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# **A rare late Mississippian flora from Northwestern Europe (Maine-et-Loire Coalfield, Pays de la Loire, France)**

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## 1. Introduction

The spread of swamp vegetation over large parts of tropical Pangaea during late Carboniferous (Pennsylvanian; 323–299 Ma) times has been linked with profound global changes in environments and biotas, including increasing levels of atmospheric oxygen, global climatic cooling, and the diversification of early terrestrial faunas in particular insects (e.g. Labandeira, 2001; Beerling, 2017). The swamps produced vast peat deposits that subsequently changed into coal (they are sometimes informally referred to as the coal swamps) and the exploitation of this energy resource during the 19<sup>th</sup> and 20<sup>th</sup> centuries resulted in their extensive geological investigation. From this, much has been learnt about the ecology and biotas of this ancient wetland biome, but its origins and early evolution are less well-understood.

Fossil evidence of pre-Pennsylvanian coal swamps is known from a few upper Mississippian deposits in Europe, North America and Asia (e.g. Vakhrameev et al, 1978; Mosseichik, 2010). Understanding the early development of this wetland biome requires evidence of the palaeofloristics and biostratigraphy of its fossil plants. For this, robust taxonomic records are required for the key fossil floras.

The present paper will revise some of the well-preserved floras found in the Pays de la Loire region of northwestern France. They are known from historic records by Brongniart (1828–1837) and Bureau (1913–1914), but other than a few short papers by Carpentier (1919, 1932, 1935, 1947) there have been no taxonomic revisions for over a century. This area has yielded floras of various ages ranging from Viséan (346–330 Ma) to Stephanian (Gzhelian; 303–299 Ma) and in his monograph Bureau (1913, 1914) combined some of these into a single treatment, producing (as Bureau himself recognised) rather anachronistic results.

The present paper will be more focused, and deal only with the early Namurian (Serpukhovian – early Bashkirian; c. 330–313 Ma) floras from a small coalfield about 20–40

km south of Angers. Although mining ceased here in the 1960s, there are important museum collections available that allow the floras to be revised in the light of modern taxonomy.

During this study, spores of early Namurian age were recovered successfully from the Maine-et-Loire Coalfield. As microfloras have never been previously reported from this region, the palynological record will be briefly discussed.

## 2. Geology

The Armorican Massif (western France) mainly consists of Proterozoic to Palaeozoic rocks that have been strongly affected by the Carboniferous Variscan orogeny. It is subdivided into North-Armorican, Central Armorican and South-Armorican domains, separated by two major Carboniferous strike-slip faults: the North-Armorican Shear Zone (NASZ) and the South-Armorican Shear Zone (SASZ). The SASZ consists of two branches, the SASZ(N) and SASZ(S) (Fig. 1A). A major suture between these two branches, the North-sur-Erdre Fault (NSEF), separates the northern Saint-Georges-sur-Loire Unit from the southern Mauges Domain (Ballèvre et al. 2009; Ducassou et al. 2011a) and disappears below the Mesozoic-Cenozoic sedimentary cover of the Paris Basin to the east.

The Saint-Georges-sur-Loire Unit (Fig. 1B) mainly consists of Ordovician to Devonian marine sediments with interbedded volcanic rocks (Lardeux, 1967) overthrusting the northern Lanvaux Unit (Cartier et al., 2001). The Mauges Unit (Fig. 1B) mainly consists of a Proterozoic basement overlain by Cambrian to Devonian deposits (Ducassou et al., 2011a) and is structurally on top of the Complex of Champtoceaux (Ballèvre et al., 2009). This Carboniferous nappe stack involves high-pressure / low-temperature metamorphic rocks, with a metamorphic peak recorded at c. 360 Ma, followed by the exhumation at c. 350–340 Ma (Bosse et al., 2000; Pitra et al., 2010). The Ancenis Basin (Fig. 1B) contains a thick interval of clastic deposits with occasional plant and fresh- to brackish-water bivalves indicating a

Mississippian age (Bureau, 1914; Ballèvre & Lardeux, 2005). Radiometric dating of detrital minerals (Ducassou et al., 2014) and igneous rocks intruding the Ancenis Basin (the Mésanger magmatism dated at  $319 \pm 3$  Ma using U-Pb on zircon; Ducassou et al., 2011b) suggest that sedimentation in the basin (i) may have started as early as Tournaisian but is at least in part Viséan in age and (ii) took place during the exhumation of the metamorphic rocks of the Champtoceaux Complex (Ducassou et al., 2014).

The Pays de la Loire coalfield, which comprises the Maine-et-Loire coalfield and the Loire Atlantique coalfield, extends from Nort-sur-Erdre to Doué-la Fontaine (Fig. 1B) along the Nort-sur-Erdre Fault and directly north of the Ancenis Basin. This coalfield contains mainly immature (micaceous and feldspar-rich) siliciclastic conglomerates to fine-grained sediments, interbedded with coal seams and tuffs (“Pierre carrée”: Bureau, 1910; Arnaud and Brossé, 1981) that have been interpreted as Namurian in age (Bureau, 1910; Carpentier, 1918). They are interpreted as deposited in pull-apart basins formed during the dextral displacement along the Nort-sur-Erdre Fault (Diot and Blaise, 1978; Barthet, 2005).

Provenance analysis performed on these deposits suggest very local sources, and indicate a significant decrease of the drainage area, when compared with the Ancenis Basin (Ducassou et al. 2014). The Westphalian deposits reported from between Chalonnes-sur-Loire and Thouarcé (Bureau, 1914), a few kilometres north of the Nort-sur-Erdre fault, occur within the Saint-Georges-sur-Loire Unit (Fig. 1B) and are thus preserved in a different structural context.

### 3. Material and Methods

This paper is based largely on the collections of the Muséum des sciences naturelles d'Angers (specimens identified by the prefix MHNAn.). In addition, reference is made to

specimens in the Museum National d'Histoire naturelle, Paris (specimens identified by the prefix MNHN).

Plants were recorded from 11 localities (Fig. 1, Fig. 2).

*Chaudefonds-sur-Layon*: (1) Malécots mine and Malécots quarry; (2) Ardennay mine, (including St Barbe-des-Mines shaft); (3) Hillside on the north bank of the Layon, opposite La Brosse and Vouzeau.

*Saint-Aubin-de-Luigné*: (4) Saint-Aubin shaft, La Roche Moreau and La Haie Longue (Vein of du Chêne shaft and du Bocage shaft).

*Chalonnnes-sur-Loire*: (5) Chalonnnes-sur-Loire mines (shafts 1, 4 and du Désert shaft); (6) de la Prée mine (Shafts 3, 4 and 5).

*Saint-Georges-sur-Loire*: (7) Saint-Georges-sur-Loire mine (shaft close to Port-Girault and de la Mazière shaft).

*Montjean-sur-Loire*: (8) Garenne quarry, Mr Poulain's quarry, Saint-Nicolas shaft (South coal seam (Carpentier, 1920, 1928)).

*Concourson-sur-Layon*: (9) Concours-sur-Layon mine.

*Beaulieu-sur-Layon*: (10) de Beaulieu, shaft of the hillside and Saint Joseph shaft.

*Martigné-Briand*: (11) coal seam near Martigné-Briand.

The fossils are preserved as adpressions (impressions or heavily coalified compressions) with little likelihood of cuticles being present. They were identified where possible to fossil-species as defined in the International Code of Nomenclature (ICN – Turland et al., 2018). This allowed different taxonomic names to be given to fossils representing different plant parts, even if those fossils originated from the same parent plant species (see Cleal & Thomas, 2010). However, they have not been attributed to supra-generic taxa other than classes due to the uncertainty of the taxonomic classification of these fossils at the family and order rank, especially of vegetative remains such as mainly dealt with here. The synonymies

quoted for each species are restricted to records from the Maine-et-Loire coalfield.

Photographs of the specimens were taken using a Nikon Camera D5100.

Chronostratigraphy follows the Heerlen Regional Scheme, which is still generally used in studies in European Carboniferous terrestrial sequences (Wagner, 1974). Dates where given are based on the v2020/01 International Commission on Stratigraphy chronostratigraphic chart (Cohen et al, 2020). The numerical analyses (Unconstrained Seriation Analysis and Detrended Correspondence Analysis [DCA]) of the distribution of species occurring at the different localities were performed with the PAST statistical package (Hammer et al., 2001).

Identification of the original specimen collection locations was collated through a mix of fieldwork, historical record searches, and correlation with ancient and modern maps. These data were combined in QGIS (QGIS Development Team, 2020), a geographic information system, to produce illustrative maps.

Palynological samples were collected in 2018 from the Malécots mine spoil tip and Malécots quarry (Fig. 1). Grey and dark grey shales (claystone, silty claystone) underwent chemical treatment using techniques described by Riding and Kyffin-Hughes (2004) and were analysed microscopically in order to obtain the Namurian miospore material.

## 4. Results

### 4.1. Systematic palaeontology (macrofloras)

*Class:* LYCOPSIDA (LYCOPODIOPSIDA) Bartl. 1830 (Fig. 3)

*Remarks.* Bureau (1913) recorded but did not illustrate a decorticated lycosid stem from Chalennes-sur-Loire as *Knorria imbricata* Sternberg. Such decorticated stems have little botanical interest and so will not be discussed further.

*Genus:* **Thaumasiodendron** Bureau, 1906

*Remarks.* The generic type is a stem adpression (part and counterpart) from the Maine-et-Loire coalfield (MNHN.F.12233.1/2). Bureau distinguished it from *Lepidodendron* by the presence of what he interpreted as spirally attached, short, persistent leaves. There are undoubtedly such short leaves in the proximal part of the specimen but in the more distal part there are sporangia directly attached to the stem; in some places, it is possible to see megaspores present (Bureau, 1913, pl. 49, fig. 1A). Other lycopsid stems with directly attached sporangia include *Omphalophloios* White (Bek et al., 2015; Opluštil et al., 2010; Wagner & Álvarez-Vázquez, 2015) and *Polysporia* Newberry (Bek et al., 2009) but attributing specimens to these taxa requires data on the *in situ* spores present. Since we have not examined the generic type, and they are stratigraphically older than the other fossils of this type, we have decided provisionally to retain Bureau's taxonomic names.

*Thaumasiodendron andegavense* Bureau, 1906

1906 *Thaumasiodendron andegavense* Bureau, 4 figs.

1913 *Thaumasiodendron andegavense* Bureau; Bureau, pl. 49.

1935 *Thaumasiodendron*: Carpentier, pl. 14, fig. 1.

*Description.* Stem with helically arranged leaf cushions; thickened oval to bluntly subtriangular, obliquely inserted sporangia, 5–6 mm long, 4–5 mm wide, attached directly to stem. Scattered among these sporangia are round megaspores.

*Remarks.* *Thaumasiodendron andegavense* is only known from the type specimens MNHN.F.12233.1/2 (Bureau, 1906, 1913) and a second specimen later figured by Carpentier (1935).

*Localities.* de la Prée Mine (shaft 5), Chalennes-sur-Loire (types figured by Bureau, 1906, 1913). The specimen figured by Carpentier (1935) originated from Malécots quarry.

*Genus:* **Lepidodendron** Sternberg, 1820

*Remarks.* Bureau (1914) recorded a specimen from du Désert shaft at Chalennes-sur-Loire as *Lepidodendron aculeatum* Sternberg, 1820. He had not collected it himself but found it in the collections of the Natural History Museum Nantes, and he noted that the lithology was not typical for the coal-bearing deposits of the Maine-et-Loire coalfield. Since *L. aculeatum* is normally restricted to Pennsylvanian age floras, we have excluded it from the following analysis. Bureau (1914) also recorded specimens as *Lepidodendron lycopodioides* Sternberg, 1821 but they could not be located and none were illustrated.

*Lepidodendron veltheimii* Sternberg, 1825 (Fig. 3A)

1913 *Lepidodendron veltheimianum* Sternberg; Bureau, pl. 39, fig. 4.

1932 *Lepidodendron veltheimianum* Sternberg; Carpentier, pl. 3, fig. 6.

*Description.* Stems with rhomboidal, protuberant leaf cushions, 3–4 times longer than wide. Cushions 4–25 mm long, 2–7 mm wide; with acute, sometimes slightly sinuous upper and lower angles; lateral angles rounded. Where preserved, a rounded, subtriangular or rhomboidal leaf scar occurs on the leaf cushions; scars isodiametric or longitudinally slightly elongate, occupying much of cushion width, and positioned just over halfway up the leaf cushion. A marked keel occurs below and above the leaf scars. Some specimens show irregularly distributed, longitudinally slightly elongated ulodendroid scars, 30–35 mm long, 25 mm wide, others have protruding *Halonia*-like structures.

*Remarks.* These are by far the most abundant lycopsid stems found in the Maine-et-Loire floras. Although most of the Maine-et-Loire specimens that we saw were decorticated, one showed the external surface of the stem with the characteristic leaf cushions of *Lepidodendron veltheimii*; well preserved stems from here with leaf cushions were also figured by Bureau (1913). All of these better preserved specimens compare well with the

holotype of *L. veltheimii* (Kvaček & Straková (1997, pl. 54, fig. 4); also with specimens attributed to this species by Crookall (1964, pl. 64, figs 3–5; pl. 70, fig. 8; pl. 71, figs 1, 2) and Purkyňová (1970, pl. 1, figs 6–9; pl. 2, fig. 5). The Crookall specimens in particular show the diagnostic features of *Lepidodendron* as defined by Thomas & Meyen (1984), including intra- and infra-foliar parichnos, and a ligule pit; the latter feature in particular precludes them from belonging to the other widespread Mississippian arborescent lycopsid *Lepidodendropsis* Lutz, 1933, which is eligulate.

*Lepidodendron veltheimii* is one of the most widespread of the Mississippian arborescent lycopsids, ranging from the middle of the *Triphyllopteris* Zone (upper Tournaisian) to the top of the *Calymmotheca larischii* Zone (top of the Arnsbergian) (Wagner, 1984). Mosseichik (2010) has recorded it from localities across Europe and eastern North America, notably in Donets, Upper Silesia and Britain.

