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The Carboniferous (Serpukhovian) macroflora from the “Coteaux du Pont Barré”, Beaulieu-sur-Layon (Maine-et-Loire), South of the Armorican Massif, France

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ABSTRACT

The “Coteaux du Pont Barré” in Beaulieu-sur-Layon is a Regional Natural Reserve which is home to exceptional flora and fauna. Recently fossil plants have been discovered at the site adding to its natural heritage significance. The exposure which is part of the “Sillon Houiller de la Basse-Loire” contains Serpukhovian-age (330–320 Ma) remains of sphenophytes, ferns, and lyginopteridopsid and cycadopsid pteridosperms, which are described for the first time as well as the geology of the site. Most Carboniferous macroflora previously described from the Maine-et-Loire has been based on *ex situ* specimens from now abandoned and inaccessible coal mines. The newly described macroflora shows evidence of *in situ* remains and differs somewhat in composition from those reported from the coal workings, especially in the total absence of lycopsids and *Calymmotheca* pteridosperms, and instead having abundant medullosalean foliage (*Neuralethopteris*). The co-occurrence of *Sphenopteris elegans* and *Neuralethopteris densifolia* suggests a slightly younger age compared to the macrofloras documented from the coal-bearing deposits. However, this could be an ecological consequence of the flora growing in better-drained substrate habitats.

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1. Introduction

The coal-swamps that extended over large areas of palaeotropical Euramerica during the Pennsylvanian and Cisuralian (late Carboniferous and early Permian) was one of the most important Palaeozoic terrestrial biomes (e.g. DiMichele et al. 2001; Greb et al. 2006; Cleal et al. 2012; Cleal 2021a, b), providing the habitat in which many biotic groups diversified including insects, arachnids, reptiles and gymnosperms, and having a major impact on atmospheric composition and climate through enhanced transpiration and carbon sequestration. As a result, this biome has attracted considerable interest from geologists and palaeontologists, to try to determine its long-term impact on Earth history.

However, the earliest evolution of the coal swamp biome in the latest Mississippian (Serpukhovian) is less well understood. Palaeobotanical remains (hereafter referred to as macrofloras – see Pardoe et al. 2021) of the Serpukhovian proto-coal swamps are well preserved in the Pays-de-Loire region of north-western France and were documented in detail notably by Bureau (1913–1914) and more recently by Strullu-

Derrien et al. (2021, 2022). Most of this evidence was derived from coal workings that are no longer accessible and, although many of the fossils are still available in museum geoheritage collections, it is difficult to interpret the depositional context of the macrofloras.

In this paper, we document a macroflora that was recently collected from an exposure, the “Coteaux du Pont Barré”, along the Layon River in Beaulieu-sur-Layon, 20 km south of Angers (Maine-et-Loire). The site is well known, especially for its extant flora long studied by the botanist Robert Corillion (1908–1997), who first established the protection of the area (Corillion 1957). The macroflora was discovered some years ago by the winemaker who owned the site and his collaborators. Nowadays, most of the site belongs to the “Domaine Belargus”, a leading biodynamic winery in the Loire Valley, and is managed for its protection by the “Ligue de Protection des Oiseaux (LPO) Anjou”.

This macroflora differs in composition from those reported earlier from the coal workings in this area, which we have interpreted as representing

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vegetation that grew in comparatively less well-drained habitats.

2. Geological setting

The studied outcrop is part of the “Sillon houiller de la Basse-Loire” (Bureau 1913-1914), a narrow (0.5 to 2

km) zone of Carboniferous coal-bearing outcrops extending over a length of about 100 km. This zone is bounded between two major domains, the Saint-Georges-sur-Loire Unit to the north, and the Mauges Unit to the south (Figure 1a, b; e.g. Cartier et al. 2001; Cartier and Faure 2004; Ballèvre et al. 2009; Lin et al. 2019). The deposition setting for these coal-bearing strata is interpreted as narrow pull-apart basins, deve-

