

Pennsylvanian fossil flora from the Velebit Mountains and Lika region (SW Croatia)

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Late Pennsylvanian age deposits in the Velebit Mts and Lika region of Croatia are mainly marine, but also include relative thin terrestrial intercalations yielding diverse fossil floras. A revision of the fossil floras, based on about 200 specimens in the collections of the Croatian Natural History Museum (Zagreb) and National Museum (Prague), has revealed 19 species, strongly dominated by medullosaleans, sphenophytes and marattialean ferns. These fossils represent the remains of the lowland vegetation that was growing on the southern side of the Variscan Mountains, and can be compared with similar floras found in northern Spain and the Carnic Alps. Similar aged floras also occurred in intramontane sequences further north and west in Europe but these often tend to be dominated by marattialean ferns and cordaitaleans rather than alethopterid medullosaleans as in the Croatian floras. These differences are probably the result of the higher elevation and better drainage of the intramontane basins. Biostratigraphically the Croatian floras belong to the *S. angustifolium* Zone of Stephanian B (late Kasimovian or earliest Gzhelian) age. • Key words: Pennsylvanian, palaeobotany, Croatia.

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Most Carboniferous strata in Croatia are of marine origin and contain few remains of terrestrial plants (Sremac 2012). The most notable exceptions are found in terrestrial intercalations within the mainly marine sequence in the Velebit Mts and Lika region in the western part of the country (Fig. 1). These were first reported by Němejc (1936) and many of the specimens he described are now stored in the National Museum (Prague). Further plant fossils were collected by M. Salopek and his team during the 1935–1938 geological mapping of this area (Salopek 1942, 1948) and these are in the Croatian Natural History Museum (Zagreb). Most recently, staff of the Croatian Natural History Museum have found a new locality with terrestrial plants, at Strmotić potok creek.

Němejc (1936) suggested that these plant fossils are of Stephanian (Late Pennsylvanian) age and so represent some of the palaeotropical vegetation that developed during the major interglacial of the Late Palaeozoic Ice Age (Gastaldo *et al.* 1996; Cleal & Thomas 1999, 2005). As with the better

known fossil floras of this age found in northern Spain (summarised by Wagner & Alvarez-Vázquez 2010a) these Croatian fossil floras represent vegetation growing on the southern side of the Variscan Mountains. This is in contrast to some of the other classic floras of this age found in France, Germany and the Czech Republic (*e.g.* Doubinger 1956, Remy *et al.* 1963, Vetter 1968, Šimůnek *in* Pešek 1994, Doubinger *et al.* 1995, Šimůnek & Martínek 2009), which occur in intramontane basins formed within the Variscan Orogen. As there has been no taxonomic study on these Croatian floras other than that of Němejc (1936), a revision is clearly overdue. The present study combines data from both the Němejc (1936) collection in Prague, and the more recently collected material in Zagreb, to provide the most comprehensive taxonomic overview of these floras to date. The biostratigraphical and floristic context of the floras will also be re-examined, with the aim of improving our understanding of the vegetation history of southeastern Europe during the Late Pennsylvanian interglacial.

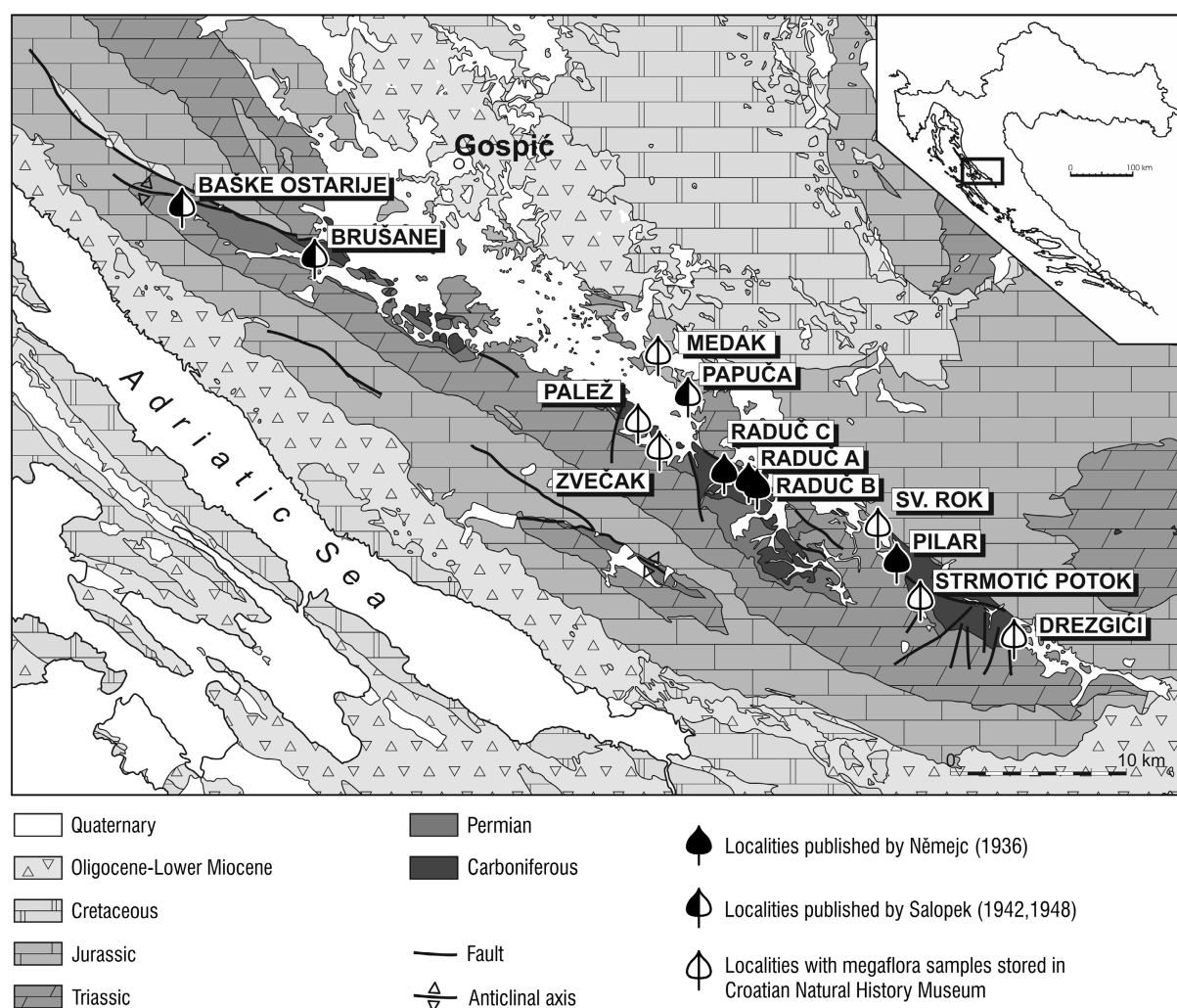


Figure 1. Simplified geological map with megaflores bearing localities (map based upon Ivanović *et al.* 1973; Šušnjar *et al.* 1973; Sokač *et al.* 1976b, c).

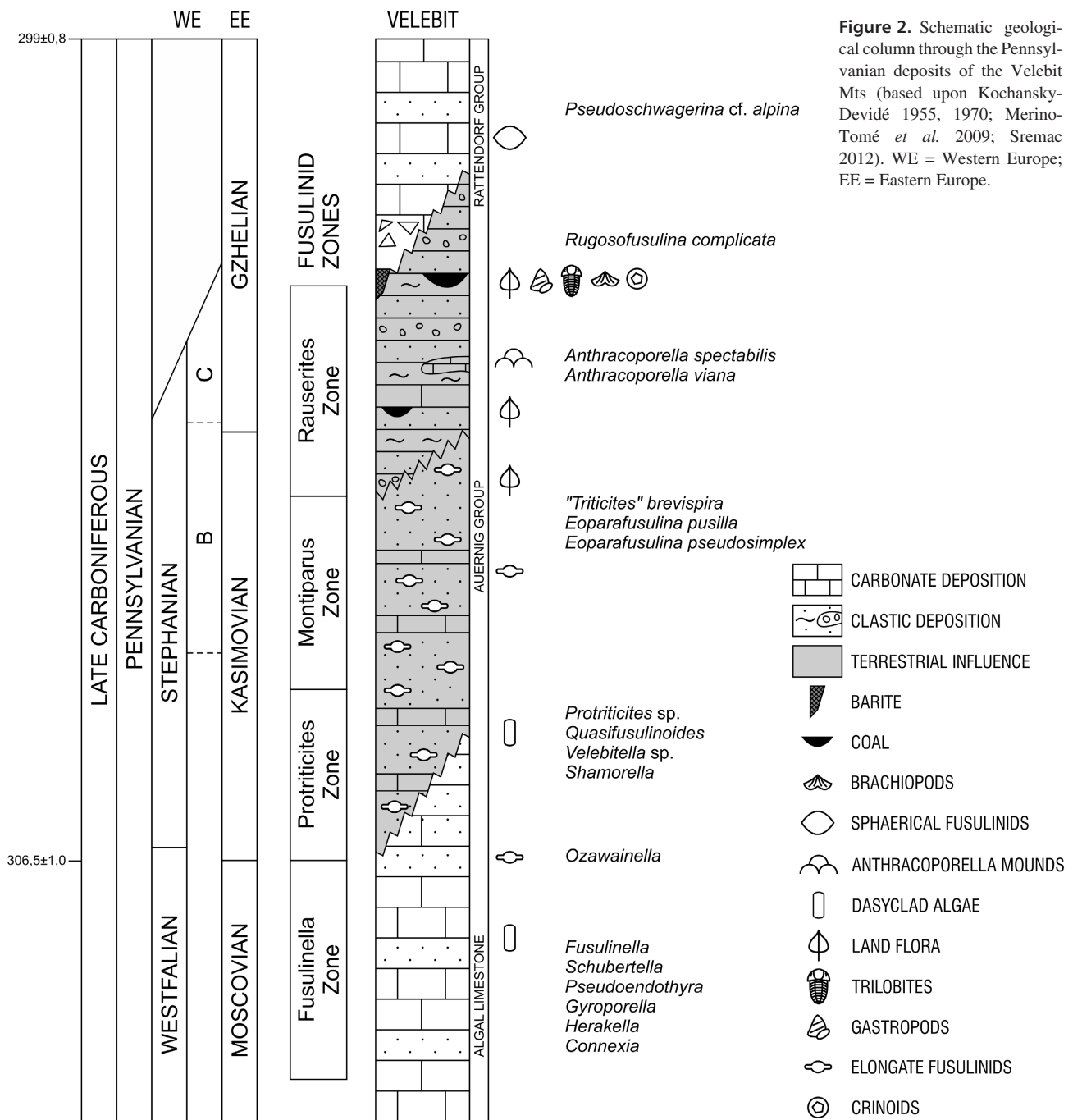
Geological background

The first detailed analysis of the geology of the Velebit Mts and Lika region was by M. Salopek and his team during the 1935–1938 mapping of the area (Salopek 1942, 1948). Subsequent more detailed mapping, for the purpose of the Basic Geological Map of Yugoslavia, took place in the second half of the 20th century; Carboniferous deposits are shown on sheets Gospić L33-127 (Sokač *et al.* 1974, 1976a), Obrovac L33-140 (Ivanović *et al.* 1973, 1976) and Udbina L33-128 (Šušnjar *et al.* 1973, Sokač *et al.* 1976b). The last cycle of mapping for the Basic Geological Map of Croatia, which included the research area, resulted in a 1:300,000 map with explanatory notes edited by Velić & Vlahović (2009).

