

A synopsis of Westphalian–earliest Stephanian medullosalean and allied plant fossils from the Central and Western Bohemian basins, Czech Republic

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The Medullosales were among the most diverse seed-plant clades in the Pennsylvanian palaeotropical, peat-forming wetlands and their fossil foliage constitutes valuable biostratigraphical and palaeofloristic indices. However, there have been several recent taxonomic revisions of the intramontane floras of the Central and Western Bohemian basins, as well as a number of unpublished records that were not incorporated into previous palaeogeographical studies. In this paper, we collate all of the currently available data on medullosalean foliage from the middle and upper Pennsylvanian Kladno Formation from these basins. The different autochthonous and allochthonous floras of the Radnice Member were coded separately to see if the habitats that represent may have had an effect on the analysis. The new dataset suggests that the roof shale floras, although still distinct from those of the lowland paralic basins, are more comparable to the similar aged intramontane Saar-Lorraine floras than was suggested previously. The apparent palaeofloristic difference between the Central and Western Bohemia and Saar-Lorraine floras seems to have been at least partly because the data for the former area included species from both ash deposits that representing peat substrate vegetation and roof shale floras representing clastic substrate vegetation. • Key words: Medullosan pteridosperms, Pennsylvanian, Radnice Member, Nýřany Member, Westphalian.

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The Central and Western Bohemian basins were part of an intramontane depositional area in the Variscan Orogen, in which localised peat-forming wetlands developed in a high-elevation setting (Pešek 1994, 2004). The exact elevation remains uncertain but modelling of the palaeogeomorphology and drainage patterns by Opluštil (2005) suggested that they may have been up to 1000 m above sea-level, at least during middle Westphalian times. We will, therefore, refer to them as upland wetlands *sensu* Thomas & Cleal (2017).

Abundant fossil floras in these deposits have attracted palaeobotanists since the early 19th century (*e.g.* Sternberg 1820–1838, Ettingshausen 1852, 1854) and are evidently the remains of vegetation broadly similar to that of the lowland paralic swamps of the Variscan foreland (*e.g.* Cleal 2018) but preserved in a higher-elevation, wetland setting. However, there are clear differences in the species present (Gothan 1915, 1951, 1954; Cleal 2008a, b) and it is now evident that these upland floras had an important influence on the overall dynamic evolution of the Euramerican peat swamp vegetation (Cleal 2008b, Cleal *et al.* 2009, Thomas & Cleal 2017, Šimůnek & Cleal 2018, Cleal & Cascales-

Miňana 2019). Since there is increasing evidence that plant diversity fluctuations in these swamps either caused or were caused by climate change (*e.g.* Cleal & Thomas 1999, 2005; Gastaldo *et al.* 1996; Pfefferkorn *et al.* 2008, 2017; Cleal *et al.* 2009, 2011) these vegetation dynamics are crucial for understanding the evolution of global life and environments at this time.

Some of the most diverse components of this swamp vegetation belonged to the Medullosales, an order of early gymnospermous seed-plants characterised by large, complex fronds, large ovules and a vascular system formed from a dissected stele. There have been several taxonomic studies on the foliage of these plants in the Central and Western Bohemian basins (Němejc 1936, 1949; Havlena 1953; Šimůnek 1988, 2004, 2007; Šimůnek & Cleal 2002, 2004, 2011, 2013) but there has been no synoptic analysis of the group as a whole. The aim of this paper is to present the first such analysis for the Middle Pennsylvanian-age Kladno Formation of the Central and Western Bohemian basins. We have included those taxa for which there is strong evidence of medullosalean affinities (*e.g.* *Neuropteris* Brongniart, *Alethopteris* Sternberg), as well as a few

whose affinities are less well-established but are usually linked with this order (*e.g. Havlenaea* Šimůnek & Cleal). We re-examine the relationship between these floras and those of the lowland areas of the Variscan foreland and of the other intramontane areas. Does this require the floristic model of Cleal (2008a, b) to be modified, and does it throw any new light on the dispersal patterns of these species and the palaeoecology of these important coal basins?

Through the rest of the paper, we will use the acronym CWBB for the Central and Western Bohemian basins. The term Variscan Euramerica refers to Variscan Orogen, and its associated foreland area and intramontane basins (Cleal 2008b). The chronostratigraphy used is what is widely referred to as the Heerlen regional scheme as summarised by Wagner (1974) (Fig. 1).

Geological background and localities

Pennsylvanian-age coal-bearing deposits occur in the Bohemian Massif in a series of coalfields, from west to east known as the Plzeň, Manětín, Kladno-Rakovník, Radnice, Žihle, and Mšeno-Roudnice basins (Pešek 2004) (Fig. 2). The Bohemian Massif was formed through crustal thickening and uplift as part of the Variscan Orogeny, and for a time was at elevations of 2–3 km above sea-level (Opluštil *et al.* 2013). However, subsequent gravitational collapse and erosion substantially lowered the elevation, and then normal and/or strike-slip faulting in late middle–late Westphalian times resulted in a complex depositional basin to form. During this initial time of sediment deposition, the area was probably at an elevation of up to *c.* 1,000 m above sea level (Opluštil 2005). The resulting lithosome consists of a range of alluvial deposits alternating with coals. The Westphalian–earliest Stephanian part of the sequence is assigned to the Kladno Formation, with two subdivisions, the Radnice and Nýřany members.

Radnice Member

The Radnice Member (*e.g.* Němejc 1953, Wagner 1977, Šimůnek *in* Pešek 2004, Opluštil *et al.* 2016) belongs to the *Paripteris linguaeifolia* Zone *sensu* Wagner (1984) and probably the lower (*Neuropteris semireticulata*) sub-zone *sensu* Cleal (1991) and Cleal & Thomas (1994). This indicates a late Duckmantian or early Bolsovian age (Opluštil *et al.* 2016). For the purposes of this analysis, eight fossiliferous units are recognised (Fig. 3, Tab. 1).

Roof shales in Plzeň coal group. – These stratigraphically lowest coals in the region are only locally developed, mainly in the Plzeň and Merklín basins. There are between

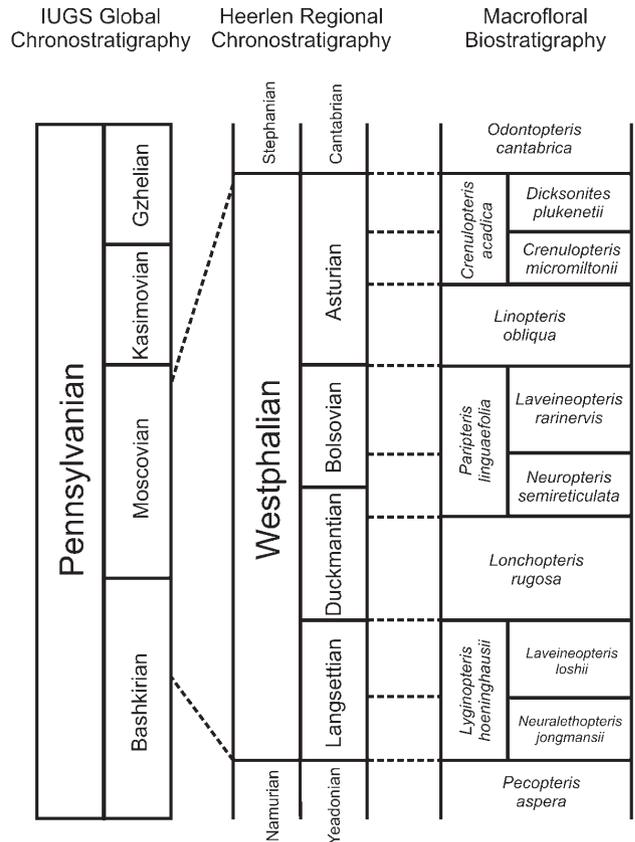


Figure 1. Summary of the Pennsylvanian stages in the IUGS Global Stratigraphic Scheme, the stages and substages in the Heerlen Regional Chronostratigraphy used in Europe (Wagner 1974), and the plant biozones developed by Wagner (1984) and modified by Cleal (1991). From Cleal & Cascales-Miñana (2019, fig. 2).

two to five coal seams in the group, whose roof shale yields mostly parautochthonous floras. Notable occurrences in the Plzeň Basin are in ironstone nodules at Bílá Hora and Blatnice, and shales at the Krimich I Mine (Nýřany-Pankrác), Merklín relic.

Whetstone Horizon (Bělka tuff). – The main coal reserves in the region are the Lower and Upper Radnice seams in the lower Radnice Member, up to 8 m and 14 m thick respectively (Pešek 1994). The two seams are separated by a 3–7 m thick tuffaceous deposits known as the Whetstone Horizon, which is found in all the coalfields in the CWBB where the Radnice coal group are mined.

The Whetstone Horizon normally consists of two layers. The lowermost layer (0.4–0.6 m thick) of yellow to white tuff known as Bělka represents a single volcanic ash fall that buried the landscape, and contains autochthonous remains of the peat substrate vegetation (Opluštil *et al.* 2007, 2009a, b, 2014); it has been dated at *c.* 314.3 Ma (Opluštil *et al.* 2016) and thus of late Duckmantian (= early Moscovian) age. The upper layer consists of

laminated tuffites and tuffaceous mudstones known as Brousek (Whetstone). This represents re-worked ash deposits (Opluštil *et al.* 2009a) containing a mixture of autochthonous remains of plants that were left protruding out of the ash deposits, parautochthonous remains caught up during the re-working of the ash, and allochthonous remains of extra-basinal vegetation.

The Whetstone Horizon has long been known as a classic source of plant fossils, especially from the Radnice Basin from where Sternberg (1821, 1823, 1825, 1833, 1838) described many specimens (notably from Svinná – see also Opluštil *et al.* 2007) and where there have been major recent excavations at Ovčín-Průvčice (Opluštil *et al.* 2009a, b, 2014). Other major palaeobotanical sites are the Stradonice locality in the Lísek relic (Ettingshausen 1852); and localities in the Plzeň Basin (Nýřany, Uxa mine, Blatnice, Marie and Prokop mines), Kladno-Rakovník Basin (Kladno, Prago III Mine), and the Malé Přílepy and Štílec relics (Opluštil *et al.* 2007).

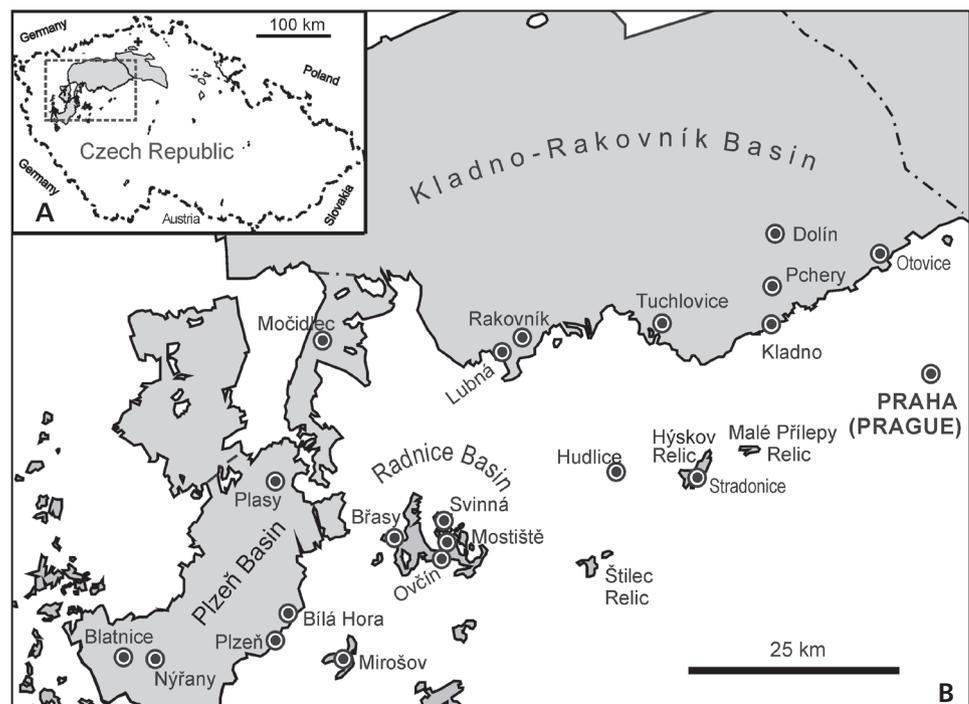
Tuffaceous intercalations (“Opuky”) in Upper Radnice Seam. – These are thinner volcanic layers within the Upper Radnice Seam found mainly near the southern margins of the Kladno-Rakovník and Radnice basins (Pešek 1994). There are seven “opuka” intercalations in the Kladno-Rakovník Basin, whereas the Radnice Basin has only four that tend to have lower ash content. One of the tuffaceous layers in the Kladno-Rakovník Basin has been dated at *c.* 313.8 Ma (Opluštil *et al.* 2016) and thus also of late Duckmantian (= early Moscovian) age. Macrofloras are especially well-

known from the Ronna and Schoeller mines near Kladno, and the František Mine at Otovice (Opluštil *et al.* 2007). The fossils described by Sternberg (1820, 1821, 1825, 1838) from Břasy in the Radnice Basin are also probably from this level and were included in the “Opuky” records.

Roof shale (“Mydláky”) of Upper Radnice Seam. – Wherever the Upper Radnice Seam has been worked, the roof shales have often yielded well-preserved parautochthonous floras (Pšenička & Opluštil 2011). Notable discoveries in the Radnice Basin were made at Mostiště and Vranovice (Sternberg 1820, 1821, 1825; Ettingshausen 1854). There have also been discoveries in the Plzeň and Kladno-Rakovník basins (in above mentioned mines), and in the Lísek and Merklín relics.

