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The floristic relationship between the upland and lowland Carboniferous wetlands of Variscan Euramerica — Evidence from some medullosalean pteridosperm fronds

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Abstract

Alethopteris grandinii represents remains of fronds of a medullosalean pteridosperm (probably a small tree) that rapidly migrated across the lowland wetland habitats of Variscan Euramerica in middle Asturian (late Moscovian) times. This was probably caused by changing drainage patterns within the lowland coal swamps, in response to climate and landscape changes. However, these medullosaleans had first appeared rather earlier, in early Bolsovian (early Moscovian) times, in upland wetland habitats. These upland habitats may have pre-adapted these plants to the changed condition in the lowland coal swamps.

Keywords: Carboniferous, Coal swamps, Medullosales, Upland, Migration

1 Introduction

During Pennsylvanian (late Carboniferous) times, large parts of palaeotropical Euramerica were covered by wetlands, often referred to as coal swamps because of the extensive coal deposits that were formed from their peats. These heavily vegetated wetlands consisted of a complex of clastic and peat substrates habitats formed in a fluvio-lacustrine setting. During most of Westphalian (late Bashkirian to late Moscovian) times, the vegetation tended to be dominated by arborescent lycopsids, with subsidiary ferns, sphenophytes, and pteridospermous and cordaitean gymnosperms; later in Westphalian and Stephanian (latest Moscovian to Gzhelian) times, marattialean ferns and alethopterid medullosaleans became the dominant plants.

Although at any one time the general character of the coal swamp vegetation was broadly similar across Euramerica, some palaeobiogeographical variation has been recognised, especially between the paralic lowland areas and the intra-montane basins (Gothan 1915, 1925, 1951, 1954; Thomas 2007; Cleal 2008a, 2008b; Cleal et al.

2010a; Fig. 1). We now believe that these floristic differences provide important insights into how the coal swamp vegetation evolved during Pennsylvanian times, especially in response to the landscape and climate changes occurring at this time (Gastaldo et al. 1996; Cleal and Thomas 1999, 2005; Opluštil and Cleal 2007; Cleal et al. 2010a, 2011).

In this paper we examine evidence for the migration of vegetation from upland to lowland wetland habitats during late Moscovian times, with particular reference to the Saar-Lorraine Basin that straddles the border between France and Germany (Schindler and Heidtke 2007). This basin formed in a half-graben between the Rheno-Hercynian and Saxo-Thuringian zones of the Variscan Orogen (Kneuper 1964, 1966; Korsch and Schäfer 1995; Schäfer and Korsch 1998) and is one of the best documented of the Westphalian age intramontane basins, with an Upper Paleozoic sedimentary fill of c. 10 km thickness. We will be focussing in particular on a group of medullosalean pteridosperms that bore fronds of the fossil-genus *Alethopteris* von Sternberg, which in late Moscovian and Kasimovian times was a major component of the Euramerican wetland vegetation; in the lowland paralic basins, its appearance was part of a major vegetational change represented by the base of the *Crenulopteris acadica* Zone, formerly known as the *Lobatopteris*

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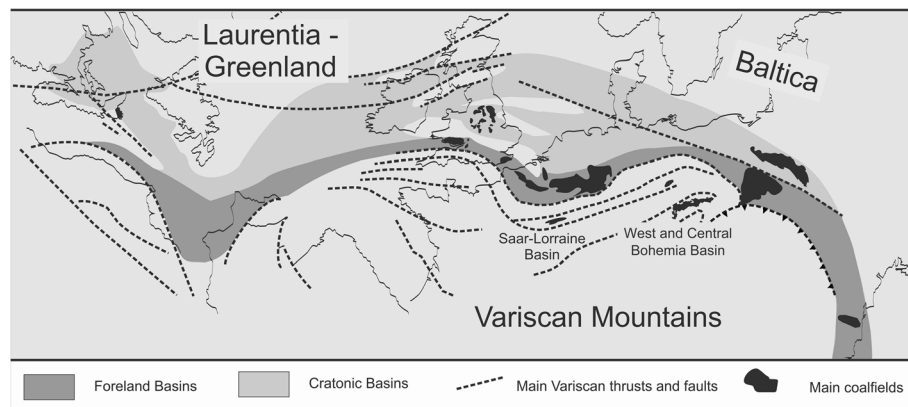Full list of author information is available at the end of the article

Fig. 1 Palaeogeographical map of Variscan Euramerica during middle Westphalian times, showing large area of paralic coal swamps and the two main intramontane basins, Saar-Lorraine and West and Central Bohemia. Adapted with permission from Cleal et al. (2010a, their Fig. 1)

vestita Zone (Wagner 1984; Cleal 1991). However, we will show that there is evidence that these plants were present rather earlier in the upland wetlands such as the Saar-Lorraine Basin.

