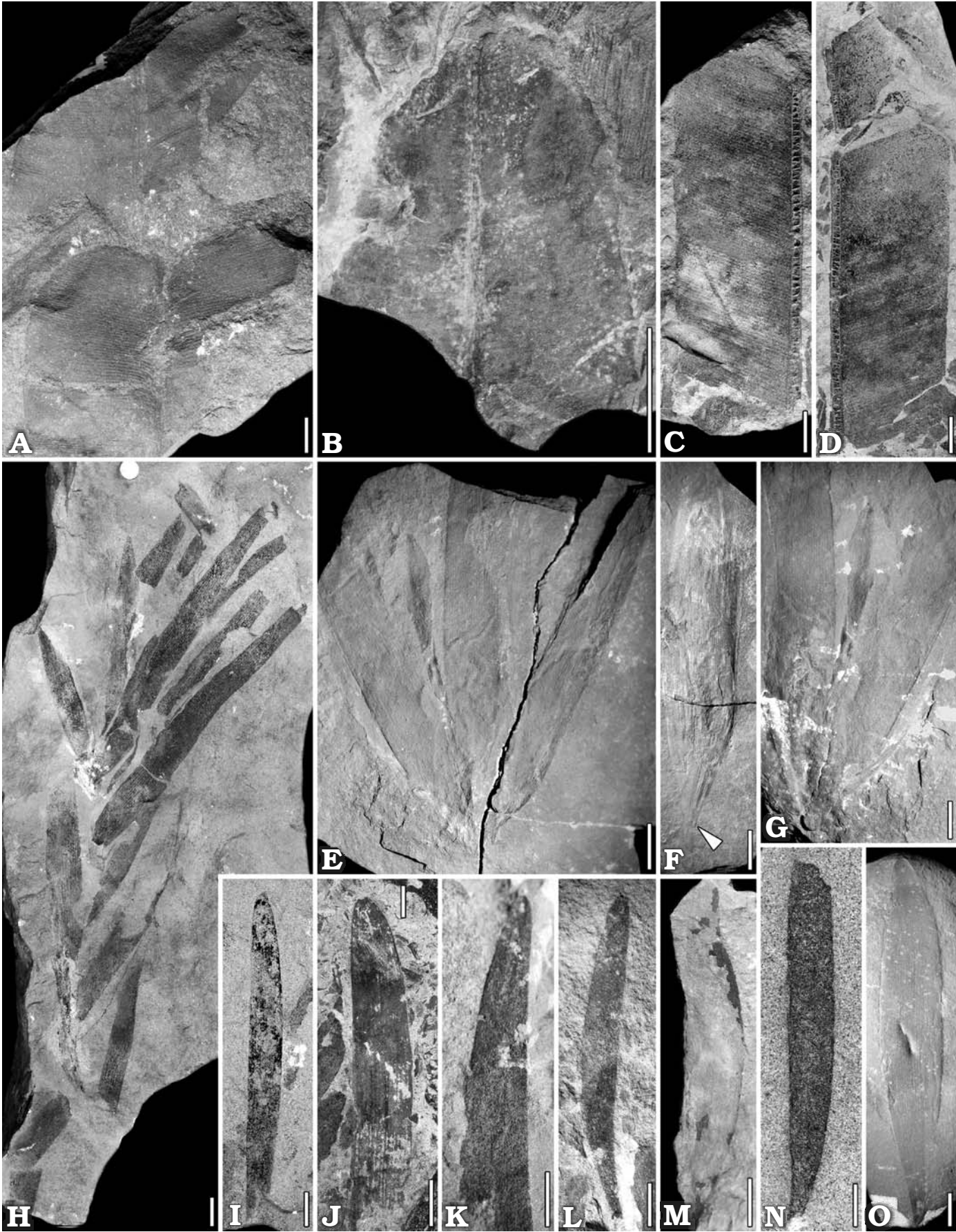
2000 *Arberophyllum spetsbergense* (Vasilevskaya 1972); Doweld 2000: 93.

Material.—Spitsbergen: Fleur de Lyshamna (NRM S080073, S080087, S080107–S080109); Hyrnefjellet (VSEGEI 10979-28, 10979-72–10979-74, 10979-95–10979-97); Wimanfjellet (VSEGEI 10979-08, 10979-29); Teistberget (VSEGEI 10979-66, 10979-75). Barentsøya: Schweinfurthberget (VSEGEI 10979-61). Edgeøya: Kapp Lee (NRM S080205, S080239; VSEGEI 10979-24, 10979-25, 10979-53, 10979-71, 102-29-12). Hopen: Kollerfjellet (?VSEGEI 21/12163, 22/12163). Carnian (Upper Triassic).