Clastic and carbonate rocks of Pennsylvanian age crop out in a ca 50 km long belt in this region, representing the core of the Velebit Anticline (Fig. 1). Marine shelf limestones dominate in the lower and upper parts of the succes-

sion, and these contain calcareous algae, fusulinids, molluscs, trilobites, brachiopods and crinoids (Fig. 2). A Moscovian to Gzhelian age for these deposits is indicated by microfossils (Kochansky-Devidé 1955, 1970).

Terrestrial plant fossils occur in the middle part of the succession, in deposits that are lithologically and faunally similar to the Auernig or Pramollo Group of Kasimovian–Gzhelian age (= *Rauserites* Zone *sensu* Merino-Tomé *et al.* 2009), present in the Austrian, Slovenian and Italian Alps (Fritz & Krainer 2006, 2007; Ronchi *et al.* 2012). Quartz-rich conglomerates, cross-bedded sandstones and graywackes, and bioturbated fossiliferous shales and sandstones are common in the lower part of the group. The upper part is characterized by evident transgressive-regressive cycles caused by Gondwana glaciation, known as “Auernig cyclothems” (McCann *et al.* 2008 and references therein). Limestone intercalations containing marine fossils were deposited during sea-level highstands, while siliciclastic deposits with sporadic occurrences of terres-



trial plant remains represent periods of sea-level low-stands. More detailed description of these rocks, with a list of older references is given by Sremac (2012).

Materials and methods

This study was based on about 200 specimens, mostly leaves, with some stems and reproductive structures. Of these, 151 are in collections in Zagreb, either at the Croatian Natural

History Museum or the University of Zagreb (GPZ). These include remains from nine localities, collected since 1935, including the newly discovered Strmotić potok Creek locality (Table 1). There are also 47 specimens in the collections of the National Museum (Prague) under accession number 24860, which comprise part of the material described by Němejc (1936).

All specimens are either impressions or poorly preserved compressions, and yield no cuticles or provide any other anatomical evidence. The descriptions are, therefore,

Table 1. Distribution of the species in the Velebit Mts fossil flora.

	Brušane	Drezgići	Medak	Oštarije	Palež W.	Papuča	Strmotić	Sv. Rok	Zvečak
<i>?Lepidodendron</i> sp.				+			+		
<i>Annularia spinulosa</i>							+		
<i>Asterophyllites equisetiformis</i>	+								
<i>Calamites suckowii</i>							+		
<i>Acitheca polymorpha</i>			+				?		
<i>Lobatopteris</i> cf. <i>corsinii</i>							+		
<i>?Cyathocarpus</i> spp.		+					+		
<i>Oligocarpia gutbieri</i>									+
Fern fragment								+	
<i>Eusphenopteris rotundiloba</i>							+		
<i>Dicksonites plukenetii</i>							+		
<i>Alethopteris zeilleri</i>							+		
<i>Alethopteris pennsylvanica</i>	+								
<i>Trigonocarpus</i> aff. <i>grandis</i>							+		
<i>Trigonocarpus</i> sp.							+		
<i>Neuropteris</i> sp.		+			+				
<i>Odontopteris schlotheimii</i>	+								
<i>Callipteridium pteridium</i>							+		
<i>Taeniopteris carnotii</i>							+		

based purely on the morphology of the plant remains. The fossils were photographed in the Croatian Natural History Museum by R. Drempešić using high resolution cameras: Canon EOS 350 D (photo: N. Borčić) and Olympus SP-570 UZ.

Systematic palaeontology

Class Lycopsidea Scott, 1909

Order Lepidocarpacea Thomas & Brack-Hane, 1984

Family uncertain

Genus *Lepidodendron* Sternberg, 1820

?Lepidodendron sp.

Figure 3A–C

(?)1936 *Lepidodendron* sp.; Němejč, p. 11, fig. 3.

(?)1936 *Lepidostrobus geinitzi* Zeiller; Němejč, p. 12, fig. 4.

Material. – Eight specimens of bark, leafy shoot and cone (specimens 12, STR1, STR2, STR8, STR18; plus three unnumbered). Also another possible stem and two cones in the Němejč Collection in the National Museum (Prague).

Description. – Three examples of stem/bark with large, helically arranged, rhomboidal leaf cushions 25 mm long, 15 mm wide, with rounded lateral angles (Fig. 3A). Cushions

do not protrude significantly from stem surface, and separated by a 2 mm wide inter-cushion area. Small, isodiametric leaf scar in middle of each cushion, ca 2 mm in size, with marked lateral lines extending from scar to lateral angles of cushion; in some cases a weakly developed keel also extends from the scar up to the apical angle of the cushion. A (?) ligule mark occurs ca 2 mm above scar. No other structure or ornamentation visible on scars.

Associated with the barks are slender shoots, preserved for up to 90 mm bearing slender leaves, 10–12 mm long and <0.5 mm wide (Fig. 3B). The leaves were helically attached (as shown by the small leaf scars visible on the facing side of the stem) at about right angles to the stem. There are also occasional long, linear leaves, at least 140 mm long and 3 mm wide, with what appear to be a single longitudinal vein, which may represent *Cyperites*-like stem leaves of this lycopsid.

Also present are incomplete fragments of large cones (Fig. 3C), preserved for a length of up to 80 mm, and originally about 30 mm wide (based on the distance between the cone axis and the distal ends of the sporophylls). Cone axis 2 mm wide. Sporophylls helically attached at 60–80° (this variation may be partly taphonomic), extend for about 13 mm from the axis, where they bend sharply towards the distal end of the cone, forming the distal blade of the sporophyll. Details of the sporangia are difficult to see but some look as though they have megaspores. The sporophyll blade is up to 30 mm long, 2–3 mm wide, with an acute apex, and seems to extend away from the main body of the cone.

Remarks. – The identity of these unusual fossils is unclear. Despite an extensive review of the literature, we have been unable to find any comparable species with such distinctive large, rhomboidal leaf cushions. It is assumed that they are lycopsid and the presence of a possible ligule just above the leaf scars suggests they probably represent *Lepidodendron* bark. There is some similarity with *Lepidodendron feistmantelii* Zalesky, 1904 (as documented by Thomas 1970) but the type of that species is rather older (Moscovian), and the leaf cushions are smaller and more protuberant from the stem surface. There is also some comparison with the specimen figured by Wagner & Alvarez-Vázquez (2010a, pl. 25, fig. 1) as “*Lepidodendron*” *gaudryi* Renault & Zeiller, 1888 but the upper and lower angles of the leaf cushions are rather sinuous, a feature not seen in the Velebit Mts specimens. A third comparison is possible with “*Lepidodendron*” *clipeiforme* Vetter (Doubinger et al. 1995, figs 17–19), which has similarly large leaf cushions but lacking the lateral lines seen in the Velebit Mts specimen. The type of Vetter’s species appears to show persistent leaves and so should not be regarded as a *Lepidodendron* as interpreted by Thomas & Meyen (1984). Until better material is uncovered, the Velebit Mts specimens are best referred to simply as (?)*Lepidodendron* sp.

Němejc (1936) figured a specimen of a *Lepidodendron* stem in which the leaf cushions are of similar shape, but of more oval outline. This might be the same as the species documented in the present paper, but the poor preservation makes it impossible to be sure. Němejc (1936) also figured a cone that is very similar to, but less well preserved than the cones documented here.

Class Equisetopsida Agardh, 1825
Order Equisetales Dumortier, 1829
Family Calamostachyaceae Meyen, 1978

Genus *Annularia* Sternberg, 1821

Annularia spinulosa Sternberg, 1821

Figure 3E

- 1804 Schlotheim, pl. 1, fig. 4.
- 1820 *Casuarinites stellatus* Schlotheim. – Schlotheim, p. 397 (*nom. illegit.*).
- 1821 *Annularia spinulosa* Sternberg, p. 32, pl. 19, fig. 4.
- 1825 *Bornia stellata* Schlotheim ex Sternberg, tent. p. 28.
- 1936 *Annularia stellata* Schlotheim. – Němejc, p. 10, pl. 2, figs 6–8.
- 2000 *Annularia spinulosa* Sternberg. – Barthel, p. 37, figs 1–5.
- 2004 *Annularia spinulosa* Sternberg. – Barthel, p. 20, figs 17, 18.

Material. – Seventeen specimens of leafy shoot (specimens 1, 2, 15, plus 14 unnumbered). Also one specimen in the Němejc Collection in the National Museum (Prague).

Description. – Leafy shoots preserved for up to 110 mm long, with whorls of slender leaves spaced at 22 mm in more distal parts of the shoot, reducing to 10 mm in shoot apex. Few whorls are complete, but mostly seem to have ca 20–30 leaves. Leaves 12–25 mm long, <2 mm wide. In some whorls the leaves are of equal length, in others the lateral whorls (as preserved on the rock) are rather longer. Leaves lanceolate, widest in the middle or somewhat more distal part, and terminated in a narrowly rounded apex. Leaves of a whorl basally but narrowly fused. A single thick vein runs along entire length of leaf.

Remarks. – Historically this species has tended to be named *Annularia stellata* (Schlotheim ex Sternberg) Wood, but Barthel (2000, 2004) has shown that *A. spinulosa* Sternberg has precedence. The Velebit Mts specimens compare closely with the type specimens, which were photographically reproduced by Barthel (2000, fig. 1).

Annularia sphenophylloides (Zenker) Gutbier, 1821

- 1833 *Galium sphenophylloides* Zenker, p. 398, pl. 5, figs 6–9.
- 1837 *Annularia sphenophylloides* (Zenker); Gutbier, p. 436.
- 1936 *Annularia sphenophylloides* Zenker. – Němejc, p. 11, pl. 1, fig. 15.

Material. – One small specimen of leafy shoot (Němejc Collection, National Museum Prague).

