

Taxonomic revision and palaeoecological interpretation of the plant assemblage of Bernissart (Barremian, Belgium)



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ABSTRACT

The Lower Cretaceous plant assemblage of Bernissart (Mons Basin, Belgium) was studied in detail during the 1900s, but no recent revisions have been performed. The taxonomy of plant taxa recovered from this site is updated, which includes one undetermined “aquatic plant” taxon, nine fern taxa (*Cladophlebis* sp., *Hausmannia dichotoma*, *Phlebopteris dunkeri*, Matoniaceae indet., *Ruffordia goeppertii*, *Onychiopsis psilotoides*, *Coniopteris* sp., *Korallipteris* sp., and *Weichselia reticulata*), aff. genus *Taeniopteris* (of unknown affinity), and five undetermined conifer organs (one stem, two types of seed, one cone, and a dispersed bract). Two lithologies are identified, both consisting of grey clays, one with a smooth surface while the other is more irregular. The large number of available specimens has permitted the study of the species richness and relative abundance of the locality and both lithologies. The taphonomical analysis of the specimens including the preservation of the remains, fragment size, and associations between taxa, together with the diversity analyses, results in four assemblages: “algae” in the water column of the lake; a vegetation composed of *Weichselia* and *Phlebopteris* closest to the lake margin; *Hausmannia*, *Onychiopsis* and the other ferns further away from the margin; and Matoniaceae indet., conifers and aff. *Taeniopteris* even further away from the depositional site. In general, the plant assemblage at Bernissart consists of open vegetation, which probably belonged to an early successional stage that was burnt frequently by wildfires.

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1. Introduction

Famous for the discovery of a large group of complete Iguanodonts (Godefroit et al., 2012), the Bernissart locality has as well yielded an abundant and diversified fossil plant assemblage (Dupont, 1878; Seward, 1900b). First reported by Dupont (1878), this flora was later studied in detail by Seward (1900b). It appeared to be one of the most important Early Cretaceous floras in Europe, with a very similar taxonomic composition to the English Wealden flora(s) (Seward, 1894; Watson, 1969; Watson and Alvin, 1996).

Although the Bernissart flora was never restudied after these early pioneer works, the Mons Basin Wealden facies have been subject to several studies focusing on plant macro- and mesofossils and on

palynomorphs (Harris, 1953; Alvin, 1953, 1957, 1960, 1971; Dejax et al., 2007; Gomez et al., 2012; Yans et al., 2012; Barral et al., 2016).

During the Early Cretaceous, Europe consisted of a vast archipelago under subtropical latitudes, with a warm, humid climate (Hay and Floegel, 2012). Although floras at this time are widely dominated by fern and conifer taxa, the Barremian limestones of Las Hoyas and El Montsec (Spain) notably record the first unequivocal angiosperm macro-remains in Europe (Gomez et al., 2015).

Here we undertake a comprehensive actualization of the plant taxonomy at Bernissart. We provide precise descriptions of the fossil material and suggest a paleoecological reconstruction based on the abundance, diversity and taphonomy of the extraordinarily large available sample.

2. Geological settings

Bernissart is located 25 km west of Mons, in southwestern Belgium, in the northern part of the Mons basin (Baele et al.,

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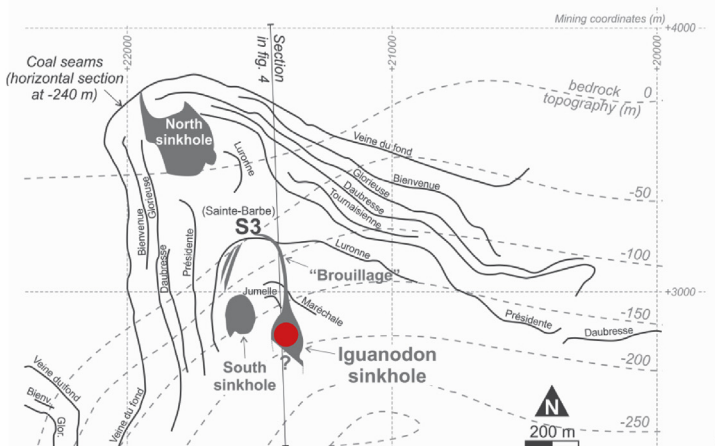
2012) (Fig. 1A–B). This basin corresponds to an east-west subsiding zone where Meso-Cenozoic sediments accumulated. Rather small, the subsiding area (40 by 15 km) is mainly controlled by intrastratal dissolution of deep evaporite beds in the Mississippian (Carboniferous) basement. This dissolution process as well led to the creation of several sinkholes, or natural pits (Spagna et al., 2012; Quinif & Licour, 2012). The natural holes

acted as a trap for the sediment, fauna, and flora, present there at that moment.

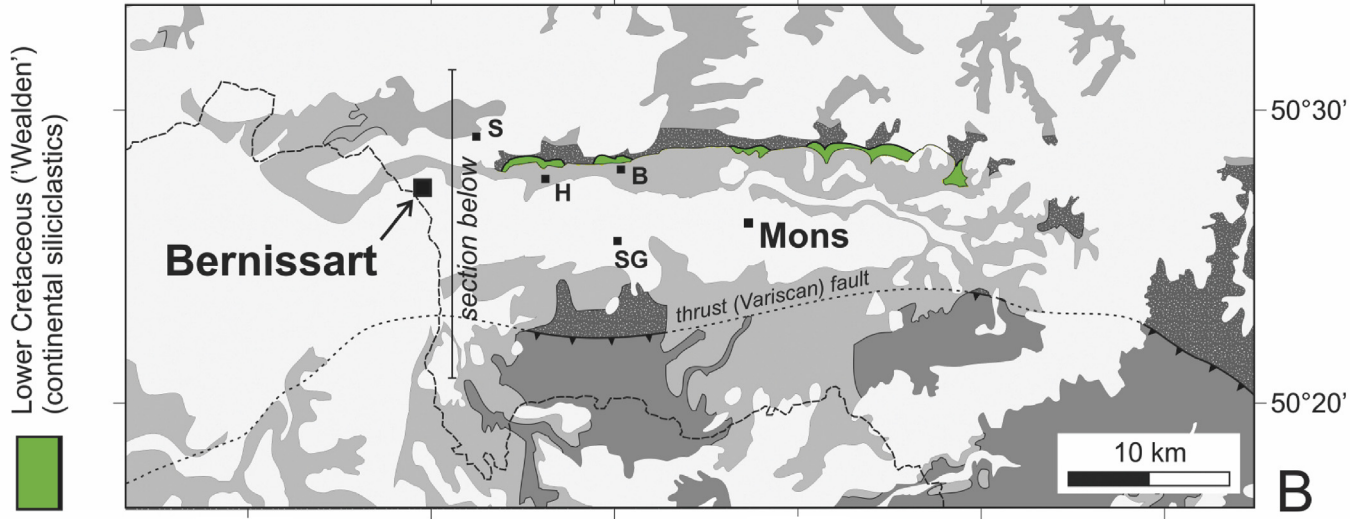
Three Sinkholes have been spotted around Bernissart (Fig. 1C). They are the North, the South, and the Iguanodon sinkholes. The latter yielded the famous Bernissart Iguanodons. They were found in a Barremian/Aptian lacustrine clay, attributed to the Sainte-Barbe Clays Formation (Cornet and Schmitz, 1898; Cornet, 1927),



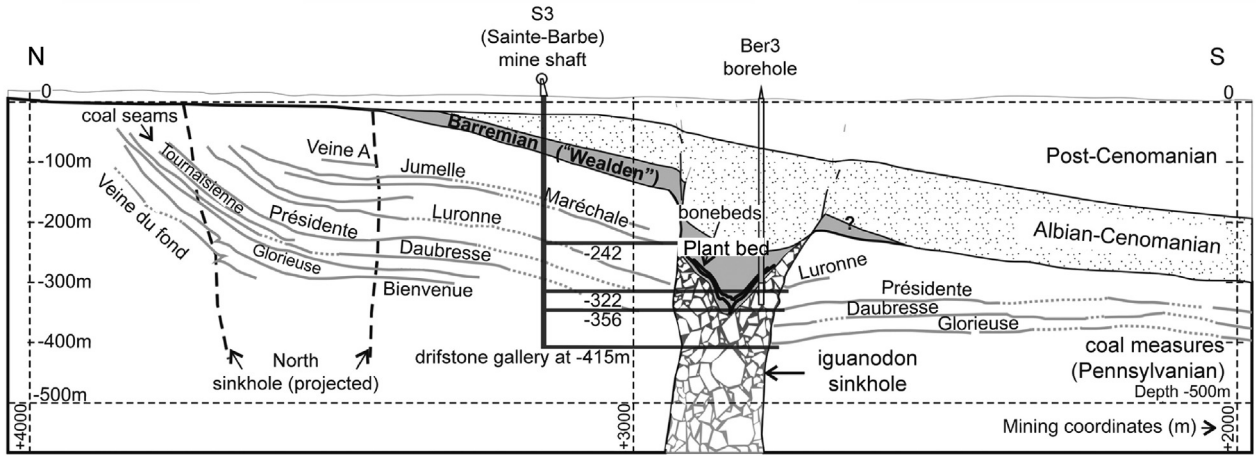
A



C



B



D

Fig. 1. Localization of the locality of Bernissart. A, map of Belgium marking the Mons Basin. B, localization of Bernissart in the Mons Basin. C, detailed map of the locality including the different sink holes. D, schematic drawing of the Bernissart pit.

together with rich fauna and flora. The age of this formation has been determined based on palynologic data as ranging from the middle Barremian to the earliest Aptian (Dejax et al., 2007). The analysis of several drill cores made in the Iguanodon Sinkhole show plant remains to be abundant throughout (Prestianni, personal observation). The plants studied here have been recovered from the -322 m tunnel only. Unfortunately, the information on the exact provenance of these fossils is lost because the specimens were mixed up before labelling when brought to the surface.

The environment at the top of the Iguanodon pit of Bernissart was formerly interpreted as lacustrine (Van den Broeck, 1898) or lacustrine to swampy (Yans, 2007; Schnyder et al., 2009; Spagna et al., 2012).

3. Material and method

A total of 3701 specimens from the Bernissart plant collection housed at the Royal Belgian Institute of Natural Sciences (identified in this collection with a specimen number preceded by the institutional abbreviation IRSNB) were revised. They mostly consist of small fragments of carbonized compressions and some impressions. The material shows a wide range of plant fragment sizes and preservation qualities, suggesting a reduced collection bias.

By contrast with the Iguanodons, the documentation associated with the collecting of the plant material is very scarce. Dinosaurs were sampled underground with great care of their original position. Many drawings and situation maps are available for the latter in the collections of the RBINS. However, as far as we know, plants were sampled above ground within the collecting residues. A detailed stratigraphic and sedimentological analysis is thus impossible. Nevertheless, two lithofacies were identified. Lithofacies 1 consists in a thinly laminated light grey clay with impressions and compressions of charred plant remains. The rock surface is smooth. Lithofacies 2 is similar to Lithofacies 1 but presents a higher content in pyrite. The pyrite diagenetically degrades and leaves on the rock surface small protuberances giving to these samples a "rough" aspect.

