

Epidermal structure of a new *Blanziopteris* species from the Saberian (Kasimovian) of the Kladno-Rakovník Basin (Czech Republic)

ZBYNĚK ŠIMŮNEK & CHRISTOPHER J. CLEAL



Foliage remains from Saberian-age (late Carboniferous–Pennsylvanian) strata of the Central and Western Bohemian basin complex are interpreted as a new species of the putative medullosalean pteridosperm fossil-genus *Blanziopteris* and is named *B. feistmantelii*. It is only the second known species of *Blanziopteris* frond, the other being *B. praedentata*. Both species appear to be foliage of lianescent plants. • Key words: Medullosales, Fronds, *Blanziopteris*, Lianas, Carboniferous, Cuticular analysis, Stephanian.

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Zbyněk Šimůnek (corresponding author), Czech Geological Survey, Klárov 131/3, 118 21 Praha 1, Czech Republic; zbynek.simunek@geology.cz • Christopher J. Cleal, School of Earth Sciences, University of Bristol, Tyndall Avenue, Bristol, BS8 1TQ

An extensive belt of wetlands often referred to as coal-swamps occupied large areas of palaeotropical Euramerica during early–middle Pennsylvanian times (ca. 307–323 Ma) (Phillips 1981, Phillips & Peppers, 1984, Phillips *et al.* 1985, Cleal & Thomas 2005, Opluštil & Cleal 2007, Opluštil *et al.* 2022) coincident with an interval of relatively low sea-levels during glacial phases C3–C4 of the Late Palaeozoic Ice Age of Fielding *et al.* (2023). These swamps were dominated by arborescent lycopsids, equisetopsids and medullosalean pteridosperms (e.g. Cleal & Thomas 1994; Cleal 2021a, b) and resulted in thick peat deposits that subsequently changed into economically-important coals. However, towards the end of the Middle Pennsylvanian (Asturian/Cantabrian, late Moscovian) a combination of climate and orogenic landscape changes disrupted the coal swamps (Gastaldo *et al.* 1996, Cleal & Thomas 1999, Cleal *et al.* 2009) and by the late Cantabrian (Kasimovian) the biome had become restricted to areas south of the Central Pangaeon Mountains (e.g. N.W. Spain, Croatia, Italy), north of the mountains (northern Appalachians and mid-continent USA), and upland areas within these mountains (e.g. France, Bohemia) (Opluštil *et al.* 2022, Knight *et al.* 2023).

These remnant Late Pennsylvanian swamps saw a reduction in abundance and diversity of the arborescent lycopsids and a corresponding increase in marattialean ferns. Medullosaleans continued as important components of the vegetation, with a few species appearing to have

been closely related to Middle Pennsylvanian taxa, such as the plants producing fronds *Neuropteris ovata*, *Alethopteris zeilleri* and *Callipteridium* spp. However, several new and sometimes enigmatic forms appear in the fossil record of this time interval. One such type of frond has been previously identified as *Neuropteris pseudoblissii* Potonié based on a single hand specimen from the West and Central Bohemia coal basin (Czech Republic) (Šimůnek 1988). However, improved cuticle preparation techniques have now yielded new data from this specimen, supplemented by additional data from similar, dispersed cuticles from associated coals. The results of this study, which have shown the original identification to be incorrect, are summarised in this paper.

Throughout the rest of this paper we will use the Regional Chronostratigraphical Scheme often referred to as the Heerlen Scheme as this continues to provide the best stratigraphical resolution for the European terrestrial sequences of this age (Wagner 1974, Wagner & Winkler Prins 2016, Knight & Álvarez-Vázquez 2021).

Geological background

The specimens in this study originated from Stephanian-age deposits in the Central and Western Bohemian region of the Bohemian Massif, Czech Republic (Fig. 1). During late Carboniferous (Pennsylvanian) times, this area was

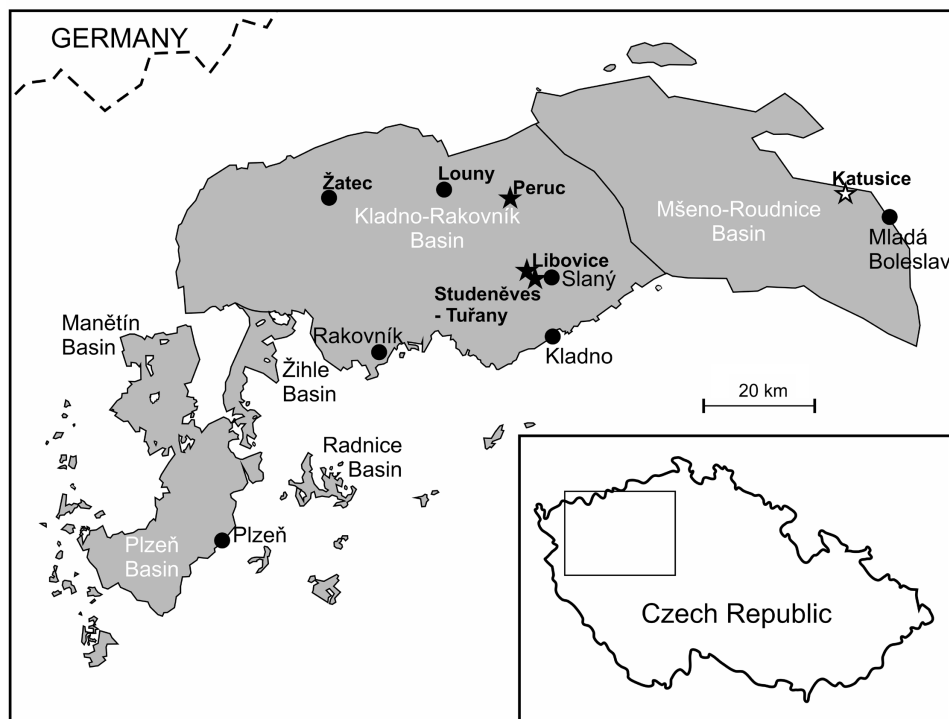


Figure 1. A map of the Czech Republic with the Carboniferous continental basins and localities of *Blanziopteris feistmantelii* in the Kladno-Rakovník Basin (with stars). Legend: black stars – Kounov Group of coals; white star – Zvětin (Klobuky) Horizon.

