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Macrofloral biostratigraphy reflects late Carboniferous vegetation dynamics in the Nord-Pas-de-Calais Coalfield, France

by AZUCENA MOLINA-SOLÍS¹ , CHRISTOPHER J. CLEAL² ,
CLAUDE MONNET¹  and BORJA CASCALES-MIÑANA^{3,*} 

¹Université de Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France; azucena.molina.etu@univ-lille.fr, clau.monnet@univ-lille.fr

²School of Earth Science, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK; chris.cleal@bristol.ac.uk

³CNRS, Université de Lille, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France; borja.cascales-minana@cns.fr

*Corresponding author

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Abstract: The Nord-Pas-de-Calais Coalfield is formed by an almost continuous succession of upper Carboniferous deposits, from which an extremely diverse macroflora has historically been described. Recent evidence has highlighted a clear pattern of changing species diversity, showing some differences from what is seen in other coalfields of Variscan Euramerica. We further study this significant macroflora, focusing on the biostratigraphical changes and their palaeo-ecological implications. Clustering and ordination analyses have indicated key floral discontinuities that enable the standard regional macrofloral biozones to be recognized in the Nord-Pas-de-Calais Coalfield. By combining these results with the previous diversity studies, six distinct phases in the evolution of the coal swamp vegetation in north-eastern France can be identified: (1) an initial invasion of peat substrate vegetation in the earliest Langsettian; (2) a rapid diversification of the clastic substrate vegetation in the early-

middle Langsettian; (3) a more gradual diversification of the vegetation of both clastic and peat substrates during the late Langsettian to middle Duckmantian glacial phase C3; (4) the appearance of more characteristically late Westphalian, but less diverse floras during the late Duckmantian to early Bolsovian C3–C4 interglacial phase; (5) a marked increase in species diversity in the middle–late Bolsovian, coinciding with the onset of the C4 glacial phase; and (6) a marked reduction in species diversity, and the appearance of new medullosaleans and marattialeans in the Asturian, possibly linked to climate change. The evidence clearly shows how this palaeotropical swamp vegetation was responding to climate change and orogenic landscape changes during Westphalian times.

Key words: biozone, Carboniferous, coal swamp, Nord-Pas-de-Calais, palaeotropics, vegetation evolution.

THE coal swamps were one of the most important early terrestrial biomes, which extended over nearly 10⁶ km² of the palaeotropics during late Carboniferous times (area estimate based on Cleal & Thomas 2005). The development of these swamps coincided with major taxonomic diversifications in terrestrial vegetation (Cleal & Cascales-Miñana 2014, 2021), vertebrates (Dunne *et al.* 2018) and insects (Jarzembowski & Ross 1996; Condamine *et al.* 2016). Peat accumulation in the swamps also acted as a major carbon sink that had a significant impact on atmospheric composition and global climate (Gastaldo *et al.* 1996; Cleal & Thomas 1999, 2005; Opluštil & Cleal 2007; Cleal *et al.* 2009a, 2012; Hibbett *et al.* 2016; Montañez 2016).

The history of the coal swamps can be broadly broken down into four phases (Cleal & Thomas 1999, 2005; Cleal 2021a, 2021b): an early phase of ‘proto-coal swamps’ in

the early Namurian (e.g. Purkyňová 1970; Gastaldo *et al.* 2009a, 2009b; Strullu-Derrien *et al.* 2021); a Westphalian phase represented by the major Carboniferous coalfields of Euramerica, and representing the first major glacial phase of the Late Palaeozoic Ice Age; a Stephanian interglacial phase mainly seen in the intramontane basins of Europe and the paralic basins of the southern foreland of the Variscan Orogen; and a Cisuralian (early Permian) phase seen in the Cathaysian coalfields mainly of China, and representing the second major glacial phase of the Late Palaeozoic Ice Age.

The development and diversification of the coal swamps in the second of these phases is best documented in the coalfields of Variscan Euramerica (i.e. that part of Euramerica adjacent to or part of the Variscan Orogen; Cleal 2008a, 2008b; Cleal *et al.* 2009a, 2009b, 2012). Species richness of the macrofloras (*sensu* Cleal *et al.* 2021)

has been used to determine the vegetation dynamics in both paralic-foreland and intra-montane settings in this area (Cleal 2005, 2007, 2008c; Opluštil & Cleal 2007; Cleal *et al.* 2009b, 2012; Uhl & Cleal 2010; Opluštil *et al.* 2017; Molina-Solís *et al.* 2023). These studies have revealed broad similarities in the vegetation dynamics across Variscan Euramerica, but also some significant differences resulting from local factors such as changes in landscape and depositional patterns as the Variscan Mountains migrated northwards (Kelling 1988; Gayer *et al.* 1993; Kroner *et al.* 2008). The vegetation dynamics in the Nord-Pas-de-Calais Coalfield in northern France (Molina-Solís *et al.* 2023) were particularly distinctive, and therefore to investigate this further a biostratigraphical analysis of the macrofloras was undertaken, with the aim of determining which taxa were driving the changes in species richness.

Throughout this paper the stages and substages of the Heerlen Regional Chronostratigraphy (Wagner 1974; Wagner & Winkler Prins 2016) have been used because these provide a better resolution of the upper Carboniferous terrestrial sequences than the stages of the SCCS Global Chronostratigraphy (Cohen *et al.* 2013), which are defined by stratotypes in marine sequences. However, we have used the SCCS subsystem divisions of Mississippian and Pennsylvanian for lower and upper Carboniferous, with a boundary approximating to the Chokierian–Arnsbergian substage boundary in the Heerlen scheme.

BIOSTRATIGRAPHICAL BACKGROUND

The distribution of plant macrofossils in the Nord-Pas-de-Calais Coalfield was first documented by Boulay (1876) and Zeiller (1888). Zeiller (1894) subsequently divided the succession into what he called zones; the latter zones have been widely referred to in the literature (e.g. Bertrand 1914, 1919; Corsin & Corsin 1970, 1971; Laveine 1987). However, they were not biozones in the currently accepted sense, defined purely by the ranges of the taxa (Cleal 1999). Rather, they were an attempt to express the differences in the macrofloras of the different lithostratigraphical intervals recognized here as formations and members; a similar approach was used by Jongmans (1928) in the Netherlands, by Renier (1928) in Belgium, and by Gothan (1929) in the Ruhr.

Dix (1934, 1937) tried to see if a similar pattern of macrofloral change could be identified in the South Wales Coalfield (UK), but using a different approach. Rather than determining the taxonomic composition of the macrofloras of pre-defined (lithostratigraphical) intervals, Dix plotted the ranges of the different taxa against the sequence of coal seams in South Wales and defined the zones purely on the distribution of the macrofloras through the stratigraphical sequence. Dix (1934) made a

preliminary comparison of her results with the data from other coalfields in continental Europe, but was hindered from further developing her ideas first by the outbreak of World War II, and subsequently by her ill health (Burek & Cleal 2005).

Wagner (1984) attempted to integrate these various biostratigraphies by defining synthetic zones based on the ranges of the macrofloral species averaged out over the various Euramerican coalfields. However, Wagner also often tried to make the zonal boundaries coincident with the chronostratigraphical stage and substage boundaries and, as a result, his scheme did not always reflect the true dynamics of vegetation change. In order to make the zones better reflect the natural vegetation dynamics, Cleal (1991) integrated the Wagner (1984) and Dix (1934) biostratigraphies and the resulting hybrid (Wagner–Cleal) scheme has been broadly adopted here (Table 1; see also Cleal & Thomas 1994; Opluštil *et al.* 2016, 2022).

Wagner (1984) described the zones in his scheme as concurrent range zones defined by the overlapping ranges of two taxa, but they were in fact defined by the overlapping ranges of several taxa and hence are more like assemblage zones. In some cases, attempts have been made to give greater precision to the biostratigraphy by focussing on certain zonal boundaries, such as the bases of the *Linopteris obliqua* Zone (Laveine 1977) and *Odonopteris cantabrica* Zone (Cleal *et al.* 2003); these are therefore now in essence interval zones.

DATA

This study was based on the plant macrofossil data given in Molina-Solís *et al.* (2023, table S1) with a few minor modifications. As with most palaeobotanical data, the taxonomic records deal with fossil taxa as defined in the *International Code of Nomenclature* (Turland *et al.* 2018), in which separate genera and species names are given to the different parts of the plants (Cleal 1986; Thomas 1989; Cleal & Thomas 2010, 2021). Following the approach used by Molina-Solís *et al.* (2023; see also Cleal *et al.* 2012, 2021), to make the data reflect as near as possible the diversity of the parent vegetation, the fossil taxa for only one plant part were recorded for each plant group: we used the stems bearing leaf scars for the lycopsids, the ovule and pre-pollen cones for the cordaitales, and the foliage for the other groups. Furthermore, to avoid overrepresenting diversity, we removed *Ulodendron haidingeri* and *Lepidodendron simile*, which are later synonyms of *Lepidodendron dilatatum* (Álvarez-Vázquez & Wagner 2014; Álvarez-Vázquez *et al.* 2018; Thomas & Cleal 2022). Similarly, we removed *Lepidodendron obovatum*, a non-illustrated record of a species that is probably

TABLE 1. Correlation of previous western European Namurian–Westphalian macrofloral zonations and the clusters identified in the present study.

Bertrand (1919)	(1914, Dix (1934)	Wagner (1984)	Cleal (1991)		Present study
			Zones	Subzones	
<i>Linopteris obliqua</i>	H	<i>Linopteris obliqua</i>	<i>Linopteris bunburii</i>		VIII
<i>Linopteris münsteri</i>	G	<i>Paripteris linguafolia</i>	<i>Paripteris linguafolia</i>	<i>Laveineopteris rarinervis</i>	VII
<i>Alethopteris davreuxii</i>	F			<i>Neuropteris semireticulata</i>	VI
<i>Alethopteris lonchitica</i>	E	<i>Lonchopteris rugosa</i>	<i>Lonchopteris rugosa</i>		V
<i>Neuropteris schlehanii</i>	D	<i>Calymmotheca hoeninghausii</i>	<i>Calymmotheca hoeninghausii</i>	<i>Laveineopteris loshii</i>	IV
	C			<i>Neuralethopteris jongmansii</i>	III
<i>Pecopteris aspera</i>	B	<i>Pecopteris aspera</i>	<i>Pecopteris aspera</i>		II
<i>Rhodia hochstetteri</i>		<i>Calymmotheca larischii</i>	<i>Calymmotheca larischii</i>		I

For the Wagner scheme, the zones names have been simplified to the first species used.

synonymous to *Lepidodendron aculeatum* (Thomas 1970; Álvarez-Vázquez & Wagner 2014). *Renaultia acutiloba* was also excluded given that Brousmiche (1983) showed that the pinnule lobes (the main diagnostic feature of the species given by Danzé 1956) are indistinguishable in shape from the better-known *Renaultia chaerophylloides*. This resulted in a dataset of 252 fossil species (Data S1).