The specimens were taxonomically classified and newly described, revising the previous identifications and descriptions by Seward (1900b). Subsequently, each fragment was counted, and the corresponding lithofacies recorded. Additionally, the maximum length of the fragment was measured. These data were recorded directly on the specimens or photographs of the latter. Measurements on pictures were performed with Image J (Schneider et al., 2012).

To perform a palaeoecological reconstruction, the abundance of each taxon, the diversity, and the taphonomy of the sample were studied. The relative abundance of each taxon was calculated for (1) the whole sample, and (2) each lithofacies. The diversity was explored by the species richness (S) and Simpson's diversity index (1-D), which was also calculated for (1) the whole sample, and (2) each lithofacies.

Taphonomical information that could be recovered from the collection was the specimen size, the lithofacies, and the presence of remains of different taxa in the same hand specimen (associations). A statistical analysis of the size of the fragments was performed. The mean, median, variance, statistical deviation, maximum and minimum were calculated for: (1) the whole sample; (2) each lithofacies; (3) each taxon; (4) each taxon for each lithofacies. Box and whiskers plots were also depicted for the two lithofacies (2) and each taxon (3). The distributions for each lithofacies (2) were compared with an unpaired Student t-test for the total sample, and per taxon. To compare mean sizes and variance between taxa (3), they were coded and grouped by the gap-weighting method (Thiele, 1993). The association between taxa

was studied through the measurement of the recurrence of different taxa co-occurrences in the same hand specimen. All these analyses were performed for each lithofacies. The randomness of the co-occurrences was tested with a Kruskal-Wallis test for each lithofacies, looking for significant differences between the total number of specimens of each taxon in the lithofacies, and the number of co-occurrences with other taxa.

The abundance studies were performed using the totality of the remains present at the collection. However, as *Weichselia reticulata* (C. Stokes et Webb) Fontaine is very abundant in the collection, the lithofacies and measurements of this taxon were only recorded for 835 of the 2734 available remains. Other taxa have been included in their totality. Statistical analyses on size and lithofacies are therefore based on 1748 specimens.

4. Results

4.1. Systematic paleontology

Class Polypodiopsida
Order Osmundales
Family Osmundaceae

Genus *Cladophlebis* Brongn., 1849

Cladophlebis sp.

Figs. 2A–C

Material examined. 105 specimens.

Description. Most specimens consist of fragments of ultimate order pinna and attached pinnules (Fig. 2A and B). Only six specimens show pinnae of the penultimate order. They range from 0.3 to 3.3 cm. The rachis of penultimate order pinnae measures up to 3.5 cm long and approximately 1 cm wide. Ultimate pinnae rachis measures up to 1 cm long and from 0.1 to 0.5 cm wide. Pinnules are always inserted alternately (Fig. 2B), the first one being in a catadromous position (Fig. 2C). They measure from 0.1 up to 0.5 cm in length and from 0.1 up to 0.2 cm in width. They all present a triangular apex but are highly variable according to their relative position in the frond (Fig. 2A–C). The margin ranges from clearly lobed to entire (Fig. 2A–C). The base may be cordate or fused to the axis (Fig. 2A and B). They tend to be more fused distally. Proportions between length and width may also considerably vary. The mid-vein is patent and forms a slightly acute angle with the pinna axis. It fades towards the apex of the pinnule, being, in most cases, undistinguishable in the last third. Secondary venation is simple and open. One to exceptionally, two dichotomies are observed. No fertile organs were found.

Interpretation. The shape of the pinnules, together with the patent mid-vein at the base and secondary vein dichotomies, clearly place these specimens in the genus *Cladophlebis*. *Cladophlebis* is a relatively diversified genus (Berry, 1911), where pinnules do not always keep the same characteristics throughout the fronds (Herbst, 1971). It is especially clear in *Cladophlebis dunkeri* (Schimp.) Seward (Seward, 1894) where two extreme morphologies with intermediate forms are described: one with triangular apex and the entire base attached, and another with longer and lobed pinnules, which become narrower towards the point of attachment. In Bernissart, some fragments are similar to *Cladophlebis browniana* (Dunker) Seward, but in this species, the apex is rounded and rarely triangular (Seward, 1894). *Cladophlebis albertsii* (Dunker) Brongn. also presents pinnules that are not attached by the whole base, but in that case, the base is asymmetrical, with only one unattached acroscopic lobe (Seward, 1894). By contrast, the specimens from Bernissart have a cordate or wholly attached base. Unfortunately, the lousy preservation (venation and pinnule morphology are not

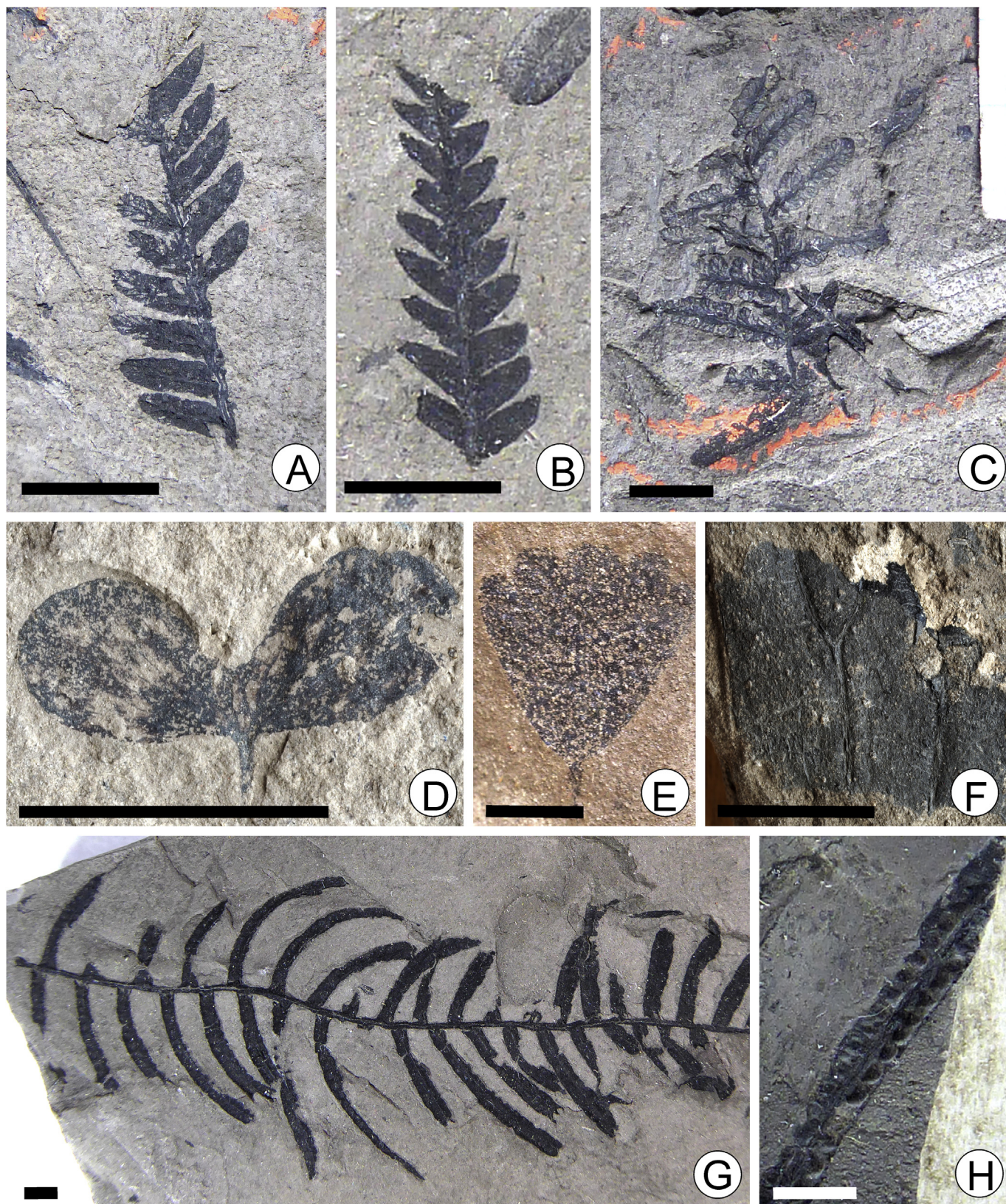


Fig. 2. Photographs of specimens. A-C, *Cladophlebis* sp., specimens IRSNB b 7841, IRSNB b 7842, IRSNB b 7788. D-F, *Hausmannia dichotoma*, IRSNB b 7807, IRSNB b 7806, IRSNB b 7786. G-H, *Phlebopteris dunkeri*, IRSNB b 7780, IRSNB b 7844. Scale bars = 0.5 cm.

very clear) makes it impossible to explore the morphological variability following methods such as the one proposed by Bodor and Barbacka (2008).

Remarks. In the original description of the flora, these remains were tentatively assigned to *Cladophlebis dunkeri* (Seward, 1900b). Seward, however, particularly insisted on the difficulty of dealing with isolated small frond fragments in this kind of material. As a result, he did not separate specimens of this species and those he identified as *Leckenbya valdensis* Seward (now *Korallipteris* sp.) (Seward, 1900 figs. 43–46). A reinvestigation of the material and detailed measurements have allowed us to separate the two genera. The main differences between the two plants are found in the general shape of the pinnule and the type of venation (see Fig. 2). Further discussion will be made in the *Korallipteris* sp. section.

Ecology. Osmundaceae during the Mesozoic have been suggested to inhabit riverbanks and/or fresh-water marshes (Van Konijnenburg-van Cittert, 2002).

Order Gleicheniales
Family Dipteridaceae

Genus *Hausmannia* Dunker 1846

Hausmannia dichotoma Dunker, 1846

Fig. 2D–F

1900 *Sagenopteris mantelli* Seward, p. 9, pl. III, fig. 55.
1900 *Protorhipis roemeri* Seward, p. 18, pl. III, fig. 34.
1900 *Adiantites* sp. Seward, p. 26, pl. III, figs. 53, 54, 57.
1901 *Hausmannia kohlmanni* Richter, p. 21.
1906 *Hausmannia kohlmanni* Richter, p. 21, pl. I, figs. 1–11; pl. II, figs. 1, 3, 4, 5, 6, 8, 9; pl. 5, figs. 1, 2, 5, 6, 7, 8; pl. 6, figs. 3, 6, 7, 9.

Material examined. 13 specimens.

Description. Specimens measure 0.8–1.7 cm long and consist of isolated pinnules and fragments of pinnule lamina (Fig. 2D–F). Two morphotypes can be observed. The first morphotype consists of a pinnule that measures 1.4 cm, with two lobes measuring 0.6 and 0.8 cm each, and entire margins (Fig. 2D); the second morphotype has pinnules with a spatulate shape, entire margins at the base, presents five lobules at the apex, and measures 0.8–1.1 cm long and 0.7–1.1 cm wide (Fig. 2E). The venation is more or less discernible in some of the specimens. It consists of simple primary veins that dichotomize at least once, and secondary veins that are perpendicular to the primary and connect to form a reticulum (Fig. 2F).