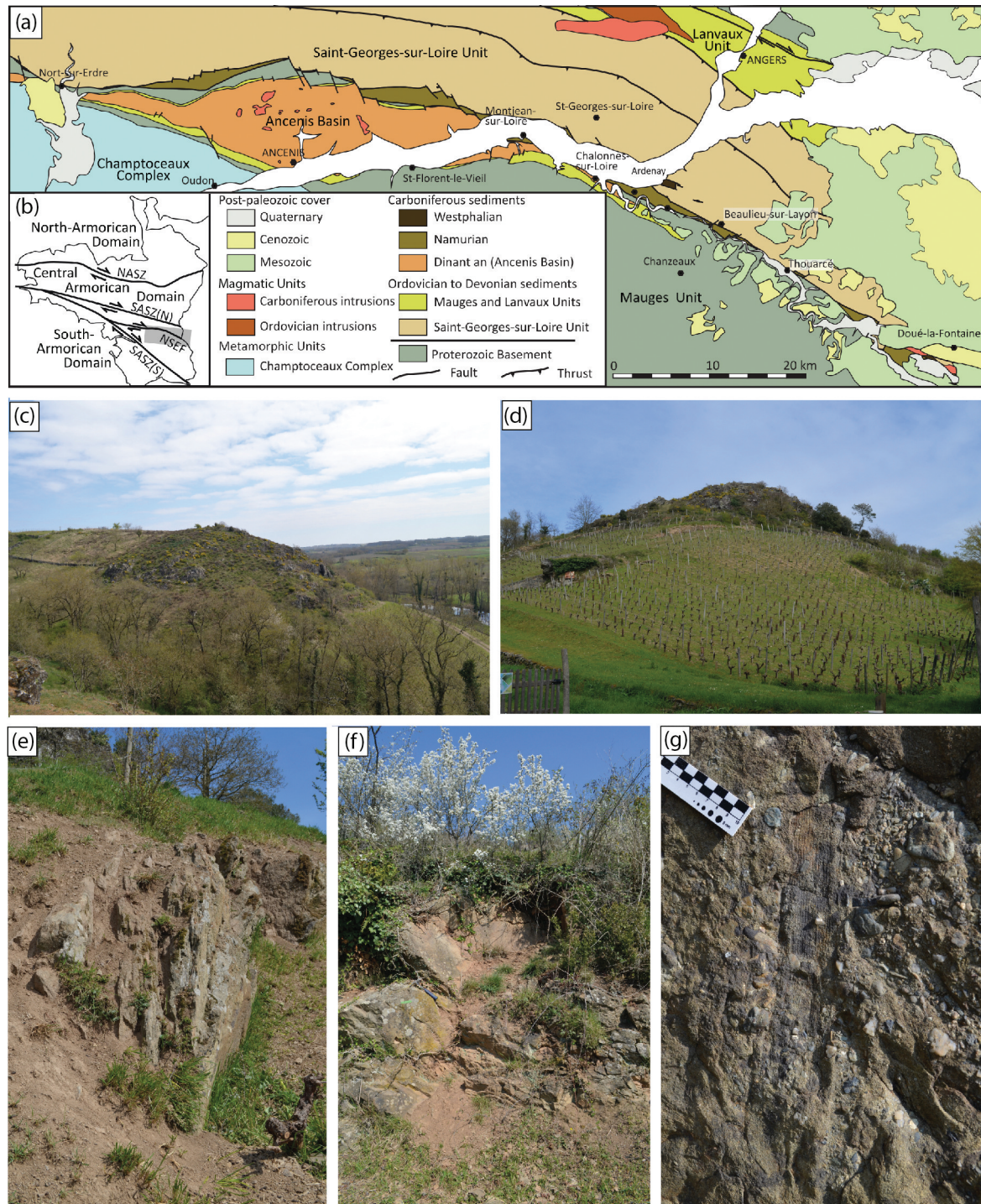


Figure 1. (a) Geological map showing the location of the studied area (Beaulieu-sur-Layon). (b) Location of the area (rectangle) within the Armorican Massif (NASZ: North Armorian Shear Zone; SASZ(N) and SASZ(S): respectively, the northern and southern branches of the South Armorian Shear Zone; NSEF: Nort-sur-Erdre Fault). (c) Overview of the “Coteaux du Pont Barré” on the right bank of the Layon River (river visible on the right side). (d) the “Coteau des Treilles” vineyard. (e-g) Different views of the outcrop. *Mesocalamites* (cast of stem) (g), along the bedding surface of a conglomerate.

loped during dextral displacement along the crustal-scale Nort-sur-Erdre Fault (Ballèvre et al. 2009).

The outcrop is located on the right bank of the Layon River, about 500 m north-west of Pont-Barré (Figures 1c, 2a). It is situated in a Regional Natural Reserve, with the majority of the outcrop located along the middle part of the slope dominating the Layon River, and above the renowned vineyard, the “Coteau des Treilles” (Figure 1d). Two main formations are seen (Blaise et al. 1986):

- (1) To the north-east, mafic schists of the Saint-Georges-sur-Loire Unit display a strongly dipping foliation to the NNE. They consist of mafic volcanics, in most cases fine-grained tuffs and breccias, sometimes containing flattened limestone clasts, up to 10–12 cm long. No fossils have been identified in these fine-grained, fully recrystallized limestones.
- (2) To the south-west of the schists are found steeply-dipping, alternating layers of Carboniferous conglomerates, sandstones sometimes grading to siltstones, and less frequently shaly layers. Several layers of conglomerates may be seen. Most conglomerates grade from clast- to matrix-supported, the coarser varieties are very poorly sorted while finer layers are much better sorted. They display well-rounded, abundant pebbles of various lithologies, namely milky quartz (derived from quartz veins), rhyolites and tuffs, schists and quartzites. The size of the pebbles is smaller in the southerly layers compared to those close to the contact with the St Georges schists, where an outcrop contains pebbles up to 30 cm. The size of the pebbles, and their nature (with large amounts of phtanites, i.e. siliceous shales) suggest a rather proximal deposit, mainly derived from the northerly situated St-Georges-sur-Loire Unit, consistent with previous observations (Blaise et al. 1986). Fossil plants have been mainly found within reddish coloured sandy-to-silty layers interbedded within conglomerates (Figures 1e-g; red star in Figure 2). These are observed *in situ* in the upper part of the vineyard slope “Coteau des Treilles”. A *Mesocalamites* (cast of stem) occurs *in situ* (Figure 1g) along the bedding surface of a polygenic conglomerate. This indicates transport and deposition of the plant remains by fast-flowing water (e.g. rivers).