Tuff, tuffites and roof shales associated with Lubná coal group. – The upper Radnice Member containing the Lubná coals is separated from the Radnice coal group by a non-sequence and is regarded as somewhat younger (Opluštil *et al.* 2016). The coals contain a number of tuff and tuffite intercalations, the best developed being the Z-tuff within the Upper Lubná Seam; this tuff is rather coarse and includes some autochthonous remains. A number of the tuffs have been dated and tend to give ages of *c.* 312.4 Ma (Opluštil *et al.* 2016) and thus of early Bolsovian (= early Moscovian) age. Plant fossils are best known from the Kladno-Rakovník Basin (the Rako and Ludvík mines, and the Filip II quarry), where they occur in both the roof shales, and intra-seam tuffs and tuffites.

Figure 2. Map of West and Central Bohemia basin showing main areas mentioned in text. Redrawn from Opluštil *et al.* (2005).



Nýřany Member

This is quite different from the underlying Radnice Member, consisting of up to 450m of higher energy, braided fluvial deposits, with thinner, less persistent coal seams (Opluštil *et al.* 2005, Bashforth *et al.* 2011). The coals are best developed in the Plzeň and Kladno-Rakovník basins, although the sequences in these two areas are difficult to correlate (Opluštil *et al.* 2016). Nevertheless, three intervals with distinct macrofloras are generally recognised. Some evidence of autochthonous plant remains was reported by Bashforth *et al.* (2011) as *in situ* stems, but the medullosalean remains appear to be parautochthonous or allochthonous. The oldest is the Mirošov Horizon (Němejc 1938), which is partly conglomeratic, but also locally includes mudstones containing plant remains. This is separated by a non-sequence from the Touškov, Nýřany and Chotíkov coal groups, in which plant fossils are known from both the roof shales and inter-seam mudstones. These stratigraphically lower two floras of the Nýřany Member belong to the upper *Crenulopteris acadica* Zone (*sensu* Wittry *et al.* 2015 – formerly named the *Lobopteris vestita* Zone *sensu* Wagner 1984), which indicate a late Asturian age. Tuffs in the lower Nýřany Member interval have been dated at *c.* 308.0 Ma and *c.* 307.0 Ma (Opluštil *et al.* 2016) and thus of late Moscovian age.

The stratigraphically youngest part of the member includes the Nevřeň Group of coals. The floras here are essentially similar to those of the lower Nýřany Member, except for the presence of *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger (*e.g.* Šetlík 1977, Opluštil *et al.* 2016), which suggests the *Odontopteris cantabrica* Zone of Cantabrian age (Wagner 1984, Cleal *et al.* 2003). A tuff has in this interval been dated at 306.0 Ma (Opluštil *et al.* 2016), of early Kasimovian age.

Plant fossils were described from the Nýřany Member by Sternberg (1825, 1838), from Mirošov and Plasy near Plzeň. The floras from here were also reviewed by Ryba (1904) and Bashforth *et al.* (2011).

Methods

A comprehensive review was made of the literature recording medullosalean foliage remains from the CWBB. This was combined with data derived from collections in the Czech Geological Survey, Prague (CGS) and the National Museum, Prague (NMP). The data were collated and grouped based on their relative stratigraphical positions, and according to facies criteria, such as those found in roof shales above coal seams, and those found in various tuff and tuffite horizons.

The resulting binary, presence/absence were then integrated with the dataset used by Cleal (2008b) in his study

of medullosalean floristics of the various basins of Variscan Euramerica, which had been modified as described in the Discussion section of the paper (the revised data are provided as a supplementary file). The palaeofloristic analyses were carried out using the same numerical methods as in Cleal (2008a, b). The order of the basins in the matrix was adjusted following an unconstrained seriation analysis. They were then analysed by cluster analysis (using the Unweighted Pair-Group Average algorithm and Raup-Crick similarity indices) and ordination analysis (Detrended Correspondence Analysis – DCA). The significance of the taxonomic differences between some of the observed grouping was tested using non-parametric Multivariate Analysis of Variance (PERMANOVA – Anderson 2001, Anderson & Walsh 2013).

Taxonomic notes

The following is not intended as a complete systematic analysis but is an inventory with notes of the species that have been recognised in the Kladno Formation. In most cases the records are based on well-established published data, which are listed in the synonymy lists. These synonymy lists have been annotated using a system similar to that used in Cleal & Shute (1995): the first valid publication of the name as used here is marked “§”; the first valid publication of the basionym is marked “*”; and illustrated specimens from the CWBB are marked “¶”. If a species is being recorded with a “cf.”, the protologue will not be included in the quoted synonymy and so its author and date of publication will be given in the subheading for that species. Where possible, the species are placed in the suprageneric groups (fossil-families) as summarised by Cleal & Shute (2003).

Family Alethopteridaceae

Remarks. – This fossil-family comprises the fronds with a bifurcate-pinnate architecture *sensu* Laveine (1997) that have a major proximal bifurcation, but lack intercalated pinnae and cyclopterids.

Alethopteris distantinervosa Wagner

Figure 4A, B

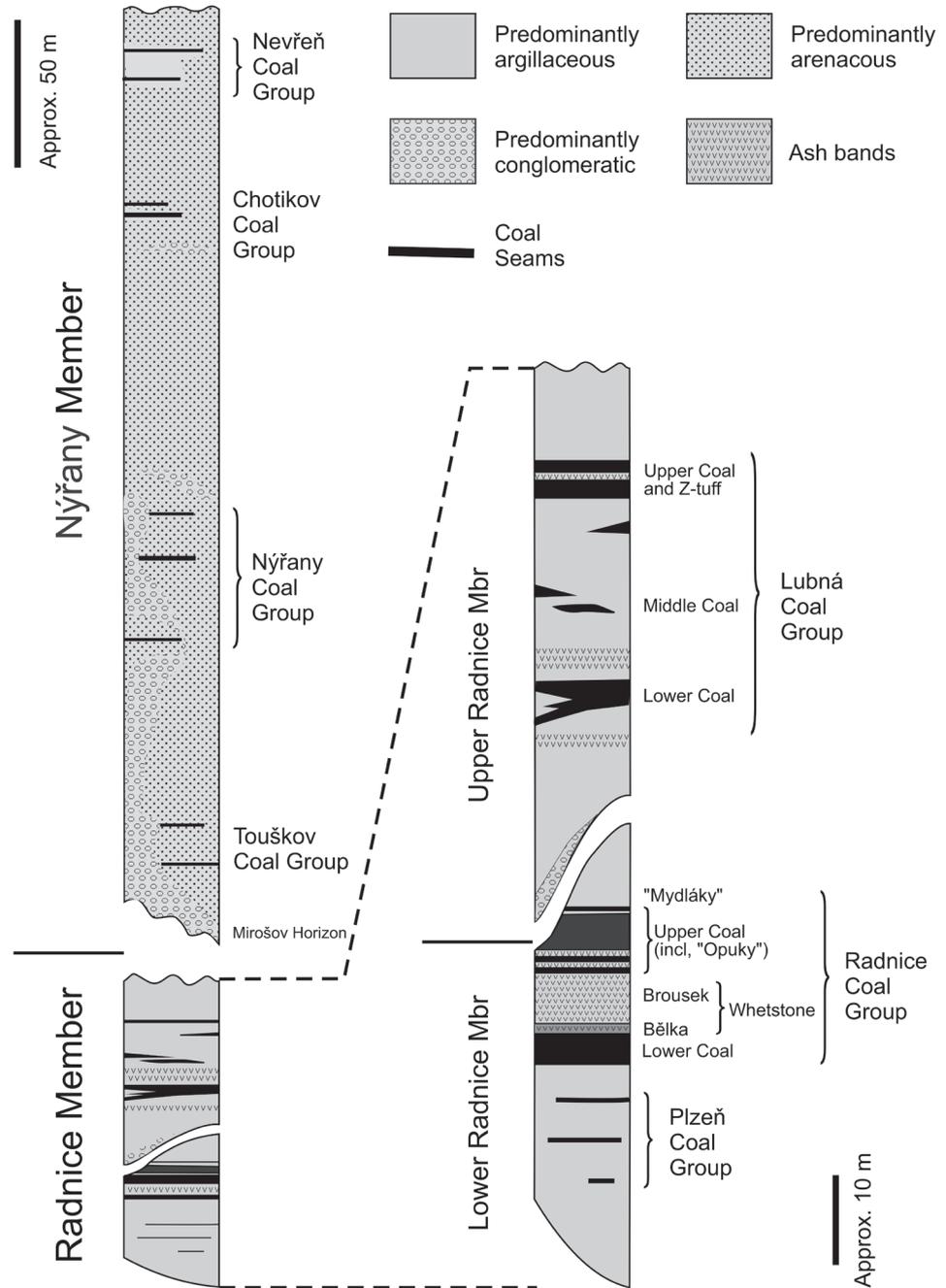
¶1936 *Alethopteris grandini* Brongniart. – Němejc (*non* Brongniart), pl. 2, fig. 3.

§1968 *Alethopteris distantinervosa*; Wagner, p. 61, text-fig. 12; pl. 16.

¶1977 *Alethopteris distantinervosa* Wagner. – Šetlík, pl. 3, fig. 2.

¶1988 *Alethopteris grandinioides* Kessler var. *distantinervosa* Wagner. – Šimůnek, text-figs 4–6; pls 3–6; pl. 7, figs 1–5.

Figure 3. Generalised lithostratigraphy of the Kladno Formation. Thicknesses vary considerably across the basin and those shown here are only intended to be indicative. Adapted and redrawn from Opluštil *et al.* (2005) and Šimůnek & Cleal (2011).



*2002 *Alethopteris distantinervosa* Wagner. – Šimůnek & Cleal, fig. 2.

*2007 *Alethopteris distantinervosa* Wagner. – Šimůnek, pl. 2, figs 1–5; pl. 5, fig. 1.

Remarks. – Although this species was originally described from fragments found in various middle Westphalian floras in Europe, it is best documented from the CWBB (Šimůnek & Cleal 2002). It is mainly known from the Radnice Member but has also been found near the base of the Mirošov Horizon in the Nýřany Member.

Alethopteris cf. pseudograndinioides Zodrow & Cleal, 1998

Figure 4G

*2018 *Alethopteris cf. pseudograndinioides* Zodrow & Cleal. – Šimůnek & Cleal, 2018, figs 1, 2.

Remarks. – This name was introduced for the species that had previously been illegitimately named *Alethopteris grandinioides* Wagner, 1968 *non* Kessler, 1916. The species mainly occurs in the upper Asturian and Cantab-

rian of the more lowland basins (e.g. Britain, northern Spain, Canadian Maritimes). The present record is based on a single specimen with cuticles, with epidermal structures very similar to that seen in the types of this species. However, this Kladno Formation specimen is stratigraphically rather older than the normally observed range of this species, in the *Crenulopteris acadica* and *Odontopteris cantabrica* zones (Wagner 1968).

***Alethopteris kettneri* Havlena**

Figure 5A, B

§1951 *Alethopteris kettneri*; Havlena, p. 499, pl. 1, figs 1, 2.

¶1988 *Alethopteris grandinioides* Kessler var. *kettneri* (Havlena). – Šimůnek, text-fig. 7; pl. 7, fig. 6; pl. 8.

Remarks. – As demonstrated by Šimůnek (1988) this belongs to the complex of species centred on what is now named *Alethopteris pseudograndinioides* (*A. grandinioides* auct.). However, it differs from the latter species in the veins being significantly more oblique to the pinnule margin and having a much lower vein density (18–22 veins per cm on the pinnule margin). It occurs in the Nýřany Member of the Plzeň Basin.

***Alethopteris lonchitica* Schlotheim ex Sternberg**

Figure 4C, D

1820 *Filicites lonchiticus*; Schlotheim, p. 411. [*nom. illegit.*]

§1825 *Alethopteris lonchitica*; Schlotheim ex Sternberg, p. 21.

¶1854 *Alethopteris Sternbergii* Goeppert. – Ettingshausen, pp. 42, 43, pl. 18, fig. 4.

¶1936 *Alethopteris lonchitifolia* P. Bertrand. – Němejc, pp. 14–17, text-fig. 9a, b.

¶2007 *Alethopteris lonchitica*; Opluštil *et al.* – Šimůnek, pl. 8, fig. 4.

¶2007 *Alethopteris lonchitica* Sternberg. – Šimůnek, p. 394, pl. 5, fig. 2.

Remarks. – We are using this name in the sense of Zodrow & Cleal (1998) for the species with relatively large pinnules and dense, non-flexuous veins found mainly in upper Westphalian and lower Stephanian floras of Euramerica; and not for the mainly lower Westphalian species that

Wagner & Álvarez-Vázquez (2008) showed to be more correctly named *Alethopteris urophylla* (Brongniart) Göppert. However, we have not followed the opinion of Wagner & Álvarez-Vázquez (2008) that the name *A. lonchitica* should be applied to the species traditionally called *Alethopteris ambigua* Lesquereux.

The specimens from the CWBB are mostly from the Radnice Member but a specimen is also known in the lower Nýřany Member. Cuticles described by Šimůnek (2007) showed epidermal structures very similar to those described by Barthel (1962) from the type region for *A. lonchitica* – Saar-Lorraine.