We will limit our discussion to the evidence available in the area of palaeotropical coal swamps between the Acadian Mountains (Pfefferkorn and Gillespie 1980) in the west, which approximates in position to the modern-day Appalachian Mountains, and the Palaeotethys Ocean in the east. This area has been named Variscan Euramerica (Cleal et al. 2010a) and at least during early Bashkirian to middle Moscovian time represented the largest area of coal swamps in Euramerica (Cleal and Thomas 2005). There are extensive adpression floras known from coal swamp habitats west of the Acadian Mountains (e.g. Pfefferkorn and Gillespie 1980; Blake et al. 2002) but their taxonomy and biostratigraphy have not been investigated in detail in recent years, making a comparison with the data from the more easterly basins difficult. We will hereafter use the Heerlen Regional Chronostratigraphy, as reviewed by (Wagner 1974) and Wagner and Winkler Prins (2016) as this still provides a far better temporal resolution of the terrestrial coal-bearing sequences of Variscan Euramerica; for a correlation between this scheme and the IUGS Global Chronostratigraphy based mainly on marine stratotypes, see Fig. 2. This will include the use of the name Asturian for what was traditionally referred to as the Westphalian D Substage (Wagner et al. 2002). For biostratigraphy, we will use the scheme developed by Wagner (1984) and modified by Cleal (1991) and Cleal and Thomas (1994); see also Fig. 2.
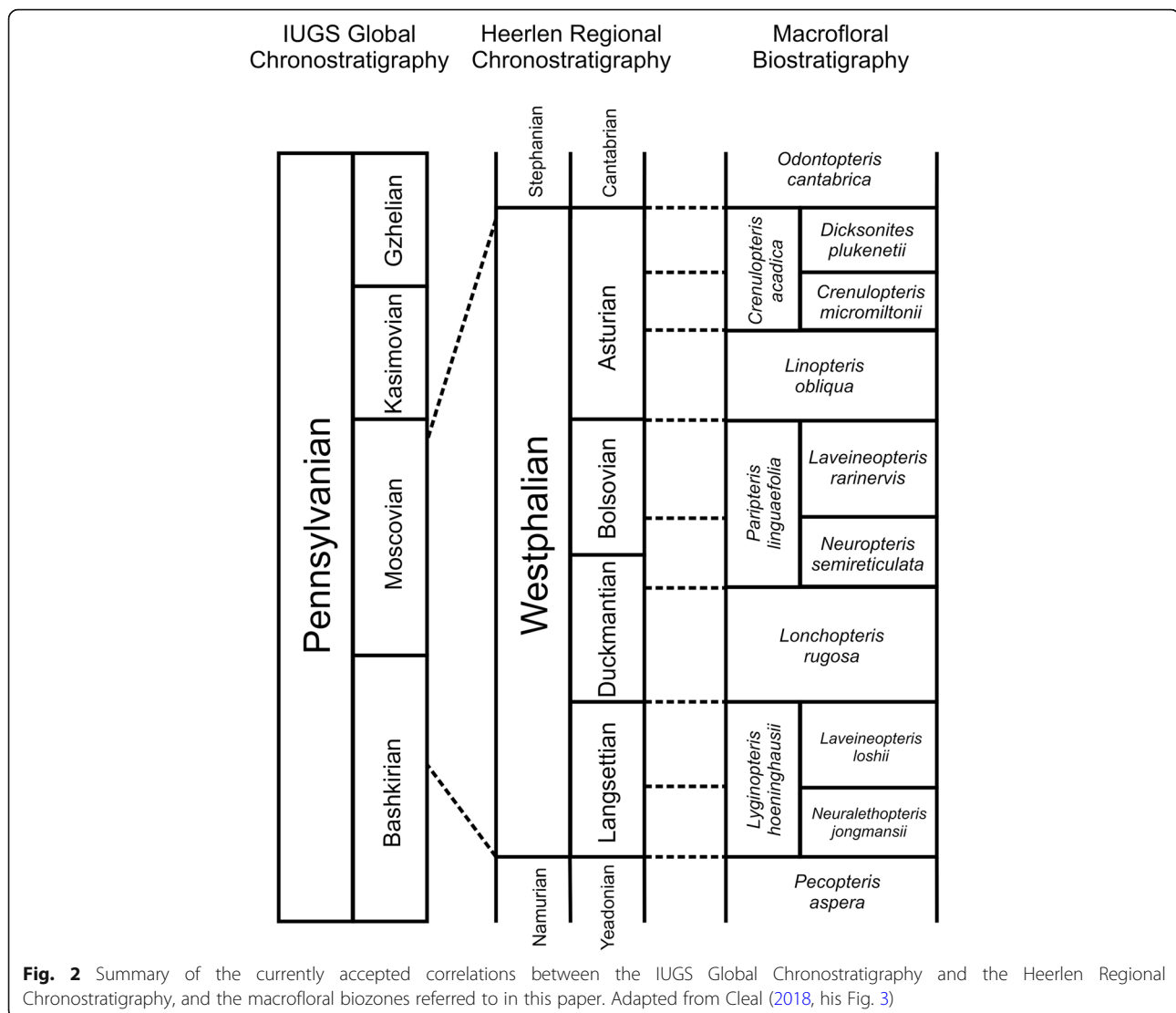
2 What were the upland wetlands?
Thomas and Cleal (2017) recently discussed what palaeobotanists have meant in the past when using the term upland floras. It became clear that most so-called

upland floras were not upland in any meaningful sense; the term was instead mainly being used to refer to vegetation of dryland or better drained lowland habitats. There is nevertheless evidence of some truly upland Westphalian vegetation in Variscan Euramerica, in the intra-montane basins of the orogen. The elevation of these basins relative to the paralic areas has been the subject of debate. Based on the distinctive nature of the vegetation, Holub et al. (1977) and Tenchov (1976, 1977) estimated elevations of 1000–2000 m above sea level, whilst Becq-Giraudon and Van Den Driessche (1994) and Becq-Giraudon et al. (1996) interpreted deposits in the Autunian basins of Central France as periglacial, from which they suggested elevations of 4000–5000 m above sea-level based. More recently, by modelling drainage patterns within the West and Central Bohemia Basin and comparing its palaeogeographical position relative to the foreland basins to the north, Opluštil (2005) estimated it formed at an elevation of about 1000 m.

3 Stratigraphical correlation
A difficulty with trying to compare the vegetation dynamics of upland intramontane and lowland paralic basins is stratigraphical correlation. In the paralic basins, marine bands resulting from eustatic flooding have provided what are in effect time-lines that allow accurate correlation (e.g. Bless and Winkler Prins 1972; Bless et al. 1972, 1977) but these are absent from the intra-montane basins. Until relatively recently, macrofloral and palynological biostratigraphy have been the main alternative means of correlation, but using these correlations to compare the vegetation dynamics in the two types of area clearly has the potential to introduce circular arguments. Correlations independent of biostratigraphy have been mainly based around ash bands, often termed tonsteins. Initially this was based around the simple lithostratigraphical correlation of the tonsteins

Fig. 2 Summary of the currently accepted correlations between the IUGS Global Chronostratigraphy and the Heerlen Regional Chronostratigraphy, and the macrofloral biozones referred to in this paper. Adapted from Cleal (2018, his Fig. 3)

between different basins and this was used to establish a detailed correlation between the intra-montane Saar-Lorraine and paralic Nord-Pas-de-Calais sequences (Bouroz 1967). More recently, high resolution radiometric dating has further improved the correlations with the West and Central Bohemia Basin (Opluštil et al. 2016) but similar work has yet to be done in Saar-Lorraine Basin.

