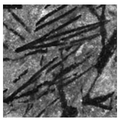
Revision of the Carboniferous genus *Rhodeites* Němejc from European and American localities

JOSEF PŠENIČKA & STEPHAN SCHULTKA



The paper deals with two Pennsylvanian species *Rhodeites gutbieri* (Ettingshausen) Němejc and *Rhodeopteridium subpetiolatum* (Potonié) comb. nov. which are mostly mistakenly placed into one species *Rhodea subpetiolata* (Potonié) Zeiller. The clear differences between the two species are given. This paper focuses on their morphological details (including cuticle), as well as stratigraphical and geographical distributions. The genus *Rhodeites* is emended. Only sterile specimens of *Rhodeites* are known up till now and so the systematic position is still unknown. This paper also discusses their ecological status in nature. • Key words: Pennsylvanian, *Rhodeites*, *Rhodeopteridium*, cuticle.

PŠENIČKA, J. & SCHULTKA, S. 2009. Revision of the Carboniferous genus *Rhodeites* Němejc from European and American localities. *Bulletin of Geosciences 84(2),* 241–256 (14 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received October 23, 2008; accepted in revised form April 9, 2009; published online May 24, 2009; issued June 30, 2009.

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This paper deals with the poorly known Pennsylvanian species of the genera *Rhodeites* Němejc (1928) and partly *Rhodeopteridium* Zimmermann (1959), which are quite characteristic for Mississippian macrofloras. Many species from both genera have been placed in the genus *Rhodea* Presl *in* Sternberg. Both genera comprised many species which were primarily regarded as members of the rhacopterids, rhodeopterids or palmatopterids, which implies they were mainly pteridosperms. The paper is focused on two species, *Rhodeites gutbieri* (Ettingshausen) Němejc and *Rhodeopteridium subpetiolatum* (Potonié) comb. nov. which are usually mistakenly placed in one species *Rhodea subpetiolatum* (Potonié) Zeiller. Both species (*Rhodeites gutbieri* and *Rhodeopteridium subpetiolatum*) are only known from a few fragmentary specimens. Due to this fact, few palaeobotanists have taken an interest in these species, with the exception of Potonié (1889), Zeiller (1899), Gothan (1912, 1913, 1929), Kidston (1923), Němejc (1928, 1937) and Josten (1991). Known specimens of both species come from localities in Europe [from Germany (Potonié 1889, Gothan 1912), the UK (Kidston 1923), from the Czech Republic (Němejc 1928), Poland (Potonié 1889)], Turkey (Zeiller 1899) as well as West Virginia (USA) (*e.g.*, Gillespie *et al.* 1978). Němejc (1928) described the largest specimen of *Rhodeites gutbieri* where the ultimate pinnae are attached to a penultimate rachis in pairs. It represents a quite different pattern of frond composition than that found among rhacopterids, rhodeopterids or palmatopterids. Němejc's specimen, which represents the best preserved specimen of *Rhodeites,* is housed in the National Museum in Prague under number E 4942. It comes from mines between Blatnice and Doubrava villages, Pilsen Basin (Czech Republic). Based on observations of this specimen, Němejc (1937) correctly established a new genus *Rhodeites.* We present for the first time morphological details of *Rhodeites gutbieri* together with its cuticles based on a redescription of Němejc's specimen, and other specimens from the Doubrava locality (Pilsen Basin) and Svinná locality (Radnice Basin; Gothan's descriptions of two specimens). We also emend the generic diagnosis of Němejc's *Rhodeites*. *Rhodea subpetiolata s.s.* is replaced by *Rhodeopteridium subpetiolatum* (Potonié) nov. comb. based on morphological characters. This paper establishes clear differences between the species *Rhodeites gutbieri* and *Rhodeopteridium subpetiolatum* (Potonié) nov. comb. which are frequently confused. Nevertheless, all known specimens of *Rhodeites gutbieri* and *Rhodeopteridium subpetiolatum* are, however, sterile so that is difficult to establish their systematic position. Němejc (1928) mentioned the possibility of a relationship between *Rhodeites gutbieri* and true ferns. Based on new observations we suggested a concept about the general plant form.

DOI 10.3140/bull.geosci.1105

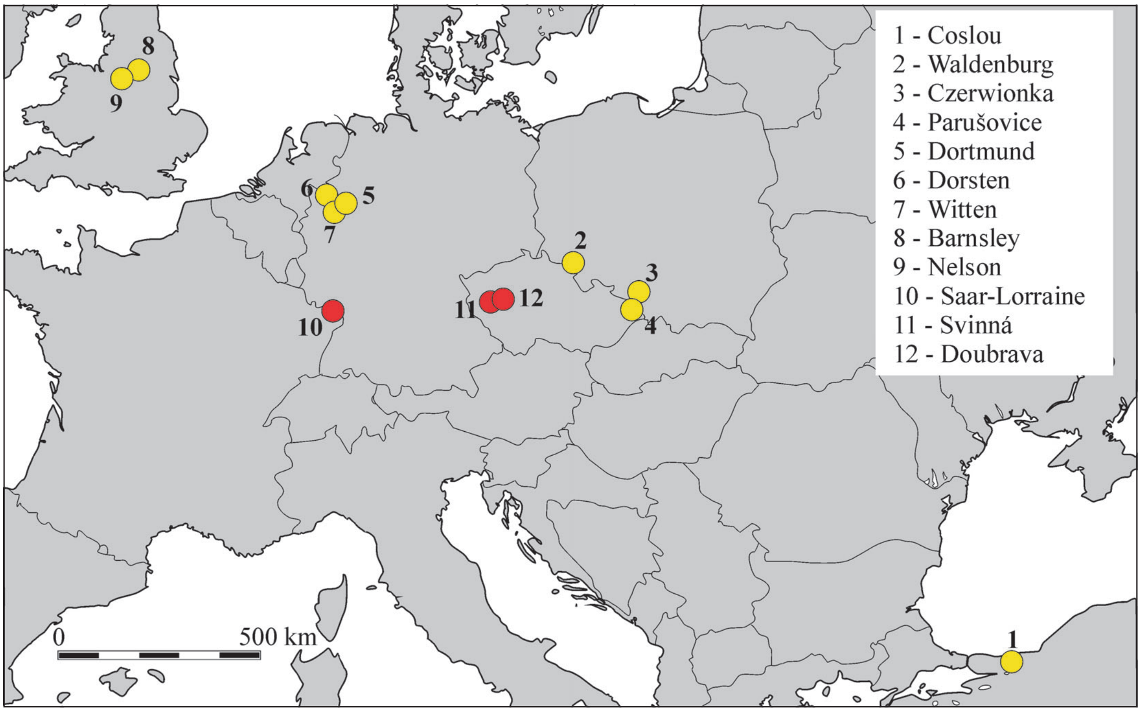


Figure 1. Map of occurrence of *Rhodeites gutbieri* (red dots) and *Rhodeopteridium subpetiolatum* (yellow dots).

Historical background

Ettingshausen [1854, p. 37, pl. 19, fig. 1 and 2 (see Fig. 2)] described and figured *Sphenopteris gutbieri* Ettingshausen. This species was established based on two specimens that came from the Svinná locality (Fig. 1) (Radnice Basin), from the Kladno Formation, Radnice Member (Bolsovian), Whetstone Horizon. This species was forgotten for a long time until Němejc (1937) took note of similarities between Ettingshausen's specimens and Potonié's *Rhacopteris subpetiolata*. He held that *Sphenopteris gutbieri* and *Rhacopteris subpetiolata* are the same species and synonymised them under the name *Rhodeites gutbieri* as Ettingshausen's name had nomenclatural priority (Ettingshausen, 1854 *versus* Poonié, 1889). It is not clear why later Němejc (1963) returned to the combination *Rhodeites subpetiolata* (including Ettingshausen's specimens) which is wrong according to the Botanical code (IBCN). Němejc (1937) also referred *Rhodea lemayi* Broussier & Bertrand, 1911 to *Rhodeites gutbieri,* but we do not agree with this as each pinnule lamina of *Rhodea lemayi* has a blunt tip while the pinnule laminae of *Rhodeites gutbieri* have acute tips.

Potonié (1889, p. 27) established *Rhacopteris subpetiolata* Potonié based on poorly preserved compression material (see Fig. 10) from the Walbrzych locality (Fig. 1), Intrasudetic Basin (Waldenburg Formation; Serpukhovian-Bashkirian). The type material consists of one specimen representing a fragmentary penultimate rachis with two unattached ultimate pinnae. This specimen is now stored in the palaeobotanical collections of the Museum für Naturkunde zu Berlin with the inventory numbers MB.Pb. 2003/0960 together with five specimens later figured by Gothan (1912, 1913, 1929). Potonié (1889) referred his species to the rhacopterids based on the character of the venation and the type of pinnules. Later Zeiller (1899) described specimens of *Rhodea subpetiolata* from the Coslou locality (Fig. 1) near the Héraclée Basin (Turkey), Coslou Formation, Asturian. Zeiller (1899) referred his specimens to the genus *Rhodea,* and pointed out that this genus belongs to the Sphenopterids and that his *Rhodea subpetiolata* belongs to the "natural" relationship between *Rhodea stachei* Stur and *Rhodea filifera* Stur. Nevertheless, his specimens were fragmentary such that it is very difficult to prove genuine relationships. Gothan (1912) described other fragmentary material from the mine Germania, near Dortmund (Ruhr Basin) ("Fettkohle", stratigraphical position: Langsettian) (Fig. 1). One year later Gothan (1913) described additional fragmentary material from the Upper Silesian Basin [Séria Mulowcowa, Orzesche Member (*i.e*. the same as the "obere Muldengruppe"), Duckmantian; borehole near Rybnik (Czervionka and Parušovice, 460 m depth)]. Later Gothan (1929) described better preserved material from the Dorsten and Witten area (Stratigraphical Position Yeadonian/Langsettian) (Fig. 1). Kidston (1923) figured specimens of *Rhodea subpetiolata* and *Rhodea gutbieri* from the "Westphalian Series" of Great Britain, of Duckmantian age. Stopa (1957) figured a specimen with *Zeilleria*-like fertile