part of an intramontane basin complex formed within the Variscan Orogen (Pešek 1994, Pešek *et al.* 1998, Pešek & Sivek 2016). In Westphalian times, this basin complex is believed to have been at an elevation of *ca.* 1,000 m above sea level (Opluštil 2005) and, since the Variscan Orogeny was continuing to evolve through to Permian times, the area may have been even higher in the Stephanian. Intramontane basins of similar age further west in the Variscan Orogen have been estimated to have been some 3,000 m above sea-level (Dusséaux *et al.* 2021) or more (Becq-Giraudon *et al.* 1996).

Material and methods

Material. – Hand-specimen (Czech Geological Survey Collection No. YA 1284) from the Libovice locality, Jiřina II Mine. Kladno-Rakovník Basin, Kounov Group of coals, Slaný Formation (Saberian Substage) (Šimůnek 1988).

Dispersed cuticles (Czech Geological Survey Collection slides 596/1-39) from the Peruc locality, Pu 3 Borehole, depth 469–471 m., Kounov Group of coals, Slaný Formation (Saberian Substage).

Dispersed cuticles (Czech Geological Survey Collection slides 652/1-7 and 660/1-36; and SEM stubs 106, 109 and 1105) from Borehole 906648, Katusice, (coordinates N: 50.446122°; E: 14.773879°, H: 311.49 m.), Líně Formation, Zvětin (Klobuky) Horizon (see: Šimůnek & Zajíc 2021, Nádaskay *et al.* 2025), Stephanian, Gzhelian.

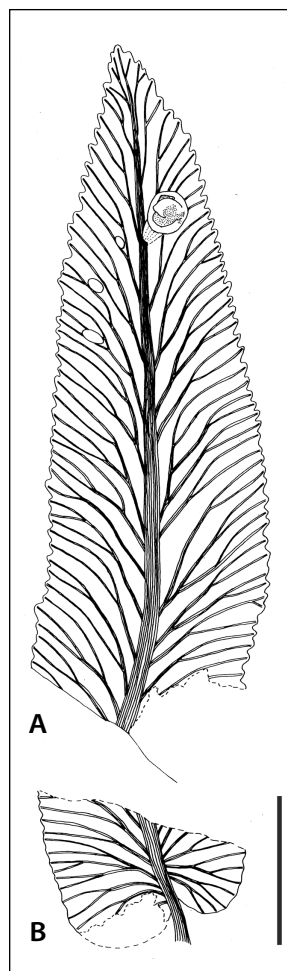


Figure 2. A drawing of venation of *Blanziopteris feistmantelii*, Libovice locality, Jiřina II coal mine (copy from Šimůnek 1988). A – holotype; B – base of a pinule from the opposite side of the slab. Scale bar = 1 cm.