4 Major changes in coal swamp floras of Variscan Euramerica

Plant species diversity fluctuated in the coal swamp vegetation in different basins of Variscan Euramerica in response to a combination of landscape and climate change (Cleal 2005, 2007, 2008c; Uhl and Cleal 2010; Cleal et al. 2010a, 2011, 2012). However, one floristic change stands out as representing a more fundamental reconfiguration of the vegetation, in late Westphalian times. This was probably related to the shift from

lycopsid- to fern-dominated vegetation that occurred in the peat-substrate habitats of Variscan Euramerica at this time (Gastaldo et al. 1996; Cleal and Thomas 1999, 2005; Opluštil and Cleal 2007; Cleal et al. 2010a, 2011). However, there was also a marked change in the clastic substrate vegetation reflected in the base of the *Crenulopteris acadica* Zone (formerly the *Lobatopteris vestita* Zone) in the Wagner (1984) and Cleal (1991) biostratigraphical scheme. As with the peat substrate vegetation, there is a marked increase in abundance and diversity of marattialean ferns (e.g. *Crenulopteris* Wittry et al., *Cyathocarpus* Weiss, *Acitheca* Schinmper; e.g. Zodrow 1990; Zodrow et al. 2006; Wittry et al. 2015). However, this is also accompanied by an increase in abundance and diversity of medullosalean pteridosperm remains, notably of *Alethopteris* von Sternberg (e.g. Cleal 1978, 1984, 2007; Zodrow and Cleal 1998; Cleal et al. 2010a, 2010b, 2012).

The rest of this paper will focus on a distinctive group of alethopterid fronds that have slender pinnules, and which appear abundantly at this floral change. They occur in both lowland and intra-montane basins, albeit recorded under different species names.

5 Taxonomic notes

The following is not intended as a detailed taxonomic analysis of these fronds. However, it is critical that we explain exactly how we are using these taxonomic names for understanding the floristics of these plants and their fossils, and therefore the palaeogeographical relationships of these basins. Where comments on the occurrences of the two taxa being discussed are not referenced, they are based on our observations on the Saarbrücken Mining School and University of Lille collections (specimens from the latter have the prefix USTL).

5.1 *Alethopteris grandinii* (Brongniart) Göppert, *nov. emend.* Cleal and Cascales-Miñana, 2019 (Fig. 3)

5.1.1 Lectotype

Specimen MNHN.F.555, Muséum d'Histoire Naturelle, Paris; Locality: Geislautern, near Völklingen, Saarland, Germany; Horizon: upper Heiligenwald Formation (upper Asturian Substage). Designated by Wagner (1968, p. 66). Figured by Brongniart (1833, pl. 91, Fig. 2); photographically refigured by Bertrand (1932, pl. 43, Fig. 2) and Wagner (1968, pl. 17, Fig. 47).

5.1.2 Synonyms

Alethopteris ambigua Lesquereux, 1879 pars. emend. Wagner, 1968; *Alethopteris pseudoaquilina* Potonié, 1893; *Alethopteris friedelii* Bertrand, 1932; *Alethopteris lesquereuxii* Wagner, 1968.

5.1.3 Diagnosis

Pinnules elongate and parallel sided or sometimes barrel-shaped, except in distal part of pinna where they become slightly subtriangular, with rounded or slightly bluntly acuminate apex; pinnules 8–17 mm long, 3–8 mm wide. Pinnule insertion usually at about right-angles. Midvein well developed and extending for most of pinnule length. Lateral veins simple, or once or twice forked at a narrow angle, usually thickly marked, and meet pinnule margin at about right-angles; marginal nervation density normally distributed, range is from 28 to 43 per cm at pinnule margin with mean ± std. = 36 ± 3. Terminal pinnule slender, parallel-sided or slightly tapered, and poorly individualised. Adaxial epidermal cells polygonal, slightly elongate along veins but isodiametric between veins. Abaxial intercostal cells with strongly undulate walls. Stomata irregularly orientated and overarched by ring of prominent papillae. Trichomes sparsely but evenly distributed over most of abaxial surface, more concentrated along pinnule margin.

Based on the emended diagnosis given by Zodrow and Cleal (1998) for *Alethopteris ambigua*.

5.1.4 Remark

Brongniart (1833) described *Pecopteris grandinii* Brongniart and *Pecopteris aquilina* Schlotheim ex Brongniart from Geislautern near Völklingen in Saarland *Alethopteris*. According to Bertrand (1932) this flora was from the formation then known as *Flambants supérieurs*, now referred to as the upper Heiligenwald Formation, and thus in the upper Asturian Substage (Laveine 1977; Cleal 1984). The types of these species have been subsequently refigured photographically by Bertrand (1932, pls. 36, 37, 43) and Wagner (1968, pl. 17, Figs. 47, 48). Both species were subsequently transferred to *Alethopteris* von Sternberg, 1825 by Göppert (1836).

It has been widely recognised that the specimens described by Brongniart (1833) as *Pecopteris aquilina* were different from those originally described as *Filicites aquilinus* by Schlotheim (1820); even Brongniart (1833) had expressed some doubt on this point. As a consequence, alternative homotypic synonyms *Alethopteris pseudoaquilina* Potonié, 1893 and *Alethopteris friedelii* Bertrand, 1932 have been proposed for *A. aquilina* Schlotheim ex Brongniart non Schlotheim. For a further discussion on this see Wagner (1968, p. 34).

Both elongate and squat pinnule forms described by Brongniart (1833) have very similar venation patterns: the midvein is usually thick and extending for most of the pinnule length, and thick lateral veins that are simple, or once or twice forked; the marginal vein density is usually about 35 per cm. Most authors have continued to keep them as separate taxa although the detailed criteria for distinguishing them have not been clearly established. As shown by Zodrow and Cleal (1998, p. 105) the pinnules in *Alethopteris* have a predominantly apical development which results in relatively constant pinnule widths but highly variable length:breadth ratios. Squat or elongate pinnule form on its own is therefore unlikely to be a reliable taxonomic indicator.

