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Article

The ferns of the Middle Triassic flora from Thale (Germany)

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With 12 figures and 2 tables

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Abstract: This is the third modern day paper on the Middle Triassic flora from Thale to be published, dealing with the ferns. Two species belong to the genus *Asterotheca*; *Asterotheca merianii* (Brongniart) Stur is one of the most common elements in the flora, while *Asterotheca thalensis* n. sp. is rarer in the assemblage. Both species yielded *in situ* round, pseudomonolete granulate spores. *Danaeopsis marantacea* (Presl in Sternberg) Schimper is the most common fern in the Thale flora; for the first time *in situ* spores from this species are described. *Rhacophyllum crispatum* (Münster in Sternberg) n. comb. might be the aphleboid structure belonging to *Danaeopsis marantacea*. *Todites gaillardotii* (Brongniart) n. comb. is here described for the first time from the Erfurt Formation (Ladinian) of Germany. Moreover, its *in situ* spores are documented as well. *Neuropteridium grandifolium* (Schimper et Mougeot) Compter is just a rare element in this flora. *Clathropteris meniscioides* Brongniart and *Phlebopteris* sp. from Thale are earliest representatives of these genera known so far; all three species are represented only by sterile frond fragments. *Cladophlebis remota* (Presl) Van Konijnenburg-Van Cittert et al. is relatively rare, while *Cladophlebis leuthardtii* Leonardi is very rare in this flora; fertile frond fragments are still missing for both species. For the first time *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg is represented by sterile and fertile material in the Germanic Basin. *Sphenopteris* vel *Cladophlebis* sp. A might be shade leaves of *Sphenopteris schoenleiniana*. *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern is a very rare element in this flora and only represented by sterile frond fragments, in contrast to *Symopteris rumpfii* (Schenk) Kustatscher et al. The latter yielded *in situ* spores (round, trilete, smooth).

Key words: Lower Keuper, Erfurt Formation, Ladinian, Middle Triassic, ferns, *in situ* spores.

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1. Introduction

The Thale flora is a nicely preserved but poorly known Keuper flora from eastern Germany. Tore Linnell described part of the flora, focusing on the two genera *Sphenozamites* and *Scytophyllum* (Linnell 1932, 1933). He provided also a list of other species, however, without descriptions and figures (Linnell 1933). Later, Franke (1936a) described *Equisetites asperrimus*, while Axsmith & Taylor (1997) included some material in their study on *Glyptolepis*. Our detailed analysis and taxonomic revision of the Thale flora was started in 2006, focussing first on the lycophytes and horsetails and later on the cycadophytes and seed ferns (Kustatscher & Van Konijnenburg-Van Cittert 2008, 2010). Here we present the third part of our study of the Thale flora, a revision of the ferns. Based on the material from the Naturhistoriska Riksmuseet in Stockholm Linnell (1933) listed the following ferns: *Neuropteridium* sp., *Pecopteris latepinnata* Leuthardt, *Pecopteris schoenleiniana* Brongniart, *Cladophlebis remota* Presl, *Bernoullia helvetica*

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Heer, *Pseudodanaeopsis marantacea* (Presl) Krasser. We have seen material in two more collections (Naturhistoriska Riksmuseet in Stockholm, Netherlands Centre for Biodiversity – Naturalis) and revised the Stockholm material. Comparisons to other fern taxa were mostly restricted to Middle-Upper Triassic ferns (with emphasis on Ladinian ones).

2. Material and methods

The precise geographic and stratigraphic position of the outcrop that yielded the Thale flora is unknown (Kustatscher & Van Konijnenburg-Van Cittert 2008). In the literature the material has been attributed generally to the Keuper (Nathorst 1912) or to the Middle Keuper (Brandes 1901, 1904; Franke 1936a, 1936b; Axsmith & Taylor 1997), which are both rich in fossil animals and plants in the Thale area (see also Schröder & Dahlgrün 1927). Palynological analyses from a specimen of the collection restricts the plant fossils to an upper Ladinian age (pers. comm. Carmen Heunisch, Landesamt für Bergbau, Energie und Geologie im Geozentrum Hannover); for a more detailed discussion see Kustatscher & Van Konijnenburg-van Cittert (2008).

The material was studied under dissecting microscope. When possible, *in situ* spore preparations were made by maceration in Schulze's reagent ($KClO_3$ and 30% HNO_3), followed by neutralisation with ammonium hydroxide (5%). The sporangia were then separated into single or groups of spores (depending on the maturity of the spores) with the aid of needles. The spores were mounted in glycerine jelly and sealed with paraplast (see also Batten 1999). Some of the sporangia and spores were examined under a Hitachi S3500N SEM scanning electron microscope (SEM) at the University of Utrecht.

The original material of P.B. Richter ("S" prefix) is stored in the Naturhistoriska Riksmuseet in Stockholm; smaller collections are stored at Netherlands Centre for Biodiversity – Naturalis ("JMS" prefix) and at the Museum für Naturkunde – Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin ("MB.Pb" prefix).

3. Systematic palaeontology

Division Pteridophytes
Order Marattiales
Family Marattiaceae
Genus *Asterotheca* Presl ex Corda 1845

Asterotheca merianii (Brongniart) Stur 1885
Figs. 1A-I, 12A

Selected synonymy:

1828a *Pecopteris meriani* Brongniart, p. 194. (*nomen nudum*)
1834 *Pecopteris meriani* Brongniart. – Brongniart, p. 289-290, pl. 91, fig. 5.
1838 *Pecopteris meriani* Brongniart. – Presl in Sternberg, p. 156.
1864 *Alethopteris meriani* Brongniart. – Schenk, p. 89-90, pl. 8, fig. 2.
1865 *Pecopteris meriani* Brongniart. – Heer, p. 48, pl. 2, figs. 2-3.
1877 *Asterocarpus meriani* (Brongniart) Heer, p. 64, 68, pl. 24, figs. 4-6.
non 1883 *Asterocarpus virginensis* Fontaine, p. 41-44, pl. 19, figs. 2-5, pl. 20, figs. 1-2, fig. 21, pl. 22, figs. 1-3, pl. 23, figs. 1-4, pl. 24, figs. 1-2.
non 1883 *Asterocarpus virginensis* var. *obtusiloba* Fontaine, p. 45-46, pl. 21, figs. 3-4, pl. 24, figs. 3-5, pl. 25, fig. 1.
non 1883 *Asterocarpus platyrachis* Fontaine, p. 46-47, pl. 25, figs. 2-6, pl. 26, fig. 1, pl. 49, fig. 2.
non 1883 *Asterocarpus penticarpa* Fontaine, p. 48, pl. 26, fig. 2.
?1883 *Pecopteris rarinervis* Fontaine, p. 48-49, pl. 26, figs. 3-4.
non 1883 *Laccopteris carolinensis* (Emmons) Fontaine, p. 102, pl. 49, figs. 11, 12, 12a.
non 1883 *Laccopteris emmonsi* (Emmons) Fontaine, pl. 48, figs. 6-7.
1885 *Asterotheca meriani* (Brongniart) Stur, p. 97.

Fig. 1. A. *Asterotheca merianii* (Brongniart) Stur 1885, most complete specimen with oppositely to suboppositely inserted pinnae (S114345). **B**. *Asterotheca merianii* (Brongniart) Stur 1885, entire pinnae (S114344). **C**. *Asterotheca merianii* (Brongniart) Stur 1885, detail of pinnules with typical venation (114803). **D**. *Asterotheca merianii* (Brongniart) Stur 1885, fertile pinnae showing the arrangement and number of sori (S114636). **E**. *Asterotheca merianii* (Brongniart) Stur 1885, fertile pinnules with the cast of the single sori showing the 4 sporangia (S114480). **F**. *Asterotheca merianii* (Brongniart) Stur 1885, sporangia fragment (S114731), scale = 50 µm. **G**. *Asterotheca merianii* (Brongniart) Stur 1885, group of slightly immature spores (MB.Pb. 2010/477), scale = 50 µm. **H**. *Asterotheca merianii* (Brongniart) Stur 1885, immature *in situ* spore with pseudoaperture visible (S114731), scale = 25 µm. **I**. *Asterotheca merianii* (Brongniart) Stur 1885, immature *in situ* spore with folds (S114731), scale = 25 µm. – Scale = 10 mm if not otherwise indicated.

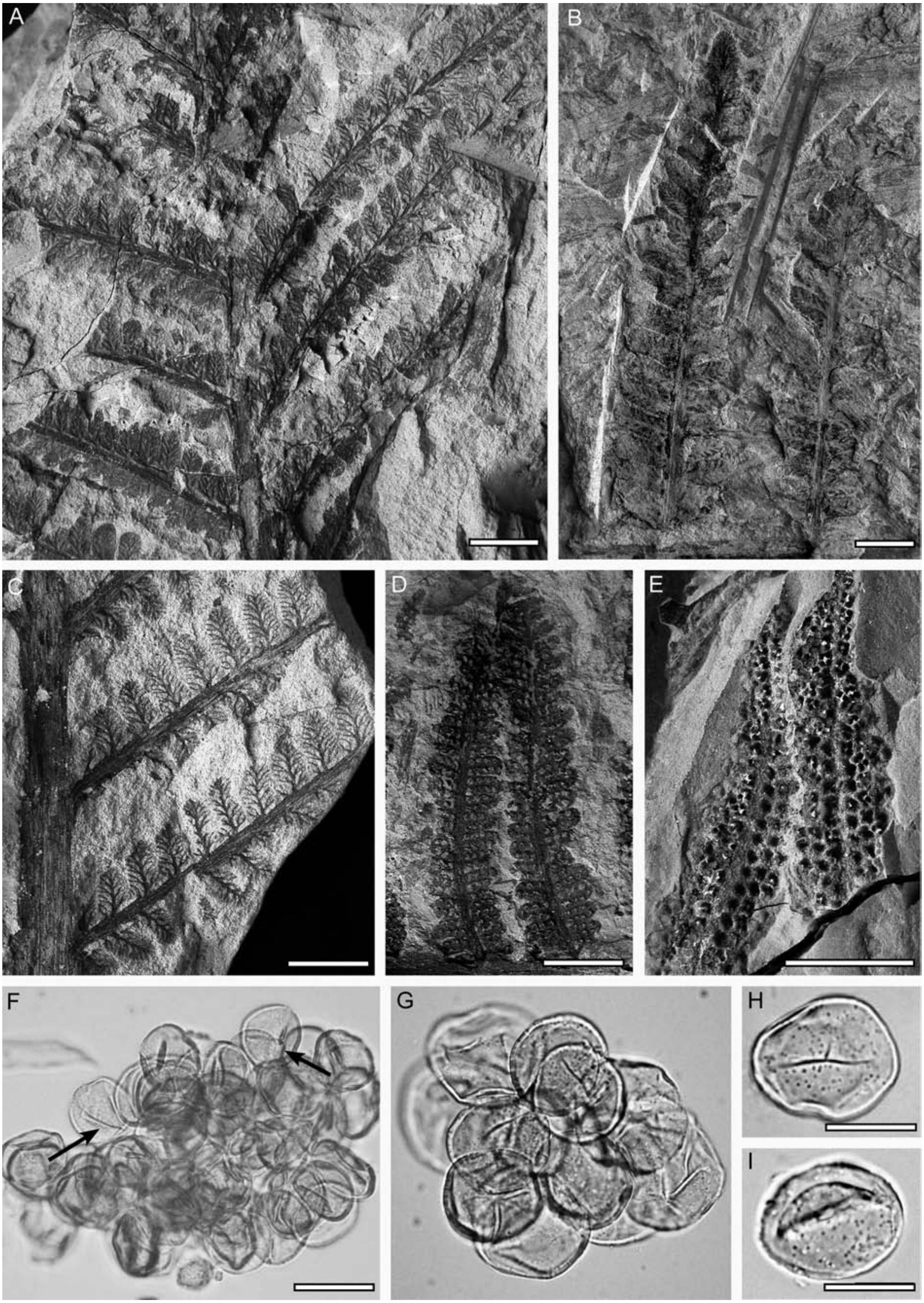

Fig. 1

1885 *Asterotheca intermedia* Stur, p. 97.
1885 *Asterotheca lacera* Stur, p. 97.
1904 *Asterocarpus meriani* Brongniart. – Leuthardt, p. 31-32, pl. 21, figs. 4-5.
1908 *Asterotheca meriani* (Brongniart) Stur. – Nathorst, p. 7-8, pl. 1, figs. 9-12.
1909a *Asterotheca meriani* (Brongniart) Stur. – Krasser, p. 17, 20-21, 32-33.
1909b *Asterotheca meriani* (Brongniart) Stur. – Krasser, p. 108.
1922a *Asterotheca meriani* (Brongniart) Stur. – Frentzen, p. 5-6, 10, 13.
1922b *Asterotheca meriani* Heer. – Frentzen, p. 25, 26.
1956 *Asterotheca meriani* (Brongniart) Stur. – Bhardwaj & Singh, p. 51-54, text-fig. 1, pls. 1-2.
1962 *Asterotheca merianii* (Brongniart) Stur. – Potonié, p. 92, pl. 9, figs. 213, 214a, b.
1968 *Asterotheca ? meriani*. – Ricour, p. 34, 40-1, text-fig. 8, pl. 11, figs. 2-5.
?1995 cf. *Bernoullia Helvetica*. – Kelber & Hansch, p. 95, 97, fig. 207.
1998 *Asterotheca meriani* (Brongniart) Stur. – Dobruskina, p. 317, 333, 342, tab. 7, 10, fig. 6D.

Description. This species is one of the most abundant ferns in the Thale flora; more than 130 sterile and fertile frond and pinna fragments have been assigned to it. The bipinnate frond fragments are up to 240 mm long and 150 mm broad with a strong rachis (basally up to 10 mm, reducing apically) and oppositely to suboppositely inserted pinnae (e.g. MB.Pb. 2001/478, S114344, S114345, Fig. 1A). The pinnae are up to 80 mm long and basally up to 15 mm wide, reducing apically to 5 mm width (e.g. S114344, S114459, Fig. 1B). The rachis of the pinnae starts almost perpendicularly from the main rachis with a width of 2 mm, reducing apically (~ 0.5 mm). The elongated pinnules (4-10 x 3-3.5 mm) with a rounded apex are attached (almost) perpendicularly and with broad basis to the rachis; there is a single apical pinnule (~10 x 5 mm, e.g. S114459**,** S114345, Fig. 1A). The midrib is distinct with 4-6 pairs of secondary veins arising at an angle of 45-60°. The secondary veins bifurcate once in the middle part of the lamina (e.g., 114803, Figs. 1C. 12A). The primary veins become particularly evident in fertile pinnules, where the bifurcations of the secondary veins become invisible. In fertile pinnules 4-5 pairs of sori plus one terminal sorus are attached to the area between the veins (e.g. S114345, S114723, S114736, Fig. 1D). The sori are less than 1 mm in diameter, consisting of 4 ovale to almost pyramidal sporangia which are basally connate. The impressions in the sediment show the free space between the single sporangia (e.g. S114480, S114636, Fig. 1D-E). Sporangia are c. 300 x 600 µm and yielded a large number (>1000) of ‘pseudomonolete’, round spores. Most specimens yielded immature spores, but in those having masses of more or less mature spores (e.g., S114731, S114745, Fig. 1F-G) the dimensions could be measured (mean diameter of c. 40 µm, varying from 28 to 45 µm). The spore wall is thin, often folded and granulate. The monolete scar is rather short, slit-like, without a margo (S114731, Fig. 1 H-I). Even immature spores never seem to be arranged in clear tetrads; but they build groups where neighbouring spores contact each other randomly but never at the monolete scar; this is why we call these spores ‘pseudomonolete’ rather than monolete.

Material. S114031, S114041, S114050, S114086, S114123, S114126, S114143, S114167, S114219, S114256, S114306, S114318, S114331, S114337, S114340, S114344-46, S114349, S114356, S114406, S114429, S114431, S114437, S114459, S114480, S114520, S114540, S114542, S114628, S114717-18, S114720-21, S114723-25, S114727-37, S114739-40, S114744, S114748-60, S114762, S114764-65, S114767-69, S114771-89, S114792-98, S114801-03, S114805, S114808-11, S114815, S114817-19, S114821-28, S114831-33, S114838, S114846, S114850, S114853, S114856-58, S115862, S115871, S115908, S115918, S115928, S114169, JMS 52375, JMS 52382a, MB.Pb. 2000/244, MB.Pb. 2000/250, MB.Pb. 2000/253, MB.Pb. 2000/254, MB.Pb. 2000/255, MB.Pb. 2010/43, MB.Pb. 2010/32b, MB.Pb. 2010/33, MB.Pb. 2010/39, MB.Pb. 2010/40.

Discussion. Brongniart introduced *Pecopteris merianii* for the first time in 1828a as *nomen nudum*, providing later (Brongniart 1834: 289-290, pl. 91, fig. 5) a diagnosis and figures of the species. Goeppert (1836: 311) transferred it, without any explanations, to the genus *Alethopteris*, Heer (1877: 68) to *Asterocarpus* and Stur (1885: 97) to *Asterotheca*. Since the genus *Asterotheca* Presl ex Corda 1845 has priority over *Asterocarpus* Heer 1877, *Asterotheca merianii* is the correct name. *Asterotheca* (compression fossils) probably represents the same genus as *Scolecopteris* Zenker 1837, which is a genus for petrefactions. As *Asterotheca merianii* has never been found as a petrefact, we still retain the species as such, and do not transfer it to *Scolecopteris* that has priority in case the two genera are really congeneric.

Stur (1888: 208) and Krasser (1909a: 6, 18, 1909b: 108) considered *Asterocarpus virginiensis* Fontaine, *A. platyrhachis* Fontaine and *A. penticarpus* Fontaine conspecific with *A. merianii*. *Asterocarpus virginiensis* is completely different because the pinnules are fused for a large part and the venation is denser. Additionally Krasser (1909a: 7) considered *Pecopteris falcatus* Emmons a synonym of *A. virginiensis* Fontaine 1883 and thus also a synonym of *Asterotheca merianii*, but *Pecopteris falcatus* shows more resemblance to a species of *Phlebopteris* than with an *Asterotheca* species. *Asterotheca platyrhachis* Fontaine 1883 is slightly similar to *A. merianii* but differs in having basally fused sterile pinnules and sori consisting of 4 or 5 sporangia. *Asterotheca penticarpus* consists of fragmentary reduced fertile parts only and cannot really be compared. The only species of Fontaine similar to *A. merianii* is *Pecopteris rarinervis* Fontaine 1883, which is only known from small sterile fragments. They might be included in *A. merianii* but the material is too rare to be sure.

Leuthardt (1904: 32, 35) distinguished *Asterotheca merianii* from *Merianopteris* (= *Pecopteris*) *augusta* Heer 1877 because of the perpendicular attachment of the pinnules and the higher number of lateral veins in the latter. It is still not clear if the latter species falls within the natural variability of *Asterotheca merianii*. In the Thale flora several specimens have been observed with a slightly higher number of lateral veins; they show, however, the same fertile leaves as *Asterotheca merianii* with 4 sporangia in each sorus. In this case just the number of sori per pinnule varies.

Krasser (1909b: 108) considered *Asterotheca lacerata* Stur 1885 apical fragments and *A. intermedia* Stur 1885 intermediate fragments of *A. merianii*; perhaps even *Hawlea* Stur 1885 was just a mature, disintegrated fertile leaf fragment of *A. merianii*. According to Krasser (1909b: 108), Stur (1888: 208) and Frentzen (1922a: 5) *Merianopteris augusta* Heer 1877, *Pecopteris augusta* Heer 1865, *Asterocarpus merianii* Heer 1877, *Asterotheca intermedia* Stur 1885 and *Asterotheca lacera* Stur 1885 are all junior synonyms of *Asterotheca merianii* (Brongniart) Stur 1885.