Description. – One fragment of shoot, with a whorl of ca 15 small, linear to spatulate leaves, 2–3 mm long.

Remarks. – This tiny fragment was identified by Němejc (1936) as *A. sphenophylloides*. Although the whorl of leaves is very small, they appear to be of the shape that characterises this species.

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

Asterophyllites equisetiformis

(Schlotheim ex Sternberg) Brongniart, 1828a

Figure 3F

- 1804 Schlotheim, pl. 1, fig. 1, pl. 2, fig. 3.
- 1820 *Casuarinites equisetiformis* Schlotheim, p. 397 (*nom. illegit.*).

1825 *Bornia equisetiformis* Schlotheim ex Sternberg, tent. p. 28.

1828a *Asterophyllites equisetiformis* (Schlotheim) Brongniart, p. 159.

Material. – One small specimen of leafy shoot (10543).

Description. – Short, leafy shoot fragment 25 mm long. Stem slender, <0.5 mm wide, with three whorls of leaves spaced 7 mm apart. Whorls with at least 11 slender, linear leaves (exact number of leaves impossible to confirm because the shoot is preserved side-on). Leaves *ca* 13 mm long, attached to stem at about right angles, but then curve towards the stem apex so the distal part is at 50–60° to stem. Leaf apex acute.

Remarks. – This is normally an abundant species in late Carboniferous coal floras but here only one specimen was found. Although not well preserved, it shows the characteristic slender, slightly curved leaves that characterise this species.

Genus *Calamites* Brongniart, 1828a nom. cons.

Calamites suckowii Brongniart, 1828b

Figure 3D

1828a *Calamites Suckowi* Brongniart. – Brongniart, p. 37 (*nomen nudum*).

1828b *Calamites Suckowi* Brongniart *pars*, p. 124, pl. 15, figs 5, 6, pl. 16, fig. 2.

1917 *Calamites Suckowi* Brongniart *pars*. – Kidston & Jongmans, p. 107.

1936 *Calamites Suckowi* Brongniart. – Němejc, p. 10, pl. 3, fig. 9.

Material. – Ten specimens of stem compressions and pith casts. Also five specimens in the Němejc Collection in the National Museum (Prague).

Description. – Poorly preserved stem fragments with regular ribs, 1.0–1.5 mm apart. Nodes are poorly preserved.

Remarks. – We have essentially followed Kidston & Jongmans (1917) in the interpretation of this species, especially in the designation of lectotypes. The specimens that we had available were too small to absolutely confirm their identification, but Němejc (1936) documented some better examples from the Velebit Mts that appear to belong to this species.

Class Marattiopsida Doweld, 2001

Order Marattiales Link, 1833

Family Psaroniaceae Unger *in* Endlicher, 1842

Genus *Acitheca* Schimper, 1879

Acitheca polymorpha (Brongniart) Schimper, 1879

Figure 4A, D

1828a *Pecopteris polymorpha* Brongniart, p. 56 (*nomen nudum*).

1834 *Pecopteris polymorpha* Brongniart, Brongniart p. 331, pl. 113, figs 2–5.

1879 *Acitheca polymorpha* (Brongniart) Schimper, p. 91, fig. 66.

1936 *Acitheca polymorpha* (Brongniart) Schimper. – Němejc, p. 6, text-fig. 1, pl. 1, fig. 13.

1959a *Polymorphopteris polymorpha* (Brongniart). – Wagner, p. 29.

2006 *Acitheca polymorpha* (Brongniart) Schimper. – Zórow *et al.*, p. 271, pls 1–9, 11–14.

Material. – Four pinna fragments (specimens 10589, 10590, STR11, plus one unnumbered). Also four specimens in the Němejc Collection in the National Museum (Prague).

Description. – Short pinna fragments with short, linguaeform pinnules <7 mm long, 3 mm wide; one pinna fragment shows a blunt terminal with small apical pinnule. Another example has two bipinnate segments with small, rounded pinnules. Pinnules attached to rachis at 80–90°; some are basally constricted, others are narrowly confluent. A non-decurrent midvein runs for two-thirds the pinnule length. Well-marked lateral veins emitted from mid-vein at *ca* 45°, bend slightly and then run in a more or less straight line to meet pinnule margin at *ca* 70°. Veins dense, forking once or twice.

Remarks. – The taxonomy of this species, including its generic position, has most recently been analysed in detail by Zórow *et al.* (2006). The pinnules in the Velebit Mts specimens are too small to show the polymorphopterid vein branching (*sensu* Wagner 1959a), which is one of the characteristic features of this species. Nevertheless, the linguaeform, basally constricted lateral pinnules with dense veining, and bluntly terminated ultimate pinnae with a small apical pinnule clearly point to them belonging to *A. polymorpha*.

Genus *Lobopteris* Wagner, 1959b

Lobopteris cf. corsinii Wagner, 1959b

Figure 4B

Material. – Two pinna fragments (specimens 7, 8).

Description. – One pinna fragment (part and counterpart)

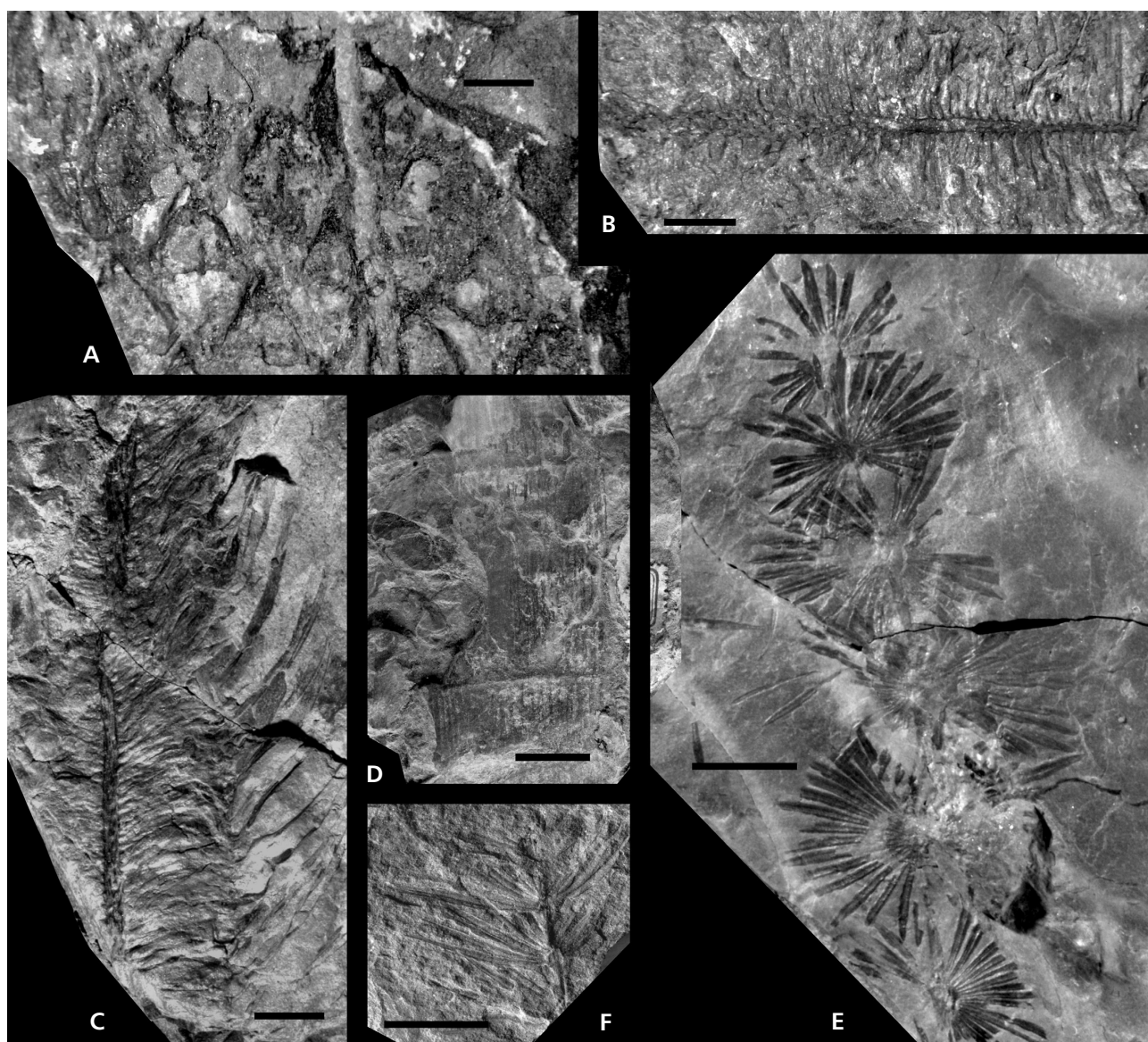


Figure 3. A, B – (?)*Lepidodendron* sp., Strmotić; A – surface of stem showing leaf cushions (specimen STR2); B – leafy shoot (specimen STR1). • C – lycopod cone, (specimen VM1). • D – *Calamites suckowii* Brongniart, Lika (specimen LIKA98). • E – *Annularia spinulosa* Sternberg, Strmotić, leafy shoot (specimen VM2). • F – *Asterophyllites equisetiformis* (Schlotheim ex Sternberg) Brongniart, Brušane (specimen 10543). All scale bars = 10 mm.

45 mm long. Rachis relatively stout, 1.5 mm wide, with irregular longitudinal striae but no punctae. Elongate, linguaeform to somewhat subtriangular, pinnatifid pinnules, <12 mm long, 2–3 mm wide, attached to rachis at 60–70°; pinnules lobed for most of length except for distalmost 2–3 mm; basiscopic lobe often enlarged and somewhat basally constricted. Thick midvein runs for most of pinnule length, a little decurrent in most proximal part. Poorly preserved lateral veins grouped in fascicles, one entering each lobe.

Remarks. – This single, poorly preserved specimen is impossible to identify with certainty, but it shows some similarities with *L. corsinii* Wagner, 1959b, especially with speci-

mens recently figured from Stephanian floras of northern Spain (Castro Martínez 2005a, pl. 32, pl. 33, figs 1, 2). Wagner (1959b) suggested that adjacent pinnules tend to be united at their base, but those figured by Castro Martínez show that this feature can be variable and the pinnules can sometimes be basally constricted, as in the Velebit Mts specimens.

Genus *Cyathocarpus* Weiss, 1869

Figure 4E

1936 *Asterotheca arborescens* Schlotheim. – Němejc, p. 6, pl. 2, figs 1–5.

- 1936 *Pecopteris* (*Asterotheca*?) cf. *paleacea* Zeiller. – Němejč, p. 6, pl. 1, fig. 12.
(?)1936 *Asterotheca candolleana* Brongniart. – Němejč, p. 7, pl. 2, figs 13, 13a.