The sequence was divided into five formations and 12 members (in French, termed *Assise* and *Faisceau*, respectively) following currently accepted lithostratigraphical nomenclature (Becq-Giraudon 1983). For analytical purposes, each member was further subdivided into three informal units (lower, middle and upper). The distribution of the fossil species was then tabulated through the resulting 36 stratigraphical units. The resulting range charts are shown in Figures 1 and 2.

METHOD

The resulting data were investigated using a set of complementary multivariate techniques. Floral discontinuities were investigated using stratigraphically constrained hierarchical cluster analyses via the unweighted pair-group method with arithmetic mean (Grimm 1987; Hammer & Harper 2006). The analyses were done by contrasting the Sørensen/Dice and Raup–Crick coefficients (Dice 1945; Sørensen 1948; Raup & Crick 1979; Shi 1993). This strategy elucidated the significant discontinuities in the macrofloral sequence, reflecting the most important changes in the macrofloral composition (Cascales-Miñana 2011; Cascales-Miñana *et al.* 2013; Pardoe *et al.* 2021). Significance of the resulting clusters was tested using one-way analysis of similarity (ANOSIM; Clarke 1993). This was

complemented by ordination analyses to investigate gradational relationships between stratigraphical intervals: non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA) (Shi 1993, 1995; Hammer & Harper 2006; Legendre & Legendre 2012; Pardoe *et al.* 2021). Data analysis was conducted using the *vegan* (v2.5.7; Oksanen *et al.* 2023) and *ade4* (v1.7.22; Dray *et al.* 2023) packages from R software (v4.1.3; R Core Team 2013).

RESULTS

Multivariate analysis identified eight stratigraphical clusters (Figs 3, 4), which provided highly significant ANOSIM values ($R = 0.95$; $p = 0.001$). They were further supported by a very low NMDS stress value (<0.05), which suggests an excellent representation of the data in reduced dimensions. The obtained cluster I–VIII model is also coherent with major floristic changes observed from range charts (Figs 1, 2). The main species that delineate these zones and associations are shown in Figures 5–9.

Cluster I

This occurs in the lower Bruille Formation (Stérelle Member), which has been dated as Arnsbergian on faunal evidence (Chalard 1960; Becq-Giraudon 1983). These low-diversity macrofloras are essentially Mississippian in character, including *Archaeocalamites radiatus*, *Cardioperis antecessens*, *Neuralethopteris larischii*, *Lepidodendron veltheimii* and *Sphenophyllum tenerrimum* (Fig. 1).

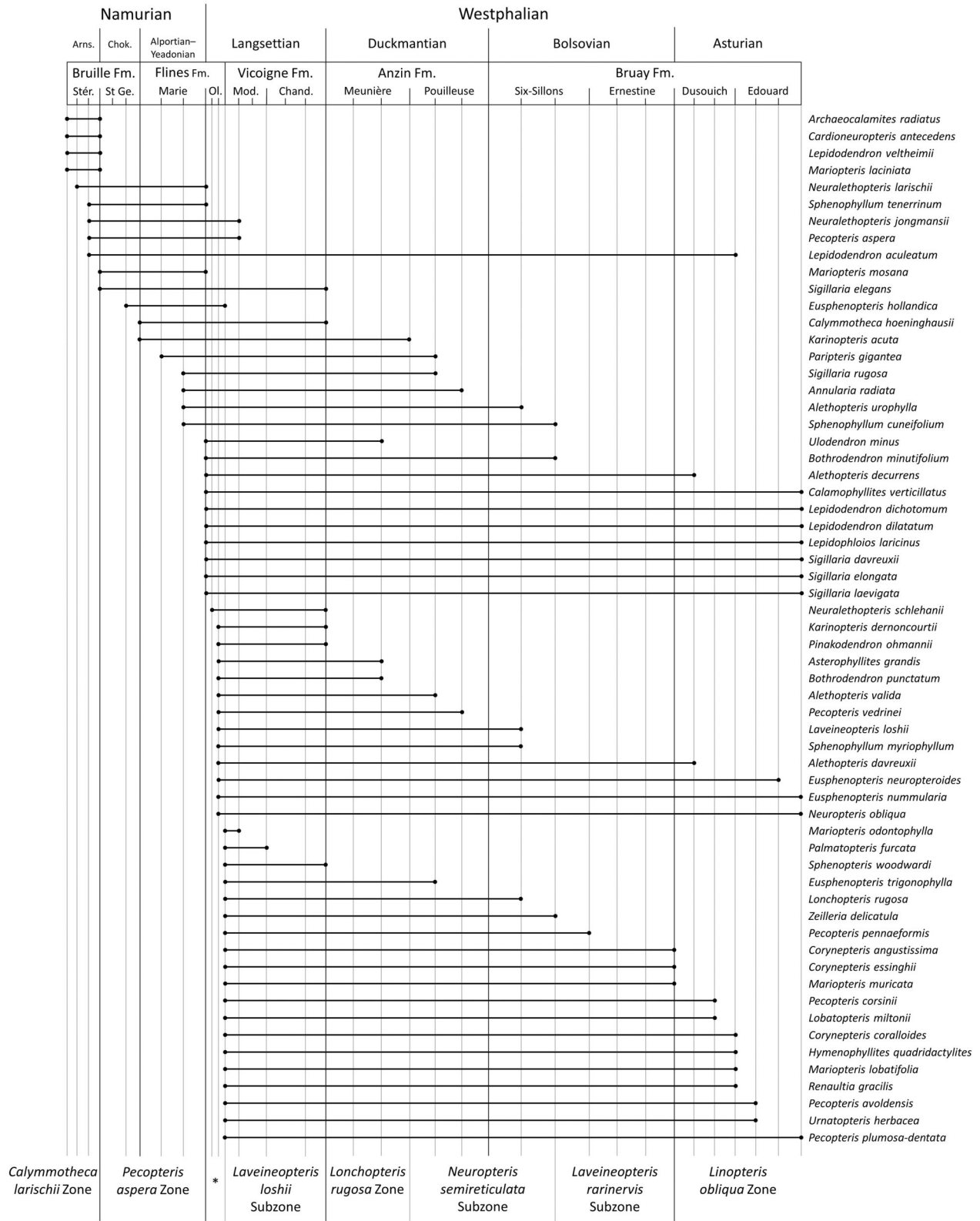


FIG. 1. Macrofloral biostratigraphy of the Nord-Pas-de-Calais Coalfield (Part 1). Stratigraphical ranges correspond to the key species of major floral changes only. Biozones according to Opluštil *et al.* (2022). Asterisk indicates *Neuralethopteris jongmansii* Subzone. Abbreviations: Arns., Arnsbergian; Chand., Chandelur; Chok., Chokierian; Mod., Modeste; Ol., Olympe; St Ge., St Georges; Stér., Stérole.