Interpretation. The occurrence of reticulate secondary veins and apically webbed pinnule lamina in both morphotypes is typical of the Dipteridaceae (Bower, 1926). The fossils described here closely resemble specimens figured by Richter as *Hausmannia* (Richter, 1906 Pl. I, II). Richter (1906) described two species that closely agree with the two morphotypes described earlier. Specimens of the first morphotype are very similar to *H. kohlmanni* Richter, while the second morphotype shows similarities with *H. dichotoma* (Richter 1906). Cantrill (1995), in a revision of the genus, discussed the similarities existing between *Hausmannia* and the extant genus *Dipteris* Reinw. He used the latter as a model to understand the ontogeny of the former. Following his interpretation, both *H. kohlmanni* and *H. dichotoma* represent morphotypes of the same natural species but at different ontogenic stages; *H. kohlmanni* being juvenile and *H. dichotoma* mature.

Remarks. Seward (1900b) identified the here described morphotype 1 as *Sagenopteris* sp., and morphotype 2 was identified as *Adiantites* sp. Surprisingly, both *Adiantites* Goepfert and *Sagenopteris* J. Presl are pteridosperm genera from the Palaeozoic and Mesozoic, respectively. Isolated fragments of lamina with reticulate secondary venation were identified as *Protorhipis roemeri* Shenk. This genus is, however, a younger synonym of *Hausmannia* (Richter, 1906).

Cantrill (1995) stated the *Protorhipis roemeri* Seward could not be changed to *Hausmannia roemeri*, as it is based on fragmentary material lacking diagnostic characteristics (Cantrill, 1995). The new assignment of the complete pinnules of Bernissart to *Hausmannia dichotoma* (morphotypes 1 and 2) permits a more complete diagnosis and a more precise identification of this material.

Ecology. The only extant genus of the Dipteraceae family, *Dipteris*, is a stream-side dweller and colonizer of disturbed sites. Some species of the genus *Hausmannia* have been interpreted as inhabiting the same areas (Cantrill, 1995). The leathery lamina of *Hausmannia dichotoma* has been suggested to be an adaptation to stress-related environments (Van Konijnenburg-van Cittert, 2002).

Family Matoniaceae

Genus *Phlebopteris* Brongn, 1837

Phlebopteris dunkeri Schenk, 1875–1876

Figs. 2G–H, 3A–B

1871 *Laccopteris dunkeri* Schenk, p. 219, pl. XXIX, figs. 3–5. [Basionym]
1875–1876 *Microdictyon dunkeri-Phlebopteris dunkeri* Schenk, p. 161, pl. XXVII, fig. 10; pl. XXVIII, figs. 11a–d.xvi.
1888 *Laccopteris dunkeri* (Schenk) Velenovský, p. 12, pl. II, figs. 3–7.
1900 *Laccopteris dunkeri* (Schenk) Seward, p. 13, pl. II, figs. 22–32.
1926 *Laccopteris rigida* (Heer) Seward, p. 80, pt. 8, figs 48–56, 58–60, 62. text-fig. 8.
1927 *Laccopteris dunkeri* (Schenk) Velenovský & Vinklár, p. 3, pl. XIV, fig. 5.; pl. XVI, fig. 5.
1953 *Phlebopteris (Laccopteris) dunkeri* (Schenk) Daber, pl. XII, fig. 2, pl. XIV, fig. 1.
1961 *Phlebopteris dunkeri* (Schenk) emend. Harris, p. 110, fig. 36 A–C.
1974 *Phlebopteris dunkeri* (Schenk) Alvin, p. 588, pl. LXXXVII, fig. 1.
1999 *Laccopteris dunkeri* (Schenk) Knobloch, p. 32, pl. VI, figs. 6, 12.

Material examined. 468 specimens.

Description. Specimen sizes range from 0.15 to 9.5 cm (Figs. 2G, 3A), and correspond to pinnae, isolated pinnules or fragments of the latter. Most specimens are fertile (Fig. 2H). Pinnae are always found broken. They measure up to 0.2 cm in width. Pinnules are loosely inserted in subopposite to alternate position. They are separated from each other by approximately 0.3–0.4 cm. Though charcoallified, the pinnule surface presents a leathery aspect, here interpreted as witnessing a thick lamina (Fig. 3B). Pinnules are elongated, linear in shape with entire margins and subtriangular apex. They range from 0.6 to 4.4 cm in length and from 0.1 to 0.3 cm in width. Venation has been observed on a few vegetative specimens. They show a very patent central vein from which secondary veins are borne at 80–90° angle, dichotomizing only once in the first 2/3 of the lamina. Tertiary venation is reticulate. Fertile and vegetative leaves share the same morphology. When fertile, they present on the abaxial face two rows of sori measuring up to 1 mm in diameter (Fig. 2H). Sori are rounded and show a placenta at the center. No indusium has been observed.

Interpretation. The general morphology and the lack of indusium on these specimens identify them as genus *Phlebopteris* (Van Konijnenburg-van Cittert, 1993). Although the absence of indusium in fossil Matoniaceae has been questioned (Klavins et al., 2004), this matter has not been addressed in the description of the fossil genera of this family yet. In genus *Phlebopteris*, the secondary venation is a differentiating characteristic. In this aspect, the remains from Bernissart concur with *Phlebopteris dunkeri*, where the secondary veins dichotomize only once, and in the first 2/3 of the lamina, whereas other species such as *Phlebopteris polyodioides* Brongn. have reticular secondary venation or

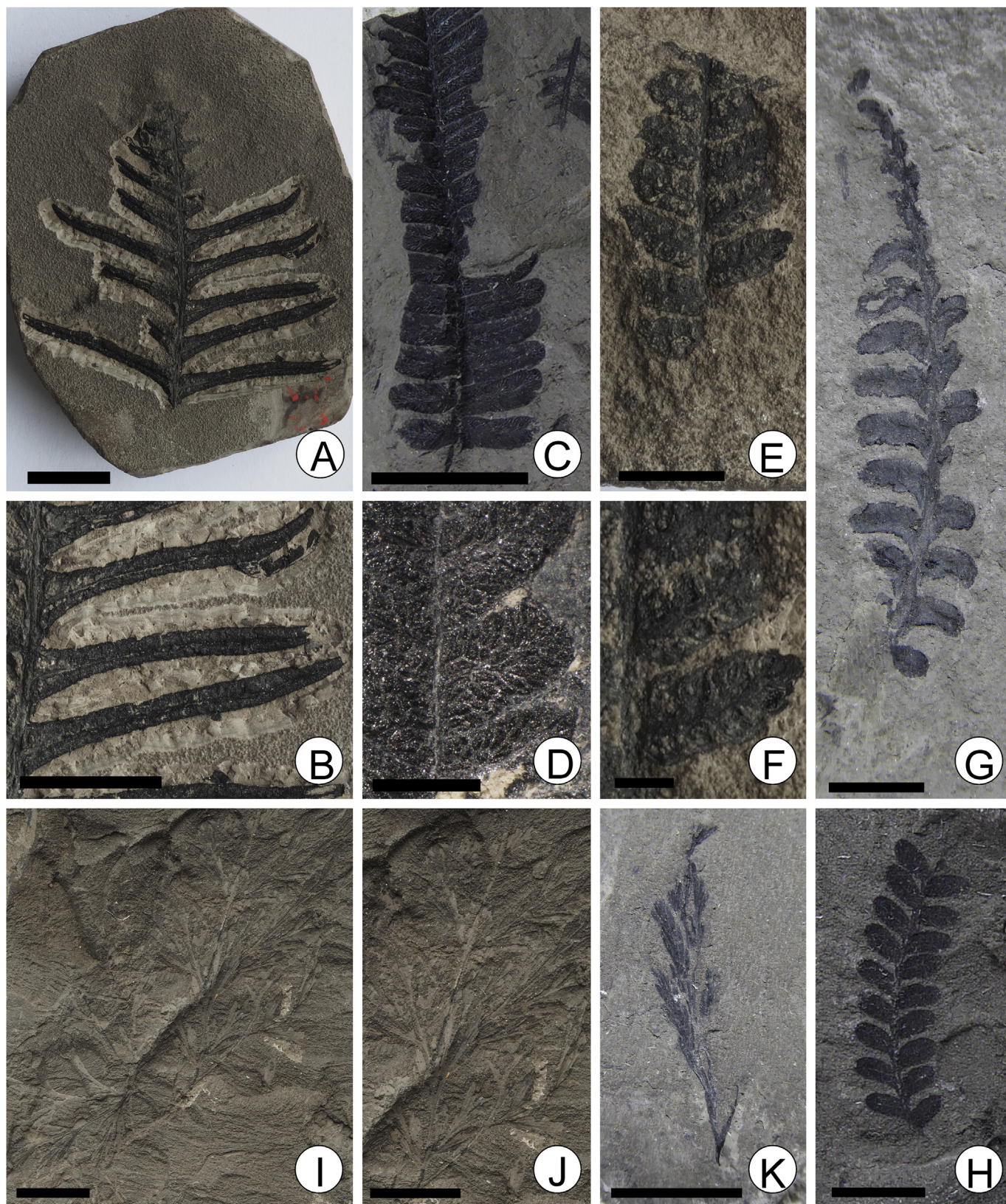


Fig. 3. Photographs of specimens. A-B, *Phlebopteris dunkeri* fertile specimens, IRSNB b 7843. C, sterile specimen of *Weichselia reticulata*, IRSNB b 7845. D, detail of the vascularization of *Weichselia reticulata*, IRSNB b 7846, scale bar = 0.2 cm. E, *Matoniaceae* indet. fertile specimen, IRSNB b 7847, scale bar = 0.5 cm. F, detail of specimen Fig. 4E, scale bar = 0.2 cm. G-H, *Korallipteris* sp., IRSNB b 7789, IRSNB b 7796. I-K, *Ruffordia goeppertii*, IRSNB b 7848, IRSNB b 7849. Scale bars = 1 cm unless otherwise indicated.

dichotomize more than once as it happens in *Phlebopteris woodwardii* Leckenby (Sender, 2012). The position of the sori is also specific, in this case, they are situated at both sides of the central vein in a more or less central position in the lamina (although closer to the central vein), which is typical of *P. dunkeri* (Harris, 1981).

Remarks. This material was identified as *Laccopteris dunkeri* Schenk by Seward (1900b). *Laccopteris* is the basionym of *Phlebopteris*, both described by Schenk in two different publications (Schenk, 1871, 1875). The assignation of these remains to *Phlebopteris dunkeri* has been corroborated in this work, as the characters observed in the fragmentary specimens agree with this species.

Ecology. This species has been considered a plant of inland heaths, sharing habitat with *Weichselia reticulata* (Harris, 1981).