***Alethopteris cf. serlii* (Brongniart) Göppert, 1836**

Figure 4E, F

¶1936 *Alethopteris Serli* Brongniart. – Němejc, text-fig. 8; pl. 2, fig. 4.

¶2007 *Alethopteris serlii* (Brongniart) Göppert. – Šimůnek, pl. 2, fig. 9; pl. 5, fig. 4.

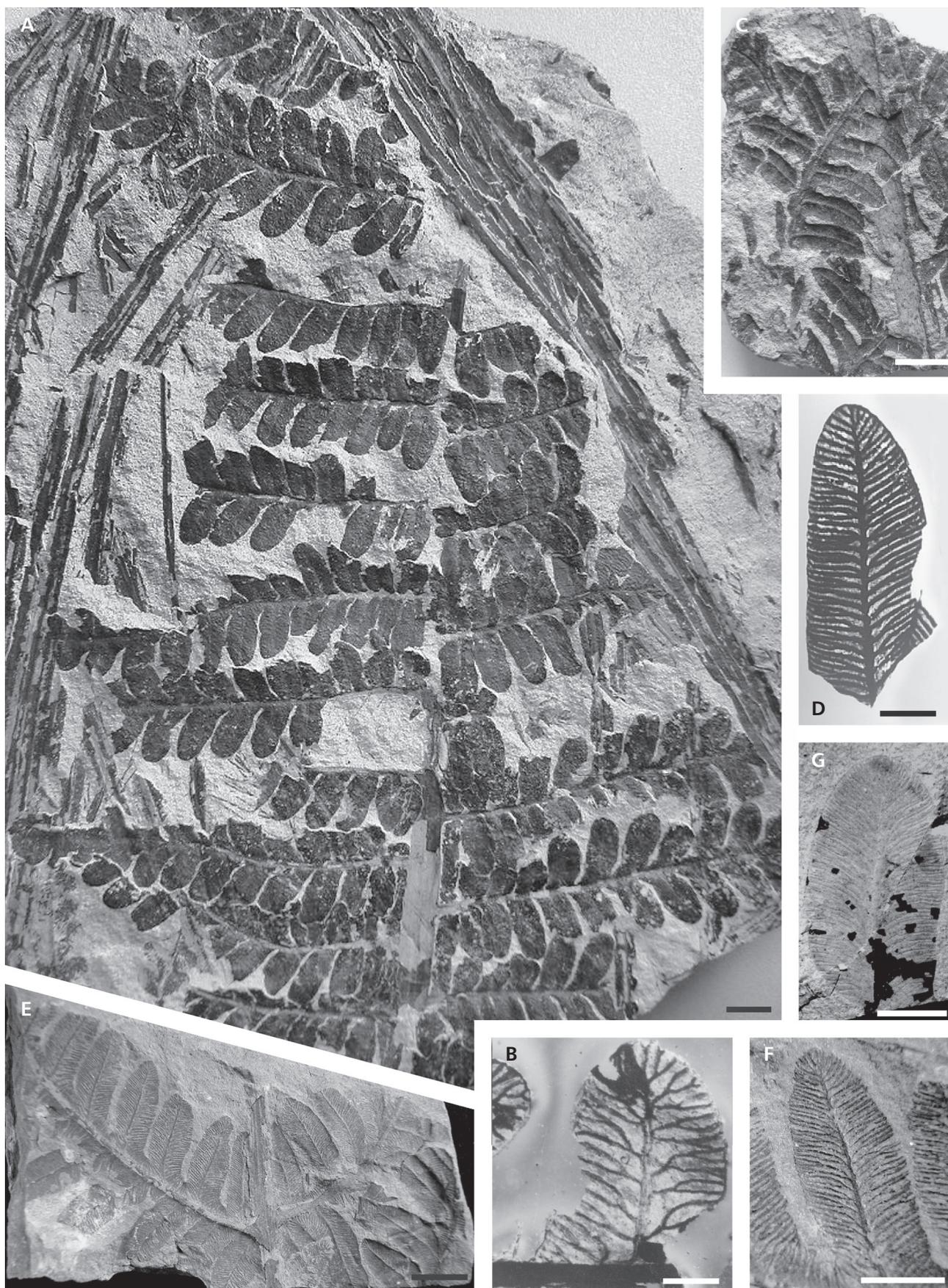
Remarks. – This species, which is normally characterised by relatively robust pinnules compared with most other *Alethopteris* species, and fine, often somewhat flexuous veins, usually occurs in upper Asturian to lower Cantabrian floras (see discussion in Zodrow & Cleal 1998). The pinnules from the CWBB assigned to *A. serlii* by Šimůnek (2007) were very similar in shape to the types of that species (e.g. Wagner 1968) and yielded cuticles very similar to those described by Zodrow & Cleal (1998) from the Sydney Coalfield. The only noticeable morphological difference was that the venation in the Bohemian specimens was not quite as flexuous, but this feature can be variable in *A. serlii*. This record is of interest as the rest of the associated flora suggests a rather older age than is normal seen for *A. serlii* (e.g. Zodrow & Cleal 1998) – the Radnice coal group, Bolsovian. For these reasons we have referred these specimens from Bohemia to *A. cf. serlii*.

***Alethopteris nemejcii* Wagner**

Figure 6A

¶1936 *Alethopteris valida* Boulay. – Němejc (*non* Boulay), text-fig. 7; pl. 1, fig. 2.

Figure 4. Medullosalean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A, B – *Alethopteris distantinervosa* Wagner; A – Kladno locality, Whetstone Horizon, (as *Alethopteris grandinioides* Kessler by Šimůnek, 1988, pl. 3, fig. 1, Pchery locality, Theodor Mine, coll. CGS, No. ZŠ 850); B –, macerated isolated pinnule with venation, Ovčín near Radnice locality, Whetstone Horizon. • C, D – *Alethopteris lonchitica* Schlotheim ex Sternberg; C – Radnice locality, Matylda Mine, Whetstone Horizon (coll. CGS, No. ZŠ 848); D – pinnule fragment with venation, Whetstone Horizon, Kladno locality, Prago III Mine. • E, F – *Alethopteris cf. serlii* (Brongniart) Göppert, Břasy near Radnice locality, Mr. Stárek’s quarry, Radnice Member, National Museum Prague, No. E 7634. • G – *Alethopteris cf. pseudograndinioides* Zodrow et Cleal, Lubná near Rakovník, Filip II Quarry, Radnice Member, Lubná Group of coals, Kladno-Rakovník Basin, Bolsovian. No. ZŠ 793b (photo: Šimůnek & Cleal 2018, pl. 1, fig. 2). Scale bars: A, C, E = 1 cm; B, D = 2 mm; and F, G = 5 mm.



§1968 *Alethopteris nemejcii*; Wagner, p. 111, text-fig. 32; pl. 41, figs 119–122.

†2007 *Alethopteris nemejcii* Wagner. – Šimůnek, pl. 2, figs 10–12; pl. 5, fig. 3.

Remarks. – This species was based on specimens from the CWBB that were originally identified as *A. valida*, but which had more triangular pinnules and denser veins. Some of the cuticles described by Šimůnek (2007) originated from the same locality that yielded the holotype of this species – Kamenný Újezd, Lazarus mine. This species occur in the Radnice Member (Duckmantian) at many localities in the Plzeň Basin and Merklín relic.

***Lonchopteris rugosa* Brongniart**

Figure 6B

§1836 *Lonchopteris rugosa*; Brongniart, p. 368.

†1876 *Lonchopteris rugosa* Brongniart. – Feistmantel, pl. 67, figs 7, 8.

†2007 *Lonchopteris rugosa* Brongniart. – Šimůnek, pl. 3, fig. 1; pl. 5, fig. 5.

Remarks. – Alethopteroid pinnules with anastomosed veining are widespread but generally rarer than true *Alethopteris*. As with most alethopteroids, the pinnules show considerable morphological variation resulting in several species having been recognised. However, Buisine (1961) has shown that venation is a more reliable taxonomic character, and that most fronds with relatively isodiametric vein meshes such as those from CWBB belong to *L. rugosa*. There is also an unillustrated record from near Plzeň by Němejc (1941, p. 213) of *Lonchopteris chandesrisii* Bertrand, 1932, a species with more elongate vein meshes, but which has otherwise only been recorded Saar-Lorraine (e.g. Bertrand 1932). This record may have been based on a poorly preserved specimen in his collection that was labelled as this species, and which originated from the Whetstone Horizon at Svinná. However, this specimen does not show the venation clearly enough to verify the identification. *Lonchopteris rugosa* is not very common in CWBB. It occurs in the Radnice Member of the Plzeň and Radnice Basin, but famous are samples from the Whetstone Horizon (Brousek) of the Stradonice locality, Hýskov relic.

Family Neurodontopteridaceae

Remarks. – This fossil-family comprises fronds with a bifurcate semi-pinnate architecture *sensu* Laveine (1997) that have a major proximal bifurcation and intercalated pinnae on the primary rachis branches. The proximal part of the frond lacks true cyclopterids, although there may be fused pinnae in this part of the frond (sometimes referred to as forma *impar* pinnae *sensu* Shute & Cleal 2002).

Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al. Figure 7A

*1827 *Neuropteris Scheuchzeri*; Hoffmann, p. 157, pl. 1b, figs 1–4.

†1854 *Neuropteris acutifolia* Brongniart. – Ettingshausen, pl. 18, fig. 5.

†1953 *Neuropteris Scheuchzeri* Hoffmann. – Havlena, pl. 7, fig. 2; pl. 8, figs 4, 5.

§1990 *Macroneuropteris scheuchzeri* (Hoffmann). – Cleal *et al.*, p. 488.

†2007 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* – Šimůnek, pl. 4, figs 5–8; pl. 5, fig. 8.

†2011 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* – Šimůnek & Cleal, pls 18, 19; pl. 21, fig. 1.

Remarks. – Isolated, large pinnules with strongly marked epidermal hairs occur frequently in many upper Westphalian and lower Stephanian floras of Europe, but there were few records in the early literature on the CWBB palaeobotany. However, Havlena (1953) figured specimens from the Radnice Member, which he compared with the var. *nordfrancia* of Bertrand (1930). He also recorded but did not figure it from the Nýřany Member.

The specimen figured as *N. acutifolia* by Ettingshausen (1854) was transferred to *N. plicata* by Havlena (1953). However, this specimen with several large acute pinnules is from the Mostitz (Mostiště) locality in the Radnice Basin, where only the Radnice Member occurs. In our view, this specimen is more likely to belong to *Macroneuropteris scheuchzeri*.

***Neuropteris plicata* Sternberg**

Figure 6E

§1825 *Neuropteris plicata*; Sternberg, p. 14 (tent.).

†1833 *Neuropteris plicata* Sternberg. – Sternberg, pl. 19, figs 1, 3.

†1833 *Neuropteris acutifolia* Sternberg. – Sternberg, pl. 19, fig. 4.

†1833 *Neuropteris obovata* Sternberg. – Sternberg, pl. 19, fig. 2.

†1904 *Neuropteris planchardii* (Zeiller). – Ryba (*non* Zeiller), pl. 15, fig. 3.

? †1904 *Neuropteris obliqua* (Brongniart). – Ryba (*non* Zeiller), pl. 16, fig. 2.

†1922 *Neuropteris plicata* Sternberg. – Šetlík, figs 1–3.

†1949 *Mixoneura plicata* (Sternberg). – Němejc, pl. 5, figs 1–5.

†1949 *Mixoneura britannica* (Gutbier) Zeiller. – Němejc (*non* Gutbier), pl. 4, figs 8–14.

†1994 *Neuropteris plicata* Sternberg. – Šimůnek, pl. 3, fig. 3.

†2011 *Neuropteris plicata* Sternberg. – Bashforth *et al.*, pl. 3, fig. 1.