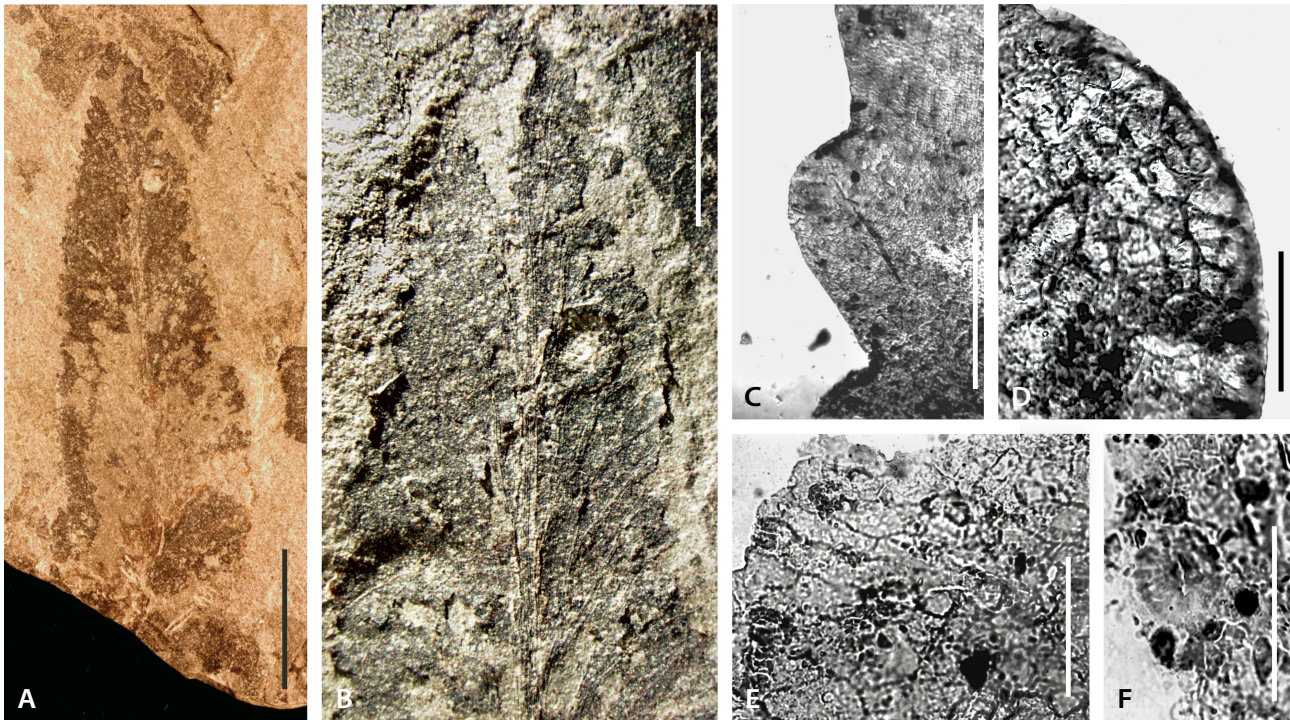


Figure 3. *Blanziopteris feistmantelii*, Libovice locality, Jiřina II mine, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Siberian (Kasimovian). A – fragment of a pinnule with dentate margin, Czech Geological Survey collection, No. YA 1284. B – terminal part of the pinnule from Fig. A enlarged to show the venation. C–F – cuticles from the specimen in Fig. A, slide 115/1; C – pinnule margin with a tooth; D – pinnule margin with a tooth showing polygonal cells of adaxial cuticle; E – abaxial cuticle with stomata; F – close up of a stoma from abaxial cuticle. Scale bars = 1 cm (A), 5 mm (B), 0.5 mm (C), 100 µm (D, E), 50 µm (F).

Methods. – Cuticles were prepared using the method outlined by Kerp (1990). Coalified pinnule fragments were isolated from the hand-specimen rock matrix using a needle and then macerated in Schulze's reagent [36% nitric acid (HNO_3) with crystals of potassium chlorate (KClO_3)] for about 13 hours. The fragments were then thoroughly washed in water followed by 10% potassium hydroxide (KOH) solution to leach out the oxidised coalified tissues. The resulting cuticles were mounted in glycerine jelly slides for optical microscope observation.

Dispersed cuticles were obtained by macerating coal in 65% HNO_3 for about 2 days and then leached out in 10% KOH. The cuticles were then mounted either on stubs for observation under scanning electron microscope, or on glycerine jelly slides for optical microscope observation.

Systematic palaeontology

Genus *Blanziopteris* Krings & Kerp, 1999

Type species. – *Blanziopteris praedentata* (Gothan) Krings & Kerp, 1999 [= *Neuropteris praedentata* Gothan 1909 in Potonié (1909)].

Lectotype of *Blanziopteris praedentata* is based on a specimen figured by Zeiller (1906) under the name

Neuropteris crenulata Brongniart in pl. 29, fig. 1 (Krings & Kerp 1999).

Remarks. – The type species of *Blanziopteris* was originally assigned to *Neuropteris* (Brongniart) Sternberg, 1825 orth. cons. (= *Filicites* sect. *Neuropteris* Brongniart, 1822) but the general aspect of the pinnules and their venation are atypical for that fossil-genus. Cleal & Shute (1995) suggested that the species could be provisionally placed in *Sphenoneuropteris* Shchegolev, 1979 but, as correctly pointed out by Krings & Kerp (1999) the diagnosis provided in the protologue of that genus is vague and the types poorly preserved, making the genus in practice unusable. Consequently, based on a detailed analysis of the foliage morphology and epidermal anatomy, Krings & Kerp (1999) placed Gothan's species in a new genus, *Blanziopteris*.

Blanziopteris feistmantelii (Šimůnek) Šimůnek & Cleal, stat. et comb. nov.

Figures 2–8

1881 *Neuropteris* cf. *crenulata* Brongniart. – Feistmantel, p. 72. pl. 1, fig. 2a, b, c.

1988 *Neuropteris pseudo-blissii* Potonié forma *feistmantelii*; Šimůnek, pp. 73, 74, pl. 1, figs 1–3, pl. 2.

Holotype. – Czech Geological Survey Collection, Specimen No. YA 1284 (Figs 2; 3A, B).

Type horizon and locality. – Provenance Libovice, Jiřina II mine, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Stephanian B (Saberian, Kasimovian).

Etymology. – Based on the family name of Karel Feistmantel (1819–1885) who first described the species.

Description. – The pinnule is lingulate-falcate with acuminate apex, crenulated margin and cordate base (Fig. 3A–C). The preserved pinnule fragment is 46 mm long and 15 mm wide. The midvein is up to 1 mm wide, moderately bent, and discernible as far as the pinnule apex. The lateral veins arise from the midvein at acute angles, divide two to three times, and reach the pinnule margin at 60–70°. Venation is widely-spaced: vein density 10–12 veins per cm on the pinnule margin.

The adaxial cuticle (Fig. 3D) is weakly cutinised; cells are polygonal, randomly oriented, 30–60 µm in size. The abaxial cuticle (Fig. 3E, F) is very weakly cutinised; cells are elongated polygonal, 45–80 µm long and 25–35 µm wide. The anticlinal walls are very thin and usually bent. The stomata are anomocytic, with pairs of elliptical guard cells with polar projections (cutin prolongations). They are 27–33 µm long (without projections) and 25–30 µm wide. The radial lamellae are visible in Figure 3F.

Description of dispersed cuticles: Adaxial cuticle (Fig. 4D, E) shows polygonal cells. Costal and intercostal fields are poorly discernible. The cells are 30–60 µm long and 25–35 µm wide (Fig. 4B, C). The anticlinal walls are straight, or slightly bent.

