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EARLY OCCURRENCE OF A PENNSYLVANIAN-AGE MEDULLOSALEAN FROND SIMILAR TO *ALETHOPTERIS PSEUDOGRANDINIOIDES* IN THE INTRA-MONTANE BASIN OF BOHEMIA

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Abstract: A single frond fragment found in the lower Bolsovian Substage of Central and Western Bohemia (the Czech Republic) closely resembles *Alethopteris pseudograndinioides* Zodrow et Cleal, a species not normally seen until rather younger, late Asturian floras. This discovery provides further evidence that some of the species that suddenly proliferated in mid-Asturian times in response to climate and/or landscape changes, originated in the upland vegetation of the Variscan Mountains.

Key words: Palaeobotany, Medullosales, Westphalian, *Alethopteris*

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Introduction

The vegetation of the Pennsylvanian-age (late Carboniferous) tropical wetlands of Euramerica underwent a major change in late Westphalian times, most notably with the replacement of lycopsids by marattialean ferns as the dominant trees of the peat-substrate habitats. This is clearly reflected in the palaeontological record of the coals (palynology and coal balls, e.g. Phillips et al. 1985), and has been variously interpreted as a response to climate change (Phillips and Peppers 1984, Phillips and Cecil 1985, DiMichele et al. 1985, DiMichele and Phillips 1996, Gastaldo et al. 1996), landscape change (Cleal and Thomas 1999, 2005), or a combination of the two (Cleal et al. 2010, 2011). However, there were also notable changes in the vegetation of the clastic substrate habitats, especially among the seed-bearing plants ("pteridosperms") whose remains tend to dominate the adpression floras found between the coal seams, with the appearance of callistophytes (*Dicksoniites* foliage) and an increase in diversity of the larger-leaved medullosaleans (especially *Alethopteris*). In most parts of Variscan Euramerica (i.e. the areas of eastern North America and Europe east of the Acadian Highlands sensu Pfefferkorn and Gillespie 1980) this change in the adpression floras is recognisable in the middle Asturian Substage and is used as an index to the base of the *Crenulopteris acadica* Zone (formerly *Lobatopteris vestita* Zone sensu Wagner 1984). However, there is some evidence that the change in adpression floras may occur a little earlier in the intra-montane basins; in the Saar-Lorraine Basin on the Franco-German border, for instance, alethopterids become noticeably more abundant in the middle Westphalian Sulzbach Formation *Paripteris linguaefolia* Zone).

The present paper reports on a rare occurrence of an alethopterid in the lower Bolsovian Substage of Central and Western Bohemia, which looks somewhat similar to *Alethopteris pseudograndinioides* Zodrow et Cleal, a species not normally seen below the middle Asturian Substage. Although it is just a single occurrence, this specimen has yielded cuticles to support our suggested identification.

Material and methods

The specimen described here is from the upper Radnice Member (lower Kladno Formation) exposed in the Filip II Quarry, Lubná, Kladno-Rakovník Coalfield, the Czech Republic. The specimen is now in the collections of the Czech Geological Survey (inventory number CGS ZŠ 793a, b).

The cuticles were prepared by macerating part of the specimen in 40% Schulze Solution and then bleaching with 10% KOH solution (Barthel 1962, Cleal and Zodrow 1989, Kerp 1991). After washing in distilled water, the cuticles

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were either mounted in glycerine jelly for light microscopy, or mounted on a stub and coated with gold for SEM.

In the Systematic palaeobotany section we have used fossil-taxa (sensu Cleal and Thomas 2010) for taxa below the rank of order, rather than trying to place them in taxa of whole living organisms.

For chronostratigraphy we have mainly used the regional Heerlen Scheme (Wagner 1974, Wagner et al. 2002) as this provides a better temporal resolution of the terrestrial sequences in Europe than the IUGS Global Chronostratigraphy. For discussions on the relationship between these two schemes, see Davydov et al. (2010) and Opluštil et al. (2016).

Geological background

The Kladno-Rakovník Coalfield represents a part of the Central and Western Bohemian Basin (also including, from west to east, the Plzeň, Manětín, Radnice, Žihle, and Mšeno-Roudnice basins – Pešek 2004) that was formed in a basin that has been interperetd as an upland, intra-montane depression with an estimated elevation of ca. 1,000 m above sea-level (Opluštil 2005).