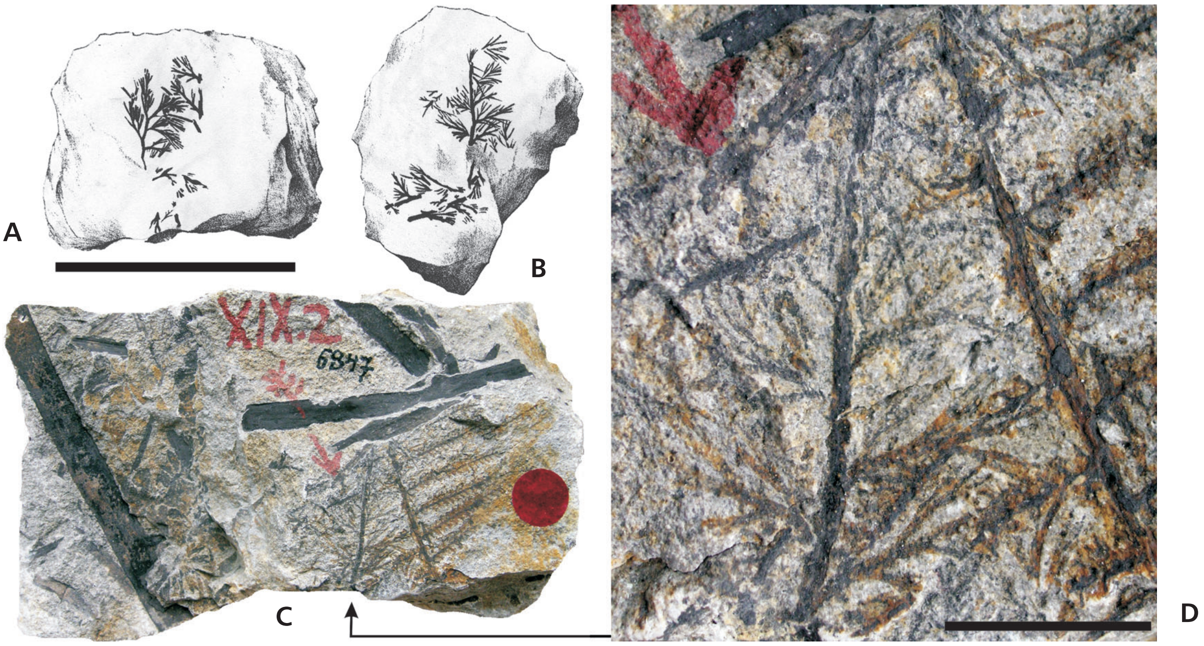


Figure 2. Ettingshausen's specimen of *Sphenopteris gutbieri* Ettingshausen from the Svinná locality, Radnice Basin, Czech Republic. • A – Ettingshausen (1854), pl. 19, fig. 1. • B – Ettingshausen (1854), pl. 19, fig. 2. • C – lectotype of *Rhodeites gutbieri* (Ettingshausen) Němejc, GBA 1854/009/0021 [pl. 19, fig. 2 in Ettingshausen (1854)]. A, B, C – scale bar 50 mm; • D – detail of figure 2C. Part of ultimate pinna with pinnules: scale bar 10 mm.

organs which should belong to *Rhodeopteridium subpetiolatum*. Brousmiche (1983) and Daber (2003) described specimens of *Sphenopteris coemansii* Andrae from the Sarro-Lorrain Basin (Bolsovian) which are markedly similar to *Rhodeites gutbieri.* Nevertheless, material studied by these authors are strictly sterile and only the pinnule's shape can be observed, nothing is known about the general character of the whole plant or about the reproductive organs.

Rhodea was established by Presl *in* Sternberg (1838) as a quite artificial genus. Because *Rhodea* Presl is a junior homonym of *Rhodea* Endlicher, which is an invalid synonym of the monocotyledon *Rhodea* Roth (Jennings 1976), Zimmermann (1959, p. 280) proposed the new generic name *Rhodeopteridium* for this group of fronds.

Material and method

Material. – Material published in this paper came from the depositories of the West Bohemian Museum in Pilsen (F 44), National Museum in Prague (E 4942), Museum für Naturkunde in Berlin (MB.Pb.2003/0209, 2003/0212, 2003/213, 2003/0214 und 2003/0788), Geologische Bundesanstalt in Vienna (GBA 1854/009/0021) and British Geological Survey, Keyworth (UK; Kidston collection; specimen Nos. 4091, 3441 and 3440).

Specimens from the West Bohemian Museum and National Museum in Prague come from old and now inactive mines between Doubrava and Blatnice, near Nýřany (Pilsen Basin; Czech Republic) (Fig. 1). Specimens housed in the Geologische Bundesanstalt in Vienna derive from the Svinná locality (Fig. 1) (Radnice Basin; Czech Republic). These specimens were collected from the Whetstone Horizon of the Radnice Member (Kladno Formation; Bolsovian) and they are preserved as "three-dimensional compressions" in yellow tuff.

Specimens housed in the Museum für Naturkunde zu Berlin are preserved in gray coloured claystone to coarse siltstones. The holotype of "*Rhacopteris*" *subpetiolata,* MB.Pb. 2003/960, sampled in 1887 and published by Potonié (1899), originated from the "Fürstlicher Tiefbau" near Waldenburg (Wałbrzych). Specimen MB.Pb.2003/214 (Gothan 1912, pl. 3, fig. 6) came from the mine Germania, near Dortmund (Fig. 1) (Langsettian); specimen MB.Pb.2003/209 (Gothan 1929, pl. 1, fig. 2) came from the mine Helene-Tiefbau, near Witten (Fig. 1) (Yeadonian/ Langsettian) and specimen MB.Pb.2003/212 (Gothan 1929, pl. 6, fig. 4) came from the coal 4, mine Baldur, near Dorsten (Fig. 1) (Duckmantian). Additional specimens came from the "Steinernes Kreuz" near Wałbrzych, mine Victor, near Neu-Lässig and mine Gustav between Rothenbach and Schwarzwaldau.

Specimens housed in the British Geological Survey, Keyworth (UK) came from the Pennine Coalfield. Specimens are preserved in grey coloured claystone. They are from Kidston's collection and were published by Kidston (1923, pl. 59). Specimen No. 4091 came from the Ward Green locality (Fig. 1) near Barnsley (Yorkshire) and belongs to Barnsley Coal (Westphalian Series; Duckmantian). Specimens No. 3441 and 3440 came from the

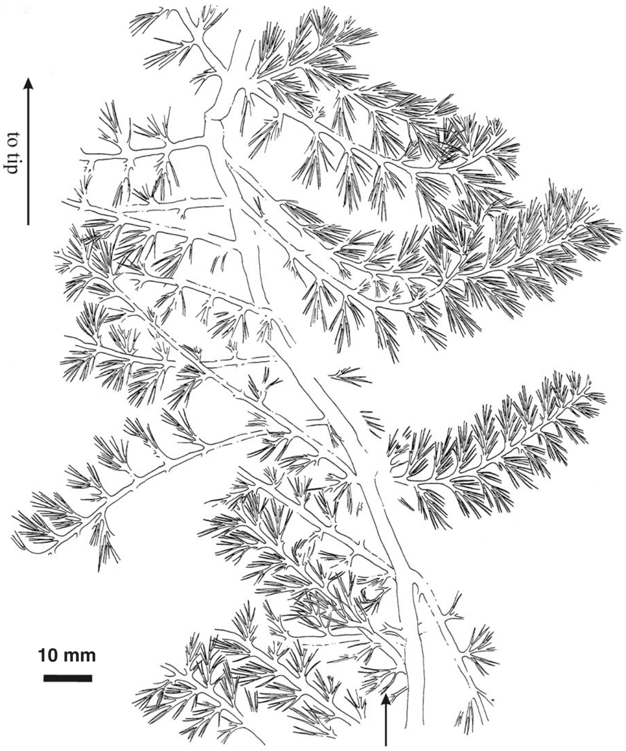


Figure 3. *Rhodeites gutbieri* Ettingshausen (Němejc); specimen E 4942; camera lucida drawing; (A) indicates aphlebia-like organs.

Hibson Road locality (Fig. 1) at Marsden Height (Arley Mine), Nelson (Lancashire) and belong to the Westphalian Series, Duckmantian.

Maceration. – Cuticles were isolated from specimens with the aid of 35 percent hydrofluoric acid for 22 hours. Subsequently, cuticles were washed in distilled water, dried and examined under a CAMECA SX100 scanning electronic microscopes (SEM). All SEM samples were gold-coated. Cuticles were quite destroyed during maceration in Schulze's solution due to the high degree of oxidation of the cuticles. All digital photos of cuticles are stored in the West Bohemian Museum, Pilsen.