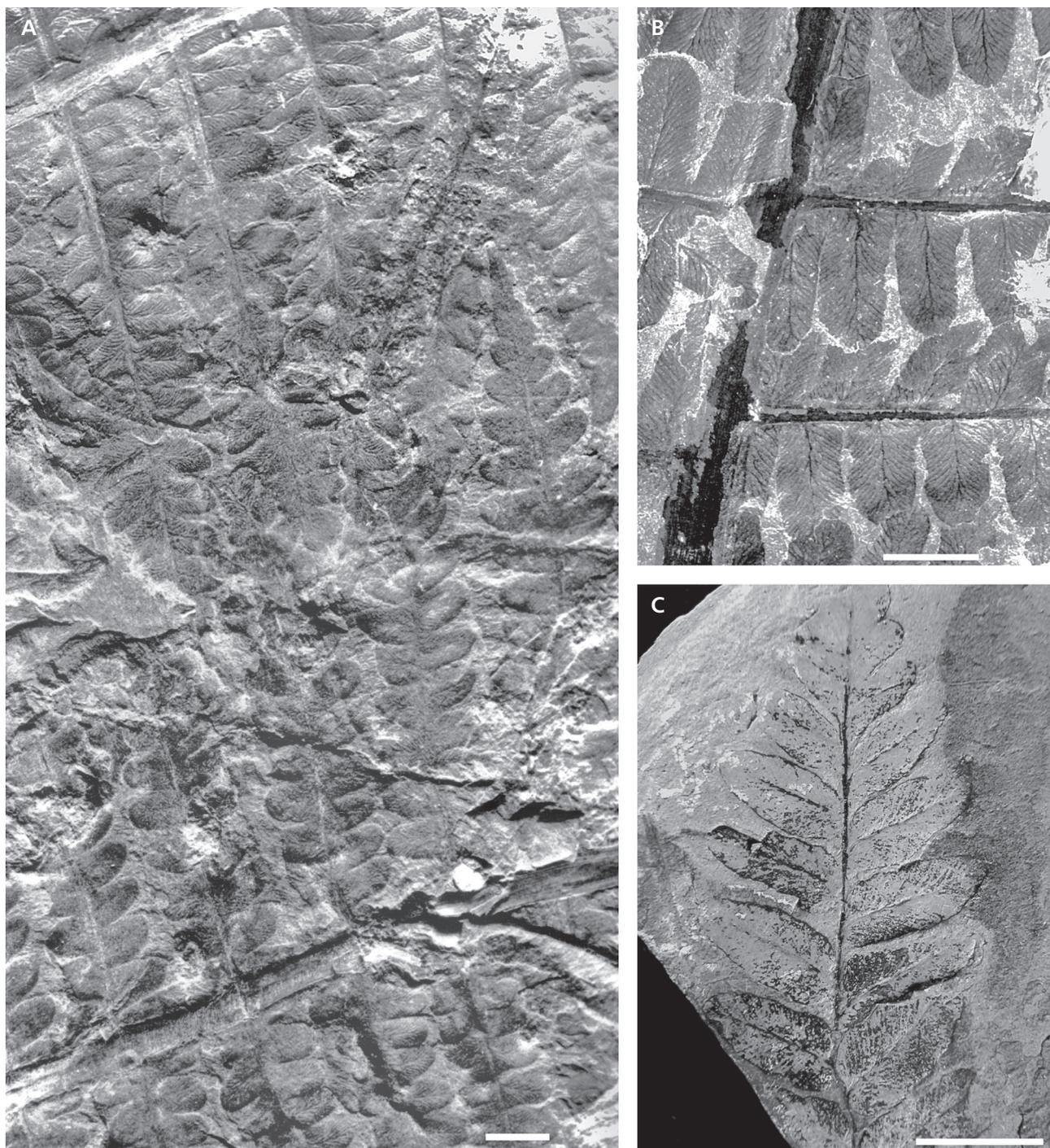


Figure 5. Medullosalean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A, B – *Alethopteris kettneri* Havlena, Nýřany locality, Křimich I Mine, Plzeň Basin, Nýřany coal group, Asturian, (Havlena 1951, pl. 1, figs 1, 2; Šimůnek 1988, pls 7, 8, fig. 6); B – coll. Dept. of Palaeontology, Fac. of Sciences, Charles University, Prague. • C – *Havlenaea coriacea* (Ettingshausen) Šimůnek & Cleal, Radnice Member, Stradonice (NMP E 4152, Barrande coll.). Scale bars = 1 cm.

*2011 *Neuropteris planchardii* Zeiller. – Bashforth *et al.* (non Zeiller), pl. 2, fig. 14.

Remarks. – The variation in *N. plicata* and the resulting confusion in early taxonomic studies was discussed by

Šetlík (1922). Němejc (1949) later transferred the species to *Mixoneura* in the sense of Bertrand (1930), for the group of species allied to *Neuropteris ovata* Hoffmann, but Laveine & Legrand (2019) have shown this to be an invalid use of the generic name; it should more correctly

be retained in *Neuropteris* (e.g. see Cleal & Shute 1995). Ryba (1904) described pinnae from the Nýřany Member as *N. planchardii* but that species is normally found in middle Stephanian floras. The illustration is rather unclear but the shape of the pinnules resembles *N. plicata*, which is well documented from these floras.

Němejc (1949) suggested that the specimens he assigned to *M. britannica* are very similar to *Neuropteris plicata* except that the vein density is much lower. However, the vein density of Němejc's specimens (40–50 veins per cm on pinnule margin) fall within the normally accepted range of this group of neuropterids (Saltzwedel 1969). The specimen figured as *N. obliqua* by Ryba (1904) is indeterminate but has a pinnule shape similar to *N. plicata*.

There is ongoing uncertainty as to the taxonomic position of this species relative to *Neuropteris ovata* Hoffmann, 1827, which has very similar shaped pinnules and venation to *N. plicata* (e.g. Saltzwedel, 1969). If these two species names did prove to be synonyms then Sternberg's would take precedence over the much more widely used *N. ovata*. However, the latter species is being increasingly circumscribed by cuticular data (e.g. Barthel 1962, Cleal & Zodrow 1989, D'Angelo & Zodrow 2016, Šimůnek & Cleal 2016) which is impossible to obtain from the types of *N. plicata*, which are impressions. For the purposes of this study we have therefore maintained the two species as separate, although the possibility of their synonymy was considered in the floristic analysis discussed later.

***Odontopteris reichiana* Gutbier**

Figure 8D, E

- §1835 *Odontopteris reichiana*; Gutbier, p. 65
- †1949 *Odontopteris reichiana* Gutbier. – Němejc, pl. 1, fig. 9; pl. 2, fig. 5.
- †2011 *Odontopteris reichiana* Gutbier. – Bashforth *et al.*, pl. 2, fig. 13.

Remarks. – The relatively small fronds of *Odontopteris* usually appear first at about the Westphalian–Stephanian boundary. Several species have been recognised, and their taxonomy has been reviewed by Šimůnek & Cleal (2004) based on their pinnule morphology and epidermal structure. The only recorded specimens of *O. reichiana* from CWBB were figured by Němejc (1949) and Bashforth *et al.* (2011), and it has been impossible to obtain cuticles from them. Nevertheless, they are morphologically very similar to the types of this species from Zwickau. Laveine & Oudoire (2016) have argued that this species is conspecific with *Odontopteris brardii* Brongniart but for the reasons explained by Šimůnek & Cleal (2004) we have maintained them as separate. *Odontopteris reichiana* is relatively rare species in the Nýřany Member of the CWBB.

Family Cyclopteridaceae

Remarks. – This fossil-family comprises fronds with a bifurcate semi-pinnate architecture *sensu* Laveine (1997) that have a major proximal bifurcation and intercalated pinnae on the primary rachis branches. Unlike the Neurodopteridaceae, however, they have true cyclopterids in the proximal part of the frond.

Callipteridium rubescens* (Presl ex Sternberg) Wagner ex Bashforth *et al.

Figure 7C

- *1838 *Neuropteris rubescens*; Presl ex Sternberg, p. 136, pl. 50, fig. 1b.
- †1904 *Alethopteris (Asterotheca) subdavreuxii* (Sterzel). – Ryba (*non* Sterzel), pl. 15, fig. 2.
- †1929 *Alethopteris rubescens* (Sternberg). – Němejc, pl. 1, figs 6–8.
- †1931 *Alethopteris rubescens* (Sternberg). – Němejc, pl. 1, fig. 1.
- †1936 *Alethopteris rubescens* (Sternberg). – Němejc, text-fig. 4; pl. 2, figs 1, 2.
- §1963 *Callipteridium rubescens* (Sternberg). – Wagner, p. 721.
- †1977 *Praecallipteridium rubescens* (Sternberg). – Šetlík, pl. 8, fig. 1.
- †2011 *Callipteridium rubescens* (Presl in Sternberg) Wagner. – Bashforth *et al.*, pl. 2, fig. 7.

Remarks. – The type of this name is from Plasy, near Plzeň, and has been refigured by Němejc (1929, pl. 1, fig. 6) and Kvaček & Straková (1997, pl. 42, fig. 2b). Němejc (1929) showed that this species has nothing to do with *Neuropteris* and Wagner (1963) suggested that it should be transferred to *Callipteridium*. Němejc (1931) later described ovules associated with this species.

This species is very similar to *Callipteridium jongmansii* (Bertrand) Wagner, 1962, which has been extensively recorded from the upper Asturian of Europe (e.g. Bertrand 1932, Wagner 1966, Laveine *et al.* 1977). It has been suggested that the names are conspecific (A. Bashforth, personal communication 2007) but the problem has yet to be the subject of a detailed published taxonomic analysis. This species is very common in the Nýřany Member of the CWBB.

***Callipteridium armasii* (Zeiller) Wagner**

Figure 9A

- †2008 *Callipteridium* cf. *armasii* (Zeiller) Wagner. – Šimůnek, fig. 16.4.

Remarks. – This record from the Nevřeň coal group of the Nýřany Member is based on specimens with smaller pin-

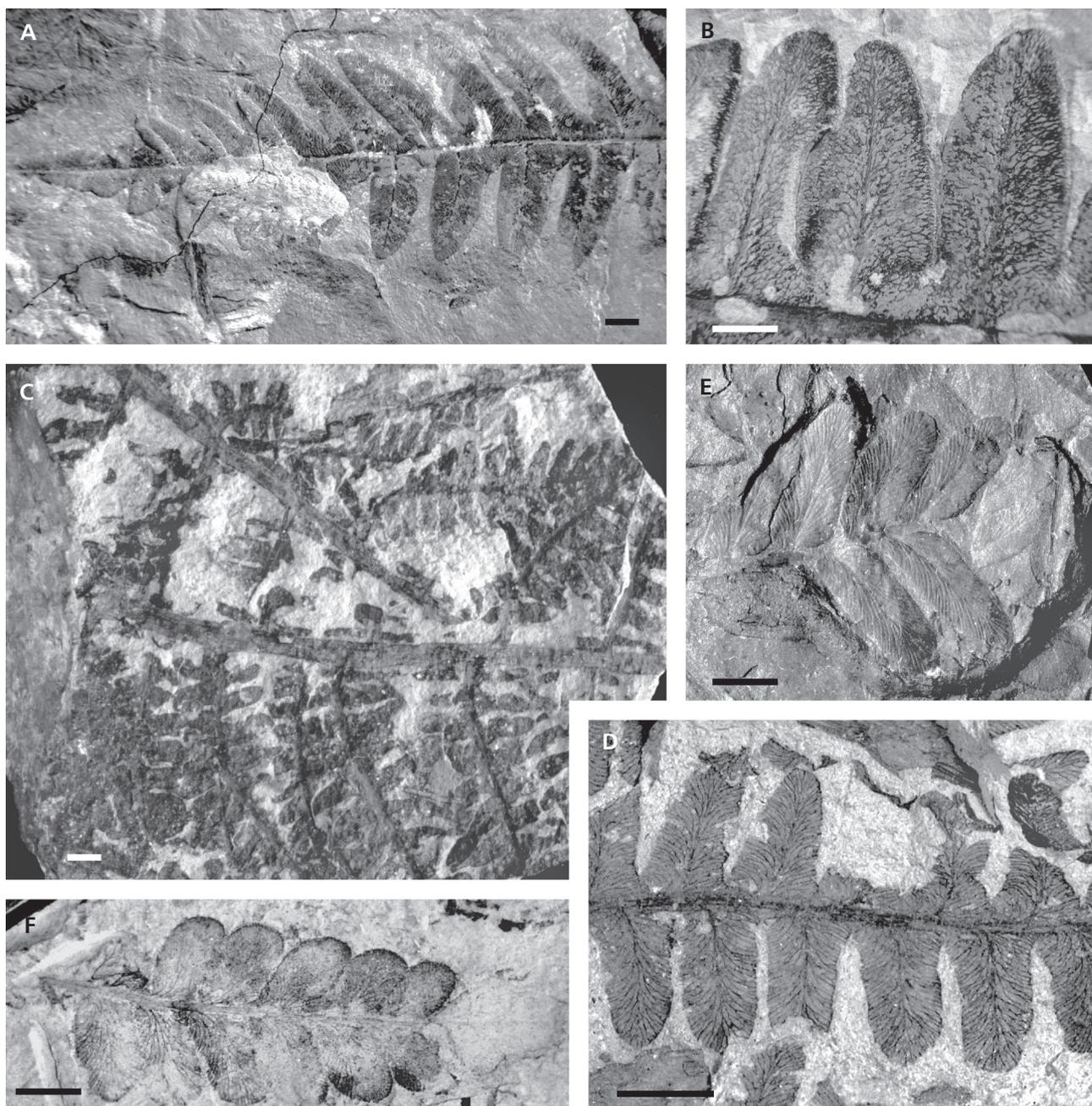


Figure 6. Medullosalean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A – *Alethopteris nemejcii* Wagner, Radnice Member, Nýřany locality, Krimich Mine, coal seam 3, NMP, No. E 7633. • B – *Lonchopteris rugosa* Brongniart, Radnice Member, Nýřany locality, Krimich Mine, coal seam 3, NMP, No. E 1250. • C, D – *Palaeoweichselia defrancei* (Brongniart) Potonié & Gothan, Whetstone Horizon, Malé Přilepy relic, NMP No. E 1302. • E – *Laveineopteris hollandica* (Stockmans) Cleal & Shute, Radnice Member, Dolin locality, D1 1 borehole, 1099, 3–1100 m, Kladno-Rakovník Basin, CGS, No. JŠ 179. • F – *Neuropteris plicata* Sternberg (previously identified as *Mixoneura britannica* (Gutbier) Zeiller), Nýřany Member, Rakovník-Šatotka locality, Moritz Mine, Kladno-Rakovník Basin, NMP, No. E 6055. All scale bars = 5 mm.

nules and less dense venation than *C. rubescens*. Laveine *et al.* (1977) suggested that this species might be the same as *C. jongmansii* and the pinnule morphotypes that characterise the two species are often found together. However, Laveine *et al.* (1977) provisionally maintained the distinction until a more complete analysis could be undertaken, a view with which we agree.

Laveineopteris loshii* (Brongniart) Cleal *et al.
Figure 7B, D

*1831 *Neuropteris Loshi*; Brongniart, p. 242, pl. 72, fig. 1; pl. 73.