The Radnice Member is divided into two units (Opluštil and Sýkorová 1999). The lower Radnice Member consists mainly of fine- to medium-grained grey, green or red-brown unbedded sediments with matrix-supported conglomerates, formed in an alluvial fan to alluvial plain environment; this interval includes the Radnice Group of Coals, with upper and lower Radnice coal seams separated by a tuffaceous layer known as the Whetstone Horizon. The upper Radnice Member is separated from the lower unit by a hiatus representing the Duckmantian-Bolsovian boundary (Opluštil et al. 2016), and consists of coarse sandstones together with the Lubná Group of coals. Several tuffite layers occur within the upper Radnice Member. The fossil described here came from a layer of laminated tuffites above the "Z-tuff", associated with the Upper Lubná Coal, and has been dated as 313.22 ± 0.04 Ma (i.e. early Bolsovian / early Moscovian age – Opluštil et al. 2016). However, other tuffaceous layers in the surrounding of Z-tuff give slightly younger ages of about 312.3 Ma, i.e. middle Bolsovian (S. Opluštil, pers. com.) Also present in this tuffite are small fragments of extra-basinal plants such as *Lesleya* and *Dicranophyllum*.

Systematic palaeobotany

Order Medullosales Corsin, 1960
Fossil-family Alethopteridaceae Corsin, 1960

Fossil-genus *Alethopteris* Sternberg, 1825

Alethopteris cf. *pseudograndinioides* Zodrow et Cleal, 1998

Pls 1, 2

Description. This species is represented here by just a single broken pinnule preserved as part and counterpart (Pl. 1, Figs 1, 2). The specimen is 10 mm wide and preserved for a length of 18 mm, with a linguaeform to slightly barreled shape, and rounded to slightly obtuse apex; the base of the pinnule is not fully preserved but shows what may be an incipient basiscopic auricle, and the acroscopic side is somewhat constricted. A prominent midvein extends for most of the pinnule length. Fine lateral veins are emitted from the midvein at an acute angle, arch broadly along most of their length, to meet the pinnule margin at about right-angles. The lateral veins fork three or four times at an acute angle, producing a marginal vein density of ca. 40 per cm.

Adaxial epidermis was thinly cutinised, but relatively large fragments could be obtained (Pl. 1, Figs 3–6). The cells of the intercostal field were isodiametric, polygonal, 45–75 mm in size. The costal field was formed by elongated polygonal to tetragonal cells that were 20–30 mm wide and 50–100 mm long. No hairs or trichome bases were observed.

Abaxial epidermis was thinly cutinised and there was a distinct differentiation between the cells of the costal and intercostal fields (Pl. 1, Fig. 7, Pl. 2, Fig. 3). The costal field, covering the lateral veins, was formed by elongate tetragonal, trapezoidal or rarely polygonal cells, 40–110 mm long and 15–30 mm wide. The intercostal fields had more irregularly shaped randomly oriented polygonal cells 30–75 mm long and 15–30 mm wide. The anticlinal walls were straight or bent.

Structured holes (Pl. 1, Fig. 8) occur rarely in the costal field of the abaxial epidermis. They are round and around 25 mm in diameter.

Anomocytic stomata were restricted to the intercostal fields of the abaxial surface and were randomly oriented (Pl. 2, Fig. 3). The guard cells were sunken and surrounded by 5 to 6 adjacent cells (Pl. 2, Figs 2, 4). The guard cells were reniform with projections in the polar areas, 32–38 mm long and 7–12 mm wide. The exterior (dorsal) walls of the guard cells had strong thickened lamellae and radial striae except in the polar regions (Pl. 2, Fig. 4). Moreover, the guard cells were strongly cutinised around the pores and at the contact areas with adjacent cells. The central part of the dorsal walls bore characteristic radial striae. The stomatal density (SD) varied from 100 (costal field included) to 130 stomata per mm^2 and the stomatal index from 15 to 18.

Comparisons. Alethopterids are generally rare in the upper Radnice Member (Němejc 1936, Šimůnek 1988, 2007, Šimůnek and Cleal 2002). The only species to be previously reported from the tuffites above the "Z-tuff" are possible fragments *Alethopteris lonchitica* Sternberg; it is better documented from the "Z-tuff" itself. However, the latter species tends to have more elongate linguaeform pinnules, and lateral veins that are less curved, rather denser and fork fewer times (usually only once or occasionally twice). The shorter pinnules in *A. lonchitica* can develop somewhat biconvex pinnules, but here the pinnules tend to have a more acute apex, in contrast to the more rounded apex in the presently described specimen. *A. lonchitica* has much denser stomata (370 per mm^2) on the abaxial surface and are surrounded by a ring of subsidiary cells (Barthel 1962, Šimůnek 1996, 2007).