Abaxial cuticle (Figs 4A, B; 5; 6) shows cells very slightly pronounced anticlinal walls, and differentiated into costal and intercostal fields. The costal cells are usually oblong, 70–120 µm long and 25–40 µm wide, and oriented parallel to the veins. The ordinary cells of the intercostal field are 30–45 µm in the diameter, irregularly polygonal with strongly bent anticlinal walls (e.g. Fig. 6A, B, E). The stomata are randomly and irregularly distributed in the intercostal field, with prominent polar projections; stomatal length 34–48 µm long (including polar projections) 20–26 µm wide (across both guard cells). Guard cells reniform, 21–27 µm long and 9–12 µm

wide. The stomatal pore is 17–22 µm long. The neighbour cells are morphologically the same as ordinary epidermal cells. The lower exterior of the guard cells shows strong radial thickenings (dorsal wood lamellae) (Figs 6C, D, F; 7F–H). The SD = 170–200 stomata per mm² and SI = 15–20 (from 5 measurements).

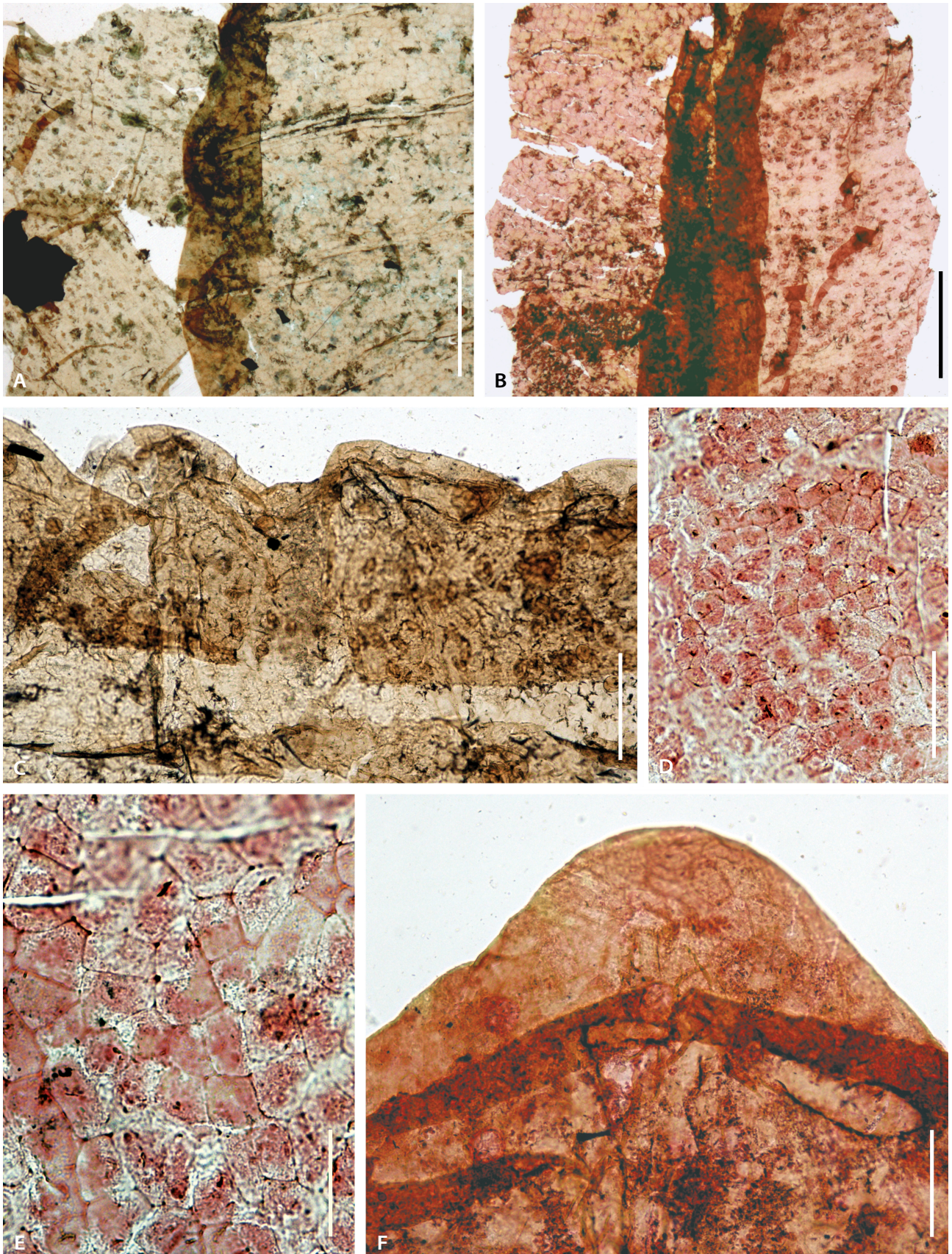
Trichomes and trichome bases occur mainly in the costal fields. The trichomes are multicellular, simple or bifurcated, 420–600 µm long and 55–70 µm wide (Fig. 5B, F, G).

Occasional possible hydathodes were observed. One example was an irregular hole *ca.* 35 mm in the diameter near the pinnule margin (Fig. 4F). A second example was an oval hole situated near the leaf margin (Fig. 5E), although this also resembles a trichome base. From the outer view in SEM to the pinnule surface, the spindle-shaped stomatal opening is seen (Fig. 8A, B).

Remarks. – This species is rare and is so far based on just one hand-specimen and some dispersed cuticles. The hand-specimen was first compared with *Neuropteris crenulata* Brongniart by Feistmantel (1881). As pointed out by Feistmantel, however, *N. crenulata* is very poorly defined, being based on just a single imperfect type probably from the Westphalian of Saar-Lorraine (Brongniart 1831), which Bertrand (1930) suggested might be a “*Sphenopteris*”, presumably a lyginopteridalean (Cleal & Thomas 2023).