Material. – Ten pinna fragments (specimens 10554, STR6, STR17, plus seven unnumbered).

Description. – Two short pinna fragments ca 40 mm long, with elongate slender pinnules attached at near to right angles to rachis. Pinnules 9–10 mm long, 2–3 mm wide, linguaform, tapered only in most distal part, with a broadly rounded apex, and narrowly confluent at base. Thick midvein extending to pinnule apex. One specimen has simple lateral veins that appear to be emitted from midvein at 30–40°, curve slightly and then extend towards pinnule margin, which they met at ca 50°. The other specimen has pinnules with a row of ovoid structures (sori) ca 1 mm in diameter on either side of the midvein, which obscures the rest of the venation.

Two other small fragments have small, linguaform pinnules attached at right angles to rachis. No evidence of veining can be seen.

Remarks. – These small fragments have the type of small pinnules normally associated in late Carboniferous wetland vegetation with *Cyathocarpus* (cf. Zoderow 1990). One has what appear to be reproductive structures on the pinnules, which could be of the asterothecoid-type, but no details are preserved. Similar specimens from Velebit were also recorded by Němejč (1936) as *Asterotheca arborescens* and *Pecopteris* cf. *paleacea*, but in our view species identification for any of these specimens is impossible.

Němejč (1936) identified a single, poorly preserved specimen as *Asterotheca candolleana*. It has elongate, pecopteroid pinnules very similar to what we have called ?*Cyathocarpus* sp. Němejč suggested that the veins were dichotomous but this is not clear from the illustration, and the original specimen has not been located.

Class Polypodiopsida Cronquist *et al.*, 1966
Order Polypodiales Link, 1833
Family Sermayaceae Eggert & Delevoryas, 1967

Genus *Oligocarpia* Göppert, 1841

Oligocarpia gutbieri Göppert, 1841

Figure 4C

- 1841 *Oligocarpia gutbieri* Göppert, p. 35, pl. 4, figs 1, 2.
1983 *Oligocarpia gutbieri* Göppert. – Brousmiche, p. 236, pls 57–61.

Material. – A single pinna fragment (specimen ZVEČAK1).

Description. – A 45 mm long near terminal fragment of tapered, bipinnate segment. Terminal part of pinna has linguaform to somewhat subtriangular pinnules, < 3–4 mm long, 2 mm wide. In more distal positions the segments become ultimate pinnae, the longest preserved for 20 mm and a width of 5 mm, obliquely attached to rachis at ca 50°. Ultimate rachises striate, slender and slightly undulate. Ultimate pinnae parallel-sided for most of length, but tapered in their distal part to a distinct, rounded apical pinnule. Lateral pinnules subtriangular to linguaform, usually basally constricted on their acroscopic side, sometimes showing minor lobbing on lateral margins; attached to rachis at 70–80° in more proximal positions, 40–60° in most distal positions. Veins poorly preserved but appear to be more or less straight and oblique to pinnule margin.

Remarks. – The most detailed published account of this species is by Brousmiche (1983) and it is on this that we have largely based our interpretation. Although we only had available one specimen, the distinctive subtriangular to linguaform pinnules and oblique veining match well with the specimens figured by Brousmiche (1983).

Order and family unknown

Fern fragments

Material. – A single specimen with several pinna fragments (specimen 10587). Also one specimen in the Němejč Collection in the National Museum (Prague).

Description. – Several fragments of pinnae with a 1 mm wide undulate rachis, bearing tapered pinnae up to 10 mm long and 6–7 mm wide. The ultimate pinnae bear small pinnules up to 2–3 mm wide, which have two or three very acute teeth. Poorly preserved veins appear to be widely forked.

Remarks. – It is impossible to identify the small specimen in the Zagreb collection beyond it being a fern, and is being recorded simply because of its very distinctive dentate pinnules.

Němejč (1936, pl. 1, figs 2, 2a) figured a single poorly preserved specimen as *Sphenopteris* cf. *weissi* Potonié. He expressed considerable reservation about the identification of the specimen and, having examined the original specimen (in the collection of the National Museum, Prague), we regard it as totally unidentifiable.

Class Lyginopteridopsida Novák, 1961
Order Lyginopteridales Corsin, 1960
Family Lyginopteridaceae Potonié, 1900

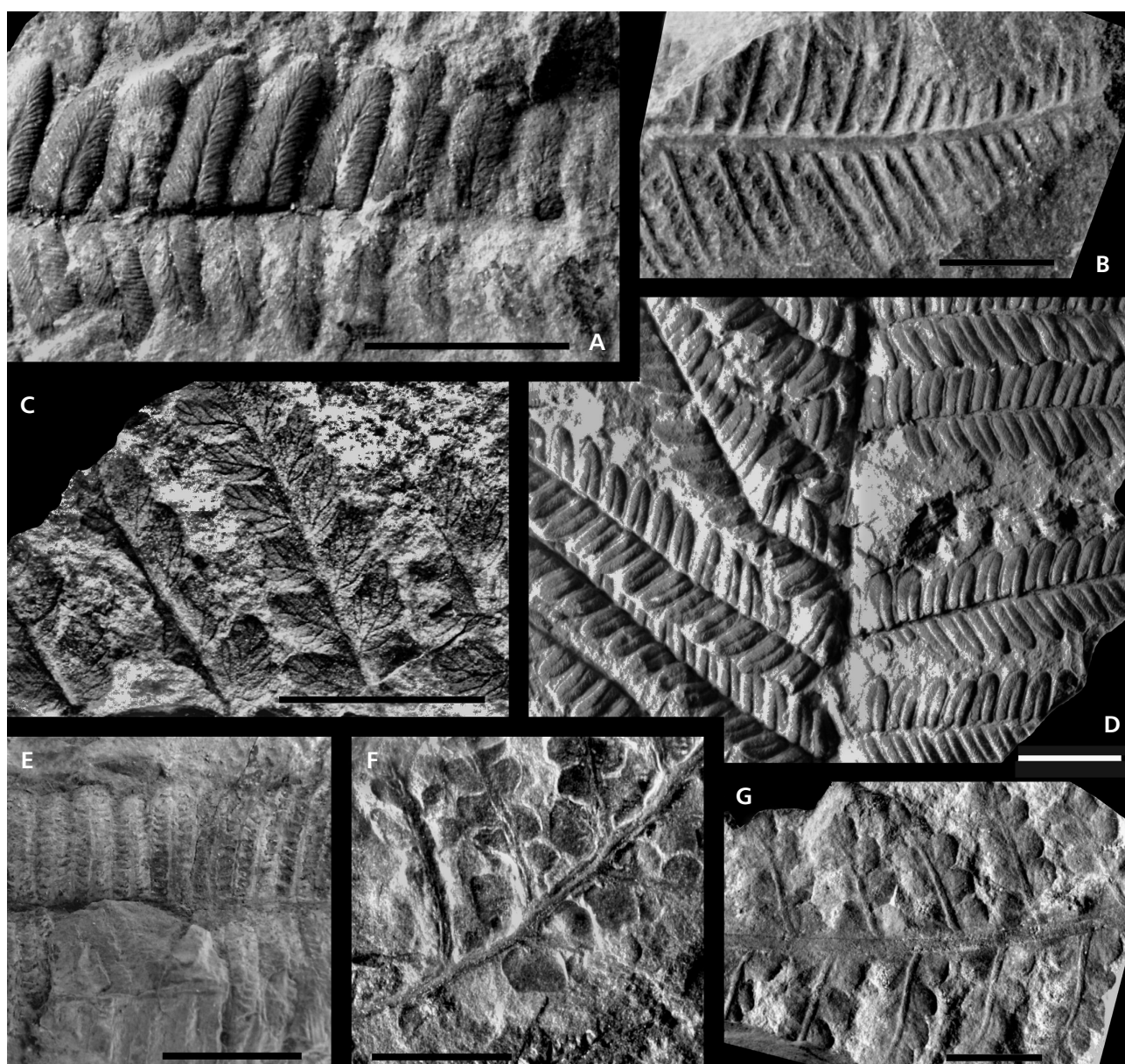


Figure 4. A, D – *Acitheca polymorpha* (Brongniart) Schimper, Baške Oštarije (specimen 10634); A – close-up of pinnules showing venation; D – part of bipinnate segment. • B – *Lobatopteris* cf. *corsinii* Wagner, Strmotić, fragment of ultimate pinna (specimen 7). • C – *Oligocarpia gutbieri* Göppert, close-up of characteristic pinnules and venation, Zvečak (specimen ZVEČAK1). • E – ?*Cyathocarpus* sp., fertile pinna, Drezgići (specimen 10554). • F – *Eusphenopteris rotundiloba* Němejč, Strmotić (specimen STR4). • G – *Dicksonites plukenetii* (Sternberg) Sterzel, unknown locality (specimen 10605). All scale bars = 10 mm.

**Genus *Eusphenopteris* Simson-Scharold, 1934
nom. cons.**

***Eusphenopteris rotundiloba* Němejč, 1937**

Figure 4F

- 1936 *Diplotmema busquetii* Zeiller. – Němejč (non Zeiller), p. 4, figs 3, 4, 4a.
1937 *Eusphenopteris rotundiloba* Němejč, p. 10, text-fig. 4.

1975 *Eusphenopteris rotundiloba* Němejč. – Van Amerom, p. 82, pl. 44.

2005b *Eusphenopteris rotundiloba* Němejč. – Castro Martínez, p. 97, pls 67, 68.

Material. – A single pinna fragment preserved as part and counterpart (specimen STR4). Also one specimen in the Němejč Collection in the National Museum (Prague).

Description. – A pinna fragment with a flexuous, longitu-

dinally ridged rachis, 50 mm long. Most ultimate pinnae are preserved as stubs attached to rachis, but three show attached pinnules. Pinnules mostly isodiametric, 3 mm in size, round, roundly subtriangular or subrhomboidal; broadly attached to rachis, except for the most proximal pinnules which are partially basally constricted. Veins (as shown on the part specimen) thick, widely spaced and dichotomous.

Remarks. – The most detailed taxonomic treatments of the species are by Van Amerom (1975) and Castro Martínez (2005b). It is by far the most widely reported eusphenopterid from Kasimovian fossil floras of Europe. Although the pinnules often have a more vaulted limb than seen in the Velebit Mts specimens (compare with the specimens figured by Castro Martínez 2005b) this can be a variable feature (as is shown by the Van Amerom specimens; see also Doubinger *et al.* 1995, fig. 215).