The only other alethopterid to be recorded from the upper Radnice Member is *Alethopteris distantinervosa* R.H.Wagner, emended by Šimůnek and Cleal (2002). The latter has very similar shaped pinnules, but the veins are much less dense (typically 18–27 per cm on the pinnules margin) and tend to fork at a wider angle. Cuticles of *A. distantinervosa* from the Whetstone Horizon described by

Šimůnek (1988) are broadly similar to those obtained from the Upper Lubná Coal specimen in the general configuration of the epidermal cells, but differ in having trichomes on the adaxial surface and papillae on the abaxial surface.

The type of *Alethopteris nemejcii* R.H.Wagner originated from the lower Radnice Member and has pinnules of similar size and similar vein density, but which are clearly more subtriangular with an acute apex than in the currently described specimen.

Němejc (1936) and Šimůnek (2007) reported *Alethopteris serlii* (Brongniart) Göppert from the lower Radnice Member, although in the lowland paralic basins it does not appear until late Asturian times (*Crenulopteris acadica* Zone – e.g. Zodrow and Cleal 1998, Cleal et al. 2010). However, *A. serlii* has generally longer and more slender pinnules, and the lateral veins often tend to be more flexuous (Wagner 1968, Zodrow and Cleal 1998). The stomatal density is similar in both species but in *A. serlii* they are orientated more parallel to the veins (Zodrow and Cleal 1998).

In floras of similar age in the lowland paralic basins of Euramerica, there is some comparison with *Alethopteris corsinii* Buisine. However, the pinnules tend to be rather more slender and lanceolate, and the veins are straighter, less forked and with a lower density (ca. 30 per cm on the pinnule margin).

Among early Westphalian alethopterids of Euramerica, only three species are notably abundant (Buisine 1961, Šimůnek 1996). *Alethopteris decurrens* (Artis) Zeiller is clearly quite different having much more slender, often almost needle-like pinnules and widely forked lateral veins. *A. decurrens* can also be distinguished by having adaxial epidermal cells that are not so markedly differentiated between the costal and intercostal fields and the guard cells of the stomata lack the thickened lamellae and radial striae (Šimůnek 1996). *Alethopteris davreuxii* (Brongniart) Zeiller has notably more lanceolate pinnules, and veins that are more flexuous, often verging on the pseudo-anastomosed, and somewhat less dense (30–36 per cm on pinnule margin); *A. davreuxii* can also be distinguished by having papillate stomata (Šimůnek 1996). *Alethopteris urophylla* (Brongniart) Göppert has less barrel-shaped pinnules, the smaller ones tending to an obliquely subtriangular form (Wagner and Álvarez-Vázquez 2008); and the stomata are smaller and oriented parallel to the veins (Šimůnek 1996).

The closest comparison to the currently described specimen is in fact a species normally found in upper Asturian floras (*C. acadica* Zone) – *Alethopteris pseudograndinioides* Zodrow et Cleal. It also has linguaeform to slightly barrelled pinnules, a well-marked midvein, and broadly curved lateral veins that fork two or four times. The most notable difference is the rather higher vein density (in *A. pseudograndinioides* it is usually 20–34 per cm – see Zodrow and Cleal 1998). It is possible that this merely represents an extreme end-member of intra-specific variation but, given its very early stratigraphical occurrence (*A. pseudograndinioides* has not previously been reliably reported from below the *Crenulopteris acadica* Zone – see Zodrow and Cleal 1998) we think this unlikely. Hence, we have named it *Alethopteris* cf. *pseudograndinioides*.

The cuticles of this Czech specimen also resemble the types of *Alethopteris pseudograndinioides* (from the upper Asturian Sydney Mines Formation, Cape Breton, Canada) in the shape and the dimensions of the epidermal cells. The stomatal guard cells of the Canadian specimens were a little smaller and narrower than in the described specimen. The Canadian specimens also show evidence of stomata that were more parallel oriented than in the described specimen. The stomatal density is a little higher in the Canadian specimen – 250 stomata per mm^2, whereas the studied specimen has only some 100–130 stomata per mm^2.