Nathorst (1908: 8, pl. 1, figs. 9-12) described and figured the sporangia and spores of *Asterotheca merianii* from Lunz. From his illustrations it can be clearly seen that the sori consisted of four sporangia (pl. 1, figs. 9-10) and he described the spores as smooth and round with some folds but he could not observe a trilete or monolete mark. Bhardway & Singh (1956: 52) described spores from Lunz specimens as circular to oval (29-50 µm in diameter) with a monolete mark. The spore wall is thick and finely granulate. The spores were attributed to the dispersed spore genus *Latosporites* Potonié et Kremp 1954. Bhardway & Singh (1956: 53) emphasised the monolete aperture in the spores of *Asterotheca merianii* while Paleozoic species such as e.g. *Asterotheca parallela* (Kidston) Radforth are generally trilete, although occasionally monolete spores were observed. Balme (1995) suggested the attribution of *Asterotheca merianii* spores to the dispersed genera *Leschikisporis* or *Punctatosporites* because of the monolete aperture. Apparently the spore morphology of *Asterotheca merianii* is quite variable, as Nathorst's spore description (1908: 8) indicated smooth, inaperturate, folded spores, and Bhardway & Singh (1956: 53) monolete, slightly granulate ones. Our own observations of *in situ* spores from Lunz material have so far only shown nearly smooth, inaperturate and typically folded spores although some appear to be 'pseudomonolete'. It is possible that these spore types constitute different ontogenetic stages, with the monolete, granulate spores being the most mature ones.

Comparisons. In *Pecopteris microphylla* Presl in Sternberg 1838 from the Keuper of Bamberg the pinnae are more deeply incised, linear to lanceolate and inserted at a more acute angle on the rachis than in our material. *Pecopteris quercifolia* Presl in Sternberg 1838 from the Keuper of Stuttgart is characterized by a dentate margin, a strong midrib and strong lateral veins that enter each segment. *Pecopteris mexicana* Newberry 1876 from the Upper Triassic of Sonora (Mexico) differs from *A. merianii* because of the smaller dimensions of the fronds, the falcate shape of the pinnules, the attachment of the sori on the basal part of the pinnules only and the delicate veins. In *Asterotheca crassa* Orlando 1968 from the Triassic of Antarctica the pinnules are inserted more loosely and at an acute angle. *Pecopteris callipteroides* Hsü et Chu in Hsü et al. 1974 from the Upper Triassic of Yungjen (China) differs from *Asterotheca merianii* because of the more acute angle of pinna attachment (70°) and the more slender pinnae (2.5-3 mm). In *Cladophlebis wielandii* Jain et Delevoryas 1967 from the Middle Triassic of Argentina the margin of the pinnules is serrate and the midrib bifurcates apically, in *Cladophlebis tenuipinnula* Holmes 2003 from the Middle Triassic of Australia the numerous secondary veins arise at acute angle from the midvein, the pinnules are smaller (4-5 x 1-1.5 mm). In *Asterotheca denmeadi* Walkom 1928 from the Triassic of Queensland the apex of the pinnules is acute, secondary veins arise at an acute angle and the number of sporangia can vary from 3 to 6, although in most cases there are 4 sporangia per sorus. In *Pecopteris* (*Asterotheca*) *hillae* Walkom 1924 from the Triassic of Queensland the pinnules are smaller than in our material (4.5 x 1.5-2 mm), the secondary veins do not bifurcate, and each fertile pinnule shows 10-14 sori. In *Asterotheca fuchsii* (Zeiller) Herbst 1977 and in *Asterotheca rigbyana* Herbst 1977 from the Upper Triassic of Argentina the pinnules are falcate; in the latter the pinnules are also smaller (5-6 x 3 mm) than in our material. The pinnules are much bigger in *Asterotheca okafujii* Kimura et Ohana 1980 from the Carnian of Japan (30 x 8 mm), attached at a more acute angle (70-80°) and with 8 sporangia per sorus. The number of sporangia per sorus in *Asterotheca cottonii* Zeiller 1903 from the Upper Triassic of Vietnam may vary between 4-5, the sori are smaller and more numerous on each pinnule and the pinnules are more widely spaced. *Asterotheca naktongensis* Oishi 1939 from the Triassic of South Korea differs because of the loosely inserted, apically inclined pinnules and the higher amount of sporangia per sorus (5-7). In *Asterotheca phenoerva* Li 1976 from the Upper Triassic of China the pinnules are more falcate with a pointed apex. *Cladophlebis szeiana* P'an 1936 from the Upper Triassic of China differs because of the overlapping pinnae, the acute angle of the pinnule attachment and the decurrent midrib. *Pecopteris* (*Aspidites*) *bullata* Bunbury 1847 from the Triassic of Virginia differs because of the more than once forking, delicate secondary veins and the restriction of the sori to the basal part of the pinnules. *Cladophlebis ichuenensis* Sze 1956 and *Cladophlebis suniana* Sze 1956 from the Upper Triassic of China differ because the pinnules are inserted at an acute angle apically, are larger (11 x 4 mm and 7 x 5 mm) and the secondary veins curve upwards.

Systematic attribution. According to several authors (e.g., Seward 1931: 304) the systematic position of this species is still unclear. Kidston (1924-1925) attributed the genus to the pteridosperms. Bhardway & Singh (1956: 54) discussed also a possible seed fern affinity since *Schopfipollenites* Potonié et Kremp 1954 and other "spores" of Medullosaceae show a monolete mark with a slight bend. Those differ, however, in size and ornamentation of the spores (Bhardway & Singh 1956: 54).

Heer (1877: 69) and Schimper (1869: 533-534) compared *Asterotheca merianii* with *Laccopteris* and attributed it, due to the type of sporangia, to the Gleicheniaceae. Compter (1894: 212) attributed it to the family of the Angiopecopterideae, since, according to Schimper & Schenk (1879), the species cannot be attributed to the Gleicheniaceae. Bhardway & Singh (1956: 54) attributed the genus to the Marattiaceae. Several authors considered *Pecopteris merianii* a fern of the *Scolecopteris* type, belonging to the Marattiaceae (e.g. Potonié 1899: 97; Leuthardt 1904: 31, Krasser 1909a: 43; Tidwell & Ash 1994: 418). Seward (1910: 409) attributed it rather to the Osmundaceae than to the Marattiaceae. Krasser (1909a: 31) and Cleal (1993: 788) assigned it to the Asterotheceae Stur in the order Marattiales. According to Vakhrameev et al. (1978: 102) it is more similar to Paleozoic than to Mesozoic Marattiales.

We think that the details of the sori, sporangia and spores make an attribution to the Marattiaceae obvious.

Distribution. According to Mader (1990) this species is restricted to the Lettenkeuper and Schilfsandstein (upper Ladinian to middle Carnian) in Central Europe. The species is rare in the Lettenkeuper and Schilfsandstein of Germany (eastern Thuringia, Schwaben and Franken, e.g., Schenk 1964; Schimper 1869; Compter 1894; Frentzen 1922a), but common in the Carnian of Switzerland (e.g., Schimper 1869; Heer 1877; Leuthard 1901; Leuthard 1904; Krasser 1909a) and Austria (Lunz, e.g. Frentzen 1922b; Krasser 1909a). It has been described from the Middle Keuper of France (Vanoise, Ricour 1968) and Italy (Sordelli 1896; Fliche 1910). Fliche (1910) mentioned it also from the Keuper of Grozon (France).

Asterotheca thalensis n. sp.
Figs. 2A-G, 12B

Etymology: After the locality, Thale.

Type specimens: Holotype S114745 (fertile specimen, yielding spores), paratype S114606 (large sterile specimen); both stored in the Naturhistoriska Riksmuseet in Stockholm (Sweden).

Type locality: Thale am Harz (Germany).

Type horizon: Erfurt Formation (Lower Keuper), upper Ladinian, Middle Triassic.

Diagnosis. At least bipinnate *Asterotheca* species. Pinnae arising (sub)oppositely from the main rachis at angles of 60-80°. Pinnules ovate with rounded apex arising at 60-80°. Pinnules inserted closely, covering partly the margin of the adjoining ones. First basiscope pinnule generally larger than the other ones and sometimes partly attached to the main rachis. Pinnules decreasing in size apically and fusing at the apex. Few secondary veins arising from the midrib, curving outwards and sometimes forking once. Fertile pinnules with 3-4 pairs of closely spaced sori, consisting of 4 elongated sporangia. Spores round in outline, 'pseudomonolete' with a granulate wall.

Description. Almost 20 specimens belong to this at least bipinnate fern species (e.g. S114606, Fig. 2A), none of which is complete. The biggest specimens are up to 100 mm long and 20 mm wide with up to 40 mm long and 10 mm wide pinnae. One bifurcated axis has been observed (S114820, Fig. 2B). Pinnae arise (sub)oppositely from the broad main rachis at angles of 60-80°. Pinnules (4-5.5 x 2.5-3 mm) are ovate with a rounded apex and arise at 60-80° from the ultimate rachis (< 1mm). Pinnules are inserted very closely, covering partly the margin of the adjoining ones. The first basiscope pinnule is generally larger than the other ones and is sometimes partly attached to the main rachis (e.g. S114766, S114814, Fig. 2C). Apically the pinnules contract in size and finally fuse at the apex (e.g. S114766, Fig. 2E). A few secondary veins arise from the midrib, curving outwards and may fork once (e.g. S114766, Figs. 2E, 12B).

Three to four pairs of closely spaced sori are located on the lower side of the pinnules, each at the end of a secondary vein (e.g. S114766, Fig. 2E). The sori (<1 mm in diameter) are formed by 4 sporangia (e.g. S114766, S114745, Fig. 2D). Sporangia are roundish to elongate (~1,5 mm long) and yielded a large number (>1000) of spores. Spores are round (27-34 µm in diameter), 'pseudomonolete' with a slightly granulate wall (e.g., S114766, Fig. 2F-G).

Material. S114047, S114239, S114252, S114522, S114524, S114536, S114598, S114606, S114716, S114719, S114722, S114726, S114745, S114747, S114766, S114770, S114790, S114791, S114799, S114804, S114807, S114813-14, S114820.

Discussion. We assign this material to the genus *Asterotheca* because of the arrangement of the 4 sporangia in the sori. However, it is clearly different from *Asterotheca merianii* because of the smaller pinnules, slightly smaller angle at which pinnae and pinnules are attached to the rachis, different venation and lower number of sori per pinnule. Moreover, the first basicopic pinnule is enlarged and partly attached to the main rachis. The venation of *Asterotheca thalensis* is usually pecopterid but tends to become more sphenopterid in apical parts. The spores of *A. thalensis* seem to be similar to those of *A. merianii* from the Thale material but appear to have a slightly thicker and more granulate spore wall.

Comparisons. *Asterotheca thalensis* is somewhat similar to *Pecopteris latepinnata* Leuthardt 1904 from the Carnian Neuewelt flora. The pinnules are more or less the same in gross morphology but are more loosely spaced and the secondary veins bifurcate more often than in *Asterotheca thalensis*. The nature of the fertile structures is not clear from the description and figure of the Swiss material; they can be sori or a single large sporangium.

Pecopteris callipteroides Hsü et Chu in Hsü et al. 1974 from the Upper Triassic of Yungjen (China) is similar to *Asterotheca thalensis* in having a larger first basiscopic pin-

Fig. 2. **A**. *Asterotheca thalensis* n. sp., paratype, bipinnate frond fragment with clear venation (S114606). **B**. *Asterotheca thalensis* n. sp., frond fragment with bifurcating axis (S114820). **C**. *Asterotheca thalensis* n. sp., frond fragment with enlarged basiscopic pinnules (arrows) (S114814). **D**. *Asterotheca thalensis* n. sp., holotype, fertile specimen showing sori (S114745). **E**. *Asterotheca thalensis* n. sp., specimen showing venation and arrangement of the sori (arrow) (S114766). **F**. *Asterotheca thalensis* n. sp., sporangial fragment (S114766), scale = 500 µm. **G**. *Asterotheca thalensis* n. sp., spore masses, spore with 'pseudomonolete' mark (S114766), scale = 25 µm. – Scale = 10 mm if not otherwise indicated.

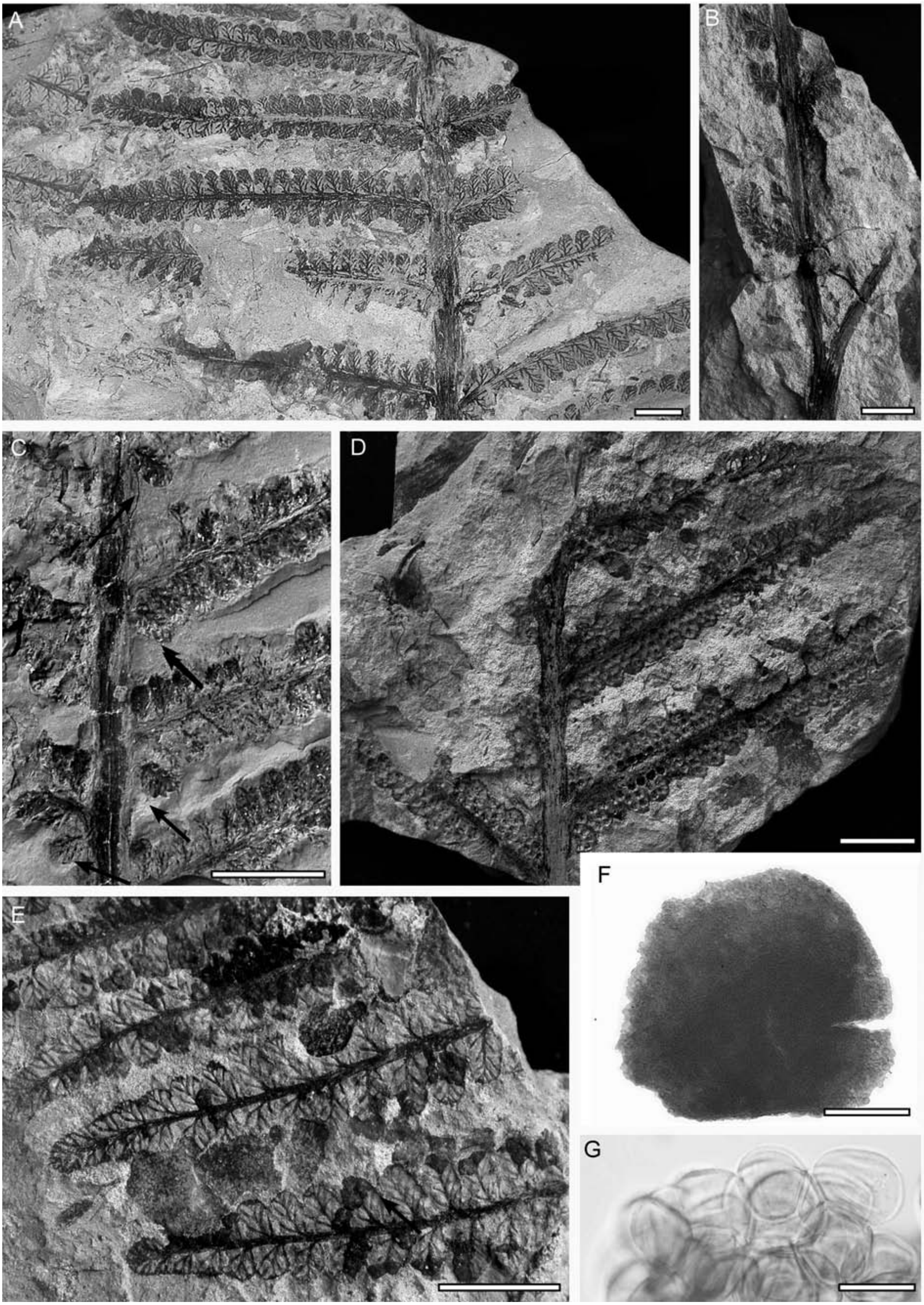

Fig. 2

nule which is partly attached to the main rachis, but differs in having larger pinnules with a dense pecopterid venation. Moreover, no fertile material is known. *Asterotheca rigbyana* Herbst 1977 from the Upper Triassic of Argentina is slightly similar in pinnule shape but the pinnules are larger and contain more sori. The secondary veins never fork. *Pecopteris mexicana* Newberry 1876 from the Upper Triassic of Sonora (Mexico) differs from *A. thalensis* in having acute pinnules and the presence of sori in the basal part of the pinnules only but the morphology of the sori is not clear. *Cladophlebis grabauiana* P'an 1936 from the Upper Triassic of China is somewhat similar in pinnule morphology and venation but differs in having a much narrower main rachis and the first basiscope pinnule is rather smaller than larger than the other pinnules. No fertile material of this species has been found so far.

Systematic attribution. We attribute *A. thalensis* to the Marattiaceae, just as *Asterotheca merianii,* based on soral and sporangial details.

Distribution. So far only known from Thale.

Genus *Danaeopsis* Heer ex Schimper 1869

Danaeopsis marantacea (Presl in Sternberg 1838) Schimper 1869
Figs. 3A-F, 12C

Selected synonymy:
1827 *Marantoidea arenacea* Jaeger, p. 28, 37, pl. 5, fig. 5.
?1835-1837 *Taeniopteris vittata* β var. *major* Brongniart. – Bronn, p. 147.
1836 *Aspidites schübleri* Goeppert, p. 351.
1838 *Crepidopteris schoenleiniana* Presl in Sternberg, p. 119.
1838 *Taeniopteris marantacaea* (Jaeger) Presl in Sternberg, p. 139.
1856 *Stangerites marantacea* Bornemann, p. 60.
1858 *Taeniopteris marantacaea* Presl. – Bronn, p. 58-59, pl. 9, fig. 3.
non 1858 *genus indeterminatum*. – Bronn, p. 59-60, pl. 9, fig. 4.
1859 *Thaumatopteris marantacaea* Heer. – Schenk, p. 191-196, pl. 4, figs. 1-2.
1861 *Stangerites arenaceus* Bornemann. – Miquel, p. 33.
1863-1864 *Danaeopsis marantacaea* Heer (*Taeniopteris marantacaea* Presl). – Schenk, p. 303, pl. 48, fig. 1.
1865 *Taeniopteris marantacaea*. – Heer, p. 48, 54, pl. 2, fig. 5.
1865 *Danaeopsis marantacaea* Heer. – Schoenlein & Schenk, p. 16-17, pl. 7, figs. 2-4, pl. 10, figs. 2c, pl. 12, fig. 3a, b.
1869 *Danaeopsis marantacaea* (Presl) Heer. – Schimper, p. 614-615, pl. 37, figs. 1-3.
1877 *Danaeopsis marantacea* Presl. – Heer, p. 64, 71, 90, pl. 24, fig. 1a-d.
1896 *Danaeopsis marantacaea* (Presl) Heer. – Sordelli, p. 42.
1904 *Danaeopsis marantacaea* Presl. – Leuthardt, p. 29-31, pl. 13, figs. 1-3.
1909a *Pseudodanaeopsis marantacaea* (Presl) Krasser, p. 17, 37.
1910 *Marattiopsis marantacea* (Presl) Seward, p. 407-408.
1921 *Danaeopsis marantacaea* Heer. – Halle, p. 1-4, 8, 10, pl. 2, figs. 27-30.
1933 *Pseudodanaeopsis marantacaea* (Presl) Krasser. – Linnell, p. 310.
1952 *Danaeopsis marantacaea*, Schenk. – Brik, p. 15-16, pl. 1, fig. 6, pl. 4, fig. 7.
non 1978 *Danaeopsis marantacaea* Heer. – Feng et al., p. 202-203, pl. 72, figs. 4-5.
1985 *Danaeopsis arenacea* (Jaeger). – Csaki & Urlichs, p. 9.
1990 *Danaeopsis arenacea*. – Kelber, p. 39, fig. 60.
1995 *Danaeopsis arenacea*. – Kelber & Hansch, p. 58, figs. 14, 117-121.
non 1998 *Danaeopsis marantacaea* (Presl) Heer. – Dobruskina, p. 317, 333, fig. 7A-K.
2001 *Marantoidea arenacea* Jaeger. – Webb, p. 217-218.

Description. More than 120 fragments of the fern fronds in the Thale flora can be attributed to this species. Most are pinna fragments; frond fragments are preserved only in few cases (e.g. S114076, S114095, S114138, S114462, Fig. 3A).

The fragments reach a length of 20 cm and a width of 33 cm (e.g., S114460, S114462, Fig. 3A). They are simply pinnate, with a main rachis c. 12 mm wide at the base, but narrowing apically to c. 6 mm. The pinnae are entire, elongated; the longest found was 187 mm long and 31 mm wide (S114462, Fig. 3A).