Bertrand (1932) was clearly aware of the difficulties. Of Brongniart's (1833) *A. grandinii* syntypes, Bertrand reported one was lost (Brongniart 1833, pl. 91, Fig. 1) and two others (Ibid., pl. 91, Figs. 3, 4) he transferred to his *A. friedelii*. The fourth syntype (Brongniart 1833, pl. 91, Fig. 2; refigured Bertrand 1932, pl. 43, Fig. 2) is poorly preserved and Bertrand also found this difficult to distinguish from what he called *A. friedelii*. He commented that, based on the syntypes alone, it would be difficult to justify separating *A. grandinii* from *A. friedelii* and that he had been unable to find any new specimens that he could attribute to *A.*
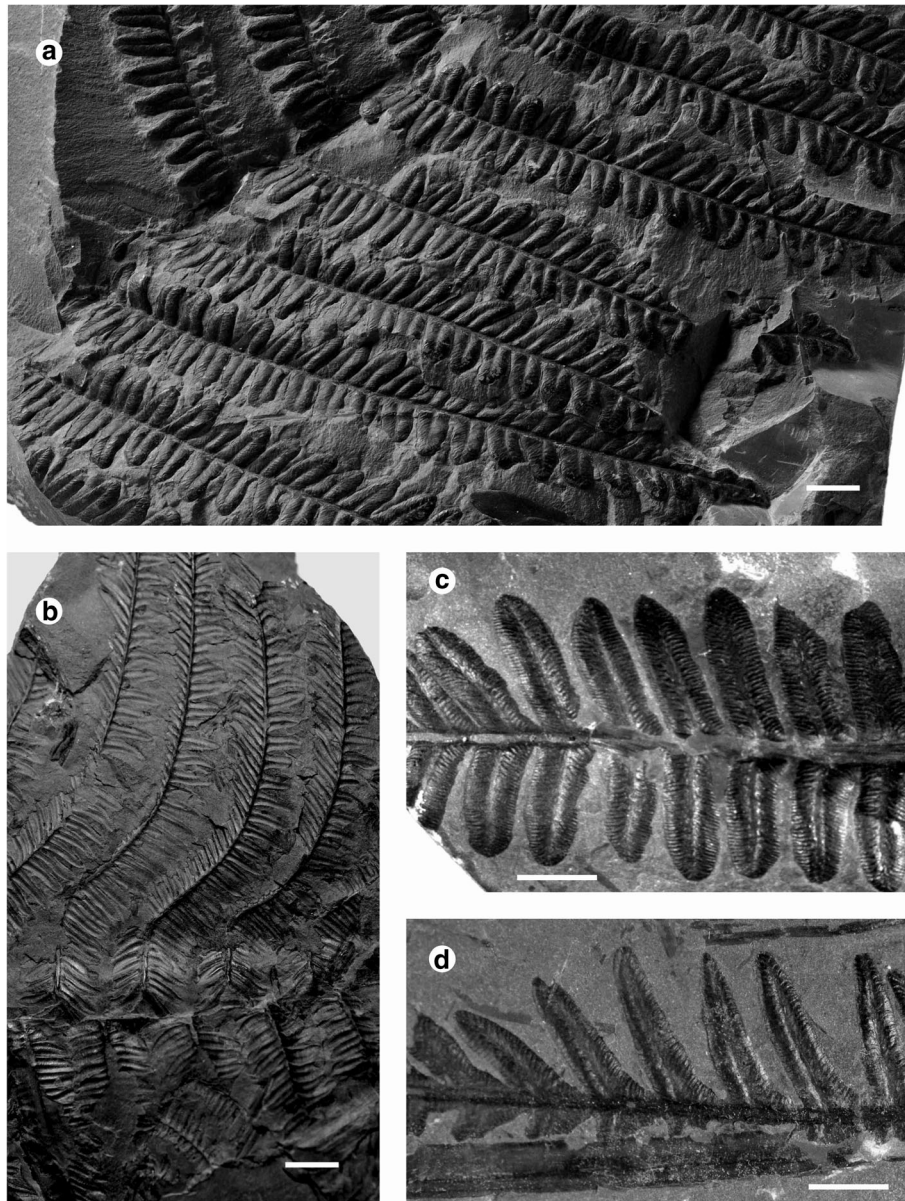
Fig. 3 *Alethopteris grandinii* (Brongniart) Göppert var. *grandinii*. **a** - Squat pinnule form; Radstock Formation (Asturian Substage), Radstock, Somerset, UK (BGS Kidst. 3850); **b** - Slender pinnule form; Heinrich Seam, Heiligenwald Formation (Asturian Substage), Wendel, Saarland, (USTL 3190); **c** - Close-up of typical pinnule form showing coarse veining; Heiligenwald Formation (Asturian Substage), Stocken Borehole (depth 1005.8 m), Saarland, (USTL 3191); **d** - Close-up of more slender pinnule form; Heiligenwald Formation (Asturian Substage), Stocken Borehole (depth 1005.0 m), Saarland, (USTL 3192). Scale bars = 10 mm (**a**, **b**); 5 mm (**c**, **d**)

grandinii as he was interpreting it; this corroborates our experience that the squat-pinnule forms are relatively rare compared with the elongate pinnules forms.