More recently, this species was named *Neuropteris pseudoblissii* forma *feistmantelii* by Šimůnek, (1988), based on a comparison with a specimen figured as *Imparipteris pseudoblissii* (Potonié) Remy & Remy by Remy & Remy (1959, fig. 192); the same specimen figured by Potonié (1893, pl. 16, fig. 4) as *Neuropteris cordata* Brongniart, which Remy & Remy (1959) had also included in *I. pseudoblissii*. However, this specimen is poorly preserved and the uneven margins of the pinnules appear to be partly the result of insect damage rather than being an original crenulation. Barthel & Amelang (2011) suggested that the original types of *Neuropteris pseudoblissii* Potonié (Potonié 1893, pl. 2, fig. 5; pl. 17, figs 1, 2) are fact just large pinnules of *Odontopteris schlotheimii* Brongniart 1828, the latter name thus taking precedence. Feistmantel’s specimen has nothing to do with *O. schlotheimii*, which has pinnules with a much thicker, often somewhat vaulted limb and thinner veins.

Figure 4. Dispersed cuticles of *Blanziopteris feistmantelii*, loc. Peruc, Pu 3 borehole, depth 469–471 m, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Saberian (Kasimovian). A – abaxial cuticle (left) and adaxial cuticle (right). Note trichomes and stomata on abaxial cuticle and 3 teeth on the pinnule margin (area in the middle of the image), slide 596/32 (Bismarck brown). B – abaxial cuticle (right) and adaxial cuticle (left). Note stomata and trichomes on abaxial cuticle, slide 596/36 (neutral red). C – pinnule margin with teeth and both cuticles. The abaxial cuticle is removed in the lower part of the image and cells of adaxial cuticle are visible, slide 596/5. D, E – adaxial cuticle with polygonal cells, slide 596/23 (safranine). F – close up of a tooth with polygonal cells of the adaxial cuticle, slide 596/24 (safranine). Scale bars = 0.5 mm (A, B), 200 µm (C), 100 µm (D, F), 50 µm (E).



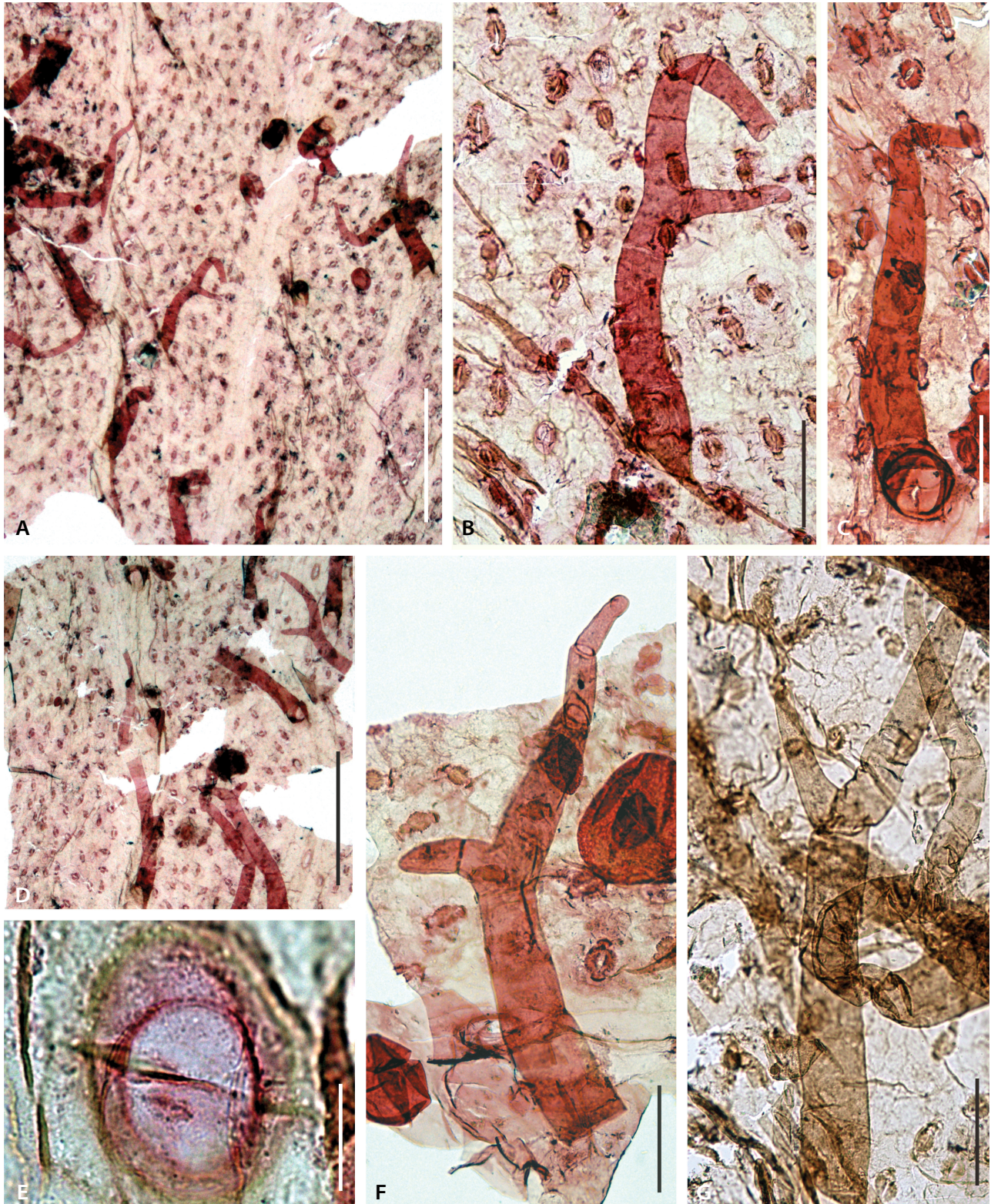


Figure 5. Dispersed cuticles of *Blazzyopteris feistmantelii*, Peruc locality, Pu 3 borehole, depth 469-471 m, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Siderian (Kasimovian). A–D, F, G – abaxial cuticles with trichomes. A – note costal and intercostal fields, stomata and unicellular or bifurcated trichomes, slide 596/25 (malachite green). B – close up of a bifurcated trichome and stomata from Fig. A. C – unicellular trichome, slide 596/22 (safranin). D – abaxial cuticle with trichomes and stomata, slide 596/26 (malachite green). E – either trichome base or hydathode on the pinnule margin on the side of adaxial cuticle, slide 596/22 (safranin). F, G – bifurcated trichomes and stomata on abaxial cuticle; F – slide 596/22 (malachite green); G – slide 596/8. Scale bars = 0.5 mm (A, D), 100 μ m (B, C, F, G), 20 μ m (E)