The contact between the St-Georges-sur-Loire and the Carboniferous sediments is not well exposed in the Pont-Barré area. At a regional scale, this contact is

generally considered as a major, crustal-scale, fault, as shown on the geological map of Thouarcé (Blaise et al. 1986). This fault has been called the Nort-sur-Erdre (or Layon) Fault, and displays a long, polyphase Variscan history (Cartier and Faure 2004; Ballèvre et al. 2009; Lin et al. 2019). In addition, it has been reactivated during several periods during the Mesozoic and the Cenozoic, as indicated in the studied area by the difference in altitude of the base of the transgression by Cenomanian sediments (Figure 2; Poirier 1935; Louail 1984; Blaise et al. 1986; Sellier 2020)

3. Material and methods

Specimens collected on the outcrops were borrowed from Erwan Guillou of the “Ligue de Protection des Oiseaux (LPO) Anjou” where they are currently stored. Later, they will be on exhibit at the “Domaine Belargus” winery located at Saint-Lambert-du-Lattay, Maine-et-Loire, France. Specimens under the names PalB 001 to PalB017 were photographed under natural light, using a Nikon D500 camera with a 180 mm macro lens.

4. Descriptions

In all cases, genera and species referred to here are fossil-taxa (*sensu* Cleal et al. 2010; Cleal and Thomas 2021), whereas suprageneric taxa are whole-plant taxa. Following Agosti et al. (2022), full details of the authorship of all taxa are given.

Class: EQUISETOPSIDA Agardh, 1825

- Genus: *Mesocalamites* Hirmer (1927) emend. Remy and Remy (1978)

Mesocalamites cistiiformis (Stur) Hirmer (1927) (Figures 1g, 3a-c, e)

(≡ *Calamites cistiiformis* Stur 1877)

Description: Linear, unbranched axes up to 20 mm wide, preserved for up to 150 mm long. Fine longitudinal ribs with bluntly acuminate ends, ca. 15 ribs per cm across axis. Clearly marked nodes across axis, with longitudinal ribs sometimes passing directly across or sometimes off-set. Internodes at least 100 mm long, as no preserved stem shows more than one node. No branch scars preserved.

Remarks: These axes represent calamite stems, some definitely as pit-casts, but others as possible stem compressions. They are characterised by long internodes, very fine longitudinal ribs that only sometimes alternate at the nodes, and an absence of branch scars, and are very similar to the specimens figured by Crookall (1969, pl. 111, Figures 1, 2), Purkynová (1970, pl. 8, Figure 4) and Josten (1983, pl. 2, Figures 1, 2) as *M. cistiiformis*.