*Locality.* Chaudefonds-sur-Layon (MHNA.2010 PB 133), Chalonnnes-sur-Loire mines, including shafts 4 and 5 (MHNA.2009 PB 006, MHNA.2009 PB 007, MHNA.2009 PB 030, MHNA.2009 PB 080, MHNA.2009 PB 195, MHNA.2009 PB 368, ? MHNA.2009 PB 386, MHNA.2009 PB 397, MHNA.2010 PB 087, MHNA.2010 PB 100, MHNA.2010 PB 101, MHNA.2010 PB 204, MHNA.2010 PB 211, MHNA.2010 PB 215), Chalonnnes-sur-Loire area (MHNA.2010 PB 530) and Saint-Aubin-de-Luigné (MHNA.2009 PB 385, MHNA.2010 PB 095). Bureau (1914) also recorded it from mines at La Haie Longue (du Chêne and du Bocage shafts) and Ardennay. Carpentier (1932) figured it from Malécots Quarry.

*Lepidodendron volkmannianum* Sternberg, 1825 (Fig. 3B)

*Description.* Stems covered with spirally-arranged, contiguous leaf cushions. Leaf cushions isodiametric, 3–13 mm in size, mainly club-shaped with an obtuse upper angle, an

elongate, sinuous lower angle and rounded lateral angles. Small rhomboidal leaf scar in upper part of leaf cushion with lateral lines extending to upper part of cushion margin. Shallow keel sometimes visible extending from scar to lower angle of cushion.

*Remarks.* Bureau (1914) only recorded *Lepidodendron volkmannianum* from the Loire Atlantique coalfield, and then from just a few localities. However, the Angers collection has three specimens (one an external sandstone cast, two preserved in siltstone) that clearly have the distinctive leaf cushions of this species. *L. volkmannianum* is most abundant in upper Visean adpression floras of central Europe, although it also occurs in the lower Namurian of southern Europe (Mosseichik, 2010).

*Localities.* La Haie Longue, Saint-Aubin-de-Luigné (MHNAn.2009 PB 028; MHNAn.2010 PB 068), Chaudefonds-sur-Layon (MHNAn.2010 PB 097).

*Lepidodendron* cf. *nathorstii* Kidston in Nathorst, 1914 (Fig. 3C)

1913 *Lepidodendron jaraczewskii* Zeller; Bureau, pl. 39, fig. 3.

1913 *Lepidodendron rimosum* Sternberg; Bureau, pl. 42, fig. 1.

*Description.* Stems with slender, fusiform leaf cushions. Larger cushions (35–45 mm long, 4–7 mm wide) protrude from stem, usually separated by inter-cushion bands 2–3 mm wide; smaller cushions (10–12 mm long, 2–3 mm wide) less protruding and separated by inter-cushion bands 4–5 mm wide. A slender, broadly sinuous line joins the top of each cushion with the base of the leaf cushion of the next but one parastichy. An oval leaf scar occurs just above the mid-axis of the cushion, 3 mm long and 7 mm wide. Also present are a number of decorticated (*Syringodendron*-like) stems with spirally arranged, vertically oval scars c. 5–7 mm long, 2 mm wide, which were probably produced by the same plants.

*Remarks.* There are several other Visean and Namurian species of *Lepidodendron* with similar slender, fusiform leaf cushions and well-developed inter-cushion areas (e.g.

*Lepidodendron lossenii* Weiss, 1884a; *Lepidodendron jaschei* Roemer, 1866; *Lepidodendron spetsbergense* Nathorst, 1894; *Lepidodendron robertii* Nathorst, 1914) but none are well documented. The best recent taxonomic analysis of these species is in Crookall (1964), who reproduced figures of the types, but there is still considerable uncertainty as to the infra-specific variation. We have opted to compare these Maine-et-Loire specimens with *L. nathorstii* as it is the best documented of these species in Crookall's monograph, but only with a "cf." as a number of key characters such as the ligule, parichnos and surface features of the inter-cushion areas could not be clearly seen.

Bureau (1913) figured two similar specimens from the Maine-et-Loire coalfield. One was identified as *Lepidodendron jaraczewskii* Zeiller, 1882, but the type of that species is stratigraphically much younger (from the Westphalian of Valenciennes) and has much smaller leaf scars, and prominent lateral lines that curve downwards from the scars. The second specimen, identified as *Lepidodendron rimosum* Sternberg, 1820, has rather smaller, more slender leaf cushions; again, the type of that species is stratigraphically much younger (middle Westphalian). In our view, these two associated stem fossils represent different growth stages of the same plant species and cannot be differentiated from what we are calling *L. cf. nathorstii*.

*Localities.* Ardenay (MHNAn.2009 PB 063, ? MHNAn.2009 PB 064), Chalonnnes-sur-Loire (MHNAn.2009 PB 392), Montjean-sur-Loire (MHNAn.2010 PB 044), Saint-Aubin-de-Luigné (MHNAn.2010 PB 069, MHNAn.2010 PB 094). The specimens figured by Bureau (1913) both came from La Haie Longue.

*Lepidodendron cf. lossenii* Weiss, 1884a (Fig. 3E)

*Description.* Fragment of stem with elongate rhomboidal leaf cushions, 6 mm long, 2 mm wide, with acute, somewhat sinuous apical angles, rounded lateral angles. Leaf scars

rhomboidal, 1.5 mm long, 1 mm wide, positioned just above the mid-position on the cushion. A possible ligule occurs above the scar. Lateral angles extend abaxially from scar to cushion margin. A prominent keel crossed by numerous lateral lines occurs on the abaxial part of the cushion.

*Remarks.* *Lepidodendron* cf. *lossenii* is represented in the Angers collection by one very distinctive specimen that was labelled as *L. acuminatum* (Göppert) Unger. Two of the syntypes of that species (Göppert, 1852, pl. 23, fig. 4; pl. 43, fig. 8) have very similar small, elongate leaf cushions with a relatively large leaf scar, but lack the very prominent lateral lines on the abaxial cushion surface seen in the Maine-et-Loire specimens. No comparable specimen was figured from the Maine-et-Loire coalfield by Bureau (1913)

The nearest comparison is with a specimen figured as *Lepidodendron lossenii* Weiss by Wagner et al. (1983, pl. 4, fig. 19) from a similar aged flora at Banajarafe in southern Spain. The type of that species (Weiss, 1884a, pl. 6, figs 6,7) also has longitudinally elongate cushions with prominent lateral marks on the abaxial surface and a relatively large leaf scar. However, the cushions are even more slender and elongate than in the Spanish or Maine-et-Loire specimens. Since the morphological variation in *L. lossenii* is unknown we have assigned the Maine-et-Loire specimen to this species with a cf.

*Locality.* Montjean-sur-Loire (MHNA.2009 PB 472).

*Lepidodendron* sp. 1 (leafy shoots) (Fig. 3F)

1913 *Lepidodendron ophiurus* Brongniart; Bureau, pl. 30, fig. 4.

*Description.* Shoots with spirally attached leaves. Leaves linear-lanceolate, 30–40 mm long, attached at about right-angles, straight for most of their length, more or less curved at their distal end.

*Remarks.* Bureau (1914) regarded these fossils as the distal twigs borne by *L. veltheimii* stems. They compare with *Lepidodendron ophiurus* (Brongniart ex Sternberg) Brongniart, 1828a but the leaves are rather larger, thicker and are not as consistently curved at the end (Thomas & Seyfullah, 2015). As the type of that species is much younger (middle Westphalian) the name has not been used for the present specimens.

*Localities.* Chalennes-sur-Loire, de la Prée mine, shaft 3 (MHNA.2009 PB 363), Saint-Aubin-de-Luigné (MHNA.2010 PB 116) and Ardenay (MHNA.2009 PB 088).

*Lepidodendron* sp. 2 (leafy shoots) (Fig. 3G)

*Description.* Shoots densely covered by leaves attached spirally at an acute angle. Leaves slender, linear, 5–7 mm long.

*Remarks.* These shoots are clearly quite different from the previous species, the leaves being much denser and more slender, and attached at a more acute angle. Bureau (1914) named similar shoots from this area as *Lepidodendron selaginoides* Sternberg, 1821. Although there is a superficial similarity to the types of that species (as photographically refigured by Kvaček & Straková, 1997, pl. 50, figs 1,3), the latter originated from the middle Westphalian of Bohemia and so we have not used this name for these Mississippian age specimens. Bureau (1914) recorded similar shoots from the Loire Atlantique coalfield as *Lepidodendron lycopodio* des Sternberg, 1821 and, although he also recorded this species from the Maine-et-Loire coalfield, none of the figured specimens were from here.

*Localities.* Chalennes-sur-Loire (MHNA.2009 PB 398) and Saint-Aubin-de-Luigné (MHNA.2009 PB 013, MHNA.2009 PB 376). Bureau (1914) also recorded shoots of this type from Chalennes-sur-Loire, Saint-Georges-sur-Loire Mine (Mazière Shaft) and the banks of the Loire River.

*Genus:* **Bothrodendron** Lindley & Hutton, 1833 (Fig. 3I)

*Bothrodendron wiikianum* (Heer) Kidston, 1889

(≡ *Lepidodendron wiikianum* Heer, 1871)

1913 *Bothrodendron kiltorkense* Haughton; Bureau (non Haughton), pl. 59, fig. 2.

1947 *Sigillaria minima* Brongniart; Carpentier (non Brongniart), pl. 26, figs 2–6.

*Description.* Stems with fine longitudinal ribs. Small, widely spaced leaf scars in a lepidodendroid arrangement with clear orthostichies; orthostichies spaced 10–12 mm apart, vertical spacing of scars c. 25 mm. Longitudinal ribs not significantly deflected around the scars. Scars round to vertically oval, 2–3 mm in size, with raised rim. In centre of scars are three marks assumed to be vascular and parichnos traces. A small notch (?ligule pit) occurs adjacent to the adaxial side of the scar.

*Remarks.* Bureau (1913) figured two *Bothrodendron*-like specimens from the Maine-et-Loire coalfield but one was decorticated and so is difficult to identify. The better-preserved specimen shows small, widely spaced leaf scars, with both vascular and parichnos scars. Unfortunately, there is no close-up of the leaf scars but a specimen in the Angers collection that has identical scars and bark patterning shows clear evidence of a ligule pit on the adaxial side of the scar. Bureau (1913) identified his specimens as *Bothrodendron kiltorkense* Haughton, 1859, but this species is now generally placed in the eligulate fossil-genus *Cyclostigma* (Chaloner & Boureau in Boureau, 1967). As the Maine-et-Loire specimens are ligulate, this precludes an assignment to *Cyclostigma* and the other characters strongly point to affinities with *Bothrodendron*.

The nearest comparison is with *Bothrodendron wiikianum*, which shows similar, small, slightly raised, widely-spaced leaf scars in a lepidodendroid arrangement, and with the longitudinal ribs of the stem deflected around the scars (e.g. Crookall, 1964, pl. 78, fig. 2). The only other Mississippian-age *Bothrodendron* species that are reasonably well

documented are *Bothrodendron kidstonii* Weiss, 1893, which has essentially unribbed stems; *Bothrodendron deperetii* Vaffier, 1901 which has much finer corrugations on the stem that are not deflected around the scar (Thomas, 1980); and *Bothrodendron wardiense* Crookall, 1964 which has a ligule pit further away from the scar.

Most of the specimens figured by Carpentier (1947) as *Sigillaria minima* have small, widely spaced leaf scars and no leaf cushions, and clearly belong to *Bothrodendron* rather than *Sigillaria*. Although the illustrations are not very clear, we assume they belong to *B. wiikianum*.

*Bothrodendron wiikianum* is rare and otherwise only reported from the Upper Devonian and Viséan of Scotland (Crookall, 1964) and the Arctic (Heer, 1871; Nathorst, 1894, 1902).

*Localities.* Chalonnès-sur-Loire (MHNAn.2009 PB 402). The specimen figured by Bureau (1913) from the Brongniart Collection (No. 4667) originated from the seam at the Chêne Shaft, la Haie Longue. The Carpentier (1947) specimen originated from the Saint-Aubin-de-Luigné mine.

*Genus: Sigillaria* Brongniart 1822 nom. cons. (Fig. 3J)

*Remarks.* Carpentier (1957 p. 299) created the new species *Sigillaria bureauii* based on two poorly-preserved, unidiagnostic specimens from Malécots quarry and the St Barbe-des-mines Shaft (Ardennay). The name has not been used by subsequent authors.

*Sigillaria minima* Brongniart, 1837

1837 *Sigillaria minima* Brongniart, pl. 158.

1913 *Sigillaria minima* Brongniart; Bureau, pl. 41, fig. 3.

1935 *Sigillaria minima* Brongniart; Carpentier, pl. 14, fig. 3.

1947 *Sigillaria minima* Brongniart; Carpentier, pl. 26, fig. 1.

*Description.* Stem with vertical rows of sub-hexagonal leaf cushions, with rounded lateral angles; two edges of cushion immediately above lateral angles slightly convex, those immediately below the lateral angles slightly convex. Large but flat leaf scar, 4 mm wide and 3 mm high, occupies much of the area of each leaf cushion. Three small cicatrices occur in a line across the upper part of scar, presumably representing the vascular and parichnos traces.

*Remarks.* Compared with most other *Sigillaria* species, the leaf scars are smaller and take up much of the cushion area. It has been suggested (e.g. Chaloner & Boureau in Boureau, 1967; Crookall, 1966) that these Maine-et-Loire specimens should be assigned to *Sigillaria elegans* Sternberg, 1825. However, the types of this species originated from a late Stephanian flora from Germany and it would seem unlikely that they would be conspecific with these Namurian stems. Other records of Namurian specimens identified as *S. elegans* from Turkey (Jongmans, 1955) and Upper Silesia (Favlena, 1982a) also probably belong to *S. minima*.