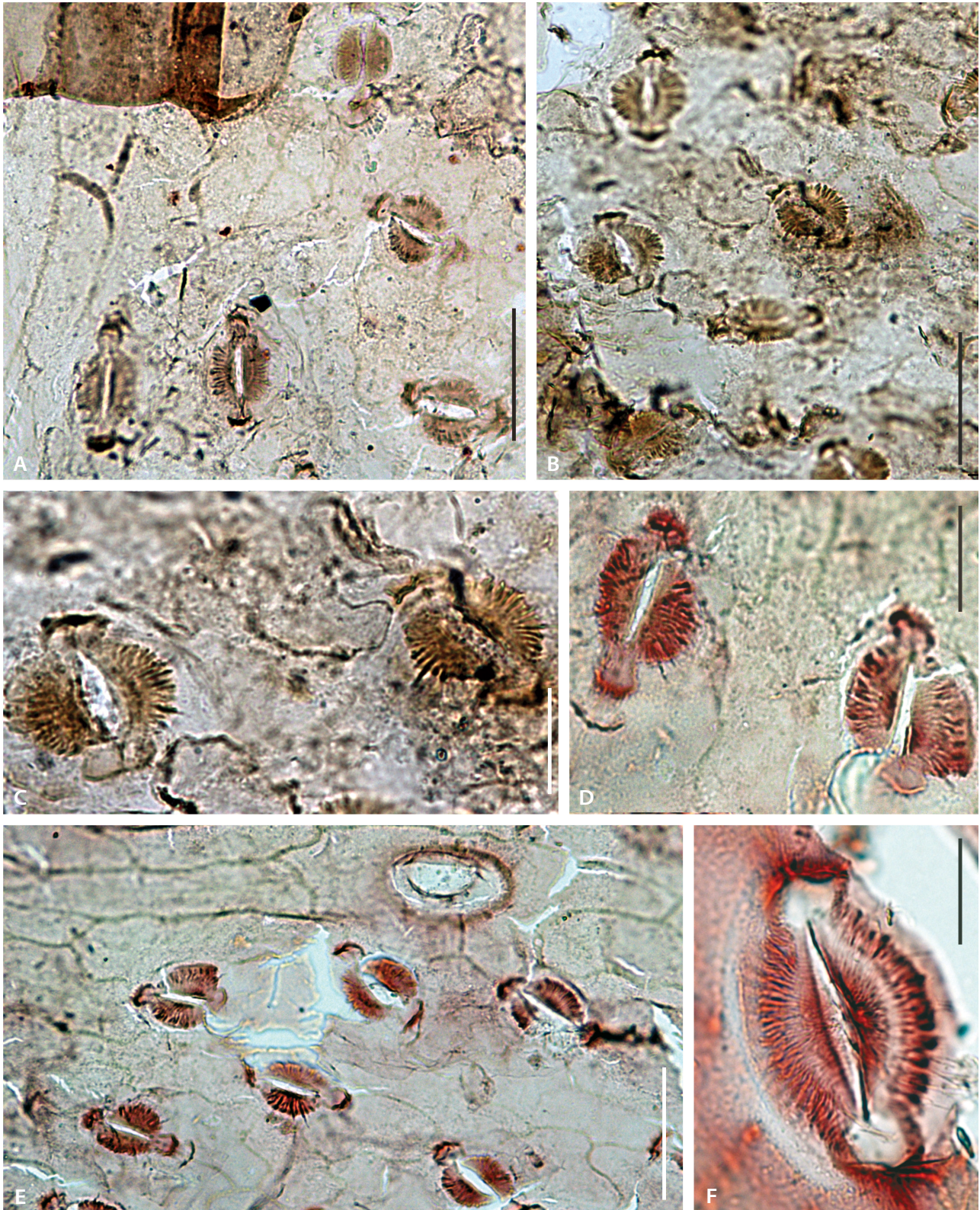


Figure 6. Dispersed cuticles of *Blanziopteris feistmantelii*, Peruc locality, borehole Pu 3 borehole, depth 469–471 m, Kladno–Rakovník Basin, Slaný Formation, Kounov Group of coals, Saberian (Kasimovian). A–E – abaxial cuticles with stomata. A – randomly oriented stomata with polar projections and radial lamellae on guard cells, slide 596/31 (malachite green). B – randomly oriented stomata, slide 596/8. C – close up of two stomata from Fig. 2. D – close up of two stomata from Fig. 5. E – randomly oriented stomata and a trichome base in the costal field, slide 596/21. F – close up of a large stoma. It is much bigger than stomata on abaxial cuticle. This probably occurs on some rachis. Slide 596/21. Scale bars = 50 μm (A, B, E), 20 μm (C, D, F).