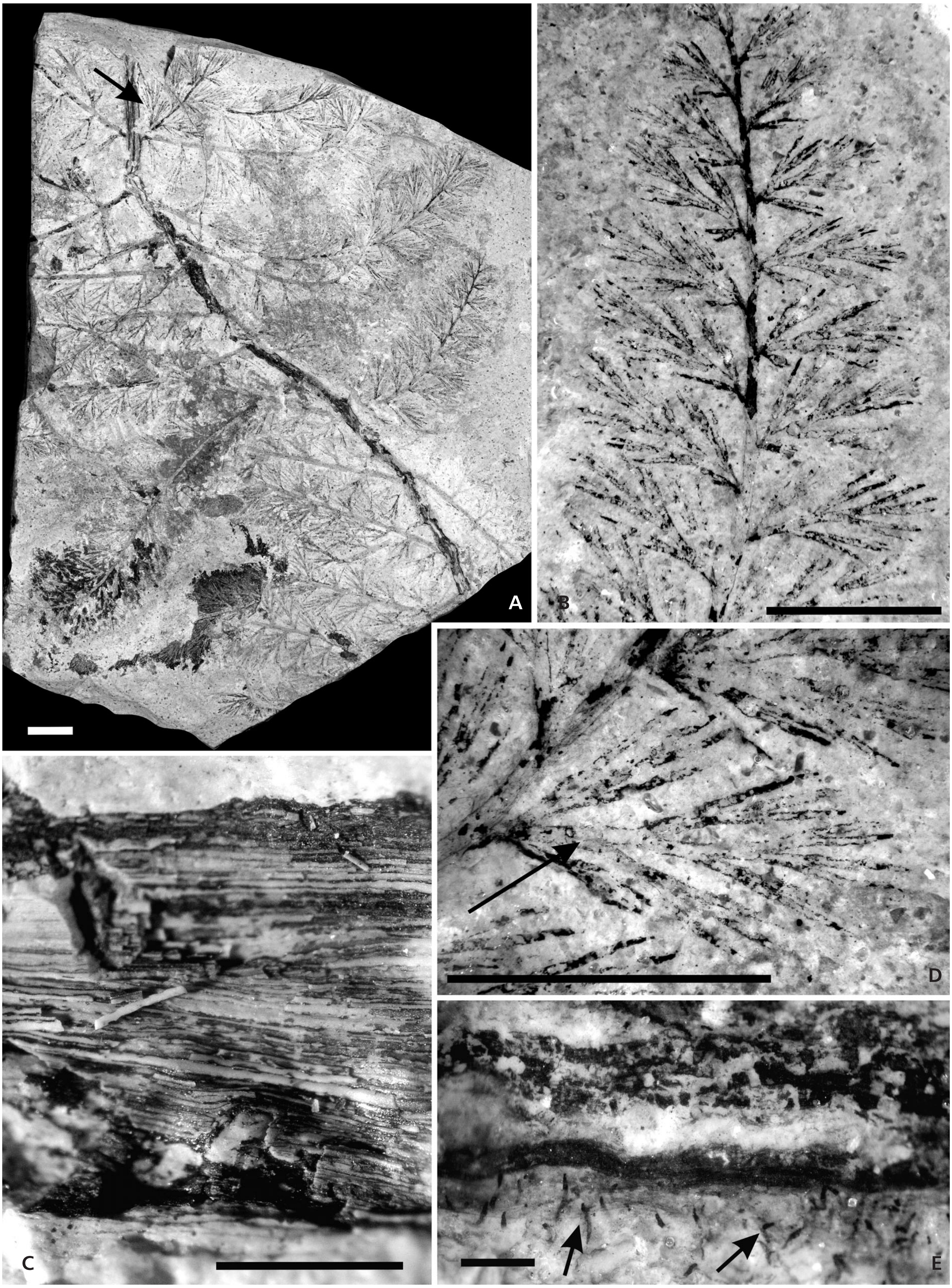
Description of *Rhodeites gutbieri*

Description of lectotype of R. gutbieri. – Specimen (GBA 1854/009/0021) shows part of an ultimate pinna (Fig. 2C, D). The ultimate rachis is 1 mm wide . Pinnules are of a palmatopterid-type and alternate on the ultimate rachis at an angle of 30°–40° (Fig. 2D). The distance between two pinnules is about 5 mm. The pinnules are 10 mm long and 7 mm wide. Pinnules are up to 7 times segmented. Each segment is differentiated in up to 4 laminar lobes with sharp tips. The midvein is well marked when leaving the ultimate rachis. Lateral veins are dichotomously divided up to 3 times and veins run into laminar lobe (Fig. 2D).

Description of other specimens of R. gutbieri from the Pilsen Basin. – Specimens [E 4942 (Figs 3, 4A) and F 44 (Fig. 5A)] show part of a penultimate pinna. The penultimate rachis is more than 160 mm long and 3 mm wide, sinusoidely warped. This rachis is partly anatomical preserved and possibly there are tracheids (Fig. 4C). These tracheids are 35–40 μm wide; nevertheless, it is not possible to establish their length and details due to their poor preservation. The rachis is densely covered by uniseriate, multicellular trichomes 0.2–0.4 mm long (Fig. 4E, arrowed). Ultimate pinnae are more than 120 mm long and 22–30 mm wide (Figs 3, 4A). The length and width of ultimate pinnae depends on the position in the whole frond. They are gradually tapering from about their middle part to the tip (Figs 3, 4A, B). The tips of ultimate rachies show poor differentiated lobes with very narrow lamina. Ultimate rachies are straight or very slightly sinusoidal at the distal end of the ultimate pinna and are 1–1.2 mm wide (Fig. 4B). Nevertheless, the divergence is still unknown. Ultimate rachises are attached to their penultimate rachis in pairs (Fig. 3) as specimens E 4942 shows. It is impossible to decide if two opposite ultimate pinna leave the rachis together (V-shaped as is known in Zygopterid ferns) or if two ultimate pinnae show an opposite position.

Pinnules are palmatopterid-type, which is characteristic for *Palmatopteris*-type and *Rhodea*-type plants, alternating on ultimate rachis at angles of 30°–40° (Fig. 4D). They are 10–13 mm long and 6–8 mm wide. Pinnules are up to 7 times segmented. Each segment is differentiated into up to 4 laminar lobes with sharp tips (Fig. 4D) which corresponds with the lectotype. The midvein is preserved as marked central lamina (Fig. 5B arrow). Lateral veins branch off with angles of around 40° to 70°, running in every laminar segment of the pinnules (Fig. 5B). Lateral veins are divided up to 3 times (Fig. 4D). Interesting are pinnules located near the base of the ultimate pinna (on the lower side) which probably represent aphlebia-like organs

Figure 4. *Rhodeites gutbieri* (Ettingshausen) Němejc; specimen E 4942 from the the Doubrava locality, Pilsen Basin; the best and most well known specimen. • A – part of penultimate pinna with several incomplete ultimate pinnae. Arrow shows aphlebia-like organs: scale bar 10 mm. • B – detail of distal part of ultimate pinna with palmatopterid-type pinnules: scale bar 10 mm. • C – detail of penultimate rachis with clearly visible tracheids: scale bar 1 mm. • D – detail of palmatopterid-type pinnule with midvein (arrowed) in central part of pinnule and lateral veins once or three time divided: scale bar 10 mm. • E – margin of ultimate rachis with several uniseriatre, multicellular trichomes (arrows): scale bar 200 μm.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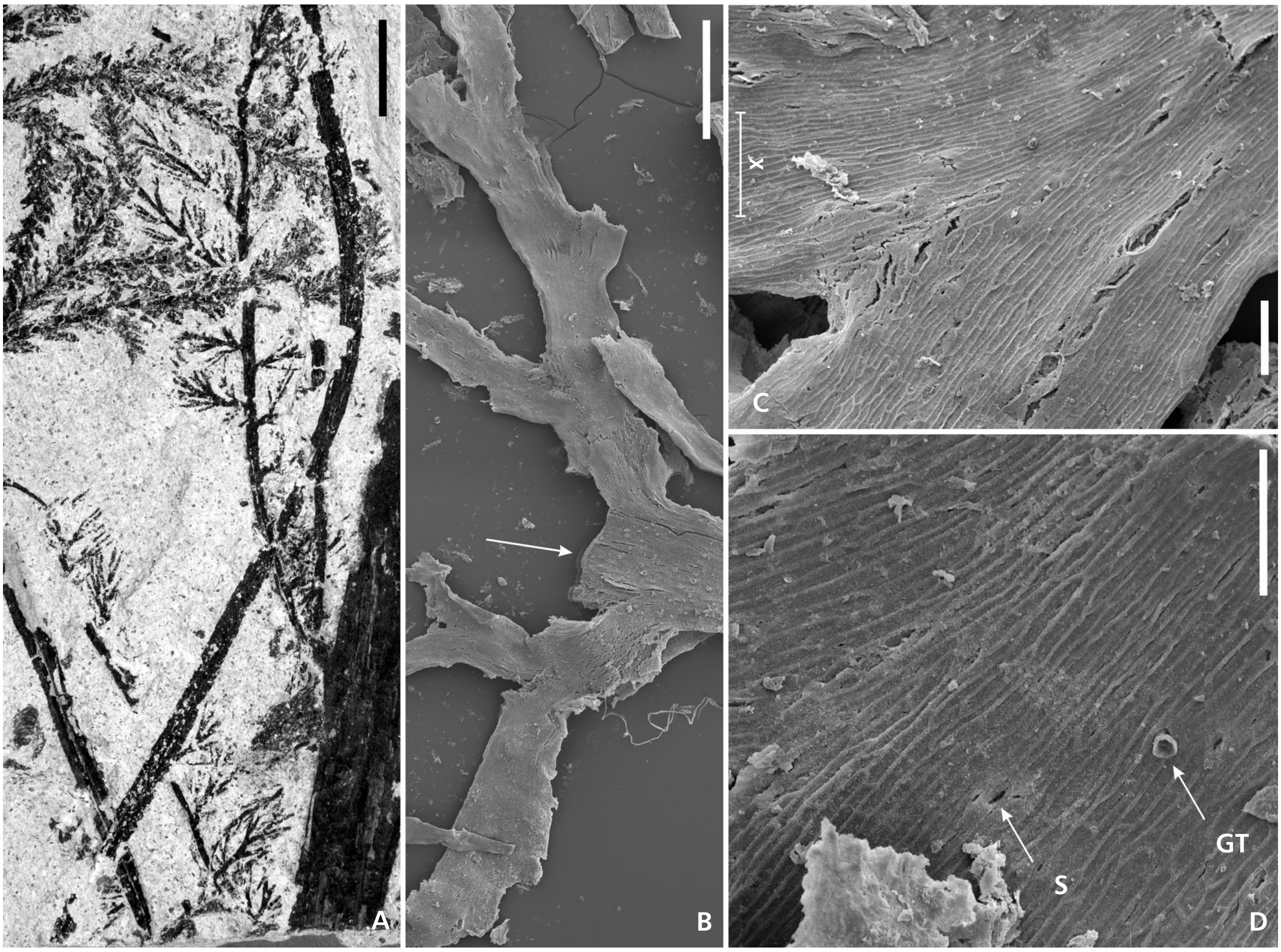


Figure 5. *Rhodeites gutbieri* (Ettingshausen) Němejc; specimen F 44 from the Doubrava locality, Pilsen Basin, Czech Republic. • A – fragment of penultimate rachis with incomplete ultimate pinnae. Pinnules are fragmentarily preserved. *Rhodeites gutbieri* is associated with *Selaginella*-like shoots: scale bar 10 mm. • B – middle part of palmatopterid-type pinnules. Central part of pinnule is represented by midvein (arrow). This part is covered by glandular trichomes. Lateral veins arise from the midvein: SEM, scale bar 1 mm. • C – adaxial cuticle with well preserved cells. Cells of costal field (X) correspond with vein. This field is characterised by elongate and narrow cells: SEM, scale bar 100 μm. • D – detail of abaxial cuticle with stomata (S) and basal part of glandular trichomes (GT): SEM, scale bar 100 μm.