Carpentier (1947) described several specimens from the Maine-et-Loire coalfield as *S. minima*, but only one appears to be a true *Sigillaria*; the others belong to *Bothrodendron wiikianum*.

*Locality.* Chalonnès-sur-Loire mines, shaft 4 (MHNA.2009 PB 091). The specimens figured by Carpentier (1955, 1947) originated from the Malécots quarry, between la Haie Longue and Ardenay and the Saint- Aubin-de-Luigné mine.

*Genus: Lepidostrobus* Brongniart, 1828a (Fig. 3D)

*Lepidostrobus variabilis* Lindley & Hutton, 1831

*Description.* Cone at least 150 mm long, up to 20 mm wide in middle part but tapering markedly both distally and proximally. Longitudinal axis 3 mm wide bearing densely packed sporophylls, probably in a helical configuration although this arrangement is difficult to

verify. Sporophylls up to 15 mm long in centre of cone; the form of the presumed sporophyll pedicel is difficult to determine as the cone is so densely packed, but the blade is 1 mm wide and broadly curved so that its distal extremity lies parallel to the axis.

*Remarks.* This cone resembles *Lepidostrobus* / *Flemingites* found in Pennsylvanian floras across Euramerica and normally regarded as being borne by arborescent lycopsids. It is very similar to the cones figured by Bureau (1913, pl. 37, figs 2–5, 7) from the Loire Atlantique floras, which Bureau named as *Lepiostrobus variabilis* Lindley & Hutton, but this name is usually used for cones with a more cylindrical shape. The specimen in the Angers collection was associated with abundant stems of *Lepidodendron veltheimii* and it is tempting to link them together. However, determining the systematic position of such cones requires data on the *in situ* spores (Brack-Hanes & Thomas, 1985; Bek & Opluštil, 2004) but these are unknown with these French specimens, and so they will be referred to as *Lepidostrobus variabilis* (following the procedure suggested by Chaloner, 1953).

*Locality.* Chalennes-sur-Loire (MHNAn.2010 PB 001).

*Genus: Lepidostrobophyllum* (Mirmer) Allen, 1961 (Fig. 3H)

*Lepidostrobophyllum veltheimianum* (Geinitz) Stepanek, I. & Vogellehner, 1985

(≡ *Lepidophyllum veltheimianum* Geinitz, 1854)

1935 *Lepidophyllum* sp.; Carpentier, pl. 13, fig. 6.

*Description.* Prominent, blade-like structures, with a smaller, linguaeform extension at the proximal end. Main blade tapered to an acute apex, 12–50 mm long, 4–9 mm wide, with a prominent longitudinal vein-like structure 2–3 mm wide. Linguaeform extension 5–7 mm long, 2–3 mm wide.

*Remarks.* These fossils resemble the disarticulated sporophylls produced by Pennsylvanian lepidocarpcean cones (Habgood *et al.*, 1988). However, they differ from the

Pennsylvanian sporophylls in having a more tapered blade with a more acute apex (compare with Boulter, 1968; Thomas, 1981). Several Mississippian species have been established for similar shaped sporophylls, including *Lepidostrobophyllum veltheimianum*, *Lepidophyllum fuisseensis* Vaffier, 1901 and *Lepidophyllum acuminatifolium* Stockmans & Willière, 1953, but it is unclear if these just represent morphological variants of a single fossil-species. For the purposes of this study we have adopted the name with the earliest published basionym, *Lepidophyllum veltheimianum*. When Geititz (1854, p. 52) first used this name, he was describing what he thought were leaves attached to the stems now known as *Lepidodendron veltheimii*. However, his diagnosis only referred to these ‘leaves’ (i.e. sporophylls) and *Lepidophyllum veltheimianum* is therefore taxonomically quite distinct from *Lepidodendron veltheimii*.

Other detached sporophylls from Viséan floras are *Lepidocarpon waltonii* Chaloner, 1952 from Scotland, and *Cantheliophorus waldenburgense* (Potonié) Bassler (Purkyňová, 1970; Thomas & Brack-Hanes, 1991) from Upper Silesia. In both cases, however, the sporophyll blade is more slender and tapered along most of its length than in the Maine-et-Loire specimens. It should be noted that the fossil-genera *Lepidocarpon* and *Cantheliophorus* are distinguished by how the sporangia are enclosed by extensions of the pedicel, which cannot be determined in the Maine-et-Loire specimens; hence we are using here the more neutral fossil-genus *Lepidostrobophyllum*.

Bureau (1913, pl. 53) figured similar sporophylls attached to a slender axis from the Loire Atlantique coalfield. Similar axes with small, isodiametric surface structures (incorrectly identified as *Lepidophloios laricinus* (Sternberg) Sternberg, 1825) was found at Ardennay, associated with numerous *L. veltheimianum* sporophylls, but no evidence of attachment was found.

*Locality.* Ardennay (MHNA.2009 PB 162, MHNA.2009 PB 163, MHNA.2009 PB 360, MHNA.2009 PB 371, MHNA.2009 PB 371, MHNA.2009 PB 394), Chalonnnes-sur-Loire, de la Prée Mine, shaft 4 (MHNA.2009 PB 060), Chaudfondes-sur-Layon (MHNA.2009 PB 382), Garenne quarry, Montjean-sur-Loire (MHNA.2009 PB 082, MHNA.2010 PB 046) and Saint-Aubin-de-Luigé (MHNA.2010 PB 108).

*Genus:* **Stigmaria** Brongniart, 1822 (Fig. 3K)

*Stigmaria ficoides* (Sternberg) Brongniart, 1822

(≡ *Variolaria ficoides* Sternberg, 1820)

1932 *Stigmaria ficoides* (Sternberg) Brongniart; Carpentier, pl. 3, fig. 4.

*Description.* Axes with spirally arranged circular (?root) scars 1–3 mm in diameter, often with a raised central area with a small median dimple.

*Remarks.* Bureau (1914) recorded these rhizophores extensively from the Maine-et-Loire coalfield, although all of his figured specimens (Bureau, 1913) came from the Loire Atlantique coalfield. Bureau distinguished seven taxonomic varieties based on variations in the shape and distribution of the root scars, but these are not recognised here.

*Localities.* Ardenay (MHNA.2009 PB 089, MHNA.2009 PB 427), Montjean-sur-Loire (MHNA.2009 PB 454, MHNA.2010 PB 147) and Chalonnnes-sur-Loire (MHNA.2010 PB 65). Bureau (1914) also recorded it from Chalonnnes-sur-Loire, de la Prée Mine (shafts 3 and 4). Carpentier (1932) figured an example from Malécots quarry.

*Class:* EQUISETOPSIDA Agardh, 1825 (Fig. 4)

*Remarks.* Stem fragments were figured by Bureau (1913, pl. 44, fig. 4) as *Equisetum antiquum* Bureau but Jongmans (1922, p. 568) suggested they were merely twigs of a calamitoid. Calamitoid roots were figured by Bureau (1913, pl. 69, fig. 1) as *Pinnularia* but none are in the collection we had to hand.

*Genus*: **Mesocalamites** Hirmer, 1927 emend. Remy & Remy, 1978

*Mesocalamites taitianus* (Kidston & Jongmans) Hirmer, 1927 (Fig. 4A, B)

(≡ *Calamites taitianus* Kidston & Jongmans, 1915)

1913 *Annularia ramosa* Weiss; Bureau, pl. 63, figs 1–2.

*Description*. Adpressions showing the outer surface of 30 mm wide stems, preserved for a length of up to 110 mm. Longitudinal ribs 1–2 mm wide with somewhat rounded or blunt ends. Weakly marked nodes spaced at intervals of 40–70 mm, with ribs mostly passing directly over them but occasionally offset. Longitudinally elongate oval branch scars 15–17 mm long, 7–8 mm wide, located at nodes; no more than one scar per node was observed. Ribs tend to be deflected around scars.

*Remarks*. These specimens are similar to the types of *Mesocalamites taitianus* as re-figured by Crookall (1969, pl. 112, figs 1–3; pl. 113, figs 1–2) from the Pendleian / Arnsbergian Upper Limestone Formation of Scotland. The types have rounder branch scars but this may be taphonomic distortion. They also have inter-nodes that are longer than broad, but this may be merely due the position within the plant, and Josten (1983, pl. 4, fig. 1) figured a specimen as *M. taitianus* with longer internodes. *Mesocalamites ramifer* (Stur) Hirmer and *Calamites cistitosus* (Stur) Hirmer also have a relatively fine ribbing and internodes that are much longer than broad, but differ in having significantly smaller branch scars (< 5 mm diameter).

*Localities*. Ardennay (MHNAn.2009 PB 393); Chalonnnes-sur-Loire (MHNAn.2009 PB 373); Chaudfondes-sur-Layon (MHNAn.2010 PB 079); Concourson-sur-Layon (MHNAn.2009 PB 159); La Haie Longue (MHNAn.2009 PB 152, MHNAn.2009 PB 164, MHNAn.2009 PB 166, 2010 PB 113); Malécots mine (MHNAn.2009 PB 056 x 6). In addition, Bureau (1914) recorded it from de la Prée mine (shafts 4 and 5), Chalonnnes-sur-Loire and Montjean-sur-Loire.

*Mesocalamites haueri* (Stur) Hirmer, 1927 (Fig. 4C)

(≡ *Calamites haueri* Stur, 1877)

1913 *Calamites cannaeformis* Schlotheim; Bureau, pl. 52, fig. 4.

1913 *Calamites Succowii* Stur; Bureau, pl. 64, fig. 3.

*Description.* Adpressions showing the outer surface of stems with coarse ribbing. Ribs up to 4 mm wide with round ends and a large round distal tubercle. Nodes clearly marked, spaced at 4–22 mm intervals, across which the ribs are offset or aligned. In some specimens the internodes are wider than long, in others they may be more than twice as long as wide. No branch scars seen.

*Remarks.* These stems differ from *Mesocalamites taitianus* in the much coarser ribbing and the more prominent distal tubercle on each rib. They compare with the specimens figured as this species by Crookall (1969, text-fig. 178; pl. 113, fig. 3; pl. 114, figs. 1–3; pl. 115, figs. 1,2; pl. 116, fig. 1), which includes a photographic re-illustration of the type.

Some authors (e.g. Jongmans, 1911) have suggested *M. haueri* is merely a form of *Calamites suckowii* Brongniart, one of the most abundant species found in Westphalian adpression floras of Euramerica. However, the ribs along the Westphalian stems are much more consistently offset at the nodes and so Stur (1877) placed these Mississippian stems in a separate species, *Calamites naueri* (≡ *M. haueri*). Bureau (1914) had referred such fossils from the Maine-et-Loire coalfield to “*C. Succowii*” (using a latinised version of the spelling of the species epithet, suggested but not formally adopted by Stur, 1887, footnote to p. 145), although he also noted a comparison with the types of *M. haueri*. He also figured a specimen with more flattened ribs as *Calamites dubius* Artis 1825, another Westphalian species from Britain, but the former also belongs to *M. haueri*.

Bureau (1913) figured other specimens from the Maine-et-Loire coalfield as *Calamites cannaeformis* Schlotheim ex Sternberg, 1825 whose type (Schlotheim, 1820, pl. 20, fig. 1)

originated from the upper Stephanian of Wettin. However, Bureau (1919) noted that Stur had seen these Maine-et-Loire specimens and had named them *Calamites haueri*.

*Localities.* Beaulieu-sur-Layon mine (MHNAn.2009 PB 153); Chalennes-sur-Loire (shaft 4), (MHNAn.2009 PB 390; Chalennes-sur-Loire (MHNAn.2010 PB 214); de la Préé mine (shaft 3) (MHNAn.2009 PB 059); Saint-Aubin-de-Luigné (MHNAn.2010 PB 118, MHNAn.2010 PB 119, MHNAn.2010 PB 122, MHNAn.2010 PB 128, MHNAn.2010 PB 161). In addition, Bureau (1913) figured it from La Haie-Longue; and Bureau (1914) recorded it from Chalennes-sur-Loire, Saint-Georges-sur-Loire mine (Port-Girault shaft); hillside on the north bank of the Layon, opposite La Brosse, Chaudefonds-sur-Layon.

*Mesocalamites* sp. (pith casts) (Fig. 4D)

?1913 *Calamites approximatifomis* Stur; Bureau, pl. 65, fig. 3.

?1913 *Calamites cistii* Brongniart; Bureau, pl. 64, figs 5, 6.

*Description.* Three-dimensionally preserved pith casts showing longitudinal ribs 2–3 mm wide. Clearly constricted nodes are spaced at 30–90 mm intervals; ribs either offset at the nodes or pass directly over them.

*Remarks.* A range of different equisetopsid pith casts occurs in this flora. Most have relatively coarse ribs similar to *M. haueri*, but at least one has finer ribs and is associated with *M. taitianus* stems. A pith cast figured by Bureau (1913) as *Calamites approximatifomis* Stur, 1877 has very coarse ribs similar to *M. haueri*, whereas his *Calamites cistii* Brongniart has finer ribs resembling *M. taitianus*. However, none of these specimens are sufficiently well preserved for a species attribution.

A single specimen in the Angers Museum (MHNAn.2010 PB 118) was labelled as *Bornia transitionis* Roemer, 1866, a species usually regarded as a cone of *Archaeocalamites*, but it is merely a preserved *Mesocalamites* pith cast with ribs and a transverse node.

*Localities.* de la Prée mine shaft 5, Chalonnes-sur-Loire (MHNA.2009 PB 147); Chalonnes-sur-Loire (MHNA.2009 PB 391); La Haie Longue (MHNA.2010 PB 082); Garenne quarry, Montjean-sur-Loire (MHNA.2009 PB 016). Other possible examples are recorded but not figured by Bureau (1914) from Montjean-sur-Loire.

*Genus:* **Asterophyllites** Brongniart, 1828a nom. cons.