Description.—*Arberophyllum spetsbergensis* leaves are common in Svalbard; their most characteristic features are the tongue- or strap-shaped lamina and the parallel veins (Fig. 9E–G, O). Leaves are consistently 100–115 mm long and 16–19 mm wide in the middle (= broadest) portion of the lamina (Fig. 9F). The leaves lack a petiole and a central rachis. The lamina tapers towards the base, which is typically 3–5 mm wide. The apex of the leaves is acutely rounded. Tapering is relatively abrupt and margins in the middle portions of the leaf are almost parallel. Veins are distinct but not very prominent. They are parallel and bifurcate close to the base of the leaf to support the whole lamina. Vein density is 12–15 veins/cm in the broadest part of the lamina. No anastomoses are visible and each vein is assumed to persist until the apex of the leaf.

Remarks.—Separation of *Arberophyllum* and *Desmiophyllum* foliage is almost impossible given the weak characters differentiating these very variable but similar appearing foliage types. If epidermal details are available, the leaves may

Fig. 9. Cycadophytes and ginkgophytes from the Carnian (Upper Triassic) strata of Svalbard. **A–D.** *Nilssoniopteris angustior* (Stur ex Krasser, 1909) → Pott, Krings, and Kerp, 2007. **A.** NRM S080078-02, from Fleur de Lyshamna. **B.** NRM S080221-02, from Kapp Lee. **C.** NRM S080235, from Kapp Lee. **D.** NRM S080236-02, from Kapp Lee. **E–G.** *Arberophyllum spetsbergensis* (Vasilevskaya, 1972) Doweld, 2000. **E.** VSEGEI 10979-95, from Hyrnefjellet. **F.** VSEGEI 10979-74, from Hyrnefjellet; note the contracted leaf base (arrowhead). **G.** VSEGEI 10979-72, from Hyrnefjellet. **H–N.** *Arberophyllum substrictum* sp. nov. **H.** NRM S080079, from Fleur de Lyshamna, holotype. **I.** NRM S080255, from Bertilryggen. **J.** NRM S080239-03, from Kapp Lee. **K.** VSEGEI 10979-94, from Agardhbukta. **L.** VSEGEI 10979-66, from Teistberget. **M.** VSEGEI 10979-77, from Wimanfjellet. **N.** NRM S080059, from Midterhukfjellet. **O.** *Arberophyllum spetsbergensis* (Vasilevskaya, 1972) Doweld, 2000, VSEGEI 10979-73, from Hyrnefjellet. Scale bars 10 mm.



be distinguished by the shape of the stomata that are elongate in *Desmiophyllum* and more circular in *Arberophyllum* (Florin 1936; Kräusel 1943; Pott et al. 2007d). However, this character, given by Florin (1936), appears to be very inconsistent even in Florin's (1936) material, hence unreliable. For macro-morphological differentiation, the number of veins in the middle (= broadest) portion of the leaves may indicate if a leaf is better placed in *Arberophyllum* (less than 20 veins/cm) or in *Desmiophyllum* (more than 20 veins/cm). Following this strategy, all the Svalbard leaves may be assigned with confidence to *Arberophyllum*. This is also supported by the circular stomata of some of the specimens identified as *Glossophyllum* sp. by Vasilevskaya (1972) that are here regarded to belong to *A. substrictum* (see below). One specimen from Hyrnefjellet indicates that the leaves of *A. spetsbergensis* were arranged in dense clusters on short shoots (Fig. 9E, G), which may have been shed as whole units (cf. Pott et al. 2007d).

Leaves of *Arberophyllum spetsbergensis* are similar to *A. substrictum* (see below) and *A. florinii*, the last of which is very common in the Carnian Lunz flora and probably the best-known *Arberophyllum* species in general (Pott et al. 2007d; Pott and Krings 2010). However, *A. spetsbergensis* leaves are distinguished from both by their shorter and broader lamina, with more prominently tapered bases and apices, and by their clustered arrangement on short shoots in contrast to the supposed convolute (or alternate) arrangement of the leaves in *A. substrictum* and *A. florinii* (see below; cf. Kräusel 1943; Pott et al. 2007d; Pott and Krings 2010). One leaf from Fleur de Lyshamna fits the description of *A. spetsbergensis* very closely, but reaches 169 mm in length, which is more than 50% longer than other specimens. *Arberophyllum spetsbergensis* is relatively common at various localities in Spitsbergen, Edgeøya, and Barentsøya.