(Fig. 3 "A" and Fig. 4A, arrowed). These pinnules are wider than other pinnules and they have a more complicated construction (richer differentiation of lamina-type lobes).

Cuticles: Cuticle of abaxial as well as adaxial side is thick and more or less identical, but there is a difference in the number of stomata per mm^2. Stomata are very rare on both abaxial and adaxial sides. The adaxial cuticle has 4 stomatal apparatuses per 1 mm^2 (stomatal index 0.3) while the abaxial cuticle has 8 stomatal apparatuses per 1 mm^2 (stomatal index 0.6).

Cells of adaxial (Fig. 5C, D and Fig. 6A, B) and abaxial (Fig. 7 and Fig. 6C, D) cuticles are differentiated in costal and intercostal fields but the margins of both fields are obscure. Therefore, the cells in the area of the veins ("costal field") appear somewhat narrower and longer (Figs 5C "X", 6A, B, D all "X", 7C "X"). Costal cells are 80–170 μm long and 5–12 μm wide, elongate and tetragonal (polygonal). The cells of intercostal field are 20–140 μm long and 10–50 μm wide, elongate and tetragonal (polygonal) (Fig. 7C arrow). Anticlinal walls of cells of both fields are straight.

Adaxial and abaxial cuticles are covered by glandular trichomes placed mainly on costal fields (Figs 5D "GT", 6D "GT"). Glandular trichomes are not well preserved themselves but they are represented by trichome bases, 10–15 μm in diameter (Figs 6B, C, D all "G", 7B "G", D). It is rarely possible to see whole or partly destroyed glandular trichomes (Fig. 7B, E–H). Trichome bases are 40–50 μm in diameter and trichomes are 50–60 μm long. Trichomes consist of a basal cell (Figs 7E, F, 8 "BC") and globose bodies (Figs 7H, 8 "BO"). Uniseriate multicellular trichomes which occur on rachises do not occur on pinnules.

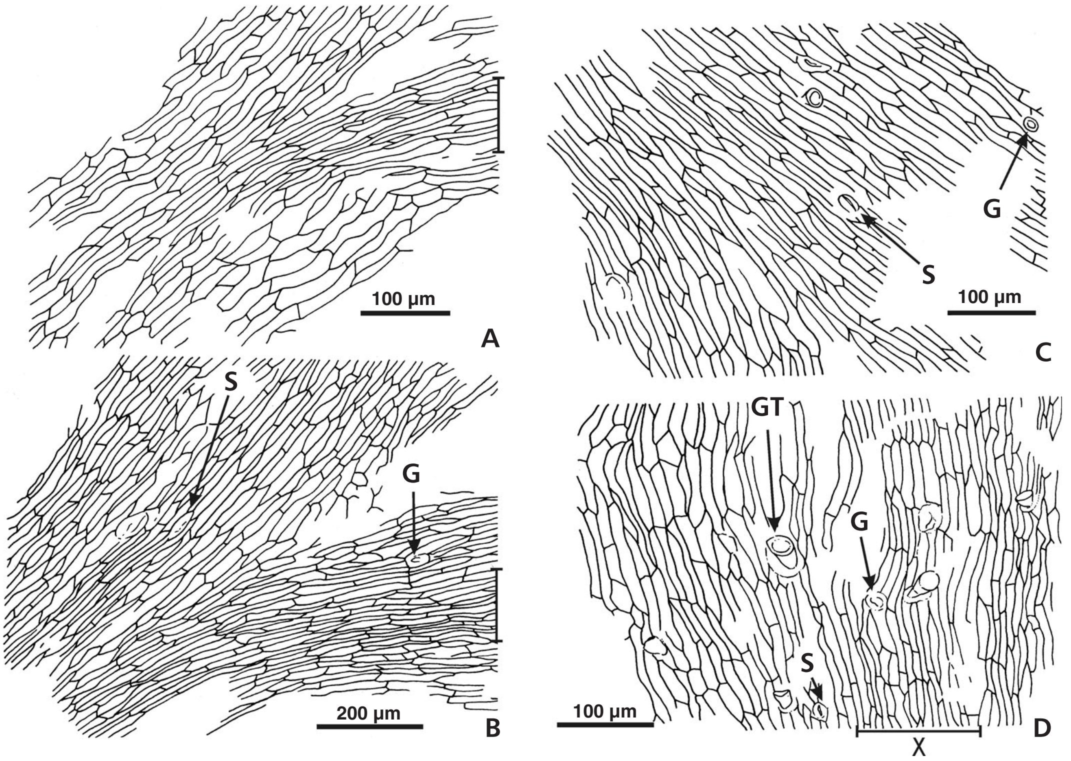


Figure 6. Cuticles from *Rhodeites gutbieri* (Ettingshausen) Němejc; specimen F 44. • A – adaxial cuticle with cells of costal field (X) and intercostal field: based on unpublished SEM photograph. • B – adaxial cuticle with cells of costal field (X) and intercostal field. Cuticle contains trichome bases (G) and stomata (S): based on Fig. 5C. • C – abaxial cuticle contains trichome bases (G) and stomata (S): based on unpublished SEM photograph. • D – adaxial cuticle with cells of costal field (X). Abaxial cuticle contains trichome bases (G), glandular trichome (GT) and stomata (S): based on unpublished SEM photograph.

Stomata (Figs 5D "S", 6B–D all "S", 7C "S", 7A, 9) are irregularly restricted on cuticles (abaxial as well as adaxial), sunken (Fig. 7A), anomocytic type 20–27 µm long and 10–12 µm wide. Guard cells are 20–26 µm long and 4–5 µm wide (Fig. 7A). Subsidiary cells are not differentiated from ordinary cells.

Description of *Rhodeopteridium subpetiolatum*

Description of holotype of Rh. subpetiolatum. – The holotype (Fig. 10) shows a poorly preserved, 65 mm long, part of a penultimate pinna. The penultimate rachis is 6.5 mm wide, straight and finely striated. Attached are three proximal parts of ultimate rachises at an angle of nearly 60° at distances of 17 and 13 mm. They show an alternate three-dimensional position.

Three ultimate pinnae are near the penultimate rachis, but are not attached and are broken at both ends. The fragments measure around 45 mm in length and are around 18 mm wide. The ultimate warty rachises look rigid, straight and are remarkably parallely embedded. Their width is 1.0 to 1.2 mm.

The pinnules are of palmatopterid type, alternating with angles between 35° and 50°. They are 10 to 13 mm long and around 5 mm wide. The pinnules are differentiated in up to four segments with one to three lobes. Lobes, if bifurcated, are up to 6 mm long, if unforked may be longer than 10 mm, with 0.3 to 0.35 mm very narrow, lamina, proximally 0.2 mm wide, tapering and fusing with the veins at the end. The midvein is around 0.1 mm wide, running up to the tips. Tips are not preserved.

Description of Rh. subpetiolatum (Potonié) comb. nov. housed in Museum für Naturkunde zu Berlin. – The specimens MB.Pb.2003/209 (Fig. 11C), MB.Pb.2003/213 (Fig. 11B) and MB.Pb.2003/0214 (Fig. 11A) show distal ends of ultimate pinnae. Ultimate rachises are 0.6 to 0.8 mm wide, nearly straight with a somewhat rigid appearance. Pinnules alternate on the ultimate rachis (Fig. 11A, C) at acute angles around 30°–50°. The gap on the ultimate rachis between two adjacent pinnules is 1.4 to 2.0 mm. In specimen MB.Pb.2003/0209 the distance between each pinnule is 4.0 to 4.4 mm. Pinnules are of palmatopterid-type, 10–15 mm long and 6–8 mm wide and are differentiated into lobed segments. There are up to four segments, each showing one to (seldom) four lobes. This ramification pattern corresponds with the vein's system. The lobes show very narrow laminae; their tips taper off.