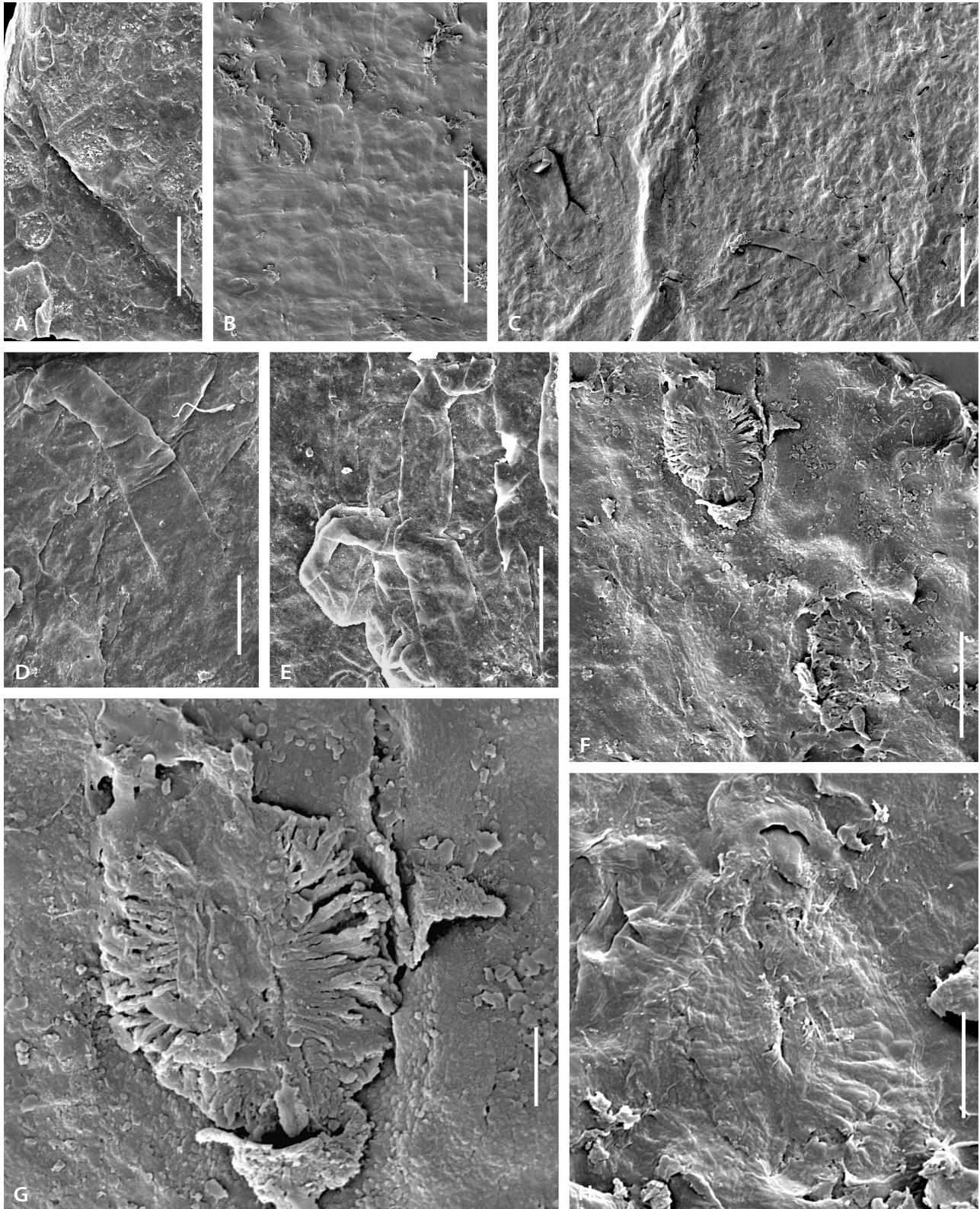


Figure 7. Dispersed cuticles of *Blanziopteris feistmantelii*, Peruc locality, Pu 3 borehole, depth 469-471 m, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Siberian (Kasimovian). Cuticles in SEM; Stub 82 = Figs A, D, E; Stub 96 = Figs B, C, F, G, H. A, B – adaxial cuticle with polygonal cells. C – abaxial cuticle with many stomata and two trichomes. D, E – close up of unicellular (D) and bifurcated (E) trichomes on abaxial cuticles. F – two stomata on abaxial cuticle; view from the inner side. G – close up of a stoma from Fig. F, with polar projection and lamellae on guard cells. H – close up of a stoma. Scale bars = 100 μm (A–C), 20 μm (F), 5 μm (G), 10 μm (H).