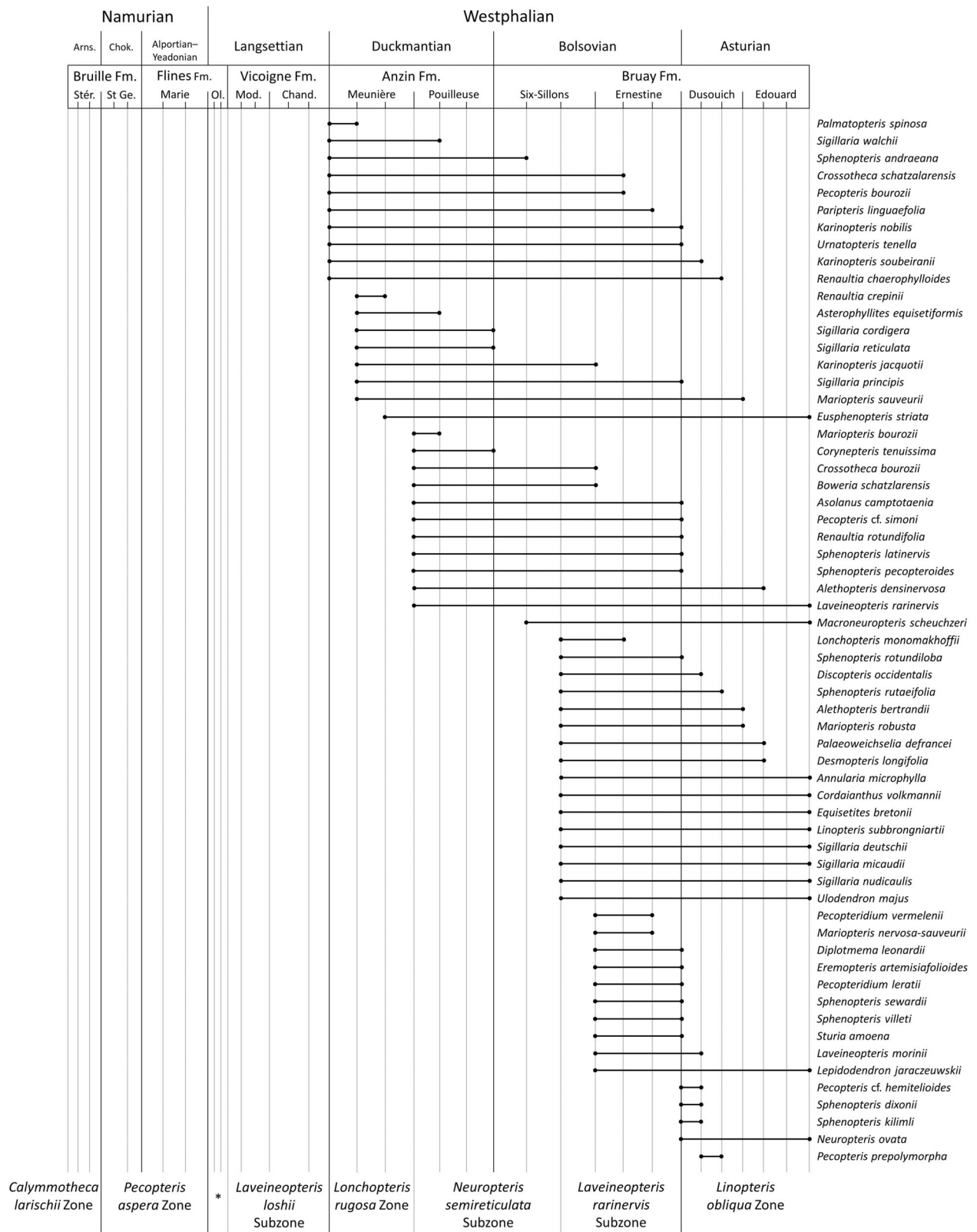


FIG. 2. Macrofloral biostratigraphy of the Nord-Pas-de-Calais Coalfield (Part 2). Stratigraphical ranges correspond to the key species of major floral changes only. Biozones according to Opluštil *et al.* (2022). Asterisk indicates *Neurolethopteris jongmansii* Subzone. Abbreviations: Arns., Arnsbergian; Chand., Chandeleur; Chok., Chokierian; Mod., Modeste; OL., Olympe; St Ge., St Georges; Stér., Stérile.

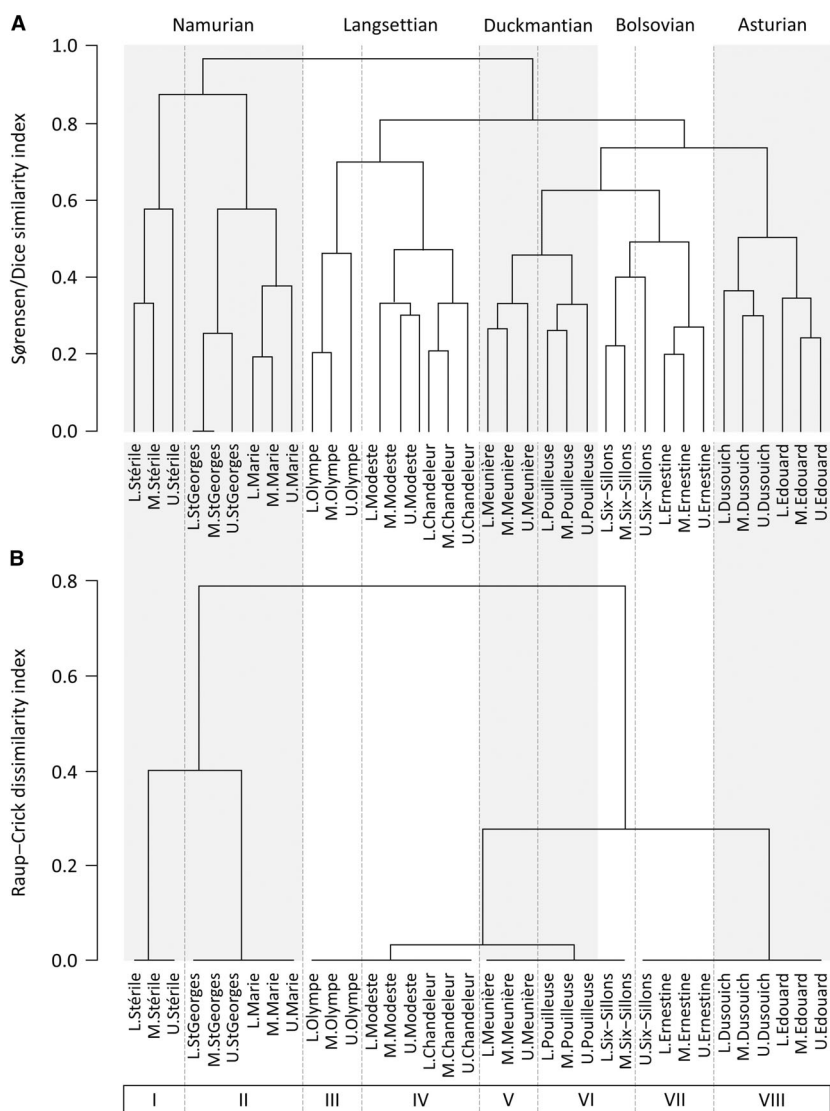


FIG. 3. Cluster analysis of the palaeofloristic composition of the Nord-Pas-de-Calais Coalfield. A, Sørensen/Dice clustering results. B, Raup-Crick clustering results.

Cluster II

These macrofloras occur in the upper Bruille Formation (St Georges Member) and lower Flines Formation (Marie Member). Although still of relatively low diversity, they represent a marked change in composition, with the appearance of *Eusphenopteris hollandica* (Fig. 5F), *Lepidodendron aculeatum*, *Mariopteris mosana* (Fig. 8A), *Neuralethopteris jongmansii*, *Pecopteris aspera*, *Sigillaria elegans* and, a little higher at the Bruille–Flines transition, by the appearance of *Karinopteris acuta* (Fig. 6D) and *Calymmotheca hoeninghausii* (Fig. 1); several of the typically Mississippian species also disappear at about the base of this interval, including

Archaeocalamites radiatus, *Cardioneuropteris antecedens* and *Lepidodendron veltheimii*.

Cluster III

This consists of the macrofloras of the Olympe Member (upper Flines Formation). It includes several species also found in the underlying Namurian macrofloras such as *Alethopteris urophylla* (Fig. 5C, D), *Calymmotheca hoeninghausii*, *Karinopteris acuta* (Fig. 6D) and *Neuralethopteris schlehanii* (Fig. 8E), but also includes the appearance of *Alethopteris decurrens* and various arborescent lycopsid species such as *Bothrodendron minutifolium*, *Lepidodendron*

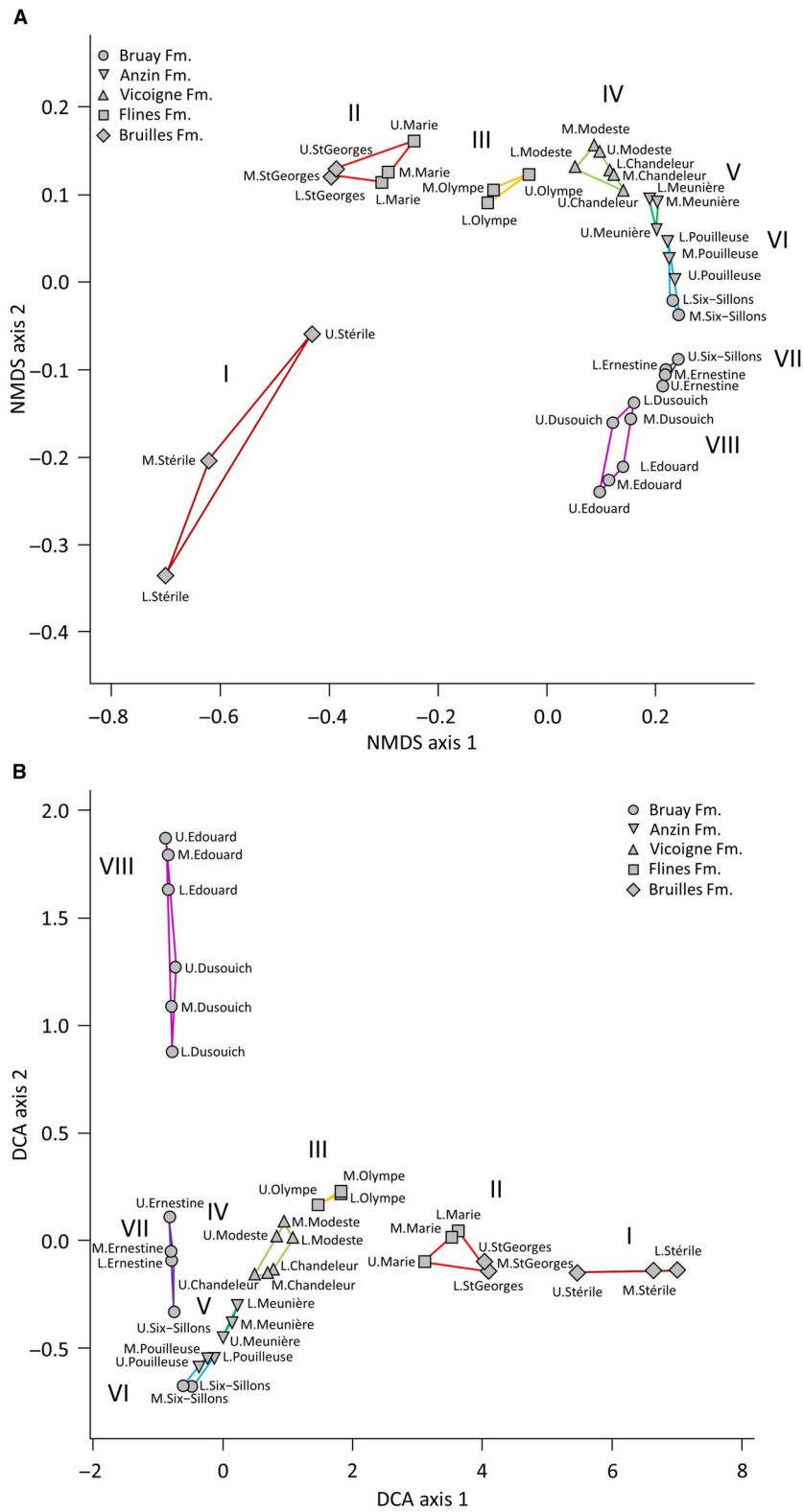


FIG. 4. Ordination analysis of the palaeofloristic composition of the Nord-Pas-de-Calais Coalfield. A, Sørensen/Dice-based non-metric multidimensional scaling (NMDS) results (stress value = 0.045). B, detrending correspondence analysis (DCA) results.