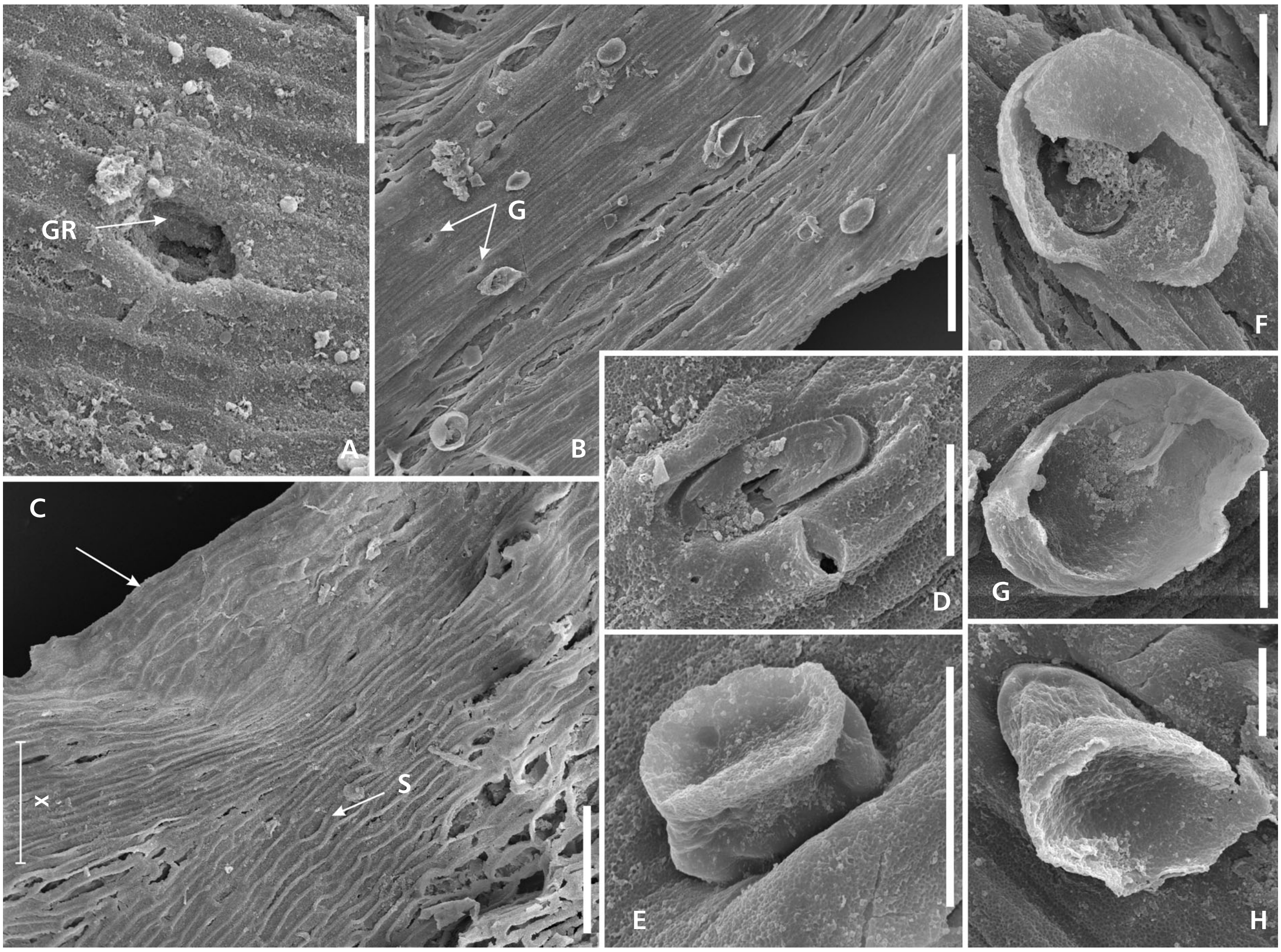


Figure 7. *Rhodeites gutbieri* (Ettingshausen) Němejc; specimen F 44 from Doubrava locality. • A – detail of sunken anomocytic stoma. Subsidiary cells are not separated from ordinary cells. Guard (GR) cells are well visible: SEM, scale bar 20 μm. • B – abaxial cuticle densely covered by glandular trichomes or trichome bases (G). These trichomes are partly destroyed: SEM, scale bar 200 μm. • C – adaxial cuticle shows cells of intercostal (arrowed) and costal (X) fields: (S) represents stomatal apparatus: SEM, scale bar 200 μm. • D – detail of trichome base of glandular trichome: SEM, scale bar 10 μm. • E – basal part of glandular trichome: SEM, scale bar 20 μm. • F – basal part of glandular trichome: SEM, scale bar 10 μm. • G – open body of glandular trichome: SEM, scale bar 20 μm. • H – open body of glandular trichome with visible basal part: SEM, scale bar 20 μm.

Specimen MB.Pb.2003/0788 (Fig. 11D) shows a straight penultimate rachis, 11.5 mm wide. Attached (Fig. 11D, arrowed) is a bent ultimate rachis, more than 66 mm long. This rachis is about 2 mm wide. Traces of attachments in slightly three-dimensional positions of two rachises are present at distances of 10 to 14 mm, while the next two are attached at a distance of around 30 mm. Pinnules are 12 mm long and around 6 mm wide, and of an outline described above; all lobes are broken.

The specimen MB.Pb.2003/0212 (Fig. 11E) from the Westphalian B of the Ruhr basin (Gothan 1919) shows a rhachis 74 mm long and 6 mm wide with attached pinnules around 11 mm long and 9 mm wide. They are attached at a distance varying from 3.5 to 11 mm (mostly around 8 mm) and show a three-dimensional arrangement. One of the pinnules at the basis of a pinna does not look as compact as those described above and even does not show that rigidity. There is a pronounced main rachis (Fig. 11E "P") with up to five lateral segments branching off which show up to 5 lobes. This type of pinnule probably represents aphlebia-like organs (Fig. 11E, arrowed).

Discussion

The studied species have not been widely mentioned in the palaeobotanical literature, due to the rareness of well preserved specimens. There are only a few specimens where it is possible to describe more than the shape of the pinnules. Due to this fact we have poor information about the whole plant concept and furthermore, there is no knowledge about reproductive organs. Nevertheless, we are presenting here new information which allowed us to push forward knowledge of both studied species.

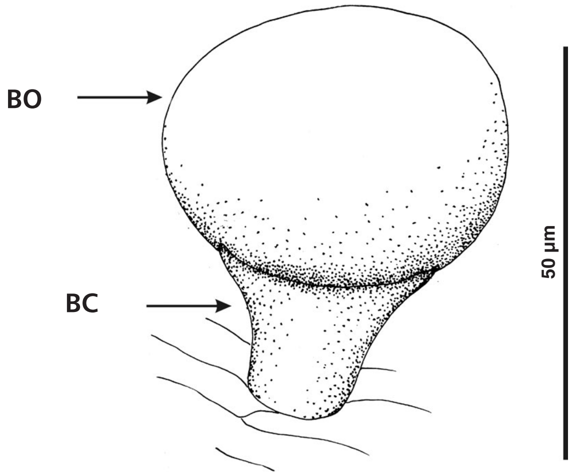


Figure 8. Reconstruction of glandular trichome, consisting of basal cell (BC) and main body (BO).

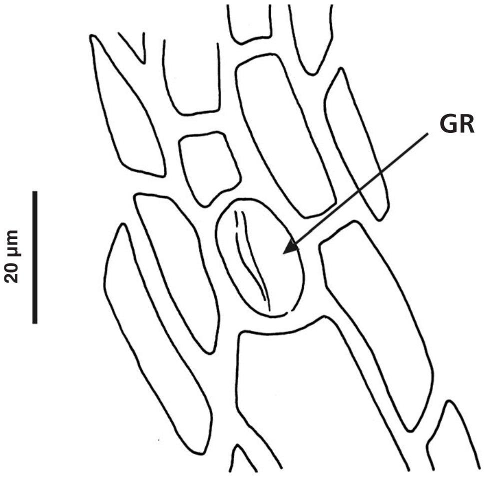


Figure 9. Anomocytic stoma surrounded by cells which are not differentiated from ordinary cells. (GR) – guard cells; based on unpublished SEM photograph.

Comparison of *Rhodeites gutbieri* and *Rhodeopteridium subpetiolatum*

Rhodeites gutbieri and *Rhodeopteridium subpetiolatum* show a great degree of similarity but also clear differences. The main differences are the attachment of ultimate rachises to the penultimate axes, which is in pairs in *R. gutbieri* as already mentioned by Němejc (1928) while the material of *Rh. subpetiolatum* published by Gothan (1913, 1929) show a weak pseudohelical arrangement.

The pinnules of both species are of palmatopterid-type with deeply divided laminar lobes. But *Rh. subpetiolatum* described by Potonié (1889) and Gothan (1912, 1913, 1929) shows an alternating, three-dimensional position of the pinnae in comparison to *R. gutbieri* which shows clearly planated fronds. Another difference seems to be the width of the penultimate rachis. Potonié's and Gothan's specimens (*Rh. subpetiolatum*) show 6 to 11.5 mm wide penultimate rachises while *R. gutbieri* has a penultimate rachis of 3 mm width. Nevertheless, the width of the penultimate rachis depends on the position of the penultimate pinna in the frond, in that rachises situated near the base of a plant are wider than rachises at the distal end of the whole plant.

Generally, pinnules of *R. gutbieri* seem to be shorter than *Rh. subpetiolatum* pinnules, which was also mentioned by Kidston (1923), but this character may be connected with too many environmental parameters to be of systematic relevance. In addition *R. gutbieri* may also show shorter pinnule stalks in comparison with *Rh. subpetiolatum* (Fig. 12).

Kidston (1923) indicated shorter segments in *R. gutbieri* than in *Rh. subpetiolatum,* which also applies to the Czech and the German material respectively. Jennings (1976) believed in the taxonomic relevance of this character but it seems to be a weak one, like the occurrence of hairs (there are none in *Rh. subpetiolatum*).

There is also a difference in the latitude of the laminar lobes. The lobes of *Rh. subpetiolatum (sensu* Potonié/Gothan) are significantly narrower than *R. gutbieri* lobes, which are closer to the shape of pinnules of *Sphenopteris (Rhodea) trichomanioides*, the type-species of this group of foliage. Lastly *R. gutbieri* has laminar lobes divided three times (Fig. 12C) while *Rh. subpetiolatum* has laminar lobes divided no more than two times (Fig. 12D).

The somewhat different branching pattern together with the tendency of the lobes to bunch together and the resulting width of segments produces a more fan-like shape of pinnules in *Rh. subpetiolatum* (Remy & Remy 1977 named it "birch-broom habit") which may be typical and a distinctive feature with regard to *R. gutbieri*.