Family Matoniaceae

Matoniaceae indet.

Figs. 3E–F, Fig. 4

Material examined. 4 specimens.

Description. Specimens measure 1.1–6 cm long. There is one specimen of a frond impression, and the other 3 specimens consist of isolated pinnae with a few attached pinnules (Fig. 3E–F). All

isolated specimens are fertile. The frond is pedate, with a central petiole head from which at least 8 once pinnate pinnae radiate. Pinnules are alternately inserted on the pinna. They are rectangular in overall shape but present a slightly truncated apex. They range from 2.5 to 3 cm in length and approximately 2.0 cm in width. The venation is impossible to determine in these specimens. Fertile specimens show two rows of sori at the abaxial side (Fig. 3F).

Interpretation. The material presently at our disposal is incomplete, it could be assigned to *Matonidium* Schenk or *Matonia* R.Br. ex Wall., based on the pedate structure and pinnule morphology. *Matonidium* has a partial indusium. In contrast, *Matonia* has a complete one covering the sori (Van Konijnenburg-van Cittert, 1993). As none of the specimens show well enough preserved sori to distinguish between these two genera, the specimens are identified as *Matoniaceae* indet.

Remarks. This material was initially determined as *Matonidium goeppertii* (Ettingsh.) Schenk by Seward (1900b). He bases its determination on a particularly well-preserved sample with sori that now appears to be lost.

Order Schizaeales

Family Anemiaceae

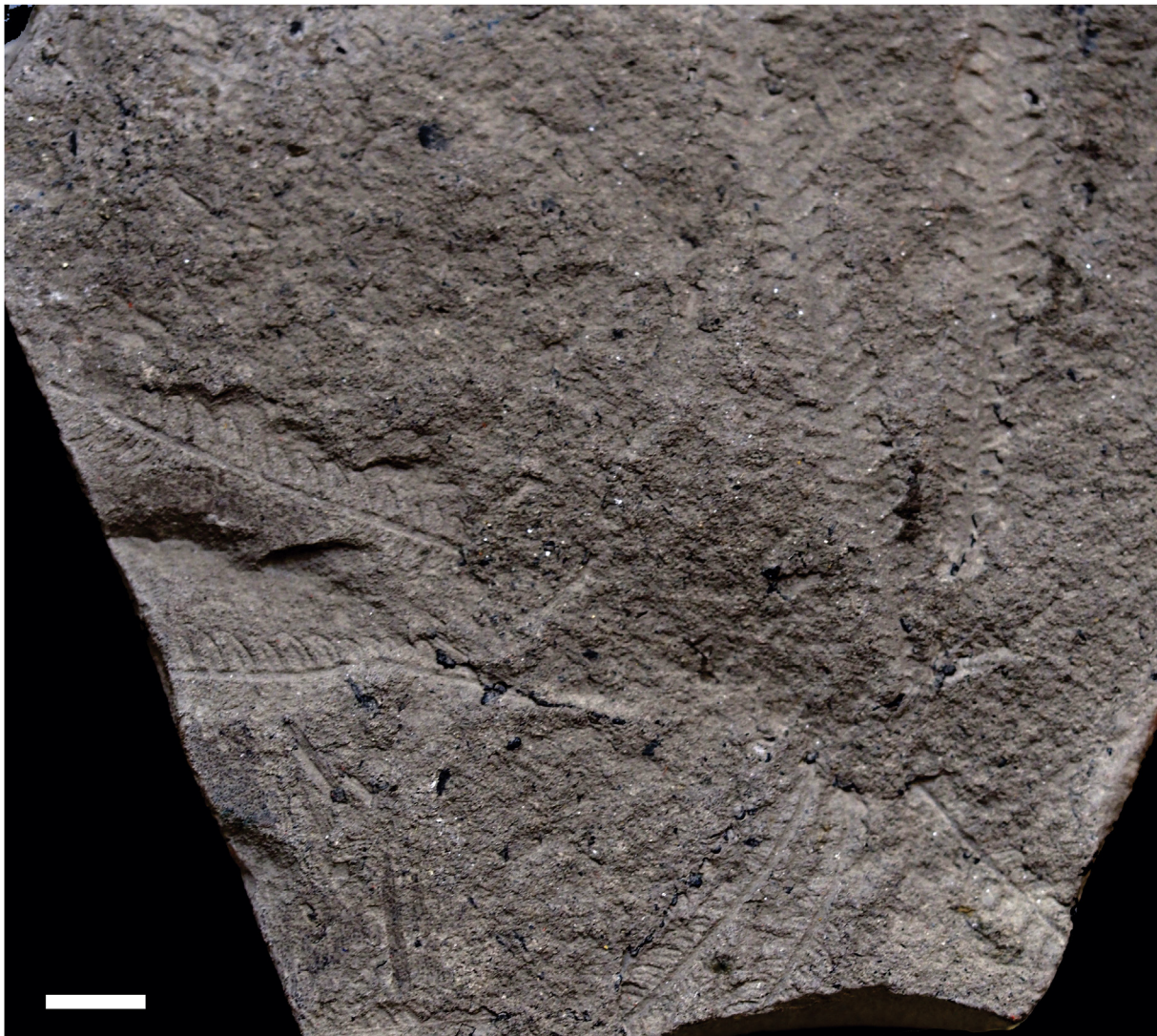


Fig. 4. Photograph of an impression of *Matoniaceae* indet. showing the pedate architecture of the frond. IRSNB b 7753, scale bar = 0.5 cm.

Genus **Ruffordia** Seward, 1894.

Ruffordia goeppertii (Dunker) Seward, 1894.

Figs. 3I–K

- 1846 *Sphenopteris goeppertii* Dunker, p. 4, pl. I, fig. 6, pl. IX, figs. 1–3. [Basionym]
 1894 *Ruffordia goeppertii* (Dunker) Seward, p. 76, pl. III, figs. 5, 6; pl. IV, pl. V, figs. 1–5; pl. VI, fig. 1, pl. X, figs. 1, 2.
 1889 *Thyrsopteris nervosa* Fontaine, p. 122, *pro parte*, pl. XXV, figs. 4, 5, 16; pl. XXXVII, figs. 2, 4; pl. XXXIX, fig. 5.
 1900 *Ruffordia goeppertii* Seward, p. 18, Pl. III fig. 33.
 1911 *Ruffordia goeppertii* (Fontaine) Berry, p. 232, pl. XXIII, figs. 3, 4.
 1956–1960 *Sphenopteris (Ruffordia) goeppertii* (Dunker) Depape & Doubinguer, p. 40, fig. 8, pl. V, figs 7, 8.

Material examined. 18 specimens.

Description. Specimens measure between 0.63 and 7.4 cm. They consist of sterile fragments of the ultimate pinna and a sterile fragment of the basal part of the frond. The latter consists in a broken petiole measuring 3.7 cm long and 0.1 cm wide. The rachis is alate, with decurrent pinnae and pinnules (Fig. 3J). Five orders of ramification can be observed, and the disposition is catadromous in all orders. Pinnae and pinnules are opposite to subopposite at the base and become alternate towards the apex. The ramification of pinnae and fusion of pinnules is complicated; many different degrees of fusion can be observed in the same pinna (Fig. 3I). The basal pinna or pinnule is the most extensive and most complicated of the sequence. Pinnae are more or less deltoid. Pinnules have a very variable morphology from linear to spatulate to flabellate and have a lobulated margin.

Interpretation. The disposition and fusion pattern observed in the specimens from Bernissart are typical of *Ruffordia* figured and described from the English Wealden (Seward, 1894; Watson, 1969) and Las Hoyas (Diéguez and Meléndez, 2000), although pinnule morphology is especially variable in the sample. *Ruffordia goeppertii* generally shows extremely variable pinnule morphology (Seward, 1894); however, the architecture of the pinnae is constant. This species is frequently confused with *Onychiopsis psilotoides* (C.Stokes et Webb) Ward, and the differences between both species will be discussed in the *Onychiopsis psilotoides* section. Other similar taxa are some *Sphenopteris* Sternb. species with elongated pinnules such as *Sphenopteris fontanei* Seward (Seward, 1894), however, the pinnules are smaller and more compact in the latter species than in the specimens from Bernissart.

Remarks. This species was previously identified by Seward (1900b) in the Bernissart flora. Some specimens that had been misidentified as *Onychiopsis psilotoides* have been included in *Ruffordia goeppertii* in the present study.

Ecology. The variability in the pinnule morphologies has been considered to be an adaptation that permits the growth of this fern in a great variety of habitats, including semiarid and wet environments (Mohr et al., 2015).

Order Cyatheaales

Family Dicksoniaceae

Genus **Onychiopsis** Yokoyama, 1890

Onychiopsis psilotoides (C.Stokes et Webb) Ward, 1905

Figs. 5A and B

- 1824 *Hymenopteris psilotoides* C.Stokes et Webb, p.424, pl. XLVI, fig.7. [Basionym]
 1828 *Sphenopteris mantelli* Brongn., p.170, pl. XLV, figs.3–7.
 1894 *Onychiopsis mantelli* (Brongn.) Seward, p.41, pl. II, fig. 1, pl. III, figs. 1–4, text-figs.4–6.

1900 *Onychiopsis mantelli* (Brongn.) Seward, p. 15, pl. I, figs. 17–19, pl. II, figs. 20–21.

1905 *Onychiopsis psilotoides* (C.Stokes et Webb) Ward n. comb. Ward, p.155.

1986 *Tanydorus psilotoides* (C.Stokes et Webb) n. comb. Skog, p.1458, figs. 1–23.

1990 *Onychiopsis psilotoides* (C.Stokes et Webb) Ward, p. 49, pl. I–VI, fig. 2–3.

Material examined. 156 specimens.

Description. Specimens consist of ultimate and penultimate pinnae and attached pinnules. They measure 0.2 cm up to 6.1 cm long. The organisation of the penultimate pinna has been observed on 6 specimens only. They alternately bear up to three ultimate pinnae that measure up to 4.2 cm long. Ultimate pinnae are inserted with an acute angle of 10–30° on the penultimate axes. They measure up to 1.3 cm when attached, but isolated ones have been observed measuring up to 6.1 cm. Pinnules are inserted in subopposite disposition (Fig. 5A–B). When well spread in the sediment, they present a more or less ovate form. However, in most cases, they are encountered folded on themselves, taking a more fascicular shape. Pinnules are relatively elongated, measuring 0.1–0.6 cm long and 0.1–0.2 cm wide. Their margin varies from crenulated to serrate in some rare cases. Venation was impossible to determine with precision.

Interpretation. *Ruffordia goeppertii* and *Onychiopsis psilotoides*, when preserved as charcoal, can be very similar and are frequently confused with each other. From the material described and figured by Seward (1894) and Friis and Pedersen (1990), *Onychiopsis psilotoides*, in contrast to *Ruffordia goeppertii*, shows an anadromous disposition of pinnae and pinnules, which are not decurrent, the most basal pinnae and pinnules are smaller and less complex than the next, and has more pinnules per pinna. The 156 specimens here identified as *Onychiopsis psilotoides*, although very fragmentary, show many non decurrent pinnules per pinna. Additionally, larger specimens show the anadromous disposition typical of *Onychiopsis psilotoides*.