Discussion

Although only a single fragment, this late Westphalian specimen is of interest as it appears to be an early but rare representative of the group of alethopterids that in late Moscovian times became major components of the adpression floras, including notably *A. psueodgrandinioides*, *Alethopteris grandinii* (Brongniart) Göppert and *Alethopteris ambigua* Lesquereux. A similar situation can be seen in the floras of the Saar-Lorraine coalfield – an intra-montane basin that straddles the Franco-German border. Here, there occur specimens in the lower Bolsovian Sulzbach and Luisenthal formations that strongly resemble *A. ambigua*, a species that in the paralic basins also does not appear until the base of the *C. acadica* Zone in the middle Asturian Substage. These Saar-Lorraine specimens, described by Bertrand (1932) as *Alethopteris friedelii* P.Bertrand, have an indistinguishable pinnule shape to *A. ambigua* (and unpublished work by the second author suggests that the epidermal structures are also similar) but differ in the veins being more widely forked.

The function of the rare structured holes observed in the abaxial cuticle is at present uncertain. Similar holes have been figured in abaxial cuticles of *Alethopteris zeilleri* (Ragot ex W.Remy et al.) R.H.Wagner by Kerp and Barthel (1993: pl. 3, figs 2–5) and *A. pseudograndinioides* by Zodrow and Cleal (1998: pl. 7, fig. 5). In both cases these were interpreted as trichome bases although no actual trichomes were observed (these are quite different from the much larger structures on the adaxial cuticle of *A. zeilleri*, which clearly are trichome bases as they have hairs attached – Kerp and Barthel 1993: pl. 2, figs 6–9). In contrast, Shute and Cleal (2002) interpreted similar structured holes in foliar remains of another medullosalean (*Laveinopteris*) as hydathodes, based on the observation that the collar surrounding the hole appeared to enter the limb of the leaf, rather than extending out of it as would be expected in a trichomes base; again, no actual trichomes were found attached to these holes. However, we have been unable to confirm the orientation of the shallow cutinised collars that appear to surround the structured holes in *A.* cf. *pseudograndinioides* and so we reserve judgement as to their function.

The guard cells of *Alethopteris* cf. *pseudograndinioides* resemble those of *Neuropteris cordata* Brongniart (Krings 2000) and *Blanzyopteris praedentata* (Gothan) M.Krings et Kerp (Krings and Kerp 1999). All these species have similar dorsal thickened lamellae and radial striae on the guard cells. Of course, there are many morphological features that enable these species to be distinguished, as well as the greater density of trichomes in *Neuropteris cordata* and *Blanzyopteris praedentata.*

Conclusions

This specimen suggests that the group of alethopterids that suddenly proliferated in late Westphalian (late Moscovian) times in the lowland paralic basins may have been already present in the upland intra-montane basins in early Moscovian times. It has been suggested that the changes in the late Westphalian floras were a result of the development of better drained substrates, and so perhaps such conditions were already present as a subset of the habitats present in the upland basins during mid-Westphalian times. Alternatively, being associated with fragments of extra-basinal plants may indicate that this alethopterid was also from a plant growing outside of wetlands. Either way, it would seem that the sudden appearance of alethopterids in the paralic basins in the middle Asturian Substage, which represent a major biozonal boundary, was a consequence of plant migration rather than a burst of evolutionary change within the lowland wetlands.

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Explanations of plates

PLATE 1

Alethopteris cf. *pseudograndinioides* Zodrow et Cleal, Lubná near Rakovník, Filip II Quarry, Radnice Member, fine-grained tuffites above Z-tuff, Lubná Group of coals, Bolsovian

1, 2. Part and counterpart of a pinnule, inv. no. CGS ZŠ 793a, b; material to slides 461/1–10.

3. Adaxial cuticle. Slide 461/7.

4, 5. Details from Fig. 3.

6. Inner view on adaxial cuticle with prominent anticlinal walls. SEM stub 42.

7. Abaxial cuticle with prominent costal areas and intercostal areas with stomata. Slide 461/7.

8. Close up of a "structured hole" from Fig. 7.

PLATE 2

Alethopteris cf. *pseudograndinioides* Zodrow et Cleal, Lubná near Rakovník, Filip II Quarry, Radnice Member, fine-grained tuffites above Z-tuff, Lubná Group of coals, Bolsovian

1. Abaxial cuticle with stomata, detail from Pl. 1, Fig. 7.
2. Close up of two stomata from Fig. 1.
3. Abaxial cuticle with costal field in upper right corner, and intercostal field with stomata in left below. Slide 461/6.
4. Close up of a stomatal complex from Fig. 3.