Secondary veins arise from the midrib at an acute angle, curving immediately towards the margin at an angle of 60-80°. Each secondary vein forks usually once near the midrib and anastomoses finally near the pinna margin (e.g. S114112, Figs. 3B, 12C). Sometimes the veins fork also near

Fig. 3. A. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, biggest frond fragment (S114462), scale = 3 cm. **B**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, pinnae with details of the venation (S114112). **C**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, fertile pinnae fragment (S114113). **D**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, sporangia fragment (S114118), scale = 50 µm. **E**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, detail of the sporangial arrangement (S114118), scale = 50 µm. **F**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, spores (S114118), scale = 50 µm. – Scale = 10 mm if not otherwise indicated.

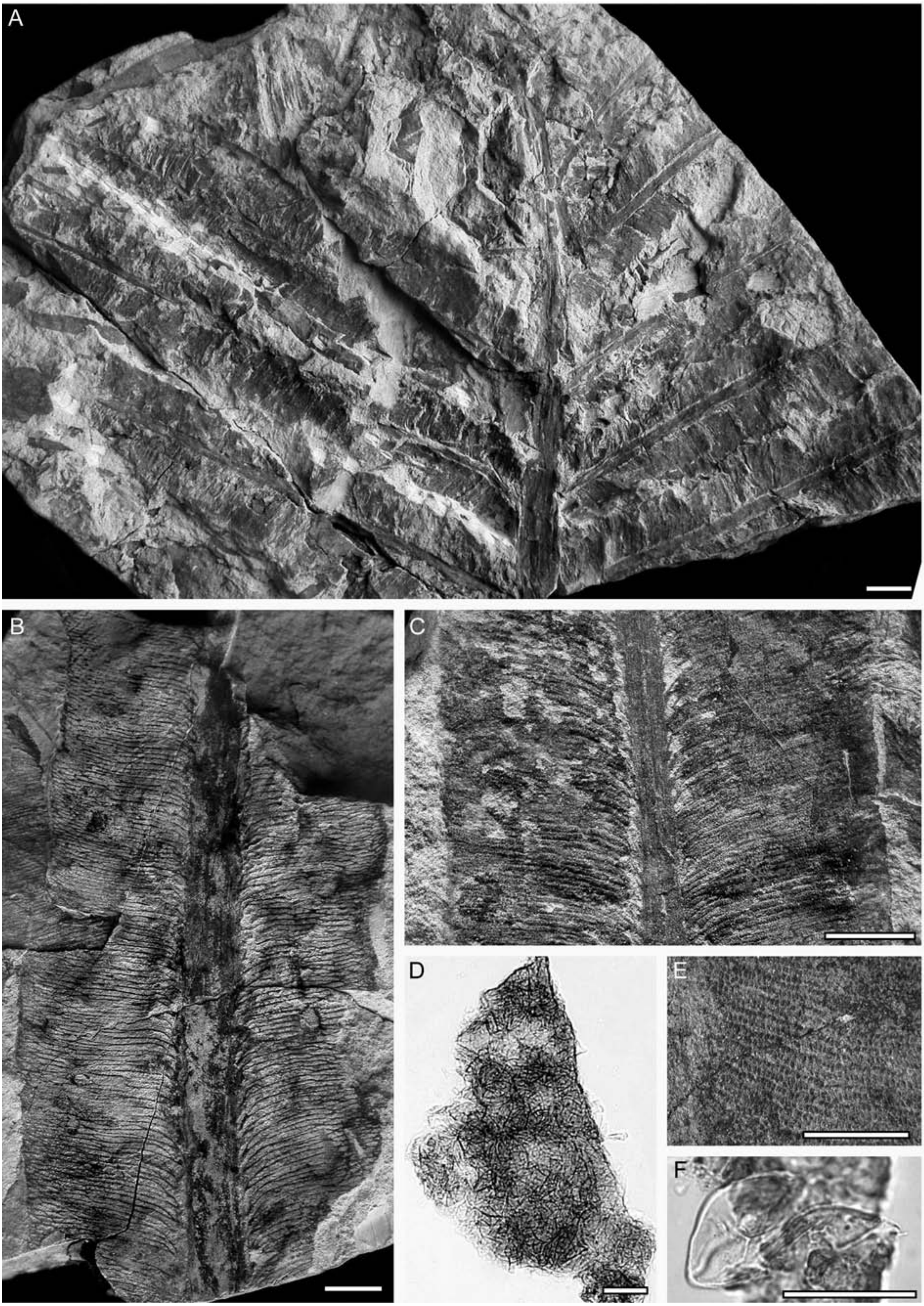

Fig. 3

the middle part of the lamina. The veins reach the margin more or less perpendicularly at a concentration that varies between 8 and 12 per centimetre.

Circa 25% of the material is fertile. Fertile pinnae are similar to sterile ones (fragments up to 130 x 43 mm, midrib 6.5-8 mm) but contain, between each pair of secondary veins, two rows of sporangia (e.g. S114100, S114113, S114141, Fig. 3C, E). The roundish sporangia are c. 0.5 mm in diameter and yielded large numbers of spores, over 1000 spores per sporangium (e.g. S114118, Fig. 3D). The spores are mainly immature and heavily folded. More mature spores are circular in outline and 40-48 µm in diameter, with a trilete mark (e.g. S114118, Fig. 3F). The spore wall appears to be smooth.

Material. S114012, S114014, S114018, S114030, S114061, S114073-85, S114088-91, S114093, S114095-109, S114111-50, S114152-53, S114166, S114293, S114317, S114326, S114352, S114355, S114437, S114460, S114462, S114465, S114467, S114523, S114532, S114537, S114545, S114551, S114553, S114585, S114593, S114601-03, S114606, S114628, S114715, S114735, S115915, S149411, JMS 52379, JMS 52388, JMS 52392, JMS 52395, JMS 52399, MB.Pb. 2000/251, MB.Pb. 2010/23, MB.Pb. 2010/27, MB.Pb. 2010/473, MB.Pb. 2010/472.

Discussion. Jäger (1827: 28) described an entire margined pinna fragment with veins arising at acute angle from the midrib but curving outwards as *Marantoidea arenacea*. Goeppert (1836: 351) moved it to the newly created genus *Aspidites* characterised by simple leaves with dichotomising, parallel secondary veins. Presl (in Sternberg 1838: 119, 138) renamed the species *Taeniopteris marantacea* and created also the new species *Crepidopteris schoenleiniana* (specimens described previously as *Pecopteris macrophylla* Brongniart and *Taeniopteris fructicosa* Schoenlein). In 1845, Presl created the genus *Danaeopsis* for a modern fern; the same generic name was used later by Heer (1877: 71) to distinguish *Taeniopteris* species with pinnate leaves. This is a case of homonymy (for more details see Zijlstra et al. 2010).

Later, several authors proposed to solve this problem in their own way. Aware of the homonymy between *Danaeopsis* Heer 1877 and *Danaeopsis* Presl 1845, Krasser (1909a: 35) transferred *D. marantacea* to *Pseudodanaeopsis* Fontaine 1883 and emended the diagnosis for the genus since, according to the author, in the latter genus veins were not supposed to anastomose near the margin. However, *Pseudodanaeopsis* might belong to the seed ferns (coriaceous leaves, no fertile structures known); Lundblad (1950: 17) proposed a gymnosperm affinity for the American species. Seward (1910: 409) moved the species to the genus *Marattiopsis* (agreed also by Potonié & Gothan 1921: 60; Emberger 1944: 246). Bornemann (1856: 60) and Miquel (1861: 33) attributed *Marantoidea arenacea* Jaeger and *Taeniopteris vittata* Brongniart 1828 to the cycadalean genus *Stangerites* Bornemann 1856 because of the coriaceous lamina and the strong veins.

Most authors (e.g. Compter 1922: 22-24; Halle 1921: 3-4; Hirmer 1927: 592) have used the name *Danaeopsis marantacaea* Presl instead of *Marantoidea arenacea* Jaeger. Only Webb (2001: 216) and Csaki & Urlichs (1985: 9) discussed the priority of the name *Marantoidea* Jaeger over *Danaeopsis* Heer, with *Marantoidea arenacea* as the type species since, according to McNeill et al. (art. 51, McNeill et al. 2006) “an alteration of the diagnostic characters or of the circumscription of a taxon does not warrant a change in its name”. Webb (2001: 216) gave also an emended diagnosis for this genus.

Since the use of the generic name *Danaeopsis* Presl 1845 for extant fern fronds has gone in disuse, a proposal has been made lately to conserve the genus *Danaeopsis* as a genus for fossil ferns (for more details see Zijlstra et al. 2010).

Comparisons. A number of Triassic species were assigned to the genera *Marantoidea* and/or *Danaeopsis*. *Danaeopsis fecunda* Halle 1921 from the Rhaetian of Scania differs from *D. marantacaea* in the smaller dimensions of the pinnae (100 x 25-30 mm), the secondary veins arising at a smaller angle (60-70°) and ellipsoidal sporangia. Additionally *Danaeopsis fecunda* yielded trilete spores with a smooth surface, up to 60-70 µm in diameter. Sze & Lee (1951: 88) suggest that *Danaeopsis hallei* P'an 1936 falls within the general variability of D. *fecunda*; thus that species will not be used here for comparison. *Taeniopteris glossopteroides* Newberry 1876 from the Upper Triassic of Mexico resembles *Danaeopsis marantacaea* in pinna shape and in the marginal anastomosing veins but is considered to be simple and not pinnate. *Danaeopsis hughesii* Feistmantel 1880 from the Mesozoic of India seems to be characterised by forking leaves and non-anastomosing veins, which would make the attribution to *Danaeopsis* doubtful (see also Potonié & Gothan 1921: 60; Sze & Lee 1951: 88; Halle 1921), attributed it to the genus *Protoblechnum*. In *Danaeopsis virginensis* Bock 1969 from the Triassic of the USA the pinnae are narrower (14-16 mm) and more widely spaced (~25 mm apart), the veins do not anastomose and the lamina continues between the pinnae. In *Marantoidea acara* Webb 2001 from the Middle Triassic of Queensland the pinnae are smaller (up to 18 cm long and 22-32 mm wide) and have an acute apex, the secondary veins cross the lamina at a more acute angle (60-80°) and the sporangia are very small (0.2-0.15 mm). In *Danaeopsis lunzensis* Stur

Fig. 4. A. *Rhacophyllum crispatum* (Münster in Sternberg) n. comb., frond fragments (S114585). **B**. *Rhacophyllum crispatum* (Münster in Sternberg) n. comb., details of the lateral segments (S114492). **C**. *Todites gaillardotii* (Brongniart) n. comb., most complete frond fragment (S114205). **D**. *Todites gaillardotii* (Brongniart) n. comb., frond fragment (S114588). – Scale = 10 mm.

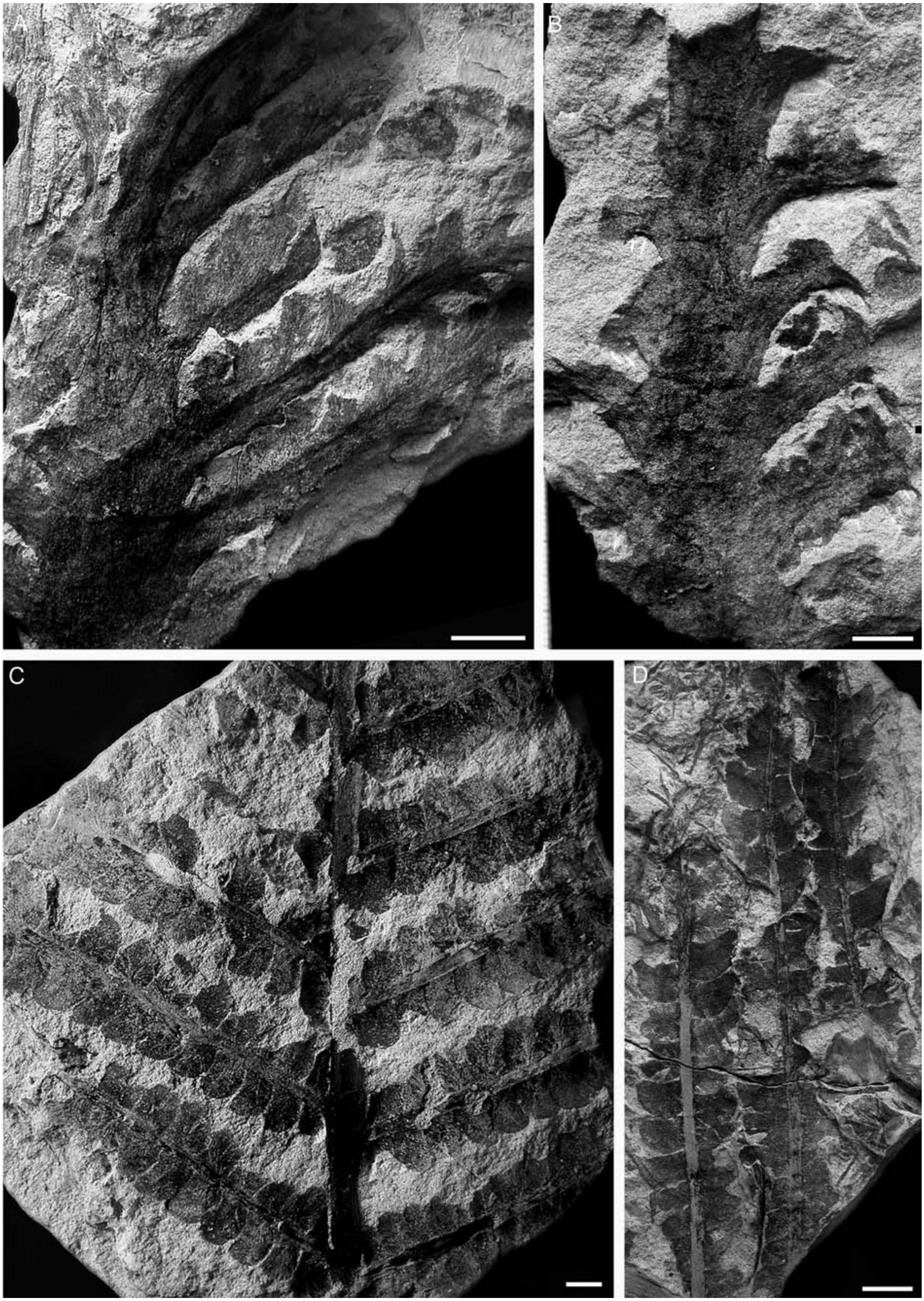

Fig. 4

ex Krasser 1909 from the Carnian of Lunz (Austria) and *Danaeopsis emarginata* Brik 1952 from the Upper Triassic Ilek Basin (Russia) the pinnae are much smaller (110 x 15-22 mm and 100 x 18-20 mm respectively). In *Danaeopsis angustipinnata* Brik 1952 from the Upper Triassic Ilek Basin (Russia) the pinnae are narrower (10-12 mm), the secondary veins reach the margin at an acute angle (70-75°) and dichotomise both near the midrib and in the middle part of the lamina but never anastomose; although the sporangia are attached in two rows on the lateral veins, this species does not belong to *Danaeopsis*. *Danaeopsis bipinnata* Brik 1952 from the Upper Triassic Ilek Basin (Russia), with its linear pinnae and dichotomising lateral veins, resembles more a *Bernoullia* species than *Danaeopsis*; the veins do not anastomose. In *Danaeopsis tenuis* Mogutcheva 1987 from the Early Triassic of Sibiria the pinnae are narrower (12-25 mm), the rachis is delicate (0.5 mm); additionally the veins bifurcate several times but never anastomose.

Fontaine (in Ward 1905: 87, pl. 15, figs. 6-9) described *Danaeopsis storrsii* from the Jurassic flora of Oregon (USA) and compared it with the Triassic *Danaeopsis marantacea* and *Danaeopsis rumpfii* (for the latter species, see *Symopteris rumpfii* below). *D. storrsii* is much smaller in size than any *Danaeopsis* species, has regularly once forking veins that never anastomose, the sporangia are probably arranged in synangia, and the area near the midrib is free from sporangia. Thus, *D. storrsii* is probably a *Marattiopsis* rather than a *Danaeopsis* species.

Systematic attribution. Most authors refer *Danaeopsis marantacea* to the Marattiaceae due to the distribution of the sporangia and its similarity to the living genus *Danaea* (e.g. Bronn 1835-1837: 147; Potonié 1899: 90; Potonié & Gothan 1921: 449; Compter 1922: 22; Kon'no 1972b: 167; Vakhrameev et al. 1978: 102; Kelber 1998: 95). Bronn (1851-1852: 29-30) attributed it to a family of its own, the Danaeaceae, in the order Marattiales. Various authors (e.g. Halle 1921: 10; Kelber 1987: 287; Tidwell & Ash 1994: 418) evidenced, however, the greater affinity with the living genus *Angiopteris* (sporangia not fused, distributed on both sides of the veins, sporangia open with a split), than with *Marattia* and *Danaea* (fused sporangia, sporangia open with a pore).

We consider *Danaeopsis* to belong to the Marattiaceae because of its macromorphology including shape and distribution of the sporangia, the spore output per sporangium (over 1000) and the spore morphology. It is not closely related to any of the living genera but is closest to *Angiopteris* because of its separated sporangia.

Distribution. In the Germanic Basin this species has been described from the Upper Muschelkalk of Chauffontaine (France, Fliche 1910), from the Lettenkeuper (upper Ladinian, Jäger 1827; Bronn 1835-1837, 1851-1852; Schenk 1864; Schoenlein & Schenk 1865; Frentzen 1922a; Kelber 1983, 1998) and from the Schilfsandstein (Carnian, Frentzen 1922a; Schenk 1864; Schimper 1869; Csaki & Urlichs 1985; Kelber 1998) of Germany. Moreover, it has been recorded from the Carnian of Austria (Lunz, e.g. Stur 1885; Krasser 1909a), Switzerland (e.g., Goeppert 1838; Heer 1877; Leuthardt 1904) and perhaps also from Italy (Raibl, Lombardia, Schenk 1866-1867; Stur 1885; Sordelli 1896).

According to Mader (1990) the species is restricted to the Lettenkeuper (upper Ladinian) and Schilfsandstein (middle Carnian) of Central Europe, but it has been mentioned also from the Carnian of China (Sze 1956b), the Lower Mesozoic of Russia (Burakova et al. 1980), and from the Rhaetian of France (Corsin et al. 1950; Saporta 1873).

Although the genus *Danaeopsis* is considered characteristic for the Chinese "northern type Flora", Sun et al. (1995) mention *Danaeopsis marantacaea* from the Early Carnian assemblage (*Abropteris yongrenensis-Pterophyllum longifolium* assemblage) of the "southern-type flora" from China.

?Family Marattiaceae
Genus *Rhacophyllum* Schimper 1869

Rhacophyllum crispatum (Münster in Sternberg) n. comb.
Figs. 4A-B, 12D

Selected synonymy:

1833 *Laminarites crispatus* Münster in Sternberg, p. 35, pl. 24, fig. 3.
1863-1834 *Schizopteris pachyrhachis* Schenk, p. 302-303, pl. 47, fig. 2.
1864 *Schizopteris pachyrrhachis* Schenk. – Schenk, p. 56, 76, pl. 7, fig. 4.
1869 *Rhacophyllum pachyrrachis* (Schenk). – Schimper, p. 687, pl. 47, fig. 3.
1877 *Rhacophyllum pachyrachis* (Schenk) Schimper. – Heer, p. 64, 74, 90, pl. 26, figs. 4-5.
1901 *Rhacophyllum pochyrachis* Heer. – Leuthardt, p. 127.
1952 *Rhacophyllum pachyrachis* (Schenk) Schimper. – Brik, p. 31-32, pl. 14, figs. 10-12.
1956a *Rhacophyllum pachyrachis* (Schenk) Schimper. – Sze, p. 148.

Fig. 5. A. *Todites gaillardotii* (Brongniart) n. comb., fertile pinnules seen from above, showing venation (S114627). **B**. *Todites gaillardotii* (Brongniart) n. comb., fertile pinnules seen from below showing sporangia (S114168). **C**. *Todites gaillardotii* (Brongniart) n. comb., detail of the venation (JMS 52387). **D**. *Todites gaillardotii* (Brongniart) n. comb., sporangial fragment with immature spores (S114164). **E**. *Neuropteridium grandifolium* (Schimper et Mougeot) Compter 1883, basal frond fragment (S114297). **F**. *Neuropteridium grandifolium* (Schimper et Mougeot) Compter 1883, apical frond fragment (S114335). **G**. *Neuropteridium grandifolium* (Schimper et Mougeot) Compter 1883, details of venation (S114300). – Scale = 10 mm.