Remarks. This material was assigned to *Onychiopsis mantelli* Brongn. by Seward (Seward, 1900b), which has been recognized as a younger synonym of *Onychiopsis psilotoides* (Ward et al., 1905). Some specimens identified by Seward as this species have been here identified as fragments of penultimate and ultimate pinnae of *Ruffordia goeppertii*.

Ecology. *Onychiopsis psilotoides* has been suggested to live in high-stress environments due to the coriaceous nature of the pinnules as well as the protected fertile bodies (Friis and Pedersen, 1990).

Family Incertae sedis

Genus **Coniopteris** Brong

Coniopteris sp.

Figs. 5C–L

1900 *Sphenopteris delicatissima* Schenk. Seward, p. 23, pl. III, fig. 49

Material examined. 27 specimens.

Description. Frond at least twice pinnate. The axis of the penultimate pinnae measures up to 0.1 cm wide and up to 3.0 cm long. Ultimate pinnae are alternately inserted at an angle of 70°–75°. Some ultimate pinnae bear sphenopteroid pinnules that are inserted in subopposite disposition and become alternate towards the apex (Fig. 5D, H, and J). Basalmost pinnules have two to three lobes, are inserted in a catadromous position, and measure around 0.12 by 0.1 cm (Fig. 5H). Pinnules become more circular to reniform towards the apex, measuring 0.06–0.09 cm long and 0.06–0.08 cm wide (Fig. 5D). Venation is palmate, typical of sphenopteroid

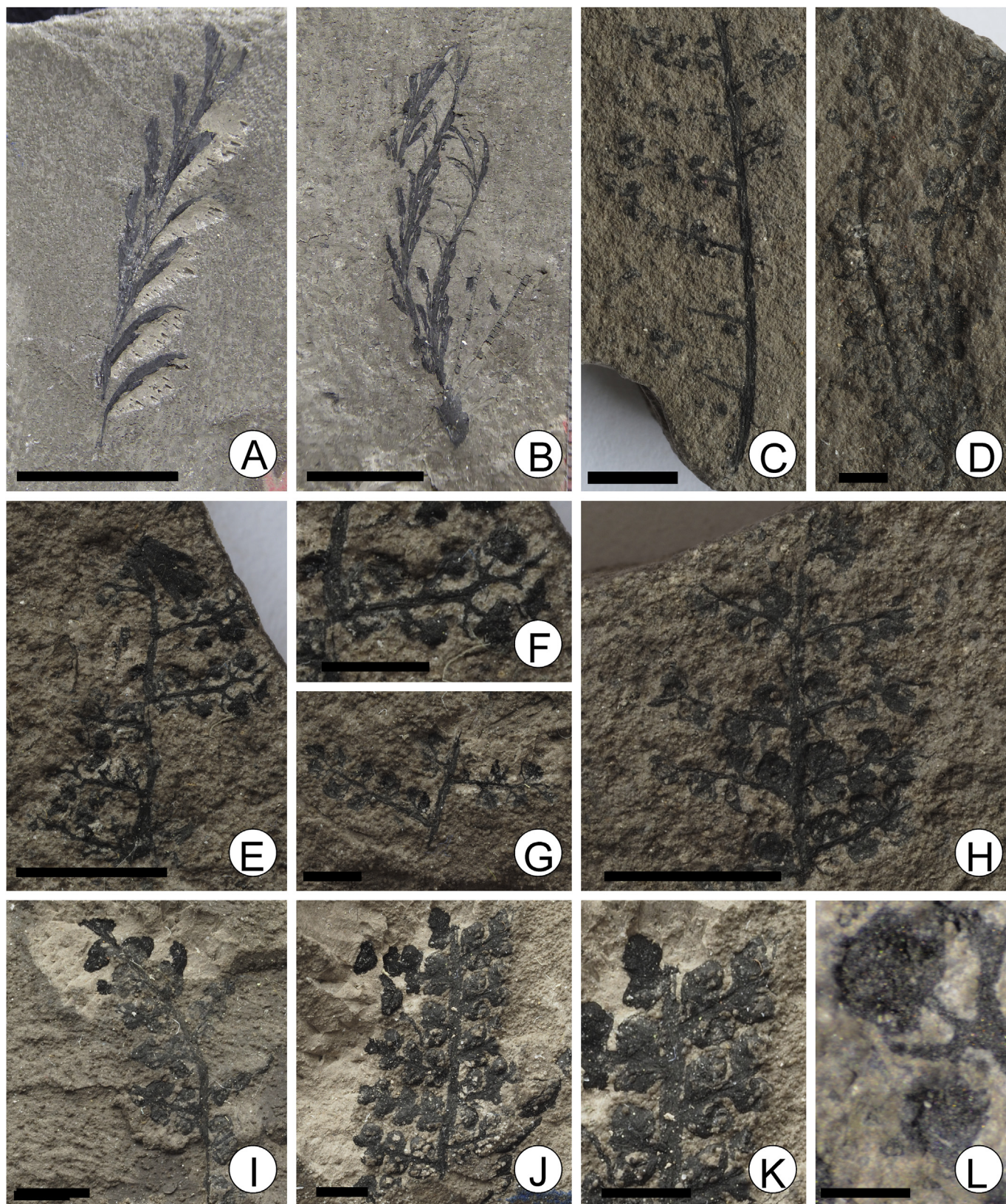


Fig. 5. Photographs of specimens. A-B, *Onychiopsis psilotoides*, IRSNB b 7772, IRSNB b 7850, scale bars = 1 cm. C-L, *Coniopteris* sp. fertile pinnae with sterile and fertile pinnules. C, moderately preserved fertile specimen, IRSNB b 7853, scale bar = 0.5 cm. D, specimen showing both fertile and vegetative leaves, IRSNB b 7855, scale bar = 0.2 cm. E, fertile specimen, IRSNB b 7851, scale bar = 0.5 cm. F, detail of specimen fig 6E, scale bar = 0.2 cm. G, fertile specimen, IRSNB b 7854, scale bar = 0.2 cm. H, specimen showing a combination of both fertile and vegetative pinnules, IRSNB b 7856, scale bar = 0.5 cm. I-K, vegetative specimens, scale bars = 0.2 cm. I, IRSNB b 7857. J, IRSNB b 7852. K, detail of specimen Fig. 5J. L, detail of a sorus of specimen Fig. 5E, scale bar = 1 mm.

pinnules. Other ultimate pinnae alternately bear stalked sori with a pedicelled indusium. The first sorus is inserted in a catadromous position (Fig. 5C, E, F, G and L). Though easy to identify, sori are challenging to describe in detail due to the bad preservation of the material. They appear to be either borne singly or in pairs. When borne singly, the stalk measures up to 1 mm in length (Fig. 5E and F). When borne in pairs, the stalk is complex and consists of a small axis that dichotomizes after 0.2–0.5 mm, giving rise to two up to 1 mm long axes bearing the sori (Fig. 5E and L). The sori are semi-circular to reniform in outline. They are 1–1.5 mm wide. Clear sporangia have not been observed.

Interpretation. The shape of the sori and their architecture is strongly reminiscent of the Dicksoniaceae or Thyrsopteridaceae families. Brongniart (1849) proposed genus *Coniopteris* as a morphogenus for pinnules with similar morphology to *Sphenopteris* and Dicksoniaceae, presenting a short petiolule, and lobed and dentate margins that become reduced and slightly pinnatifid. The genus *Coniopteris* was later revised by Harris (1961), where it was included in the Dicksoniaceae (at the time the family included Dicksoniaceae and Thyrsopteridaceae). The fertile structures here described are very similar to *Coniopteris margaretae* Harris described by Harris (1961), which present the same disposition and sori morphology as the fertile specimens assigned to *Coniopteris* from Bernissart. However, the latter species is larger (especially pinnae length). On the other hand, the specimens preserving sterile pinnules are similar to the species *Coniopteris bella* Harris based on the pinnule morphology described and figured by Harris (1961). Although sterile and fertile pinnules can be assigned to two distinct species, and anatomical connection between the two distinct morphologies has not been observed, all specimens with *Coniopteris*-like morphology recovered from Bernissart have been described together, as they probably belong to different stages of maturity of the fertile pinnae of the same species.

Remarks. Seward (1900) identified these specimens as *Sphenopteris delicatissima* Schenk, probably based on the sphenopteroid pinnules. He included all specimens with a *Coniopteris*-like morphology in *Sphenopteris delicatissima*, perhaps due to the bad preservation and small size of the specimens, which makes them complicated to interpret.

Family *Incertae sedis*

Genus *Korallipteris* Vera and Passalia 2012

Korallipteris sp.

Fig. 3G–H

Material examined. 137 specimens.

Description. Very incomplete specimens, these remains range from 0.3 up to 3.5 cm in length. They all consist of ultimate order pinnae. Their rachises measure up to 2.3 cm in length and approximately 0.5 mm in width. They bear small pinnules in alternate position (Fig. 3G–H). Pinnules are more or less ovate and characterized by a rounded apex. Most pinnules show a slight curvature toward the base. The lamina is fused to the axis and decurrent on the latter (Fig. 3G). They range from 0.1 to 0.3 cm in length and from 0.05 to 0.1 cm in width. Towards the apex of the pinna, pinnules are fused and form a small wider apical pinnule measuring up to 0.3 cm in length and 0.1 cm in width. Venation is, in most cases, challenging to observe. When observed, the mid-vein forms an acute angle with the rachis and is visible throughout the whole lamina (Fig. 3H). Secondary veins are simple and dichotomize only once. The dichotomy occurs close to the main vein.

Interpretation. As the remains here studied present a *Gleichenia*-like morphology but lack diagnostic characteristics to permit their classification at the family level, they are identified as the

morphogenus *Korallipteris*, proposed by (Vera and Passalia, 2012) to solve part of the nomenclatural problems of *Gleichenites* Goepfert. **Remarks.** These remains were previously identified by Seward (1900b) as *Leckenbya valdensis*, which was later included in *Gleichenites nordenskiöldii* (Heer) Seward by Harris (1981). However, Seward (1900b) did not describe these specimens separately from *Cladophlebis* specimens. The main difference is that *Korallipteris* sp. pinnules are decurrent and show a mid-vein that is visible throughout the whole length of the lamina. In contrast, in *Cladophlebis* the mid-vein fades towards the apex of the pinnule, and pinnules are not decurrent and are inserted at a wider angle.