†1953 *Neuropteris heterophylla* Brongniart. – Havlena (*non* Brongniart), pl. 3, fig. 2 (*non* fig. 1 – to *Laveineopteris tenuifolia*).

- §1990 *Laveineopteris loshii* (Brongniart). – Cleal *et al.*, p. 490.
- *2009a *Laveineopteris loshii* (Brongniart) Cleal *et al.* – Opluštil *et al.*, pl. 7, figs 7, 8.
- *2009b *Laveineopteris loshii* (Brongniart) Cleal *et al.* – Opluštil *et al.*, fig. 8g.
- *2007 *Laveineopteris loshii* (Brongniart) Cleal *et al.* – Šimůnek, pl. 3, figs 2–8; pl. 5, fig. 6.
- *2011 *Laveineopteris loshii* (Brongniart) Cleal *et al.* – Šimůnek & Cleal, pls 5–7.
- *2014 *Laveineopteris loshii* (Brongniart) Cleal *et al.* – Opluštil *et al.*, fig. 16a.

Remarks. – This species, often historically misidentified as *Neuropteris heterophylla* (Brongniart) Brongniart (as discussed by Laveine 1967), is extremely abundant in many floras from the Langsettian to Bolsovian of the paralic basins of Europe (Cleal & Shute 1995, 2003). It is less widespread in the CWBB, occurring mainly in the Whetstone Horizon tuffs. Feistmantel (1876) recorded it from Břasy (“Bras”) which is normally associated with an “Opuky” tuffaceous intercalation in the Upper Radnice Seam. However, Havlena (1953) expressed some doubt as to this record, as this species is more typically found in the lower Bělka part of the Whetstone Horizon and only rarely in the roof shales of the Upper Radnice Seam.

Laveineopteris tenuifolia* (Schlotheim ex Sternberg) Cleal *et al.*, *nom. cons.

Figure 9E

- 1820 *Filicites tenuifolius*; Schlotheim, p. 405, pl. 22, fig. 1. [*nom. illeg.*]
- *1825 *Neuropteris tenuifolia* (Schlotheim); Sternberg, p. 17. [*nom. cons.*]
- ?*1874 *Cyclopteris orbicularis* Brongniart. – Feistmantel, pl. 67, figs 2, 3.
- *1953 *Neuropteris tenuifolia* (Schlotheim). – Havlena, pl. 3, figs 3–6; pl. 6, fig. 3; pl. 7, figs 3, 4.
- *1953 *Neuropteris heterophylla* Brongniart. – Havlena (*non* Brongniart), pl. 3, fig. 1.
- §1990 *Laveineopteris tenuifolia* (Sternberg). – Cleal *et al.*, p. 490.
- *2007 *Laveineopteris tenuifolia* (Sternberg) Cleal *et al.* – Šimůnek, pl. 3, figs 9, 10; pl. 5, fig. 7.
- *2011 *Laveineopteris tenuifolia* (Schlotheim ex Sternberg) Cleal *et al.* – Šimůnek & Cleal, pls 8–12.

Remarks. – This species, which is differentiated from *L. loshii* mainly by having more elongate pinnules, is also widespread in the Langsettian to Bolsovian floras of the paralic coal basins, but in the CWBB, appears to be restricted to the roof shales of the Radnice Member. Ettingshausen (1854, p. 34) recorded *Cyclopteris orbicularis* Brongniart from the roof shales of the Radnice Seam (Mostišť locality), which may belong to this species.

***Laveineopteris bohemica* (Ettingshausen) Šimůnek**
Figure 9B, C

- *1854 *Neuropteris bohemica*; Ettingshausen, p. 34, pl. 13, fig. 1.
- *1854 *Neuropteris rubescens* Sternberg. – Ettingshausen (*non* Sternberg), pl. 14, figs 4, 5.
- *1929 *Neuropteris bohemica* Ettingshausen. – Němejc, pl. 1, fig. 9; pl. 2.
- *1953 *Neuropteris attenuata* Lindley and Hutton. – Havlena (*non* Lindley & Hutton), pl. 1, figs 1–5; pl. 2, figs 1–3.
- *2011 *Laveineopteris bohemica* (Ettingshausen) Šimůnek. – Šimůnek & Cleal, pls 13–15.
- *2013 *Laveineopteris bohemica* (Ettingshausen) Cleal *et al.* – Šimůnek & Cleal, figs 1–3.

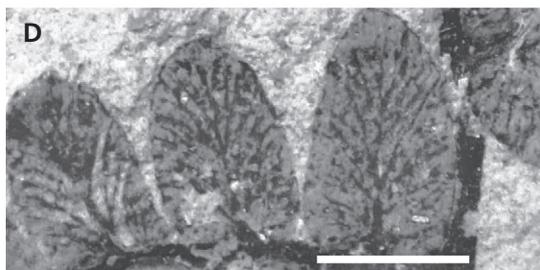
Remarks. – This species is similar to *Laveineopteris rarinervis* (Bunbury) Cleal *et al.* found abundantly in the upper Westphalian of the lowland basins of Western Europe and North America, but is distinguished by its thinner and less widely forking veins, and different epidermal structure (Šimůnek & Cleal 2011). It is conspecific with the specimens named *Neuropteris nicolausiana* Gothan from Upper Silesia (Gothan 1913) and *Neuropteris nikolausii* Gothan from Saar-Lorraine (Bertrand 1930), and appears to be a species characteristic of more upland wetland habitats.

The attribution of the specimens from the Radnice Member figured by Ettingshausen (1854) as *N. rubescens* to *L. bohemica* is based on the comments by Němejc (1929, p. 5; see also Gothan 1913, p. 213 and Havlena 1953). Němejc (1929) also figured cyclopterids and possible ovules associated with this species. *L. bohemica* is relatively common in the Radnice Member of the CWBB.

***Laveineopteris lubnensis* (Havlena) Šimůnek & Cleal**
Figure 4D

- *1953 *Neuropteris lubnensis*; Havlena, p. 58, pl. 6, figs 1, 2.
- §2011 *Laveineopteris lubnensis* (Havlena). – Šimůnek & Cleal, pls 16, 17.

Figure 7. Medullosalean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A – *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* Tlustice, Na Štilci locality, Whetstone Horizon, National Museum Akc. No. p 1635. • B, D – *Laveineopteris loshii* (Brongniart) Cleal *et al.*, Ovčín near Radnice, Whetstone Horizon. coll. West Bohemian Museum Pilsen. • C – *Callipteridium rubescens* (Presl ex Sternberg) Wagner ex Bashforth *et al.*, Močidlec (Sauberg) locality, Žihle Basin, Nýřany Member, Asturian (coll. CGS, No. ZŠ 851). Scale bars: A, B = 1 cm; C, D = 5 mm.



Remarks. – This species appears to be endemic to the tuffs and tuffites associated with the Lubná coals. Its attribution to *Laveineopteris* was based on the cuticles, which resemble those of *L. loshii* and *L. tenuifolia* described from both the CWBB (Šimůnek & Cleal 2011) and elsewhere (Barthel 1962; Cleal & Shute 1992, 1995, 2003, 2012).

***Laveineopteris hollandica* (Stockmans) Cleal & Shute**
Figure 6D

- *1933 *Neuropteris hollandica*; Stockmans, p. 31, pl. 10, fig. 1.
- †1977 *Neuropteris hollandica* Stockmans. – Šetlík, pl. 3, fig. 1.
- §1995 *Laveineopteris hollandica* (Stockmans). – Cleal & Shute, p. 20.

Remarks. – This species is similar to *L. tenuifolia* but has finer and more oblique veins. It is rare in the CWBB but Šetlík (1977, pl. 3, fig. 1) illustrated it from above the Upper Radnice Seam. It was also identified by R.H. Wagner (personal communication 2006) from the Ovčín-Přivětice excavation of the Bělka tuff.

***Palaeoweichselia defrancei* (Brongniart) Potonié & Gothan**
Figure 6C, F

- *1834 *Pecopteris defrancei*; Brongniart, p. 325.
- §1909 *Palaeoweichselia defrancei* (Brongniart). – Potonié & Gothan in Potonié, part 116.

Remarks. – There are no published reports of this species from the CWBB, but there are eight specimens in the National Museum (Prague) from the Whetstone Horizon (Bělka layer) at Malé Přílepy, which are very similar. In the absence of previous records from these coal basins, we give the following brief description.

The most complete specimen is part of an antepenultimate pinna with main rachis 7 mm wide, bearing pairs of subopposite penultimate rachises at *c.* 70 mm intervals. Also present are shorter intercalated monopinnate segments spaced *c.* 18 mm apart, up to *c.* 35 mm long with oppositely arranged subtriangular, broadly attached pinnules up to 9 mm long. Penultimate rachises 4–6 mm wide bearing alternately to suboppositely-arranged ultimate rachises at 15–20 mm intervals. Ultimate rachises obtusely attached (70–90°), mostly straight but in some cases they curve in their proximal part.

Ultimate axes bear alternately or suboppositely arranged lateral pinnules at intervals of 3–4 mm, as well as an elongate, tapered apical pinnules. Pinnule attachment varies from 70° to 90°, tending to become more acute in the distal part of pinna. Pinnules linguaeform to subtriangular with round apex, broadly attached to rachis and adjacent pinnules often narrowly confluent. Basally decurrent mid-

vein runs along $\frac{2}{3}$ – $\frac{3}{4}$ the pinnule length, reducing to $\frac{1}{4}$ pinnule length in most distal part of pinna. Broadly arched lateral veins, sometimes somewhat flexuous (although it is difficult to be sure this is not taphonomic) but no sign of pseudo-anastomosing, twice occasionally three-times forked, meeting pinnules margin at *c.* 60°.

The specimens compare closely with examples from Saar-Lorraine, the type area for this species (*e.g.* Bertrand 1932, pls 48–53; Laveine 1989, pls 31, 32); they all have somewhat tapered, often oblique pinnules and flexuous veins. Although it is more characteristic of somewhat younger (late Bolssovian to early Asturian) floras in Saar-Lorraine (Bertrand 1932) it also occasionally ranges into lower Bolssovian strata (Laveine 1989, Laveine & Goubet 1995) and so overlaps with its occurrence in the Radnice Member. According to Laveine *et al.* (1977) and Laveine & Goubet (1995) this species may be related to *Callipteridium* and so it is assigned here to the Cyclopteridaceae. In the CWBB, this species is practically known only from the Whetstone Horizon (Bělka) of the Malé Přílepy relic.

Family Parispermaceae

Remarks. – This fossil-family comprises fronds with a pseudo-pinnate architecture *sensu* Laveine (1997) that lacks a major proximal bifurcation and has intercalated pinnules on all orders of rachises. The pinnae are also characterised by being paripinnate (*i.e.* terminated by a pair of terminal pinnules) rather than imparipinnate as with the other medullolean fronds.

***Linopteris neuropteroides* (Gutbier) Potonié**
Figure 9G

- *1855 *Dictyopteris neuropteroides*; Gutbier in Geinitz, p. 23.
- §1899 *Linopteris neuropteroides* (Gutbier). – Potonié, p. 154.
- †2007 *Linopteris neuropteroides* Gutbier. – Šimůnek, pl. 4, figs 10–13; pl. 5, figs 10, 11.
- †2011 *Linopteris neuropteroides* Gutbier. – Bashforth *et al.*, pl. 2, fig. 8.

Remarks. – This widespread species is characterised by relatively large, often somewhat subfalcate pinnules and dense, elongate veins meshes. Two subspecific taxa (usually designated as forma) can be recognised: *Linopteris neuropteroides* (Gutbier) Potonié forma *neuropteroides* (referred to by Potonié 1904 as forma *major*) with larger pinnules and *Linopteris neuropteroides* forma *minor* Potonié, 1904 with consistently smaller pinnules. There are still some nomenclatural problems surrounding these taxa but for this study we continue to use these forma names. The forma *neuropteroides* occurs in the Radnice and Nýřany members, but both formas occur in the Nýřany Member.