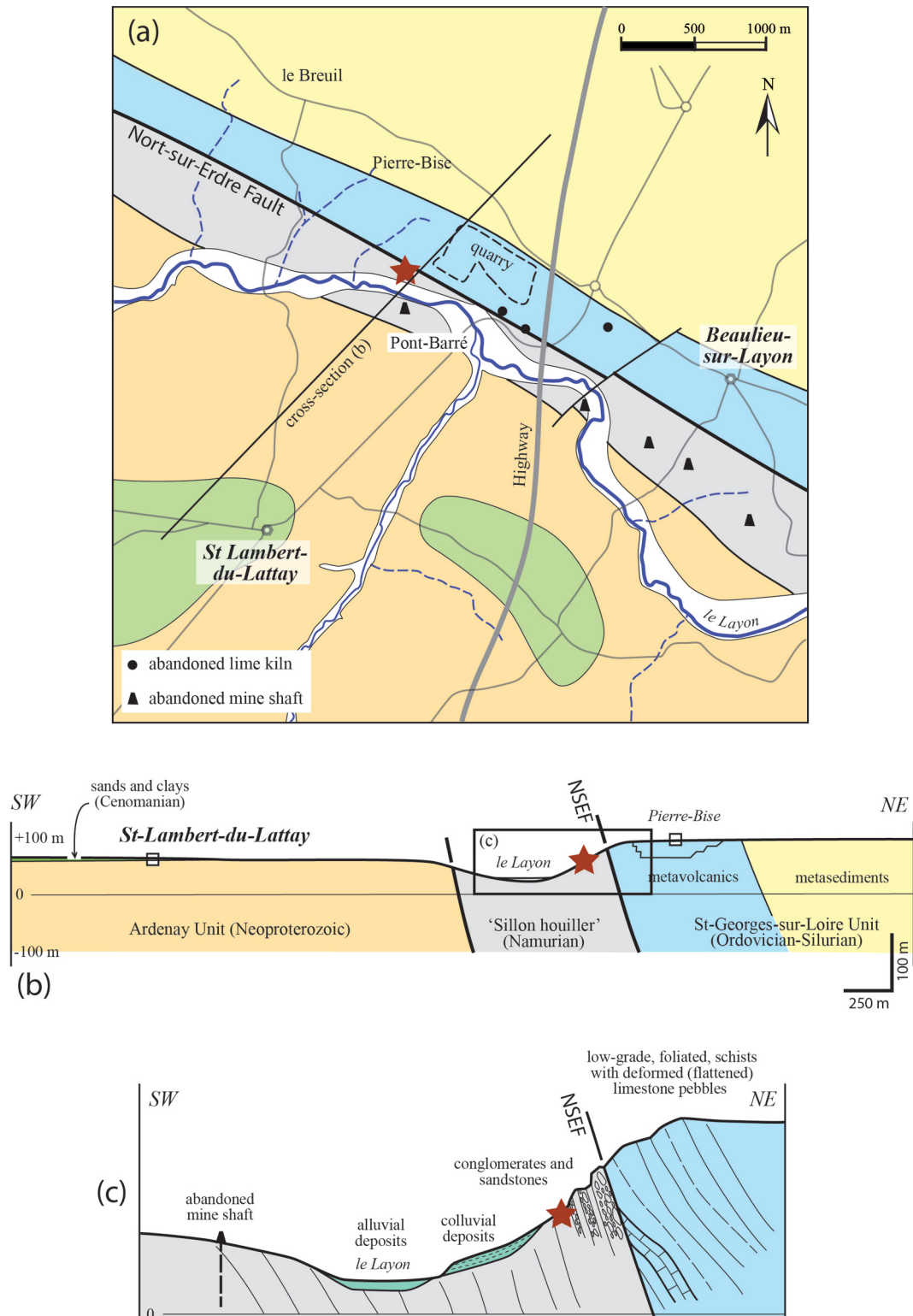


Figure 2. Geological setting of the studied site, indicated by a red star. (a) Simplified geological map of the studied area, modified from Blaise et al. (1986). The Nort-sur-Erdre Fault (NSEF) separates the Saint-Georges-sur-Loire and the Ardenay Units, to the North and South, respectively. A narrow band of Carboniferous sediments (“Sillon houiller de la Basse-Loire”) is located along the southern contact with the Nort-sur-Erdre Fault. Palaeozoic rocks are unconformably covered with a thin sheet of Cenomanian sands and clays. (b, c) Schematic cross-sections of the studied area. Note that the plant-bearing beds are observed in sandy to silty layers interbedded within conglomerates.

Jongmans (1911) combined this species with *Calamites cistii* Brongniart (1828), which also has axes with fine longitudinal ribs, long internodes and few branch scars, but the ribs in the latter species consistently alternate at

the nodes (Crookall 1969). There is also a comparison with *Mesocalamites taitianus* (Jongmans and Kidston) Hirmer (1927), but the latter has rather wider ribs, shorter internodes and large, oval branch scars.