Geographic and stratigraphic range.—Svalbard; Carnian.

Arberophyllum substrictum sp. nov.

Figs. 6A, 9H–N.

1972 *Glossophyllum* sp.; Vasilevskaya 1972: 53, pls. 17: 4–7; 18: 1–4.
?1972 *Podozamites pseudolanceolatus*; Vasilevskaya 1972: 54, pl. 19: 3.

Etymology: From Latin *substrictus*, narrow; after the narrow shape of the leaves.

Holotype: NRM S080074/S080079 (counterparts); axis with alternately arranged leaves; Fig. 9H.

Type locality: Fleur de Lyshamna, Wedel Jarlsberg Land, Spitsbergen, Svalbard, Norway.

Type horizon: De Geerdalen Formation or Bravaisberget Formation, Kapp Toscana or Sassendalen Group, Upper Triassic (most likely Carnian–Rhaetian).

Diagnosis.—Strap-shaped leaves arranged alternately on prominent axes, slightly tapering towards acutely rounded apex and slender base; venation parallel, veins bifurcating close to the base; leaves amphistomatic, epidermal cells typically isodiametric, stomatal complexes round, guard cells surrounded by 6–7 subsidiary cells each producing one papilla overarched the porus.

Material.—Spitsbergen: Bertilryggen (NRM S080255); Midterhukfjellet (NRM S080058, S080059); Fleur de Lyshamna (NRM S080074, S080076, S080078, S080079, S080087, S080089, S080104); Wimanfjellet (VSEGEI 10979-08, 10979-13, 10979-29, 10979-77); Agardhbukta (VSEGEI 10979-94); Teistberget (VSEGEI 10979-03, 10979-66, 10979-75). Edgeøya: Kapp Lee (NRM S080198, S080205, S080217, S080219, S080221, S080222, S080227–S080233, S080237, S080239); Kvalpynten (NRM S080242). Carnian (Upper Triassic).

Description.—*Arberophyllum substrictum* is characterised by strap-shaped leaves 9–11 mm wide. The longest fragment is 108 mm long suggesting a maximum leaf length of around 120 mm. No petiole is present; the leaf base is poorly preserved but typically <2 mm wide (Fig. 9L–N). Leaf apices are rounded to acute but not pointed (Fig. 9I–L). Leaves are more slender than and not as robust as those of *A. spetsbergensis*; they taper towards the base and apex more smoothly. Leaves contain distinct but not very prominent parallel veins (Fig. 9I) with a density of 7–8 veins/cm in mid-lamina. Veins bifurcate one or two times in the basal part of the leaf and proceed to the apex without further bifurcations. Epidermal anatomy is known from one specimen from Wimanfjellet (see Vasilevskaya 1972) and is superficially similar to that of *A. florinii* from the Carnian of Lunz (cf. Pott et al. 2007d). Two specimens indicate that leaves of *A. substrictum* were arranged alternately on prominent axes (Figs. 6A, 9H).

Remarks.—*Arberophyllum substrictum* is easily differentiated from *A. spetsbergensis* by its more slender shape, more gentle apical and basal taper and less densely arranged veins. The arrangement of leaves on the axes is, as far as visible, also different. *Podozamites pseudolanceolatus* Vasilevskaya, 1972 might belong here, but epidermal anatomy is unknown for that species. Vasilevskaya (1972) published one specimen under the name *Glossophyllum* sp., which had a well-preserved cuticle (see Vasilevskaya [1972] for details); this is also assignable to *A. substrictum* on the basis of its cuticle architecture. *Arberophyllum florinii* from the Carnian of Lunz is very similar to *A. substrictum*, but differs in its distinctly smaller size. *Podozamites* leaves differ from *Arberophyllum* by the more regular arrangement and architecture of the stomata and the rectangular shape of the epidermal cells (Doludenko 1967). Unfortunately, no fresh cuticle could be retrieved from any Svalbard specimen even though I tried with one promising sample. Therefore, some of the specimens assigned here to *Arberophyllum* might in fact be *Podozamites*, but for an unambiguous assignment, cuticles are essential to reveal the differences in epidermal anatomy (cf. Doludenko 1967).

Geographic and stratigraphic range.—Svalbard; Carnian.

Genus *Ginkgoites* Seward, 1919

Type species: *Ginkgoites obovatus* (Nathorst, 1886) Seward, 1919; from the Rhaetian of Bjuv, Scania, Sweden.