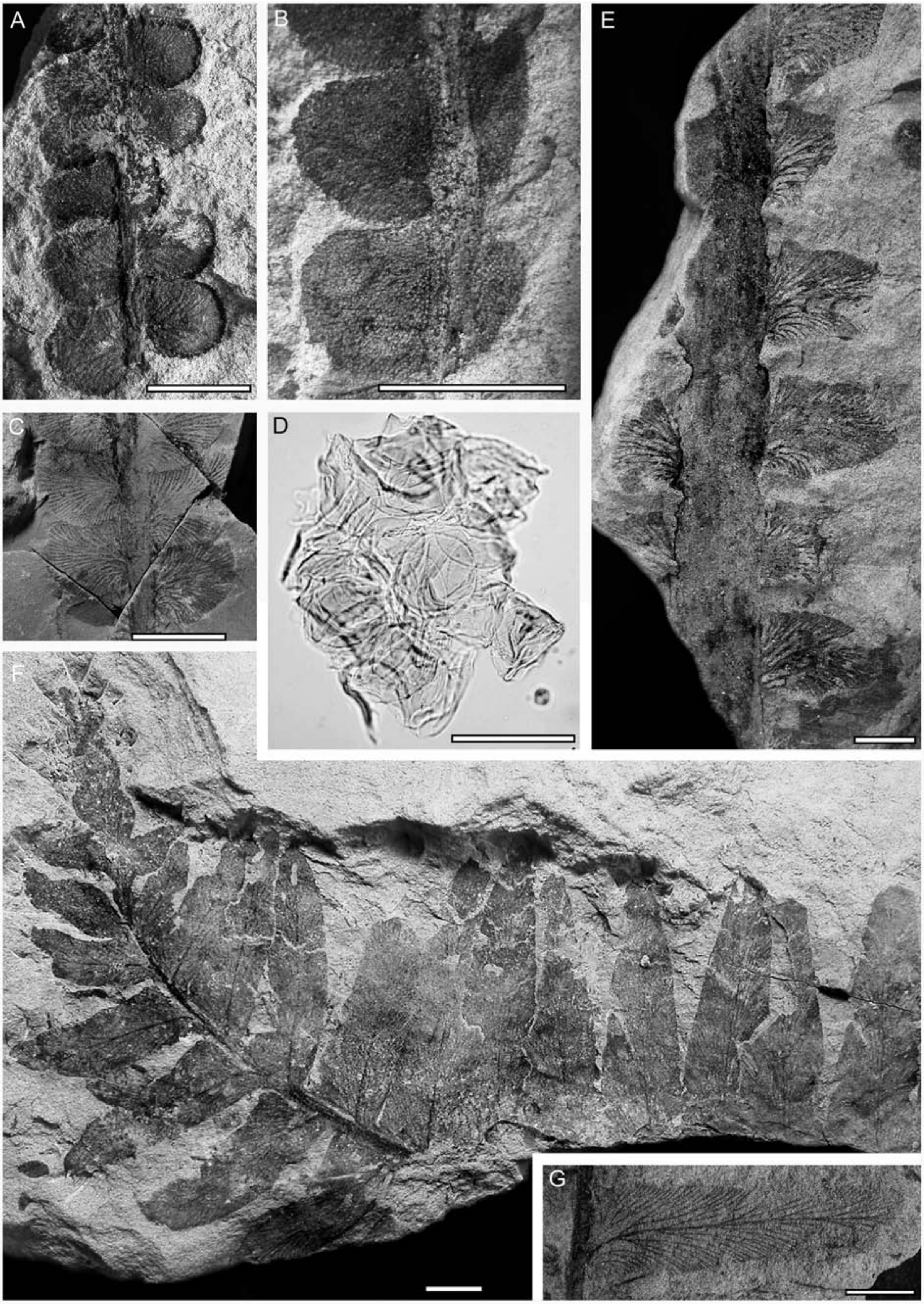

Fig. 5

1957	*Aphlebia* (*Schizopteris*) *pachyrachis* Schenk. – Jongmans & Dijkstra, p. 277.
1985	*Aphlebia pachyrachis* Schenk. – Boersma, p. 28.
1990	*Schizopteris pachyrhachis*. – Kelber, p. 44, fig. 76.

Description. Fourteen fragments of aphlebia-type structures were found in the Thale flora. The fragments are often three-dimensionally preserved or partly covered by sediment, underlying the theory that they were were stout and coriaceous. The fragments are up to 110 mm long and up to 90 cm wide (e.g. S114585, Fig. 4A). Segments (up to 60 mm long and 25 mm wide) arise oppositely from the up to 20 mm broad central part (e.g. S114585, Fig. 4A). The segments have an irregular outline with various lobes, up to 5 mm long and 3-4 mm wide (e.g. S114492, Figs. 4B, 12D). At least one vein enters each segment.

Material. S114020, S114094, S114272, S114312, S114320, S114492, S114507-09, S114524, S114585, S114678, S114700, S115892, S115951-52, MB.Pb. 2000/247, MB.Pb. 2010/469, MB.Pb. 2010/464.

Discussion. Münster in Sternberg (1833: 35) considered these structures with irregular appendices as algae. Later, Schenk (1863-1864: 302) described it as bipinnate structures with a stout rachis, irregularly lobated pinnules and “venations” and considered them ferns. Based on the fact that the plant material belonged to a different plant group, he proposed for the original specimen from Sternberg and other German material the new species *Schizopteris pachyrhachis* (Schenk 1863-1864: 303; Schenk 1864: 76-77); this his however not in accordance with the IBCN (art. 51, McNeill et al. 2006).

In 1834 Presl in Sternberg created the genus *Aphlebia* for mainly Carboniferous, lobate, flabellate or pinnate structures without veins and with a fine rhizome. Because of the contradiction existing between a frond and the absence of veins, Schimper (1969: 684) did not want to use this genus for Schenk’s species “because the name *Aphlebia* means without venation” (and indeed it is in the original generic diagnosis) and these structures showed venation. Therefore, he created the new genus *Rhacophyllum* into which he moved several species from the genus *Schizopteris* Brongniart and *Aphlebia* Presl in Sternberg.

Rhacophyllum crispatum cannot be assigned to *Laminarites* Brongniart, a genus for structures that may be algae and are completely different from this species. It does not belong to *Schizopteris*, either, because *Schizopteris* is characterised by delicate, bifurcate structures with terminal fertile organs and fine veins. The presence of both bifurcating and pinnate structures included in the genus *Aphlebia* Presl in Sternberg (Schimper & Schenk 1890: 142) makes it difficult to assign our species to *Aphlebia*. Additionally, Seward (1910: 525-528) discussed the confusion related to the existence of various generic names such as *Rhacophyllum*, *Schizopteris* etc. He proposed not to use the term *Aphlebia* “as a distinct genus, but (i) as a descriptive name for detached leafy structures similar to those figured by Presl, which are now recognised as laminar appendages of the petioles of ferns or fern-like fronds, and (ii) as an epithet for highly modified pinnules with occur at the base of the primary pinnae of pecopteroid and sphenopteroid fronds (e.g. *Dactylotheca plumosa*).”

Thus, we accept Schimper’s and Seward’s considerations for the genus, but propose to use the original (and thus correct) epithet of the species, *crispatus* or in this case *crispatum* as *Rhacophyllum* is neuter.

According to Schenk (1864: 77) the most complete specimen so far identified reached a length of 35.5 cm, but in the Thale flora the longest fragment is only 11 cm.

Comparisons. This seems to be the only *Rhacophyllum* species described so far from the Triassic. Schenk (1863-1864: 302) compared his specimens with the carboniferous *Schizopteris gutbieriana* Geinitz 1855 but evidenced the bigger dimension and the more irregular division of the Triassic species.

Systematic attribution. According to Schenk (1864: 76) the German material showed that *Laminarites crispatus* could not belong to the algae but to the ferns, since it was a secondary pinna. Schimper (1869: 687) mentioned that this species might represent the “fronde primaire” of *Danaeopsis marantacaea*. Even if no organic connection is so far known between *Rhacophyllum crispatum* and *Danaeopsis marantacea*, they might indeed belong to the same natural species. In this case also *Rhacophyllum crispatum* is belongs to the Marattiaceae.

Distribution. In the original paper Presl (in Sternberg 1838) indicated, that the material was collected in the Keupersandstein of Abtswind (“Abschwind”). Later, Kvaček & Straková (1997) considered it of Liassic age, but we do not agree with this stratigraphic interpretation and consider it still middle Keuper in age (= Carnian; pers. comm. K.-P. Kelber 2009).

Rhacophyllum crispatum has been mentioned from the Lettenkeuper (Erfurt Formation) near Würzburg (Estenfeld, Erlach; Schenk 1863-1864) as well as Schweinfurt (Kronungen, Schenk 1864), from the Schilfsandstein (Carnian) of Franconia (Abtswind in the Steigerwald, Schenk 1864), from the Carnian of Hemmiken and Ormelingen (Switzerland, Heer 1877). Brik (1952) mentioned it also from the Upper Triassic of Western Kazakstan (Sze 1956a).

Apart from the original material from Abtswind, *Danaeopsis* species have been found in all localities from which *Rhacophyllum crispatum* is known.

Order Filicales
Family Osmundaceae
Genus *Todites* Seward 1900

Todites gaillardotii (Brongniart) nov. comb.
Figs. 4C-D, 5A-D, 12G

Selected synonymy:

1828a	*Neuropteris gaillardotii* Brongniart, p. 53, 195. (*nomen nudum*)
1834	*Neuropteris gaillardotii* Brongniart, p. 245, pl. 74, fig. 3a.

non 1834 *Neuropteris gaillardotii* Brongniart, p. 245, pl. 74, fig. 3.
1847 *Neuropteris linnaeaefolia* Bunbury, p. 281, 288, pl. 1.
1856 *Neuropteris linnaeaefolia* Bunbury. – Emmons, p. 329, pl. 2, fig. 6.
1857 *Neuropteris linnaeaefolia* Bunbury. – Emmons, p. 104, pl. 6, fig. 6.
non 1869 *Neuropteris gaillardotii* Brongniart. – Schimper, p. 449.
Non 1883 *Acrostichites linnaeaefolius* Fontaine, p. 25-29, pl. 6, fig. 3; pl. 7, figs. 1-4, pl. 8, fig. 1, pl. 9, fig. 1.
non 1900 *Acrostichites linnaeaefolius* Fontaine. – Ward, p. 240, pl. 25, figs. 7-8.
1910 *Cladophlebis linnaeaefolia* Bunbury. – Fliche, p. 87-89, pl. 7, fig. 1.
?1910 *Neuropteris gaillardotii* Brongniart. – Fliche, p. 77-86, pl. 8, fig. 1.
1910 *Neuropteris gaillardotii* Brongniart. – Fliche, p. 77-86, pl. 8, fig. 2.
?1918 *Pecopteris parvifolia* Compter, p. 440-442, figs. 2a, 3.
?1922 *Neuropteris distans* Presl. – Compter, p. 25, pl. 1, fig. 7.
1936 *Cladophlebis shensiensis* P'an, p. 15-17, pl. 4, fig. 16, pl. 5, figs. 4-6, pl. 6, figs. 4-8.
1956b *Cladophlebis* (*Todites*) *shensiensis* P'an. – Sze, p. 123, pl. 10, figs. 2-3, pl. 12, fig. 5, pl. 14, fig. 1, pl. 15, figs. 1-17, pl. 21, fig. 5.
1995 *Cladophlebis distans*, Kelber & Hansch, figs. 136, 139, 284.

Basionym. *Neuropteris gaillardotii* Brongniart 1834, p. 245, pl. 74, fig. 3a.

Description. About 90 frond fragments belong to this probably bipinnate species. The fragments are up to 290 mm long and 150 mm wide, they are never completely preserved (e.g., S114205, Fig. 4C);. Linear pinna fragments arise oppositely to suboppositely from the woody, striate rachis (up to 11 mm wide); they are up to 130 mm long and 24 mm wide (e.g. S114192, S114588, Fig. 4D). Sterile pinnules are roundish (6-11 x 6-8 mm) and arise alternately from the pinna axis (2-3.5 mm). They are sometimes imbricate with a slightly constricted base (e.g. S114163, JMS 52387, Fig. 5C). The apex is often slightly curved upwards. The venation is almost neuropterid; the midrib is indistinct and gives off a large number of secondary veins, which are 2-3 times forked. Moreover, some veins arise directly from the rachis in the lower part of the pinnules (e.g. S114163, JMS 52387, Figs. 5C, 12G).

Fertile pinnules are shorter (e.g. 6-7.5 x 6 mm) with a rounded apex (S114168, Fig. 5B), and sometimes being almost circular in outline with a constricted base (S114627, Fig. 5A). The lower surface is completely covered by ovoid sporangia (200-300 µm in diameter). Only one specimen (S114164, Fig. 5D) yielded masses of immature trilete spores. Mean spore size is 35-51 µm. The spore wall appeared to be smooth. When mature, these spores could easily fall in the dispersed genus *Todisporites*.

Material. S114032, S114063, S114079, S114154, S114156-7, S114160, S114162-4, S114166, S114168, S114170, S114173-75, S114177-99, S114201, S114203, S114205-6, S114208, S114210-11, S114213-4, S114216-8, S114221-37, S114293-5, S114310, S114338, S114413, S114436, S114489, S114547, S114550,S114563, S114566, S114588, S114603, S114627, S114651, S114743, S114806, S114822, JMS 52387, MB.Pb. 2010/35, MB.Pb. 2010/88-91, MB.Pb. 2010/472, MB.Pb. 2010/467-468.

Discussion. Brongniart (1834: 245; see also Schimper 1969: 449) described *Neuropteris gaillardotii* from the Muschelkalk of Lunéville (France), a species with rounded pinnules and neuropterid dichotomising venation. Brongniart figured one specimen (1834: pl. 74, fig. 3a) without midrib, while the second specimen shows a narrow midrib as is known from *Cladophlebis remota* Presl in Sternberg. Fliche (1910: 77) proposed to unify *Neuropteris gaillardotii* with *N. remota* Presl in Sternberg, *N. distans* Presl in Sternberg, *N. schoenleiniana* Schenk, *N. perrini* Mougeot 1845, *Pecopteris triasica* Heer 1877 and *P. ruetimeyeri* Heer 1877 into one species, *Cladophlebis gaillardotii* (Brongniart) Fliche. We consider that Brongniart's specimens belong to two different species; the specimen in fig. 3a represents *Cladophlebis gaillardotii* (now *Todites gaillardotii* because of the structure of the fertil pinnules), while fig. 3 must be attributed to *Cladophlebis remota* (Presl in Sternberg) Van Konijnenburg-Van Cittert et al. 2006 because of the pinnule shape (roundish in *T. gaillardotii* against falcate with a more acute apex in *Cladophlebis remota*) and the venation (two stronger veins arising from the rachis in *T. gaillardotii*, a midrib with secondary veins in *C. remota*). Moreover no fertile remains are known from *C. remota*.

Neuropteris linnaeaefolia Bunbury 1847, a bipinnate fern species with (sub)oppositely inserted, long and narrow pinnae is conspecific with *Todites gaillardotii* in our opinion. The closely inserted pinnules are almost circular in outline with an entire margin. They lack a distinct midrib but two strong, forked secondary veins radiate from the base of each pinnule (Bunbury 1847: 281-282, pl. 1). According to Bunbury (1847: 282) "granulate structures, typical for the *Acrostichum* group", cover the lower pinnule surface (which is identical to our fertile material). Later, Fontaine (1883: 25-29), Ward (1900: 240) and Bock (1969: 96) described *Acrostichites linnaeaefolius* (Bunbury) Fontaine from the Triassic of Virginia; however, those remains show a clear midrib (although reduced in the fertile pinnules) and, thus, cannot be conspecific. The fertile leaves of *Acrostichites linnaeaefolius* (Bunbury) Fontaine as described by Bock (1969: figs. 157, 161b) resemble *Todites gaillardotii*, but the sterile pinnules are smaller (3-6 x 6 mm), with a pointed apex and sometimes slightly elongated sporangia (Bock 1969: 96-101, figs. 157, 160-161).

Cladophlebis shensiensis P'an 1936 from the Upper Triassic of China is conspecific as well. The venation pattern, pinnule shape and frond organisation are exactly the same, although P'an does not figure any fertile material. Sze (1956b: 123) stated that "the fertile pinnules are of the *Todites* type, the pinnules are very small and round with indistinct bifurcating veins. Sporangia indistinct."

Comparions. Most Triassic *Cladophlebis* and *Todites* species have larger pinnules with a clear midrib and sometimes a crenulate to undulate margin; and thus are not compared here with *Todites gaillardotii*.

Todites subtilis Duan et Chen 1979 and *T. yanbianensis* Duan et Chen 1979 from the Upper Triassic of Sichuan (China) differ from *Todites gaillardotii* because of their even smaller pinnule dimensions (1.5 x 2-2.5 mm) and narrow falcate pinnules with a pointed apex. *Todites roessertii* (Presl in Sternberg) Krystofovich 1912 from the Rhaeto-Liassic of Europe differs in its secondary veins that only fork once (see e.g., Weber 1968).

Systematic attribution. Because the sporangia cover the whole lower pinnule surface, we attribute *Todites gaillardotii* to the Osmundaceae; the immature *in situ* spores do not contradict this attribution.

Distribution. This species has been described from the Muschelkalk of Lunéville (France, Brongniart 1834; Schimper 1969), the Triassic of Virginia (USA, Bunbury 1847) and the Lettenkeuper (Ladinian) of the Germanic Basin (Kelber & Hansch 1995). P'an (1936) and Sze (1956b) described it as *Cladophlebis* (*Todites*) *shensiensis* from the Yenchang Formation (Upper Triassic) of China. Sun et al. (1995) mention *Todites shensiensis* (P'an) from the Middle Triassic of the Northern China Florist Subregion China; they consider it an indicator (together with other ferns) of the more humid climate during the late Middle Triassic in this area.

?Family Osmundaceae

Genus *Neuropteridium* Schimper in Schimper & Schenk 1879

Neuropteridium grandifolium (Schimper et Mougeot) Compter 1883

Figs. 5E-G, 12E

Selected synonymy:

1844	*Nevropteris grandifolia* Schimper et Mougeot, p. 77, pl. 36, figs. 1-2.
1869	*Neuropteris grandifolium* (Schimper et Mougeot). – Schimper, p. 447-448.
1883	*Neuropteridium grandifolium* (Schimper et Mougeot) Compter, p. 17-18, 28.
1890	*Neuropteridium grandifolium* Schimper. – Schimper & Schenk, p. 117, fig. 90.
1922	*Neuropteridium grandifolium* (Schimper et Mougeot) Compter. – Compter, p. 26-27, fig. 12.
1933	*Neuropteridium* sp. – Linnell, p. 310.
1995	*Linguifolium* sp. – Kelber & Hansch, p. 62, figs. 133-135.
non 2000	*Neuropteridium grandifolium* (Schimper et Mougeot) Schimper. – Wachtler & Van Konijnenburg-Van Cittert, p. 108, pl. 2, fig. 1.

Description. *Neuropteridium grandifolium* is common in the Thale flora (more than 40 specimens). Frond fragments reach a maximum length of 44 cm and width of 12 cm; however, no complete frond has been found. The rachis reaches in the middle part of the frond a maximum thickness of 5-12 mm and decreases towards the apex (1-2 mm). The (sub)oppositely inserted pinnules are elongate to tongue-shaped, attached with a distal auricle and a proximal decurrent margin. Basal pinnules are small (c. 15 x 11 mm, e.g., S114297, Fig. 5E); pinnule size increases rapidly to c. 44-75 x 12-35 mm but decreases again towards the apex (22-35 x 9-14 mm), with one terminal pinnule (30 x 10.5 mm, e.g., S114335, Fig. 5F). The venation is neuropterid with a delicate but clear midrib that extends about one half to two-thirds of the pinnule length; secondary veins arise at small angle, diverge and fork three to four times (e.g., S114300, Figs. 5G, 12E). No fertile material has been found.

Material. S114015, S114038, S114194, S114211, S114263, S114266, S114296-308, S114311, S114313-14, S114316-19, S114321, S114323, S114325-26, S114328-32, S114335-36, S114350, S114406, S114456, S114532, S114591, S115938, MB.Pb. 2010/23, MB.Pb. 2010/84, MB.Pb. 2010/94, MB.Pb. 2010/473.