*Asterophyllites* cf. *gothanii* Leggewie & Schonefeld in Gothan et al., 1959 (Fig. 4E)

*Description.* A single specimen with four incomplete cupped whorls of leaves spaced at 13–16 mm intervals. Each whorl consists of 10 visible leaves (probably c. 15 originally in complete whorl). Leaves 15 mm long, < 1 mm wide, their distal end not reaching the next node; leaves attached to stem at near to right-angles, curve rapidly and then extend in an essentially straight line. Each leaf has a thick midvein.

*Remarks.* The one specimen we have seen of calamitoid foliage in this flora compares with some of the types of *A. gothanii*, especially Gothan et al. (1959, pl. 39, fig. 2), notably in the dimensions and shape of the leaves, and the number of leaves per whorl. The main difference is that leaves in the Maine-et-Loire specimen are about the same length as the internodes, whereas *A. gothanii* leaves tend to be longer. However, this feature will presumably depend on the position of the whorls on the shoot. The type of *A. gothanii* originated from the Yeadonian of northern Germany, but Josten (1983) has it ranging down into the Alportian. As this Maine-et-Loire flora is still older and, as we are dealing here with a single fragment, it has been named with a cf.

The specimen was labelled as *Sphenophyllum davysii* Bureau. However, this species has elongated, cuneate leaves, sometimes with a digitate distal margin, quite different from this specimen.

*Locality.* Unknown locality (MHNA.2010 PB 107).

*Genus: Calamostachys* Schimper, 1869

*Remarks.* The specimen figured by Bureau (1913, pl. 73, fig. 9) as *Macrostachya caudata* Weiss, 1876 shows no evidence of sporangiophores and resembles a lycopsid shoot except that the leaves were in whorls.

?*Calamostachys* cf. *paniculata* Weiss, 1876 (Fig. 4F)

?1913 *Calamostachys paniculata* Weiss; Bureau, pl. 68, figs 2–4.

?1913 *Annularia ramosa* Weiss; Bureau, pl. 68, figs 5–7.

*Description.* A single poorly preserved cone with what seems to be whorls of bracts spaced at 2 mm intervals. It was preserved for a length of 25 mm and is 5 mm wide between the ends of the (?)bracts. The (?)bracts appear to be curved, their distal ends lying at c. 30° to the cone axis. Between the (?)bract whorls are dark areas that may be sporangiophores.

*Remarks.* Little is known of the cones that were produced by the plants with *Mesocalamites* stems. This poorly preserved example was the only cone found associated with *M. haueri*. It is similar in size and general structure to the specimens figured by Bureau (1913) as *C. paniculata* but, as the types of that species are late Namurian, we have assigned it to that species with a cf.

Also similar are specimens figured by Bureau (1913) as *Annularia ramosa* Weiss and by Purkyňová (1970, pl. 9, fig. 2) as *Calamostachys ramosa* Weiss, 1884b; the bracts in our specimen appear to be a little more curved but this might be due to cone maturity.

*Localities.* Saint-Aubin-de-Luigné (MHNA.2010 PB 123). The specimen figured by Bureau (1913) came from Saint-Georges-sur-Loire mine (Port-Girault shaft).

*Calamostachys occidentalis* Bureau, 1914

1913 *Calamostachys occidentalis* Bureau, pl. 68, fig. 1.

1918 (?)*Macrostachya bureaui* Carpentier, pl. 4, fig. 6.

*Description.* Shoots bearing strobili oppositely arranged (or in whorls) at intervals of 12–15 mm. Strobili 20–30 mm long, up to 5 mm wide, distally tapered. Whorls of closely-spaced bracts at 1–2 mm intervals; bracts up to 5 mm long, linear-lanceolate, attached to cone axis at about right-angles, broadly curved so their distal parts are 60–80° to cone axis. Whorls of sporangiophores attached to cone axis midway between the bract whorls, each bearing 4 sporangia directed back towards the cone axis.

*Remarks.* These cones were found associated with *Mesocalamites taitianus* stems. Unfortunately, we have been unable to locate this specimen and the original illustration was based on a drawing rather than a photograph.

*Locality.* Montjean-sur-Loire quarry.

*Genus:* **Dichophyllites** Borsuk in Borsuk & Radczenko, 1960

*Dichophyllites pachystachya* (Bureau) Boureau, 1964

1913 *Bornia pachystachya* Bureau, pl. 56, fig. 1–5; pl. 67 fig. 5, 5A.

*Description.* Leafy shoots with finely ribbed stems bearing leaves 20–30 mm long and once, twice or occasionally three times forked. In distal positions in the shoot the leaves are stiff and oblique to the stem; in more proximal parts they are attached at more obtuse angles or even abaxially curved. Associated are cylindrical strobili, up to 70 mm long, 10–15 mm wide; cone axis 1–2 mm wide, slightly thickened where whorls of sporangiophores are attached. Sporangiophores rigid, 8–9 mm long, with sporangia attached to a peltate head. No evidence of sterile bracts between sporangiophores.

*Remarks.* We have been unable to examine these fossils and our statement as to their taxonomic position is based exclusively on the views of Jongmans (1911) and Boureau (1964). However, this fossil-genus is usually interpreted as the foliage attached to *Archaeocalamites* stems and no such stems have been seen from this flora.

Localities: shaft 1, Chalennes; Mr Poulain's Quarry, Montjean-sur-Loire.

*Genus: Sphenophyllum* Brongniart, 1828a nom. cons.

*Sphenophyllum tenerrimum* Ettingshausen in Helmhacker, 1874 (Fig. 4G)

*Description:* Shoots with slender stems 2–3 mm wide, longitudinally ribbed. Whorls of leaves spaced at 5–10 mm intervals. Shoots usually preserved side-on but Bureau (1914) stated there are 10–12 leaves per whorl. Leaves 5–8 mm long, attached at about 45° and then rapidly curve so for most of their length they lie at right-angles to the stem. Each leaf subcuneiform, deeply divided with one or two orders of very slender segments, each with a blunt apex. A single vein lies in each segment.

*Remarks.* The specimens we have seen are similar to those figured by Bureau (1913) from the Loire Atlantique coalfield, with whorls of deeply incised, rather splayed leaves with bluntly terminated segments. The most detailed analysis of *Sphenophyllum tenerrimum* has been by Havlena (1982b) based on specimens from Upper Silesia, who resolved the issue of its type and discussed the morphological variation of the leaves. As pointed out by Havlena (1982b), there are a number of other sphenophyll species with deeply incised leaves from Visean and early Namurian floras, such as *Sphenophyllum charaeformis* Jongmans, 1912 and *Sphenophyllum pachyca* de Lamber, 1959; none are particularly well documented, but all seem to differ from *S. tenerrimum* in having larger and more divided leaves.

Wagner (1984) regarded *S. tenerrimum* as typically lower Namurian (*Cardioneuropteris antecedens*, *Calymmotheca stangeri* and *Calymmotheca larischi* zones). Mosseichick (2010) recorded it from across central and eastern Europe; similar specimens to those found in the Maine-et-Loire coalfield have been figured from the upper Visean of Bulgaria (Tenchov, 1987, pl. 3, figs 8, 10), and the lower Namurian of Belgium (Stockmans & Willière, 1952, pl. 1, figs 9, 10; pl. 20, figs 2–7; pl. 53, figs 2, 3).

*Localities.* Ardenay (MHNA.2009 PB 161); Chaudefonds-sur-Layon (MHNA.2009 PB 358); Saint-Aubin-de-Luigné (MHNA.2010 PB 125). Bureau (1914) also recorded but did not figure *S. tenerrimum* from Garenne quarry, Montjean-sur-Loire; de la Prée mine (shaft 4), Chalonnnes-sur-Loire and Beaulieu-sur-Layon mine.

*Sphenophyllum davyii* Bureau, 1914 pars. (Fig. 4H)

1913 *Sphenophyllum davyi* Bureau pars, pl. 70, fig. 1 (figs 2–4 uncertain).

1918 *Sphenophyllum davyi* Bureau; Carpentier, pl. 3; pl. 4, figs 1–3.

*Description.* Shoots with slender axes bearing whorls of 6–10 leaves, each leaf up to at least 25 mm long. Leaves attached obliquely to stem and then curve so that distal end at near to right-angles to stem. Leaves narrowly ob-cuneiform with numerous dichotomous veins.

*Remarks.* The taxonomic position of *S. davyii* is uncertain, and Carpentier (1928) expressed considerable reservation as to it belonging to *Sphenophyllum*. The types figured by Bureau (1914) appear to comprise a mixture of elongate leaves and it is far from certain that they all belonged to the same biological species. One of the specimens we have seen compares with Bureau (1913, pl. 70, fig. 1) and so have used the name for this. Carpentier (1918) figured what he regarded as a cone associated with similar foliage, but its structure is not clear.

*Locality.* Malécots mine, Chaudefonds-sur-Layon (MHNA. 2009 PB 056); Garenne quarry, Montjean-sur-Loire (MHNA.2009 PB 010). Specimens from Malécots quarry were also figured by Carpentier (1918).

*Class:* FILICOPSIDA Agardh, 1822 (POLYPODIOPSIDA Cronquist, Takht. & Zimmerm., 1966) (Fig. 5)

*Genus: Pecopteris* Brongniart emend. Cleal, 2015

*Remarks.* We are using this generic name in the restricted sense of Cleal (2015) for fern fossils of the filicalean family Tedeleaceae that bore sporangia that in the past have sometimes been referred to the fossil-genus *Senftenbergia* Corda, 1845.

*Pecopteris aspera* Brongniart, 1836 (Fig. 5A–F)

1913 *Dactylothea aspera* (Brongniart) Bureau; Bureau, pl. 5, figs 3, 5; pl. 6.

1913 *Senftenbergia plumosa* (Brongniart) Stur; Bureau (non Brongniart), pl. 8, figs 2 4; pl. 28, figs 3, 4.

*Description.* Fragments of tri- to quadripinnate fronds, sometimes associated with slender, linear tendril-like structures. Ultimate pinnae 20–30 mm long, narrowly lanceolate, basally constricted, alternately inserted at about right-angles to the rachis; adjacent ultimate pinnae contiguous at their base; ultimate pinnae sometimes somewhat curved or even flexuous, especially in distal parts of penultimate pinnae. Ultimate pinnae become progressively shorter along the penultimate pinnae towards their apex, and show a transition into pinnatifid and then entire pinnules. At the end of the pinnae, the lateral pinnules progressively merge into a usually linguaeform and very elongate terminal pinnule, somewhat tapered, with a blunt apex; in a few cases, pinnae terminated by a slender tendril-like prolongation. Lateral pinnules inserted near to right-angles low in pinnae, becoming somewhat obliquely in distal part of pinnae. Pinnules 2–5 mm long, 2–3 mm wide, broadly attached to rachis; smaller pinnules rounded, larger pinnules linguaeform tending to subtriangular and even subfalcate. Midvein straight and well-marked; lateral veins widely spaced, slightly curved, one or twice forked.

*Remarks.* The types of *P. aspera* originated from Montrelais in the Loire Atlantique coalfield (Brongniart, 1836) and compare very closely with the specimens from the Maine-et-

Loire coalfield figured by Bureau (1913) and those in the Angers collection. Following Radforth (1939) and Dalinval (1960) we have included this species within the tedeleacean fossil-genus *Pecopteris* as interpreted by Cleal (2015). This was based on a specimen in the Brongniart Collection in Paris (MNHN.F.308.2) figured by Bureau (1913, pl. 7, fig. 1) as a fertile example of *P. aspera*, which had sporangia of the *Dactylotheca* / *Senftenbergia*-type. However, this needs further verification through the study of other specimens. The slender tendril-like structures associated with these frond fragments, and the occasional slender prolongation of ultimate pinnae suggest the plant had a climbing habit, similar to *Pecopteris plumosa* (Artis) Brongniart, 1836 (Opluštil et al., 2007).

There are few other Visean or lower Namurian fern species with pecopteroid pinnules. Purkyňová (1970) described some fragments as *Pecopteris namurica* Purkyňová with senftenbergid sporangia, but the pinnules are more colliquely attached to the rachis compared with *P. aspera*. *Pecopteris plumosa* can extend down into the middle Namurian and has a similar venation to *P. aspera*, but the pinnules are larger pinnules and more linguaeform. Bureau (1913) figured some pinna fragments from the Maine-et-Loire floras as *P. plumosa*, but these have the more subtriangular pinnules associated with *P. aspera*.

According to Wagner (1984), *P. aspera* is a stratigraphically long ranging species from middle Visean to the uppermost Namurian.

*Localities.* Ardenay (MHNA.2009 PB 087, MHNA.2009 PB 230, MHNA.2009 PB 463), Chalonnes-sur-Loire (MHNA.2009 PB 223), de la Prée mine including shaft 3 (MHNA.2009 PB 040, MHNA.2009 PB 226, MHNA.2009 PB 227, MHNA.2009 PB 229, MHNA.2009 PB 359), La Haie Longue (MHNA.2010 PB 111, MHNA.2010 PB 127), La Roche Moreau, Saint-Aubin-de-Luigné (MHNA.2010 PB 120), Montjean-sur-Loire (MHNA.2009 PB 330, MHNA.2010 PB 006; also possible stem MHNA.2009 PB 459), Garenne quarry, Montjean-sur-Loire (MHNA.2009 PB 083, MHNA.2009 PB 084,

MHNA.2009 PB 085, MHNA.2009 PB 087), Saint-Aubin-de-Luigné (MHNA.2010 PB 130, MHNA.2010 PB 139; also possible rachis MHNA.2010 PB 124), Mazière and Port-Girault shafts, Saint Georges-sur-Loire (MHNA.2010 PB 137), Vouzeau, Chaudefonds-sur-Layon (MHNA.2009 PB 261). Bureau (1914) also recorded *P. aspera* from Saint-Nicolas shaft (South Vein), Montjean-sur-Loire; Mr Poulain's quarry, Montjean-sur Loire and Martigné-Briand.