Ginkgoites sp.

For illustration see Vasilevskaya (1983: pls. 5: 4; 6: 1).

Material.—Hopen: Kollerfjellet (?VSEGEI 17/12163); Carnian (Upper Triassic).

Remarks.—One specimen yielding cuticle has been described by Vasilevskaya (1983) from Kollerfjellet on Hopen. The specimen was not available for study because the repository of the specimens figured in Vasilevskaya (1983) is unknown. Confident identification of the specimen is virtually impossible due to the poor quality of Vasilevskaya's (1983) figures. However, *Ginkgoites* is not unexpected in the Carnian of Svalbard as the genus has been reported from the very similar coeval flora of Lunz (Pott and Krings 2010) and the cuticle illustrated by Vasilevskaya (1983) has some typical ginkgoalean epidermal features (e.g., papillate epidermal cells, circular and papillate stomata).

Division incerti divisionis

Order Caytoniales Harris, 1964

Family incertae familiae

Genus *Sagenopteris* Presl in Sternberg, 1838

Type species: *Filicites nilssoniana* Brongniart, 1825 (see Harris 1964); from the Hettangian of Höör, Scania, Sweden.

Sagenopteris sp.

Fig. 6C.

1972 Planta indet.; Vasilevskaya 1972: 55, pl. 19: 1, 2.

Material.—Spitsbergen: Hyrnefjellet (VSEGEI 10979-78); Carnian (Upper Triassic).

Description.—A fragmentary, 65.1 mm long, petiolate leaflet comes from Hyrnefjellet. The basally tapering lamina is 30.9 mm wide at its widest preserved part and is characterised by a midvein giving off numerous anastomosing secondary veins at an angle of c. 20°, arching to c. 50° towards the leaf margin (Fig. 6C). Vein density is c. 20 veins/cm at the leaf margin.

Remarks.—Only one specimen of *Sagenopteris* sp. was found in the Svalbard assemblages. It was originally published as *Planta indet.* by Vasilevskaya (1972), and indeed, its systematic assignment is somewhat problematic. The leaf also resembles examples described as *Gontriglossa* species from the Carnian Molteno Formation of southern Africa (Anderson and Anderson 1989). However, *Gontriglossa* is a typical Gondwanan taxon and has never been reported from the Northern Hemisphere. The only fossils from the Northern Hemisphere approaching the specimen under study are the petiolate leaflets of *Sagenopteris*, as described e.g., from the Middle Jurassic of Yorkshire or the Late Cretaceous of Greenland and assigned to the Caytoniales (Harris 1964; Boyd 1992). Anastomosing veins are also known from *Anthrophyopsis* foliage from the Rhaetian of e.g., Iran, but differences in the shape of the lamina and the venation are readily recognisable (Schweitzer and Kirchner 1998). A leaf identified as *Glossopteridium* from the Rhaetian of Poland

by Bochenski (1957) is similar to the leaves of *Sagenopteris* or *Glossopteris*. *Sagenopteris* is known from Rhaeto-Liassic to Late Cretaceous deposits, but has not yet been described from older strata. Specimens of *Sagenopteris* and *Gontriglossa* are strikingly identical even in epidermal anatomy right down to stomatal morphology (cf. Harris 1964; Anderson and Anderson 1989). Specimens of both genera have been identified as *Glossopteris* earlier (e.g., Brongniart 1830; Lindley and Hutton 1833; Thomas 1958), but their heterogeneity has been shown (Anderson and Anderson 1989). The reconstructions of the habit of the plants and the arrangement of the leaves highly differ from each other; Anderson and Anderson (1989) gave evidence by impressive fossils, whereas Harris (1964) did not publish photographs of any fossil specimens, but merely gave quite fragmentary line drawings. I assign the Svalbard specimen to *Sagenopteris* even though it would constitute the oldest representative of the genus, but I refrain from referring it to a formal species due to its fragmentary nature.

Discussion

Age of the flora.—The distribution of the fossil localities suggests that all assemblages come from the Carnian–Norian De Geerdalen Formation of the Kapp Toscana Group (see Fig. 1). A Carnian rather than a Norian age is suggested for most assemblages based on compositional similarities to Carnian assemblages elsewhere in Europe (Dobruskina 1994). Most assemblages contain at least one typical Carnian index taxon, such as *Neocalamites merianii*, *Asterotheca merianii*, *Danaeopsis marantacea*, *Pterophyllum filicoides*, or *P. brevipenne*. Solitary *Arberophyllum* from Midterhukfjellet is also a typical Carnian taxon. *Dictyophyllum* occurring at Wimanfjellet and Kapp Lee is more typically Norian or younger, but this taxon may come from a different layer than the bulk of the assemblage or may extend the range of the genus down into the Carnian.