Order Callistophytales Rothwell, 1981

Family Callistophytaceae Stidd & Hall, 1970

Genus *Dicksonites* Sterzel, 1881

Dicksonites plukenetii (Schlotheim *ex* Sternberg)

Sterzel, 1881

Figure 4G

1804 Schlotheim, pl. 10, fig. 19.

1820 *Filicites Pluckenetii* Schlotheim. – Schlotheim, p. 410 (*nom. illegit.*).

1825 *Pecopteris Plukenetii* Schlotheim *ex* Sternberg. – Schlotheim, p. xix.

1881 *Dicksonites Pluckeneti* (Schlotheim) Sterzel, p. 223.

Material. – A single pinna fragment (specimen 10605).

Description. – Short pinna fragment 47 mm long and exposed showing lower surface. A 2 mm wide, longitudinally striate rachis bears ultimate pinnae at *ca* 80°. Ultimate pinnae 12 mm long, 6 mm wide, parallel-sided and terminated by blunt, poorly individualised apical pinnule. Pinnules roundly subtriangular to subrhomboidal with a vaulted limb, 3 mm long, 3 mm wide.

Remarks. – Although we only found one specimen, the very characteristic roundly subtriangular pinnules with a somewhat vaulted limb make the identity beyond doubt.

Class Cycadopsida Brongniart, 1843

Order Medullosales Corsin, 1960

Family Alethopteridaceae Corsin, 1960

Genus *Alethopteris* Sternberg, 1825

Alethopteris zeilleri (Ragot *ex* Remy *et al.*)

Wagner, 1964

Figure 5A

1960 *Alethopteris zeilleri* Jongmans, p. 67, pl. 30, figs 154–155a (*nomen nudum*).

1963 *Alethopteris grandini* Brongniart forma *zeilleri* Ragot *ex* Remy *et al.*; p. 133, pl. 3, figs 1, 2.

1964 *Alethopteris zeilleri* Ragot; Wagner, p. 837 *et seq.*

1968 *Alethopteris zeilleri* Ragot. – Wagner, p. 158, pls 63, 64.

Material. – 67 pinna fragments (specimens 2, 3, 6, 13, 16, STR7, STR9, STR10, STR12, STR13, STR14, STR15, plus 55 unnumbered).

Description. – Pinnae fragments up to 130 mm long, 20 mm wide, mainly parallel-sided but tapering in most distal part to a small terminal pinnule. Pinnules mostly robust, up <16 mm long, 9 mm wide, inserted at *ca* 80° on rachis. Pinnules mostly parallel-sided or slightly barrelled, with round apex; pinnules somewhat decurrent on basiscopic side, usually a little constricted in acroscopic side. Thick midvein only slightly decurrent at base and extending for most of pinnule length. Lateral veins leave midvein at *ca* 45°, bend very quickly then extend in a more or less straight line to meet the pinnules margin at 70–90°. They fork once or usually twice to produce a marginal vein density of 30–35 per cm.

Remarks. – Wagner (1968) argued that there was a progressive change in pinnule shape and venation from upper Moscovian fronds that he identified as *Alethopteris grandinioides* Kessler (later renamed *Alethopteris pseudograndinioides* Zedrow & Cleal, 1998) to the Kasimovian *A. zeilleri*. It has since been shown that there is also a similarity in the ovules and pollen-bearing organs produced by the same plants (Cleal *et al.* 2010).

Although this species only occurs at one locality (Strmotić) it is abundant there.

Alethopteris pennsylvanica Lesquereux, 1858

Figure 5B, C

1854 *Alethopteris pennsylvanica* Lesquereux, p. 422 (*nomen nudum*).

1858 *Alethopteris pennsylvanica* Lesquereux, p. 864, pl. 11, figs 1, 2.

1968 *Alethopteris pennsylvanica* Lesquereux. – Wagner, p. 117, pls 45–47.

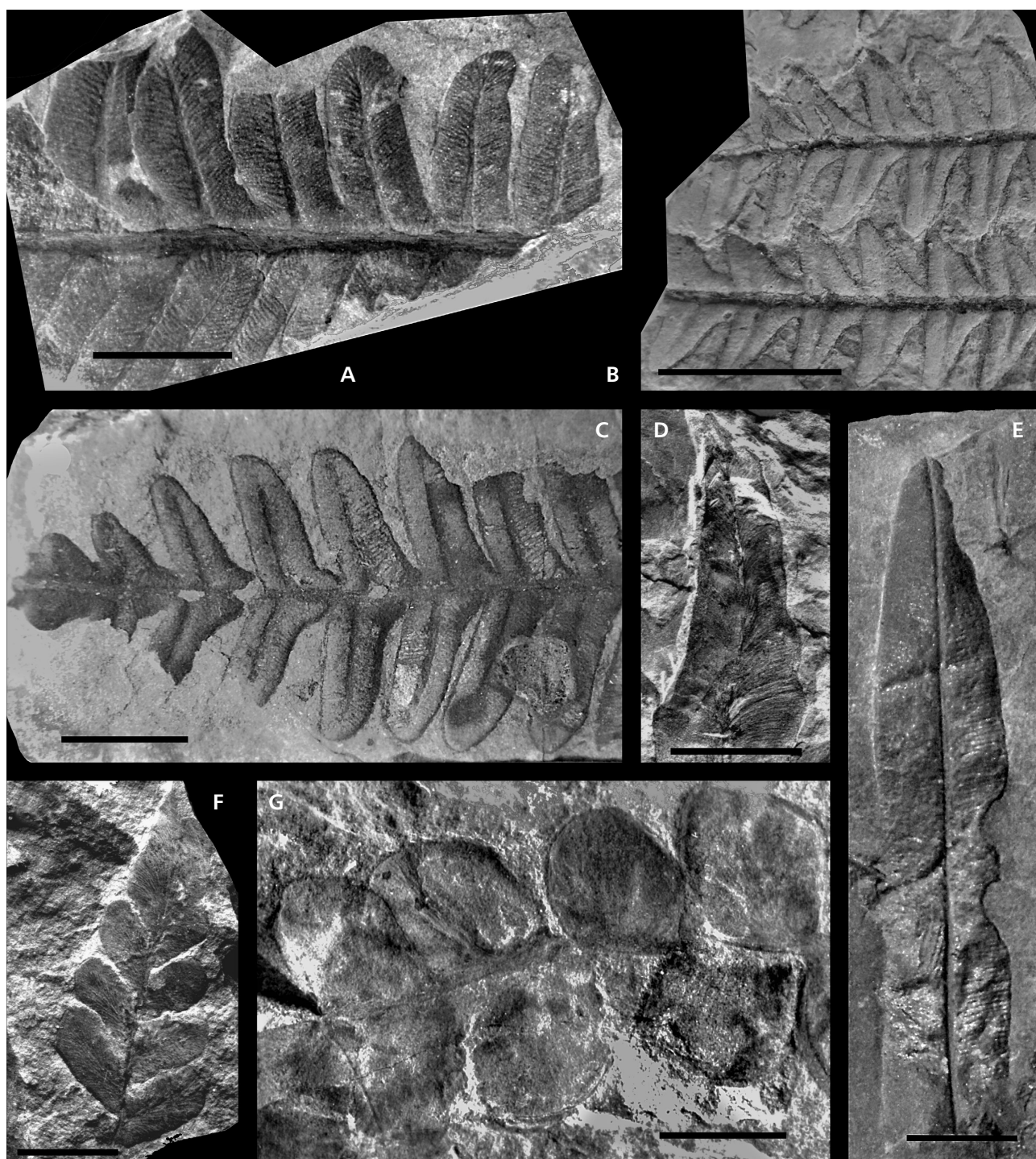


Figure 5. A – *Alethopteris zeilleri* (Remy *et al.*) Jongmans, Strmotić (specimen 3). • B, C – *Alethopteris pennsylvanica* Wagner, Brušane; B – small pinnules probably from high in pinna (specimen 10541); C – fully developed pinnules (specimen 10528). • D, F – *Neuropteris* sp.; D – Drezgići (specimen 10526); F – Palež W. (specimen 10566). • E – *Taeniopteris carnotii* Zeiller, leaf showing (?) insect damage, Strmotić (specimen 10776). • G – *Odontopteris schlotheimii* Brongniart, Brušane (specimen 10575). All scale bars = 10 mm.

Material. – Eight pinna fragments (specimens 10499, 10528, 10561, 10572, 10579, 10612, 10557, 10541).

Description. – Pinna fragments <60 mm long, mainly

parallel-sided but tapering in most distal part. No complete apical pinnule preserved, but one specimen (10528) shows part of what looks like a short, slender, tapered apical pinnule. Lateral pinnules inserted at 80–90° along most of

pinna, becoming more obliquely inserted (50–60°) towards pinna apex, attached to upper side of rachis. Pinnules elongate, slender, mostly 12–17 mm long in their fully developed form, but in one specimen at least 25 mm long; pinnules straight or slightly curved acroscopically, parallel-sided for most of length, tapering in distal part to an essentially round apex. Pinnules have decurrent base only on basiscopic side; adjacent pinnules separate or only narrowly confluent. Pinnule limb vaulted with thick midvein lying in deep furrow; midvein rarely decurrent and extends for most of pinnule length. Lateral veins leave midvein at *ca* 45°, bend very sharply then extend in a more or less straight line to meet pinnule margin at near to right-angles. Veins mostly once forking or sometimes simple, marginal vein density *ca* 32 per cm.

Remarks. – Our interpretation of this species is largely based on Wagner (1968). Our specimens bear some comparison with *Alethopteris zeilleri*, especially in the venation, and when the Velebit Mts collection was viewed as a whole it was difficult to tell them apart. However, when the specimens were separated according to locality of origin, it became clear that the assemblage from Brušane had consistently more slender pinnules than the *A. zeilleri* specimens from Strmotić.

The best-known Kasimovian *Alethopteris* species with slender pinnules is *Alethopteris leonensis* Wagner, 1964 (for more complete analyses of this species, see Wagner 1965, 1968 and Wagner & Álvarez-Vázquez 2010b). However, *A. leonensis* differs in having somewhat tapered and decurrent pinnules with a less rounded apex, a less prominent midvein and less dense lateral veins. Also similar is *Alethopteris ambigua* Lesquereux, 1880 (?*Alethopteris lesquereuxii* Wagner, 1968) from the upper Moscovian Stage, but the pinnules of the latter differ in being more closely spaced, adjacent pinnules being usually non-confluent, and the lateral veins being more oblique to the pinnule margin.

A. pennsylvanica is a rare species that has only been reported from Pennsylvania, northern Spain and (now) Croatia.

Genus *Trigonocarpus* Brongniart, 1828

Trigonocarpus aff. *grandis* Lesquereux, 1884

Figure 6C

Material. – Five specimens with several compressions of ovules (specimens 9, 14, plus three unnumbered).