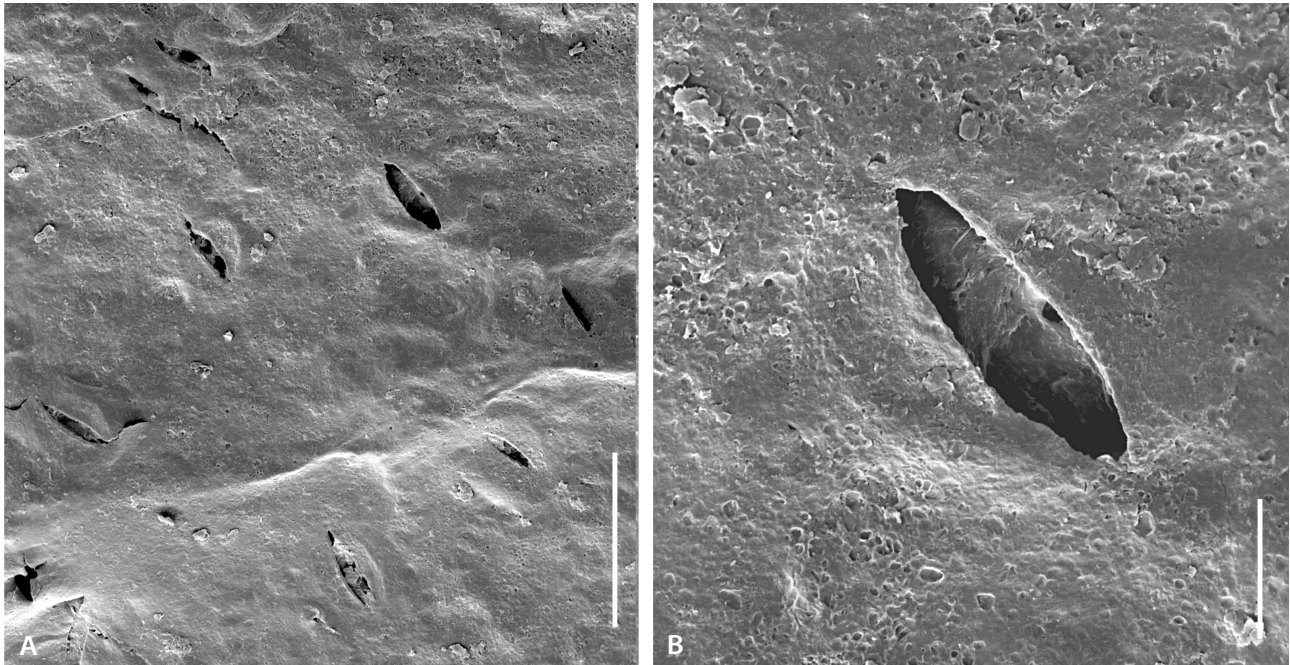


Figure 8. A, B – abaxial dispersed cuticles of *Blanzyopteris feistmantelii* with outer view of stomata in SEM, Peruc locality, Pu 3 borehole, depth 469–471 m, Kladno-Rakovník Basin, Slaný Formation, Kounov Group of coals, Saberian (Kasimovian). Stub 96. A – scale bar = 50 µm; B – close up of a stoma from Fig. A in view from the outside, scale bar = 10 µm.

Although originally assigned to *Neuropteris*, Feistmantel's specimen differs from more typical neuropterids in the pinnule being more falcate with crenulate margins, the thin midvein and widely forked lateral veins, and the branched epidermal trichomes (e.g. compare with Cleal & Shute 1995, 2012). These features offer a much closer comparison with *Blanzyopteris praedentata* (Krings & Kerp 1999; Krings 2000; Krings *et al.* 2003, 2004) and we believe that these features are sufficiently similar to justify placing this Czech specimen in *Blanzyopteris*. Compared to the type of *B. praedentata* the Czech specimen has more tapered pinnules with a more acute apex and more consistently crenulate margins, but it is difficult to be sure if this difference is taxonomically significant as the range of variation in pinnule morphology of the former species is still not fully known. However, as *B. praedentata* has not been previously reported from Bohemia, we have kept the Czech specimen as taxonomically distinct, assigning it to a new species which we name *Blanzyopteris feistmantelii*, adopting the same variety epithet used by Šimůnek (1988) when the taxon was originally described at a lower rank.

There is also comparison with the fragmentary specimens identified as cf. *Blanzyopteris praedentata* from the upper Stephanian of New Mexico (DiMichele *et al.* 2013, fig. 16). These also have tapered, falcate pinnules but differ from *B. feistmantelii* in being larger, at least 70 mm long and 20 mm wide. Given that we are dealing with small numbers of specimens, it is difficult to be sure of the taxonomic significance of this size difference.

Discussion

This is only the second species of *Blanzyopteris* to have been reported in the literature. Like the other species (*B. praedentata*) *B. feistmantelii* occurs in Saberian-aged strata in an intramontane setting. There are also records (as *Neuropteris praedentata*) from northern Spain (Wagner 1963), Saar-Lorraine (Doubinger & Germer 1975), the Caucasus (Novik 1978) and New Mexico, USA (DiMichele *et al.* 2013), but all based on poorly preserved specimens; the Spanish fossils were subsequently renamed *Mixoneura wagneri* Lorenzo, 1980. Nearly all known specimens of *Blanzyopteris* are fragmentary and the only specimens showing part details of the frond architecture are the lectotype (Krings & Kerp 1999, fig. 1a) and the specimens from Blanz – Montceau figured as drawings by Langiaux (1984, figs 217–219).

The systematic position of *Blanzyopteris* is uncertain as no reproductive structures or rachial or cauline anatomy are known, but many authors have placed it in the Medullosales (e.g. DiMichele *et al.* 2006). Zeiller (*in* Renault & Zeiller 1890, p. 235) suggested the frond had a basal dichotomy of the main rachis similar to that seen in many medullosaleans (e.g. Laveine 1997) and this idea could be supported by the offset angle of the upper part of the main rachis; a similar arrangement is seen in the bifurcate semi-pinnate fronds *Macroneuropteris* (Cleal *et al.* 1998). Laveine (1967) also reported intercalated pinnules on the penultimate rachises, also typically found

in medullosalean fronds. Other authors, however, have suggested that the foliage consisted of pinnate fronds lacking a basal dichotomy (Laveine 1967, Krings *et al.* 2003) although some medullosalean fronds also have this style of frond architecture, notably the parispermaceans (*sensu* Laveine *et al.* 1993, Cleal & Shute 2003). Until we have more evidence about these fronds their systematic position must remain uncertain and should perhaps be regarded as a satellite taxon (*sensu* Thomas & Brack-Hanes 1984; Cleal & Thomas 2010, 2021) within the Medullosales.

We have seen no evidence of the climbing organs as reported for *B. praedentata*. However, the branched trichomes on the *B. feistmantelii* are suggestive that these pinnules were also from fronds of a climbing liana.

Conclusions

A second species is recognised within the fossil-genus *Blanziopteris*, which is named *B. feistmantelii*. Like the type species of that genus, it occurs in the upper Stephanian of an upland, intramontane basin and probably represents foliage of lianescent plants.

Acknowledgements

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