FIG. 5. Main species of the palaeofloristic associations from the Nord-Pas-de-Calais Coalfield (Part 1). A, *Alethopteris davreuxii* Brongniart (Medullosales); fragment of frond showing the insertion of primary pinnules; USTL 4178, Westphalian (Duckmantian) Anzin Formation. B, *Alethopteris densinervosa* Wagner (Medullosales); detail of secondary pinnules with venation; USTL 4146, Westphalian (Bolsovia) lower Bruay Formation. C–D, *Alethopteris urophylla* (Brongniart) Göppert (Medullosales); primary pinnules from distal part of frond: C, USTL 4180, Westphalian (Langsetian) Vicoigne Formation; D, USTL 4181, Westphalian (Bolsovia) lower Bruay Formation. E, *Alethopteris valida* Boulay (Medullosales); fragment of primary pinnule showing the typical venation; USTL 4156, Westphalian (Duckmantian) Anzin Formation. F, *Eusphenopteris hollandica* (Gothan & Jongmans) Novik; detail of secondary pinnules; USTL 4210, Namurian (Alportian–Yeadonian) lower Flines Formation. Specimens are housed in the palaeobotanical collections of the University of Lille. Scale bars represent: 1 cm (A–E); 0.5 cm (F).

dichotomum, *Lepidodendron simile*, *Sigillaria davreuxii* and *Sigillaria elongata* (Fig. 1).

Cluster IV

A visual inspection of the range chart shows many species appearing at about the base of the Vicoigne Formation and this important change is clearly represented in the cluster analysis using Sørensen/Dice coefficients, but less so in the two ordination analyses, and very little in the cluster analysis using Raup–Crick coefficients (Fig. 3B). This discrepancy in the analyses, which will be discussed later, seems to occur because the change is mainly due to species appearances with few accompanying extinctions. Characteristic species of this cluster include *Alethopteris davreuxii* (Fig. 5A), *Alethopteris urophylla* (Fig. 5D), *Eusphenopteris nummularia*, *Eusphenopteris trigonophylla*, *Karinopteris acuta* (Fig. 6D), *Laveinopteris loshii*, *Lobatopteris miltonii*, *Lonchopteris eschweiliana* (Fig. 7C), *Mariopteris muricata* (Fig. 8B), *Neuraletopteris schlehanii* (Fig. 8E), *Neuropteris heterophylla* (Fig. 9A), *Neuropteris obliqua* and *Pecopteris pennaeformis*.

Corsin (1962) differentiated the macrofloras of the Modeste and Chandeaur members, with the former being characterized by *Palmatopteris furcata*, *Paripteris gigantea*, *Sigillaria elegans*, *S. laevigata*, *Sphenophyllum cuneifolium* and *Sphenopteris laurentii*; and the latter by *Alethopteris valida* (Fig. 5E), *Karinopteris daviesii*, *Lonchopteris eschweiliana*, *L. rugosa*, *Mariopteris muricata* and *Neuropteris heterophylla*, and, to a lesser extent, *Paripteris gigantea*. However, this distinction is not noticeable in our range chart (Figs 1, 2) or in any of the numerical analyses (Figs 3, 4).

Cluster V

The macrofloras remain essentially similar throughout the Vicoigne Formation and into the lower Anzin Formation. However, a weak vegetation change is evident at the base of the Anzin Formation, most notably in the cluster analysis using Sørensen/Dice coefficients and along axis 2 in

both ordinations (Figs 3A, 4). The change is most distinguished in the extinction of several taxa characteristic of Langsetian and earlier floras, including *Calymmotheca* spp. (notably *C. hoeninghausii*), *Karinopteris acuta* (Fig. 6D), *Neuraletopteris* spp. (notably *N. schlehanii*) and *Paripteris gigantea*. The cluster is nevertheless characterized by the abundance of *Alethopteris valida* (Fig. 5E), *Karinopteris daviesii* (Fig. 6E), *Laveinopteris tenuifolia* (Fig. 7A), *Lonchopteris eschweiliana* (Fig. 7C), *Lonchopteris rugosa* (Fig. 7D), *Mariopteris muricata* (Fig. 8B), *Neuropteris heterophylla* (Fig. 9A) and *Pecopteris volkmannii* (Fig. 9D). Other important Meunière species are *Paripteris gigantea*, *Pecopteris pennaeformis*, *Sigillaria elongata*, *S. scutellata* and *Sphenophyllum myriophyllum* (Fig. 1).

Cluster VI

The base of cluster VI represents one of the most significant changes in the macrofloras, involving both species appearances and (at about the same level) extinctions, and is most marked in the Raup–Crick cluster analysis and on axis 2 of the DCA ordination (Figs 3, 4). The cluster VI macrofloras range throughout the Pouilleuse Member and lower to middle Six-Sillons Member, and are characterized by abundant *Alethopteris davreuxii* (Fig. 5A), *Alethopteris densinervosa* (Fig. 5B), *Alethopteris urophylla* (Fig. 5D), *Fortopteris latifolia* (Fig. 6C), *Macro-neuropteris scheuchzeri* (Fig. 7E), *Mariopteris sauveurii* (Fig. 8D), *Paripteris pseudogigantea* (Fig. 9B) and *Pecopteris avoldensis* (Fig. 9C); also *Asolanus camptotaenia*, *Boweria schatzlarensis*, *Corynepteris tenuissima*, *Eusphenopteris neuropteroides* (Fig. 6A), *Eusphenopteris striata* (Fig. 6B), *Lonchopteris rugosa* (Fig. 7D), *Pecopteris volkmannii* (Fig. 9D), *Renaultia rotundifolia*, *Sphenopteris pecopteroides* and rare *Reticulopteris muensteri* (Fig. 9E).

Cluster VII

The range chart shows another significant change at the upper Six-Sillons Member (lower Bruay Formation), and this is confirmed by both the cluster analysis and a

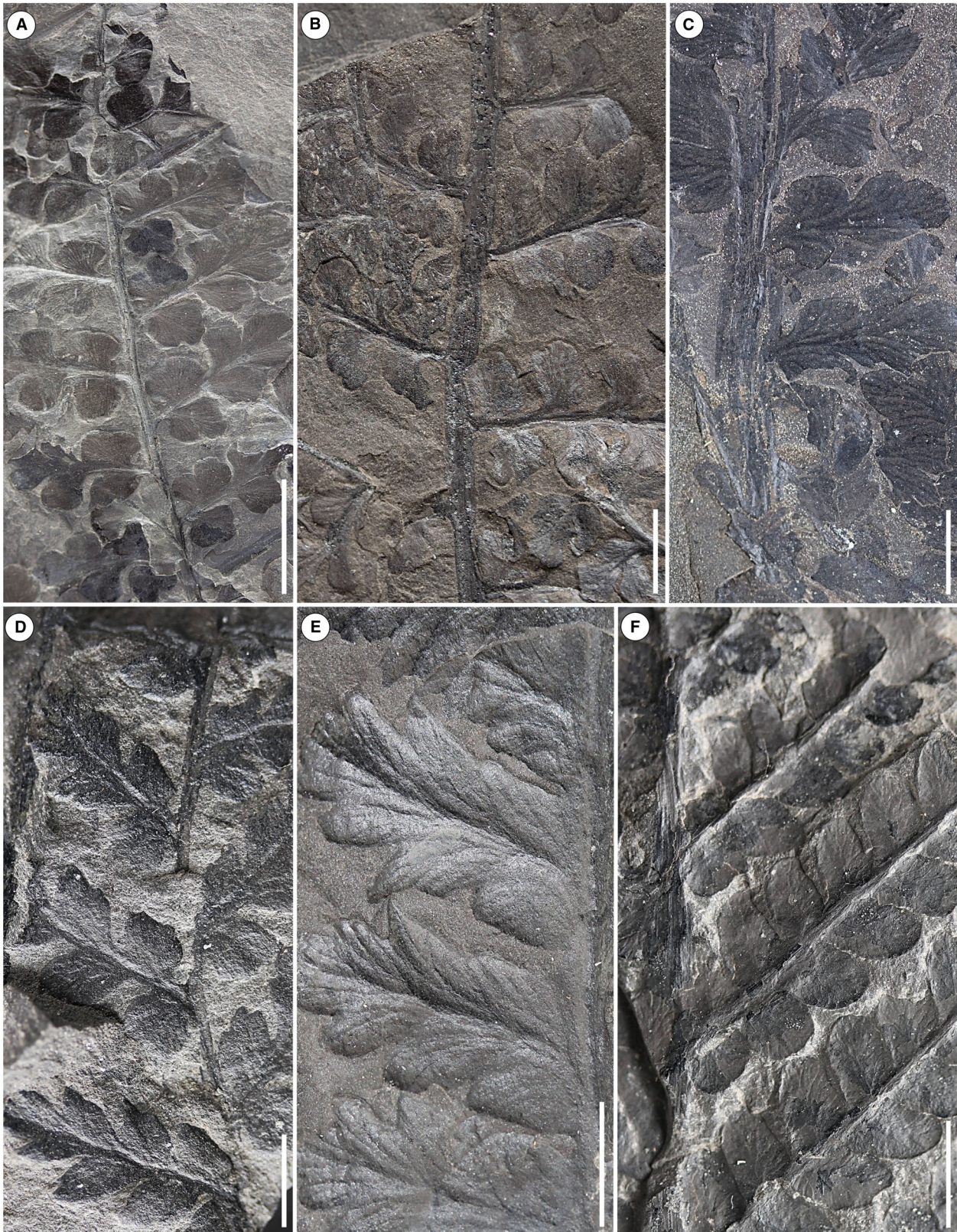


FIG. 6. Main species of the palaeofloristic associations from the Nord-Pas-de-Calais Coalfield (Part 2). A–B, general view of secondary pinnules: A, *Eusphenopteris neuropteroides* (Boulay) Novik (Lyginopteridales); USTL 4197, Westphalian (Duckmantian) Anzin Formation; B, *Eusphenopteris striata* (Gothan) Novik (Lyginopteridales); USTL 4202, Westphalian (Duckmantian) Anzin Formation. C–E, detail of secondary pinnules with venation: C, *Fortopteris latifolia* (Zeiller) Boersma (Lyginopteridales); USTL 4187, Westphalian (Bolsvian) lower Bruay Formation; D, *Karinopteris acuta* (Brongniart) Boersma (Lyginopteridales); USTL 4165, Westphalian (Langsetian) Vicoigne Formation; E, *Karinopteris daviesii* (Kidston) Boersma (Lyginopteridales); USTL 4169, Westphalian (Duckmantian) Anzin Formation. F, general view of a primary pinnule; *Laveineopteris rarinervis* (Bunbury) Cleal *et al.* (Medulloales); USTL 3402, Westphalian (Asturian) upper Bruay Formation. Specimens are housed in the palaeobotanical collections of the University of Lille. Scale bars represent: 1 cm (A); 0.5 cm (B–F).

notable increase in axis 2 scores of the DCA ordination (Figs 3B, 4B). However, many of the species that appear here are relatively rare (e.g. sphenopteroid ferns and sigillarians, such as *Sphenopteris rotundiloba*, *S. rutaefolia* or *Sigillaria nudicaulis*), the notable exceptions being *Eusphenopteris neuropteroides* (Fig. 6A), *Eusphenopteris striata* (Fig. 6B), *Laveineopteris rarinervis* (Fig. 6F), *Linopteris subbrongniartii* (Fig. 7B), *Mariopteris sauveurii* (Fig. 8D), *Palaeoweichselia defrancei*, *Paripteris pseudogigantea* (Fig. 9B) and *Reticulopteris muensteri* (Fig. 9E).