Description. – Large ovules <80 mm long, 30 mm wide, ovoid with widest part about half way along length. All ovules are compressed but at least one shows a central

ovoid body (?sclerotesta) 50 mm long, 25 mm wide. Surface of ovule shows irregular, longitudinal ribbing.

Remarks. – These large ovules are closely associated with *Alethopteris zeilleri* foliage. A similar association was noted by Doubinger *et al.* (1995) at St-Étienne (France) and is unlikely to be coincidental. They also compare with ovules described by Cleal *et al.* (2010) as *Trigonocarpus grandis* from the upper Middle Pennsylvanian Sydney Mines Formation of Cape Breton (Canada) and associated with *Alethopteris pseudograndinioides* var. *subzeilleri* (Wagner) Zodrow & Cleal, 1998. The Croatian ovules appear to be a little more slender than the Canadian ones, but in view of the small number of available specimens from the Velebit Mts floras this may not be significant.

Trigonocarpus sp.

Material. – A single ovule (specimen STR3).

Description. – One small ovule, 20 mm long, 16 mm wide; preserved as external cast with a thin layer of carbon on the surface, and shows little in the way of structure.

Remarks. – A second, much smaller form of *Trigonocarpus* also occurs at Strmotić. It is possible that it is merely a *T.* aff. *grandis* ovule that had not fully developed. However, there is sufficient discrepancy in size for the small form to be recorded separately.

Family Neurodontopteridaceae Laveine *ex*
Cleal & Shute, 2003

Genus *Neuropteris* (Brongniart) Sternberg, 1825

Neuropteris sp.

Figure 5D, F

Material. – Two pinna fragments (specimens 10526, 10566).

Description. – Pinna terminal with slender rachis and incomplete large, lanceolate apical pinnule, 17 mm long, 7 mm wide. Six obliquely-attached, linguaeform pinnules <9 mm long, 6 mm wide; the larger pinnules are partly constricted basally, attached to rachis by about one-third of pinnule width, and have weakly developed basiscopic auricle. Midvein extends for half pinnule length in larger pinnules. Lateral veins leave the midvein at a narrow angle and arch broadly to meet pinnule margin at *ca* 50°. Marginal vein density *ca* 35 per cm.

A second specimen has one incomplete pinnule 40 mm

long, 16 mm wide, with gradually tapered margins (tip not preserved), a prominent acroscopic bulge and a more irregular basiscopic lobe. Midvein strongly marked, extending for most of pinnule length. Lateral veins emitted at *ca* 10°, and arch broadly to meet pinnule margin at 70–80°. The veins fork at a narrow angle two or three times, to produce marginal vein density of *ca* 35 per cm.

Remarks. – The general aspect of the pinnules of the pinnate specimen compared with *Neuropteris ovata* Hoffmann, 1826, an abundant species in upper Moscovian and Kasimovian floras, and *Neurocallipteris neuropteroides* (Göppert) Cleal et al., 1990 (= *Gleichenites neuropteroides* Göppert, 1836), a species from the Gzhelian Stage. The isolated, large subtriangular pinnule is also compatible with both species. Since these two species are difficult to separate without cuticles (Cleal & Shute 1995) we have named these specimens simply as *Neuropteris* sp.

Genus *Odontopteris* (Brongniart) Brongniart, 1831

Odontopteris schlotheimii Brongniart, 1828a

Figures 5G, 6B

- 1804 Schlotheim, p. 33, pl. 3, figs 5, 6.
- 1820 *Filicites osmundaeformis* Schlotheim, p. 413 (*nomen illegit.*).
- 1828a *Odontopteris schlotheimii* Brongniart; Brongniart, p. 60.
- 1936 *Odontopteris subcrenulata* (Rost) Zeiller. – Němejc (*non* Rost), p. 9, pl. 2, fig. 15.
- 2006 *Odontopteris schlotheimii* Brongniart. – Barthel, p. 56, figs 138–143.

Material. – Two pinna fragments (specimens 10575, 10577).

Description. – Two pinna fragments with squat pinnules, 7–12 mm long, 7–10 mm wide, squat-linguaeform to rounded, basally slightly constricted or broadly attached to rachis. Midvein absent, subsidiary veins apparently arising directly from rachis. Veins relatively thick, only slightly arched and fork two to three times. Marginal vein density *ca* 20 per cm on pinnule apex.

Remarks. – This is a very distinctive species, assumed to be medullosalean, probably equivalent to the anatomically preserved fossil-species *Medullosa endocentrica* Hamer & Rothwell, 1988 (see Cleal & Shute 2012). The most detailed taxonomic analysis is by Barthel (2006), who showed that the name *O. schlotheimii* has to take precedence over *Odontopteris osmundaeformis* Schlotheim.

The only species with which this is likely to be confused is *Odontopteris cantabrica* Wagner, which was first

described from the lower Stephanian Stage of northern Spain (Wagner et al. 1969). Wagner (*in* Wagner et al. 1969) suggested that it might be possible to regard *O. cantabrica* as a variety of *O. osmundaeformis* (*i.e.* *O. schlotheimii*), but, in view of the long stratigraphical gap between the known ranges of the two forms, it is preferable to regard them as distinct fossil-species. It is also noteworthy that *O. cantabrica* does not have the large, neuropteroid pinnules that form such a distinctive part of the *O. schlotheimii* fronds. Cuticle evidence may help here but, although they are known for *O. cantabrica* (Cleal et al. 2007; Zdzrow & Mastalerz 2009; Zdzrow et al. 2009, 2012) they are unknown for *O. schlotheimii*.

Němejc (1936) figured a poorly preserved odontopteroid from the Velebit Mts with large pinnules as *Odontopteris subcrenulata*. The figured photograph does not show the venation clearly enough, but it seems most likely that it belongs to the species we are calling here *O. schlotheimii*.

Family Cyclopteridaceae Corsin, 1960

Genus *Callipteridium* (Weiss) Zeiller in Renault & Zeiller, 1888

Callipteridium pteridium (Schlotheim) Zeiller in Renault & Zeiller, 1888

Figure 6A

- 1804 Schlotheim, p. 59, pl. 14, fig. 27.
- 1820 *Filicites pteridius* Schlotheim, p. 406 (*nom. illegit.*).
- 1832 *Filicites pteridius* Schlotheim, p. 8, pl. 14, fig. 27.
- 1888 *Callipteridium pteridium* (Schlotheim). – Zeiller in Renault & Zeiller, p. 194, pl. 19, figs 1–3.
- 1936 *Callipteridium pteridium* Schlotheim. – Němejc, p. 8, pl. 2, figs 7, 8.

Material. – Nine pinna fragments (specimens 4, 10497, 10530, 10531, 10545, 10634, X11, X12, X13). Also nine specimens in the Němejc Collection in the National Museum (Prague).

Description. – Fragments of bipinnate segments <70 mm long and wide. Penultimate rachis longitudinally striate, 2–3 mm wide, with ultimate rachises attached at 60–80°. Ultimate pinnae <10 mm wide, parallel-sided for most of length, but tapered gradually in their distal part to an elongate apical pinnule. Lateral pinnules mostly 5–6 mm long, 2–3 mm wide in their fully-developed form, attached to upper side of rachis at 70–80°, becoming more oblique (<50°) in the distal parts of pinnae. Pinnules somewhat vaulted, linguaeform, or in distal parts of pinnae sometimes subtriangular, straight or somewhat acroscopically curved, with

broadly round apex. Pinnule base not significantly decurrent, with adjacent pinnules being narrowly confluent. Thick midvein lies in a shallow furrow and extends for *ca* two-thirds of pinnule length. Lateral veins emitted from midvein at a narrow angle (*ca* 10–20°), bend slightly and meet pinnule margin at 70–80° on acroscopic side, 60–70° on basiscopic side. Lateral veins fork once, sometimes twice in larger pinnules (the second fork usually being on the distal branch produced by the first fork) to produce a marginal vein density of 38–40 per cm.

Remarks. – The taxonomy and nomenclature of *Callipteridium* is in confusion, with its relationship with *Callipteridium gigas* (Gutbier) Weiss, 1870 (= *Pecopteris gigas* Gutbier, 1849), *Callipteridium striatum* Wagner, 1964 and *Callipteridium zeilleri* Wagner, 1964 remains unresolved. Our single specimen provides no helpful evidence on this matter. However, *C. pteridium* is the earliest legitimately published of these names, and the Velebit Mts specimens compare well with typical specimens of that species (*cf.* Wendel 1980).

Family uncertain

Genus *Taeniopteris* Brongniart, 1831

***Taeniopteris carnotii* Zeiller in Renault & Zeiller, 1888**
Figure 5E

1888 *Taeniopteris carnoti* Zeiller; Zeiller in Renault & Zeiller, p. 282, pl. 22, fig. 10.

1936 *Taeniopteris carnoti* Zeiller. – Němejc, p. 9, pl. 1, fig. 14, pl. 2, fig. 14 (not 17 as quoted in text).

2012 *Taeniopteris carnoti* Zeiller. – Jarzembowski, pl. 1.

Material. – A single leaf preserved as part and counterpart (specimen 10776).

Description. – A leaf fragment 68 mm long, 12 mm wide, parallel-sided for most of length, tapering in distalmost 25 mm to a narrowly rounded apex. Leaf limb essentially flat. Thick midvein extends for all of leaf length. Lateral veins emitted from midvein at 45°, bend quickly and then run in an essentially straight line to meet the leaf margin at 80°; marginal vein density *ca* 22 per cm.

Remarks. – Němejc (1936) identified these Velebit Mts specimens as *T. carnotii*, which he regarded as having similar sized leaves and vein density. They also compare in leaf shape with *Taeniopteris jejuna* Grand'Eury, 1877 (*e.g.* Doubinger *et al.* 1995, figs 338, 339; Castro Martínez 2005b, pl. 33) but this species tends to have somewhat less

dense veining (usually <20 per cm). A better comparison is with the fragment figured by Fritz *et al.* (1990, fig. 97) as *T. jejuna*, which has a venation nearer to that of the Velebit Mts specimen.

Other species recorded by Němejc (1936)

Not all of the specimens described by Němejc (1936) have been located. Consequently, we have not been able to verify all of the species recorded in his study: *Ptychocarpus unitus* (Brongniart) Weiss, *Nemejcopteris feminaeformis* (Schlotheim *ex* Sterzel) Barthel, *Crossothea pinnatifida* (Gutbier) Potonié, *Linopteris duplex* Bertrand, *Cyclopteris* sp., *Cordaites palmaeformis* Göppert, *Cordaicaarpus ovoideus* (Göppert & Berger) Seward and *Carpolithus* sp.