Comparison of studied species with other plants of similar pinnule-type

Potonié (1889, 1899) placed this species (*Rh. subpetiolatum*) in *Rhacopteris* Schimper based on the similarity of pinnules which are differentiated into deep and sharp lobes that correspond with veins. *Rhacopteris* Schimper, 1869, is characterised as a plant with linear, pinnate frond, narrowing towards the base and contracted into a point at the apex; rachis straight or rarely slightly sinusoid, alternately organized rachises; pinnules flabelliform, semiflabelliform or rhomboidal, entire, crenate, lobed or divided into narrow linear segments, placed at right angles or slightly oblique to the axes (Schimper 1869, Kidston 1923). Pinnules of some Rhacopterids may appear like *Rh. subpetiolatum.* Nevertheless, all known species of *Rhodeopteridium*, including the studied specimens, do not conform to the *Rhacopteris* characteristics, which corresponds with Zeiller's (1899),

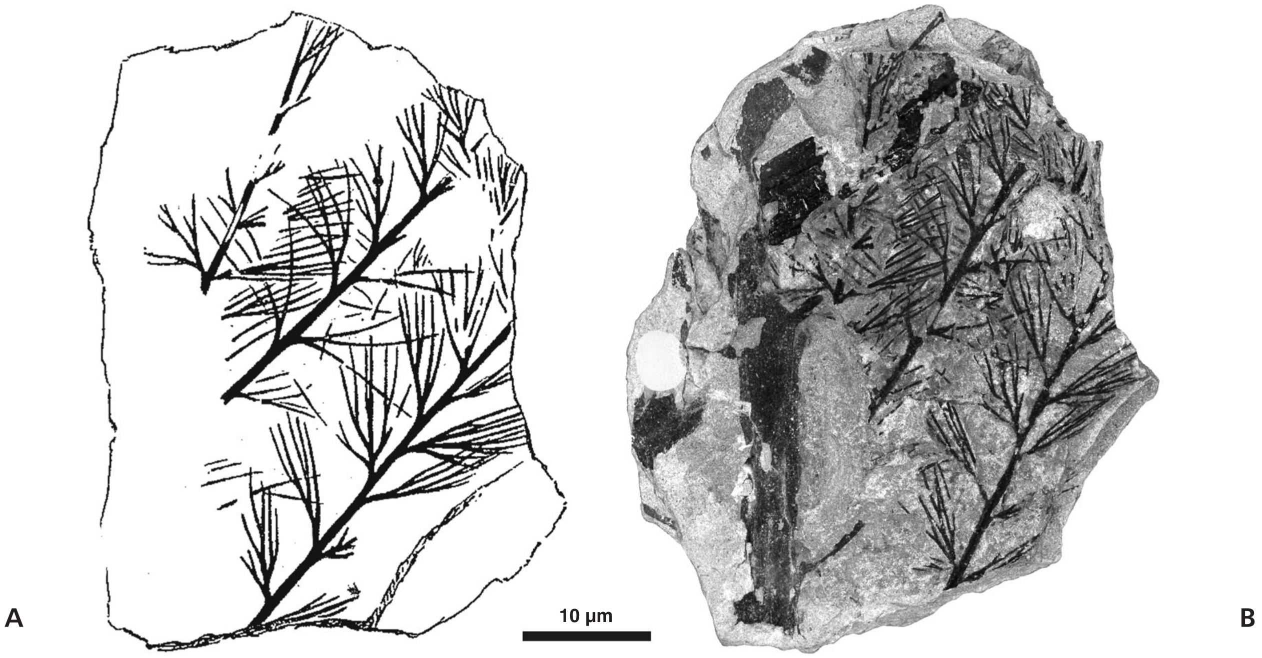


Figure 10. *Rhodeopteridium* (*Sphenopteris*) *subpetiolatum* (Potonié) comb. nov. • A – figured by Potonié (1889, p. 27) based on poorly preserved compression material from Intra-Sudetic Basin (Waldenburg Formation). • B – holotype; MB.Pb. 2003/960; specimen corresponds with Potonié's (1889) figure (see Fig. 10A).

Gothan's (1912, 1913, 1929), Kidston's (1923) and Němejc's (1928) opinions. Consistently all the four authors assigned the studied species to the genus *Rhodea* Presl *in* Sternberg.

Rhodea was established by Presl *in* Sternberg (1838) as a quite artificial genus. Because *Rhodea* Presl is a junior homonym of *Rhodea* Endlicher, which is an invalid synonym of the monocotyledon *Rhodea* Roth (Jennings 1976), Zimmermann (1959, p. 280) proposed the new generic name *Rhodeopteridium* for this group of plants. *Rhodeopteridium* is characterised by pinnatifid fronds with sphenopterid pinnules, differentiated into very narrow laminar lobes. When such species are found in a fertile condition they are removed from *Rhodeopteridium* and placed in genera founded on characters derived from their fertile organs (for example *Zeilleria* Kidston *et al.*). Stur (1877) separated his new genus *Diplotmema* from *Rhodea (Rhodeopteridium)* based on the character of producing fronds with just one major dichotomy in its proximal part. Later Potonié (1892) separated from Stur's (1877) specimens (respectively species) the new genus *Palmatopteris* Potonié for fern-like plants with double dichotomy of the main rachis with sphenopterid pinnules, differentiated into very narrow laminar lobes.

Nevertheless, all three genera *Rhodeopteridium*, *Diplotmema* and *Palmatopteris* have rachises of all orders in alternate organization as in *Rh. subpetiolatum* and they are never organised in pairs as in *R. gutbieri* (specimen E 4942). Due to this fact Němejc (1928) suggested this species with palmatopterid-type pinnules, combined with paired ultimate pinnae, has to be placed into a different genus, for which a new genus was later established *Rhodeites* (Němejc 1937, p. 6). He characterised the new genus: "…the secondary pinnae are arranged in pairs on the stronger and more or less winded primary rachis; but no aphlebiae at the base of such pairs could be stated…".

Kidston (1923) had already proposed the idea that *Rhodeites* (*Sphenopteris*) *gutbieri* and *Rh. subpetiolatum* may be the same species. Only 15 years later, Němejc (1937) synonymized *R. gutbieri* and *Rh. subpetiolatum,* integrating both taxa within the species *R. gutbieri* which was later accepted by Josten (1991).

The robust character "arrangement of ultimate pinnae in pairs" supports our opinion confirming *Rhodeites* as a monospecific genus, clearly separated from the genus *Rhodeopteridium,* including all species showing pinnatifid fronds with sphenopterid or palmatopterid pinnules, differentiated into very narrow laminar lobes and with a three-dimensional, pseudohelical arrangement of ultimate rachises.

Short comment on the affinity of *Rhodeites gutbieri*

We stated above that only sterile specimens of *Rhodeites* are known up till now. Nevertheless, during maceration of *Selaginella*-like cones (specimen F 44; West Bohemian