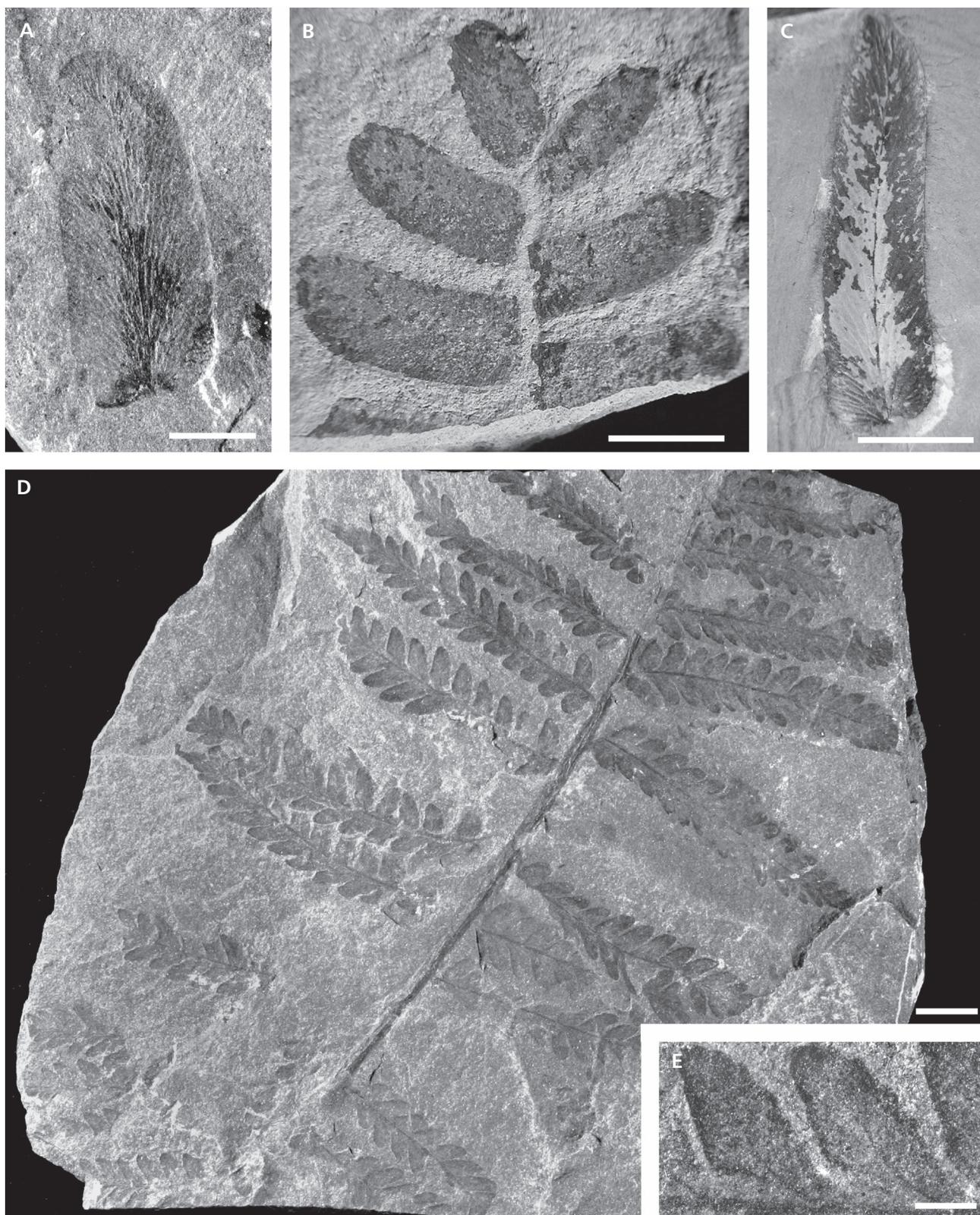


Figure 8. Medullosalean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A – *Linopteris obliqua* (Bunbury) Zeiller, Nýřany Member, Skvrňany locality, Šn 13 borehole, wedge 309.2–309.5 m, Plzeň Basin, No. ZŠ 849. • B – *Paripteris linguaeifolia* (Bertrand) Josten, Radnice Member, Lubná group of coals, Rakovník locality, Rako mine. Kladno-Rakovník Basin, NMP No. E 7635. • C – “*Mixoneura*” *muensterifolia* Němejc, Pejpina u Hudlic locality, Hýskov relic, Radnice Member, No. E 6011. • D, E – *Odontopteris reichiana* Gutbier. Nýřany Member, Mines between Blatnice and Doubrava, photo: Němejc (1949, pl. 2, fig. 5) Nat. Muz. E 6028. Scale bars: A = 5 mm; B–D = 1 cm; E = 2 mm.

***Linopteris obliqua* (Bunbury) Zeiller**

Figure 8A

- *1847 *Dictyopteris obliqua*; Bunbury, p. 427.
- §1899 *Linopteris obliqua* (Bunbury). – Zeiller, p. 46.
- *2011 *Linopteris obliqua* (Bunbury) Zeiller. – Bashforth *et al.*, pl. 2, fig. 12.
- *2011 *Linopteris palentina* Wagner. – Bashforth *et al.*, pl. 2, fig. 11.

Remarks. – This differs from *L. neuropteroides* by having usually smaller, more linguaeform pinnules and more isodiametric veins meshes. It typically occurs in uppermost Bolsovian to Cantabrian floras in Europe. Bashforth *et al.* (2011) figured two pinnules as *L. obliqua* and *L. palentina*. The pinnule identified as *L. obliqua* is very similar to specimens from its type area documented by Zодrow *et al.* (2007; see also Zодrow & McCandlish 1978). The other specimen has somewhat finer vein meshes but the pinnule size is rather smaller than is typical for *L. palentina* (Wagner 1964a, pl. 1, fig. 7; Wagner *et al.* 1983, pl. 12, figs 2–4). Since *L. palentina* has not been reported from outside of Iberia and, given the infraspecific variation in pinnule shape and venation of these species, we have assigned both Czech specimens to the same species, which we call *L. obliqua*. This species is not very common in the Nýřany Member of the CWBB.

***Linopteris weigeli* (Sterzel) Daber**

Figure 9F

- *1881 *Dictyopteris weigeli*; Sterzel, p. 76.
- §1955 *Linopteris weigeli* (Sterzel). – Daber, p. 37.
- *1977 *Linopteris weigeli* (Sterzel). – Šetlík, pl. 6, fig. 2.
- 2009 *Linopteris weigeli* (Sterzel). – Kahlert & Schultka in Hoth *et al.*, p. 80, pl. 4, fig. 7 (holotype).

Remarks. – This species is distinctive because of the dimensions of its pinnules. The vein meshes are larger than in *L. neuropteroides* but of similar elongate aspect. It is a very rare species in the Nýřany Member of the CWBB.

***Paripteris linguaefolia* (Bertrand) Josten**

Figure 8B

- *1930 *Neuropteris linguaefolia*; Bertrand, p. 31.
- *1953 *Neuropteris linguaefolia* Bertrand. – Havlena, pl. 6, figs 4, 5.
- §1966 *Paripteris linguaefolia* (Bertrand). – Josten, p. 573.
- *2007 *Paripteris linguaefolia* (Bertrand) Laveine. – Šimůnek, pl. 4, fig. 9; pl. 5, fig. 9.

Remarks. – Pinnules of this species tend to have linguaeform pinnules and only a weakly developed midvein, in contrast to *P. gigantea* (Sternberg) Gothan pinnules which tend to be more falcate and a prominent midvein. Havlena (1953, p. 50) recorded *P. gigantea* from the Kladno Formation, but all of his figured specimens were from the Lower Silesia region (from where Sternberg's type originated). This species is normally associated with Langsetian and lower Duckmantian floras, although it does rarely range up into the upper Duckmantian (*e.g.* Laveine 1967). However, since all of the recorded localities for this species in the Kladno Formation also yielded typical examples of *P. linguaefolia*, it seems likely that Havlena's records of *P. gigantea* represent variation in *P. linguaefolia*.

Family uncertain

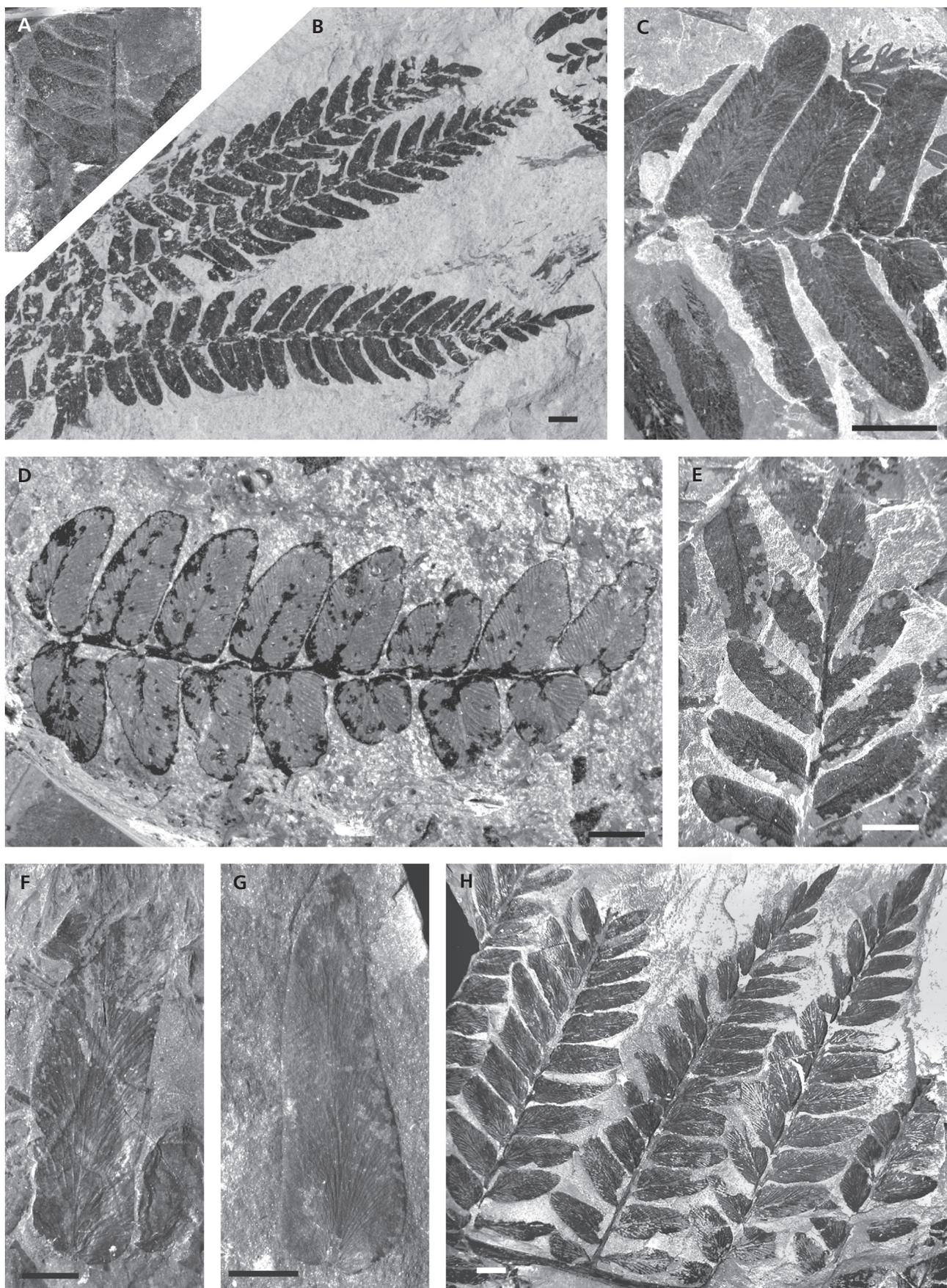
Remarks. – The frond architecture of these species is unknown and, since the pinnae are morphologically quite different from other medullolean species, it is impossible at this time to place them in a fossil-family.

***Havlenaea coriacea* (Ettingshausen) Šimůnek & Cleal**

Figure 5C

- *1852 *Neuropteris coriacea*; Ettingshausen, pp. 9, 10, pl. 2, fig. 1.
- *1876 *Neuropteris acutifolia* Brongniart. – Feistmantel, pl. 66, fig. 4.
- *1949 *Mixoneura praeovata*; Němejc, text-fig. 2; pl. 4, figs 1–7.
- *1949 *Mixoneura grandifolia*; Němejc, text-figs 3, 4.
- *2007 *Neuropteris praeovata* (Němejc) Cleal & Shute. – Šimůnek, pl. 1, figs 1, 7; pl. 3, figs 11, 12; pl. 4, figs 1, 2.
- *2007 *Mixoneura grandifolia* Němejc. – Šimůnek, pl. 1, fig. 4.
- *2011 *Havlenaea praeovata* (Němejc). – Šimůnek & Cleal, pls 1, 2.

Figure 9. Medullolean frond fragments from the Kladno Formation, Central and Western Bohemian basins. • A – *Callipteridium armasii* (Zeiller) Wagner, Nýřany Member, Radčice locality, Plzeň Basin, (Šimůnek 2008, fig. 16/4) CGS, No. ZŠ 320. • B, C – *Laveineopteris bohémica* (Ettingshausen) Šimůnek; B – Doubrava-Blatnice locality, Plzeň Basin, No. F 2051 (West Bohemian Museum, Pilsen); C – Filip II Quarry, Lubná near Rakovník locality (CGU ZŠ 429). • D – *Laveineopteris lubnensis* (Havlena) Šimůnek & Cleal, Radnice Member, Lubná near Rakovník locality, Filip II Quarry (CGU ZŠ 431). • E – *Laveineopteris tenuifolia* (Schlotheim ex Sternberg) Cleal *et al.*, *nom. cons.*, Radnice Member, Motyčín near Kladno locality, No. E 1343. • F – *Linopteris weigeli* (Sterzel) Daber, Nýřany Member, Košnice locality, Ko 1 borehole, 892–892.8 m, Kladno-Rakovník Basin, No. JŠ 167. • G – *Linopteris neuropteroides* (Gutbier) Potonié forma *neuropteroides*, Křimice locality, Km 11 borehole, 260.4–261.4 m, Nýřany Member, No. ZŠ 847. • H – *Havlenaea stradonitzensis* (Andrä) Šimůnek & Cleal, Radnice Member, Strádonice (NMP E 3794). All scale bars = 5 mm.



§2016 *Havlenaea coriacea* (Ettingshausen). – Šimůnek & Cleal, pl. 1.

Remarks. – The taxonomy of this species has been discussed in most detail by Šimůnek & Cleal (2011, 2016). Pinnule morphology is highly variable but the different forms were shown to grade into each other, and all have similar epidermal structures. Němejc (1930) recorded but did not figure specimens from Stradonice as *Neuropteris ovata* Hoffmann, but on the specimen labels he wrote that they were not typical and rather older stratigraphically than the types of that species. He later made them the types of a new species, *N. praeovata* Němejc, 1949, but he was evidently unaware that the type of *N. coriacea* Ettingshausen, 1852 also belongs to this species and so the latter name must take precedence (see Šimůnek & Cleal 2016 for further details).