Discussion. The species is known from the Middle Triassic of France and Germany. The Italian specimens described by Wachtler & Van Konijnenburg-Van Cittert (2000) as *Neuropteridium grandifolium* have lately been re-interpreted as *N. elegans* (see Van Konijnenburg-Van Cittert et al. 2006). The specimens described by Kelber & Hansch (1995) as *Linguifolium* sp. belong to *Neuropteridium grandifolium* even if the auriculate acroscopic base is not always visible.

Comparisons. *Neuropteridium voltzii* (Brongniart 1828) Schimper in Schimper & Schenk 1879 and *Neuropteridium elegans* (Brongniart 1828) Schimper in Schimper & Schenk 1879 from the Buntsandstein of the Vosges differ from *Neuropteridium grandifolium* because of the smaller and narrower pinnules (40-80 x 10 mm and 15-25 x 6-7 mm respectively) and the absence of an auriculate acroscopic margin. In *Neuropteridium coreanicum* Koiwai 1927 from the Triasssic of Korea the pinnules are smaller (20-40 x 10-15 mm), with an undulate margin, closer spaced and more strongly curved upwards (40-50°). In *Neuropteridium moombraense* Walkom 1928 from the Upper Triassic of

Fig. 6. A. *Clathropteris meniscioides* Brongniart 1828, frond fragment (S114341). **B**. *Clathropteris meniscioides* Brongniart 1828, detail of the reticulate venation (S114341). **C**. *Phlebopteris* sp., pinnae fragment with clear venation pattern (MB.Pb. 2010/471). **D**. *Phlebopteris* sp., frond fragment (MB.Pb. 2010/471). – Scale = 10 mm.

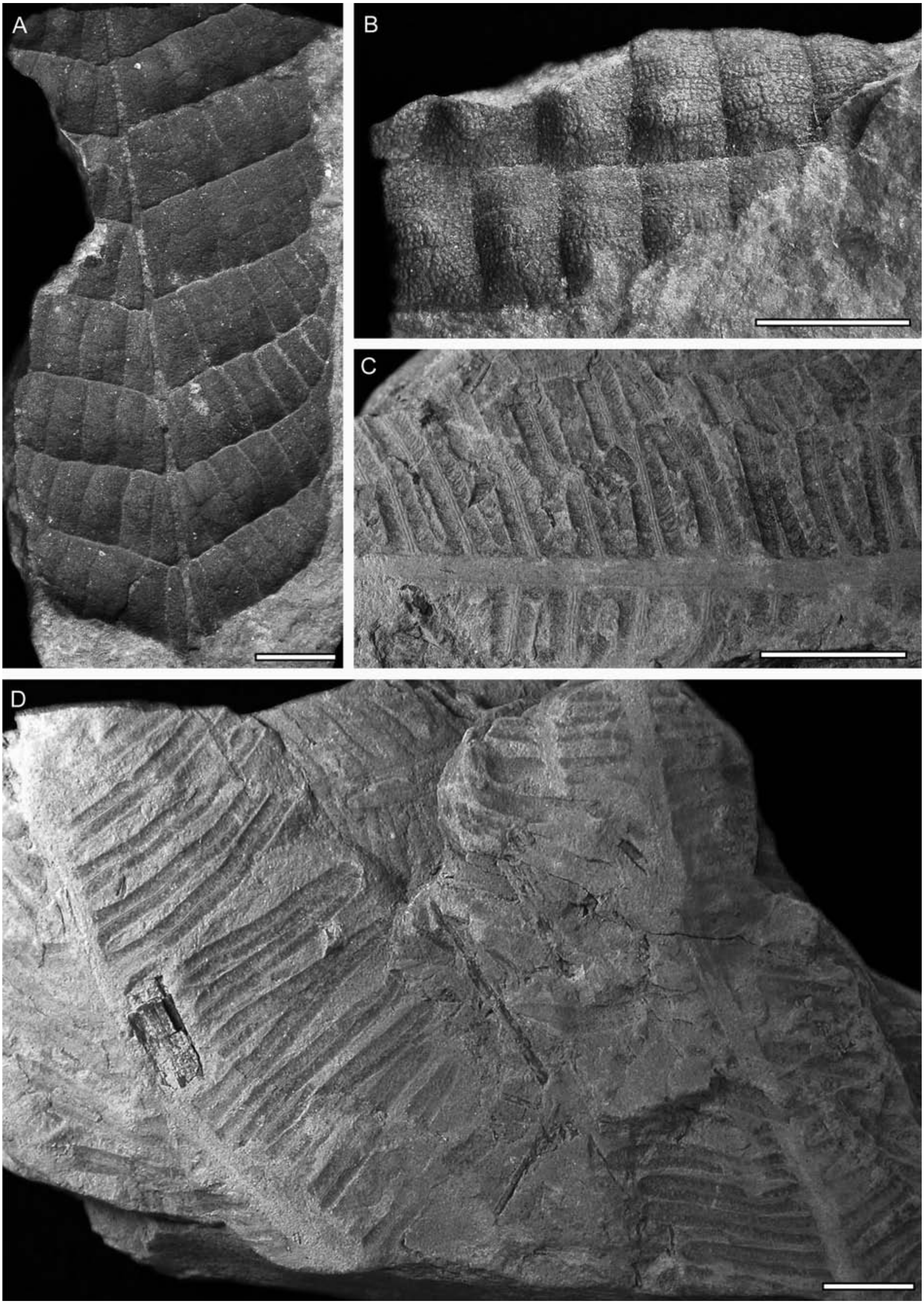

Fig. 6

Queensland the pinnules are attached at an acute angle and with a strongly contracted base. *Neuropteridium marginatum* Zhou et Li 1979 from Early Triassic of China is much smaller than our species and resembles more an *Asterotheca* species than a species of *Neuropteridium* because the venation is completely pecopterid. *Neuropteridium curvinerve* Wang et Wang 1990 from the Lower Triassic of China has much smaller pinnules than *Neuropteridium grandifolium*.

Systematic attribution. Although several *Neuropteridium* species definitely belong to the Osmundaceae (Van Konijnenburg-Van Cittert et al. 2006) we cannot attribute *Neuropteridium grandifolium* with certainty to this family as no fertile material is known.

Distribution. Although this taxon was described originally from the Buntsandstein of the Vosges (France, Schimper & Mougeot 1844), Frentzen (1922a) considered it a typical element of the German Lettenkeuper, while according to Mader (1990) it is restricted to the Upper Buntsandstein-Lettenkeuper (Anisian-Ladinian) of Central Europe. Today the species is known from the Buntsandstein (Grès bigarré) of the Vosges (France, Schimper 1869; Schimper & Mougeot 1844) and Göttingen (Germany, Schlüter & Schmidt 1927). It is also well distributed in the Lettenkeuper (Erfurt Formation) of Thuringia (e.g. Apolda, Compter 1883, 1922; Schmidt 1928), Thale (Linnell 1933) and perhaps also in Swabia (Frentzen 1922a).

Family Dipteridaceae

Genus *Clathropteris* Brongniart 1828

Clathropteris meniscioides Brongniart 1828

Figs. 6A-B, 12L, 12N

Description. Two specimens have been found. The frond fragments are up to 80 mm long and 40 mm wide, characterised by typical reticulate venation with net meshes of 8-10 x 4-6.5 mm. Each of the vein meshes is subdivided once more by a small reticulum less than 1 mm wide (S114341, Figs. 6A, Fig. 12N). One specimen was fertile, but the sporangia have fallen off and are only indicated by small dots between vein meshes (S114341, Fig. 6B).

Material. S114341, S114342.

Discussion. *Clathropteris* is considered a typical Upper Triassic and Jurassic genus. So far it has never been found in older sediments. Additionally, the sediment containing these fossils is more compact and carbonatic than the other rock samples from Thale, and of a darker grey color. Thus, we cannot completely be sure, that the specimens have been collected in the same stratigraphic level as the other specimens of the collection. The specimens are thus decribed here but not discussed in detail. Even if the specimens are small and we are not sure of their exact age, we can still attribute them to *Clathropteris meniscioides* because of their typical venation (e.g., Harris 1931; Kelber & Hansch 1995).

Systematic attribution. *Clathropteris meniscioides* has been considered a member of the Dipteridaceae based on its venation pattern and sporangial details.

Distribution. According to Frentzen (1922a: 7) this species is restricted to the Schilfsandstein (= Carnian) of Germany (e.g. Stuttgart), but it has been listed also from the Carnian of Neue Welt (Bronn 1851-1852: 34), and from the Rhaetian of e.g., Greenland, Germany, France and Sweden (Harris 1931; Weber 1968; Kelber & Hansch 1995). Lately this species has been recorded from the Lower Jurassic of Antarctica (Bomfleur & Kerp 2010).

Family Matoniaceae

Genus *Phlebopteris* Brongniart 1836

Phlebopteris sp.

Figs. 6C-D, 7A

Selected synonymy:

?1995 *Phlebopteris* sp. – Kelber & Hansch, p. 58, fig. 122.

Description. Only three frond fragments are assigned to this species. The rock samples are densely covered with pinnate frond fragments up to 65 mm long and 40 mm wide (pinnae converge to a none preserved petiole) (MB.PB. 2010/470, MB.PB. 2010/471, Fig. 6D). The elongated pinnules (25 mm long and 3-3.5 mm wide) with a rounded apex arise perpendicularly from the rachis (2 mm wide) and are characterised by a strong midrib. The secondary veins arise at about 60-70° and reach the margin perpendicularly, forking once or twice (MB.PB. 2010/471, Fig. 6C). The two fertile specimens show imprints of the sori consisting of circa eight free sporangia. Most of the sporangia have fallen of and only the receptaculum can be seen (MB.Pb. 2010/470, Fig. 7A).

Material. MB.Pb. 2010/470, MB.Pb. 2010/471.

Discussion. *Phlebopteris* (and its junior synonym *Laccopteris* Presl in Sternberg 1838) is considered the oldest known genus in the family Matoniaceae and is characterized by exindusiate sori arranged in two rows along the midrib. Our specimens can be assigned to the genus because of the pinna arrangement, the venation and the soral details. However, the material is limited and, therefore, it is difficult to make a specific attribution, although the similarity to *P. muensteri* seems to be the greatest (see below for comparions). Previously Kelber & Hansch (1995: 58, fig. 122) figured a specimen as *Phlebopteris* sp. from the Lower Keuper of Germany. Unfortunately, it is too badly preserved to compare it in detail with the three specimens from Thale.

Comparisons. *Phlebopteris muensteri* (Schenk) Hirmer et Hörhammer 1936 from the Late Triassic to Early Jurassic of Europe has up to 12 cm long pinnules, with a clear midrib and usually twice forked secondary veins, although once forked veins occur (see e.g., Van Konijnenburg-Van Cittert 1993). This is quite similar to the specimens described here. However, because of the fragmented nature of the Thale material, we do not attribute these specimens to this species, but if more material is found, it is possible that the German Ladinian material might belong to *Phlebopteris muensteri*. *Laccopteris* (= *Phlebopteris*) *lunzensis* Stur 1885 from the Carnian Lunz flora might be conspecific with *Phlebopteris muensteri*. It has never been figured but the description (see also Krasser 1909b) fits with that of *Phlebopteris muensteri* (see e.g., Van Konijnenburg-Van Cittert 1993).

Phlebopteris smithii (Daugherty) Arnold 1947 from the Carnian of the USA has pinnules that are 1-2.5 cm long and 2-3.0 mm broad. Thus they are slightly smaller than the material from Thale. Moreover, the secondary veins only fork once (see Ash et al. 1982).

Systematic attribution. Apart from the absence of an indusium, the genus *Phlebopteris* compares easily to the living genus *Matonia* and thus belongs to the fern family Matoniaceae.

Distribution. The Thale specimens are the only defined representatives of the genus *Phlebopteris* in the Ladinian since the specimen figured in Kelber & Hansch (1995) cannot be definitely attributed to the genus because of poor preservation, and thus the oldest members of the family known so far.

Pteridophyta incertae sedis

Genus *Cladophlebis* Brongniart 1849

Cladophlebis remota (Presl) Van Konijnenburg-Van Cittert et al. 2006

Figs. 7B, 12H

Selected synonymy (see also Van Konijnenburg-Van Cittert et al. 2006):

non 1820 *Neuropteris distans* Presl in Sternberg, p. 17.
1838 *Neuropteris distans* Presl in Sternberg, p. 136, pl. 40, fig. 4 (*nomen invalidum*, ICBN art. 34).
1838 *Neuropteris remota* Presl in Sternberg, p. 220.
1864 *Neuropteris remota* Presl. – Schenk, p. 75-76, pl. 1, fig. 1, pl. 2, fig. 3.
?1865 *Neuropteris remota* Presl. – Schoenlein & Schenk, p. 13-15, pl. 8, figs. 3-7; pl. 9, fig. 1.
?1865 *Pecopteris triasica* Heer, p. 54, pl. 2, fig. 7.
1865 *Neuropteris ruetimeyeri* Heer, p. 53, pl. 2, fig. 6.
1869 *Anotopteris distans* Presl. – Schimper, p. 470-472, pl. 33, nom. illeg. (ICBN art. 52.1).
1874 *Neuropteris remota* Presl. – Compter, p. 6.
1877 *Pecopteris ruetimeyeri* Heer. – Heer, p. 64, 70, pl. 25, figs. 10-12.
?1877 *Pecopteris triasica*. – Heer, p. 64, 69, pl. 25, figs. 1-2.
1885 *Neuropteris remota* Presl. – Quenstedt, p. 1095, pl. 90, fig. 17.
?1888 *Neuropteris remota?* Presl. – Szajnocha, p. 220-221, 226-228.
1922c *Anotopteris* (*Cladophlebis*) *distans* Presl. – Frentzen, p. 3, 6, 22-24, pl. 2, figs. 4, 6.
1922c *Pecopteris ruetimeyeri* Heer. – Frentzen, p. 6, 25-26, pl. 2, fig. 5.
1953 *Cladophlebis ruetimeyeri* (Heer). – Leonardi, p. 10, pl. 1, fig. 15, pl. 3, fig. 6.
1953 *Cladophlebis* sp. – Leonardi, pl. 1, figs. 3-4.
1989 *Scytophyllum bergeri*. – Kelber, fig. 73.
1990 *Cladophlebis distans*. – Kelber, p. 40, figs. 23b, 24a, 70, 71, 78.
1995 *Cladophlebis distans*. – Kelber & Hansch, p. 66, figs. 137-138.
2006 *Cladophlebis remota* (Presl) Van Konijnenburg-Van Cittert et al., p. 960-962, pl. 5, figs. 5-6, pl. 6, fig. 4, text-fig. 5B.

Description. Only a few pinna fragments in the collections were attributed to this species. They are up to 80 mm long and 30 mm wide. Falcate pinnules (up to 9-13 x 6.5-8 mm) with a pointed apex, marked midrib and forked lateral veins are attached (sub)oppositely to a 1-3 mm wide rachis (e.g. S114271, S114593, Figs. 7B, 12H). No fertile material has been found so far.

Material. S114018, S114117, S114155, S114158-9, S114161, S114171, S114176, S114200, S114271, S114593, S114687, S114712, S115911, S115915, MB.Pb. 2010/105.

Discussion. For a detailed discussion on the nomenclature of *Cladophlebis remota* see Van Konijnenburg-Van Cittert et al. (2006: 960). As an additional remark, we can now say that *Neuropteris ruetimeyeri* Heer (= *Cladophlebis ruetimeyeri*) from the Keuper flora of Neuewelt is conspecific with *Cladophlebis remota* (see already Schoenlein & Schenk 1865: 15). Moreover, *Pecopteris triasica* probably represents a small, badly preserved leaf fragment of *Cladophlebis remota*. *Pecopteris parvifolia* Compter 1922 from the Erfurt Formation (Ladinian) of Apolda is not well enough described for a comparison; it could, however, also belong to *C. remota*. Kelber (1986) figured leaves of *Cladophlebis remota* colonized by *Spirorbis*, indicating that they floated in the water sometimes before burial.

Comparions. *Pecopteris quercifolia* Presl in Sternberg 1838 from the Keuper of Stuttgart differs from *C. remota* because of its dentate margin and simple pinnate leaves. In *Pecopteris mexicana* Newberry 1876 from the Upper Triassic of Mexico the leaves are smaller and the veins are delicate, and fork only once. In *Cladophlebis brownii* Ash 2005 from the Upper Triassic of Arizona the rachis is stout (3 cm), the midrib curved and the pinnules smaller with connecting laminas. In *Cladophlebis wielandii* Jain et Delevoryas 1967 from the Middle Triassic of Argentina the pinnules are alternately attached, oblong-lanceolate in shape, with a serrate margin and an apically bifurcating midrib. In *Cladophlebis conferta* Holmes 2003 the midrib is delicate, the pinnules are much shorter and are attached at an acute angle (~45°); in *Cladophlebis octonerva* Holmes 2003 the pinnules are obtuse to triangular and secondary veins are more distant. In *Cladophlebis retallackii* Holmes 2003 the midrib is strongly decurrent and the lateral veins are thrice forked, in *Cladophlebis sinuata* Holmes 2003 (all four from the Middle Triassic of Australia) the margin is undulate and the midrib is fine, with secondary veins attached at 45°. In *Cladophlebis subfalcata* Fontaine 1883 and *Cladophlebis ovata* Fontaine 1883 the pinnules are thin and delicate; in *Cladophlebis auriculata* Fontaine 1883 the base of the broadly ovate pinnules is auriculate. In *Cladophlebis pseudowhitbiensis* Fontaine 1883 (all four from the Upper Triassic of the USA) the pinnules alternate and venation is indistinct apart from the midrib. In *Todites chilensis* Herbst et Troncoso 1998 from the Upper Triassic of Argentina, *Cladophlebis microphylla* Fontaine 1883 from the Upper Triassic of the USA, *Cladophlebis yungjenensis* Chu in Hsü et al. 1975 from the Upper Triassic of China and *Cladophlebis curvifolia* Prynada 1962 from Upper Triassic of Russia the leaves and pinnules are smaller (3-4 x 1.5-2 mm, 4-6 x 1-3.5 mm and 10 x 3-3.5 mm respectively).

In *Todites fukutomii* Kimura et Ohana 1980 and *Todites yamanoiensis* (Yokoyama) Kimura et Ohana 1980, *Cladophlebis bitchuensis* Oishi 1932 (all from the Carnian of Japan) and *Cladophlebis calcariformis* Chu in Hsü et al. 1975 (in Chen et al. 1979) from the Upper Triassic of China the pinnae arise at an acute angle and the pinnules are much more elongated (16 x 5.3 mm, 13-21 x 7-11 mm, 10-18 x 5-6 mm and 19-22 x 0.8-11 mm respectively). In *Todites tamurae* Kon'no 1972b and *Todites sarawakensis* Kon'no 1972b, both from the Upper Triassic of East Malaysia, the margin is undulate. *Todites subtilis* Duan et Chen 1979 and *Todites yanbianensis* Duan et Chen 1979 from the Upper Triassic of Sichuan (China) differ because of the smaller dimensions of the pinnules and the delicate secondary veins (5-6 x 4-5 mm). In *Cladophlebis ishiiana* Kon'no 1972b the pinnae and pinnules are inserted at an acute angle and the pinnules are bigger (15-24 x 6-9 mm), in *Todites katoi* Kon'no 1972b (both from the Upper Triassic of East Malaysia) the pinnae imbricate. In *Cladophlebis pseudodelicatula* Oishi 1932 from the Carnian of Japan the pinnules are linear to elongate-lanceolate (length generally five times the width). In *Cladophlebis yanschinii* Prynada 1962 from the Upper Triassic of Russia they are much bigger and perpendicularly inserted (25-35 x 8 mm). *Cladophlebis acutipennis* Oishi 1940 from the Carnian of Japan has small and acuminate pinnules with an indistinct venation. *Cladophlebis szeiana* P'an 1936 differs because of its oblong pinnules with a contiguous base and a rounded apex, *Cladophlebis grabauiana* P'an 1936 (both from the Upper Triassic of China) because of the slender rachis, and the distinct, decurrent midrib.

Systematic attribution. Since fertile leaves have never been found, some authors suggested a seed fern affinity (see also Kelber 1987: 286, 1998: 95), others suggested it to be a tree fern (Leuthardt 1901: 128). We think that a fern assignement is the most likely based on macromorphology.