*Genus: Zeilleria* Kidston, 1884

*Zeilleria antiquum* (Bureau) Cleal et al., comb. nov. (Fig 5G)

1913 *Hymenophyllum antiquum* Bureau, pl. 13, fig. 1; n<sup>o</sup>. 20, figs 1–2.

?1920 *Zeilleria moravica* (Ettingshausen) Bureau; Carpentier (non Ettingshausen), pl. 8, figs 10–12.

*Description.* Very slender, more or less zigzag penultimate rachises, preserved for up to 30 mm long, bearing alternating ultimate pinnae spaced 3–4 mm apart; in more proximal parts of the penultimate pinnae, the ultimate pinnae are near to right-angles to the rachis, but become more obliquely attached in more distal positions. Ultimate pinnae up to 15 mm long, but progressively become shorter along most of the penultimate pinna, and in more distal parts fuse to become discrete pinnules. Ultimate rachis slender and narrowly winged, bearing up to 12 pinnules on either side. Pinnules digitate, with very thin limb, alternate, linguaeform or sublinear, up to 4 mm long; largest pinnules have a terminal lobe, and 6–8 basally confluent, oval or sublinear lateral lobes, about 0.5 mm long. A very slender vein enters each lobe.

*Remarks.* Bureau (1914) assigned this species to the genus of extant ferns

*Hymenophyllum* Smith, 1793 (Bureau in error attributed this name to Kaulfuss, 1824). Many authors (e.g. Brousmiche, 1983) have placed such Palaeozoic fossil fern fronds with lobed

pinnules where the reproductive structures are unknown in *Sphenopteris* (Brongniart) Sternberg, 1825 but this is also difficult to support as the latter's type is a pteridosperm, *Sphenopteris elegans* (Brongniart) Sternberg.

The only other known fossil-genus of small-pinnuled ferns is *Zeilleria*, which has synangia comprising four to eight sporangia borne at the end of the pinnule lobes. Bureau (1914) described similar structures at the end of each lobe in this species from Maine-et-Loire, but only figured them as drawings and none of the material we had available exhibits comparable structures. Kidston (1923, p. 280) moreover expressed some doubt as to the interpretation of these structures in Bureau's specimens. Nevertheless, in the absence of an alternative generic name, we have proposed the combination *Zeilleria antiquum*.

The only other known comparable species of similar age is *Renaultia launoitii* Stockmans & Willière, 1952, but this has pinnules with wider and sometimes more subdivided lobes, and rather different reproductive structures.

Carpentier (1920) figured pinnules as fertile *Z. moravica*. It is difficult to be certain from the small photographs but they originated from a locality (Garenne quarry, Montjean-sur-Loire) that has yielded sterile foliage similar to *Z. antiquum*. We have therefore transferred Carpentier's specimens to the latter species.

*Localities.* Garenne quarry, Montjean-sur-Loire (MHNA.2009 PB 081, MHNA.2009 PB 087, MHNA.2009 PB 459, MHNA.2010 PB 045).

*Zeilleria moravica* (Ettingshausen) Bureau (Fig. H)

1913 *Zeilleria moravica* (Ettingshausen) Bureau, pl. 18, figs 1–4.

*Description.* Fronds at least tripinnate with widely-spaced pinnae. Ultimate pinnae with a thin, often flexuous 3 mm wide rachis, with strongly marked longitudinal striae. Pinnules usually c. 5 mm long, occasionally up to 10 mm long, widely spaced; pinnules digitate, with

slender filiform, widely-spaced divisions, each with a single longitudinal vein. Lobes of sterile pinnules have acute apex. Lobes of fertile pinnules terminated by four capsules fused at their base, and which at maturity open to form stellate structure.

*Remarks.* *Z. moravica* has been assigned to various fossil-genera of sterile foliage, but Bureau (1914) described what appear to be *Zeillera*-like sori structures at the end of the pinnule lobes (see also Carpentier, 1919; and Purkyňová, 1970, under the name *Rhodeopteridium* (*Zeillera*) sp.). In none of these specimens is the preservation good and no spores have been recovered to help confirm the generic assignment. Kidston (1924) moreover pointed out that the sori (if this is what they are) are rather larger than is typically seen in the Pennsylvanian aged *Zeillera*. Nevertheless, in the absence of an alternative genus into which the species could be placed, it is retained here in *Zeillera*.

No other fern species of this age has comparably shaped pinnules. Kidston (1924) compared it with *Rhodea smithii* Kidston, but this has rather larger digitate pinnules with thicker lobes, and appears more like the fronds of lyginopteridalean pteridosperms such as *Palmatopteris subgeniculata* (Stur) Potonié. *Rhodeopteridium alloiopteroides* Purkyňová, *Rhodeopteridium paskoviense* Purkyňová and *Rhodeopteridium flabellatum* (Brongniart) Purkyňová (Purkyňová, 1970).

Other than from the Loire floras, *Z. moravica* is best known from the upper Viséan and lower Namurian of the Midland Valley of Scotland (Kidston, 1924).

*Locality.* Chalonnès-sur-Loire (MHNA.2009 PB 461, MHNA.2010 PB 103), Malécots mine, Chaudfondes-sur-Layon (MHNA.2009 PB 334). Bureau (1913) figured specimens from Chalonnès-sur-Loire, Saint-Georges-sur-Loire mine (Port-Girault shaft); he also recorded it from Beaulieu-sur-Layon.

*Class:* LYGINOPTERIDOPSIDA Novak 1961 (Fig. 6)

*Remarks.* In the following descriptions, frond architecture is described using the terminology of Cleal & Shute (1991) and Laveine (1997).

*Genus:* **Sphenopteris** (Brongniart) Sternberg, 1825

*Remarks.* *Sphenopteris* is being used here in a restricted sense for the group of lyginopteridalean fronds centred on the type species *Sphenopteris elegans* (Brongniart) Sternberg. The fronds were bifurcate pinnate, the pinnules lobed or deeply incised (digitate) and the rachises often show distinctive transverse marks due to sclerotic thickenings.

In addition to the species described below, Bureau (1914) named a single *Sphenopteris*-like specimen from the Maine-et-Loire coalfield with very small, delicate, digitate pinnules as *Diplotmema depauperatum* Bureau. However, as only one specimen has ever been reported, the status of *D. depauperatum* is difficult to assess.

*Sphenopteris elegans* (Brongniart, Sternberg, 1825 (Fig. 6A,B)

(≡ *Filicites (Sphenopteris) elegans* Brongniart, 1822)

1913 *Diplotmema elegans* (Cöppert) Stur non Brongniart; Bureau, pl. 23, figs 2, 3; pl. 24, figs 1, 2; pl. 24 bis, fig. 1.

1913 *Palmatopteris furcata* (Brongniart) Potonié; Bureau (non Brongniart), pl. 24 bis, figs 2, 3.

*Description.* Bifurcate pinnate fronds with rachises showing short transverse marks and very fine longitudinal striae. Antepenultimate rachises 13–15 mm wide; penultimate rachises alternate, up to 200 mm long, c. 5 mm wide. Pinnae more or less tapered along entire length, up to 200 mm long, 120 mm wide at base. Pinnules 10–12 mm long, 8–10 mm wide, triangular or oval-triangular, petiolate, very deeply incised into two to four segments on each side of pinnule. Pinnule segments generally short; may be simple, linear, or divided once or

sometimes twice into subsidiary segments; ultimate pinnule segments linear with more or less acute apex. Adjacent pinnule segments closely spaced but never touching. Each ultimate lobe of pinnule has a single longitudinal vein.

*Remarks.* *S. elegans* has been widely named *Diplothemema adiantoides* (Schlotheim) Gothan, 1913 ( $\equiv$  *Filicites adiantoides* Schlotheim, 1820). However, Schlotheim's (1820) study predates the starting point for palaeobotanical nomenclature (ICN, Art. 13.1) and the earliest legitimately published name for this species is *Sphenopteris elegans* (Brongniart) Sternberg, 1825 ( $\equiv$  *Filicites elegans* Brongniart, 1822). As this was the only species mentioned in the protologue of the section *Filicites* (*Sphenopteris*) this became the type of the genus *Sphenopteris* (Cleal & Thomas, 2018).

Bureau (1914) compared his specimens with *S. elegans* as figured by Göppert (1836, pl. 10, fig. 1; pl. 11, figs 1, 2) and Stur (1877, pl. 13, fig. 5; pl. 14, figs 1–6), rather than the type figured by Brongniart (1822, p. 2, fig. 2). Bureau regarded the original Brongniart (1822) type as belonging to a different species, which he illegitimately named *Calymmatotheca silesiaca* Bureau. However, Bureau gave no reason for distinguishing separate species and most subsequent authors (e.g. Midston, 1923) have regarded them as conspecific; it is also of note that the Brongniart, Göppert and Stur specimens all originated from the Waldenburg Formation ( $\equiv$  Ostrava Formation) in Lower Silesia.

Patteisky (1929) suggested that two forms of *S. elegans* can be distinguished in Upper Silesia. The most typical form (corresponding to the holotype) has pinnules with relatively broad lobes and occurs in the lower Ostrava Formation (Petřkovice and Hrušov members). There is then a stratigraphical gap in the range in Upper Silesia until the Porub Member, where there is a similar form but with more deeply divided pinnules and more slender lobes, which he called fa. *silesiaca* (this appears to be different from *Calymmatotheca silesiaca* Bureau). However, according to Purkyňová (1970) the two forms often occur together

throughout the Ostrava Formation (although fa. *silesiaca* is a little more abundant in the upper part of the formation) and she did not recognise the taxonomic distinction. The specimens figured by Purkyňová (1970, pl. 29, figs 1–4) mostly originated from the lower Ostrava Formation and compare closely with the typical form of *S. elegans*, and to the specimens from the Maine-et-Loire coalfield.

One of the specimens figured by Bureau (1913, pl. 23, fig. 2) has the distinctive bifurcate pinnate frond architecture of *S. elegans*, albeit in what appears to be a young frond. The specimen also clearly shows the transverse bars across the rachis resulting from sclerotic thickenings, which is a characteristic feature of *Sphenopteris* sensu stricto fronds, and which helps distinguish them from *Calymmotheca* (see later).

Bureau (1914) also recorded specimens as *Diplomazina dissectum* (Brongniart) Stur from the Maine-et-Loire coalfield, although none were illustrated. Bureau (1914, p. 83) regarded *D. dissectum* as similar to *Sphenopteris elegans* but with rather larger pinnules. Since at least one of the localities listed by Bureau (1914) for *D. dissectum* also yielded abundant *S. elegans* it seems likely that they represent variation within a single species. Bureau (1913) figured two other fragments from the Maine-et-Loire coalfield with slightly larger pinnules as the Pennsylvanian-age species *Palmatopteris furcata*, but again these are almost certainly just variants of *S. elegans*.

*Sphenopteris elegans* is typically early Namurian in age (e.g. Wagner, 1984) and has been extensively documented from Scotland (e.g. Kidston, 1923) and Upper Silesia (e.g. Gothan, 1913; Patteisky, 1929; Purkyňová, 1970).

*Locality.* Beaulieu-sur-Layon mine (MHNA.2009 PB 049, MHNA.2009 PB 309, MHNA.2009 PB 418, MHNA.2009 PB 350, MHNA.2010 PB 075, MHNA.2010 PB.529); de la Prée mine (MHNA.2009 PB 058). Bureau (1914) recorded but did not figure specimens as *D. dissectum* from La Haie-Longue mine and Saint-Joseph shaft, Beaulieu-sur-

Layon. The specimens figured by Bureau (1913) as *Palmatopteris furcata* originated from Saint-Georges-sur-Loire mine.

**Genus: *Calymmotheca* Stur, 1877**

*Remarks.* This fossil-genus represents a distinctive group of early seed-plants with bifurcate pinnate fronds bearing relatively small, lobed to digitate pinnules, and with rachises with distinctive mesh-shaped markings resulting from sclerotic thickenings in the outer cortex. Stur (1877) originally characterised the genus by the presence of fructifications that he interpreted as sporangia that had split or burst open, but which are now regarded as being terminal clusters of ovules. However, it is clear from the diagnosis provided by Stur (1877, p. 255) that the circumscription was to include the fronds as well as the clusters of ovules that they bore.

Stur (1877) included 18 species within *Calymmotheca*, 11 of which were described by him. Three were based on clusters of uni-ovulate cupules (*Calymmotheca schimperi* Stur, *Calymmotheca haueri* Schimper, *Calymmotheca minor* Stur), which have yet to be linked with foliage. More complete specimens were made the basis of *Calymmotheca stangeri* Stur, *Calymmotheca linkii* Stur, *Calymmotheca divaricata* Stur, *Calymmotheca larischii* Stur, *Calymmotheca moravica* Stur, *Calymmotheca subtrifida* Stur, *Calymmotheca schlehanii* Stur and *Calymmotheca rothschildii* Stur. *C. moravica* has since been transferred to *Zeilleria* (see above) and *C. subtrifida* has also been interpreted as a true fern (Zimmermann, 1958, p. 603). The remaining six species appear to represent a taxonomically coherent group of fronds of early seed-plants.

Patteisky (1957) renamed the genus *Lyginopteris* Potonié, 1897 based on the presence of distinctive mesh-shaped markings on the rachises that also occur in *Lyginopteris* stem petrifications. If this were to be accepted, then the generic name *Lyginopteris* would have to

be suppressed in favour of the earlier heterotypic synonym *Calymmotheca*. It is certainly true that the type of the former generic name (*Lyginopteris oldhamia* (Binney) Potonié, 1897) bore *Calymmotheca* fronds but it is not certain that all stems of this type have this type of foliage; for instance, Tournaisian *Lyginopteris* stems (e.g. Barnard & Long, 1975) are much older than the currently known stratigraphical range of *Calymmotheca* fronds. In other groups of seed-plant fossils, the taxa of frond adpressions and stem petrifications are kept separate; for instance, *Medullosa* stem petrifications bore fronds that can be attributed to a range of different fossil-genera recognised in the adpression record (e.g. Chal & Shute, 1995, 2012). In this study we therefore restrict the fossil-genus *Calymmotheca* to adpressions of fronds and associated fructifications.