Nevertheless, Bertrand (1932) continued to recognise *A. grandinii* as a distinct species from his *A. friedelii*, based mainly on a fifth specimen in the Brongniart collection, also from the Geislautern locality, which he (Bertrand) designated as a "cotype" (figured Bertrand 1932, pl. 43, Fig. 4; pl. 43 bis). This shows relatively squat, basally confluent pinnules with a midvein that does not extend to the pinnule apex, and thus agrees with the emended diagnosis given by Bertrand (1932, p. 76) for *A. grandinii*. As pointed out by Bertrand, however, the specimen is from the distal part of a penultimate pinna in the transition area between pinnules and ultimate pinnae, where the latter would be expected to have atypically squat pinnules of this type. Since it was reportedly associated with specimens showing the elongate types of pinnule used to characterise *A. friedelii*, it is difficult to see the justification for establishing a separate species on this specimen alone.
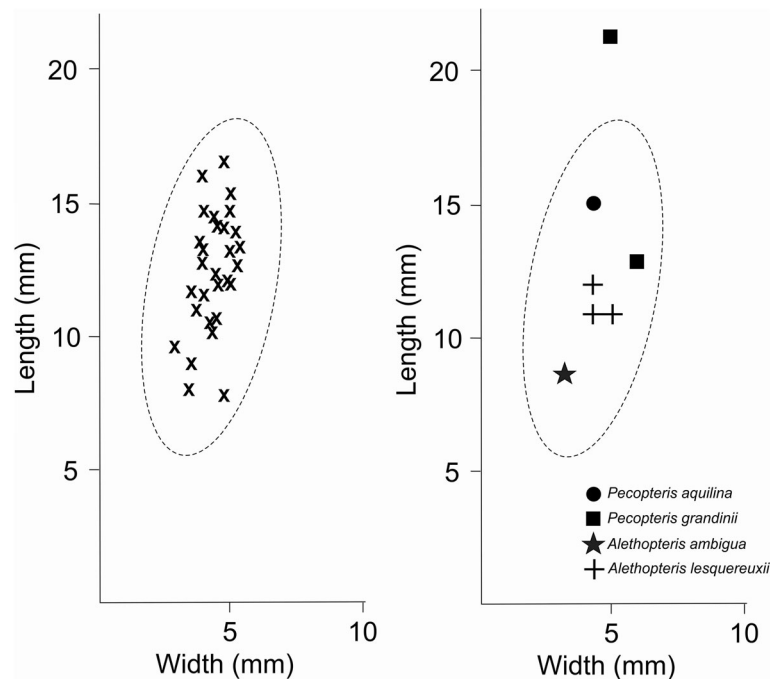
Fig. 4 Left shows the sizes of pinnules in an assemblage originally identified as *Alethopteris ambigua* (now referred to *A. grandinii*) from the Asturian Hub Seam of the Sydney Coalfield (originally documented by Zodrow and Cleal 1998). Right shows the sizes of the types of *Pecopteris aquilina* and *P. grandinii* from Geislautern, Saarland, plotted in the same dimension space; also of the types of *Alethopteris ambigua* and *A. lesquereuxii*

Bertrand compared a sixth specimen, this time from "Saarbrücken", with *A. grandinii* (Bertrand 1932, pl. 43, Fig. 3; pl. 44). Although some of the pinnules correspond to Bertrand's emended diagnosis for *A. grandinii*, he noted that the apical pinnules are very similar to those seen in *A. friedelii*. Bertrand was clearly uncertain as to the identity of this specimen, which he named *Alethopteris* cf. *grandinii*. A seventh specimen, this time from a much older stratigraphical level at Dudweiler (Bertrand 1932, pl. 45) was described as similar to *A. grandinii*, but sufficiently distinct to be assigned to a separate variety; this will be discussed later.

In conclusion, we can find little justification for taxonomically distinguishing the types of *A. grandinii* and *A. fiedelii*. This moreover is in agreement with our observations on the extensive collections of this type of alethopterid in the collections of the Saarbrücken Mining School and University of Lille, where both pinnule forms almost invariably occur in close association. In our view, *A. grandinii* and *A. friedelii* should be regarded as heterotypic synonyms, of which *A. grandinii* is the earlier published name.

In Saar-Lorraine Basin, these frond fragments with the distinctive *A. grandinii* venation appear at about the stratigraphical level of the ash band Tonstein 60 in the upper Heiligenwald/La Houve Formation (Laveine

1977; Cleal 1984). This coincides with the base of the *Crenulopteris acadica* (*Lobatopteris vestita* auct.) Zone of Wagner (1984) in the middle Asturian Substage. Morphologically very similar pinna remains occur in the more lowland and paralic basins of northern Spain, southern Britain and the Canadian Maritimes (Wagner 1968; Cleal 1978, 2007; Thomas and Cleal, 1994; Zodrow and Cleal, 1998) usually recorded as *Alethopteris ambigua* Lesquereux pars. emend. Wagner, 1968 or *Alethopteris lesquereuxii* Wagner, 1968 (the latter two species were argued to be conspecific with one another by Zodrow and Cleal, 1998). *A. grandinii* and *A. ambigua* also have essentially indistinguishable epidermal structures, the former having been described by Barthel (1962) and the latter by Zodrow and Cleal (1998); Barthel (1962) incorrectly used the name *Alethopteris davreuxii* (Brongniart) Göppert for these fossils, but this refers to a rather different, Duckmantian to Bolsovian species with rather larger pinnules and often a pseudoanastomosed venation (see Buisine 1961). Wagner (1968) in fact argued that *A. ambigua* is conspecific with *A. friedelii*, using the former name as this had priority. However, if we accept *A. grandinii* as also being conspecific with *A. ambigua*, then the former must take priority over *A. friedelii* as well.

To further corroborate the similarity of these species, Fig. 4 shows a graphical plot of the range of

pinnule sizes found in an assemblage of fossils associated with the Hub Seam in the Sydney Coalfield, Cape Breton, Canada, based on data reported in Zodrow and Cleal (1998). This is accompanied by a plot of the sizes of the types of *A. grandinii*, *A. friedelii* and *A. ambigua* (also of *Alethopteris lesquereuxii* Wagner) on the same dimension space. The only one of these types that does not lie within this dimension space is one of the *A. grandinii* types, which is a little longer but of similar width. However, given the apical development pattern of alethopterid pinnules, this may be of little significance and just regarded as an extreme outlier of the normal range of morphological variation. Since these types all have essentially the same venation patterns, we suggest that they merely represent variation in pinnule shape within the frond of one biological species.