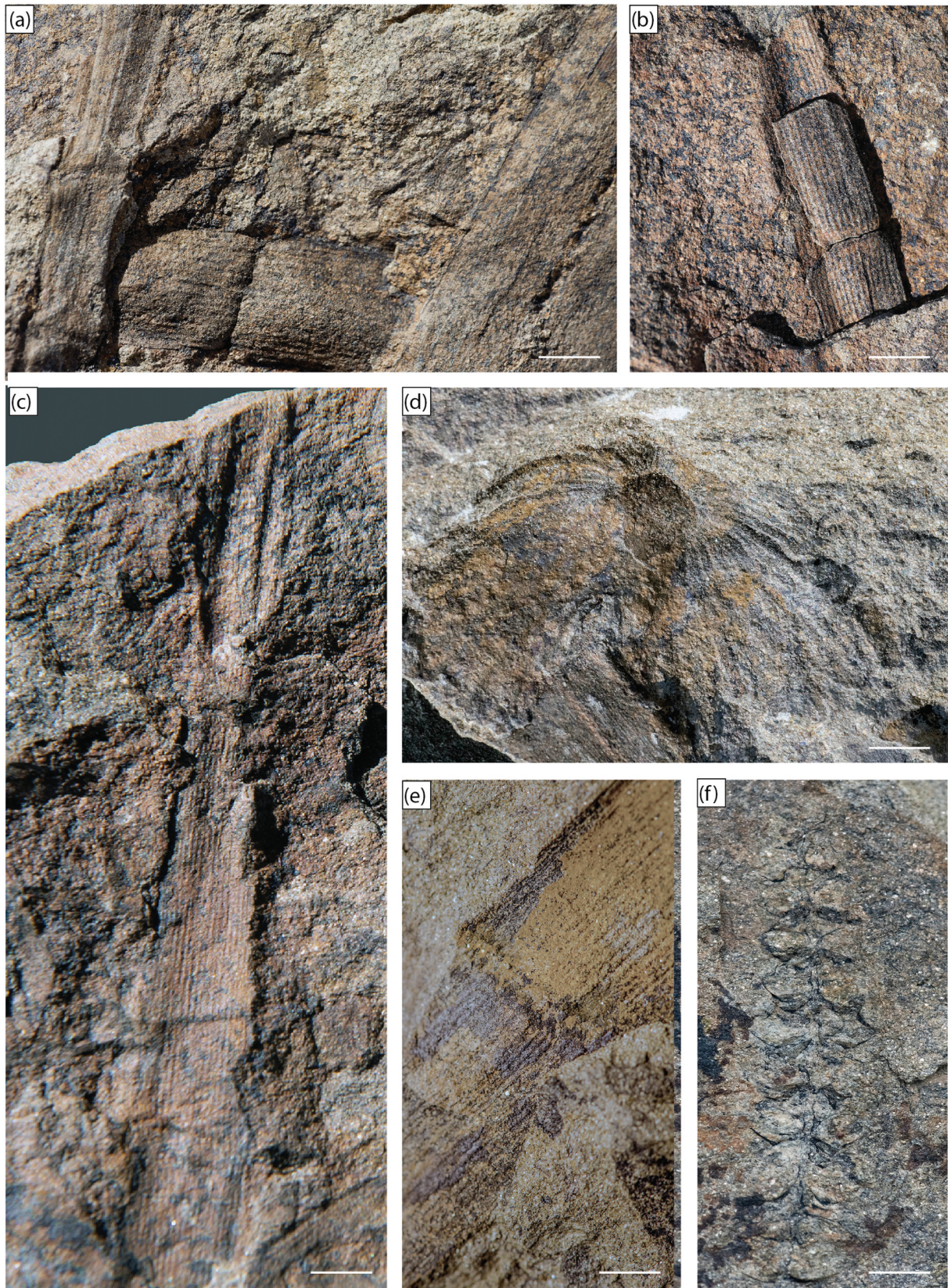


Figure 3. (a–c, e) *Mesocalamites cistiiformis* (Stur) Hirmer (PalB 001–003, PalB 005); (a, b) pith casts; (c) ?cast of stem; (e) cast of stem showing leaf-attachment scars. (d) *Annularia* cf. *radiata* (Brongniart) Sternberg (PalB 004), leaf whorl. (f) *Palaeostachya* cf. *mostensis* Purkynová (PalB 006), part of strobilus showing bracts and axillary ?sporangiophores. Scale bars: 0.42 cm (a); 0.55 cm (b); 0.47 cm (c); 0.84 cm (d); 0.50 cm (e); 0.30 cm (f).