Distribution. According to Mader (1990) *Cladophlebis remota* is restricted to the Lettenkeuper and Schilfsandstein in Central Europe (see also Schenk 1864; Schoenlein & Schenk 1965; Frentzen 1922a; Kelber 1983). Additionally, the species has been recorded from the Middle Triassic of the Dolomites (N-Italy, e.g. Leonardi 1953; Kustatscher & Van Konijnenburg-Van Cittert 2005; Van Konijnenburg-Van Cittert et al. 2006) and the Carnian of Raibl and perhaps of Lunz (Schenk 1866-1867; Heer 1877; Leuthardt 1901; Krasser 1909a; Frentzen 1922a). In Neuewelt *Merianopteris ruetimeyeri* Heer (= *Cladophlebis remota*) is, together with *Merianopteris augusta*, the dominant fern (Leuthardt 1901). Perhaps some material also comes from the Upper Triassic of Cacheuta in Argentina (Szajnocha 1888).

Cladophlebis leuthardtii Leonardi 1953
Figs. 7C, 12I

Selected synonymy (see also Kustatscher & Van Konijnenburg-Van Cittert 2005):

1953	*Cladophlebis leuthardtii* Leonardi, p. 11, pl. 2, figs. 1-5.
1953	*Cladophlebis rütimeyeri* var. *heeri* Leonardi, p. 11, pl. 1, fig. 1.
1964	*Cladophlebis* sp. – Leonardi, p. 201, pl. 5, fig. 7.
1968	*Cladophlebis* cf. *denticulata*. – Leonardi, p. 179, pl. 28, fig. 7.
1986	*Cladophlebis leuthardtii*. – Calligaris, p. 9, fig. B29.
2000	*Cladophlebis leuthardtii* Leonardi. – Wachtler & Van Konijnenburg-Van Cittert, p. 109, pl. 1, fig. 3.
2005	*Cladophlebis leuthardtii* Leonardi. – Kustatscher & Van Konijnenburg-Van Cittert, p. 34.

Description. Only two specimens in the collections have been attributed to this species. The pinnate frond fragments are up to 35 mm long and 17 mm wide with up to 20 mm long and 5 mm wide. The rachis is less than 1 mm wide, the pinnules are falcate and small (2-2.5 x 1.5 mm); delicate, bifurcating secondary veins arise from the midrib (e.g. S114279, S114200, Figs. 7C, 12I).

Fig. 7. A. *Phlebopteris* sp., details of the fertile pinnules showing attachment areas of the sori (MB.Pb. 2010/470). **B**. *Cladophlebis remota* (Presl) Van Konijnenburg-Van Cittert et al. 2006, pinnae fragments (S114271). **C**. *Cladophlebis leuthardtii* Leonardi 1953, frond fragment (S114200). **D**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, pinna fragment (S114291). **E**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, details of the pinnules (S114283). **F**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, detail of fertile pinnae (S114244), scale = 0.5 mm. **G**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, fertile frond fragment (S114244). – Scale = 10 mm if not otherwise indicated.

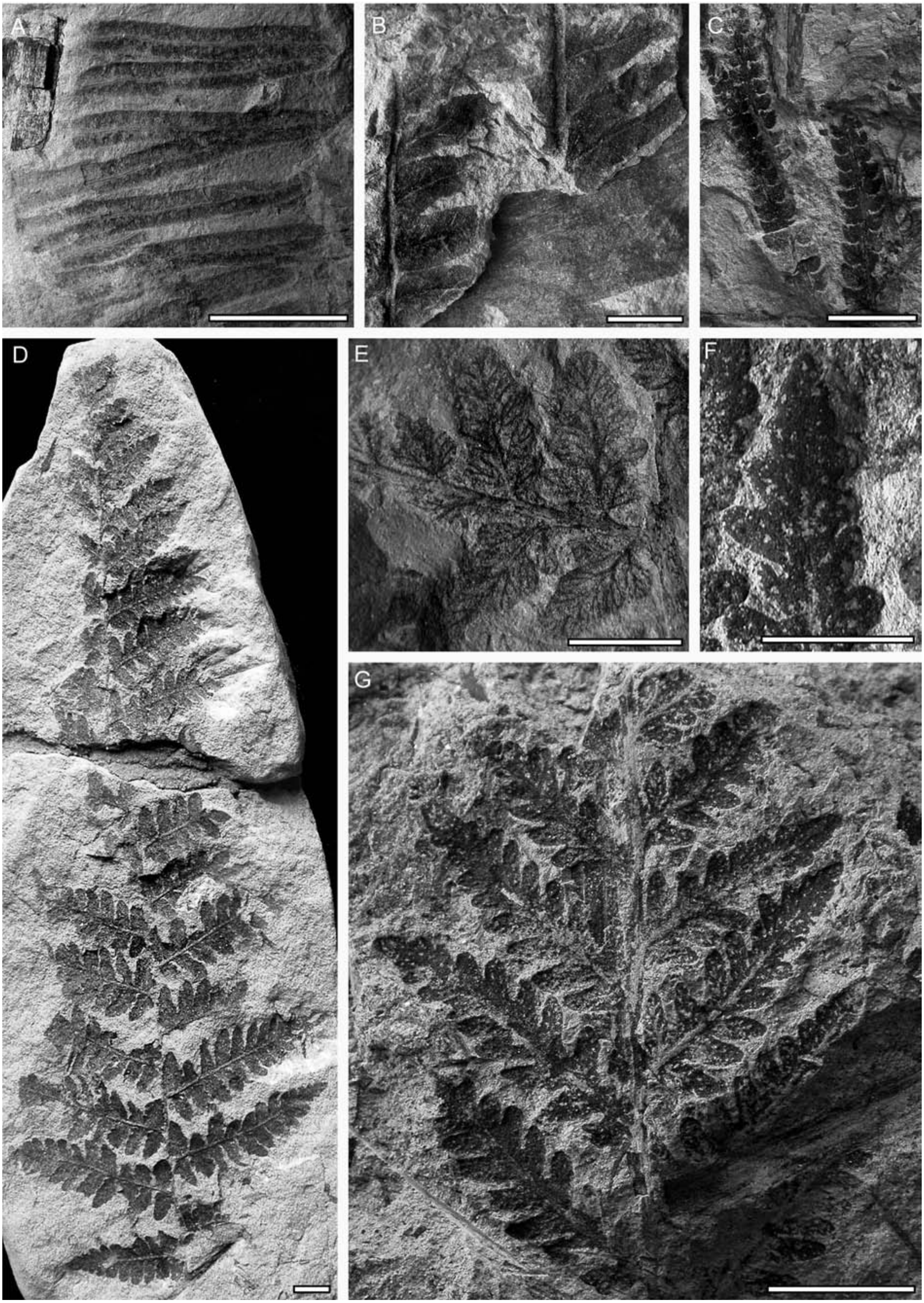

Fig. 7

Material. S114285, S114200, S114279.

Discussion. The two specimens have been attributed to this species because of the typical falcate shape of their small pinnules. They resemble closely the material from the Dolomites described by Leonardi (1953) and Wachtler & Van Konijnenburg-Van Cittert (2000). It cannot be completely excluded that these specimens are young leaves or leaves of a young individual of *Cladophlebis remota* but the falcate pinnules precludes this.

Comparisons. *Pecopteris quercifolia* Presl in Sternberg 1838 from the Keuper of Stuttgart (Presl in Sternberg 1838: 159, pl. 50, fig. 3) differs from *Cladophlebis leuthardtii* because of the dentate margin and the bigger dimension of the pinnules. In *Cladophlebis remota* and in *Todites gaillardotii* the pinnules are bigger (9-13 x 6.5-8 mm and 6-11 x 6-8 mm respectively) and the pinnules are roundish in the latter. *Pecopteris mexicana* Newberry 1876 from the Upper Triassic of Mexico resembles *C. leuthardtii* in frond morphology, pinnule shape and venation pattern, but the dimensions of the species are unknown. Additionally, in the fertile material of *P. mexicana* 1-5 sori are situated on the lower side of the pinnules while in *Cladophlebis leuthardtii* there is no information on the fertile structures. *Cladophlebis brownii* Ash 2005 from the Upper Triassic of Arizona differs because of the stout rachis (3 cm), the curved midrib and the connection of the laminas between the adjacent pinnules. In *Cladophlebis paucinerva* Holmes 2003 and *Cladophlebis tenuipinnula* Holmes 2003 from the Middle Triassic of Australia, *Cladophlebis gracilis* Sze 1956 from the Middle-Late Triassic of China, *Cladophlebis subfalcata* Fontaine 1883, *Cladophlebis auriculata* Fontaine 1883, *Cladophlebis ovata* Fontaine 1883, *Cladophlebis microphylla* Fontaine 1883 and *Cladophlebis pseudowhitbiensis* Fontaine 1883 (all five from the Upper Triassic of Pennsylvania, USA) the pinnules are bigger and the pinnules inserted at a larger angle. In *Cladophlebis acutipennis* Oishi 1940 from the Carnian of Japan the pinnules are small and narrow, acuminate, with an indistinct venation; unfortunately the author gives no dimensions and it is impossible to detect if the pinnules are as small as in our case. *Sphenopteris birsina* Heer 1877 from the Carnian of Neuewelt resembles *C. leuthardtii* in pinna shape and venation but no information on the dimensions of the Swiss specimens are given, thus it is impossible to compare it with our material.

Distribution. This species was previously described only from the Upper Ladinian of the Dolomites (e.g., Wachtler & Van Konijnenburg-Van Cittert 2000; Kustatscher & van Konijnenburg-Van Cittert 2005).

Genus *Sphenopteris* (Brongniart) Sternberg 1825

Sphenopteris schoenleiniana (Brongniart) Presl in Sternberg 1838

Figs. 7D-G, 8A-C, 12K

Selected synonymy:

1835	*Pecopteris schoenleiniana* Brongniart, p. 364, pl. 126, fig. 6.
1838	*Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg, p. 132.
1864	*Sphenopteris schoenleiniana* (Brongniart) Presl. – Schenk, p. 80-81, pl. 2, fig. 2, 2a.
1865	*Pecopteris schoenleiniana* Brongniart. – Schoenlein & Schenk, p. 151-156, pl. 9, fig. 2, 2a.
1871	*Pecopteris schoenleiniana* Brongniart. – Stur, p. 203.
1888	*Pecopteris schoenleiniana* Brongniart. – Szajnocha, p. 220-221, 225-226, pl. 1, fig. 9.
1922c	*Sphenopteris schoenleiniana* (Brongniart) Presl. – Frentzen, p. 3, 6, 30-32, pl. 3, fig. 3.
?1990	*Sphenopteris schoenleiniana* (Brongniart) Presl. – Kelber, p. 40, fig. 72.
1995	*Sphenopteris schoenleiniana*. – Kelber & Hansch, p. 58, 95, figs. 123, 125-126.
2006	*Sphenopteris schoenleiniana* (Brongniart) Presl. – Van Konijnenburg-Van Cittert et al., p. 959, pl. 5, figs. 3-4, 7.

Description. There are *c.* 50 specimens of this at least tripinnate fern species, most of which are only pinna fragments (e.g. S114280, S114283, S114290-01). The largest frond fragments are up to 235 mm long and 73 mm wide (e.g. S114291, S114452, Fig. 7D). The primary rachis is 1-2 mm wide with pinnae (up to 51 mm long and 31 mm wide) arising at angles of 45-60°. The penultimate pinnules measure up to 29 x 6 mm basally and 5-9 x 2-5 mm apically. In the basal part of the leaves of the second order pinnules show sometimes an undulate margin or divide once more into pinnules of the third order (4 x 1.5-2.5 mm, S114283, Fig. 7E). The ultimate pinnules are very variable in shape: from lingulate, spatiolate to ovate, slightly curving forwards or imbricate, with a more or less constricted base, a lobate, serrate or entire margin and a rounded apex (Fig. 12K).

The fertile frond fragments (e.g. S114253, S114274, S114244, Fig. 7F-G) are at least tripinnate. The most complete one is 57 mm long and 50 mm wide. The main rachis is *c.* 2.5-3 mm wide; the pinna fragments measure up to 38 x 31 mm. The penultimate pinnules are 29-34 mm long (apically 10 mm) and 17 mm wide (apically 5.6 mm). The ultimate pinnules measure up to 2.5 x 1.8 mm. The small sporangia are attached at the end of the secondary veins (S114244, Fig. 7F). So far, no *in situ* spores were recovered, but we extracted some small, thin epidermal remains from a specimen. They show costal and intercostal zones with stomata randomly arranged in the intercostal zones. Stomata have 2 guard cells and usually 4 subsidiary cells with a small papilla. Normal epidermal cells are polygonal with slightly undulate cell walls (S114244, Fig. 8A-C).

Material. S050055, S114165, S114200, S114207, S114212, S114215, S114240-41, S114244-45, S114248, S114253, S114255, S114259, S114266-68, S114273-75, S114283-84, S114286-89, S114291-2, S114309, S114309, S114347, S114431, S114452, S114455, S114552, S114651, S114720, S114800, S114816, S114829, S149409, JMS 52391, MB.Pb. 2000/249b, MB.Pb. 2000/249c, MB.Pb. 2000/249d, MB.Pb. 2000/258, MB.Pb. 2010/28, MB.Pb. 2010/34a, MB.Pb. 2010/34b, MB.Pb. 2010/38b, MB.Pb. 2010/85, MB.Pb. 2010//96, MB.Pb. 2010/97, MB.Pb. 2010/98.

Discussion. *Sphenopteris* is a morpho-genus for bi- to tripinnate fronds with pinnules constricted at their base. The midrib is straight or flexuous and produces forking secondary veins that depart at a steep angle and extend toward the margin either singly or in small groups. Although most *Sphenopteris* species are from the Palaeozoic, there are a number of Mesozoic representatives (see Taylor et al. 2009: 680).

Brongniart (1835-1836: 364) introduced the species *Pecopteris schoenleiniana* for a small frond fragment with a quite variable pinna shape. According to Frentzen (1922c: 32) and Mader (1990: 1159) *Sphenopteris schoenleiniana* is characterised by heterophylly, representing sun and shadow leaves. Sun leaves have subdivided second-order pinnae, whereas shadow leaves "exhibit undivided second-order pinnae that are also broader at the base". If this is true, the specimens now described as *Sphenopteris* vel *Cladophlebis* sp. A might represent the shade leaves of *Sphenopteris schoenleiniana*. According to Szajnocha (1888: 226) *Sphenopteris lobifolia* Morris 1845 is identical with *S. schoenleiniana* and should, thus belong to this species.

Comparisons. Fronds are bipinnate in *Sphenopteris myriophyllum* Brongniart 1828 from the Buntsandstein of France (tripinnate in our specimens), the rachis is stout (delicate in our specimens) and the pinnae are more curved forwards, obtuse, ovate and irregularly lobed than in *S. schoenleiniana*. *Sphenopteris oppositifolia* Presl in Sternberg 1838 from the Keuper of Germany differs from *S. schoenleiniana* because of the cuneate pinnules with a dentate margin, undulate midrib and the secondary veins arising at a very acute angle from the midrib. *Sphenopteris clavata* Presl in Sternberg 1838 from the Keuper of Germany is characterised by elongate to lanceolate pinnules with incised lobes and restricted bases (against the lobed pinnules with entire margin in *S. schoenleiniana*). *Sphenopteris kirchneri* Goeppert 1841 from the Keuper of Bamberg (Germany) differs in the prominent basal pinnae with an acute middle lobe and never forking veins. In *Sphenopteris braunii* Goeppert 1841 from the Keuper of Germany the apex of the pinnules is more acute and the pinnules are inserted at an acute angle. In *Sphenopteris patentissima* Goeppert 1841 the pinnae arise at an acute angle; the veins bifurcate several times.

Sphenopteris birsina Heer 1877 from the Carnian of Neuewelt described originally by Heer (1865: 2, fig. 4) as *S. roessertiana* Presl in Sternberg, is represented only by one small apical specimen with inclined oval pinnules with an acute apex and strong midrib. Its fragmentary preservation does not permit us to compare it closely with *S. schoenleiniana*. *Sphenopteris sitholeyi* Bock 1969 from the Upper Triassic of North America is characterised by fan-shaped to ovate pinnules, with open dichotomous venation but without midvein and is thus clearly distinct from *S. schoenleiniana*. In *Sphenopteris speciosa* Holmes 2003 from the Middle Triassic of Australia the pinnae overlap close to the main rachis and are much bigger than in our case (100 x 45 mm), the pinnules have five pairs of deeply incised lobes while in our material the shape of the pinnules is much more variable. In *Sphenopteris eskensis* Walkom 1928 from the Upper Triassic of Queensland the pinnules are wedge-shaped with a crenulate margin. In *Sphenopteris arizonica* Daugherty emended Ash 1999 from the Upper Triassic of Arizona (petrified forest) the pinnae are linear-lanceolate and narrower than in our material (30 mm long and 9-12 mm broad); additionally the narrow flange of lamina running decurrently from each primary pinna along the margin of the main rachis to the pinna below has not been observed in our specimens.

Systematic attribution. Species assigned to the genus *Sphenopteris* probably belong to different plant groups including ferns and pteridosperms (e.g. Kelber 1998: 96; Taylor et al. 2009: 680-683). In our case, the presence of fertile pinnae enables us to attribute this species without doubt to the ferns, but a family attribution is impossible because of lack of sporangial details.

Distribution. *Sphenopteris schoenleiniana* has been recorded as a rare element from the Lettenkeuper (upper Ladinian) and Schilfsandstein (Stuttgart Formation, Carnian) of Germany (e.g., Presl in Sternberg 1838; Schenk 1864; Schoenlein & Schenk 1965; Frentzen 1922a; Schmidt 1928; Kelber & Hansch 1995).

According to Mader (1990) *Sphenopteris schoenleiniana* is restricted to the upper Ladinian (Lettenkeuper) in Central Europe; Van Konijnenburg-Van Cittert et al. (2006) described it also from the upper Anisian of the Dolomites and Szajnocha (1888) mentioned it from the Upper Triassic of Argentina.

Sphenopteris vel *Cladophlebis* sp. A
Figs. 8D-F, 12M

Description. About 30 specimens are described as *Sphenopteris* vel *Cladophlebis* sp. A (e.g. S114265, S114264, Fig. 8E). No complete frond has been found so far, the biggest specimens of this tripinnate material are up to 90 mm long and 50 mm wide (e.g. S114280, S114526, S114264, Fig. 8E). The pinnae (up to 50 x 13 mm) have a narrowly triangulate outline and arise from a 2-3 mm broad rachis. The first basiscopic pinnules are slightly smaller than the other ones (e.g. JMS 52380, Fig. 8D). The other pinnules are ovate with a rounded apex (7-10 x 3.5-4 mm) and arise at angles of ~ 80° from the narrow rachis (< 1mm). The margin is entire, only in the most basal pinnules the margin undulates slightly (e.g. JMS 52380, Fig. 8D); the basiscopic margin attaches decurrently to the rachis, the acroscopic margin seems to be constricted. Apically the pinnules reduce in size (3.5-5 x 3-3.5 mm) and finally fuse near the apex. Secondary veins arise from the delicate midrib, then fork generally once (e.g. S114264, Figs. 8F, 12M). No fertile leaf fragments have been found.

Material. S114020, S114070, S114092, S114102, S114204, S114209, S114219, S114238, S114242-43, S114246-7, S114249-51, S114254, S114257, S114258, S114261-62, S114264-5, S114269-70, S114276, S114278, S114280-81, S114290, S114526, S114553, S114610, S114627, S114807, S114859, JMS 52380, MB.Pb. 2000/249, MB.Pb. 2010/92.

Discussion. The fronds are at least tripinnate; the frond morphology with its narrow rachis is rather similar to *Sphe-*

nopteris schoenleiniana but the pinnule attachment (apart from the basiscopic decurrent margin), the distinct midrib and the secondary venation are more like a *Cladophlebis* than a *Sphenopteris*; therefore we describe this material preliminarily as *Sphenopteris* vel *Cladophlebis* sp. A.

Frentzen (1922c: 31-32) mentioned that the pinnae of the second order of *Sphenopteris schoenleiniana* are quite variable in size and shape and might represent sun and shade leaves of that species. If this is true, the specimens now described as *Sphenopteris* vel *Cladophlebis* sp. A might represent the shade leaves of what we described here as *Sphenopteris schoenleiniana*.