5.1.5 Occurrences
Saarland, upper Heiligenwald Formation: Flöz Beust (Luisenthal, Viktoria and Gerhardt Mines), Flöz Elisabeth (Göttelborn Mine), Flöz Constanze (Luisenthal; Bertrand 1932), Borehole Saarbrücken Süd 1 (depth 1091.3 m), Borehole Bisten 4 (depth 1169.3 m), Borehole Marienau 1 (depth 944.8 m), Borehole Marienau 2 (depths 800.5 m, 843.0 m, 1032.3 m and 1035.6 m), Borehole Marienau 4 (depths 850.5 m, 942.5 m, 990.3 m, 990.5 m, 991.4 m and 991.7 m), Borehole Pfaffenkopf (depths 76 m and 116 m) and Borehole Stocken (depths 733.3 m, 733.5 m, 734.3 m, 998.5 m, 1005.0 m, 1005.8 m and 1006.8 m); also from an uncertain stratigraphical horizon at Geislautern (Bertrand 1932). Lorraine, upper "Assise" Flambants: Veine François (La Houve; Bertrand 1932), Borehole Cocheren 11 (depths 1217.9 m and 1217.9 m), Borehole Cocheren 8 (depth 991.9 m), Borehole Cocheren 9 (depth 1133.5 m), Borehole Créhange 1 (depths 1499.0 m and 1501.3 m), Borehole Folschuillerd (depth 1008.5 m), Borehole St Fontaine 1 (depths 369.2 m and 394.7 m) and Borehole St Fontaine 4 (depths 572.0 m and 833.6 m). Sydney Coalfield, Cape Breton: between Mullins and Point Aconi seams (upper Morien Group; Zodrow and Cleal 1998). British Isles, upper Warwickshire Group, notably South Wales (Swansea 2 ft. to Coalbrook seams; Cleal 2007), Radstock and Pennines Basins (Cleal 2018). Northern Spain: numerous localities in Palencia and León (Wagner 1968). Zonguldak-Amasra Basin, Northeast Turkey (Jongmans 1955; identifications verified by CJC). USA: Mazon Creek (Wittry 2006), Missouri and Pennsylvania (Wagner 1968; exact relationship of these floras to the European regional chronostratigraphy at present uncertain).

5.2 *Alethopteris grandinii* (Brongniart) Göppert var. *duboisii* Bertrand *nov. emend.* Cleal and Cascales-Miñana, 2019 (Fig. 5)
5.2.1 Lectoype
Specimen 1874, Benecke Collection, Musée de Géologie, Université l'Strasbourg; Locality: Gegenortesschacht, Dudweiler, Saarbrücken; Horizon: Sulzbach Formation ("Charbons gras" – Bolsovian Substage). Figured by Bertrand (1932, pl. 45).

5.2.2 Emended diagnosis
Pinnules elongate and parallel sided or sometimes barrel-shaped, except in distal part of pinna where they become slightly subtriangular, with rounded or slightly bluntly acuminate apex; pinnules 4–20 mm long, 2–3 mm wide. Pinnule insertion usually at about right-angles. Midvein well developed and extending for most of pinnule length. Lateral veins simple, or once or twice, usually thinly marked, forked at a wide angle, sometimes tending to flexuous, and meet pinnule margin at about right-angles; marginal nervation density mainly between 35 and 45 per cm. Terminal pinnule slender, parallel-sided or slightly tapered, and poorly individualised.

5.2.3 Remark
In most basins in Variscan Euramerica, *A. grandinii* first appears in the middle Asturian Substage and is one of the indices for the base of the *Crenulopteris acadica* Zone (Wagner 1984; Cleal 1991; Cleal and Thomas 1994). However, Wagner (1968) had previously stated that the slender pinnule form, which he called *A. ambigua*, could also range down into the Bolsovian Substage. An examination of his list of occurrences shows that this is mainly based on specimens from Saar-Lorraine Basin documented by Bertrand (1932, pl. 37, Fig. 1; pls. 38, 39; pl. 40, Fig. 2, pl. 41; pl. 42, Figs. 1, 2); other examples were subsequently figured by Laveine (1989, pls. 18, 19, Fig. 2). These specimens have very similar shaped pinnules to *A. grandinii* except that the squatter, barrel-shaped forms are perhaps even rarer, but Bertrand's figured specimens appear to have more finely-marked, and more widely forking lateral veins, that can tend towards being flexuous.