Cluster VIII

The cluster analysis with Sørensen/Dice coefficients shows a significant break in the macrofloral sequence at the base of the Dusouch Member (upper Bruay Formation) (Fig. 3A). This change is also clearly reflected by significantly higher scores on axis 2 of the DCA ordination and, to a lesser extent, low axis 2 scores on the NMDS ordination (Fig. 4). One of the advantages of DCA ordination is that it can show which taxa are causing assemblages to have high or low scores on specific axes, and in this case the high axis 2 scores are due to the presence of typically late Westphalian species including *Neuropteris ovata*, *Laveineopteris dussartii*, and several rare marattialean and callistophyte species. In addition, there are many species also found in the earlier macrofloras such as *Laveineopteris rarinervis* (Fig. 6F), *Mariopteris nervosa* (Fig. 8C) and *Reticulopteris muensteri* (Fig. 9E).

DISCUSSION

Biostratigraphy and floral characterization of the Nord-Pas-de-Calais Coalfield

The biostratigraphical model proposed here compares well with the previously established biozonations for the Nord-Pas-de-Calais (Zeiller 1894; Bertrand 1914, 1919; Corsin & Corsin 1970, 1971), as well as the synthetic regional scheme developed by Wagner (1984) and Cleal (1991); see also Opluštil *et al.* (2022). There is also

broad agreement with the various informally recognized palaeofloristic associations recognized by Corsin (1962) (Figs 10, 11). However, our zones have the merit of having been developed using objective numerical analyses of the data.

The recognition of two macrofloral clusters (I and II) for the Namurian part of the succession separated at about the boundary between the Stérile and St Georges members (boundary of Arnsbergian and Chokierian sub-stages; Chalard 1960; Becq-Giraudon 1983) is in broad agreement with most of the earlier schemes; only Zeiller (1894) did not differentiate these Namurian biozones, referring to them together as subzone A₁, probably due to the relative low diversity of these macrofloras in Nord-Pas-de-Calais. The stratigraphically older cluster represents typically Mississippian macrofloras, and corresponds to the *Mariopteris lacinata* Subzone of Corsin & Corsin (1971) and the *Calymmotheca larischii* Zone in the Wagner–Cleal biostratigraphy. Similar low-diversity floras are known from South Wales (Dix 1933), Belgium (Stockmans & Willière 1953), Upper Silesia (Purkyňová 1970), the Donets (Novik 1974) and northern Turkey (Jongmans 1955); the general low diversity of these macrofloras is interpreted as a consequence of the widespread regression that took place at the onset of the Pennsylvanian, resulting in a non-depositional gap immediately after the Mississippian (Wagner 1984).

Cluster II corresponds to the *Neuraethopteris larischii* – *Pecopteris aspera* Subzone of Corsin & Corsin (1971) and the *Pecopteris aspera* Zone in the Wagner–Cleal scheme. Comparable macrofloras are generally rare in Euramerica but have been reported from the Ruhr Coalfield (Josten 1983), Belgium (Stockmans & Willière 1953) and the Svoge in Bulgaria (Tenčov 1977).

Clusters III and IV range throughout the Langsetian part of the succession, corresponding to the *Calymmotheca hoeninghausii* Zone of the Wagner–Cleal scheme and approximately to Zeiller's (1894) Zone A₂ and Corsin & Corsin's (1971) *Neuraethopteris schlehanii* – *Lyginopteris hoeninghausii* – *Karinopteris acuta* Subzone (upper *Neuraethopteris* Zone). The base of the interval is the most important change in the Nord-Pas-de-Calais macrofloras as shown by both cluster analyses (Fig. 3), and



FIG. 7. Main species of the palaeofloristic associations from the Nord-Pas-de-Calais Coalfield (Part 3). A, *Laveinopteris tenuifolia* (Sternberg) Cleal *et al.* (Medullosales); general view of secondary pinnules with venation; USTL 4191, Westphalian (Bolsovian–Asturian) Bruay Formation. B, *Linopteris subbrongniartii* Grand'Eury (Medullosales); fragment of terminal part of primary pinnule; USTL 3335, Westphalian (Bolsovian–Asturian) Bruay Formation. C, *Lonchopteris eschweiliana* Andrä (Medullosales); fragment of frond showing the insertion of primary pinnules; USTL 4152, Westphalian (Langsettian) Vicoigne Formation. D, *Lonchopteris rugosa* Brongniart (Medullosales); fragment of frond showing the characteristic disposition of pinnules; USTL 4150, Westphalian (Duckmantian) Anzin Formation. E, *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* (Medullosales); detail of secondary pinnules with venation; USTL 4189, Westphalian (Bolsovian) lower Bruay Formation. Specimens are housed in the palaeobotanical collections of the University of Lille. Scale bars represent: 1 cm (A–D); 0.5 cm (E).

represents the appearance and diversification of the typical coal swamp vegetation (Molina-Solís *et al.* 2023).

The Langsettian macrofloras were not divided in the Zeiller (1894) or Corsin & Corsin (1971) biostratigraphies, but Dix (1934) distinguished Zones C and D, which Cleal (1991) then used to differentiate the *Neuralopteris jongmansii* and *Laveinopteris loshii* Subzones of the *Calymmotheca hoeninghausii* Zone. Cluster III, as differentiated in both cluster and ordination analyses (Figs 3, 4), corresponds to the *N. jongmansii* Subzone and involves a major increase in diversity of the arborescent lycopsids (*Bothrodendron*, *Lepidodendron*, *Sigillaria* and *Ulodendron*). This reflects the expansion of the coal swamp biome that occurred over much of the Variscan Foreland at the start of the Westphalian (marked by the *Subcrenatum* goniatite level), to form the first major tropical rainforests (Cleal & Thomas 1994; Cleal *et al.* 2009b). Examples of these macrofloras are generally rare, the best documented examples being from the Nant Llech beds in South Wales (Dix 1933).

The cluster IV macrofloras of the Modeste and Chandeaur members reflect a major diversification among pteridosperms, including some of the most characteristic adpression taxa found in the lower Westphalian of the Variscan Foreland. This cluster corresponds to the *Laveinopteris loshii* Subzone in the Wagner–Cleal scheme and its appearance coincides with the disappearance of marine bands such as that above the Farewell Rock in the Lower Coal Measures of South Wales (Cleal 2007) and the base of the Bochum Formation in the Ruhr (Josten 1991).

Cluster V in the Meunière Member is broadly equivalent to the *Lonchopteris rugosa* Zone in the Wagner–Cleal scheme and to Zone E in the Dix (1934) scheme. They represent the most diverse coal swamp macrofloras from the lower half (Langsettian–Duckmantian) of the Westphalian in Nord-Pas-de-Calais (Molina-Solís *et al.* 2023) and can be compared with similarly diverse floras such as at the Barnsley Seam in Yorkshire (Cleal 2005), the Upper Nine Feet Seam in South Wales (Cleal 2007), and the Essen Formation in the Ruhr (Josten 1991; Uhl & Cleal 2010). However, an examination of the Nord-Pas-de-Calais range chart (Figs 1, 2) indicates that the base of this cluster is less sharply marked than some of the other

cluster or biozone boundaries recognized here, and that other more subtle compositional changes also occur at other levels throughout the Meunière Member. The general pattern of upper Langsettian to middle Duckmantian macrofloras, therefore, seems to involve a gradual vegetation change rather than a sudden turnover reflecting a major ecological disruption. The gradual nature of this change explains the discrepancies in the number of biozones and their boundaries in previously proposed biostratigraphies (Fig. 11). However, our more objective, numerical analysis of the data appears to corroborate that the Meunière Member macrofloras represent a coherent, identifiable floristic biozone, equivalent to the *Lonchopteris rugosa* Zone of the Wagner–Cleal scheme.

The cluster and ordination analyses (Figs 3, 4) show the base of cluster VI to be the most important change in the Westphalian macrofloras. It can be correlated with the base of the *Paripteris linguaefolia* Zone (*Neuropteris semireticulata* Subzone) in the Wagner–Cleal scheme and of Zone F of Dix (1934), and coincides with the re-appearance of several marine bands in the British successions (Table 1). Zeiller (1894), Bertrand (1914, 1919) and Corsin & Corsin (1970, 1971) placed the equivalent biozonal change rather higher in the Nord-Pas-de-Calais succession, in the upper Pouilleuse Member. This is probably because marine flooding did not occur here until rather later. For instance, in the British coalfields there is a series of marine bands throughout the upper Duckmantian and lower Bolsovian (Waters *et al.* 2001), whereas in Nord-Pas-de-Calais there is only one significant marine band in this interval (the *Rimbert*), at the Duckmantian–Bolsovian boundary. Nevertheless, our numerical analyses indicate that a significant change in the Nord-Pas-de-Calais macrofloras occurs at about the Meunière–Pouilleuse member boundary, which is equivalent in age to the base of the *Paripteris linguaefolia* Zone in the Wagner–Cleal scheme.