Zeiller (1883, p. 182) changed the orthography of this generic name to *Calymmatotheca* for linguistic reasons. However, the currently accepted *Code* (ICN, Art. 60.1) stipulates that original spelling has to be retained even if it is not linguistically correct.

*Calymmotheca dubuissonis* (Brogniart) Stur, 1877 (Fig. 6C)

(≡ *Sphenopteris dubuissonis* Brogniart, 1830)

*Description.* Fronds basally bifurcate, apparently at an acute angle (although the angle may have been narrowed through taphonomy). The petiole / primary rachis below the dichotomy is up to 6 mm wide with clear anastomosed surface markings. The bifurcation produces bipinnate to tripinnate primary pinna branches. Secondary pinnae attached both below and above the main frond dichotomy, spaced about 20 mm apart, oppositely arranged below the dichotomy, alternately or suboppositely above the fork, attached at 70–80°; secondary pinnae up to 100 mm long, parallel-sided in proximal part, gradually tapered in distal part. Up to c. 20 alternately arranged, almost contiguous pinnules borne on either side of the secondary rachises at 70–80° in proximal parts of the pinna, becoming more oblique

(50–60°) in more distal positions. Pinnules up to 8 mm long; the smallest are oval, intermediate forms subtriangular with one to three lateral lobes on each side, and the largest sub-linguaeform with up to four lobes on each side; all pinnules with a single, blunt terminal lobe with obtuse apex, similar in size to the distalmost lateral lobes. Lateral lobes rounded, sometimes partly basally constricted and oblique to midvein; in the larger pinnules the lobes have a somewhat undulate margin. A single vein enters each lobe from the midvein and then branches once or twice.

*Remarks.* The type of *C. dubuissonis* originated from Montreuil's, Loire Atlantique coalfield (Brongniart, 1830, pl. 54, fig. 4a, b) and additional specimens were figured from here by Bureau (1913). Bureau (1914) reported that he had been unable to locate the type (it is still not recorded in the on-line Type and Figured Catalogue of the Muséum d'Histoire Naturelle, Paris) but that he had discovered a second, very similar specimen (in the collections of the Muséum d'Histoire Naturelle, Nantes) that had a label in Brongniart's handwriting identifying it as *S. dubuissonis*. Brongniart's illustration of the holotype as a whole specimen is rather diagrammatic but the close-up shows a pinnule with oblique, basally constricted lobes very similar to Bureau's specimens.

Bureau (1914) also recorded but did not figure *C. dubuissonis* from Maine-et-Loire and there are well-preserved examples in Angers Museum, some of which are figured here.

The generic attribution of *C. dubuissonis* to *Calymmotheca* is based on the basal dichotomy of the frond and on the distinctive mesh-shaped surface markings on the rachises reported by Bureau (1914), although the specimens in the Angers collections do not show this particularly clearly. Bureau (1914) reported that isolated cupulate structures, similar to those attributed by Stur (1877) to *Calymmotheca*, were associated with these fronds but none were in direct attachment.

Bureau (1914) regarded these fossils as conspecific with *Calymmotheca stangeri*. However, Kidston (1924, p. 470) and Patteisky (1957, p. 63) argued that the pinnules of *C. dubuissonis* are more oblique to the rachis, are more divided and have more acute lobes (compare for instance with Stur, 1877, pls 8, 9; Kidston, 1924, pls 105, 106, 107, figs 1–6; Patteisky, 1957, pl. 2, figs 1–8; Purkyňová, 1970, pl. 33, figs 2–5; pl. 34, figs 1, 2; Purkyňová, 1979, pl. 3, fig. 1). The ultimate pinnae also tend to be more parallel-sided and closely spaced along the penultimate rachises.

Bureau (1914) also included the type of *Filicites bermudensis* Schlotheim, 1820 nom. illegit. ( $\equiv$  *Sphenopteris distans* Sternberg, 1825) in the synonymy of *C. dubuissonis*. However, the former species has smaller, more delicate pinnules with more slender lobes (Kidston, 1923, pl. 61, fig. 3; pl. 67, fig 3; Patteisky, 1957, pl. 1, figs 1–3).

In addition to the Loire specimens, the only other well-documented record of *Calymmotheca dubuissonis* is from the Vendée region a little to the south (Mathieu, 1937, pl. 3).

*Localities.* Beaulieu-sur-Layon mines (MHNAAn.2009 PB 012, MHNAAn.2009 PB 375, MHNAAn.2009 PB 476, MHNAAn.2010 PB 008, MHNAAn.2010 PB 086, MHNAAn.2010 PB 208); Chalonnnes-sur-Loire (MHNAAn.2010 PB 025, MHNAAn.2010 PB 096); La Haie Longue (MHNAAn.2010 PB 085), Claudefonds-sur-Layon (MHNAAn.2010 PB 144). Bureau (1914) also recorded *C. dubuissonis* from Montjean-sur-Loire; la Mazière shaft, Saint Geoges-sur-Loire; La Haie Longue; Saint Joseph shaft, Beaulieu sur-Layon; banks of the Loire.

*Calymmotheca divaricata* (Göppert) Stur, 1877 (Fig. 6F)

( $\equiv$  *Cheilanthites divaricatus* Goppert, 1836)

*Description.* Relatively delicate bifurcate pinnate fronds with bipinnate (sometimes tending to tripinnate) primary rachis branches; rachises often with a longitudinal furrow and

covered with small scars (? hair bases). Secondary pinnae oppositely attached below the main fork, alternately to suboppositely attached above the fork; in all observed cases, pinnae are attached at near to right-angles at c. 15 mm intervals. Secondary pinnae parallel-sided for most of length, but tapering towards apex in distal part. Tertiary pinnae or pinnules (depending on size of frond) alternately to suboppositely, obliquely attached ( $50\text{--}70^\circ$ ) at c. 5 mm intervals. Pinnules usually subtriangular, except the larger ones which are parallel-sided in their proximal part, up to 10 mm long, 5 mm wide; pinnules deeply digitate with up to three slender, oblique lobes on either side, plus a terminal lobe; lobes with round apex, and themselves further divided into two or three lobes in larger pinnules. A single prominent vein lies in each lobe.

*Remarks.* These frond fragments have delicate, digitate pinnules, quite different from *C. dubuissonis*. Bureau (1914, p. 252) only recorded *C. divaricata* from the Loire Atlantique coalfield and figured a particularly fine example from there (Bureau, 1913, pl. 15, fig. 1). However, there are specimens in the Angers collections, originating from the Maine-et-Loire coalfield, which clearly also belong to the same species.

Bureau (1914) named these fossils *Calymmotheca tenuifolia* (Brongniart) Stur var. *divaricata* (Stur) Bureau. However, the type of that species (*Sphenopteris tenuifolia* Brongniart, 1830) originated from the Saint-Georges-Chatelais mine of Maine-et-Loire, from where Bureau (1914) also reported taxa normally associated with latest Westphalian and Stephanian floras such as *Cyathocarpus arborea* (Sternberg) Weiss and *Cyathocarpus cyatheus* (Sternberg) Mosbrugger. In contrast, the holotype of the variety (*Cheilanthes divaricatus* Göppert, 1836) originated from similar, late Mississippian-aged strata in Upper Silesia. The protologue of Göppert's species included only a poor illustration but Stur (1877, pl. 13, figs 1–3) figured better material from Upper Silesia and this compares very closely

with the French specimens; Stur (1877, p. 166) in fact commented that he had seen specimens in the Bureau Collections that belonged to *C. divaricata*.

Patteisky (1957) named *C. divaricata Lyginopteris fragilis* (Schlotheim) Patteisky, 1929 (see also Kidston, 1923, p. 89). Although Schlotheim's (1820) publication was invalid, the species epithet was subsequently validated as *Sphenopteris fragilis* Schlotheim ex Brongniart, 1828a. However, the typification of the species is ambiguous. Schlotheim (1804, p. 46) originally stated that the type originated from Chaumont in Haute-Marne but later (Schlotheim, 1820, p. 408) that it was from Breitenbach suggesting it was latest Stephanian in age (Cleal, 2008a); he also in 1820 stated that he had seen a specimen from the early Namurian Waldenburg Flora in Silesia. As the illustration of the type is unclear (Schlotheim, 1804, pl. 10, fig. 17) *L. fragilis* name is best abandoned.

Patteisky (1957) regarded *Calymmotheca falter nainii* (Stur) Stur, 1877 and *Calymmotheca linkii* (Göppert) Stur, 1877 as varieties of *L. fragilis* that are distinguishable on minor differences in the terminal pinnules. However, the illustrations of their types (Stur, 1875, pl. 6, fig. 1 and Göppert, 1836, pl. 2, fig. 1) show that these two species have much less divided pinnules with rounder lobes than *C. divaricata*.

*Calymmotheca divaricata* is typical of lower Namurian floras (mainly the *C. stangeri* Zone) especially of Upper Silesia (Stur, 1875, 1877; Patteisky, 1935, 1957) and the Midland Valley of Scotland (Kidston, 1923).

*Localities.* de la Prée Mine (shaft 4), Chalonnnes-sur-Loire, (MHNAn.2009 PB 341); de la Prée mine (shaft 5), Chalonnnes-sur-Loire (MHNAn.2009 PB 228), Malécots mine (MHNAn.2009 098 ); unrecorded locality (MHNAn.2010 PB 098, MHNAn.2010 PB 135).

*Calymmotheca tridactylites* (Brongniart) Stur, 1877 (Fig. 6D)

(≡ *Sphenopteris tridactylites* Brongniart, 1830)

1913 *Calymmatotheca tridactylites* (Brongniart) Stur; Bureau, pl. 13, fig. 1.

*Description.* Bipinnate fragments from a possibly tripinnate primary rachis branch. Rachises stiff with a longitudinal groove. Ultimate pinnae alternate, attached at 15–25 mm intervals, parallel-sided in proximal part, gradually tapered in distal part. Pinnules obliquely attached to rachis, mainly subtriangular, usually 6–12 mm long, 3–5 mm wide, basally partly constricted, deeply lobed with obtuse rounded segments; basal lobes relatively erect, more distal lobes more obliquely inserted. A single vein enters each pinnule in its proximal part, and then dichotomises so an ultimate vein enters each lobe.

*Remarks.* These pinnae with small, subtriangular pinnules are very distinctive and cannot be confused with any other species of *Calymmatotheca*.

*Localities.* Chaudfonds-sur-Layon (MHNA.2010 PB 021) and an unrecorded locality (MHNA.2010 PB 023). The specimen figured by Bureau (1913) was from Montjean-sur-Loire.

*Calymmatotheca distans* (Sternberg) comb. nov.

(≡ *Sphenopteris distans* Sternberg 1825)

1913 *Diplothemema distans* (Sternberg) Schimper; Bureau, pl. 19.

*Description.* Stems up to 20 mm wide bearing alternately or helically arranged 8–10 mm wide petioles. Preservation is insufficient to demonstrate frond architecture in detail but there appears to be a dichotomy of the primary rachis, with pinnae attached below the fork.

Ultimate rachises slender, bearing widely-spaced, delicate pinnules, up to c. 8 mm long, 4–5 mm wide; pinnules rounded, deeply 3–5 lobed; lobes oblong, obtuse and spread out in fan.

*Remarks.* Bureau (1913) figured several specimens as *Calymmatotheca distans* from Beaulieu-sur-Layon, remarking that it is very rare here and is often associated with *C. dubuissonis*; it is possible, therefore, that they are merely fragments of young *C. dubuissonis*.

fronds. However, since these small-pinnuled forms appear sufficiently distinct, and they compare well with typical *C. distans* (e.g. Kidston, 1923, pl. 67, fig 3; Patteisky, 1957, pl. 1, figs 1–3) we have kept them taxonomically separate.

*Calymmotheca distans* is widely known as *Lyginopteris bermudensisiformis* (Schlotheim) Patteisky, 1929 (e.g. Kidston, 1923; Patteisky, 1957) but the basionym of that name (*Filicites bermudensisiformis* Schlotheim, 1820) was not validly published (ICN, Art. 13.1). The earliest validly published name is *Sphenopteris distans* Sternberg, 1825 but the combination *Calymmotheca distans* has not previously been validly published; we therefore propose it here.

Stur (1875) recognized two varieties of *C. distans* that he named var. *schlotheimii* (more correctly to be named var. *distans*) and fragments with more robust pinnules that he named var. *geinitzii*). The specimens from Maine-Loire clearly correspond to *C. distans* var. *distans*.

*Calymmotheca distans* is typical of the *C. stangeri* to upper *C. antecessens* Zones, especially of Upper Silesia (Stur, 1875, 1877; Patteisky, 1935, 1957) and the Midland Valley of Scotland (Kidston, 1923).

*Locality.* shaft on the hillside, Beaulieu-sur-Layon (MNHN-F-12029.1A ; MNHN-F-12029.2).

*Genus:* **Karinopteris** Boersma, 1972

*Karinopteris* cf. *acuta* (Brongniart) Boersma, 1972 (Fig. 6E)

1913 *Mariopteris acuta* (Brongniart) Zeiller; Bureau, pl. 24 bis, figs 4, 5.

*Description.* Oval-lanceolate bipinnate segments, up to c. 100 mm long, 40 mm wide, bearing alternately arranged ultimate segments spaced c. 25 mm apart. Rachises longitudinally ridged and with fine punctae (? trichome bases). Pinnules basally constricted, subtriangular, divided into 2–3 rounded lobes with smooth margins; basisopic pinnule of

each pinna swollen relative to other adjacent pinnules. Single vein enters each pinnule and then dichotomises and radiates into each lobe.