Havlena (1953, p. 70) suggested that the specimen figured by Feistmantel (1876) as *N. acutifolia* was more correctly assignable to “*M. praeovata*” (\equiv *H. coriacea*). However, the specimens figured by Havlena (1953, pl. 8, figs 1, 2) as *Neuropteris coriacea* are in fact a *Mariopteris*, as hinted at by Havlena.

***Havlenaea stradonitzensis* (Andrä) Šimůnek & Cleal**
Figure 9H

- *1864 *Odontopteris* sp. – Andrée, pl. 4, fig. 4a.
- *1876 *Odontopteris reichiana* Gutbier. – Feistmantel (*non* Gutbier), pl. 67, figs 4, 5.
- *1879 *Aspidites stradonitzensis*; Andrä, p. 104.
- *1949 *Odontopteris stradonicensis* (Andrä). – Němejc, pl. 1, figs 1–8.
- *1954 *Neuropteris stradonicensis* (Andrä). – Gothan, pl. 4, fig. 3.
- *2007 ‘*Odontopteris*’ *stradonicensis* (Andrä) Němejc. – Šimůnek, pl. 1, fig. 2; pl. 4, figs 3, 4.
- §2011 *Havlenaea stradonitzensis* (Andrä). – Šimůnek & Cleal, pls 3, 4.

Remarks. – This species is similar to *H. coriacea* but has more odontopteroid-looking pinnules. The specimens figured by Feistmantel (1876) as *O. reichiana* originated from the Whetstone Horizon from where that species is unknown. They compare closely with specimens from the type locality for *H. stradonicensis*, such as those figured by Šimůnek & Cleal (2011). This species is common in the Whetstone Horizon (Brousek) of the Stradonice locality, Hýskov relic.

“*Mixoneura*” *muensterifolia* Němejc
Figure 8C

§1949 *Mixoneura muensterifolia*; Němejc, p. 15, text-fig. 1; pl. 3, figs 10–14.

*2007 *Mixoneura muensterifolia* Němejc. – Šimůnek, pl. 1, fig. 4.

*2011 “*Mixoneura*” *muensterifolia* Němejc. – Šimůnek & Cleal, pl. 20.

Remarks. – Němejc (1949) assigned this species to *Mixoneura sensu* Bertrand (1930), which was intended for species intermediate between *Neuropteris* Brongniart and *Odontopteris* Brongniart. Current views of this fossil-genus are rather different (*e.g.* Wagner 1964b, Wagner & Castro 1998, Laveine & Legrand 2019). However, there is no obvious existing fossil-genus to which this species could be assigned, and it is insufficiently well preserved to make the basis of a new genus. We have therefore retained the provisional nomenclature suggested by Šimůnek & Cleal (2011). This species occurs relatively rarely in the Whetstone Horizon (Brousek) of the Stradonice locality, Hýskov relic.

Palaeofloristic analyses

For the *P. linguaefolia* Zone analysis, data from the different facies of the Radnice Member (as summarised above) were separated and then incorporated into the Cleal (2008b) dataset (the basins included in the Cleal 2008b analysis are shown in Fig. 10). It is evident from the dataset (Tab. 1) that the floras from all three roof shales (from the Plzeň, Upper Radnice and Lubná seams) were broadly similar and were therefore combined. The species listed in Cleal (2008b) for the Intra-Sudetic Basin (upper Prkenný Důl–Žďárky and Petrovice members of the Žacléř Formation) were also modified following the revision by Opluštil *et al.* (2017); and those from northern Turkey based on some of the records in Opluštil *et al.* (2018). The Donets data were excluded as, although Boyarina (2016) has recently published a biostratigraphical review, there has been no comprehensive taxonomic treatment of the medullosaleans since Novik (1952).

The resulting cluster and ordination analyses for the *P. linguaefolia* Zone medullosaleans are shown in Fig. 11. This reveals an essentially three-fold structure, representing the floras referred to by Cleal (2008b) as the Rhine Palaeoprovince and Silesia Palaeoprovince, and a loose cluster of the intramontane basin floras of the CWBB and Saar-Lorraine. Unlike in the Cleal (2008b) model, the CWBB floras are now clustering rather closer to those of Saar-Lorraine, except for the Lubná tuffs and tuffites floras. If the latter data are removed from the model (also the singleton Intra-Sudetic Basin flora), a PERMANOVA test based on the Raup-Crick coefficients confirmed that the resulting three groups are statistically significantly different ($F = 69.3$, $p_{(same)} \leq 0.01\%$).

Unlike in the Cleal (2008b) analysis, a single, combined analysis was performed for the *Crenulopteris*

Table 1. Distribution of medullosalean fossil-species in the Radnice Member, Central and Western Bohemian basins. Taphonomy: Para. – parautochthonous; Auto. – autochthonous; Mixed – mixed autochthonous, parautochthonous and allochthonous. Symbols: X – rare; (?) – not sure; ● – common; ●* – common in one locality.

	Plzeň coal group (Para.)	Radnice coal group				Lubná coal group		
		Whetstone Horizon		Upper Radnice Seam		Z-tuff (Auto.)	Laminated tuffites (Mixed)	Mudstones (Para.)
		Bělka (Auto.)	Brousek (Mixed)	“Opuky” (Mixed)	“Mydláky” (Para.)			
<i>Alethopteris cf. pseudograndinioides</i>							X	
<i>Alethopteris distantinervosa</i>	X	●	(?)	X	X			X
<i>Alethopteris lonchitica</i>	(?)	X	(?)	X	X	X	?	X
<i>Alethopteris nemejcii</i>	●				●			
<i>Alethopteris cf. serlii</i>			X		●			
<i>Havlenaea coriacea</i>			●	X				
<i>Havlenaea stradonitzensis</i>			●					
<i>Laveineopteris bohemica</i>	●	X	X	X	●			●
<i>Laveineopteris hollandica</i>		X			X			
<i>Laveineopteris loshii</i>	X	●			X			
<i>Laveineopteris lubnensis</i>						●*	●	
<i>Laveineopteris tenuifolia</i>	●				●			●
<i>Linopteris neuropteroides f. neuropteroides</i>	X			X	●			●
<i>Lonchopteris rugosa</i>			●					
<i>Macroneuropteris scheuchzeri</i>	●	●	●	●	X	X	X	
<i>Mixoneura' muensterifolia</i>	X		X					
<i>Palaeoweichselia defrancei</i>		X						
<i>Paripteris linguaeifolia</i>	X				X		X	●

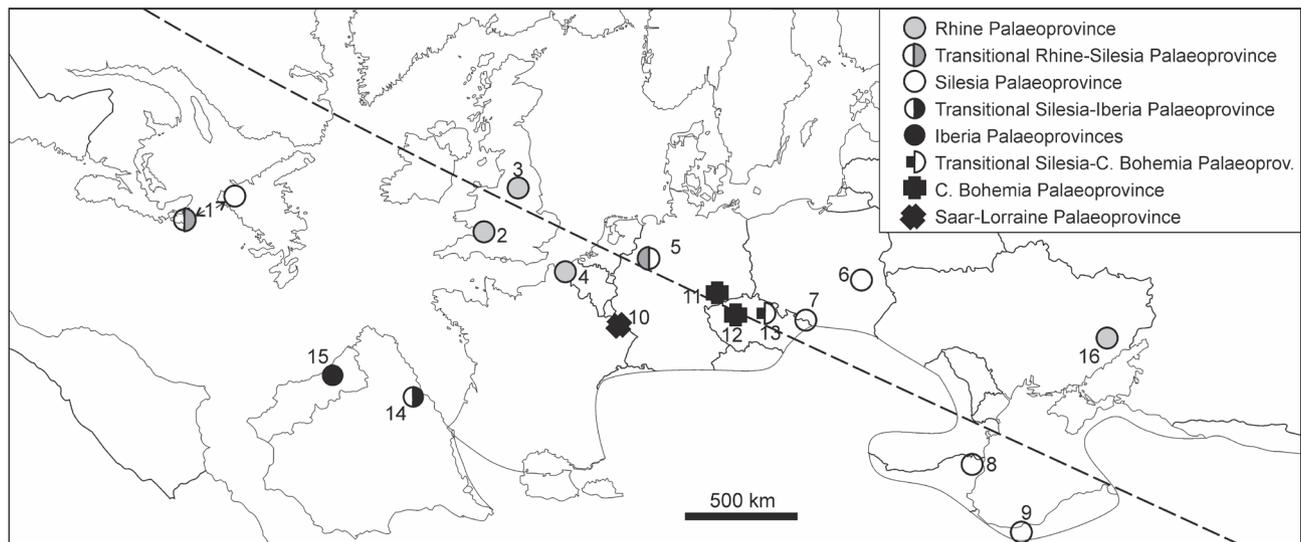


Figure 10. Location of 16 coal basins dealt with in this study, plotted on a late Carboniferous palinspastic map. Legend: 1 – Canadian Maritimes; 2 – SW Britain; 3 – Pennines; 4 – Franco-Belgian Basin; 5 – NW Germany; 6 – Lublin; 7 – Upper Silesia; 8 – Dobrudzha; 9 – N Turkey; 10 – Saar-Lorraine; 11 – Zwickau; 12 – CWBB; 13 – Intra-sudetic Basin; 14 – NW Spain; 15 – Portugal; 16 – Donets. The dashed line approximates to the position of the palaeoequator in late Carboniferous times. Reproduced from Cleal (2008b, fig. 2).

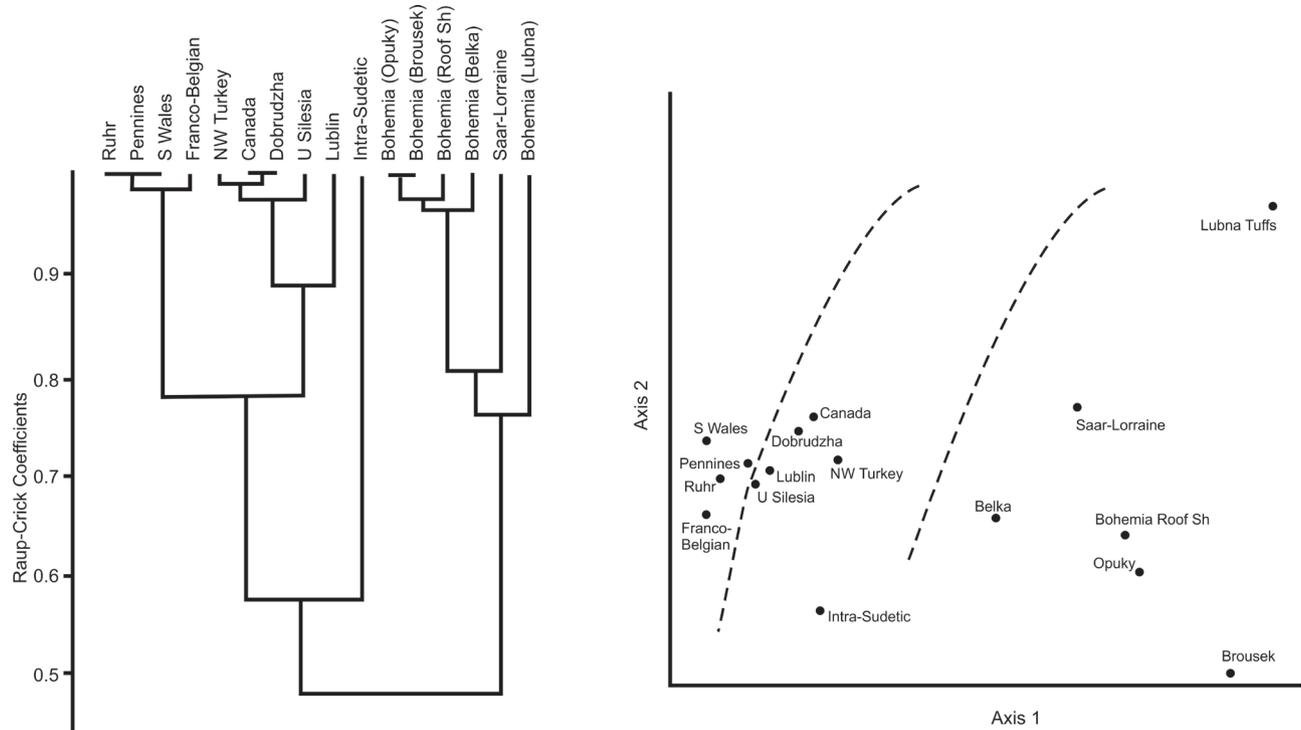


Figure 11. Palaeofloristic analyses of the *P. linguaefolia* Zone floras with the new data for the Radnice Member. The areas demarcated on the DCA ordination reflect the major groupings revealed by the cluster analysis. See text for details of methods used.

acadica and *Odontopteris cantabrica* zones. Although the zonal boundary is biostratigraphically important as it indicates the Westphalian–Stephanian stage boundary (Cleal *et al.* 2003), there are not major differences in the medullosaleans present. Consequently, the species listed for the Nýřany Member are treated as a whole. Data for the Intra-Sudetic Basin were modified following Opluštil *et al.* (2017). As with the Radnice Member, there is a clear separation of two phytochoria for the lowland paralic areas, and a loose cluster of the central European intramontane basins (Fig. 12). The situation of the Iberian floras (NW Spain and Portugal) remains uncertain and clearly requires further investigation.