Only the Hyrnefjellet assemblage may be slightly younger, probably Norian, based on the presence of species typically of that age (i.e., *Clathropteris obovata*, *Sagenopteris* sp.; see also statement of Dobruskina [1994] on the occurrence of the layers yielding the plant fossils). Some of the specimens assigned to *Paratatarina ptchelinae* from Fleur de Lyshamna (indicated as “below the *Pterophyllum* layer”) may also derive from this younger layer as they are of similar preservation as *P. ptchelinae* specimens from Hyrnefjellet. The position of this younger layer, below the older layers at Fleur de Lyshamna may be due to overfolding or thrust-faulting as indicated by Dallmann et al. (2001) for this area.

According to Dobruskina (1994), the plant fossils occur in two beds of the De Geerdalen Formation, in the upper Carnian, extending into the Norian (Mørk et al. 2013; Vigran et al. 2014), whereas the fossiliferous Lunz strata (see below for comparison) have been dated as Julian (= middle Carnian; cf. Roghi 2004). Dobruskina's (1994) account is

based on that of Vasilevskaya (1972) and the stratigraphic position of the fossiliferous beds may have been revised by more recent geological studies (see Harland 1997b; Mørk et al. 2013; Vigran et al. 2014). Fossils compared with the Late Triassic Central-East Asian *Pterophyllum firmifolium* from Teistberget and Hopen may derive from loose (ex situ) rocks on a beach, as indicated by their poor preservation, their wave-abraded edges, and by logbook/diary entries (see Introduction).

The striking similarity of the Svalbard flora and the Carnian floras of Lunz in Austria and Neuwelt in Switzerland strongly supports a Carnian age. This had been proposed by Vasilevskaya (1972) and stressed by Dobruskina (1994) before the thorough revision of the Lunz flora by Pott (2007), Pott et al. (2007c, f, 2008a, b), and Pott and Krings (2010). All three floras share a large number of taxa, such as *Neocalamites merianii*, *Equisetites conicus*, *Asterotheca merianii*, *Danaeopsis marantacea*, *Arberophyllum* spp., *Clathropteris* spp., *Pterophyllum filicoides*, *P. brevipenne*, and *Nilssoniopteris angustior*. The fern genera *Phlebopteris*, *Sphenopteris*, and *Cladophlebis* are typical of Carnian deposits and may also occur in Lunz and/or Neuwelt (CP personal observation, May 2011). Although the Svalbard flora shares some taxa with Ladinian floras of central Europe, a Late Triassic age is indicated by the presence of Carnian-diagnostic species (cf. Vasilevskaya 1972; Dobruskina 1994; Dallmann et al. 2001; Kelber and Nitsch 2005).

Distribution of the floral elements.—Collection bias has strongly affected the composition of the plant fossil assemblages recovered from Svalbard. However, there is a general similarity in the composition of the assemblages. The highest numbers of taxa are documented from Wimanfjellet (13 taxa), Kapp Lee (10) and Fleur de Lyshamna (8). These localities also provided the highest number of specimens (collectively 136 of the 227 studied specimens; Table 2). Hyrnefjellet yielded a large number of specimens but only five species. All taxa are rather arbitrarily distributed among the localities apart from Hyrnefjellet (Table 2). The most common taxa are *Neocalamites merianii* (occurring at 12 localities), *Paratatarina spetsbergensis* (10), *Asterotheca merianii* (9), *Pterophyllum filicoides* (9), *Arberophyllum substrictum* (8) and *Arberophyllum spetsbergensis* (7). *Nilssoniopteris angustior* (4) is rather common, but the remaining taxa are mostly known from one or two localities each (Table 2). The distribution of plants suggests a rather uniform flora across Svalbard, and the taxa are typical of Carnian deltaic environments as represented by the Lunz flora (Pott et al. 2008b).

