The taxonomy of middle Westphalian medullosalean foliage known as 'Alethopteris grandinioides early form' from the Central and Western Bohemian basins

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A b s t r a c t. Fossils from the Whetstone Horizon of central Bohemia, previously referred to as the 'early form of *A. grandinioides* Kessler', are shown to be indistinguishable in pinnule morphology and venation from *Alethopteris distantinervosa* Wagner. This new evidence allows the diagnosis of *A. distantinervosa* to be emended, providing better information on its morphological variation and epidermal structure. *A. distantinervosa* occurs in floras of late Duckmantian to Bolsovian and possibly early Westphalian D age in central Bohemia, Saar-Lorraine, Ibbenbüren, and South Staffordshire. *A. grandinioides* Kessler *sensu* Wagner, *non* Kessler s.s. (= *A. pseudograndinioides* Zodrow and Cleal) does not appear to occur in floras older than middle Westphalian D in age.

Key words: Upper Carboniferous, Middle Westphalian, biostratigraphy, Gymnospermae, Pteridospermae, Alethopterides, taxonomy, biogeography, Late Paleozoic of central and western Bohemia

Introduction

Alethopteris grandinioides Kessler, 1916 was established for medullosalean pteridosperm foliage based on a type from the Westphalian D of Saarland, Germany. This holotype is now lost and Kessler's photographic illustration of it is poor (Bertrand and Corsin 1933) and so for many years the name was virtually ignored. However, Wagner (1968) resurrected this name for a species found mainly in the middle Westphalian D to lower Cantabrian, which also rarely ranges down into the upper Duckmantian. For some 30 years, Wagner's taxonomic treatment was generally accepted.

In a revision of the species, Zodrow and Cleal (1998) concluded that *A. grandinioides sensu* Wagner in fact covers three morphospecies.

- 1. The lost holotype, which almost certainly belongs to *Alethopteris grandinii* (Brongniart) Göppert.
- 2. The specimens of middle Westphalian D to Cantabrian age, which includes Wagner's (1968) proposed neotype. This species does not occur in Saar-Lorraine and so cannot be conspecific with Kesssler's holotype (Zodrow and Cleal 1998, p. 86). Following ICBN Article 9.16 (Greuter et al. 2000) Wagner's proposed neotype must therefore be rejected. Consequently, Zodrow and Cleal assigned this material to a new species, *Alethopteris pseudograndinioides*.
- 3. The late Duckmantian to Bolsovian aged specimens. Zodrow and Cleal (1998) did not have available any of this group of specimens and they had to base their interpretation on the published literature. Consequently, they merely referred to it as the '*A. grandinioides* early form'. The present paper examines the taxonomy of this '*A. grandinioides* early form'.

A. grandinioides early form' from the Whetstone Horizon

The best-preserved and most abundant pre-middle Westphalian D examples of A. grandinioides sensu Wagner, 1968 are from the Whetstone Horizon (Radnice Member, lower Bolsovian) of the Central Bohemian Basin. Němejc (1936) first described them as Alethopteris grandinii (Brongniart) Göppert, alongside other specimens with similar shaped pinnules but more flexuous veining. Wagner (1968) referred these specimens with more flexuous veins to a new species, Alethopteris distantinervosa. However, Šimůnek (1988) found that the morphological distinction was not clear-cut, as some of the Whetstone Horizon specimens showed both pinnule morphotypes. He also showed that pinnules with these different veining patterns yielded virtually indistinguishable cuticles. However, their epidermal structure is significantly different from that of A. pseudograndinioides, in having trichomes, larger and more randomly oriented stomata, and more sinuous cell walls (Zodrow and Cleal 1998, pp. 87-88).

To see if the morphological distinction between *A. distantinervosa* and the 'early form' is real, we looked at three characters regarded as critical by Šimůnek (1984, 1988) based on specimen from the Whetstone Horizon.

- 1. Pinnule dimensions. An almost complete overlap was found in the ranges of their lengths and breadths (Fig. 1).
- 2. Venation. A complete gradation was found between pinnules with an *A. distantinervosa*-like venation (Figs 2b, e–h), pinnules with an 'early form' type venation (Figs 2i, j, l, m), and pinnules with an intermediate type venation (Figs 2a, c, k).
- 3. Incisions between pinnules. Again, a complete grada-



Fig. 1. Variation in pinnule length and breadth of *Alethopteris distantinervosa*, from Bolsovian floras of the Central and Western Bohemian basins (shown as black circles). Also shown are the lengths and breadths of pinnules previously referred to as *A. grandinioides*, from contemporaneous floras of the same basins (marked as "×"). Based on data from Šimůnek (1984).

tion was found in this feature (Fig. 2). Moreover, some pinnules with essentially *A. grandinioides*-like venation have wide and blunt incisions (e.g. Fig. 2j) while others with *A. distantinervosa*-like venation have relatively narrow incisions (e.g. Fig. 2f).

These results thus confirm Němejc's (1936) view that these two morphotypes represent end members of a continuous range of variation within one species. However, we cannot agree with him that they belong to *A. grandinii*, which is quite a different middle Westphalian D to Cantabrian species, very similar to *A. ambigua* (see Cleal 1984, Zodrow and Cleal 1998). In our view, the correct name is *A. distantinervosa*.