Macrofloras similar to the Nord-Pas-de-Calais cluster VI are known from the Middle Coal Measures of South Wales such as the Four Feet Seam (Dix 1934; Cleal 2007). They are also known from the Middle Coal Measures of northern England (Cleal 2005) and the Horst and Dorsten formations of the Ruhr (Uhl & Cleal 2010), but in

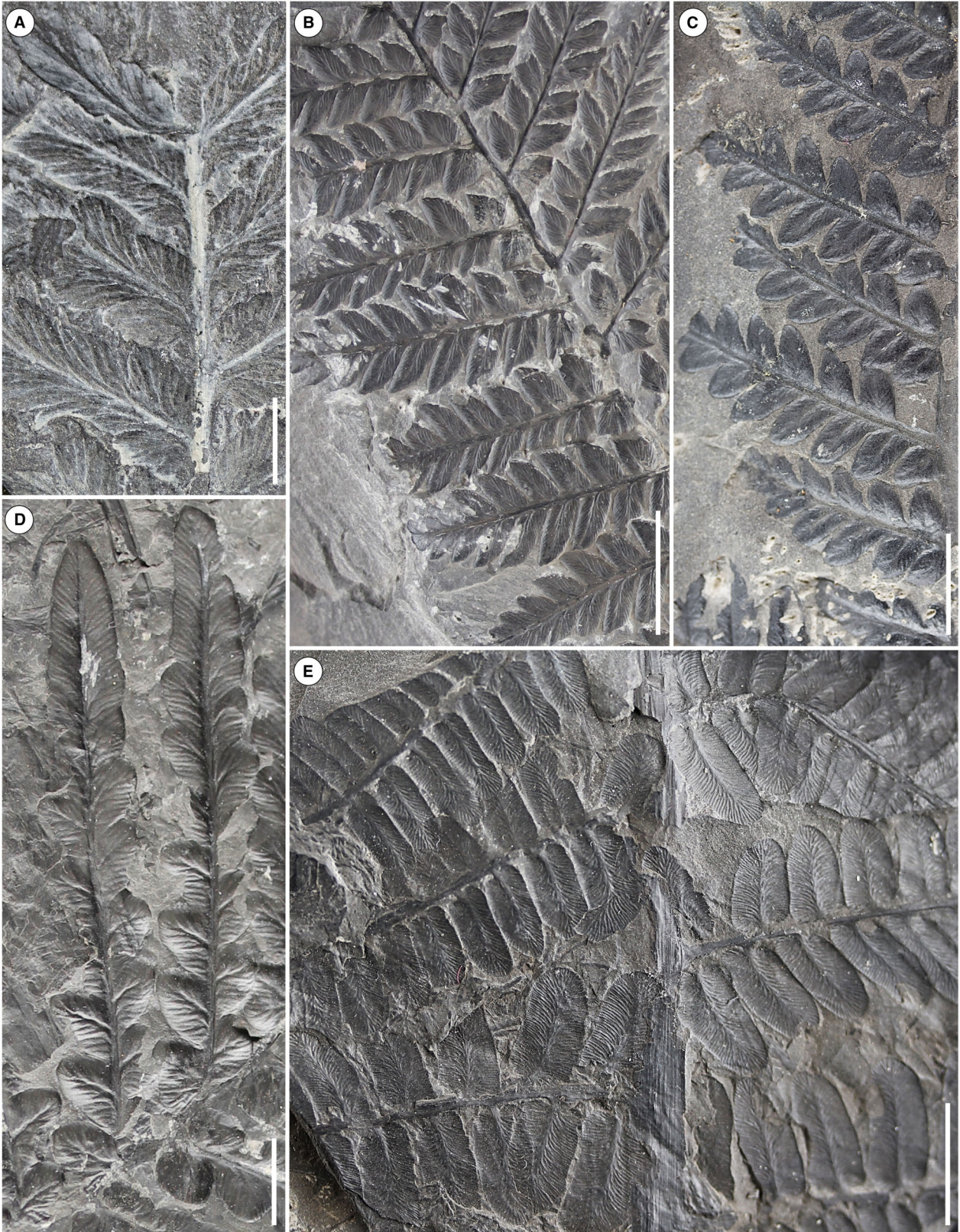


FIG. 8. Main species of the palaeofloristic associations from the Nord-Pas-de-Calais Coalfield (Part 4). A, *Mariopteris mosana* Willière (Lyginopteridales); detail of secondary pinnules with venation; USTL 4208, Namurian (Alportian–Yeadonian) lower Flines Formation. B, *Mariopteris muricata* Schlotheim (Lyginopteridales); general view of frond showing the typical bifurcation and pinnules disposition; USTL 4163, Westphalian (Duckmantian) Anzin Formation. C, *Mariopteris nervosa* Brongniart (Lyginopteridales); general view of distal part of frond showing the pinnules disposition; USTL 4184, Westphalian (Asturian) upper Bruay Formation. D, *Mariopteris sauveurii* (Brongniart) Stur (Lyginopteridales); fragment of secondary pinnules showing the characteristic venation; USTL 4158, Westphalian (Bolsovian) lower Bruay Formation. E, *Neuralethopteris schlehanii* Stur (Medullosales); fragment of frond showing the insertion of primary pinnules and secondary venation; USTL 4174, Westphalian (Langsettian) Vicoigne Formation. Specimens are housed in the palaeobotanical collections of the University of Lille. Scale bars represent: 0.5 cm (A); 2 cm (B); 1 cm (C–E).

both these areas vegetation diversity was in decline, probably due to changing landscape and sedimentation patterns. Indeed, there is a clear increase in arenaceous deposits in the Horst and Dorsten formations, indicating a change in landscape to upper delta and higher energy fluvial systems (e.g. Uhl & Cleal 2010). It is difficult to be sure whether such changes in species diversity are caused by sampling ('artefacts'), although in the Pennines data at least some of the stratigraphically younger but lower diversity floras (e.g. from the Shafton Coal) are reasonably well-sampled. Furthermore, similar-age macroflora, but from upland coal swamps, are known from the Sulzbach Formation of Saar-Lorraine (Laveine 1989), the lower Radnice Member of West and Central Bohemia (Pešek 1994), and the Žďárky Member of the Intra Sudetic Basin (Opluštil *et al.* 2017).

The appearance of cluster VII macrofloras in the upper Six-Sillons Member is accompanied by a significant increase in species richness (Molina-Solís *et al.* 2023) and is clearly represented in the cluster analysis using Raup–Crick coefficients (Fig. 3B) and in axis 2 of the DCA ordination (Fig. 4B). It was recognized in the biostratigraphy of Zeiller (1894) as the base of Zone C and the base of the *Fortopteris latifolia* – *Linopteris subbrongniartii* – *Mariopteris nervosa* – *Laveinopteris tenuifolia* Zone by Corsin & Corsin (1971). The appearance of *Laveinopteris rarinervis* suggests an equivalence with the *L. rarinervis* Subzone in the Wagner–Cleal scheme and Zone G of Dix (1934) (Table 1). Macrofloras of this type are relatively unusual, the most diverse being from the lower Pennant Formation of South Wales, such as that from the No. 2 Rhondda Coal (Cleal 1978, 2007), and the Tracy Coal of the South Bar Formation of Cape Breton, Canada (Bell 1938; Zodrow & Cleal 1985).

The base of cluster VIII coincides with the base of the C₂ Subzone of Zeiller (1894) and that of the *Eusphenopteris* ('*Diplothemema*') *leonardii* Subzone of Corsin & Corsin (1971). The most obvious change to the macrofloras is a dramatic decline in species richness, especially of the lyginopteridaleans and of sphenopteroid ferns (e.g. species of *Renaultia* and *Urnatopteris*), which appears to be not merely an effect of poor sampling or an 'edge-effect' (Molina-Solís *et al.* 2023). However, this level also

involves the appearance of *Neuropteris ovata*, which is usually taken as marking the base of the *Linopteris obliqua* Zone, which, in turn, is taken as an indicator of the base of the Asturian ('Westphalian D') Substage (Laveine 1967, 1977). *Linopteris obliqua* Zone macrofloras are best documented elsewhere in South Wales (Cleal 1978, 1997, 2007) and Saar-Lorraine (Cleal 1984a; Laveine 1989) and, to a lesser extent, in the Canadian Maritime Provinces (Bell 1938; Zodrow & Cleal 1985) and northern Spain (Wagner & Álvarez-Vázquez 1991, 2010).

Evolution of Nord-Pas-de-Calais swamp vegetation

The results of this analysis are in general agreement with the various previous biostratigraphical schemes (Table 1). These schemes were developed using different methodological approaches, suggesting that the underlying pattern of macrofloral change that they show is robust and provides a good indication of the vegetational dynamics in the Westphalian-age coal swamps.