We could not locate the specimen that Němejc (1936, pl. 1, fig. 10) figured as *Pecopteris plumosa* (Artis) Brongniart, but another specimen that he labelled as this species closely resembles what we call *?Cyathocarpus* sp.

Němejc (1936) recorded numerous specimens as *Alethopteris bohémica* Franke. However, when the specimens themselves were examined, most had a far less dense venation than is characteristic of that species, and could mostly be attributed to either *Alethopteris zeilleri* or *Alethopteris pennsylvanica*.

Discussion

Biostratigraphy

The stratigraphical ranges of the biostratigraphically important species that we have identified in the Velebit Mts flora are shown in Fig. 7, plotted against the now standard set of biozones for the Upper Pennsylvanian Series (see Wagner 1984, Wagner & Alvarez-Vázquez 2010a). This clearly indicates that they belong to either the *S. angustifolium* or *A. conferta* Zone and, if the identity of the *Lobopteris corsinii* can be confirmed, the evidence strongly points to the former. Wagner (1984) regarded the *S. angustifolium* Zone as an indicator of the Stephanian C Stage (now Substage) but he has subsequently revised this downwards to the Stephanian B Substage (Wagner 1998, Wagner & Alvarez-Vázquez 2010a). According to Wagner & Alvarez-Vázquez (2010a) this would equate to the upper Kasimovian or lowermost Gzhelian Stage in the IUGS chronostratigraphy for the Carboniferous System (Heckel & Clayton 2006). Microfaunal data (Fig. 2; Kochansky-Devidé 1955, 1970; Merino-Tomé *et al.* 2009; Sremac 2012) have indicated a very similar age for these Croatian deposits.

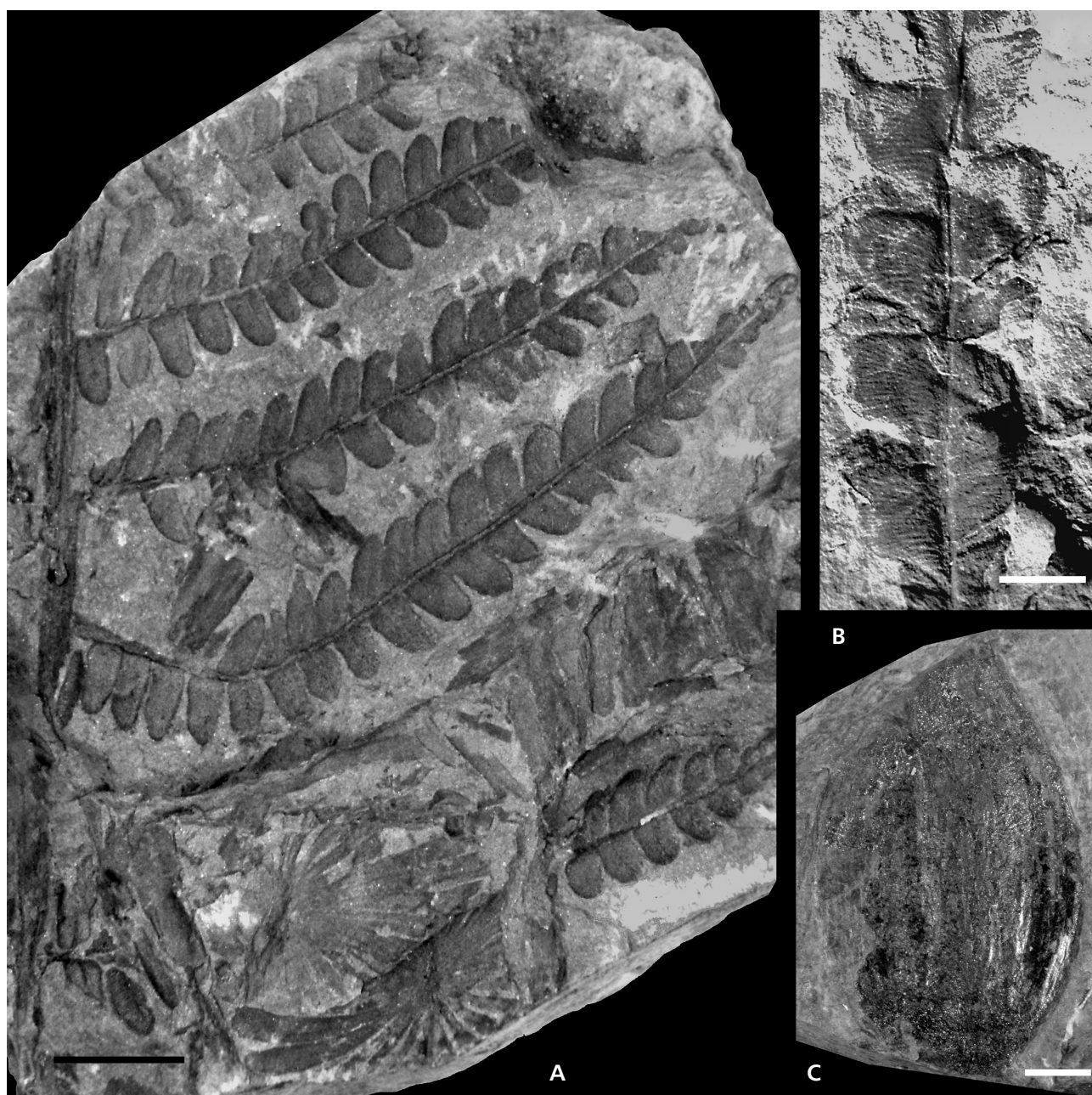


Figure 6. A – *Callipteridium pteridium* (Schlotheim) Zeiller, Oštarije (specimen 10545). • B – *Odontopteris schlotheimii* Brongniart, Brušane (specimen 10577). • C – *Trigonocarpus* aff. *grandis* Lesquereux, Strmotić (specimen STR). All scale bars = 10 mm.

Composition of fossil flora

Table 2 summarises the relative abundances of the 19 fossil species that we have seen in the Carboniferous floras from the Velebit Mts. This should not be regarded as a systematically sampled census but was merely a count of the number of specimens in the collections of the Croatian Natural History Museum and the National Museum (Prague). It nevertheless provides a reasonable impression of the overall balance of the plant groups present. It is immedi-

tely evident that the flora is dominated by medullosaleans (mainly *Alethopteris*), sphenophytes and marattialean ferns (notably *?Cyathocarpus*), which together make up over 90% of the assemblage. Notable absentees are *Sphenophyllum* and cordaitanthaleans (although fragments of both were reported from here by Nĕmejc 1936).

One of the few sources of statistical data on Stephanian floras with which these figures can be compared is in Castro Martínez (2005a), who gave comparable data from the Stephanian B La Magdalena Coalfield in northern Spain.

Table 2. Census of plant fossils from the Velebit Mts Carboniferous floras, according to species and major plant groups. This is based on specimens in both the Croatian Natural History Museum (Zagreb) and National Museum (Prague). N – Number of specimens.

	N	Major plant group	N
? <i>Lepidodendron</i> sp.	11	Lycopsids	11
<i>Annularia spinulosa</i>	18		
<i>Annularia sphenophylloides</i>	1	Sphenophytes	35
<i>Asterophyllites equisetiformis</i>	1		
<i>Calamites suckowii</i>	15		
<i>Acitheca polymorpha</i>	8		
<i>Lobatopteris</i> cf. <i>corsinii</i>	2	Marattialean ferns	21
? <i>Cyathocarpus</i> spp.	11		
<i>Oligocarpia gutbieri</i>	1	Other ferns	3
Fern fragment	2		
<i>Eusphenopteris rotundiloba</i>	2	Lyginopteridaleans	2
<i>Dicksonites plukenetii</i>	1		
<i>Alethopteris zeilleri</i>	76		
<i>Alethopteris pennsylvanica</i>	18		
<i>Trigonocarpus</i> aff. <i>grandis</i>	5		
<i>Trigonocarpus</i> sp.	1	Medullosaleans	122
<i>Neuropteris</i> sp.	2		
<i>Odontopteris schlotheimii</i>	2		
<i>Callipteridium pteridium</i>	18		
<i>Taeniopteris carnotii</i>	1	(?)Cycadaleans	1

These Spanish floras also tend to be dominated by medullosaleans, sphenophytes and Marattiales, although not to the same degree (usually together comprising 50–70% of the total), but also with significant components of *Sphenophyllum* and non-marattialean ferns. In contrast, the Westphalian floras from the Variscan Foreland (such as analysed by Davies 1929, Cleal *et al.* 2012) consistently have a much higher proportion of sphenophytes (often over 50% of the total), lycopsids and cordaitanthaleans, presumably reflecting the wetter substrates in these earlier wetland habitats.

Floristic comparisons

Floras of comparable age are relatively poorly known in Euramerica, mostly situated in the eastern part of the Euramerican tropical belt (Fig. 8).

The most extensively collected are from northern Spain, notably from the Villablino Coalfield and, although no definitive monograph on these floras has been published, there are numerous published papers (as summarised by Wagner & Alvarez-Vázquez 2010a). The list of Stephanian B floras from Villablino given by Wagner & Alvarez-Vázquez (2010a) is rather longer than that from the Velebit Mts, mainly because they have been derived

through more extensive collecting from more localities, but they include virtually all of the species found in the Velebit Mts sites. The only exceptions are *Odontopteris schlotheimii*, which based on the Wagner & Alvarez-Vázquez (2010a) records, is totally absent from Spain, and *Taeniopteris carnotii*, which is a very rare species. A number of other similar but less diverse floras are also listed by Wagner & Alvarez-Vázquez (2010a) mainly from the western and northeastern margins of the Cantabrian Basin.

The Pramollo Group (Kasimovian–Gzhelian) floras of the Carnic Alps are of broadly similar age to the Croatian floras and reportedly share a number of taxa, such as *Annularia spinulosa*, *Acitheca polymorpha*, *Eusphenopteris rotundiloba* [recorded as *Eusphenopteris nummularia* (Gutbier) Novik], *Dicksonites plukenetii*, *Alethopteris zeilleri* [recorded as *Alethopteris serlii* (Brongniart) Göppert] and *Callipteridium pteridium* (Fritz *et al.* 1990; Fritz & Krainer 2006, 2007; Ronchi *et al.* 2012). However, there are also many notable differences, such as the greater diversity of lycopsids, sphenophylls and marattialean ferns in the Carnic floras.