*Remarks.* *Karinopteris* cf. *acuta* is very rare in the Maine-et-Loire floras and only represented by relatively small fragments. They have the general morphology associated with *Karinopteris* pinnae as documented by Boersma (1972; see also Danzé-Corsin, 1953 under *Mariopteris acuta*). Bureau (1914) identified them as *M. acuta*, the type of *Karinopteris*. The pinnule lobes seem rather more rounded than is typical for that species. However, as the taxonomy of these early mariopteroid fronds has still to be properly worked out, we have provisionally attributed these Maine-et-Loire specimens to *K. acuta* with a cf.

*Localities.* Beaulieu-sur-Layon mine (MHNAn.2010 PB 022); La Roche Moreau, Saint-Aubin-de-Luigné (MHNAn.2010 PB 160). Bureau (1914) also recorded it from Saint-Georges-sur-Loire mine (Port-Girault and Marière shafts).

*Class:* CYCADOPSIDA Brongniart, 1843 (Fig. 7A)

- *Genus:* **Cardioneuropteris** Gogarova et al., 1993

*Cardioneuropteris antecessans* (Stur) Strullu-Derrien *et al.* comb. nov.

(≡ *Neuropteris antecessans* Stur, 1875).

1913 *Neuropteris antecessans* Stur; Bureau, pl. 9, fig. 3.

?1913 *Neuropteris schleani* Stur; Bureau, pl. 12, fig. 4; pl. 13, figs 2, 3.

*Description.* Single fragment showing small oval-elliptical, basally constricted pinnules, c. 5 mm long, 3 mm wide, obliquely (60–70°) attached to rachis. Strong midvein runs for  $\frac{2}{3}$  of pinnule length; lateral veins fork once and meet pinnule margin at 60–80°.

*Remarks.* This small fragment compares well with the types of *Neuropteris antecessans* (Havlena, 1969a). This is a widespread species found in late Mississippian (Asbian to Arnsbergian) floras of Europe, especially in the Silesian and Saxo-Thuringian basins (Hübers

et al., 2014). According to Wagner (1984) it is restricted to the *Neuropteris antecedens* Zone but there is also clear evidence of it in the overlying *Calymmotheca stangeri* Zone (as summarised by Mosseichik, 2010).

Goganova et al. (1993) showed that many late Mississippian fronds with *Neuropteris*-like pinnules had bifurcate pinnate architecture and so did not belong to *Neuropteris* as defined for instance by Cleal & Shute (1995). Goganova et al. (1993), therefore, transferred examples of such fronds from Kazakhstan to a new fossil-genus, *Cardioneuropteris*.

Goganova et al. observed that Stur's (1875) types of *N. antecedens* seem also to have a bifurcate pinnate architecture but that this needed to be confirmed through the discovery of larger specimens of that species. However, the photograph of the most complete of the types (Havlena, 1969a, pl. 17, fig. 2; pl. 18, fig. 2) is a large, somewhat curved tripinnate segment, suggesting that it was the primary rachis branch of a bifurcate pinnate frond (see also Havlena, 1969b, pl. 11, fig. 12). Consequently, we propose here the transference of Stur's species to *Cardioneuropteris*.

Bureau (1913) figured some pinnules as "*Nevropteris schleanii*" (i.e. *Neuralethopteris schlehanii* (Stur) Laveine) from the same locality. We have not seen these specimens and it is impossible to be sure from the illustrations, but it is feasible that they are elongate forms of *C. antecedens*.

*Locality.* Port-Girault shaft, Saint-Georges-sur-Loire (MNHN-F-4646).

**Genus: *Rhabdocarpus* Göppert & Berger in Berger, 1848**

*Rhabdocarpus bochschanus* Berger, 1848 (Fig. 7A)

1913 *Rhabdocarpus bochschanus* Berger; Bureau, pl. 75, fig. 6

*Description.* Large ovoid (?) ovules, 35 mm long, 15 mm wide, with a prominent longitudinal rib on the exposed surface, and a c. 10 mm long apical beak.

*Remarks.* These putative ovules are associated with the *Cardioneuropteris antecessens* frond fragments and it is tempting to regard them as originating from the same plant species, but no actual attachment has been found. Arber (1914) regarded *Rhabdocarpus boschianus* as a form of the medullosalean ovule *Trigonocarpus parkinsonii* Brongniart auct. but they are much more slender than that species. Similarly, slender but somewhat smaller ovules were reported by Goganova et al. (1993) with late Mississippian *Cardioneruopteris* fronds from Kazakhstan.

Another possible example of a large medullosalean ovule in the Angers collections (MHNA.n.2010 PB 061) from Martigné-Briand was identified as *Hexanospermum rugosum* Bureau, 1914 but the preservation is inadequate to confirm the identification, or even that it is the remains of an ovule.

*Locality.* Saint-Georges-sur-Loire mine (MHNA.n.2009 PB 377).

*Class:* CORDAITOPSIDA Lesquereux, 1880 (Fig. 7B)

*Genus:* **Cordaites** Unger, 1850

*Cordaites* spp. (Fig. 7B)

1913 *Cordaites borasifolius* (Sternberg) Unger; Bureau, pl. 71, fig. 1.

1913 *Cordaites principalis* (Germar) Geinitz; Bureau, pl. 71, figs 2, 3.

*Description.* Fragments of large, linear leaves up to 70 mm wide and 0.5 m long. Simple, longitudinal veins, separated by fine, parallel striations.

*Remarks.* Although these would be very early examples, they appear to have the type of venation normally associated with cordaitopsid leaves, in particular the numerous, parallel, thick main veins and the thinner false veins (?sclerotic fibres). Bureau (1914) assigned them to species normally found in Westphalian floras based mainly on the leaf shape and to an extent the veining. However, it has been shown that *Cordaites* leaves can only be reliably

identified if cuticles are preserved (e.g. Šimůnek, 2007) and in this case they are not. Since there are no well-defined *Cordaites* species from floras of similar age, we have referred to the Maine-et-Loire specimens simply as *Cordaites* spp.

*Locality.* Montjean-sur-Loire (MHNAn.2010 PB 032), ?Ardennay (MHNAn.2009 PB 160). The specimens recorded by Bureau (1913, 1914) originated from Port-Girault shaft, Saint-Georges-sur-Loire and Saint-Nicolas shaft (South coal seam), Montjean-sur-Loire.

## 4.2. Palynology

The analysis of three samples revealed a low content of organic material consisting mostly of small phytoclasts (brown and black, structured wood remains). The miospores that could be extracted were relatively small (Fig. 8). The spore material was partly well-preserved (e.g. Fig. 8.A, 8.E) and partly less-well-preserved (sample NamA-Sp02).

*Lycospora* and *Verrucosisporites* species occur, and other elements having a sculptured exine (Fig. 8). Such spores have been recognized also in non-illustrated, investigated sample material. The composition of the palynological material was similar in both the outcrop at Malécots quarry and the spoiling at Malécots mine.

## 5. Discussion

The distribution of the adpression taxa in the eleven main localities represented in the Angers collection and recorded in the literature was analysed using Unconstrained Seriation Analysis, which arranges both taxa and localities to maximise the presences along the diagonal of the data matrix (Brower & Kile, 1988). The results were used to construct Table 1. A Detrended Correspondence Analysis of the data (Fig. 9) has suggested that three weakly constrained groups of localities can be recognised:

(A) Malécots mine and quarry: mainly lycopsids and equisetopsids, and few pteridosperms.

(B) Ardennay mine, Chaudefonds-sur-Layon, Saint-Aubin-de-Luigné, Chalennes-sur-Loire mines, de la Prée mines and Montjean-sur-Loire: the most diverse floras with many lycopsids, equisetopsids, fern and *Calymmotheca* species. A reconstruction of the forest represented by this group is given in Fig. 10.

(C) Beaulieu-sur-Layon and Saint-Georges-sur-Loire mines: mainly characterised by the presence of *Cardioneuropteris* and *Karinopteris*, and with fewer lycopsid, equisetopsid and *Calymmotheca* species.

In the absence of any systematic sampling of these floras, it is difficult to say too much at this stage about these groups. However, there appears to be a broad transition along Axis 1 (whose eigenvalue represents about a half of the total variance in the data set) from floras dominated by lycopsids and equisetopsids (low scores) to floras with few lycopsids and equisetopsids and more pteridosperms including rare medullosaleans (high scores). It is possible that this is revealing a transition between lycopsid-dominated floras from flood-plain clastic swamps and mesophilic (pteridophyllous) communities of river valleys, similar to that seen in the Viséan floras of the Moscow Basin (Mosseichik & Ruban, 2010). There is little evidence of the “flöz-fern” floras recognised as drifted fragment in the similar-aged Petřkovice and Hrušov members of Upper Silesia (Havlena, 1961; Gastaldo et al. (2009a, b), typically including taxa of a more Viséan aspect such as *Cardiopteridium*, *Archaeopteridium*, *Sphenopteridium* and *Archaeocalamites*. Gastaldo et al. suggested that *C. antecedens* was an essentially “flöz-fern” element, and this only occurs very rarely in the Maine-et-Loire coalfield floras, in just Group C.

In purely biostratigraphical terms, the most robust biozonal model is that of Wagner (1984). Based on this, the co-existence in the Maine-et-Loire coalfield floras of

*Cardioneuropteris antecedens*, *Pecopteris aspera*, *Calymmotheca divaricata*, *Sphenopteris elegans*, *Mesocalamites* spp. and *Karinopteris* sp. places it in the lower *Calymmotheca stangeri* Zone (the lower *Lyginopteris* Zone in the “Global Macrofloral Zone” scheme of Mosseichik, 2010). Radioisotopic data from Upper Silesia strata yielding similar floras are middle Pendleian in age in the Heerlen Regional Chronostratigraphical scheme or early Serpukhovian in the IUGS Global Chronostratigraphy (Jirásek et al., 2018). This is older than the age suggested by Ducassou et al. (2011b) based on the radioisotopic date of  $319 \pm 3$  Ma (i.e. Bashkirian) of the associated Mésanger Granite. This was based on the assumption that the rhyolitic tuffs within the coal-bearing sequence were produced at the same time as the pluton emplacement. The biostratigraphical evidence instead suggests that either the volcanic activity pre-dated the pluton emplacement, or that they were the product of a more prolonged interval of igneous activity.

In the floristic scheme of Cleal (1994) the Maine-et-Loire coalfield floras belong to the Europe Palaeoarea, representing the Mississippian fossil floras of Europe, North America and northwest Africa. For floras of late Mississippian age, Mosseichik (2010) distinguished Southern Europe and Central Europe palaeoprovinces, the former including the Maine-et-Loire coalfield floras, together with contemporaneous floras from the Pyrenees (Babin et al., 1995) and Cordoba area in Spain (Wagner et al., 1983). Mosseichik characterised the Southern European Palaeoprovince by the presence of *Mesocalamites*, *Calamites*, *Sphenopteris* and *Rhodeopteridium*, and the absence of *Neuropteris*, *Lyginopteris* and *Archaeopteridium* (other notable absentees appear to be *Cardiopteridium* and *Rhacopteris*). As Mosseichik pointed out, however, the Loire floras are from the northern margins of this province and may be transitional between the Iberian floras and those of the central Europe province such as Scotland, Belgium and Upper Silesia; there are for instance several *Calymmotheca* species in the Loire floras.

An added complication is that most of the Iberian and central Europe floras were found in paralic deposits, whereas the Maine-et-Loire coalified floras may have originated from an intra-montane setting, which could have influenced the composition of the floras. These deposits are preserved in the internal zone of the Variscan belt, in small basins formed during the dextral displacement along the Nort-sur-Erdre fault (Barthet, 2005) shortly after the exhumation of high-pressure/low temperature metamorphic rocks (Champtoceaux Complex, Bosse et al. 2000; Pitra et al. 2010). This mountain range may not have been as elevated as previously suggested (e.g. Becq-Gireaudon et al., 1996). Recent isotopic analyses of meteoric-derived fluids from the south Armorican shear zones seem to indicate only a moderate palaeoelevation (Dusséaux et al. 2019). The provenance analysis performed on the sediments from the Maine-et-Loire coalfield indicates that the detrital material mostly derived from the metamorphic rocks of the Champtoceaux Complex, hence suggesting a local source and a small drainage area for this basin (Ducassou et al. 2014). This depositional context could explain the presence of taxa such as *Cardioneuropteris* that may have had an extra-basinal (“flöz-fern”) origin. Nevertheless, the rather different palaeogeographical setting for these coal deposits in Maine-et-Loire may provide part explanation for their distinctive floral composition. It is also important to point out that most of the floras incorporated into Mossbrink’s (2010) analysis have not been revised in over half a century; our experience with the Maine-et-Loire coalfield flora has shown that taxonomic revisions of the other floras will be required before reliable palaeoarea / palaeoprovince floristic analyses will be possible (contrast with the work done on Middle Pennsylvanian floras of Euramerica, e.g. Cleal, 2008b,c).

Although these fossil floras were obtained from coal-bearing deposits, they are rather different in character to those associated with the better known Westphalian coal sequences of Europe (e.g. Cleal, 2005, 2007; Uhl & Cleal, 2010). If the Maine-et-Loire floras are

corrected using the approach of Cleal et al. (2012) with the aim of translating fossil-species diversities into whole-plant species diversities, landscape-scale species richness appears to be substantially lower – about 20 species, in contrast to about 50 for the Westphalian floras. There is also a clear difference in the taxonomic makeup of the floras, with these early Namurian floras containing a significantly higher proportion of lycopsid species and a lower proportion of medullosaleans. Some caution must be exercised at this stage from drawing too many ecological conclusions from these observations as the Maine-et-Loire floras have not been the subject of systematic sampling. Nevertheless, the evidence seems to suggest that a significant change in the make-up of these coal swamp floras took place later in Namurian times as the biome expanded over larger areas of tropical Pangaea.