PLATE 1

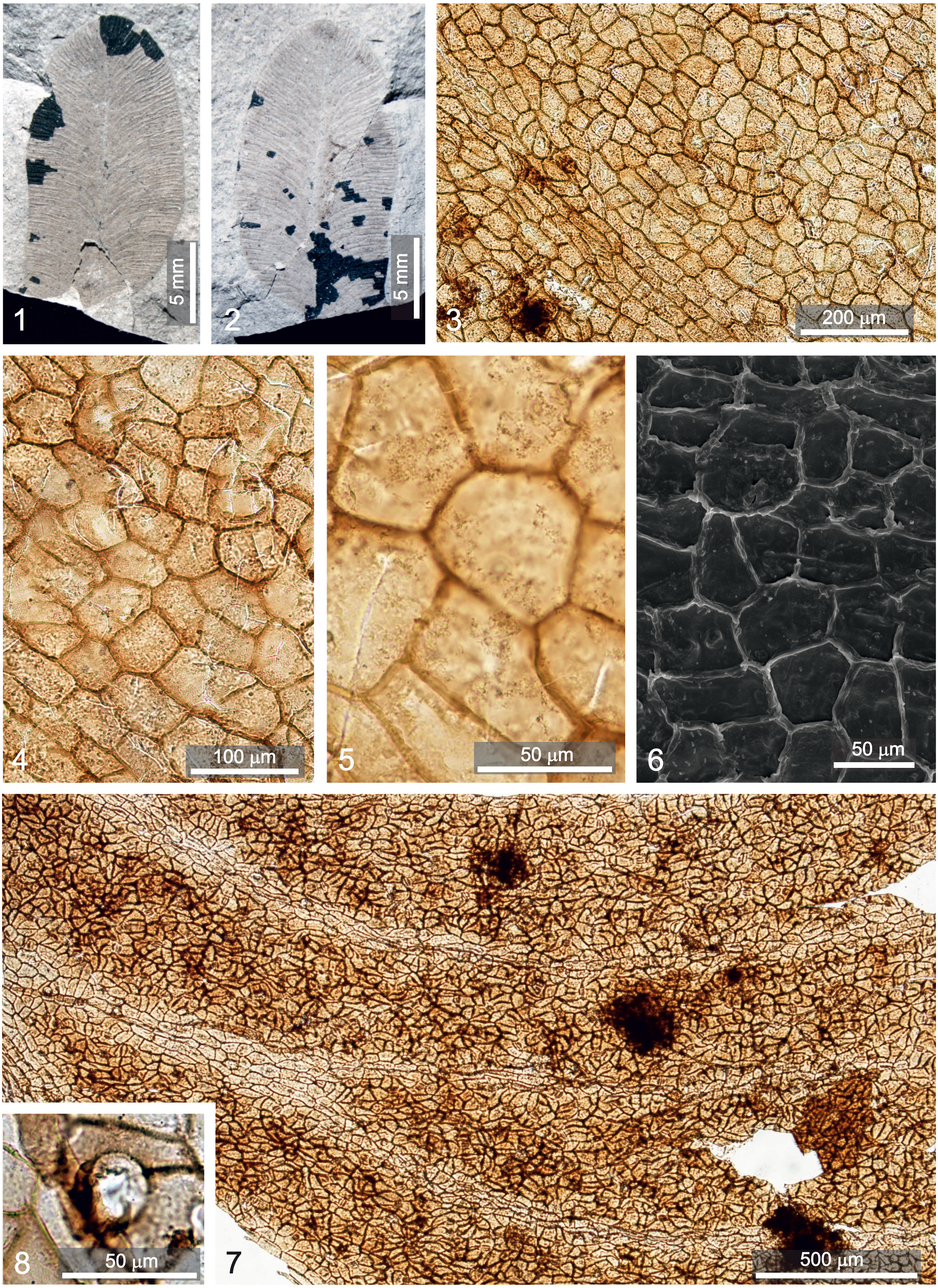

PLATE 2