Sphenophytes occur in almost all localities, usually represented by *Neocalamites merianii*. Similarly widely distributed among the localities is the marattialean *Asterotheca merianii*, a Ladinian–Carnian key species. Other ferns, representing all major fern groups existing at that time (i.e., Marattiaceae, Gleicheniaceae, Matoniaceae, and Polypodiaceae) are less widely distributed, usually with very restricted ranges. The highest fern diversity is report-

ed from Wimanfjellet, with six different species, whereas the two other well-sampled localities (Fleur de Lyshamna, Kapp Lee) are rather poor in ferns but more dominated by bennettitaleans and ginkgophytes. Both latter groups are well represented and occur at localities in all parts of Svalbard. The record of the Rhaetian *Sagenopteris* likely derives from a younger layer (see above), which is reflected in other Norian–Rhaetian taxa from the same locality, such as *Clathropteris obovata*.

In a brief and little known account, Vasilevskaya (1983) reported on a few more specimens and species from Hopen, which have been included in the present study. Later, Vasilevskaya (1987) reported on an additional questionable pteridosperm species from Svalbard, viz. *Vitaephyllum(?) spetsbergense* Vasilevskaya, 1987, based on collections from 1981 from Flowerdalen at Botneheia Mountain at Sassenfjorden. *Equisetites* cf. *Equisetites glandulosus*, *Paratatarina*, *Taeniopteris*, *Glossophyllum*, and *Desmiophyllum* were also found together with this species by Vasilevskaya (1987). None of these fossils except *Vitaephyllum(?) spetsbergense* were figured and none was available for study, but it is assumed that they are identical to the respective species described above (viz. *Equisetites* cf. *Equisetites conicus*, *Paratatarina spetsbergensis*, *Nilssoniopteris angustior*, *Arberophyllum spetsbergensis*, and *A. substrictum*).

Ecological implications.—The Svalbard flora likely grew in a near-shore, deltaic and locally lagoonal environment (Dallmann et al. 2001), similar to that invoked for the Lunz/Neuwelt ecosystem (Pott et al. 2008b). The grey shale, siltstone and sandstone beds of the Kapp Toscana Group are characterised by shallow marine and coastal fluvio-deltaic sediments. The ecosystem likely covered a large geographical area and developed within the incipient rift between Greenland and Scandinavia (Fig. 10). For the Rhaetian, extensive evidence for this North Atlantic floral sub-province is present in form of floras of similar composition restricted to the coastal plains of southern Sweden (Scania; Pott and McLoughlin 2009; Pott 2014), eastern Greenland (Jameson Land; e.g., Harris 1926, 1931; Pott 2014) and northern central Europe (e.g., Poland; Reymanówna 1963). For the Carnian, less evidence is available, since fossiliferous strata are rare. The Carnian strata in Jameson Land are barren (Kaj Raunsgaard Pedersen, personal communication 2012); even palynological analyses did not yield any pollen (e.g., Pedersen and Lund 1980). In southern Sweden, strata older than the Norian are not exposed, and no fossils are available (e.g., Lindström and Erlström 2006). The flora from the famous Carnian Krasiejów biota in south-western Poland is generally poor in species and mainly consists of poorly studied conifers and other gymnosperms making a comparison with Svalbard and Lunz impossible (Dzik and Sulej 2007). High-latitude Carnian floras eastwards are rare. A few accounts have been reported from Franz Josef Land, Novaya Zemlya, and Far East Siberia; however, their composition becomes progressively different further eastward from the Svalbard assem-

Table 2. Distribution of taxa and specimens within the fossil localities in Svalbard. * *Paratatarina pichelinae* is here occurring in a different layer. See text. ** Vasilevskaya (1983) mentioned additional specimens from Lyngfjellet and Iversenfellet of Hopen yielding *Pterophyllum* sp. and *Glossophyllum* sp. The specimens were not figured and assignment of the species is equivocal. *** Vasilevskaya (1987) described additional specimens including one additional species from Flowerdalen at Botneheia Mountain at Sassenfjorden (viz. *Vitaephyllum spetsbergense*), which were not available for study, and therefore are not included in this synopsis.