Ecology. Extant Gleicheniaceae live in damp soil in sunny places. However, most Cretaceous Gleicheniaceae are preserved as fusain, as is the case in Bernissart, suggesting they inhabited upland areas subject to fire (Van Konijnenburg-van Cittert, 2002). These Cretaceous representatives of the family have been suggested to be a significant component of fern “savannahs” (Skog and Dilcher, 1994) and early successional vegetation (Crabtree, 1988)

Family *Incertae sedis*

Genus *Weichselia* Stielher, 1857

Weichselia reticulata (C.Stokes et Webb) Fontaine emend. Alvin 1971

Fig. 3C–D

1824 *Pecopteris reticulata* C. Stokes et Webb, pl. XLVI, fig. 5, pl. XLVII, fig. 3. [Basionym]

1857 *Weichselia ludovicae* Stiehler, p. 73–75, pls. XII, XIII.

1883 *Lonchopteris virginensis* Fontaine, p. 53–54, pl. XXVIII, figs. 1, 2; pl XXX, figs. 1–4.

1894 *Weichselia mantelli* Seward, p. 116, pl. X, fig. 3, text-fig 12, 13.

1900b *Weichselia mantelli* (Brongn.) Seward, p. 20, pl. I, figs. 3–16; pl. III, figs. 41, 42, 47, 56.

1900b *Conites minuta* Seward, p. 28, pl. IV, figs. 60–62, 64.

1914 *Weichselia peruviana* (Neumann) Zeiller, p. 654, pl. II, fig. 6–13, text-fig, D1, D2, E.

1953 *Weichselia reticulata* (C.Stokes et Webb) Daber, p. 407, pls. II–IV, Abbs. 2, 3.

1953 *Stiehleria similidae* (Stiehler) Daber, p. 410, pls. V–X, Abb. 4.

1968 *Weichselia reticulata* (Stiehler) Daber, p. 78, pls. 1–3, text-figs. 1, 2.

1971 *Weichselia reticulata* (C.Stokes et Webb) Fontaine in Ward emend. Alvin, p. 5, figs. 1–5, pls. I–IX.

Material examined. More than 2700 specimens.

Description. The specimens range from 0.1 up to 13.6 cm long and consist in fragments of the rachis, pinnae, as well as isolated pinnules. Rachis diameter ranges from 0.13 to 3.3 cm wide. Pinnae are borne in opposite to subopposite position basally and are alternate distally (Fig. 3C). They are inserted at 0.2–1 cm from each other and form an angle of 50°–90° with the rachis. Pinnules are inserted in “butterfly” position, hiding characteristics of the axis of the pinna distally (Fig. 3C). The first pinnule is always inserted in a catadromous position. Pinnules are thick, with a slightly revolute margin, and lacking petiolules. They are rectangular with a rounded apex. Their general morphology becomes triangular towards the apex, and they are inserted adjacent to each other. They measure from 0.05 to 0.7 cm long and 0.05 to 0.3 cm wide. Venation is simple reticulate with 2–4 vein meshes (Fig. 3D).

Interpretation. The organization of the fronds associated to the reticulate venation of the pinnules undoubtedly validate the identification of the material as belonging to the species *Weichselia reticulata*. The pinnules have a similar morphology to that observed in the Matoniaceae indet. specimens mentioned previously. However, in *Weichselia reticulata* pinnules are more elongated, larger,

and inserted in opposite positions at the base of the pinna, rather than alternate, as it happens in the Matoniaceae indet. specimens. Additionally, the reticulate venation separates these specimens from *Cladophlebis*, where the venation is open.

Remarks. These remains have been identified as *Weichselia mantelli* Brongnart by Seward (1900b). This species has been recognized as a younger synonym of *Weichselia reticulata* (Ward, 1899). Due to similarities in frond architecture and spore morphology, this plant is generally placed within or close to the Matoniaceae (e.g. Alvin, 1971). Its affinities are, however, still a matter of debate (e.g. Silantjeva and Krassilov, 2006; but see Blanco-Moreno et al., 2020). As the soral clusters have not been found in anatomical connection with the rest of the plant (Alvin, 1971; Diez et al., 2005; Silantjeva and Krassilov, 2006; Sender et al., 2015) and the architectural similarities could be convergent, in this case, we have preferred to maintain it as *incertae sedis*.

Ecology. The butterfly disposition of the pinnules, together with other anatomical traits such as the resistant cuticle, sunken stomata, and thick sclerotic outer layer of the axes, have been previously suggested to be xerophytic (Watson and Alvin, 1996). This has been interpreted as indicative that *Weichselia reticulata* was adapted to extreme drought conditions. Its presence in subaqueous depositional environments would be due to transport from its natural habitat via flooding (Alvin, 1974). Other authors interpret these traits as indicative of a mangrove-like vegetation (Silantjeva and Krassilov, 2006).

Division Spermatophyta

Class Coniferophyta *incertae sedis*

Fig. 6B–I

Material examined. 5 seeds, 1 cone, 1 cone bract, 3 stem fragments. **Description.** A total of eight specimens of conifer material have been recovered from Bernissart. They mainly consist of fertile structures and include three stem fragments. The stems are straight, unbranched, and covered by leaf scars, which are rhomboidal to round in morphology (Fig. 6I), and measure 4–6 cm in length and 0.5–1 cm wide. All specimens are preserved as impressions but present small fragments of charred material.

The cone measures 2.7 by 1.3 cm. It is preserved as an impression and consists of 6 rows of bracts that are rhomboidal and overlap over each other (Fig. 6E). The dispersed bract is preserved as a charred compression and is larger (0.7 cm); it is rhomboidal in shape and has no visible ornamentation (Fig. 6F).

The seed material consists of four specimens. Three of them are elongated (Fig. 6C and G–H), and measure 0.5–0.7 by 1–1.5 cm. The other two are rounded (Fig. 6B and D) and measure 0.5 and 0.7 cm in diameter. They are all charred, and the preservation does not permit the observation of ornamentation. Detailed morphology is not visible due to bad preservation.

Remarks. Seward (1900) identified the stem material as *Pinites* sp. However, we have maintained it as *incertae sedis* due to the lack of information. For the diversity and taphonomy analysis, we have used *Pinites* sp. to clearly indicate we refer to the stems and avoid confusion with the seed specimens assigned to Coniferophyta *incertae sedis*. More work must be done on the identification of the conifer material, which has proved impossible with the techniques available to us at this moment.

Incertae sedis

Genus aff. *Taeniopteris* Brongn., 1828

Fig. 6A

Material examined. 2 specimens.

Description. Fragments of leaves, measuring at least 6.3 cm long and 0.7 cm wide. Linear, with entire margin. Patent, thick mid-vein. Secondary venation not preserved.

Interpretation. The material is not well preserved and is fragmented. Base and apex morphology, as well as venation characters cannot be observed in any of the specimens available and no cuticle is preserved. *Taeniopteris* is widely used for sterile leaves with entire margins that belonged to Marattiales or Cycadophyta (Cycadales and Bennettiales), this assignation is used when the remains cannot be assigned to a natural group (Van-Konijnenburg-Van Cittert et al., 2017), as it occurs in this case.

Remarks. Seward (1900b) assigned these two specimens to aff. *Taeniopteris* and in this work, the assignation is maintained. The lack of informative characters makes it impossible to classify this material further. These specimens are referred to as *Taeniopteris* for the diversity and taphonomy analyses.

Incertae sedis aquatic plant

Fig. 7

Material examined. 36 specimens.

Description. Specimens are incomplete and measure 0.5–10 cm. They consist of slender (less than 0.5 mm wide), dichotomizing axes preserved as impressions, or whitish compressions (Fig. 7). All axes have an equivalent width. The most complete specimen does not present a clear main axis, and numerous axes emerge from the same area at the base and subsequently dichotomize at least three times (Fig. 7).

Interpretation. Seward (1900b) assigned remains of possible algae to the morphogenus *Algites* established by Seward (1894) for fossil algae where taxonomic affinities cannot be ascertained. It is undoubtedly a dustbin genus with little, if any, taxonomic value. The material here described clearly differs from the two species described as *Algites* sp. by Seward (1894) in the English Weald.

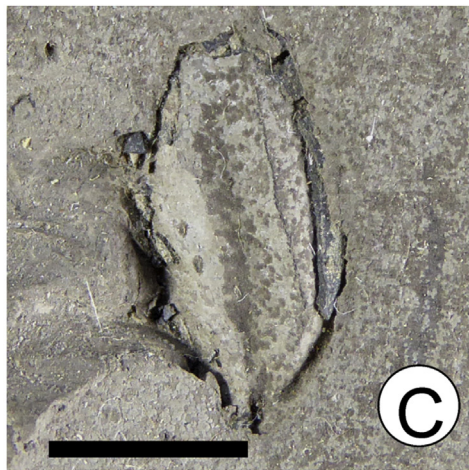
Noncalcareous and singularly freshwater algal remains are rarely encountered in the fossil record. Often simple in organization, their identification is made difficult by the many convergences existing within the different groups but also by the lack of preservation of several key features (particularly the reproductive ones). As far as we know, there is no other mention of freshwater macrophyte *Algites* in the Lower Cretaceous. Although we can consider these remains as aquatic, the relatively lousy preservation and their simple organization prevents us from discussing them in detail and would make any determination little more than a tentative wishful identification.

Remarks. The specimens figured by Seward (1900b) do not show much detail and were not identified in the collection. These specimens are identified as “algae” in the diversity and taphonomy analyses.

4.2. Species richness and relative abundance

The species richness for the total sample (S) is 12. Additionally, our results show a reasonably low Simpson's diversity index ($1-D = 0.43$), due to the high abundance of *Weichselia reticulata*, which accounts for 74% of the remains in the collection (Fig. 8). If we study the relative abundance of the rest of the taxa present, without *Weichselia reticulata*, *Phlebopteris dunkeri* accounts for 48%, *Onychiopsis psilotoides* for 16% and *Korallipteris* sp. for 14%. *Cladophlebis* sp. is slightly less abundant, 11% of the remains, and the rest of the elements of the flora are anecdotic (0.2%–4%).

Lithofacies 1 and 2 have a very similar number of specimens, 51% of the sample is preserved in lithofacies 1, while 49% is present in lithofacies 2. However, lithofacies 2 shows a higher species richness than lithofacies 1 ($S = 11$ vs $S = 9$). “Algae” have only been found in lithofacies 1, and Matoniaceae indet., *Pinites* and *Taeniopteris* were only collected from lithofacies 2 (Fig. 8). Similarly, to



the species richness, Simpson's diversity index is also higher for lithofacies 2 (1-D = 0.73 vs 1-D = 0.65). The difference in this index between both lithofacies indicates differences in the relative abundance of remains of each taxon (Fig. 8). Both are dominated by *Weichselia reticulata*, but the relative abundance of this species is higher for lithofacies 1, 53% vs 40% in lithofacies 2. *Weichselia reticulata* excluded, the abundance of *Phlebopteris dunkeri* is very similar in both lithofacies (51% in lithofacies 1, and 48% in lithofacies 2). The same happens with *Cladophlebis* sp., *Korallipteris* sp. and *Coniopteris* sp. However, the abundance of *Onychiopsis psilotoides* is a key difference in the composition of the flora for both lithofacies, it accounts for 21% in lithofacies 2, and only for 10% in lithofacies 1.