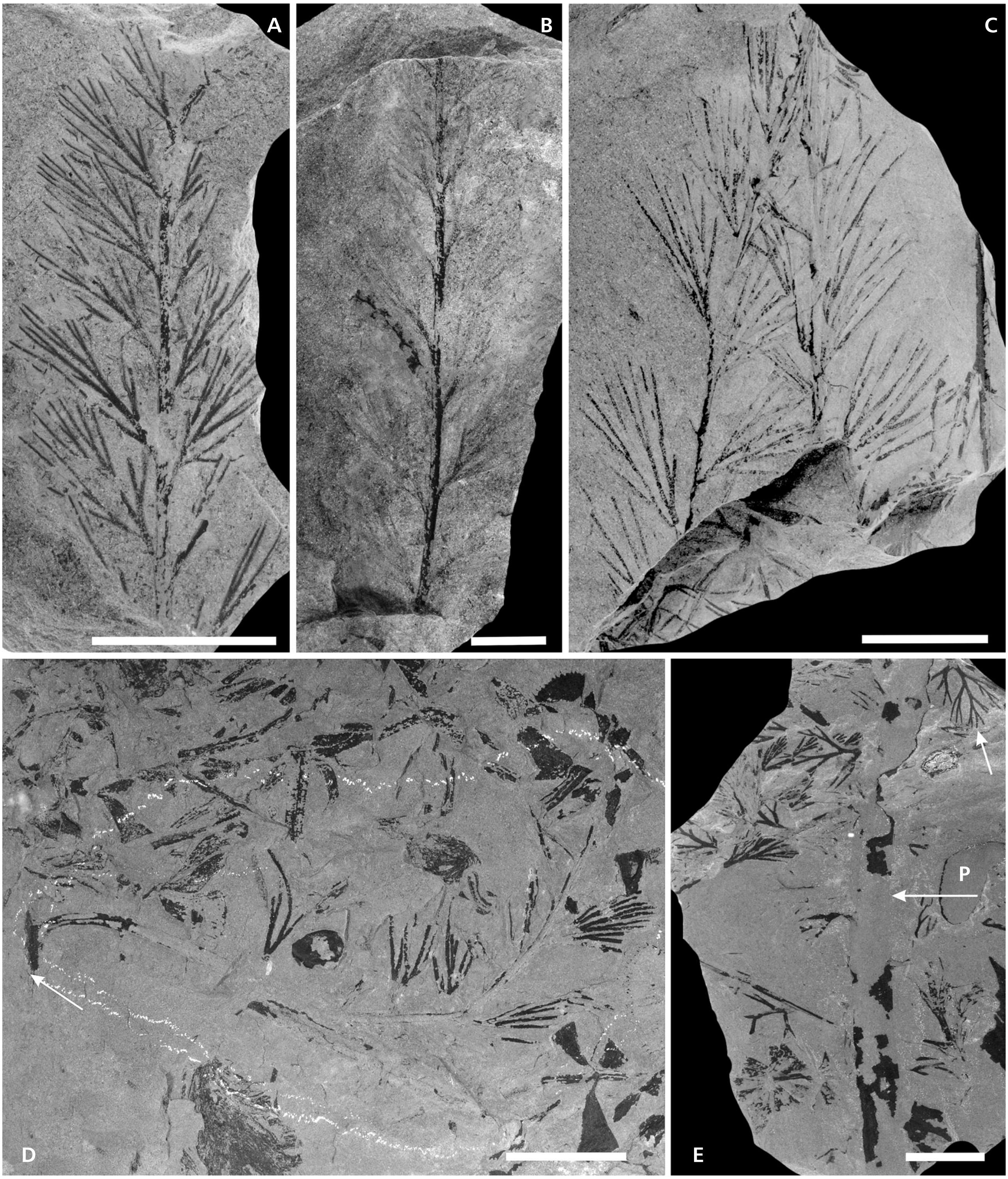


Figure 11. *Rhodeopteridium subpetiolatum* (Potonié) comb. nov. • A – part of distal end of ultimate pinna with well preserved pinnules: MB.Pb.2003/214 – Gothan (1912), pl. 3, fig. 6 (locality – mine Germania, Dortmund, Germany): scale bar 10 mm. • B – part of distal end of ultimate pinna with pinnules: MB.Pb.2003/213 – Gothan (1929), pl. 1, fig. 3 (locality – mine Germania, Dortmund): scale bar 10 mm. • C – distal part of two ultimate pinnae with palmatopterid-type pinnules: MB.Pb.2003/209 – Gothan (1929), pl. 1, fig. 2 (locality – mine Helene-Tiefbau, Witten): scale bar 10 mm. • D – fragment of ultimate pinna attached to penultimate rachis (arrowed): MB.Pb.2003/788 – Gothan 1913, pl. 1, fig. 3 (locality – mine near Orzesche, Upper Silesia, Poland): scale bar 10 mm. • E – fragment of penultimate rachis (P) and aphlebia-like organs (arrowed): MB.Pb.2003/212 – Gothan (1929), pl. 6, fig. 4 (locality – Flöz 4, Zeche Baldur, Dorsten): scale bar 10 mm.

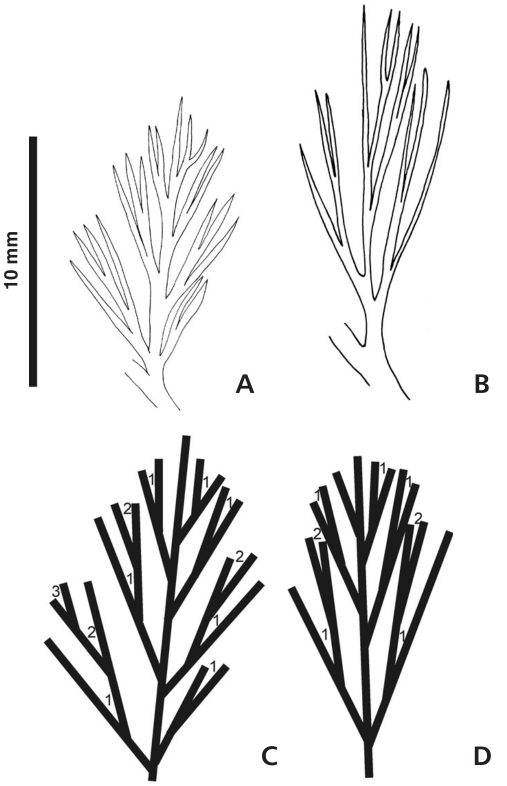


Figure 12. A – pinnule of *Rhodeites gutbieri* (Ettingshausen) Němejc (specimen E 4942). • B – pinnule of *Rhodeopteridium subpetiolatum* (Potonié) comb. nov. of Gothan's specimen MB.Pb.2003/214. • C – *Rhodeites gutbieri* – schematic drawing of dividing lateral veins (max. 3 times). • D – *Rhodeopteridium subpetiolatum* – schematic drawing of dividing lateral veins (max. 2 times).

Museum in Pilsen) very interesting sporangia were obtained, probably from *R. gutbieri*, which will be published as *Echinosporangites libertite* Pšenička & Bek. *Ec. libertite* has never been observed in organic connection with any of the associated pinnules or rachises. Associated plant remains included *Selaginella* sp., *Corynepteris angustissima* (Sternberg) Němejc and *R. gutbieri*. Although we cannot be sure about the precise affinity of *Ec. libertite* dispersed sporangia [with spores comparable to *Schopfites* Kosanke (Pšenička & Bek 2009)], we have some indirect evidence identifying their parent plants. Sporangia and *in situ* spores of two of them (*Selaginella* sp. and *C. angustissima*) are known and are not comparable with the morphology of *Ec. libertite*. Thus the supposition arises that *R. gutbieri*, as the third associated plant, is the hypothetical parent plant of these sporangia. If sporangia *Ec. libertite* really belongs to *R. gutbieri,* it may belong to the true ferns.

The affinity to ferns is also supported by the fact that ultimate pinnae are organised in pairs, which is known in zygopterid ferns such as *C. angustissima* (Sternberg) Němejc. *C. angustissima* as well as *R. gutbieri* have dense haired and sinusoid warped penultimate rachises (or stems). In contrast to *R. gutbieri, C. angustissima* produced aphlebia-like structures on the rachis. Nevertheless, it is not possible to clearly refer *R. gutbieri* to the fern, pteridosperm or progymnosperm plant group.

Comparison of cuticles

Cuticles from *Rhodeites gutbieri* are described for the first time during palaeobotanical history. A general database of Carboniferous fern or fern-like cuticles still does not exist. The papers that deal with this topic are more or less isolated (*i.e.* Barthel 1962, Pšenička 2005). Therefore comparisons of cuticles are more or less limited.

Barthel (1962) described similar cuticles from *Sphenopteris adiantoides* (Schlotheim) H. Potonié: cuticles that are not differentiated into costal and intercostal fields; ordinary cells are elongated, 15–25 μm wide and 100–250 μm long; adaxial and abaxial cuticles contain trichome bases; stomata occur on the abaxial cuticle only; stomata are 35–45 μm long and 25 μm wide. The common characteristic of *S. adiantoides* and *R. gutbieri* cuticles is the lack of differentiation in costal and intercostal fields. But Barthel (1962) pointed out that this feature depends on preservation and size of cuticles. Other characteristics are the elongation of cells and that adaxial/abaxial cuticles exhibit trichome bases 15 μm in cross-section. *S. adiantoides* also has palmatopterid type pinnules, characterised by deeply lobed pinnule to laminar segments, corresponding with veins (Barthel 1962, pl. 6, fig. 88) which resemble the palmatopterid pinnules of the studied species. Nevertheless, Barthel (1962) described pinnules of *S. adiantoides* as hypostomatic (stomata on lower surface only) while pinnules of *R. gutbieri* appear rather aphistomatic (stomata on both surfaces). Barthel (1962) also mentioned the 35–45 μm size of *S. adiantoides* stomata while *R. gutbieri* has sunken stomata 20–27 μm long.

The *R. gutbieri* stomata are not only aphistomatic but also anomocytic (subsidiary cells are indistinguishable from other cells in size and aspect). This type of stomata appears in most true fern families (Van Cotthem 1970). Even if this type of stoma points to a relationship with some fern species, pinnules of *R. gutbieri* bear glandular trichomes, which have not been described in any living ferns.

Ecological comment

All known specimens of *Rhodeites gutbieri* occur in an about 0.5 m thick *in situ* volcanic ash bed at the base of the Whetstone Horizon (Radnice Member, Kladno Formation). Mašek (1963) interpreted the basal bed of the Whetstone Horizon as a rhyolitic sand-grained tuff, and the laminated "whetstone" above it as a graded ash tuff bed. The

Figure 13. Idealised reconstruction of *Rhodeites gutbieri* (Ettingshausen) Němejc.

in situ volcanic ash buried plants at the place of their original growth (Opluštil *et al*. 2007). Taphocoenosis preserved in the tuff bed more or less corresponds with original phytocoenosis. It is also possible to recognise individual plant storeys (Opluštil *et al*. in press). *R. gutbieri* is associated with *Selaginella* sp., *C. angustissima* (on the specimen from the Doubrava locality), *C. angustissima* and *Sphenophyllum majus* (Bronn) Kidston (on the specimen from the Svinná locality). All specimens of these plants occur near the base of the *in situ* volcanic ash bed about 0–30 mm above roof of the Lower Radnice Seam. This part of the bed mostly contains remains of plants that belonged to the herbaceous storey. Due to this fact, *R. gutbieri* was also part of this storey. The ultimate rachis (or stem) is notably long (more than 160 mm) and s-warped, and resembles a stem of zygopterid ferns as for example *C. angustissima.* We assume that *R. gutbieri* had a similar habit (Fig. 13) and life strategy, as creeping and climbing plants occupying the herbaceous storey. The flora preserved in the tuff bed colonized the planar (rheotrophic) mire occasionally supplied by clastics during flooding events (Opluštil *et al*. in press). *R. gutbieri* is therefore an element of disturbed peat to mixed peat-clastic mires.

The specimen of *Rh. subpetiolatum* from Orzesche in Upper Silesia, Poland (MB.Pb.2003/0788) is associated with *Sphenophyllum cuneifolium* a widespread scrambling plant and the specimen MBPb.2003/0212 with *Calamites* sp., *Mariopteris muricata* and even with *Sph. cuneifolium.*

Stratigraphical distribution of both studied species

The stratigraphical distribution of both studied species is clearly differentiated into two main stratigraphical horizons as Fig. 14 shows. *Rhodeites gutbieri* is limited to deposits of the Lower Moscovian (Bolsovian age). The regional distribution of *Rhodeites gutbieri* is the Pilsen Basin (Czech Republic) and the Sarro-Lorrain Basin (France) ("*Sphenopteris coemansii*" *sensu* Brousmiche 1983). *Rhodeopteridium subpetiolatum* in contrast is characteristic for the Bashkirian Stage (from Yeadonian to Duckmantian age) (Fig. 14) and occurred in the Intra-Sudetic Basin area (Poland). This species also occurred in the upper Bashkirian Stage (Duckmantian) in the Upper Silesian Basin (Poland), East Pennine and Burnley basins (UK) (Fig. 14). In Germany *Rhodeopteridium subpetiolatum* is known from the Ruhr Basin and belongs to the middle Bashkirian Stage (Yeadonian and Lengsettian).