Species	Localities	Spitsbergen										Barents-øya		Edgeøya			Hopen						Localities per species			
		Bertilryggen	Amadeusberget	Edlundfjellet	Sassenfjorden***	Trehøgden	Midterhukfjellet	Fleur de Lyshamna	Wimafjellet	Wichebukta	Teistberget	Agardhbukta	Hyrnefjellet	Vossbukta	Schweinfurthberget	Kapp Lee	Kvalpynten	Kapp Pechuel Lösche	Negerpynten	Nørdestfjellet	Lyngfjellet	Blåfjell		Kollerfjellet	Husdalen	Werenskioldfjellet
<i>Neocalamites merianii</i>	Ladinian–Carnian	X	X	X	X	X	X	X	X	X	X					X	X	X		X	X	X				
<i>Neocalamites</i> sp.	Carnian				X																					
<i>Equisetites</i> sp. cf. <i>E. conicus</i>	Carnian								X																	
<i>Asteroteca merianii</i>	Ladinian–Carnian	X			X		X	X	X	X			X				X		X							
<i>Danaeopsis</i> sp. cf. <i>D. marantacea</i>	Ladinian–Carnian								X							X										
<i>Dictyophyllum exile</i>	Norian–Middle Jurassic															X										
<i>Dictyophyllum</i> sp.	Norian–Middle Jurassic								X																	
<i>Clathropteris</i> cf. <i>C. obovata</i>	Norian–Middle Jurassic											X														
<i>Clathropteris</i> sp.	Carnian–Middle Jurassic							X	X																	
<i>Phlebopteris</i> sp. cf. <i>P. muensteri</i>	Carnian–Lower Cretaceous	X					X	X	X																	
<i>Cladophlebis</i> sp.	Ladinian–Lower Cretaceous	X																								
<i>Cladophlebis</i> sp. cf. <i>C. remota</i>	Carnian						X	X	X																	
<i>Sphenopteris</i> sp.	Carnian			X																						
<i>Paratatarina pichelinae</i>	Carnian	X	X		X		X*	X	X	X	X	X	X	X	X	X	X	X				X				
<i>Ptilozamites</i> sp.	(?Anisian–)Rhaetian–Lower Jurassic																						X			
<i>Pterophyllum filicoides</i>	Carnian						X	X	X	X	X	X	X	X	X	X	X	X		X**	X	X	X	X	X**	
<i>Pterophyllum brevipenne</i>	Carnian						X	X	X																	
<i>Pterophyllum</i> sp. cf. <i>P. firmifolium</i>	Carnian–Norian									X							X		X							
<i>Pterophyllum</i> sp.	Carnian				X																					
<i>Nilssoniopteris angustior</i>	Carnian				X		X	X									X					X				
<i>Arberophyllum spetsbergensis</i>	Carnian						X	X	X	X	X	X	X	X	X	X	X					X	X	X	X**	
<i>Arberophyllum substrictum</i>	Carnian	X				X	X	X	X	X	X	X	X			X	X									
<i>Ginkgoites</i> sp.	Carnian																					X				
<i>Sagenopteris</i> sp.	Carnian (<i>Gontriglossa</i>), Rhaetian–Jurassic											X														
	Species per locality	5	1	2	2	4	1	8	13	1	5	2	5	1	2	9	3	3	1	2	1	2	4	2	1	2
	Specimens studied	15	2	3	4	5	2	39	26	3	5	2	25	6	4	66	3	7	3	7	0	2	13	1	6	0
																										249

blage (Vasilevskaya 1972, 1984a, b, 1985; Dobruskina 1994) in terms of generic and specific composition. These floras mostly share the same genera, but have different species of, i.e., *Equisetites*, *Neocalamites*, *Cladophlebis*, *Asterotheca*, *Arberophyllum*, *Pterophyllum*, and additional taxa appear (e.g., *Drepanozamites*, *Anomozamites*, *Desmiophyllum*; cf. Dobruskina 1994).

The similarity of the Svalbard flora to the central European floras such as Lunz and Neuwelt, amongst others, and their distinct difference from coeval floras further east argues for a generally rather poor and uniform flora in deltaic environments within the central part of Laurasia with its northern and southern shores. Geographic latitude (Svalbard around 60° N and Lunz around 30° N; see Fig. 10) influenced the composition of the floras apparently less than longitudinal distribution. Whereas the more southern non-coastal Carnian–Norian floras from the Chinle Formation and the Newark Basin have almost no taxa in common with the central European floras (cf. Ash 1980), the floras from Svalbard and Lunz/Neuwelt share a large number of taxa. According to Dobruskina (1994), the Carnian floras of central Europe and Svalbard have little in common with coeval floras from the Donetsk Basin and further east. The shared occurrence of key-Carnian species between the floras of central Europe and Svalbard may thus indicate that the North Atlantic floristic sub-province, which was well-developed by the Rhaetian (Pott and McLoughlin 2011: fig. 10), was already established by the Carnian (Fig. 10).