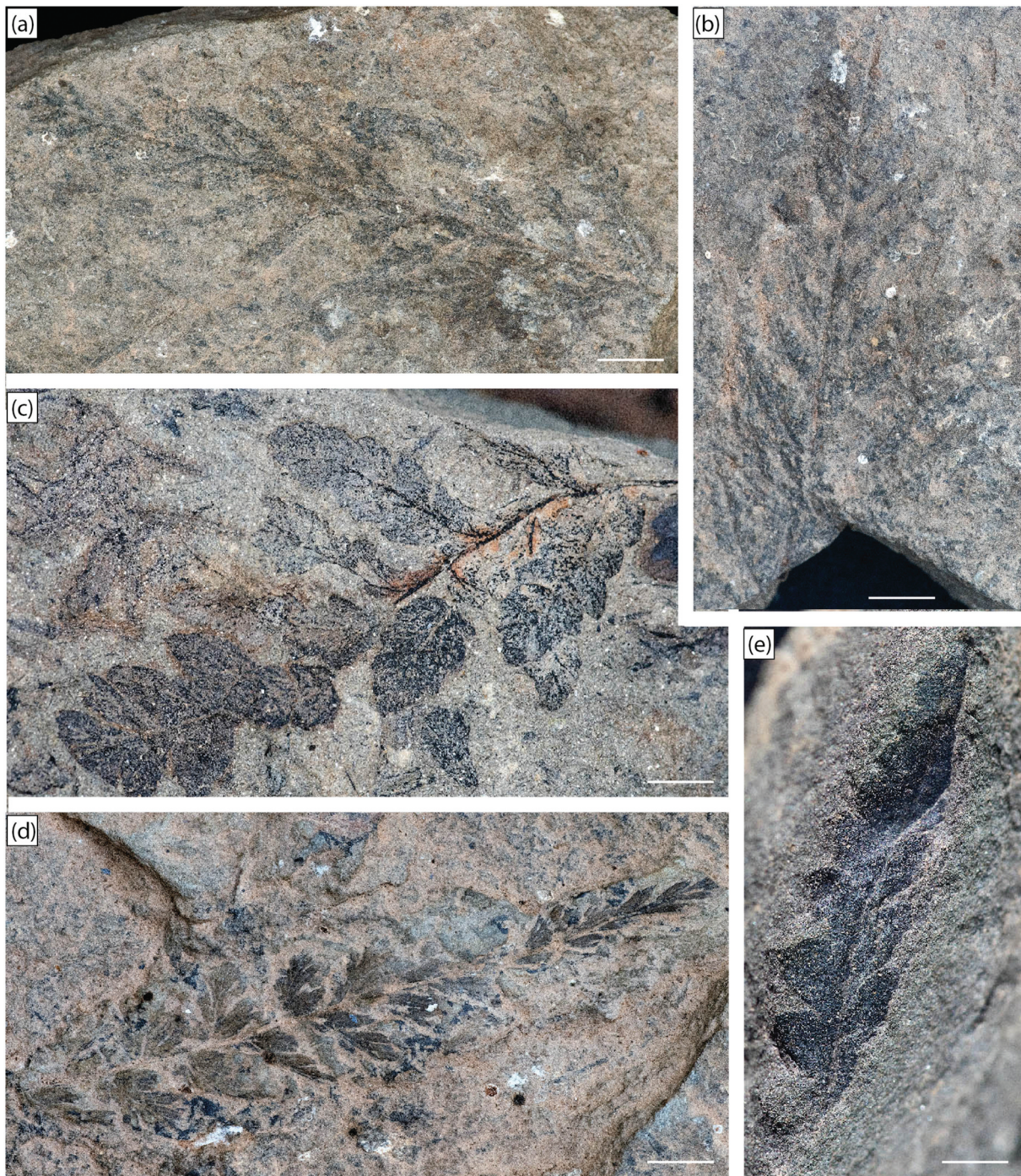


Figure 4. (a, b) *Pecopteris plumosa* (Artis) Brongniart (PalB 007, 008), slender, obliquely attached pinnules. (c, e) ?*Mariopteris* sp. (PalB 010, 011), linguiform, pinnatifid pinnules typical of *Mariopteris*. (d) *Sphenopteris elegans* (Brongniart) Sternberg (PalB 009), ultimate pinna with typical incised pinnules. Scale bars: 0.37 cm (a), 0.40 cm (b, c); 0.55 cm (d); 0.15 cm (e).

Specimens PalB 001–004, PalB 005.

- Genus: *Annularia* Sternberg KM von (1821)

Annularia cf. *radiata* (Brongniart) Sternberg KM von (1825) (Figure 3d)

Description: A single specimen of a stem ca. 5 mm wide with 25–20 leaves attached at a node (the number of leaves in the incompletely preserved leaf whorl is estimated). Leaves are basally fused to form a 1-mm-wide collar around the stem. Leaves ca. 20 mm long, 2 mm wide, linear-lanceolate, widest in middle, with acute apex.

Remarks: Since this single specimen represents the foliage on a relatively wide stem, it is difficult to definitely ascertain the shape of the leaf whorl. However, the general shape of the leaves and the presence of a basal collar makes it most comparable to *A. radiata* and *Annularia ramosa* Stur, (1887). These species of sphenophyte foliage are poorly constrained, and we have used *A. radiata* as the comparison simply because it is the more widely used name.

Specimen PalB 004

- Genus: *Palaeostachya* Weiss (1876)

Palaeostachya cf. *mostensis* Purkynová (1970) (Figure 3f)

Description. Strobilus slightly tapered, maximum (proximal) width 9 mm, preserved for a length of 41 mm. Strobilus axis ca. 1 mm wide with whorls of at least 4 bracts at intervals of 4–5 mm. Bracts initially directed proximally, straight for the first half of length and then curve so their distal part is ca 45° to strobilus axis. Large carbonaceous mass (?sporangiphore) attached to axil of bract and strobilus axis.

Remarks. This strobilus clearly shows what are presumably the sporangiphores in an axillary position, indicating that it belongs to *Palaeostachya*. Most sphenophyte strobili from Namurian macrofloras belong to *Calamostachys* (e.g. Stockmans and Willièrè 1953; Josten 1983), but Purkynová (1970) described *Palaeostachya* strobili from the upper Arnsbergian (uppermost Serpukhovian) of Upper Silesia. Although we have only one specimen of this strobilus, it is of generally similar size and shape and so we tentatively compare it with Purkynová's specimens.

Specimen PalB 006

Class: FILICOPSIDA Brongniart (1822)

- Genus: *Pecopteris* (Brongniart) Sternberg KM von (1825) emend. Cleal (2015)

(≡ *Filicites* (*Pecopteris*) Brongniart (1822))

Pecopteris plumosa (Artis) Brongniart (1836) (Figure 4a, b)

(≡ *Filicites plumosus* Artis 1825)

Description: Bipinnate pinna fragments up to 40 mm long. Penultimate rachis straight and slender (1 mm wide). Ultimate rachises slender (ca. 0.5 mm wide), alternately arranged and oblique to penultimate rachis. Ultimate pinnae up to 15 mm long, spaced 5 mm apart, gradually tapered along most of length. Pinnules alternate, oblique, subtriangular with rounded to acute apex, ca 2 mm long, 1 mm wide. The venation is unclear, but each pinnule appears to have a prominent midvein along most of its length.

Remarks: This specimen is very similar to the *P. plumosa* figured by Dalinval (1960, pl. 11, Figure 1; pl. 12, Figure 2) and Josten (1983, pl. 46, Figure 3), and corresponds to the forma *delicatula* of that species.

Specimens PalB 007–008

Class: LYGINOPTERIDOPSIDA Novák (1961)

- Genus: *Sphenopteris* (Brongniart) Sternberg KM von (1825)

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

Sphenopteris elegans (Brongniart) Sternberg KM von (1825) (Figure 4d)

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

Description: Once-pinnate fragments of fronds up to 55 mm long, 12 mm wide, gradually tapered to a deeply incised terminal segment. Rachis slender (<1 mm wide), straight or slightly deflected. Lateral pinnules alternate, obliquely inserted at 45° or less in the distal part of pinna, gradually changing to 60–70° in more proximal positions. Pinnules rhomboidal, up to 6 mm long, 5 mm wide, deeply incised into up to eight segments, each segment especially in more proximal parts of pinnule further divided into up to three subsidiary segments; segments/subsegments narrowly lanceolate with bluntly acuminate apex. Thin, basally decurrent midvein extends for most of the pinnule length and producing thin lateral veins, one for each ultimate segment. Pinnule lamina well developed so that there are only narrow gaps between each segment.