The specimens from Héraclée Basin (Turkey) were reported from Duckmantian/Bolsovian age deposits (Fig. 14) and are thus outside the stratigraphical distribution of other known specimens of *Rhodeopteridium subpetiolatum* as well as *Rhodeites gutbieri.* Based on the fact that Zeiller's specimens look poorly preserved and fragmentary, and are only mentioned in the text by Ralli (1933), the occurrence of *Rhodeopteridium* in this Turkish coal basin is not sufficiently secured.

Systematic palaeobotany

Class *Incertae sedis*
Order *Incertae sedis*
Family *Incertae sedis*

***Rhodeites* Němejc (1937) emend.**

Type species. – *Rhodeites gutbieri* (Ettingshausen, 1854) Němejc, 1928. Czech Republic. Pennsylvanian, lower Moscovian (Bolsovian).

Emended diagnosis. – Pinnatifid fronds; ultimate pinnae gradually tapering; tip of ultimate rachis with poorly differentiated lobes and very narrow lamina; ultimate rachises straight or slightly sinusoidal at the distal end of the ultimate pinna, attached to penultimate rachis in pairs; pinnules palmatopterid-type, alternating on ultimate rachis, segmented, each segment differentiated into laminar lobes with sharp tips; aphlebia-like organs present.

***Rhodeites gutbieri* (Ettingshausen, 1854) Němejc, 1936 emend.**

1854 *Sphenopteris gutbieri* n.; Ettingshausen; pl. 19, figs 1, 2.
1928 *Rhodea subpetiolata* Potonié. – Němejc; p. 6, figs 1, 2.
1937 *Rhodeites gutbieri* (Ettingshausen) n. – Němejc; p. 6.
1963 *Rhodeites subpetiolata* (Potonié) Němejc. – Němejc; p. 381, pl. 42, fig. 4.
1983 *Sphenopteris coemansii* Andrae. – Brousmiche; pl. 84, figs 2–4.

Lectotype. – Fig. 2C, D; specimen GBA 1854/009/0021; housed in Geologische Bundesanstalt in Vienna (Austria).

Type locality. – Svinná locality; Radnice Basin (Czech Republic).

Type horizon. – Whetstone Horizon, Radnice Member, Kladno Formation; Pennsylvanian, lower Moscovian (Bolsovian).

Diagnosis. – Pinnatifid fronds; penultimate rachis sinusoid warped, densely covered by uniseriate, multicellular trichomes 0.2–0.4 mm long. Ultimate pinnae gradually tapering from *ca* middle part to the tip; tip of ultimate rachis with poorly differentiated lobes with very narrow lamina. Ultimate rachises straight or very slightly sinusoidal at the distal end of the ultimate pinna, attached to penultimate rachis in pairs.

Pinnules palmatopterid-type, alternating on ultimate rachis at 30°–40°, 10–13 mm long and 6–8 mm wide. Pinnules up to 7 times segmented. Each segment differentiated in up to 4 laminar lobes with sharp tips. The midvein preserved as marked central; lateral veins branching off at angles around 40° to 70,° running in every laminar segment of the pinnules, divided up to 3 times. Aphlebia-like organs present near base of ultimate pinna (on lower side).

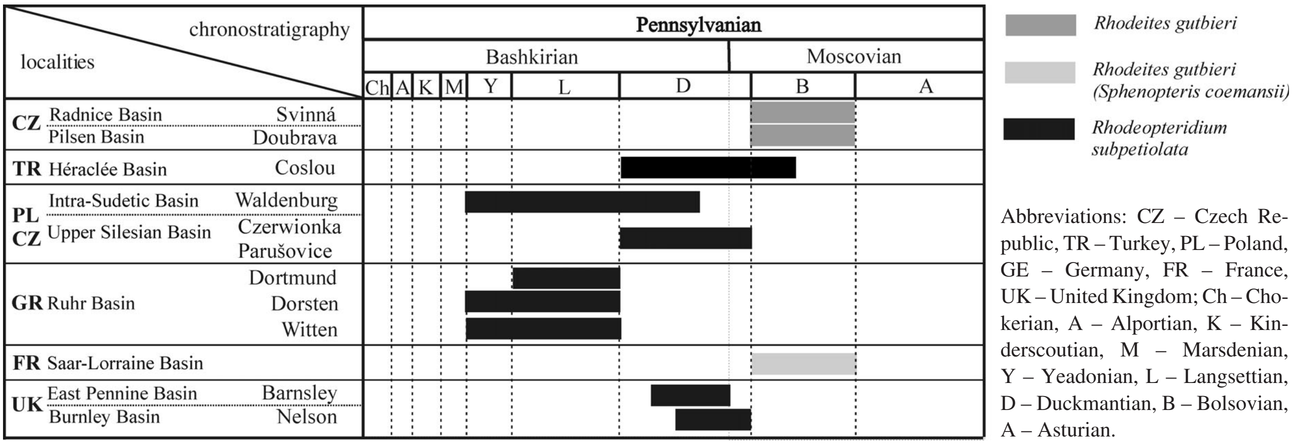
Cuticles: Cuticle of abaxial as well as adaxial side thick and more or less identical. Sunken, anomocytic stomata rare on abaxial as well as on adaxial sides. Cells of adaxial and abaxial cuticles differentiated in costal and intercostal fields but the margin of both fields obscure. Costal cells elongateand tetragonal (polygonal). Anticlinal walls straight. Adaxial and abaxial cuticles covered by glandular trichomes located in costal fields, consisting of a basal cell and globose bodies.

Class Pteridospermopsida?
Order *Incertae sedis*
Family *Incertae sedis*

***Rhodeopteridium* Zimmermann, 1959**

***Rhodeopteridium subpetiolatum* (Potonié, 1889) comb. nov.**

1892 *Rhacopteris subpetiolata* n.; Potonié; p. 26, text-fig. p. 27.
1896 *Rhacopters subpetiolata* n. – Potonié; p. 21, text-fig. 6.
1899 *Rhacopteris subpetiolata* n. – Potonié; p. 132, text-fig. 121.
1899 *Rhodea subpetiolata* (Potonié) Zeiller; Zeiller; p. 27.
1912 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan; pl. 3, figs 6, 7.
1913 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan; pl. 1, fig. 3.
1921 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan & Potonié; p. 82, fig. 75.
1923 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan; p. 43, fig. 41.
1923 *Rhodea subpetiolata* (Potonié) Zeiller. – Kidston; pl. 59, fig. 1.
1923 *Rhodea gutbieri* (Ettingshausen) n. – Kidston; pl. 59, figs 2, 3.
1929 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan; p. 20, pl. 1, figs 2, 3; pl. 6, fig. 4.
1954 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan & Weyland; p. 133, fig. 111.
1957 *Rhodea subpetiolata* (Potonié) Zeiller. – Gothan & Remy; p. 99, figs 89, 90.
1957 *Rhodea (Zeilleria) subpetiolata* (Potonié) Zeiller. – Stopa; p. 186, pl. 25, figs 1–3.



Abbreviations: CZ – Czech Republic, TR – Turkey, PL – Poland, GE – Germany, FR – France, UK – United Kingdom; Ch – Chokerian, A – Alportian, K – Kinderscoutian, M – Marsdenian, Y – Yeadonian, L – Langsettian, D – Duckmantian, B – Bolsovian, A – Asturian.

Figure 14. Stratigraphical distribution of *Rhodeites gutbieri* (Ettingshausen) Němejc and *Rhodeopteridium subpetiolatum* (Potonié) comb. nov. from basins where both species are know.

1977 *Rhodeites gutbieri* (Ettingshausen) Němejc. – Remy & Remy; p. 206, fig. 91.

1991 *Rhodeites gutbieri* (von Ettingshausen) Němejc. – Josten; p. 230, pl. 101, fig. 5; pl. 103, fig. 3.

Holotype. – See Fig. 10A, B; Specimen MB.Pb.2003/0960; Museum für Naturkunde zu Berlin, Germany.

Type locality. – Fürstlicher Tiefbau, near Waldenburg, Intra Sudetic Basin, Poland.

Type horizon. – Pennsylvanian, Westphalian A/B (Langsettian/Duckmantian).

Diagnosis. – Ultimate rachises nearly straight with somewhat rigid appearance; three dimensional, pseudohelical arrangement of ultimate rachises; Pinnules palmatopterid-type, alternate on ultimate rachis at acute angles of around 30° to 50°, 10–15 mm long and 6–9 mm wide, with a length/width ratio of ~1.8, differentiated in up to four segments, build up by one to (seldom) four lobes; lobes straight and showing very narrow laminae, their tips are tapering off; Aphlebia-like organs present. Fructification of *Zeilleria*-type.

Cuticles: Cells of cuticles slightly differentiated in costal and intercostal fields, both areas merging without any clear border, cells elongate (length/width ratio ~ 4:1)and tetragonal (polygonal). Anticlinal walls straight.

Acknowledgements

This work was supported by the Grant Agency of the Czech Republic (205/07/1059), Grant Agency of Academy of Science (IAA 301110701) and IGCP 469 projects. We would like to thank Anna Langrová, and Zuzana Korbelová from the Institute of Geology, Academy of Science of the Czech Republic, Prague for examination under CAMECA SX100 scanning electronic microscope (SEM). We also thank Barbara Meller for taking photographs of Ettingshausen's type housed in the Geologische Bundesanstalt, Wien. Milan Libertín (National Museum in Prague) is cordially acknowledged for help with the study of Němejc's specimens. We acknowledge J. Svoboda for the hand drawing of the *Rhodeites* plant. We would like to thank to C. Radke for taking photographs of Gothan's specimens and J. Dunlop for revision of English.

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