'A. grandinioides early form' from other localities

Wagner (1968) included four late Bolsovian specimens from the North Staffordshire Coalfield (Great Britain) in this species. The two that he figured (Ibid., pl. 21, fig. 63; pl. 22, fig. 66) are short pinna fragments with broken pinnules, and are too small to identify. He also included a much larger and better-preserved specimen from the upper Duckmantian of the South Staffordshire Coalfield, (figured by Crookall 1955, pl. 4). This closely resembles the specimens from the Whetstone Horizon flora with more narrowly forking veins. Interestingly, Wagner (1968, pl. 16, fig. 45) figured a second specimen from about the same stratigraphical level in the same coalfield, which has widely forking veins and was identified as A. distantinervosa. Although not from the same locality, these two specimens may reflect a similar variation in venation to that seen in the Whetstone Horizon flora.

Wagner (1968) also included the late Bolsovian spec-

imens from Nord-Pas-de-Calais figured by Buisine (1961, pl. 56) as Alethopteris pontica Zeiller. Other similar specimens from contemporaneous strata in this coalfield were figured by Zeiller (1888, pl. 38, fig. 1) and Wagner (1968, pl. 21, figs 61, 62). These specimens have much larger pinnules (up to 30 mm long and 10 mm wide) with a more triangular shape and flatter limb, and more narrowely forking veins that A. distantinervosa.

Finally, Wagner (1968) identified some specimens from the Bolsovian of Saarland as *A. grandinioides*, one of which was subsequently figured by Doubinger and Germer (1974, pl. 21). These have a

midvein that extends for most of the pinnule length, whereas in *A. pseudograndinioides* it rarely extends for more than three-quarters of the pinnule length. Also, the veins are much finer and denser (c. 40 veins per cm along the pinnule margin) than is typical for *A. pseudograndinioides* (which usually has vein densities of between 20 and 34). As pointed out by Cleal and Zodrow (1998), there is a comparison with *Alethopteris lonchitica* Sternberg, especially with specimens such as that figured by Bertrand (1932, pl. 33, fig. 1), which also came from Saar-Lorraine.

Conclusions

In conclusion, the specimens from the Whetstone Horizon referred by Wagner (1968) to *A. grandinioides* belong in fact to *A. distantinervosa*. This requires an emendation of to the diagnosis and circumscription of the latter species, so as to incorporate both the wider range of morphological variation and the epidermal evidence described by Šimůnek (1988).

Alethopteris distantinervosa Wagner, 1968, emend. Šimůnek and Cleal

- 1914 Alethopteris Grandini (Brongniart) Göppert; Kidston (*non* Brongniart), p. 103 [specimen figured by Wagner 1968, pl. 16, fig. 45].
- 1936 Alethopteris Grandini (Brongniart) Göppert; Němejc (non Brongniart), p. 12, text-fig. 6a, b, pl. 2, fig. 3.
- 1955 Alethopteris Grandini (Brongniart) Göppert; Crookall (*non* Brongniart), pl. 4 (*non* pl. 6, fig. 2 – to *A. quadrata* Wagner).



Fig. 2. Variation in pinnule shape and venation in Alethopteris distantinervosa.

a–g – Whetstone Horizon (lower Bolsovian); a, e, f from Theodor Mine, Pchery, near Kladno; b, d from Pokrok Mine, Ovčín, near Radnice; c from Matylda Mine, Břasy, Radnice Basin; and g from Svinná, near Radnice; h-m – Lubná Group of Coals (upper Bolsovian), Lubná near Rakovník, h from Nostic (Ervín) Mine (refigured from Němejc 1936, pl. 2, fig. 3); i-m – Roof of No. 1b Seam (Lubná Group of Coals – upper Bolsovian), Ludvík Mine, Lubná, near Rakovník, Kladno-Rakovník Basin, (k – refigured from Šimůnek 1988, text-fig. 1, pl. 2, fig. 5). All shown at ×3 magnification.

- 1968 Alethopteris distantinervosa Wagner, p. 61, pl. 16 [protologue].
- 1968 Alethopteris grandinioides Kessler var. grandinioides; Wagner (non Kessler), pp. 72, 79 (only references to specimens from Whetstone Horizon, and the above listed Crookall specimen).
- 1988 Alethopteris grandinioides Kessler var. grandinioides; Šimůnek (non Kessler), p. 382, text-figs 1–3, pls 1–2.
- 1988 Alethopteris grandinioides var. distantinervosa

(Wagner) Šimůnek, p. 383, text-figs 4–6, pls 3–6; pl. 7, figs 1–5 [includes cuticles].

E m e n d e d i a g n o s i s : Robust, ribbon-shaped pinnules, 5–15 mm long, 3–7 mm wide. Pinnule apices rounded. Midvein thin, decurrent, reaching almost into the pinnule apex. Lateral veins rather widely spaced, forking once or twice at wide to narrow angles, reaching pinnule margin at 60–90°. Vein density 18–27 per cm along pinnule margin. Epidermal cells with sinuous walls. Uniseriate trichomes borne on both surfaces. Stomata randomly oriented on abaxial surface; guard cells 30–42 µm long.

Holotype: Specimen 5211, Geologisch Bureau, Heerlen, the Netherlands. Originated from the upper Bolsovian Glückenburg Seam, Ibbenbüren Pit Oeynhausen, Slg. Dreibholz, Germany (Wagner 1968, p. 61).

Distribution: Ibbenbüren, Germany (upper Bolsovian); Central Bohemian basins, Czech Republic (upper Duckmantian–lower Westphalian D); Saar-Lorraine (upper Duckmantian–basal Bolsovian); South Staffordshire Coalfield, Great Britain (upper Duckmantian).

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