Discussion

Radnice Member

The underlying structure of the revised *P. linguaefolia* Zone palaeofloristic model (Fig. 10) is similar to that in Cleal (2008b), with two phytochoria being differentiated on the foreland areas: the Ruhr Palaeoprovince (the Pennines, South Wales, Franco-Belgian and Ruhr basins) and the Silesia Palaeoprovince (Upper Silesia, Lublin, Dobrudzha, Northern Turkey and Canada). However, there is now a much closer grouping of most of the intramontane

CWBB and Saar-Lorraine floras. In the Cleal (2008b) analysis CWBB and Saar-Lorraine were assigned to their own separate phytochoria (palaeoprovinces) but here we will group them together as the Bohemia-Saar-Lorraine Palaeoprovince.

The distinctive aspect of the Bohemia-Saar-Lorraine Palaeoprovince in the middle Westphalian is largely due to the absence of many of the abundant and characteristic species found in the lowland basins such as *Laveineopteris rarineris*, *Neuropteris obliqua* (and related forms as discussed by Josten 1962), *Alethopteris urophylla* and *Alethopteris decurrens*. There are in contrast relatively few species that unite the floras of the intramontane basins. Exceptions are *Laveineopteris bohemica* and *Palaeoweichselia defrancei*, but even here there are also links with the paralic basin floras: *L. bohemica* also occurs in Upper Silesia and northern Turkey, on the margins of the foreland basin, and *P. defrancei* has been reported as occurring rarely in Nord-Pas-de-Calais. These connections with marginal parts of the Variscan foreland may have provided the corridors via which these species could disperse between these intramontane basins.

In the paralic basins, the roof shale floras representing mainly the vegetation of clastic substrate habitats tend to be rather different from the vegetation of the peat substrate habitats represented in the coals (Gastaldo *et al.* 1995). In contrast, the vegetation preserved in the Radnice Member

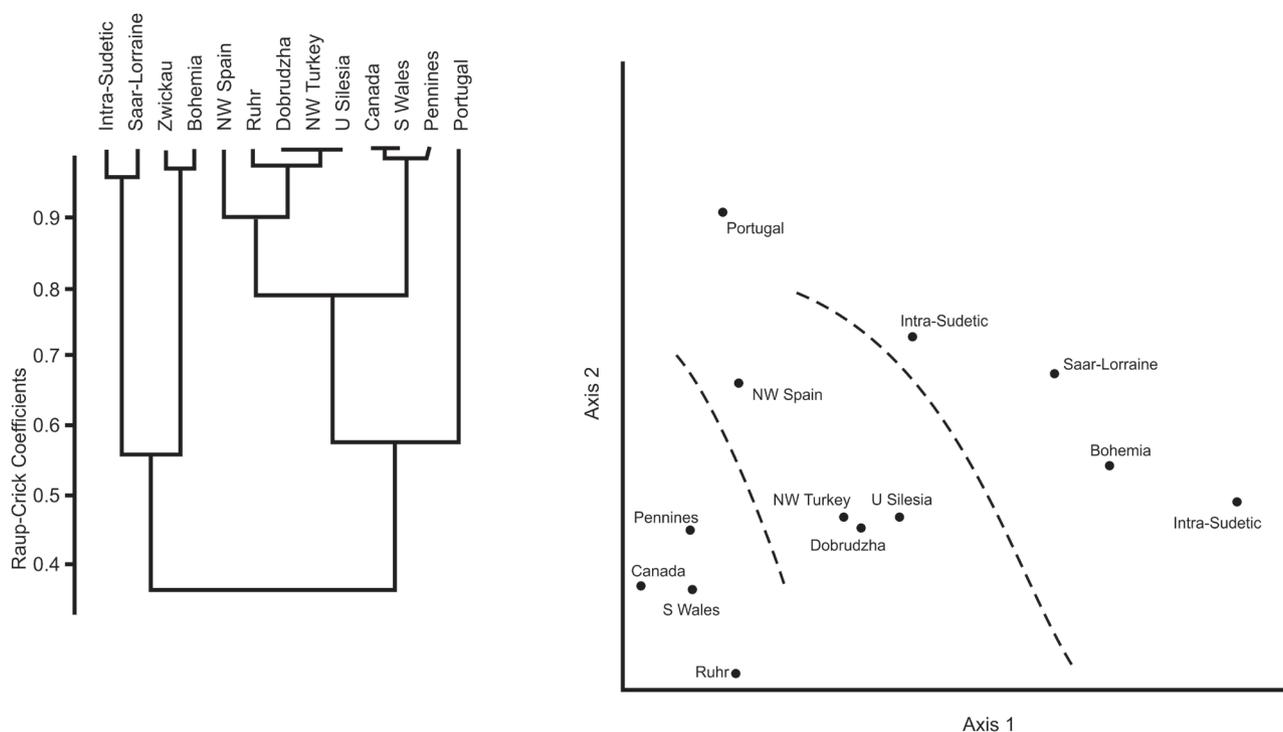


Figure 12. Palaeofloristic analyses of the *C. acadica* and *O. cantabrica* zones floras with the new data for the Nýřany Member. The areas demarcated on the DCA ordination reflect the major groupings revealed by the cluster analysis. See text for details of methods used.

roof shales does not seem to differ markedly from the peat substrate vegetation such as found in the Bělka tuff (e.g. Opluštil *et al.* 2007, 2009a, b, 2014). The explanation for this difference from what is seen in the paralic basins is unclear as the palaeoecology of the Radnice Member roof shale floras is has not been investigated in detail. Perhaps the narrower palaeogeomorphology of this intramontane basin (Opluštil 2005) constrained the drainage system from developing extensive floodplains with clastic substrate habitats, and the roof shales are preserving allochthonous remains of plants that were growing on localised peat substrates elsewhere in the basin, or perhaps on better-drained fan delta systems. This is evidently a subject that requires further investigation.

The distinction of the floras from the Lubná tuffs and tuffite appears to be mainly due to the presence of the endemic *Laveineopteris lubnensis* and the stratigraphically early occurrence of *Alethopteris pseudograndinioides*, and the absence of taxa found abundantly in the other the CWBB floras such as *Havlenaea* spp., *Laveineopteris bohémica*, *L. tenuifolia*, *Alethopteris nemejcii* and *Linopteris neuropteroides*. However, these tuffs and tuffites are known from only a very restricted number of localities, which clearly merit further investigation.

Opluštil & Cleal (2007) reported what appeared to be a significantly higher floral diversity in the Radnice Member compared with other adpression floras of simi-

lar age in Variscan Euramerica. However, the data presented here suggests that this was due to combining taxonomic lists from different facies and therefore habitats in the CWBB data and that, at least for the Medullo-sales diversities within habitats were not significantly higher.

Nýřany Member

The study also confirms the clear differences suggested by Cleal (2008b) between the Nýřany Member floras and those of contemporaneous deposits in the paralic basins such as Britain and the Canadian Maritimes (Fig. 11). Again, however, this is mainly due to the absence from the intramontane floras of a number of species regarded as characteristic of the lowland floras such as *Laveineopteris rarineris*, *Alethopteris pseudograndinioides*, *Alethopteris ambigua* and *Alethopteris serlii*. There are a few species recorded from the CWBB but not from similar-aged strata in the lowland basins (e.g. *Alethopteris kettneri*, *Linopteris weigeli*, *Odontopteris reichiana*) but these tend to be relatively rare (Tab. 2). Also as with the Cleal (2008b) analysis, the Nýřany Member floras broadly group with those of the contemporaneous Heiligenwald Formation floras of Saar-Lorraine, the other major intramontane basin in Europe at this time.

Table 2. Distribution of medullosalean fossil-species in the Nýřany Member, Central and Western Bohemian basins. Symbols: X – rare; ● – common.

	Mirošov Horizon or its equivalent	Chotíkov and Nýřany coal groups	Nevřeň coal group
<i>Alethopteris distantinervosa</i>	X		
<i>Alethopters kettneri</i>		X	
<i>Alethopteris lonchitica</i>	X		
<i>Callipteridium rubescens</i>	●	●	X
<i>Callipteridium armasii</i>			X
<i>Neuropteris plicata</i>	●	X	X
<i>Macroneruopteris scheuchzeri</i>	X	X	
<i>Linopteris neuropteroides</i> f. <i>neuropteroides</i>	X	X	X
<i>Linopteris neuropteroides</i> f. <i>minor</i>		X	X
<i>Linopteris obliqua</i>	X		
<i>Linopteris weigelii</i>		X	
<i>Odontopteris reichiana</i>		X	
“ <i>Mixoneura</i> ” <i>britannica</i>		X	

Plant migration between intramontane and paralic basins

Cleal (2008b) argued that there was a dynamic relationship between the medullosalean floras of the lowland and of the intramontane basins of Variscan Euramerica. It is evident that some of the species seen in the Radnice Member originated in the lowland paralic basins in early Westphalian (or earlier) times, and migrated into the CWBB as wetland conditions developed there during late Duckmantian–early Bolsovian times, notably *Laveineopteris loshii*, *Laveineopteris tenuifolia*, *Alethopteris lonchitica* and *Linopteris neuropteroides*. These tend to be abundant and widespread species in the paralic areas (e.g. Wagner 1968, Cleal & Shute 1995, Cleal *et al.* 2009) suggesting they may have been remains of adaptable plants that would have found it easier to extend their ranges into the new upland habitats.

However, there are also examples of taxa that seem to have originated in the intramontane basins and only later extended their ranges into the lowland paralic areas. For instance, Cleal & Cascales-Miřana (2019) suggested that alethopterids similar to *Alethopteris grandinii* (Brongniart) Göppert appeared significantly earlier (early Bolsovian) in the intramontane Saar-Lorraine Basin, and only later (middle Asturian) migrated into the lowland paralic areas when there were landscape changes resulting from the Variscan Orogeny. Although *A. grandinii* has not been reported from the CWBB, there are fragmentary remains of other alethopterids in the Radnice Member that are normally associated with late Asturian and younger floras

in the paralic basins: *Alethopteris pseudograndinioides* and *Alethopteris serlii* (e.g. Wagner 1968). These Radnice Member fossils are fragmentary and their identification still provisional, but the records are supported by cuticle evidence. They therefore provide some additional support to the idea that at least some of the alethopterids normally associated with late Asturian and later floras in the lowland paralic areas had their origins in more upland wetland habitats.

A similar possible relationship between upland and lowland medullosaleans has also been argued for the small-pinnuled *Laveineopteris* species (Cleal 2008b, řimůnek & Cleal 2011), with *L. bohémica* occurring in late Duckmantian and early Bolsovian floras in the Bohemia-Saar-Lorraine Palaeoprovince, *L. rarinervis* occurring in late Bolsovian to Cantabrian floras of the Ruhr Palaeoprovince, and both species occurring with overlapping stratigraphical ranges in the Silesia Palaeoprovince. Thomas (1997) has suggested that herbaceous lycophyte species may also have originated in the intramontane basins in Westphalian times and only later extended their ranges into the lowland paralic areas.

There were (as far as we know) no animals that could have facilitated seed dispersal at this time. The large size of the seeds of the medullosaleans (Cleal *et al.* 2010, Sims 2012) must, therefore, have affected their migration patterns. Water transport by rivers may have been an important vector in some species and might explain the observation that some medullosaleans appear to have migrated downstream from upland to lowland basins. There were, nevertheless, other species that appear to have

migrated in the opposite direction, presumably in response to changing habitats in the upland basins; as pointed out by Laveine *et al.* (1993), long-distance migration of medullosaleans may have been achieved simply by seeds being shed and landing not far from the parent plant. Significantly, no medullosalean species occur only in both intramontane basins (CWBB and Saar-Lorraine) but not in at least parts of the foreland basins. This suggests that there was little or no direct migration of these species between the intramontane basins over the intervening highlands. This issue of the long-distance migration of these large-seeded plants, often in response to environmental change, also clearly needs further investigation.

Conclusions

This first comprehensive taxonomic synopsis of medullosalean pteridosperm foliage from the intramontane CWBB has confirmed that there are clear differences in the balance of species present compared with the lowland paralic basins, but not significantly higher species diversity as was previously suggested (Opluštil & Cleal 2007). Although there are some species restricted (or mainly restricted) to the CWBB, the differences are mainly due to the absence of several characteristic and abundant, paralic basin species. The analysis also suggests that there is a closer similarity than previously suggested in the medullosalean floras found in the CWBB and the other major, middle–late Westphalian intramontane basin of Variscan Euramerica, in Saar-Lorraine.

The reasons for these differences between the intramontane and paralic basin medullosalean floras is unclear. If there was a significant difference in elevation (and this has still not been fully confirmed) it could have affected temperature or even precipitation patterns. Alternatively, the intramontane basins may have had different substrate conditions due to differences in drainage patterns, and perhaps this altered the species compositions. These differences potentially have wider implications as it has been suggested that plant migration from the intramontane basins may have been a significant factor in the vegetation changes observed in the paralic basins (*e.g.* Thomas 1997, Cleal *et al.* 2009, Thomas & Cleal 2017, Šimůnek & Cleal 2018, Cleal & Cascales-Miñana 2019). Evidently, the ecological factors that drove these temporal and palaeofloristic differences among the medullosaleans at this time will require further work.

This study has also suggested that, in contrast with the paralic basins, there was relatively little difference in the peat and clastic substrate vegetation in the CWBB. However, whether there was also a broad similarity in the peat and substrate vegetation in other intramontane basins such as Saar-Lorraine remains unknown.

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