Typical taxa of central European Carnian floras, such as *Equisetites arenaceus* (Jaeger, 1827) Schenk, 1864 and cycads or conifers (see e.g., Kelber and Nitsch 2005) were not found to date on Svalbard. *Equisetites arenaceus* is a large sphenophyte that dominated Ladinian–Carnian swamps and deltaic environments (Kelber and Van Konijnburg-van Cittert 1998). Due to its large size, it may have had special ecological requirements and favoured more tropical or warm climate, whereas *Neocalamites merianii* may have been able to grow at 60° N. Cycads are absent from Svalbard whereas they are rather common in the Lunz flora (Pott et al. 2007a; Pott and Krings 2010), which may indicate special ecological requirements of the plants (cf. Norstog and Nichols 1997). However, cycads are also absent from the Carnian of Neuwelt (CP personal observation, August 2008). Conifers are completely absent from the Svalbard flora, which may result from the environmental setting of the Svalbard sediments; in the Lunz flora, they are also underrepresented (Pott and Krings 2010); in the Yorkshire Jurassic, for example, conifers are generally rare and supposed to represent the flora of the land above the flood-plain level (Harris 1979), but range throughout the complete Deltaic series.

Bennettitalean distribution.—The Svalbard flora is interesting in terms of the distribution of Bennettitales. Bennettitaleans had their diversity and distributional heyday in the very latest Triassic (Rhaetian) to Middle Jurassic (e.g., Harris

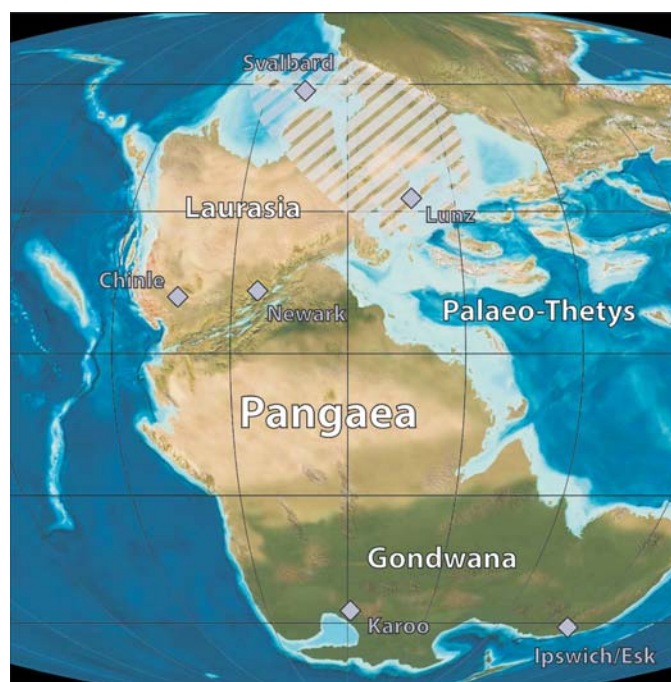


Fig. 10. World map of the Late Triassic (Carnian, 220 Mya) showing the position of key floras comprising bennettitaleans (grey diamonds) and supposed North-Atlantic floral sub-province (striped area). Base map: Ron Blakey, CP Geosystems, Inc., Flagstaff, AZ, USA.

1926, 1932, 1969; Pott and McLoughlin 2009; Pott et al. 2010b; Pott 2014). The demise of the group is also intriguing. Most bennettitalean genera show a dramatic decline through the mid-Cretaceous, contemporaneous with the rise of the flowering plants (e.g., Watson and Sincov 1992; Pott et al. 2010b; Friis et al. 2011). Some hypotheses for their demise invoke competitive displacement by diversifying opportunistic angiosperms. Recent detection of a bennettitalean in the Oligocene of Australia, however, reveals that bennettitaleans survived long after the rise of the angiosperms and the end-Cretaceous mass-extinction, but may have been isolated in high-latitude refugia (McLoughlin and Pott 2010; McLoughlin et al. 2011).

Whereas the stepwise demise of the bennettitaleans is quite well documented, the origin of the group sometime in the Middle Triassic remains obscure. As convincing examples of bennettitaleans from older strata have not yet been found (Pott et al. 2010b), Carnian fossils remain the oldest indubitable examples of this group (Pott et al. 2010a). However, the bennettitaleans from Svalbard expand the known geographic range of this group from southern Gondwana to northern Laurasia during the Carnian indicating that bennettitaleans were cosmopolitan already by the Carnian (Fig. 10; e.g., Ash 1980; Anderson and Anderson 1989) suggesting that the group had a much earlier origin (cf. Pott et al. 2007c, 2010b; Pott 2014). Thorough investigation of Carnian floras from other regions of the world, which have not been considered in this study, ought to provide significant insights into the origin and diversification of this enigmatic group of seed plants.

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