There are a number of contemporaneous coal-bearing sequences in the Massif Central and surrounding areas of southern France (as summarised by Vetter 1986). Of these, the St-Étienne Formation (Grüner Member) of St-Étienne and the Bourran Formation of Decazeville have yielded the best-documented floras (*e.g.* Vetter 1968, Doubinger *et al.* 1995). The St-Étienne Formation has most of the species found in the Velebit Mts with the notable exceptions of *Eusphenopteris rotundiloba*, *Dicksonites plukenetii* and *Odontopteris schlotheimii* (although there is the very similar species *Odontopteris pseudoschlotheimii* de Maistre). From Doubinger *et al.* (1995, table 8) it would seem that the St-Étienne floras also have relatively high proportions of sphenophytes and alethopterid medullosaleans, but in contrast to the Velebit Mts floras there are also abundant marattialean ferns, cordaites and conifers, and *Taeniopteris* is also more abundant. The situation is similar in the Bourran Formation, except that the alethopterid medullosaleans are much rarer, and the odontopteroid medullosaleans and callistophytaleans somewhat more abundant.

The Breitenbach Formation in Saarland (Germany) has also yielded a *S. angustifolia* Zone flora (Hemmer 1920, Doubinger 1956, Cleal 2008). Whilst sharing many species in common with the Velebit Mts fossil flora (*e.g.* *Annularia spinulosa*, *Acitheca polymorpha*, *Odontopteris schlotheimii*, *Callipteridium pteridium*) the former lacks several of the alethopterid species, *Eusphenopteris rotundiloba* and *Dicksonites plukenetii*.

There are some similarities with the floras from the Rosice-Oslavany Formation in the lower part of the Boskovice Basin succession in southern Bohemia (Šimůnek & Martinek 2009). Both share a number of taxa including

Stages	Moscovian	Kasimovian			Gzhelian	
Substages	Cantabrian	Barruelian	“Saberian”	Stephanian B	Stephanian C	middle / upper Autunian
Biozones	<i>Odontopteris cantabrica</i>	<i>Lobatopteris lamuriana</i>	<i>Alethopteris zeilleri</i>	<i>Sphenophyllum angustifolium</i>	<i>Autunia conferta</i>	<i>Annularia spicata</i>
<i>Lobatopteris corsinii</i>			—			
<i>Oligocarpia gutbieri</i>						
<i>Eusphenopteris rotundiloba</i>		—				
<i>Alethopteris pennsylvanica</i>				—		
<i>Odontopteris schlotheimii</i>				—		
<i>Callipteridium pteridium</i>				—		

Figure 7. Stratigraphical ranges of the six stratigraphically informative species in the Upper Pennsylvanian fossil flora from the Velebit Mts, Croatia. The ranges of *Calamites suckowii*, *Annularia spinulosa*, *Asterophyllites equisetiformis*, *Acitheca polymorpha*, *Dicksonites plukenetii* and *Alethopteris zeilleri* are not shown as they range throughout the stratigraphical interval represented; and the range of *Taeniopteris carnotii* is not known in any detail. The ranges are plotted against the biozones proposed by Wagner (1984) and modified by Wagner & Alvarez-Vázquez (2010a). The correlation of the zones with the Heerlen substages and IUGS stages is based on Wagner (1998) and Wagner & Alvarez-Vázquez (2010a).

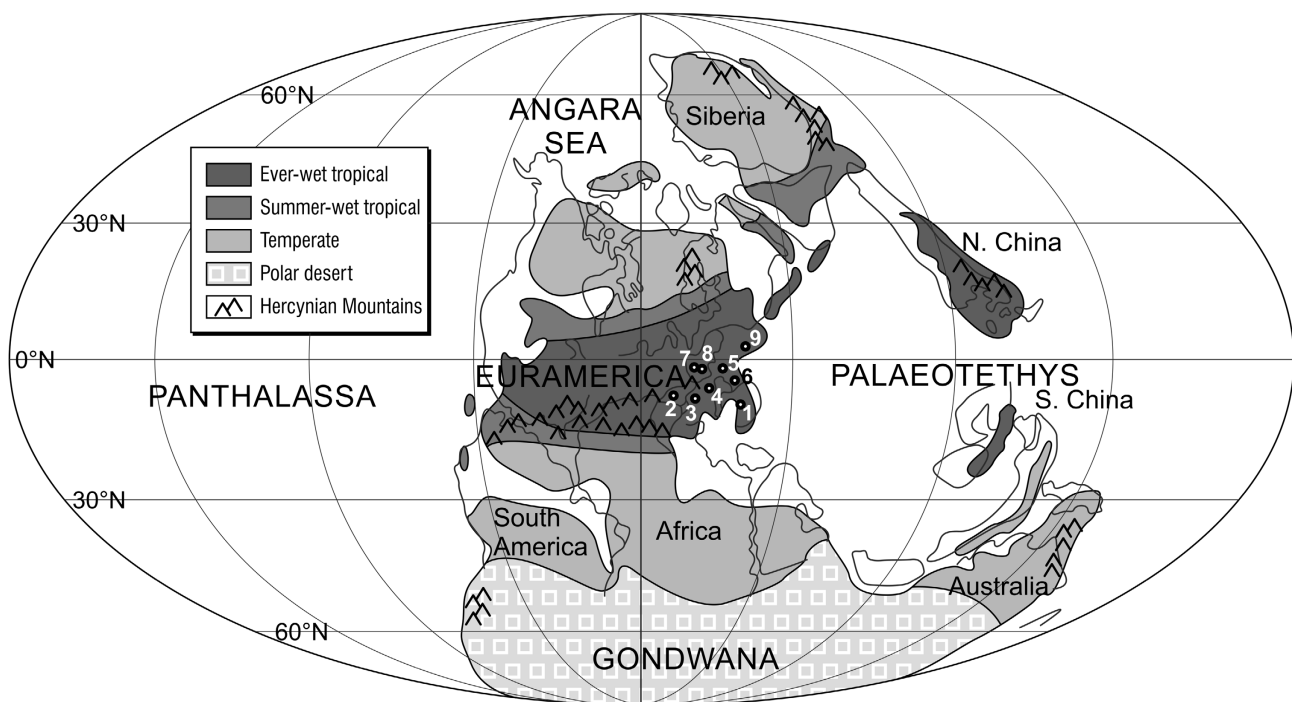


Figure 8. Localities with Stephanian B flora in Euramerica. Palaeogeographic reconstruction based upon Falcon-Lang (2003), DiMichele *et al.* (2010). 1. Croatia – Velebit Mts And Lika region; 2. Spain – Villablino and La Magdalena; 3. France – Massif Central; 4. Germany – Saarland, Saxony-Anhalt; 5. Austria – Carnic Alps; 6. Slovenia – Karavanke Mts; 7. Czech Republic – Bohemia Basin; 8. Poland – Intrasudetic Basin; 9. Ukraine – Donets Basin.

Annularia spinulosa, *Asterophyllites equisetiformis*, *Acitheca polymorpha*, *Dicksonites plukenetii*, *Alethopteris zeilleri* and *Odontopteris schlotheimii*. The Boskovice floras tend to have a far higher proportion of marattialean fern remains than seen in the Velebit Mts, as well as having a much wider range of medullosalean pteridosperms (but unlike the Croatian floras are not dominated by alethopterids).

Also of similar *S. angustifolia* Zone age is the Líně Formation in the Central and Western Bohemia Basin (Pešek 1994). Based on the floral species list from here by Šimůnek (*in* Pešek 1994, table 4) there are a number of species in common including *Alethopteris zeilleri*, *Odontopteris schlotheimii*, *Callipteridium pteridium*, *Dicksonites plukenetii* and *Acitheca polymorpha*. However,

there are a number of discrepancies, notably the absence from the Líně Formation of *Alethopteris pennsylvanica*, *Oligicarpia gutbieri*, *Eusphenopteris rotundiloba*, *Lobopteris corsinii*, *Annularia spinulosa* and any lycopsids (other than *Asolanus camptotaenia*), and the absence from the Velebit Mts of conifers and cordaites. This may reflect the rather different ecological setting of the Líně Formation, which was formed in a fluvio-lacustrine environment in an intra-montane setting (as summarised in Pešek 1994) and would have incorporated remains of vegetation from surrounding habitats with drier substrates (e.g. conifers and cordaites), whereas the taxa present in the Velebit Mts but not in the Líně Formation probably represent more lowland, wetter substrate vegetation.

Wagner (1984) reported that similar aged floras occur in the area of Wettin (Saxony-Anhalt, Germany) and according to Remy *et al.* (1963) the Wettin Formation includes *Alethopteris zeilleri* and *Callipteridium pteridium*. However, there has been no recent taxonomic review of these floras so a detailed comparison is impossible.

The Gzhelian Stage in the Donets Basin (Ukraine) has abundant floras that should be approximately contemporaneous with those from the Velebit Mts (Novik 1952) but none of the associations summarised and in part described by Shchegolev (1975, 1991) are similar. Unlike the Croatian floras, ferns and sphenophylls dominate, and medullosaleans are relatively rare and *Alethopteris* is absent [the only alethopterid recorded from these strata by Novik (1952) is *Alethopteris discreta* (Weiss) Zalessky, a species which Wagner & Castro Martínez, 1998 have transferred to *Neuropteris obtusa* (Brongniart) Wagner & Castro Martínez]. The contemporaneous floras from the Caucasus described in detail by Shchegolev (1979) are similarly rich in ferns and relatively rare in medullosaleans.

Conclusions

Continental interbeds within the mainly marine Upper Pennsylvanian sequence of the Velebit Mts and Lika region of Croatia have yielded abundant plant macrofossils indicating a Stephanian B (late Kasimovian or earliest Gzhelian) age. They are thus remains of some of the youngest Pennsylvanian wetland vegetation still remaining in Europe, as landscape changes and increased drainage triggered by Variscan tectonics caused the biome to contract and fragment. This was also when the wetland biome was migrating east into Cathaysia, and it has been argued that the relatively localised distribution of the European wetlands at this time may have acted as a taxonomic bottleneck that caused the differences in overall taxonomic balance between the Pennsylvanian Euramerican and successor Permian Cathaysian vegetation (Hilton & Cleal 2007). Understanding Late

Pennsylvanian Euramerican plant biogeography is clearly important for interpreting this major biome migration, as well as the transition from Palaeophytic to Mesophytic floras (*sensu* Cleal & Cascales-Miñana 2014).

The Croatian assemblage compares most closely with similar age floras in northern Spain, notably from the Villablino Coalfield, and the Pramollo Group of the Carnic Alps. It epitomises the lowland vegetation that developed during latest Carboniferous times on the southern side of the Variscan Mountains, along the northern coast of the Palaeotethys. In contrast, the fossil floras of similar age from the intramontane basins, notably of France, Germany and the Czech Republic, tend to have a greater diversity of marattialean ferns, and also often to include sphenophylls, cordaites and conifers, probably reflecting the higher elevation of these basins.

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