Focusing on the individual taxa and their presence on each lithofacies, only four taxa are more abundant in lithofacies 1 than lithofacies 2: "algae" (100% in lithofacies 1), *Ruffordia goeppertii* (72%), *Weichselia reticulata* (58%), and *Hausmannia dichotoma* (54%). The rest of the taxa are more abundant in lithofacies 2, *Onychiopsis psilotoides* is considerably so with 72% of the total remains. In comparison, the other taxa are only slightly more abundant in lithofacies 2 (59%–54% of the remains) (Table 1).

4.3. Taphonomy

4.3.1. Preservation of remains

The preservation of the material recovered corresponds mainly to fusain compressions (96.7% of the total remains). Only 3.2% of the remains are preserved as impressions, and 0.1% as iron oxides. For all taxa except *Ruffordia*, Matoniaceae indet., *Taeniopteris*, and "algae", burnt remains correspond to more than 90% of the remains recovered. Burnt Matoniaceae indet. remains make up for 67% of the remains, in the case of *Ruffordia* for 56% of the remains, and *Taeniopteris* 50%. All "algae" specimens are preserved as white compressions.

4.3.2. Fragment size

The analysis of the fragment size per taxon results in five groups according to their mean (Fig. 9): (1) *Korallipteris* sp. and *Coniopteris* sp. show the smallest mean size; (2) *Phlebopteris dunkeri*, *Weichselia reticulata*, *Cladophlebis* sp. and *Hausmannia dichotoma* also show relatively small sizes; (3) *Onychiopsis* fragments are larger; (4) Matoniaceae indet. and *Ruffordia* present especially large sizes; and finally (5) *Pinites* and *Taeniopteris* show the largest mean size. Most specimens of *Ruffordia goeppertii* and *Pinites* are not complete, so even larger sizes would be expected for these taxa in the site. On the other hand the variance of the fragment size can be separated into 5 groups: (1) *Cladophlebis*, *Korallipteris* sp., *Coniopteris* sp. and *Hausmannia dichotoma* have the smallest variance; (2) *Phlebopteris*, *Onychiopsis*, and *Pinites* show a larger variance; (3) the size of *Weichselia* fragments is more variable; (4) *Ruffordia* and *Taeniopteris* show a high variance for fragment size; and finally (5) Matoniaceae indet. has the most significant variance of the sample. "Algae" specimens were not included in this analysis, as they are always found incomplete.

The distribution of fragment size for the two lithofacies is significantly different (sig = 0.02 for Student t-test, Fig. 9), however, most taxa show significantly similar size distributions in both sediments except for *Weichselia reticulata* and *Onychiopsis psilotoides*. Mean size and variance are both larger for lithofacies 1. The mean and median size is larger in lithofacies 1 for most taxa (Table 1), except for *Onychiopsis psilotoides* and *Hausmannia*

dichotoma. Similarly, variance and standard deviation values are higher in lithofacies 1 for all taxa except for *Onychiopsis psilotoides*.

4.3.3. Plant associations

Plant remains of different taxa are found in association in 104 hand specimens. The associations are more frequently found in lithofacies 2 and are also more diverse. The specimens found in association for each taxon could be due to random distribution in lithofacies 2 (Kruskall-Wallis test Sig. > 0.05), however, this is not the case in lithofacies 1 (Kruskall-Wallis test Sig. < 0.05). There are 24 different combinations in the association of taxa (Table A1). The most abundant association is between *Phlebopteris dunkeri* and *Weichselia reticulata*, and it is equally present in both lithofacies (50% on each). *Pinites*, Matoniaceae indet., and *Taeniopteris* have not been found in association with any other taxon.

Hausmannia dichotoma and "algae" are found in association with other taxa only in lithofacies 1. *Hausmannia dichotoma* is associated only with *Weichselia reticulata*, whereas "algae" are found with the latter and *Ruffordia goeppertii* (the three taxa together or separately). On the other hand, two associations have been recorded from lithofacies 2 only: *Onychiopsis psilotoides* with *Coniopteris* sp., and the first with *Cladophlebis* sp. No associations have been observed between *Coniopteris* sp., and *Cladophlebis* sp. or *Korallipteris* sp. Additionally, *Ruffordia goeppertii*, is only present with *Weichselia reticulata*, *Phlebopteris dunkeri*, and "algae". The rest of the taxa can be found in association with others in both lithofacies (Fig. 10).

5. Discussion

5.1. Relative abundance and size differences

For each taxon, the remains relative abundance is generally interpreted as the relative abundance of the plant in the community to which it belonged. The autecology (especially organ shedding behaviours) and size of the plant, together with the taphonomical processes it has undergone, may, however, produce a bias in the production and preservation of fragments and lead to erroneous interpretations (Barral et al., 2016). Therefore, the taphonomy of each taxon, together with the inferred autecology and size of the plant, must be carefully studied and included in the reconstruction of the vegetation.

For the ferns, the number of fragments was probably not affected by their autecology, as ferns generally do not shed their leaves naturally; they are abscised traumatically (Martín-Closas and Gomez, 2004). In this case, the traumatic factor was fire, as most remains are burnt. On the other hand, plant size could be significant, especially in the case of the outstanding abundance of *Weichselia reticulata*. This plant was much larger than the other fern taxa, and one single frond of *Weichselia reticulata* could have produced around 14,500 fragments of the mean size of the *Weichselia* fragments here analyzed (based on the inferred size of the frond by Blanco-Moreno et al., 2019). From a taphonomic perspective, remains are charred in most cases, permitting increased preservation, as they waterlog faster than uncharred remains (Nichols et al., 2000). It could lead to an underestimation of the presence of taxa that were not so frequently burnt, such as *Ruffordia*. For these reasons, in the interpretation of the palaeovegetation in this work, we do not address taxonomic dominance and only establish a zonation of vegetation based on the depiction of the distance from

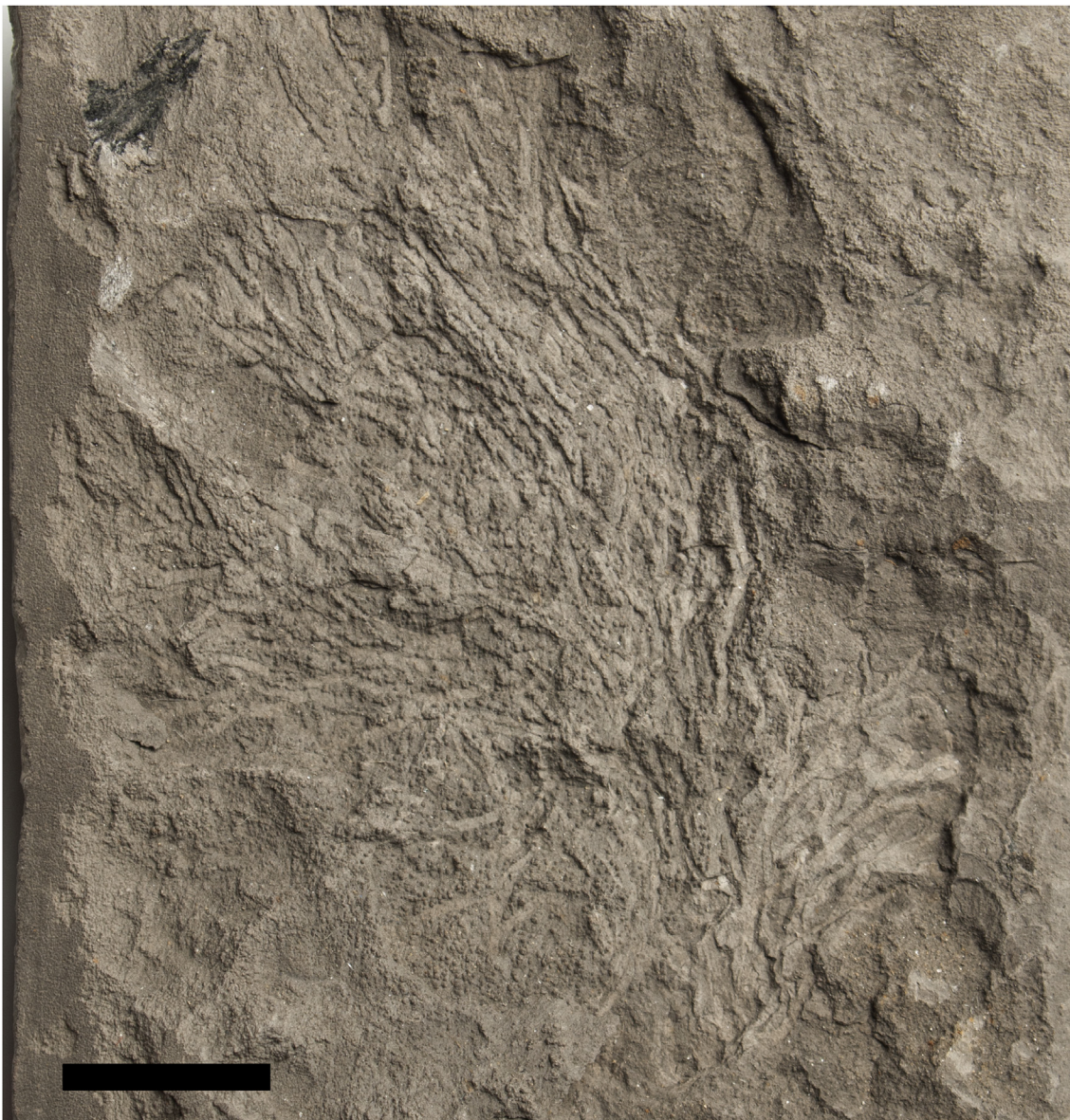


Fig. 7. Photograph of a specimen of Incertae sedis aquatic plant. IRSNB b 7840, scale bar = 0.5 cm.

the depositional site of each taxon by their relative abundance combined with fragment size.

The differences observed in the size distribution of the fragments per taxon have a taphonomical component that is also affected by taxonomy. From a necrobiotic point of view, burnt remains are generally smaller than impressions when remains from the same taxon are analyzed (Blanco-Moreno et al., 2017). Furthermore, in this study, we observe size differences between taxa with the same preservation and similar sizes in the two lithofacies for most taxa, suggesting fragmentation when burning depends on the plants' anatomy and architecture. For example, the similarity in fragment size distribution of plants with similar secondary pinnae architecture such as *Cladophlebis*, *Phlebopteris* and *Weichselia* could be due to similar fragmentation. When the fossil record is analysed, a pattern in the fragmentation of the taxa can be observed: *Ruffordia* is frequently found as large fragments in the fossil record (e.g. Diéguez and Meléndez, 2000; Sender et al., 2004; Mohr et al., 2015), *Onychiopsis* seems to fragment into ultimate pinnae, and generally only isolated pinnules of *Hausmannia* have

been recovered (e.g. Richter 1906; Cantrill, 1995). Extant pines fragment into small twigs like the ones observed in *Pinites* and the large and coriaceous leaves of *Taeniopteris* would not have fragmented easily. Differences in the degree of articulation and completeness of the remains could also be related to the biostratinomic process if fragmentation occurred during the transport of the remains (i.e. Ferguson 1985). However, Nichols et al. (2000) observed that charred remains do not suffer much attrition (and therefore further disarticulation) during transport in water.