These differences on the face of it may appear to be relatively subtle and be merely due to taphonomy: for instance, the apparent width of the veins can be influenced by whether the abaxial or adaxial surface of the pinnule is being examined. However, when the extensive collections of plant fossils from Saar-Loraine Basin in the University of Lille and the Saarbrücken Mining School were examined, a consistent pattern emerged: specimens from above Tonstein 60 in the Heiligenwald
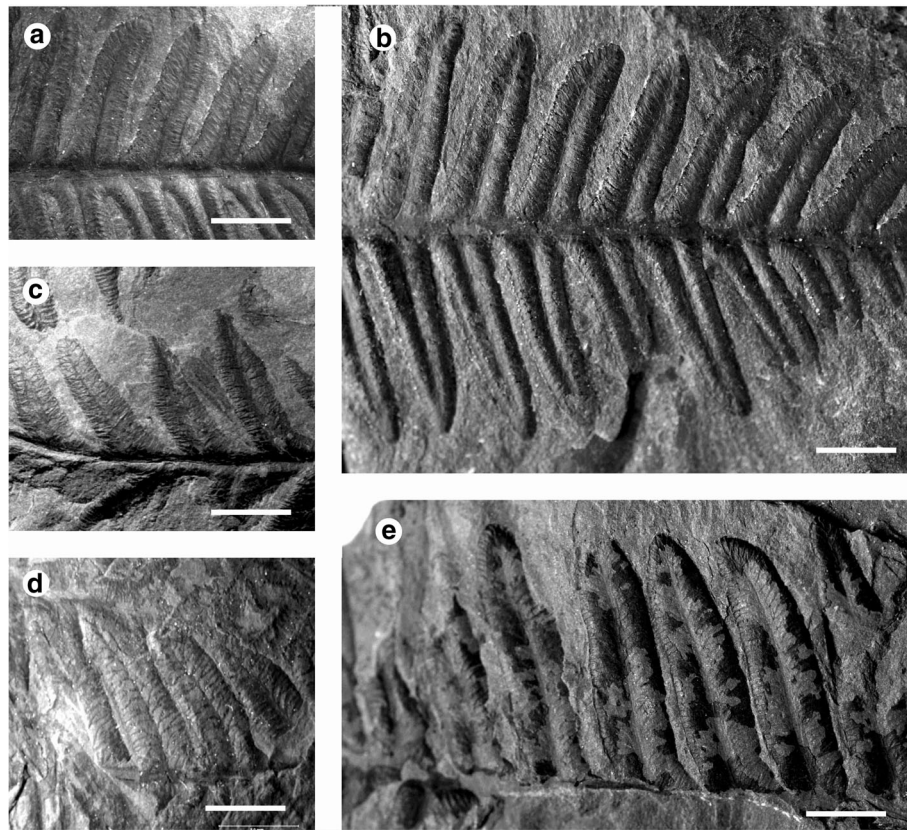
Fig. 5 *Alethopteris grandinii* (Brongniart) Göppert var. *duboisii* Bertrand; range of different pinnule morphologies, but all showing fine, somewhat flexuous veining; all scales bars = 5 mm. **a**, **b** - Lower Heiligenwald Formation (lower Asturian Substage), Créhange 1 Borehole (depth 1799.6 m), (USTL 3193); **c** - Lower Heiligenwald Formation (lower Asturian Substage), Hallering 1 Borehole (depth 1341.5 m), (USTL 3194); d - Lower Heiligenwald Formation (lower Asturian Substage), Tritteling Borehole (depth 1041.0 m), (USTL 3195); e - Seam 5, Sulzbach Formation (Bolsovian Substage), Jägersfreude Mine, Saarland, (USTL 3196)

Formation were of the typical *A. grandinii* variety with narrowly forking veins, and all those from lower stratigraphical levels had the widely forking to flexuous veining pattern.

Among the specimens figured by Bertrand (1932, pl. 45) one was interpreted by him as sufficiently different from typical *A. grandinii* to merit distinction as a separate variety; *A. grandinii* var. *duboisii* Bertrand. The specimen originated from a horizon on the Sulzbach Formation and thus of Bolsovian age. Bertrand distinguished this specimen from typical *A. grandinii* by the wider spacing of the pinnae, but this is a very variable feature in such fronds. More significantly, however, the lateral veins are thinner and more widely forking, almost tending to being flexuous. This would therefore appear to correspond with the plant fossils we have observed in the Sulzbach, Luisenthal and lower Heiligenwald formations in Saar-Lorraine Basin — the early form of *A. grandinii*.

It is perhaps a debatable point as to whether Bertrand's trinomial, varietal nomenclature should be used, or whether it would be better to interpret this early form of *A. grandinii* as a separate species and give it the name "*duboisii*". However, as the range of pinnule forms in the two taxa are almost identical, and the characteristic venation needed to distinguish them can sometimes be difficultly found in isolated specimens, we have opted to keep the taxonomic distinction at the varietal rank.

Other examples showing this type of venation were included by Bertrand (1932, pl. 37, Fig. 1; pls. 38, 39; pls. 40, 41; pl. 42, Figs. 1, 2).

5.2.4 Occurrences

Only known from the Saar-Lorraine Basin. Saarland, Sulzbach Formation: Flöz 13 (König, Helene and Friedrichsthal mines), Flöz 10 (Helene and Maybach mines), Flöz 9 (Velsen Mine), Flöz 7, 6 and 1 (unknown localities), Flöz 5 (Jägersfreude Mine; Bertrand 1932), Flöz 4 (Heinitz and Maybach Mines), Flöz 3 (König, Camphausen and Reden Mines), Flöz 1 (Frankenholz Mine; Bertrand 1932), Borehole Marianau 1 (depths 920.3 m, 690.9 m, 691.2 m, 691.3 m and 691.5 m), Borehole Papiermühle (depth 419.1 m) and Borehole Stocken (depths 1097.5 m, 1233.0 m, 1233.3 m and 1314.8 m). Saarland, Luisenthal Formation: 0.80 Flöz

(Reden Mine), Flöz IIR (Helene Mine), Flöz Kallenberg (Reden Mine). Saarland, Lower Heiligenwald Formation: Flöz Polly 1 (Kohlwald Mine). Lorraine, lower "Assise" Flambants: Pit V, Merlebach (Veine 5 and 16; Bertrand 1932), Borehole Chasseurs (depths 656.5 m, 794.0 m, 825.6 m and 910.4 m), Borehole Créhange 1 (depths 1799.4 m and 1799.6 m), Borehole Fockloch (depth 535.4 m), Borehole Folschviller 23 (depth 15.8 m), Borehole Hallering (depth 1341.5 m), Borehole Merbette (depths 1007.9 m and 1007.9 m), Borehole Merlebach (depth 278.6 m), Borehole Oratoire (depth 808.9 m), Borehole Simon 21 (depth 297.1 m), Borehole St Fontaine 1 (depths 709.8 m, 781.8 m, 933.5 m, 940.9 m, 956.7 m and 1051.4 m), Borehole St Fontaine 2 (depths 509.8 m, 1038.4 m and 1049.6 m), Borehole St Fontaine 4 (depths 942.4 m, 976.9 m, 1086.1 m, 1086.1 m and 1098.4 m), Borehole St Fontaine 6 (depth 1103.5 m) and Borehole Tritteling (depths 1044.8 m, 1079.5 m, 1102.0 m, 1102.2 m and 1102.3 m).