Comparisons. The most similar species from literature is *Cladophlebis grabauiana* P'an 1936 from the Upper Triassic of China but it differs from *Sphenopteris* vel *Cladophlebis* sp. A because of the more rigid slender rachis, the angle of pinna attachment (45°) and the smaller size of the pinnules.

Distribution. This taxon seems to have been described only from the Thale flora.

Genus *Chiropteris* Kurr ex Bronn 1858

Chiropteris lacerata (Quenstedt) Rühle von Lilienstern 1931
Figs. 8G, 12J

Selected synonymy (see also Rühle von Lilienstern, 1931a):

1852 *Cyclopteris lacerata* Quenstedt, p. 710.
1858 *Chiropteris digitata* Kurr ex Bronn, p. 61-63, pl. 10, figs. 1-4.
1862 *Chiropteris digitata* Kurr. – Schenk, p. 179.
1864 *Chiropteris digitata* Kurr. – Schenk, p. 86-88, pl. 2, fig. 4.
1865 *Chiropteris digitata* Kurr. – Schoenlein & Schenk, p. 16, pl. 11, fig. 1a, b; pl. 13, fig. 6.
1867 *Cyclopteris lacerata* Quenstedt. – Quenstedt, p. 853, fig. 171.
1869 *Chiropteris kurriana* Schimper, p. 643, pl. 43, figs. 1-2.
1910 *Chiropteris digitata* Kurr. – Wills, p. 313.
1922c *Chiropteris digitata* Kurr. – Frentzen, p. 3, 6, 32-33, pl. 3, figs. 5, 8.
1931a *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern, p. 255-262, text-figs. 1-4, pls. 7-9.
1931b *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern, p. 232.
1990 *Chiropteris digitata*. – Kelber, p. 40-41, figs. 61b, 69.
1995 *Chiropteris digitata*. – Kelber & Hansch, p. 58, 62, text-figs. 15, 127-130.

Description. Only few fragmentary specimens of this species have been found in the flora. They are generally small, up to 60 mm long and 35 mm wide and are characterised by their typical net venation with a central vein in each segment (e.g. S114431, Figs. 8G, 12J).

Material. S114347, S114431, S114629, JMS 52390, MB.Pb. 2010/104.

Discussion. In 1852, Quenstedt described, without figuring, *Cyclopteris lacerata* from the Lettenkeuper of Bibersfeld (Germany), as a palmate type of leaf divided into 6 segments and showing net venation. Bronn (1858: 61), referring to the (never published?) manuscript of Kurr, described *Chiropteris digitata* as a funnel-shaped structure formed by several leaflets without evident midrib and with a netlike venation. Schenk (1862: 179) interpreted the netlike structure as anastomosing secondary veins with a clear midrib. Rühle von Lilienstern (1931a: 255) revised the species and created the correct combination *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern 1931. He considered the leaves to be up to 20 cm wide with an up to 15 cm long petiole, arising directly from rhizomes (Rühle von Lilienstern 1931a: 255).

The species *Chiropteris lacerata* Arber 1913 ex Arber 1917 from the Rhaetian of New Zealand is a junior synonym and thus invalid.

Comparisons. The fragments present in this flora are small and do not permit any close comparisons. Specimens of *C. lacerata* from other floras, enable us, however, to compare the taxon with others known from literature.

Chiropteris barrealensis Frenguelli 1942 from the Rhaetian of Barreal (Argentina) differs because of its smaller dimension (38 mm long), the asymmetric cordate form of the leaf and the venation type (narrow, polygonal meshes only present near the margin). According to Rühle von Lilienstern (1931a: 263-264) *C. lacerata* differs from *Chiropteris cuneata* (Carruthers) Seward 1903 from the Triassic of Queensland because of the entire margin, the lack of any midrib and the delicate secondary veins, from *Chiropteris zeilleri* Seward 1903 from the Rhaetian of South Africa because of the orbiculate lamina, the deeply irregular segments and the large, polygonal meshes, from *Chiropteris arberi* Rühle von Lilienstern 1931 from the Rhaetian

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Fig. 8. **A**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, cuticle fragment (S114244), scale = 50 µm. **B**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, cuticle fragment with polygonal epidermal cells and stomata (S114244), scale = 50 µm. C. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, detail of cuticle with stomata (S114244), scale = 50 µm. **D**. *Sphenopteris* vel *Cladophlebis* sp. A, frond fragment with reduced basiscopic pinnules (JMS 52380). **E**. *Sphenopteris* vel *Cladophlebis* sp. A, frond fragment (S114264). **F**. *Sphenopteris* vel *Cladophlebis* sp. A, showing venation pattern (S114264). **G**. *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern 1931, frond fragment with typical netstructure and midrib (arrow) (S114431). – Scale = 10 mm if not otherwise indicated.

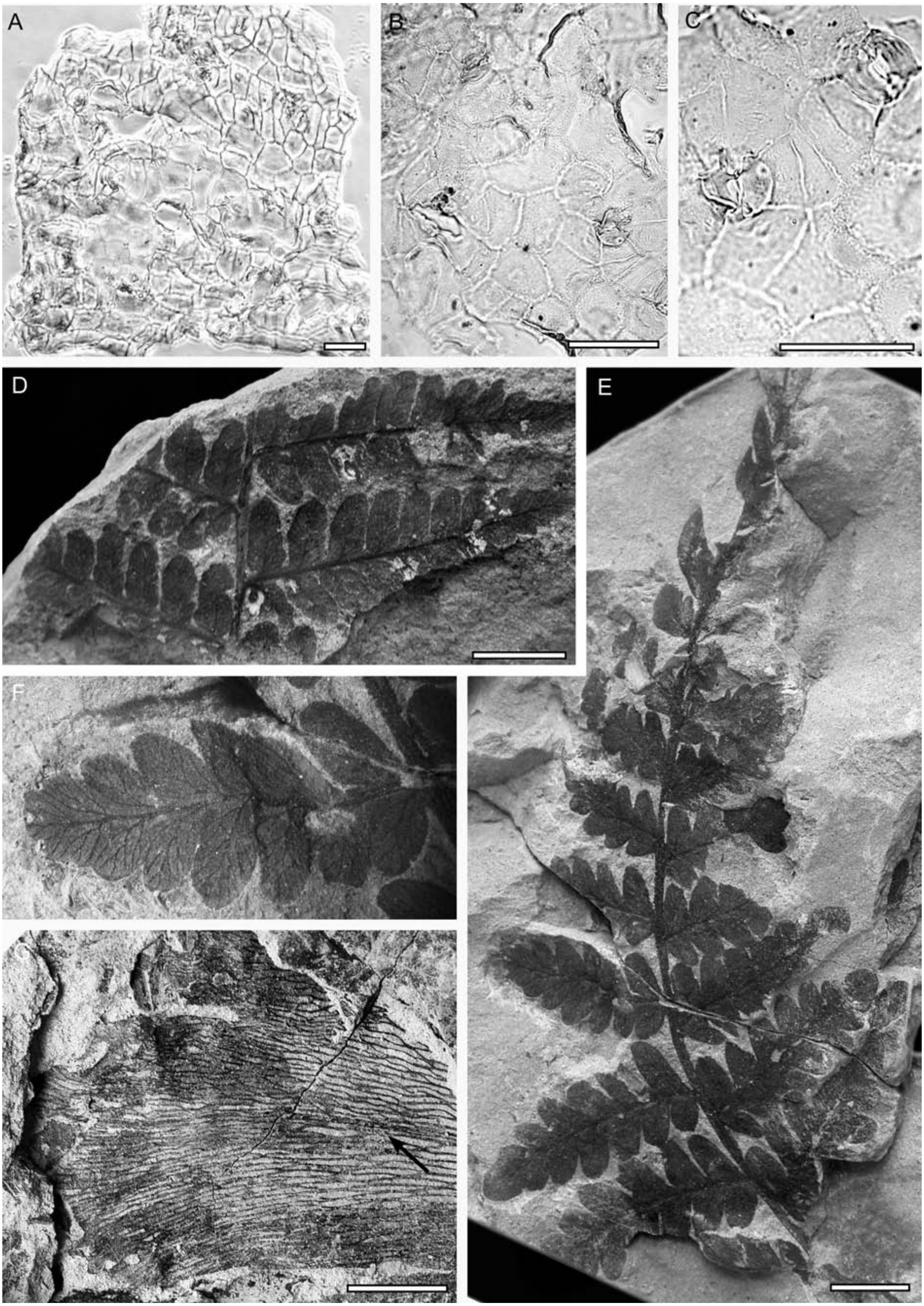

Fig. 8

of New-Zealand because of the dentate margin and the fine veins. *Chiropteris copiapensis* Steinmann et Solms-Laubach in Solms-Laubach & Steinmann 1899 from the Rhaetian of Chile differs from *C. lacerata* because of the flabellate leaves, the irregularly undulate to lacinate distal margin and the rhomboidal net meshes (Frenguelli 1942: 345-347). In *Chiropteris tasmanica* Walkom 1925 from the Mesozoic of Tasmania the veins of the small leaves (up to 35 mm long, 30 mm wide) branch dichotomously and only occasionally anastomose. The leaves of *Chiropteris biloba* Bell 1956 from the Upper Triassic of New Zealand are much smaller (~ 40 mm long and 35 mm wide) and deeply incised into two distinct segments. In *Chiropteris waitakiensis* Bell 1956 from the Upper Triassic of New Zealand the leaves are subdivided into four or more straplike segments by repeating dichotomy; apart from the anastomosing veins the macrostructure resembles a ginkgophyte. In *Chiropteris taizihoensis* Zhang 1980 and *C. yuanii* Sze 1956 from the Upper Triassic of China the leaves are of much smaller dimensions (1.5-2.5 mm). *Chiropteris kawasakii* Kon'no 1972a from the Late Triassic of East Malaysia is characterized by reniform leaves with a slender petiole, an entire or slightly undulated margin and several main veins.

Systematic attribution. The systematic position of *Chiropteris* is still unclear; the genus might even belong to various plant groups. Schimper (1869: 643) mentioned a close resemblance between *Chiropteris* and *Sagenopteris* (Caytoniales) due to the net venation. The two genera differ, however, in the leaf structure (funnel-shaped in *Chiropteris* and 2 pairs of closely spaced leaflets in *Sagenopteris*) and venation (the lateral veins arise at an acute angle from the midrib in *Sagenopteris*, while in *Chiropteris* the lateral veins are almost parallel to the delicate midrib). *Chiropteris lacerata* has been considered closely related to *Ophioglossum palmatum* L. (Schimper & Schenk 1890: 152; Potonié 1899: 91; Zeiller 1900: 55; Frentzen 1922c: 32); Schmidt (1928: 71) assigned it thus putatively to the Ophioglossaceae. Seward (1910: 431) and Hirmer (1927: 679) rejected attribution of the genus to the Ophioglossaceae and assigned it to the ferns in general. Rühle von Lilienstern (1931a: 261) interpreted some roundish structures on the lower side of the leaves as sporangia and considered the Matoniaceae or Dipteridaceae as the closest fern families (Rühle von Lilienstern 1931a: 269). Indeed the Dipteridaceae is the only fern family with a net venation.

Mägdefrau (1956: 234) suggested a close affinity to the polypodiaceous *Neocheiropteris palmo-pedata* because of the roundish "fertile structures" and the palmate leaf shape; but pointed out that no clear relationship to any family could be given. Some authors even consider it a ginkgoalean type of leaf (see Kelber 1998: 95; Taylor et al. 2009: 749) and Fraas (1910: 110) suggested an affinity with the cycadophytes.

We consider that the affinity of *Chiropteris* will not be clear until fertile structures have been found, but that an attribution to the Dipteridaceae is the most likely because of the leaf morphology and venation pattern.

Distribution. This species is well distributed in the Lettenkeuper (Erfurt Formation, upper Ladinian) of Baden-Württemberg and Bavaria (Germany) and rare in the Schilfsandstein (Carnian) of Stuttgart and Württemberg (Germany, Schenk 1862, 1864; Schimper 1869; Frenzen 1922a; Rühle von Lilienstern 1931a, 1931b; Kelber & Hansch 1995). This species also might be present in the Lower Keuper of England (Wills 1910), the Carnian of Neue Welt (Switzerland, Schoenlein & Schenk 1865) and the Rhaetian of Australia and New Zealand (Walkom 1925a, b).

Fig. 9. **A**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), epitype, fertile specimen (SMNS P24165). **B.** *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), epitype, large sterile specimen (S114030). **C**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), holotype (BSPG 2008 LXI 01). **D**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), holotype, detail of the fertile pinnules (BSPG 2008 LXI 01). – Scale = 10 mm.

Next Double Page:

Fig. 10. **A**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), detail of the pinnules with undulate margin, giving almost the idea of a third subdivision (S114837). **B**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), apical frond fragment (S114048). **C**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), apical frond fragment (S114027). **D**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), pinnule with clear venation pattern (S114052). **E**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), fertile pinnules (S114017). – Scale = 10 mm.

Fig. 11. **A**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), fertile frond fragment (S114016). **B**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), lower surface of fertile pinnules with sporangia fallen off, arrow indicates the curved lamina that protected originally the lower lamina (S114006). **C**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), sporangial fragment (S114006), scale = 50 µm. **D**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), spore group (S114006), scale = 50 µm. **E**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), spores (S114017), scale = 25 µm. **F**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), spore with evident trilete mark (S114017), scale = 25 µm. – Scale = 10 mm if not otherwise indicated.