Remarks: These pinna fragments with deeply incised, somewhat obliquely attached pinnules, with bluntly acuminate ultimate segments, compare well with *S. elegans* as illustrated by Kidston (1923) and Purkynová (1970). Although the pinnule shape is typical for this species, their size is rather small, but this is probably just a function of them coming from a relatively distal position in the pinna. There are some similarities with the Westphalian *Palmatopteris furcata* (Brongniart) Potonié (1893), but the pinnules of the latter are not so oblique to the rachis and have more bluntly terminated pinnule lobes. *S. elegans* typically ranges between the upper *Cardioneuropteris antecedens* and *Calymmotheca larischii* Zones (Wagner 1984; Opluštil et al. 2021)

Specimen PalB 009

- Genus: *Mariopteris* Zeiller (1878)

-? *Mariopteris* sp. (Figure 4c, e)

Description. Linguaeform, pinnatifid pinnules with rounded to bluntly acuminate apex and partly constricted base, 10–15 mm long, 3–5 mm wide. Thin, strongly decurrent midvein extends for much of the pinnule length. Lateral veins alternate and produce a bunch of final veins in each of the pinnule lobes (details of the veining pattern not preserved).

Remarks. These fragments compare with remains of *Mariopteris* fronds from Pennsylvanian macrofloras such as *Mariopteris muricata* (Sternberg) Zeiller (1878), but are too small to make a definite species assignment.

Specimens PalB 010, 011

Class: CYCADOPSIDA Brongniart, 1843

- Genus: *Neuraethopteris* Cremer (1893) emend. Laveine (1967)

Neuraethopteris densifolia Josten (1983) (Figure 5)

Description. Linguaeform, more-or-less bilaterally symmetrical pinnules with parallel margins, broadly rounded apex and constricted base, up to 9 mm wide;

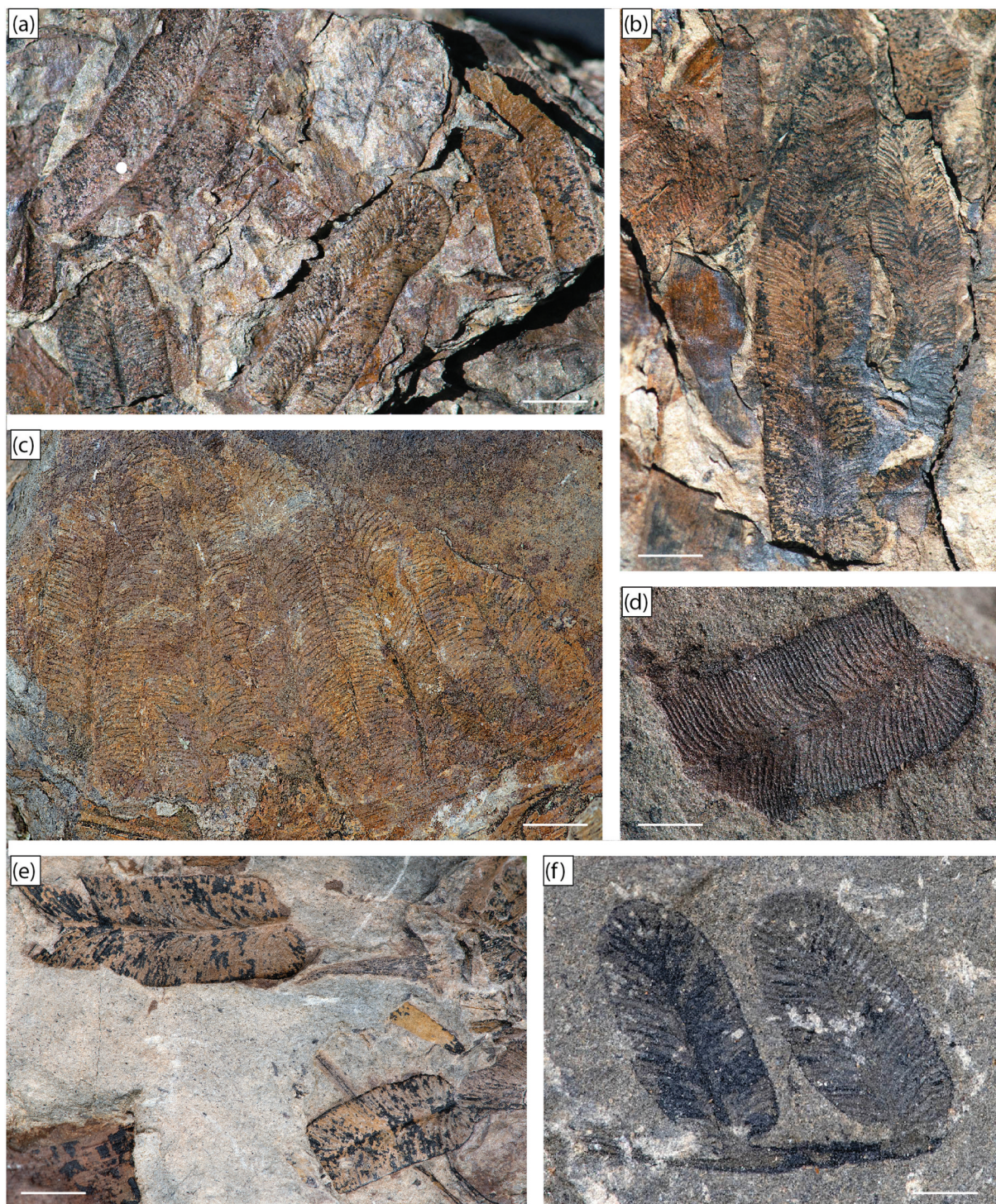


Figure 5. *Neuralethopteris densifolia* Josten (PalB 012–017), with pinnules of very variable length-to-breadth ratio, but consistent venation, as is typical for this fossil-genus. Scale bars: 0.47 cm (a); 0.50 cm (b, c); 0.40 cm (d); 0.70 cm (e); 0.30 cm (f).