The core of this study has been the collections at Angers Museum and these mainly originated from the Maine-et-Loire coalfield. We did not therefore deal in detail with the floras from the other mines in the areas such as at La Tardivière, Languin and Montrelais. Bureau (1914) combined these fossils with those from the Maine-et-Loire coalfield in his monograph, and there are undoubtedly many species in common, such as *Pecopteris aspera*, *Sphenopteris elegans* and *Lepidodendron cf. nathorstii*, and it is likely that the floras are of very similar age. However Bureau's (1914) records also suggest that there are differences and this is likely as some coal seams in the Pays de la Loire coalfield are of Stephanian age. However, this will require a more detailed taxonomic analysis of the records from these other mines, preferably using the original specimens rather than just the published records, and this is beyond the scope of the present study.

Palynological analysis has the potential for providing further meaningful evidence for age determinations and palaeoenvironmental reconstructions (e.g. Cleal et al., in press). Due to the sparse palynological record of the sample material in this study, there was a lack of data for comprehensive species analyses and distribution patterns. Nevertheless, the miospore

record of the Malécots mine and Malécots quarry localities has shown a clear presence of *Lycospora* (Fig. 8A). *Lycospora* spores were produced by Lepidocarpaceae (e.g. Brack-Hanes and Thomas, 1983; Balme, 1995) and microfossils of this family are well-represented at the palynologically investigated localities such as *Lepidodendron veltheimii* and related species (Table 1). Part of the illustrated small, brown, ornamented spores (Fig. 8.D–H) were probably produced by Filicopsida (zygopterids, botryopterids) or are of uncertain affinities (lycopsids, filicopsids, cycadopsids; e.g. Balme, 1995).

This is the first record of spores having been successfully recovered from deposits of the Maine-et-Loire coalfield but further more detailed palynological investigations will be required to delve deeper into the stratigraphical and environmental questions, if the material allows. It is, for example, currently not clear whether the predominantly relatively small miospores reflect special local depositional environments (with accumulation of small organic particles) or are the dispersed products of plant communities that were growing around Locality 1 or in the wider area.

## 6. Conclusions

The Maine-et-Loire coalfield has yielded fossil floras with 33 fossil-species, representing about 20 whole-plant species of lycopsids, equisetopsids, filicopsids, lyginopterids, cycadopsids (medullosaieans) and cordaitopsids. They are remains of an essentially wetland vegetation, with some localities yielding more lycopsid-dominated floras that probably grew on wetter substrates, and others yielding assemblages dominated more by pteridosperms and ferns probably from somewhat better-drained substrates. However, excepted for a single occurrence of *Cardioneuropteris*, no evidence has been seen of the “flöz-fern” floras reported from similar aged deposits in Upper Silesia and thought to represent allochthonous remains of basin-margin or extra-basinal vegetation. The floras belong to the *Calymmotheca stangeri*

Zone indicating a middle Pendleian (i.e. Serpukhovian) age. They appear to represent vegetation of an intra-montane basin that may be an ecotone between the early Namurian floras of the Iberian Peninsula and the more diverse floras of central and eastern Europe. This potentially has considerable significance as the floristics and biostratigraphy of these late Mississippian floras will throw light on the early evolution of coal swamp vegetation – a biome that subsequently during Pennsylvanian times dominated large areas of tropical Pangaea, producing coal deposits that have proved of immense economic importance, and by acting as a carbon sink had a major influence on the evolution of climate and atmosphere at this time. The present paper represents the first step in developing an improved understanding of these important Serpukhovian fossil floras. It paves the way to overdue taxonomic revisions of other floras of the same age; illustrations will allow future comparisons to be made with confidence.

In regard to microfloras, the first Namurian spores are recorded from deposits of the Maine-et-Loire Coalfield. *Lycospora* sp. (from lycopsids) and small ornamented spores (from filicopsids and of uncertain affinities) are present at Malécots mine and Malécots quarry. This palynological evidence will serve as a basis for subsequent palaeoenvironmental and stratigraphical studies.

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## Figure captions

Fig. 1. Geological map. A) Location of the studied area (rectangle) within the Armorican Massif (NASZ: North Armorican Shear Zone; SASZ(N) and SASZ(S): respectively the northern and southern branches of the South Armorican Shear Zone B; NSEF: Nort-sur-Erdre Fault. B) Geological map of the studied area, showing the locations of historic coal mines and extraction sites.

Fig. 2. Cartographic illustrations showing locations of historic coal mines and extraction sites plus related lime kilns (Maine-et-Loire department, France). A) Overview map from Montjean-sur-Loire in the North-West to Doué-La-Fontaine in the South-East. B) Small scale map showing mine and kiln distribution in and around Montjean-sur-Loire. C) Small scale map showing mine distribution near Chalonnes-sur-Loire; D) Medium scaled map showing mine locations around Concourson-sur-Layon and at Martigné-Briand. Location number: 1) Malécots mine and Malécots quarry, Chauderonds-sur-Layon ; 2) Ardennay mine, (including St Barbe-des-Mines shaft), Chauderonds-sur-Layon; 3) Hillside on the north bank of the Layon, opposite La Brosse and Verzeau, Chauderonds-sur-Layon ; 4) Saint Aubin shaft, La Roche Moreau and La Haie Longue, Saint-Aubin-de-Luigné 5) Chalonnes-sur-Loire mines (shafts 1, 4 and du Décor, shaft); 6) De la Prée mine (Shafts 3, 4 and 5), Chalonnes-sur-Loire; 7) Saint-Georges-sur-Loire mine; 8) Saint-Nicolas shaft, Montjean-sur-Loire; 9) Concourson-sur-Layon mine; 10) Beaulieu-sur-Layon mines; 11) Coal seam near Martigné-Briand. Base map data copyrighted OpenStreetMap contributors and available from <https://www.openstreetmap.org>.

Fig. 3. LYCOPSIDA. A. *Lepidodendron veltheimii* (MHNA.2010 PB 530). B. *Lepidodendron volkmannianum* (MHNA.2009 PB 028). C. *Lepidodendron cf. nathorstii* (MHNA.2009 PB 392). D. *Lepidostrobis variabilis* (MHNA.2010 PB 001). E.

*Lepidodendron cf. lossenii* (MHNAAn.2009 PB 472). F. *Lepidodendron* sp. 1 (leafy shoot) (MHNAAn.2010 PB 116). G. *Lepidodendron* sp. 2 (leafy shoots) (MHNAAn.2009 PB 398). H. *Lepidostrobophyllum veltheimianum* (MHNAAn.2009 PB 394). I. *Bothrodendron wiikianum* (MHNAAn.2009 PB 402). J. *Sigillaria minima* (MHNAAn.2009 BP 091). K. *Stigmaria ficoides* (MHNAAn.2009 427). Photos by C. Strullu-Derrien.

Fig. 4. EQUISETOPSIDA. A, B. *Mesocalamites taitianus* (MHNAAn.2009 PB 393; (MHNAAn.2009 PB 164). C. *Mesocalamites haueri* (MHNAAn.2010 PB 122). D. *Mesocalamites* sp. (pith cast) (MHNAAn.2009 PB 391). E. *Asperophyllites cf. gothanii* (MHNAAn.2010 PB 107). F. *Calamostachys cf. paniculata* (MHNAAn.2010 PB 123). G. *Sphenophyllum tenerrimum* (MHNAAn.2009 PB 161) H. *Sphenophyllum davyii* (MHNAAn.2009 PB 010). Photos by C. Strullu-Derrien.

Fig. 5. FILICOPSIDA. A–F. *Pecopteris obovata* (MHNAAn.2009 PB 230, MHNAAn. 2010 PB 111, MHNAAn.2009 PB 229, MHNAAn.2009 PB 359, MHNAAn.2009 PB 083, MHNAAn.2009 PB 261). G. *Zeilleria antiquum* (MHNAAn.2010 PB 045). H. *Zeilleria moravica* (MHNAAn.2009 PB 461). Photos by C. Strullu-Derrien.

Fig. 6. LYGINOPTERIDOPSIDA. A, B. *Sphenopteris elegans* (MHNAAn.2009 PB 309, MHNAAn.2010 PB 075). C. *Calymmotheca dubuissonis* (MHNAAn.2009 PB 375). D. *Calymmotheca tridactylites* (MHNAAn.2010 PB 021). E. *Karinopteris cf. acuta* (MHNAAn.2010 PB 022). F. *Calymmotheca divaricata* (MHNAAn.2009 098). Photos by C. Strullu-Derrien.

Fig. 7. CYCADOPSIDA (A) and CORDAITOPSIDA (B). A. *Rhabdocarpus bochschanus* (MHNAAn.2009 PB 377). B. *Cordaites* sp (MHNAAn.2009 PB 160). Photos by C. Strullu-Derrien.

Fig. 8. Namurian spores recovered from the Maine-et-Loire coalfield at Malécots mine and quarry (Locality 1). A. *Lycospora* sp., NamA-Sp01-1, 36  $\mu\text{m}$ ; B. *Lycospora* sp., degraded, NamA-Tr-S11, 29  $\mu\text{m}$ ; C. *Lycospora* sp., degraded, silicified, NamA-Sp02-S11, 51  $\mu\text{m}$ ; D. spore cluster of trilete, ornamented spores, NamA-Sp01-1, 28  $\mu\text{m}$  (front spore); E. verrucate spore, NamA-Tr-S12, 43  $\mu\text{m}$ ; F. verrucate spore, partly degraded, NamA-Tr-S12, 23  $\mu\text{m}$ ; G. *Convolutispora* sp., NamA-Sp02-S11, 28  $\mu\text{m}$ ; H. spore cluster, *Verrucosisporites* in front, NamA-Sp02-S11, 51  $\mu\text{m}$  (front spore). Photos by E. Stolle.

Fig. 9. Plot of first two axes of Detrended Correspondence Analysis of data in Table 1. All data were used in the analysis, but the two localities with only one species each are not shown in the plot.

Fig. 10. Reconstruction of the Mississippian forest based mainly on the group B localities: the most diverse flora with many lycopsids, quisetopsids, fern and *Calymmotheca* species. Illustration by Victor O. Leshyk (<http://victorieshyk.com/paleo.html>)

### Highlights:

- The Maine-et-Loire coalfield has yielded a Serpukhovian-late Mississippian flora
- Represented are early examples of Palaeozoic coal swamp vegetation
- This is the first taxonomic review of the flora for over a century
- The flora belongs to the *Calymmotheca stangeri* Zone of the South European province
- There is evidence of a transition between floras from swamps to river valleys

## Abstract

Numerous localities in the Maine-et-Loire coalfield in northwestern France have yielded diverse adpression floras belonging to the *Calymmotheca stangeri* Zone, indicating an early Namurian (Serpukhovian – late Mississippian) age. The floristic affinities are with the South European Palaeoprovince, although there is some evidence of an ecotonal relationship with the Central European Palaeoprovince to the north. The geological context of the deposits suggest that the floras may represent vegetation from an intra-montane setting, although at lower elevations compared with the Pennsylvanian-age Variscan intra-montane basins. This represents some of the earliest known examples of coal swamp vegetation, although compared with the Pennsylvanian-aged coal swamps there was a significantly higher proportion of lycopsid species and a lower proportion of laedullosaleans. Most of the Maine-et-Loire fossiliferous localities yielded diverse assemblages of lycopsids, equisetopsids, ferns and *Calymmotheca* species, and these were used to develop a pictorial reconstruction of this early coal swamp vegetation. However, two of the localities yielded adpressions and associated palynofloras with a greater predominance of lycopsids and sphenopsids, suggesting vegetation of wetter habitats. Two other localities yielded species of a more Pennsylvanian aspect such as *Cardioneuropteris* and *Karinopteris*, which may represent drier substrate vegetation.

## **Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table 1. Distribution of plant fossil-species in the main fossiliferous localities of the Maine-et-Loire area. Localities are grouped and shaded based on the DCA analysis (Fig. 9). Locality

	1	9	6	2	5	4	3	8	11	10	7
<i>Thaumasiodendron andegavense</i>	*		*								

numbers refer to list in Section 3.

<i>Calymmotheca divaricata</i>	*		*		*				
<i>Sigillaria minima</i>	*				*		*		
<i>Stigmaria ficoides</i>	*		*	*	*			*	
<i>Lepidodendron</i> sp. 1			*	*			*		
<i>Lepidodendron veltheimii</i>	*		*	*	*	*	*		
<i>Mesocalamites taitianus</i>	*	*	*	*	*	*	*	*	
<i>Sphenophyllum davyii</i>	*								*
<i>Lepidostrobus variabilis</i>				*	*				*
<i>Bothrodendron wiikianum</i>				*	*	*			*
<i>Lepidostrobophyllum veltheimianum</i>			*	*		*	*	*	
<i>Lepidodendron</i> cf. <i>nathorstii</i>					*	*			
<i>Sphenophyllum tenerrimum</i>			*		*	*	*	*	*
<i>Lepidodendron volkmannianum</i>						*	*		
<i>Dichophyllites pachystachya</i>				*	*				
<i>Zeilleria moravica</i>	*			*	*			*	*
<i>Sphenopteris elegans</i>			*		*				*
<i>Pecopteris aspera</i>			*	*	*	*	*	*	*
<i>Mesocalamites haueri</i>				*	*	*	*	*	*
<i>Lepidodendron</i> sp. 2				*	*		*		*
<i>Calymmotheca tridactylites</i>						*	*		
<i>Calymmotheca dubuissonis</i>				*	*	*	*	*	*
<i>Lepidodendron</i> cf. <i>lossenii</i>							*		
<i>Calamostachys occidentalis</i>							*		
<i>Zeilleria antiquum</i>							*		
? <i>Calamostachys</i> cf. <i>paniculata</i>					*				*
<i>Karinopteris</i> cf. <i>acuta</i>					*			*	*
<i>Cordaites</i> sp.									*
<i>Calymmotheca distans</i>								*	
<i>Cardioneuropteris antecedens</i>									*
<i>Rhabdocarpus bochschanus</i>									*

### Highlights:

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