6 Discussion

The base of the *Crenulopteris acadica* Zone in Variscan Euramerica represented a major change in the vegetation in Variscan Euramerica during Westphalian times, marked by a significant increase in abundance and diversity in the adpression floras of alethopterid medullosaleans and marattialean ferns. It was probably related to the diachronous change from lycopsid- to marattialean-dominated vegetation in the peat-substrate vegetation (as reflected in the coal ball and palynological record) that seems to have occurred in mid-Westphalian times in eastern Variscan Euramerica, late Westphalian times in western Euramerica and early Stephanian times in west of the Acadian Mountains (Gastaldo et al. 1996, Cleal et al. 2010a, 2011). This change has been variously interpreted as due to climate change (e.g. DiMichele et al. 1985; DiMichele and Phillips 1996; Pfefferkorn et al. 2008), landscape change due to Variscan tectonics (Cleal and Thomas 1999) or a combination of the two (Cleal et al. 2010a, 2011). However, understanding this vegetational change also requires some understanding of where these species came from: did they evolve within the coal swamps or is the apparent change the result of plant migration?

The evidence reviewed in this paper indicates that at least one of the alethopterid species that appears at this level in the lowland basins (*A. grandinii*) may have originated in the upland wetlands of Saar-Lorraine, first appearing there some 4 million years earlier, based on the chronology of Opluštil et al. (2016). Care must be taken not to draw too many conclusions; we are after all dealing with fossil-taxa of foliage and not taxa of whole organisms. However, these frond fragments found in the earlier Saar-Lorraine floras have virtually indistinguishable pinnule shapes and epidermal structure to the later

forms, and only differ in relatively subtle aspects of the venation; hence they are only separated taxonomically at the rank of variety.

This may not be the only example of Westphalian age plants appearing earlier in intra-montane basins than in paralic areas. *A. grandinii* does not occur in the other major late Westphalian intramontane basin (the West and Central Bohemia Basin) but in the upper Asturian-lower Cantabrian Nýřany Member there are abundant remains of another of the species associated with the base of the *Crenulopteris acadica* Zone: *Alethopteris pseudograndinioides* Zodrow and Cleal (Šimůnek 1988). However, there has also recently been a record of a fragment of foliage in the early Bolsovian Radnice Member that closely resembles *A. pseudograndinioides* (Šimůnek and Cleal, 2018), also suggesting that the alethopterids associated with the mid-Asturian floral change may have originated in upland wetland habitats. A similar suggestion has also been made by Thomas (1997, p. 149) for anisophyllous herbaceous lycopsids, which first appeared in intra-montane basins in Bolsovian aged floras, and do not occur in the lowland paralic basins until late Asturian times.

In stratigraphically earlier floras there are also indications of upland–lowland migration of species. *Laveineopteris bohemica* (von Ettingshausen) Šimůnek (= "*Neuropteris*" *nicolausiana* Gothan) found in lower Bolsovian floras of both Saar-Lorraine and West and Central Bohemia (Bertrand 1930; Šimůnek and Cleal 2011, 2013) is morphologically similar to *Laveineopteris rarinervis* (Bunbury) Cleal et al., 1990 from the upper Bolsovian and younger floras of the lowland and paralic parts of Variscan Euramerica (e.g. Laveine 1967; Cleal 2007). In the upper Duckmantian part of the Radnice Member of the West and Central Bohemia Basin there are sphenophytes recorded as *Annularia longifolia* Brongniart (e.g. von Ettingshausen 1854) that look remarkably similar (albeit a little larger) to *Annularia spinulosa* von Sternberg, which does not normally appear in the lowland basins until the upper part of the Duckmantian Substage (e.g. Cleal 2007).

We know of few examples of the reverse, lowland to upland migration of species. The only possible exception is *Laveinopteris tenuifolia* (von Sternberg) Cleal et al., which in the lowland basins ranges from the lower Langsettian through to the basal Asturian substages, but in the Saar-Lorraine sequences does not appear until the Bolsovian Subtage (e.g. Bertrand 1930; Laveine 1989); it is so-far unrecorded from West and Central Bohemia (Šimůnek and Cleal, 2011).

7 Conclusions

The medullosan pteridosperms that bore *Alethopteris grandinii* (= *A. ambigua auct.*) and possibly *Alethopteris pseudograndinioides* fronds occurred in the upland

wetland basins of Variscan Euramerica in early Bolsovian times, and only migrated into the lowland wetlands in middle Asturian times, some 4 million years later. An explanation for this migration will require further investigation. The vegetation change represented by the base of the *Crenulopteris acadica* Zone has been linked with landscape and climatic changes possibly resulting in better-drained substrates (e.g. Cleal et al. 2010a), although the continued development of coal deposits indicates we are still dealing with wetland habitats. Perhaps there was some aspect of these upland wetlands that pre-adapted some plants to conditions in the changed environments of the lowlands. Especially in the West and Central Bohemia Basin, we now have considerable data on the middle Westphalian vegetation and ecology of the peat substrate habitats through the work on the in situ floras found in the Whetstone Horizon, an ash-band within the Radnice Coal Seam (e.g. Opluštil et al. 2007, 2009, 2014; Libertín et al. 2009). However, the ecological relationship between this vegetation and the clastic substrate vegetation preferentially preserved in the adpression floras is still uncertain (Opluštil et al. 2007, 2014). It has been suggested that the clastic substrates between the coals of the Radnice Member tend to be relatively coarse (Opluštil and Pešek 1998; Opluštil et al. 1999) suggesting they may have been somewhat better drained than those of lowland clastic substrate habitats; but whether this would have been sufficient to pre-adapt some of the upland plant species to the changed, post middle Asturian conditions in the lowlands is uncertain. No comparable data are so far available from Saar-Lorraine. With the alethopterids, maybe the large size of the ovules (e.g. Cleal et al. 2010b) may have favoured upland to lowland migration due to purely gravitational factors. Whatever the explanation, it is clear that a better understanding of the ecological relationships between the upland and lowland wetland habitats of Variscan Euramerica will be critical for a proper understanding of coal swamp vegetational dynamics.

Abbreviations
auct.: auctorum (of other authors); emend.: emended; ft.: feet (as in imperial scale measurements); Ibid.: Ibidem (in the same place); *nov. emend.*: new emendation; std.: standard deviation

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