The present study used numerical analyses to identify the underlying distributional patterns. Constrained cluster analysis using Raup–Crick coefficients produced the clearest groupings, which confirms evidence from previous studies (e.g. Cleal 2008a, 2008b; Cleal *et al.* 2012; Fig. 3B). The Raup–Crick coefficients were particularly sensitive for detecting the macrofloral changes when there are comparable numbers of species extinctions and appearances, such as at the base of the Olympe and Pouilleuse members (Fig. 3B). However, when there are mainly only species appearances with few accompanying extinctions, or mainly only species extinctions and few appearances, the Raup–Crick coefficients are much less sensitive. This is because Raup–Crick coefficients are not true measures of similarity, but represent the probability of observing at least *n* common species between the compared samples (Raup & Crick 1979). When the observed difference between assemblages is mainly due to either a loss or a gain of species, Raup–Crick coefficients will show little change because it is assumed that the missing taxa in the smaller sample are the result of a random effect such as sampling effort. Sørensen/Dice

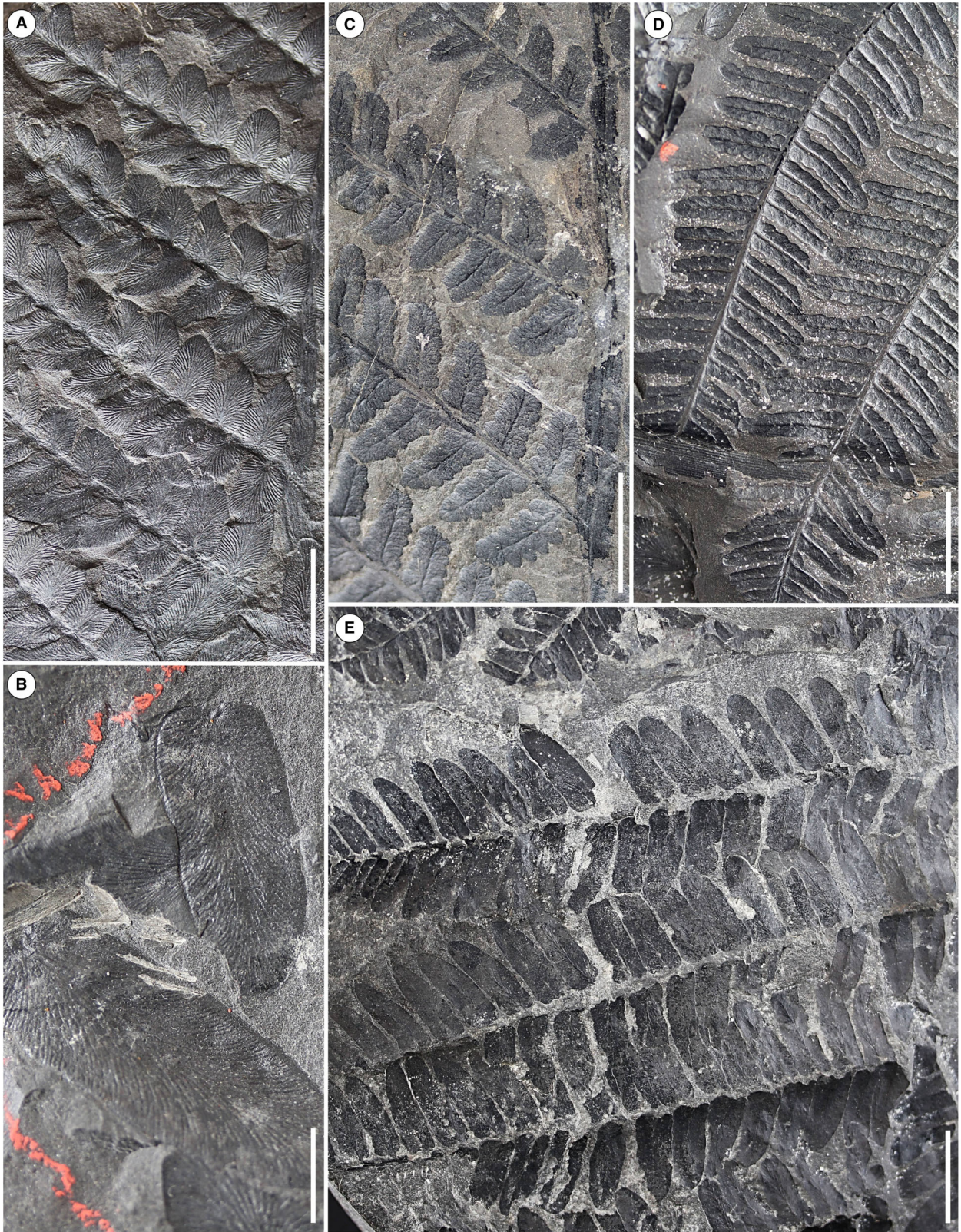


FIG. 9. Main species of the palaeofloristic associations from the Nord-Pas-de-Calais Coalfield (Part 5). A, *Neuropteris heterophylla* Brongniart (Medullosales); fragment of frond showing the insertion of secondary pinnules; USTL 4194, Westphalian (Langsetian) Vicoigne Formation. B, *Paripteris pseudogigantea* Potonié (Medullosales); fragments of secondary pinnules; USTL 3874, Westphalian (Bolsovian) lower Bruay Formation. C–E, fragments of frond showing the secondary pinnules: C, *Pecopteris avoldensis* Stur (non-marattialean ferns); MBL36 (DalINVAL 1960, pl. 57, fig. 2), Westphalian (Bolsovian) lower Bruay Formation; D, *Pecopteris volkmannii* Sauveur (non-marattialean ferns); MBL180 (DalINVAL 1960, pl. 26, fig. 1), Westphalian (Duckmantian) Anzin Formation; E, *Reticulopteris muensteri* Eichwald (Medullosales); USTL 4171, Westphalian (Bolsovian–Asturian) Bruay Formation. Specimens are housed in the palaeobotanical collections of the University of Lille. Scale bars represent: 1 cm (A, C, D); 0.5 cm (B); 2 cm (E).

WE chronostratigraphy			Lithostratigraphy		Palaeofloristic associations ^{1,2}	Macrofloral zonations				
Epoch	Stage	Subst.	Fm.	Mbr.		Zeiller's zonation ³	HBNPC floral zones ⁴		WE floral zones ⁵	
							Zone	Subzone	Zone	Subzone
Early Pennsylvanian	Namurian	Alportian–yeaddonian	Flines	Marie	<i>Pecopteris aspera</i> <i>Neuraethopteris schlehanii</i> <i>Eusphenopteris hollandica</i> <i>Mariopteris mosana</i> <i>Calymmotheca hoeninghausii</i> <i>Karinopteris acuta</i>	A ₁	Neuraethopteris	<i>Neuraethopteris larischii</i> , <i>Pecopteris aspera</i>	<i>Pecopteris aspera</i>	<i>Neuraethopteris larischii</i>
										<i>Sigillaria elegans</i>
Late Mississippian	Arnsbergian	Chok.	Bruille	St Ge.	<i>Pecopteris aspera</i> <i>Neuraethopteris schlehanii</i> <i>Mariopteris mosana</i>					
				Stérile	<i>Karinopteris laciniata</i> <i>Cardioneuropteris antecessens</i> <i>Lepidodendron veltheimii</i>			<i>Karinopteris laciniata</i>		<i>Calymmotheca larischii</i>

FIG. 10. Palaeofloristic associations and relative position of the Namurian macrofloral biozonations in the Nord-Pas-de-Calais Coalfield. In floral associations, species appear in decreasing order of abundance. Sources: 1, Corsin (1962); 2, Loboziak (1971); 3, Laveine (1987); 4, Corsin & Corsin (1971); 5, Opluštil *et al.* (2022). Abbreviations: Chok., Chokierian; Fm., Formation; HBNPC, Houillères du bassin du Nord et du Pas-de-Calais; Mbr, Member; St Ge., St Georges; Subst., Substage; WE, western European.

coefficients, in contrast, provide a more direct indication of both how many species are in common between assemblages and how many are absent in one but not the other (although the absences have less effect than in the related Jaccard similarity analysis). Consequently, Sørensen/Dice coefficients have shown, more clearly than the Raup–Crick coefficients, the pulse of species appearances at the base of the Modeste Member and of extinctions at the base of the Dusouich Member (Fig. 3A). This demonstrates the value of using different

approaches in parallel in such studies, given that each will elucidate a different aspect of the structure of a complex dataset.

Ordination is intended to identify gradational relationships rather than discontinuities in data (Pardo *et al.* 2021) and hence is less successful in elucidating biozonal boundaries. Nevertheless, ordination has been helpful in confirming the underlying structure of the data revealed by cluster analysis, especially given that it arranges the data in a multidimensional space, rather than

WE chrono-stratigraphy		Litho-stratigraphy		Palaeofloristic associations ^{1,2}	Macrofloral zonations											
Epoch	Stage	Subst.	Fm.		Mbr.	Zeiller's zonation ³	HBNPC floral zones ⁴		WE floral zones ⁵							
							Zone	Subzone	Zone	Subzone						
Middle Pennsylvanian	Westphalian	Asturian	Bruay	Ed.	<i>Linopteris subbrongniartii</i> <i>Laveineopteris rarinervis</i> <i>Macroneuropteris scheuchzeri</i> <i>Alethopteris densinervosa</i> <i>Fortopteris latifolia</i> <i>Mariopteris nervosa</i> <i>Pecopteris avoldensis</i> <i>Diplotmema leonardii</i>	C ₂	<i>Fortopteris latifolia</i> , <i>Linopteris subbrongniartii</i> , <i>Mariopteris nervosa</i> , <i>Laveineopteris tenuifolia</i>	<i>Diplotmema leonardii</i>	<i>Linopteris obliqua</i>							
				Dus.												
				Ernestine												
		Bolsovian	Bruay	Six-Sillons	<i>Neuropteris flexuosa</i> <i>Paripteris pseudogigantea</i> <i>Mariopteris sauveurii</i> <i>Reticulopteris münsteri</i> <i>Eusphenopteris striata</i> <i>Eusphenopteris neuropteroides</i>	B ₃	<i>Neuropteris semireticulata</i> , <i>Laveineopteris tenuifolia</i>	<i>Paripteris linguaefolia</i>	<i>Neuropteris semireticulata</i>							
				Anzin	Pouilleuse						<i>Alethopteris davreuxii</i> <i>Lonchopteris rugosa</i> <i>Pecopteris volkmannii</i> <i>Mariopteris sauveurii</i> <i>Eusphenopteris neuropteroides</i> <i>Eusphenopteris striata</i>	B ₂	<i>Alethopteris davreuxii</i> , <i>Pecopteris pennaeformis</i> , <i>Pecopteris volkmannii</i>	<i>Lonchopteris rugosa</i>	<i>Lonchopteris rugosa</i>	
					Meunière						<i>Lonchopteris rugosa</i> <i>Lonchopteris eschweilleriana</i> <i>Karinopteris daviesii</i> <i>Pecopteris volkmannii</i> <i>Neuropteris heterophylla</i>					
		Early Pennsylvanian	Langsettian	Vicoigne	Chandeleur	<i>Alethopteris valida</i> <i>Lonchopteris eschweilleriana</i> <i>Neuropteris heterophylla</i> <i>Lonchopteris rugosa</i> <i>Mariopteris muricata</i> <i>Karinopteris daviesii</i>	A ₂	<i>Neuralethopteris</i>	<i>Neuralethopteris schlehanii</i> , <i>Calymmotheca hoeninghausii</i> , <i>Karinopteris acuta</i>	<i>Calymmotheca hoeninghausii</i>						
					Modeste	<i>Alethopteris urophylla</i> <i>Karinopteris acuta</i> <i>Lonchopteris eschweilleriana</i> <i>Alethopteris valida</i>										
				Flines	Olympe	<i>Neuralethopteris schlehanii</i> <i>Calymmotheca hoeninghausii</i> <i>Karinopteris acuta</i> <i>Alethopteris urophylla</i>						<i>Neuralethopteris jongmansii</i>				