largest preserved pinnule 40 mm long. Most pinnules are isolated, but the few that are attached are at 80–90° to the rachis. Prominent midvein extends for most of the pinnule length. Lateral veins alternately arise from midvein and narrow angle, rapidly arched in a somewhat angular pattern and then extend to the pinnule margin, which it meets at 70–90°. Lateral veins fork up to four times depending on pinnule width, producing a vein density of 45–50 per cm on pinnule margin.

Remarks. Although these pinnate fragments are small, the basally constricted, bilaterally symmetrical pinnules with a strong midvein clearly places them within the fossil-genus *Neuralethopteris*, and the often elongate pinnules with a dense, slightly angular venation indicates *N. densifolia*. This is a rare species that has only previously been recorded from the Ruhr in north Germany (Josten 1983; Jenchen and Schultka 1993), where it occurs in the *Pecopteris aspera*

Zone of Kinderscoutian to Yeardonian age (Wagner 1984; Opluštil et al. 2021).

Specimens PalB 012–017.

5. Interpretation of the macroflora

Compared with many of the Maine-et-Loire macrofloras described by Bureau (1913–1914) and Strullu-Derrien et al. (2021), which originated from grey, coal-bearing sequences, the Pont Barré macroflora is relatively low in diversity. It also differs in the total absence of lycopsids and of *Calymmotheca* pteridosperms and instead has abundant medullosalean foliage (*Neuralethopteris*). Similar fern – pteridosperm macrofloras of about the same age from Upper Silesia are interpreted as the remains of vegetation from better-drained substrates and are termed “flöz-fern” macrofloras (Havlena 1961; Gastaldo et al. 2009a, b). This ecological interpretation appears to be supported by the Pont Barré macroflora being preserved in coloured, reddish clastic sediment, which could indicate well-drained conditions and a low water table (see, for instance, comments by Besly and Turner 1983; Besly and Fielding 1989). As the Pont Barré fossils are relatively fragmentary and preserved in a high-energy water deposited stratigraphical sequence, they are clearly allochthonous. However, since there is no evidence of taxa such as *Adiantites*, *Pseudadiantites* and *Rhacopteridium* that have been interpreted as allochthonous remains of hinterland vegetation (e.g. Wagner 2001), it is likely that this macroflora was derived from vegetation growing in well-drained alluvial habitats within the basin (see discussion by Thomas and Cleal 2017).

It is difficult to place biostratigraphically such a low diversity macroflora and the co-occurrence of *Sphenopteris elegans* and *Neuralethopteris densifolia* appears to be in conflict as their previously known ranges do not overlap. However, the lower limit of the range of *N. densifolia* is not well constrained, being based on the less well-documented floras of the lower Namurian of the Ruhr (Josten 1983), whereas the upper limit of the range of *S. elegans* is better constrained to the lower Chokierian such as in Upper Silesia (Purkynová 1970). In our view, the Pont Barré macroflora can probably be assigned to the *Calymmotheca larischii* Zone indicating an Arnsbergian or early Chokierian age in the Heerlen Regional Chronostratigraphy, making it a little younger than the macrofloras documented from the coal-bearing deposits of this area (Strullu-Derrien et al. 2021); this would make a closer comparison with the macrofloras from the Poruba Formation of Upper Silesia (e.g. Purkynová 1970), which also includes *Neuralethopteris*.

6. Conclusions

The “Coteaux du Pont Barré” at Beaulieu-sur-Layon (Maine-et-Loire, France) has yielded a newly discovered macroflora of late Mississippian age. The allochthonous fossils occur in coloured, reddish clastic deposits suggesting relatively well-drained conditions, and reflect a vegetation dominated by medullosalean pteridosperms, tedeacean ferns and sphenophytes. It is markedly different from most of the other macrofloras from the “Sillon houiller de la Basse-Loire” (e.g. Strullu-Derrien et al. 2021), which are more diverse and tend to be dominated by lycopsids (e.g. *Lepidodendron*) and *Calymmotheca* (pteridosperm) fronds, and are probably the remains of vegetation from swampier, poorer-drained habitats. The Pont Barré macrofloras therefore provides a valuable, contrasting insight into the vegetation that formed the origins of the coal swamp biome, which in early Westphalian (early Pennsylvanian) times expanded to cover swathes of tropical Euramerica.

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Author contributions

CS-D designed the research program; CJC and CS-D contributed to the palaeobotany; MB, HL, ARTS contributed to the geology; J-PG photographed the fossil plants (except 3e) and CS-D photographed the site and the outcrop; CJC, MB, CS-D wrote the first version of the manuscript; all authors contributed to the final version of the manuscript.

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