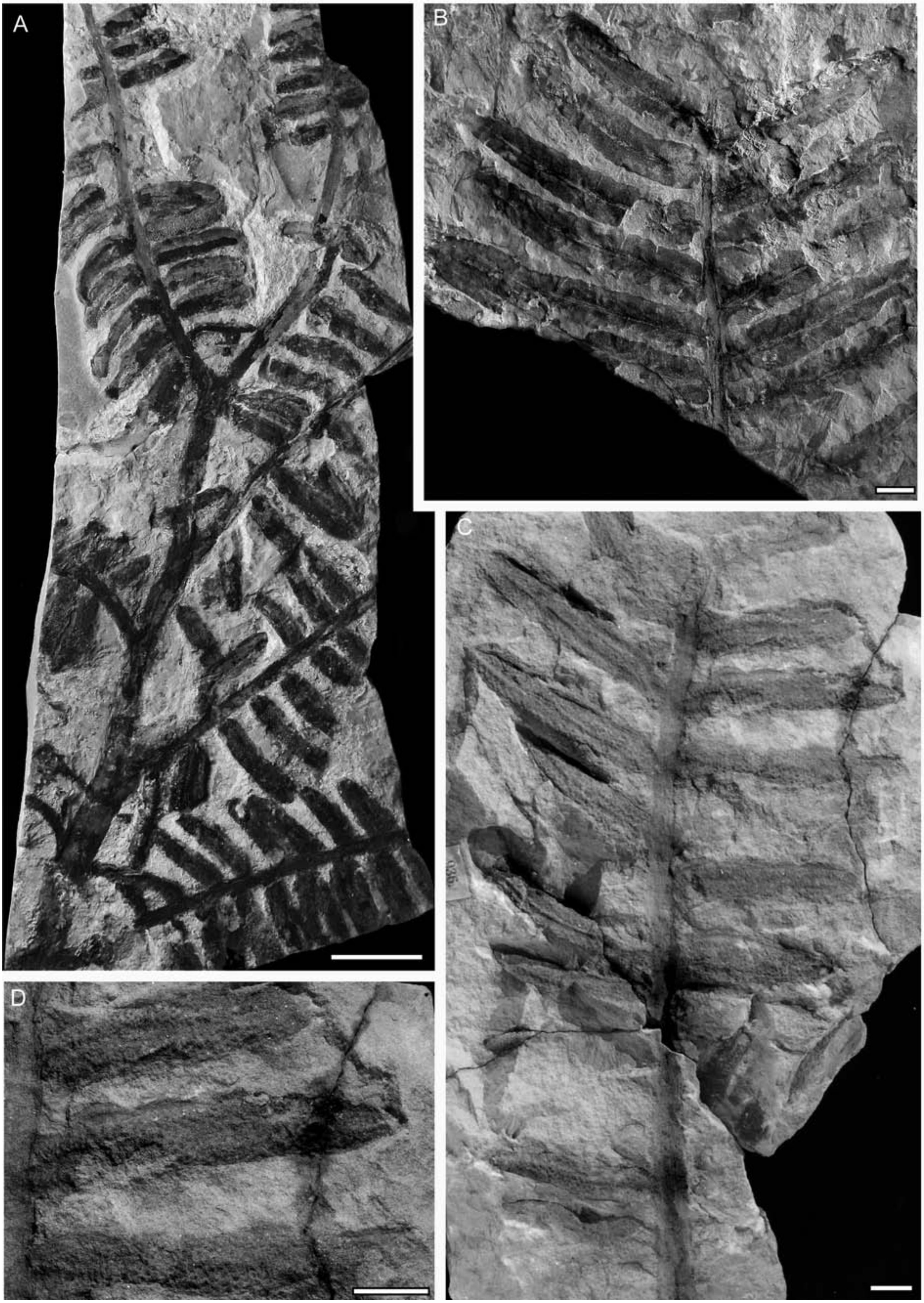

Fig. 9

Fig. 10

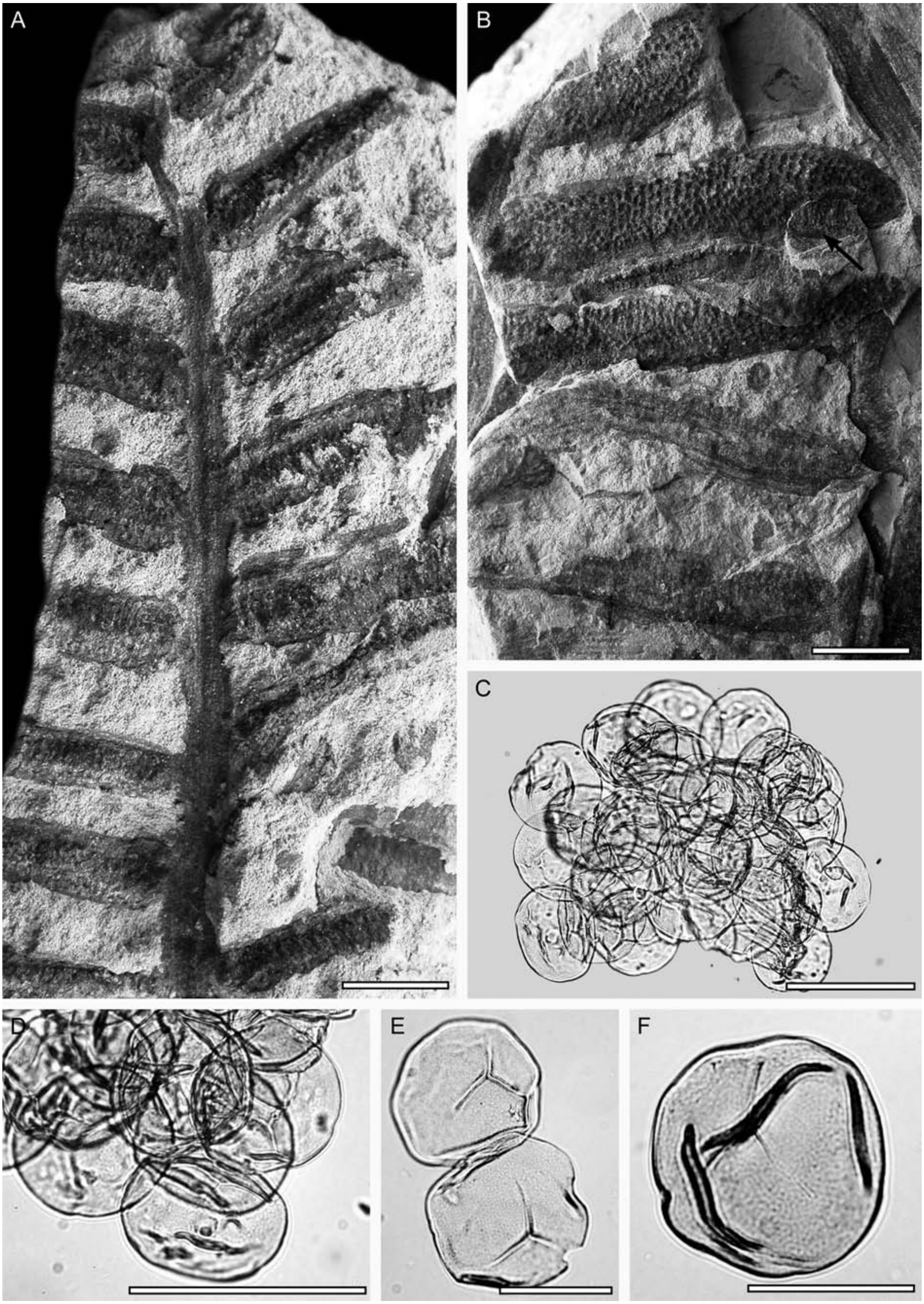

Fig. 11

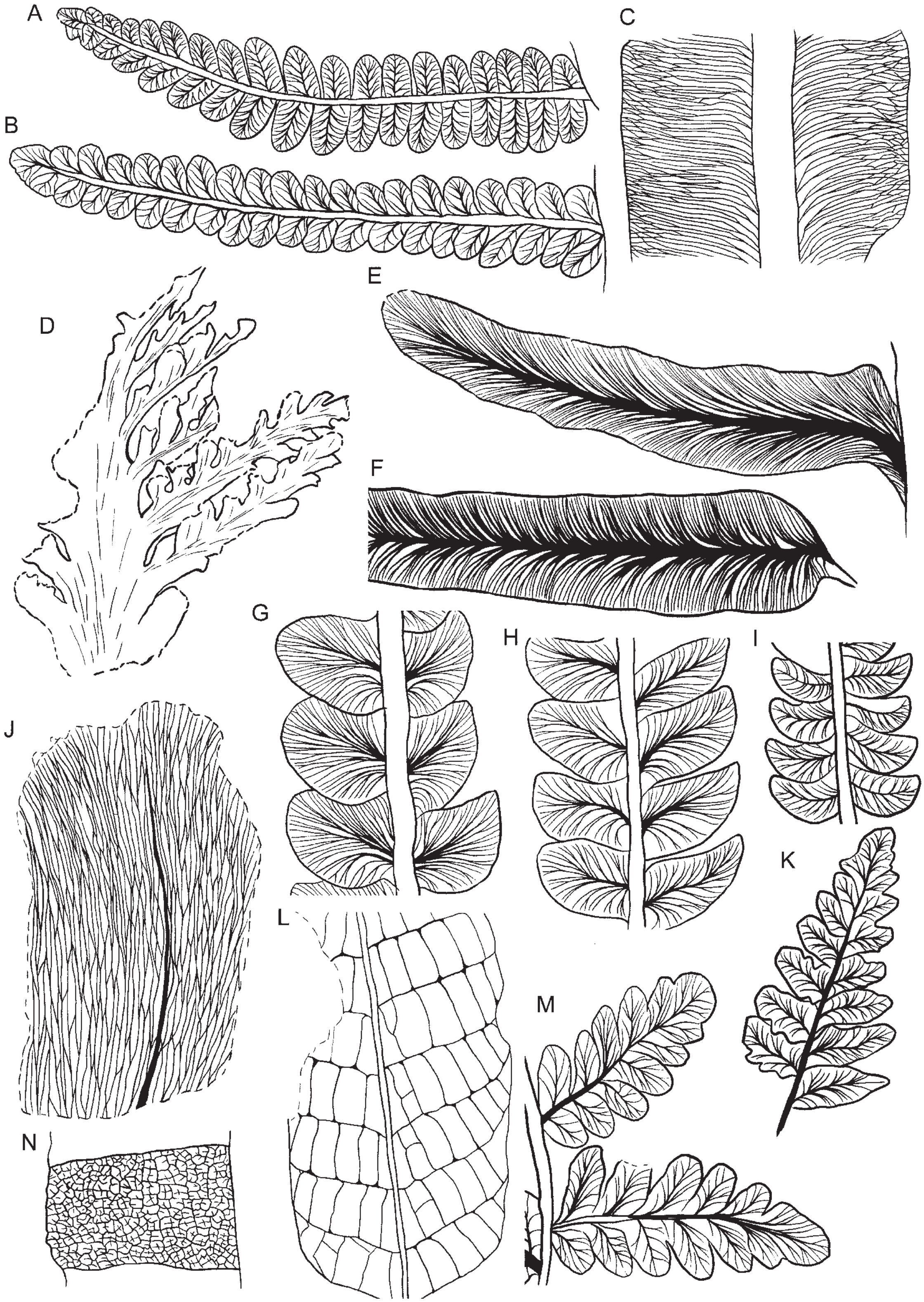

Fig. 12

Genus *Symopteris* Hsü 1979

Symopteris rumpfii (Schenk 1864) Kustatscher et al. (2011)

Figs. 9A-D, 10A-E, 11A-F, 12F

1864 *Cycadites rumpfii* Schenk, p. 61, pl. 6, fig. 1.
non 1869 *Danaeopsis rumpfii* (Schenk) Schimper, p. 615.
?1890 *Bernoullia helvetica* Heer. – Sandberger, p. 235-236. (list only)
1922a *Bernoullia franconica*. – Frentzen, p. 6, 10, 13. (*nomen nudum*)
1922b *Bernoullia franconica*. – Frentzen, p. 23, 26-27. (*nomen invalidum*)
1926 *Bernoullia franconica*. – Frentzen, p. 476-478.
1933 *Bernoullia helvetica* Heer. – Linnell, p. 310.
non 1990 "*Bernoullia franconica*". – Kelber, p. 39, fig. 67.
non 1995 "*Bernoullia franconica*". – Kelber & Hansch, p. 58, fig. 124.

Description. *Symopteris rumpfii* is a common fossil in the Thale flora (over a 110 specimens), occurring usually as fronds and pinna fragments, both sterile (e.g. S114002-01, S114003, S114026, S114030, S114031, Fig. 8A) and fertile (e.g. S114016, S114022, S114030, Fig. 10E), although isolated pinnules are frequent (e.g. S114001-02; S114024, S114052).

The fronds are at least bipinnate; the main rachis is about 10-15 mm wide. Alternately attached pinnules arise at an angle of 50-70° from the axis (3-7.5 mm wide). The sterile pinnules are linear to lanceolate with a rounded apex (e.g. S114002, S114030, S114837, Fig. 9B, 10A). The margin is generally entire, but sometimes undulate or even crenulate giving almost the idea of a third subdivision (e.g. S114037, S114052, Fig. 10A, D). The distal margin is slightly constricted, the proximal one decurrent, although in some specimens both margins seem to be constricted (preservation?). The size of the pinnules varies noticeable; generally the length is *c*. 31-85 mm and the width 7-17 mm, with a maximum of 110 x 14 mm (e.g. S114030, Fig. 9B). Apically, the pinnules decrease in size (20-23 x 7-8 mm) and show a broad attachment of the base; at the apex the pinnules fuse (e.g. S114011, S114033, S114048, Fig. 10B). The strong midrib (1-2 mm) decreases slightly in width. Secondary veins arise at an acute angle (45-50°) then curve outwards, forking in the middle and once more in the outer part of the pinnules (e.g. S114001-02, S114029, S114052, Figs. 10D, 12F). They are somewhat organised in groups (fasciculate) which seem to correspond to the segments created in some specimens by the crenulate/undulate margin.

Fertile pinnules have never been found on the same pinnae as sterile ones. They are much smaller (26-46 x 4-12 mm) than the sterile ones and are ovate-elongate with a rounded apex (e.g. S114008, S114016, S114017, Figs. 10E, 11A). The midrib is rarely visible. The lamina is slightly recurved downwards at the margins. The lower surface of the fertile pinnules is covered by sporangia, 2-3 mm long and about 0.5 mm wide (e.g. S114016, S114017, S114040, Figs. 10E, 11A), a 1-2 mm long sporangia-free band characterises the margin of the pinnule. When the sporangia have been removed, the lower surface is foveolate showing the location of the attachment scars of the sporangia (0.5-1.0 mm in diameter, e.g. S114006, Fig. 11B). The sporangia seem to be arranged in irregular rows along the veins. Spores are round, trilete with a thin, slightly punctate spore wall (35-38 µm in diameter, Fig. 11C). The trilete scar extends ½-2/3 of spore radius (e.g., S114006, S114017, Fig. 11C-F).

Material. S050054, S114001-03, S114005-14, S114016-17, S114019-24-31, S114033-38, S114040, S114043-54, S114057-61, S114064-65, S114067-69, S114071-72, S114076, S114084-87, S114110, S114131, S114166, S114187, S114198, S114220, S114277, S114298, S114301, S114304, S114307, S114318, S114322, S114337, S114339, S114406, S114421, S114490, S114502, S114505-06, S114510, S114521, S114536,

Fig. 12. Schematic drawings of the main venaition pattern. **A**. *Asterotheca merianii* (Brongniart) Stur 1885, schematic drawing of a sterile pinna with bifurcated secondary veins. **B**. *Asterotheca thalensis* n. sp., schematic drawing of a sterile pinna. **C**. *Danaeopsis marantacea* (Presl in Sternberg 1838) Schimper 1869, schematic drawing of a basal part of a sterile pinna fragment with marginal anastomousing veins. **D**. *Rhacophyllum crispatum* (Münster in Sternberg) n. comb., schematic drawing of a frond fragment with irregular segments. **E**. *Neuropteridium grandifolium* (Schimper et Mougeot) Compter 1883, schematic drawing of a sterile pinnule with secondary veins biforking several times. **F**. *Symopteris rumpfii* (Schenk 1864) Kustatscher et al. (2011), schematic drawing of a sterile pinnule with secondary veins organized in groups (fasciculate). **G**. *Todites gaillardotii* (Brongniart) n. comb., schematic drawing of sterile pinnules with the midrib and some additional veins arising from the midrib. **H**. *Cladophlebis remota* (Presl) Van Konijnenburg-Van Cittert et al. 2006, schematic drawing of sterile pinnules with distinct midrib and bifurcating secondary veins. **I.** *Cladophlebis leuthardtii* Leonardi 1953, frond fragment (S114200), schematic drawing of sterile pinnules with the delicate veination. **J**. *Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern 1931, schematic drawing of a leaf fragment with evident net venation and distinct central vein. **K**. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg 1838, schematic drawing of a sterile pinna with veriable pinnules' shapes and delicate veination. **L**. *Clathropteris meniscioides* Brongniart 1828, schematic drawing of a sterile frond fragment with the typical reticulate structure. **M**. *Sphenopteris* vel *Cladophlebis* sp. A, schematic drawing of a sterile frond fragment with delicate midrib and secondary veins. **N**. *Clathropteris meniscioides* Brongniart 1828, drawing of the veination pattern, detail of the small reticulum of the third order veins.

S114830-31, S114835-37, S114842-43, S114846-47, S114849-50, S114852, S114855, S114861-62, S115882, S115941, S149403, JMS 52376, JMS 52378, JMS 52383, JMS 52396, JMS 52397, MB.Pb. 2000/247, MB.Pb. 2000/247a, MB.Pb. 2000/257, MB.Pb. 2010/24a, MB.Pb. 2010/24b, MB.Pb. 2010/25-26, MB.Pb. 2010/29-31, MB.Pb. 2010/41, MB.Pb. 2010/466, MB.Pb. 2010/105.

Discussion. The genus *Bernoullia*, with its type species *Bernoullia helvetica,* was introduced by Heer in 1877 for dimorphic fronds with fertile pinnules on specialised fronds, or both sterile and fertile pinnules attached to the same rachis. The generic name *Bernoullia* is already in use for a genus of extant Bombacaceae (Oliver 1873), which is validly described and has priority over *Bernoullia* Heer. This was recognised previously by Xu et al. (1979), who then introduced the new generic name *Symopteris* as a substitute for *Bernoullia* Heer 1877 (for more details see Kustatscher et al. 2011).

Schenk (1864) introduced *Cycadites rumpfii* for pinnate leaves with a stout rachis and pinnules inserted alternately or suboppositely. The pinnules were elongated with a restricted basis, a rounded apex and a thick midrib. Later, Frentzen (1922: 6) introduced *Bernoullia franconica* as a *nomen nudum* referring to material indicated by Sandberger (1890) (see also Kelber 1990: 39; Kelber & Hansch 1995: 58). The elaborate description of the species followed in 1926 (Frentzen 1926: 476), however, still without any figures, which were to follow in the (never published?) “Monographie der Keuperfloren Süddeutschlands”. The author referred to four specimens, one of which was already described and figured by Schenk (1864: pl. 6, fig. 1) as *Cycadites rumpfii*. This holotype, originally stored at the University of Würzburg and lately moved to the Bayrische Staatssammlung für Paläontologie und Geologie (Munich), is not a sterile fragment with leathery lamina as suspected by Schenk (1864: 61) but a fertile specimen of the genus *Symopteris*. Thus, *Cycadites rumpfii* (here transferred to the genus *Symopteris*) has priority over *Bernoullia franconica* (the latter was not validly created since it was not figured in 1922, when it was described). Linnell (1933: 310) indicated *Bernoullia helvetica* Heer 1877 in the flora from Thale, without, however, discussing or describing the species.

Remarks. *Danaeopsis rumpfii* as described by Schimper (1869: 615) was not based on the original material from Schenk but on a large specimen in the Naturkundemuseum in Stuttgart. The *Cycadites (Danaeopsis) rumpfii* material from Stuttgart is considered to belong to *Scytophyllum bergeri* (see Kustatscher & Van Konijnenburg-Van Cittert 2010).

Comparisons. We distinguish *Symopteris rumpfii* from *Symopteris (Bernoullia) helvetica* from the Carnian of Neuewelt because the sterile and fertile pinnules are found on the same leaves in *S. rumpfii*. Moreover, the lamina of the fertile pinnules in *S. helvetica* is much more recurved covering the sporangia for an extended distance. Furthermore, in *Symopteris helvetica* and *Symopteris (Bernoullia) lunzensis* (Stur 1885) Xu from the Carnian of Lunz the secondary veins are fasciculate with each secondary vein giving origin to a group of third order veins.

Distribution. According to Frentzen (1922b) this species is restricted to the German Lettenkeuper (see also Frentzen 1922a; Hirmer 1927) although perhaps it has been found also in the Schilfsandstein (Schmidt 1938).

4. Conclusions

The ongoing detailed taxonomic re-evaluation of the Thale flora has increased the number of fern taxa from 6 to 14. All six species recorded by Linnell (1933) were found although most of them have been renamed and eight additional species were encountered. This provides evidence that the ferns are the most numerous and diverse of the plant group in the flora.

Three species were assigned to the Marattiaceae (*Asterotheca meriani* (Brongniart) Stur, *Asterotheca thalensis* n. sp. and *Danaeopsis marantacea* (Presl in Sternberg) Schimper). Considering that *Asterotheca meriani* and *Danaeopsis marantacea* are the two most common species in the flora (each more than 120 specimens), the Marattiaceae are the dominant fern family. *Rhacophyllum crispatum* (Münster in Sternberg) n. comb. is so far the only aphleboid structure recorded in the Mesozoic. It is quite possible that it belongs to *Danaeopsis marantacea*.

The two Osmudaceous ferns in the Thale flora are *Todites gaillardotii* (Brongniart) n. comb. and *Neuropteridium grandifolium* (Schimper et Mougeot) Compter, although the latter cannot be assigned to the family definitively because no fertile material has been found so far. However, other members of the genus *Neuropteridium* definitely belong to the Osmundaceae.

Clathropteris meniscioides Brongniart may be the oldest record of the species, genus and even of the family Dipteridaceae, but since the lithology of the specimen containing these fossils is different from that of other Thale samples, we cannot completely be sure that the specimens were collected at the same stratigraphic level as the rest of the collection although they are labelled as such. *Phlebopteris* sp. is certainly the oldest record for the family Matoniaceae. The specimen from the Lower Keuper of Germany figured in Kelber & Hansch (1995: fig. 122) cannot be definitely attributed to the genus because of its poor preservation. Although the specimens are fertile, the material is too limited to make a defined specific attribution.

In the ferns *incertae sedis Cladophlebis remota* (Presl) Van Konijnenburg-Van Cittert et al. and

Table 1. Comparison table of the sterile characters of the various species from Thale.

	Frond shape	Main rachis	Pinna attachment	Pinnule attachment	Pinnule shape	Venation
Asterotheca merianii	bipinnate	up to 10 mm	(sub) oppositely, almost perpendicular	almost perpendicular	elongate, rounded apex	strongly pecopterid
Asterotheca thalensis	at least bipinnate	4-6 mm	(sub) oppositely, 60-80°	closely inserted, first basiscopic pinnae larger	ovate, rounded apex	secondary veins few, curving outwards
Danaeopsis marantacea	pinnate	c. 6-12 mm	/	~ 60°, oppositely	entire, elongated	secondary veins anastomosing near the margin
Todites gaillardotii	bipinnate	up to 11 mm, striate	(sub) oppositely, ~70°	closely inserted, sometimes overlapping	roundish, base slightly constricted, apex slightly curved upwards	neuropterid, short midrib, some veins arising from rachis
Neuropteridium grandifolium	pinnate	5-12 mm	/	suboppositely with a distal auricule and proximally decurrent	elongate -tongue shape	neuropterid, midrib ½ to 2/3 of pinnules shape
Clathropteris meniscoides	/	/	/	/	elongate with incised margin	net venation
Phlebopteris sp.	bipinnate	/	Converging towards petiole	perpendicular	elongate	secondary veins forking ones or twice
Cladophlebis remota	at least bipinnate	/	/	suboppositely	falcate	clear midrib, forked lateral veins
Cladophlebis leuthardtii	at least bipinnate	/	/	almost perpendicular	small falcate	delicate bifurcating secondary veins
Sphenopteris schoenleiniana	at least tripinnate	1-2 mm	45-60°	alternately	variable, constricted base	sphenopterid
Sphenopteris vel *Cladophlebis* sp. A	at least tripinnate	around 2 mm	suboppositely to alternately	mainly alternately	ovate with round apex, first basiscope pinnules smaller	more pocopterid than sphenopterid
Chiropteris lacerata	funnel-shape	/	/	/	segments	net venation with delicate midrib in each segment
Bernoullia franconica	at least bipinnate	3-7.5 mm	/	alternate	linear to lanceolate, sometimes with undulate margin	fasciculate

Cladophlebis leuthardtii Leonardi are rare elements. *Cladophlebis remota* is generally considered to be one of the dominant ferns of the German Lettenkeuper (Frentzen 1922a). However this was not the case in the Thale flora. *Cladophlebis leuthardtii* has been recorded for the first time outside the Dolomites. *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg is a common element in the Thale flora, represented by sterile and fertile material. The frond morphology of *Sphenopteris* vel *Cladophlebis*

Table 2. Comparison of the fertile characters of the various species from Thale.

	Fertile fronds morphology	Sori present/absent	Arrangement of sporangia	Spore morphology	Spore dimensions
Asterotheca merianii	similar to sterile	present 4-5 pairs	4 connate sporangia per sorus	circular, pseudomonolete, smooth to slightly granulate	28-45 µm
Asterotheca thalensis	similar to sterile	present 3-4 pairs	4 connate sporangia per sorus	circular, pseudomonolete, granulate	27-34 µm
Danaeopsis marantacea	similar to sterile	absent	2 rows of sporangia between secondary veins	circular, trilete, smooth	40-48 µm
Todites gaillardotii	slightly different from sterile	absent	lower surface covered with sporangia	circular, trilete, smooth	35-51 µm
Clathropteris meniscoides	similar to sterile	present	sporangia indicated by small dots between vein meshes		
Phlebopteris sp.	similar to sterile	present	circa 8 free sporangia in the sorus	/	/
Sphenopteris schoenleiniana	slightly different	absent	at the end of secondary veins	/	/
Bernoullia franconica	different	/	lower surface covered with numerous sporangia	circular, trilete, punctate	35-38 µm

sp. A is rather similar to *Sphenopteris schoenleiniana* but the pinnule attachment and the venation are more like a *Cladophlebis* than a *Sphenopteris* species. These fronds may be the shade leaves of *Sphenopteris schoenleiniana*, a theory already stated by FRENTZEN (1922c). *Chiropteris lacerata* (QUENSTEDT) RÜHLE VON LILIENSTERN is a very rare element in this flora, although it is well represented in other German Lettenkeuper floras such as Bedheim (MOHR et al. 2008). *Symopteris rumpfii* (SCHENK) KUSTATSCHER et al. 2011 is described for the first time from the Thale flora, together with its *in situ* spores.

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