FIG. 11. Palaeofloristic associations and relative position of the Westphalian macrofloral biozonations in the Nord-Pas-de-Calais Coalfield. Sources: 1, Corsin (1962); 2, Loboziak (1971); 3, Laveine (1987); 4, Corsin & Corsin (1971); 5, Opluštil *et al.* (2022). Abbreviations: Ed., Edouard; Dus., Dusouch; Fm., Formation; HBNPC, Houillères du bassin du Nord et du Pas-de-Calais; Mbr, Member; Subst., Substage; WE, western European.

in a simple one-dimensional structure. In this study, the DCA was particularly informative (Fig. 4B). Axis 1 accounts for *c.* 80% of the total variance of the data. Although the two groups of Namurian floras were clearly distinguished (clusters I and II), much of the Westphalian shows an essentially gradual decrease in axis 1 scores throughout the succession (Fig. 4B). However, the Asturian macrofloras (Dusouich and Eduard Members; cluster VIII) are clearly separated by much higher axis 2 values (axis 2 represents *c.* 20% of the total variance) suggesting a significant vegetational change (Fig. 4B). The high scores on axis 2 show that this is largely due to the presence of taxa such as *Neuropteris ovata*, *Laveineopteris dusartii*, and various callistophytes and marattiales; the appearance of which taxa has been linked to the significant vegetation changes that occurred in the late Westphalian in response to alterations in landscape and climate (e.g. Cleal *et al.* 2009a, 2012).

By comparing this biostratigraphy with the species diversity curve described by Molina-Solís *et al.* (2023, fig. 6), it is possible to interpret the broad pattern of vegetation change throughout the Nord-Pas-de-Calais succession. The mixed marine–terrestrial Namurian deposits preserve a low-diversity, essentially allochthonous macrofloral record (clusters I and II), possibly derived from the early coal swamp vegetation found some 500 km to the southwest in the lower Loire area (e.g. Strullu-Derrien *et al.* 2021, 2022, 2023). More autochthonous vegetation remains appear at the base of the Langsettian (lower Westphalian), with the presence of a lycopsid-dominated pioneer community (cluster III). Shortly after, coinciding with a lowering of sea level probably linked to the onset of Late Palaeozoic Ice Age glacial phase C3 (Fielding *et al.* 2008, 2023), there is a rapid increase in diversity of the coal swamp vegetation. However, although this diversification (the base of cluster VI) was partly due to increased numbers of arborescent lycopsid species that represented the ecological keystone taxa of the biome (DiMichele & Phillip 1995), it was mainly due to diversification of the clastic substrates vegetation. Whether this is because the better-drained clastic substrates could support a more diverse vegetation, or there was a greater diversity of habitats with such substrates, or both, is presently unclear.

Through the rest of the Langsettian to the upper Duckmantian, the coal swamp macrofloras continue to gradually diversify (Molina-Solís *et al.* 2023, fig. 6). There is a minor change at the *Vanderbeckei* Marine Band, known locally as the *Poissonnière* Marine Band (boundary between clusters IV and V), but, overall, the history of the coal swamp vegetation during the *c.* 2 myr from the middle Langsettian to the late Duckmantian is characterized by gradual change and diversification.

The next major change, between clusters V and VI at the base of the Pouilleuse Member (Fig. 3), introduces macrofloras that have more of an upper Westphalian character; this was interpreted by Trueman (1946) as being the most important change to have occurred in terrestrial habitats in Euramerica during the Westphalian (see also Dix 1937; Dix & Trueman 1937). It also sees a flattening of the species diversity curve (Molina-Solís *et al.* 2023, fig. 6), which seems to be concurrent with a similar flattening seen in South Wales and the Ruhr, and even a downturn in the Central Pennines. In the British coalfields this coincides with the recurrence of intervals of marine flooding probably due to an interglacial causing raised sea levels (between glacial phases C3 and C4; Fielding *et al.* 2023). Although marine flooding in this interval was less prevalent in Nord-Pas-de-Calais (the only reported marine band in this interval is the *Rimbert*, at the Duckmantian–Bolsovia boundary), it seems to have had a clear (if indirect) impact on the composition of the coal swamp vegetation here.

The onset of the Late Palaeozoic Ice Age glacial phase C4 of Fielding *et al.* (2008, 2023) and the resulting drop in global sea levels seems to coincide with the appearance of cluster VII macrofloras occurring at the middle Bolsovian Six-Sillons Member (Fig. 3). The change is weakly identifiable in both ordinations and cluster analyses (although less clearly in the Sørensen/Dice cluster analysis, Fig. 3A). This coincides with a significant increase in species diversity, especially among the herbaceous (non-marattiale) ferns and medullosaleans (Molina-Solís *et al.* 2023, fig. 6). The macrofloral change can be comparable to the base of the *Laveineopteris rarinervis* Subzone as identified in South Wales (Cleal 2007), which has been interpreted as the result of the cessation of marine flooding here. The later (early Bolsovian) flooding events are not represented in the Nord-Pas-de-Calais succession. However, they also seem to have had an indirect (‘far-field’) impact on the vegetation in the latter area. Figures S1, S2 show a series of reconstructions of typical areas of the upper Carboniferous coal swamps from the paralic basin of the Nord-Pas-de-Calais.

The start of cluster VIII marked by the appearance of Asturian-age macrofloras also involves a significant reduction in species diversity (Molina-Solís *et al.* 2023, fig. 6). A similar significant drop in diversity was reported in the upper Bolsovian in South Wales (Cleal 2007), where it was shown not to be correlated with any significant depositional changes and may have been caused by climate change. This change in the macrofloras has been the subject of several detailed studies in other areas (Laveine 1977; Cleal 1978, 1984a, 1984b, 2007; Zodrow & Cleal 1985; Wagner & Álvarez-Vázquez 1991, 2010; Cleal *et al.* 2009a, 2009b) and seems to represent a significant

change in the vegetation during the later evolution of the coal swamp biome in Euramerica.

CONCLUSION

This study has demonstrated the value of using a range of approaches to investigate vegetation dynamics in deep time, including species diversity analysis, ordination and cluster analyses involving different similarity coefficients. Each method gives different insights into the structure of the palaeobotanical data, enabling elucidation of a new macrofloral biozonation scheme for the Nord-Pas-de-Calais Coalfield. Using this approach it has also been possible to establish the broad pattern of vegetation change in the Westphalian-age (late Bashkirian to early Moscovian) coal swamps of this coalfield, and how it potentially relates to climate and landscape change. This history may be summarized as occurring in six distinct steps:

1. Earliest Langsettian: an initial invasion of peat substrate vegetation dominated by arborescent lycopsids.
2. Early to middle Langsettian: a rapid diversification of vegetation of the clastic substrates, probably due to the exposure of extensive areas of continental shelf.
3. Late Langsettian to middle Duckmantian: a steady diversification of both peat and clastic substrates vegetation, with the onset of glacial phase C3.
4. Late Duckmantian to early Bolsovian: a reduced species diversity and the appearance of more characteristically late Westphalian floras, possibly linked to the C3–C4 interglacial phase.
5. Middle to late Bolsovian: further gradual changes to more typically late Westphalian vegetation, possibly linked to the C4 glacial phase.
6. Asturian: a marked reduction in species diversity and the appearance of new medullosaleans and marattialeans, possibly linked to climate change.

However, further detailed comparisons are needed with other comparable sequences of Variscan Euramerica, including both those that have already been studied in detail (e.g. Britain, the Ruhr) and others that have been less well-documented such as in Belgium and the Netherlands. This extensive area of ancient swamp represents a valuable natural laboratory with the potential for testing ideas concerning the relationship between wetland vegetation, landscape and climate in deep time.

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Author contributions. **Conceptualization** Christopher J. Cleal (CJC), Borja Cascales-Miñana (BC-M); **Formal Analysis** Claude Monnet (CM); **Funding Acquisition** BC-M; **Investigation** Azucena Molina-Solís (AM-S), CJC, BC-M; **Methodology** CM; **Project Administration** BC-M; **Software** CM; **Visualization** AM-S, CJC, BC-M. **Writing – Original Draft** CJC, BC-M; **Writing – Review & Editing** AM-S, CJC, CM, BC-M.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1551>):

FIG. S1. Palaeofloristic reconstructions of the Nord-Pas-de-Calais Coalfield (Part 1). A, main morphologies of lycopsids, Equisetales and Cordaitales: *Lepidodendron*; *Ulodendron*; *Lepidophloios*; *Sigillaria*; *Sphenophyllum*; *Archaeocalamites*; *Calamites*; *Cordaites*. B, main morphologies of seed ferns: *Alethopteris*; *Diplotmema*; *Neuropteris*; *Mariopteris*; *Tetratmema*. Reproduced with permission from Corsin & Corsin (1970, pls. 22–23).

FIG. S2. Palaeofloristic reconstructions of the Nord-Pas-de-Calais Coalfield (Part 2). A, main morphologies of herbaceous and tree ferns: *Pecopteris*; *Corynepteris*; *Sphenopteris*; *Rhodesia*. B, Westphalian (Bolsovian) landscape of Nord-Pas-de-Calais: *Mariopteris*; *Paripteris*; *Pecopteris*; *Neuropteris*; *Reticulopteris*; *Diplotmema*; *Crossotheca*; *Alethopteris*; *Calamites*; *Sphenophyllum*; *Sigillaria*; *Dicksonites*; *Ulodendron*; *Lepidodendron*; *Cordaites*. Reproduced with permission from Corsin & Corsin (1970, pls. 24–25).

Data S1. Raw data used in this study.

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