From a biostratinomic point of view, the large differences in mean size and variance for each taxon indicate that there is not a strong homogenizing agent in this site. However, the differences in fragment size observed in the two lithofacies in general, and in *Weichselia* and *Onychiopsis* in particular, indicate different biostratinomic conditions for each one. Size in lithofacies 2 is less variable than lithofacies 1, suggesting transport of the remains that would homogenise the size of the fragments to some extent. The randomness observed in the co-occurrences in lithofacies 2 in contrast with lithofacies 1 also supports a more homogeneous

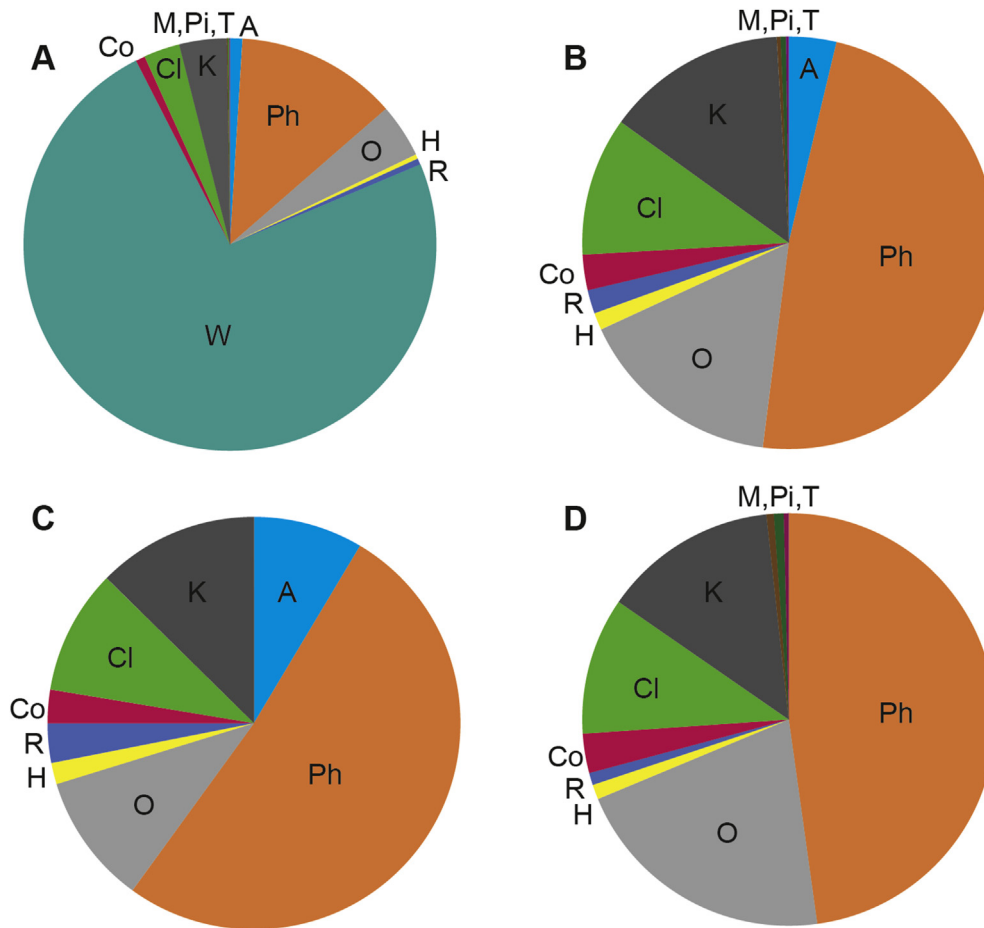


Fig. 8. Proportion of each plant taxon in the locality. A, total sample. B, sample excluding *Weichselia reticulata*. C, lithofacies 1. D, lithofacies 2. Abbreviations: A, "Algae"; Ph, *Phlebopteris*; O, *Onychiopsis*; H, *Hausmannia*; R, *Ruffordia*; W, *Weichselia*; Co, *Coniopteris*; Cl, *Cladophlebis*; K, *Korallipteris*; M, *Matoniaceae* indet.; Pi, *Pinites*; T, *Taeniopteris*.

Table 1
Descriptive statistics separated by lithofacies for all the taxa included in the study. Size statistics in cm.

Taxon	Lithofacies	n	mean	median	variance	St. Dev	max	min
All sample	1	900	1.65	1.30	1.58	1.25638	13.56	0.10
	2	862	1.52	1.21	1.06	1.02882	9.50	0.13
"Algae"	1	36	—	—	—	—	—	—
	2	0	—	—	—	—	—	—
<i>Cl. dunkeri</i>	1	41	1.35	1.10	0.45	0.67	3.30	0.50
	2	56	1.32	1.20	0.42	0.65	3.00	0.30
<i>Hausmannia dichotoma</i>	1	7	1.09	1.00	0.09	0.30	1.70	0.80
	2	6	1.33	1.40	0.08	0.28	1.70	1.00
<i>P. dunkeri</i>	1	216	1.63	1.30	1.11	1.05	7.30	0.30
	2	249	1.45	1.20	0.78	0.88	9.50	0.15
<i>W. reticulata</i>	1	479	1.74	1.39	2.02	1.42	13.56	0.10
	2	342	1.44	1.11	1.03	1.02	6.84	0.13
Matoniaceae indet.	1	0	—	—	—	—	—	—
	2	3	2.93	1.40	7.05	2.66	6.00	1.40
<i>Korallipteris</i> sp.	1	53	1.01	1.00	0.26	0.51	3.50	0.40
	2	71	0.93	0.90	0.21	0.46	2.50	0.30
<i>R. goeppertii</i>	1	13	3.00	3.10	3.77	1.94	7.40	0.63
	2	5	2.51	2.90	1.26	1.12	3.50	1.10
<i>O. psilotoides</i>	1	43	1.63	1.55	0.56	0.75	3.50	0.40
	2	109	2.22	2.10	1.14	1.07	6.08	0.20
<i>Coniopteris</i> sp.	1	11	1.26	1.10	0.37	0.61	2.40	0.50
	2	16	1.13	1.05	0.17	0.42	2.00	0.40
aff. <i>Taeniopteris</i>	1	0	—	—	—	—	—	—
	2	2	5.05	5.05	3.125	1.76777	6.3	3.8
<i>Pinites</i>	1	0	—	—	—	—	—	—
	2	4	5.275	5.55	0.76917	0.87702	6	4

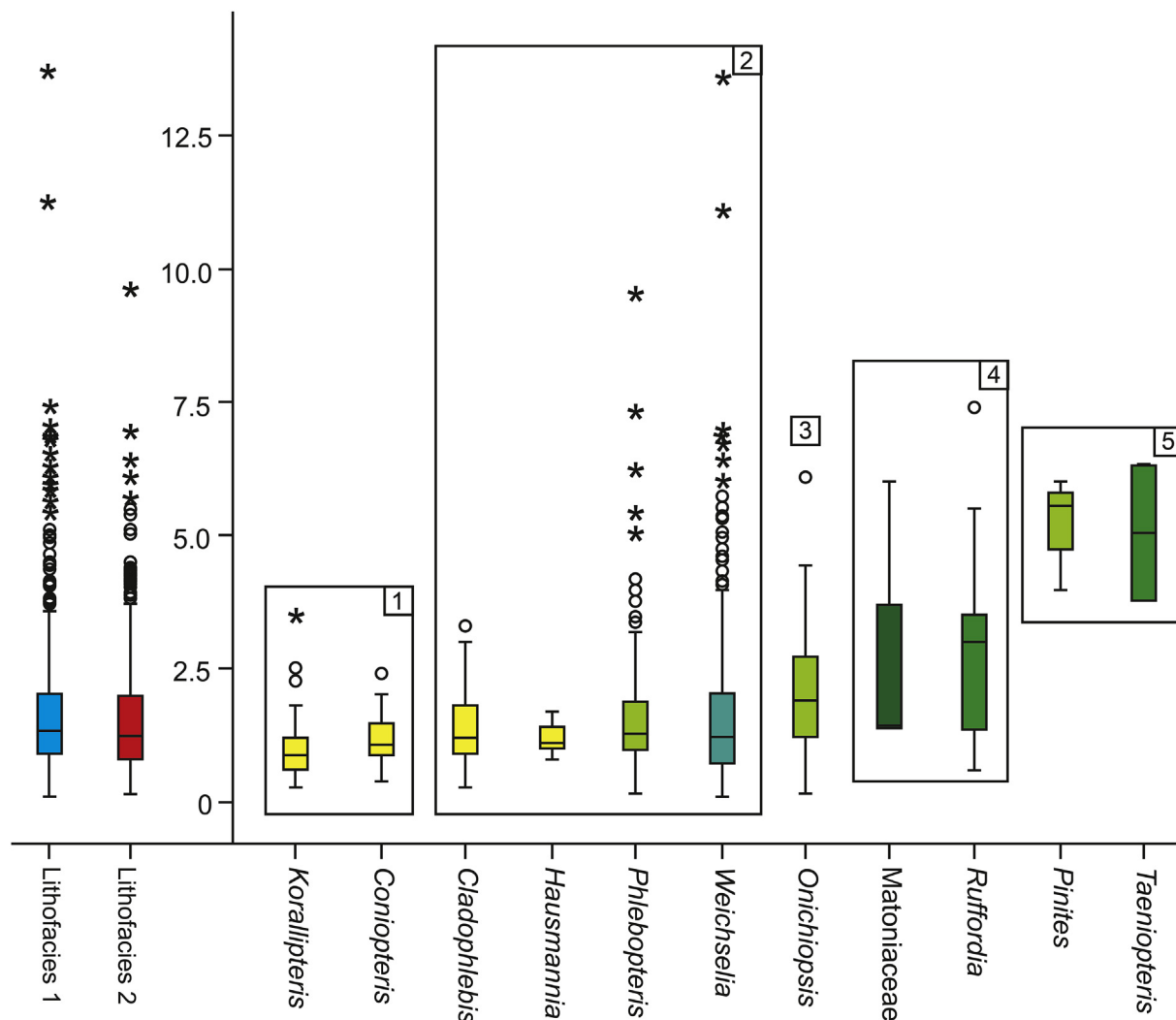


Fig. 9. Fragment length distribution for each lithofacies, and each taxon. Numbered boxes indicate the groups according to the mean. There are 5 variance groups, ordered by ascending variance from lighter to darker colours. Size in cm.

deposition in this lithofacies. Additionally, the largest mean of fragment size recorded belong to taxa exclusively found in lithofacies 2, except for *Ruffordia*, which consists mainly of impressions, which are generally larger than charred remains (Blanco-Moreno et al., 2017). The smaller mean size in lithofacies 2 in contrast to lithofacies 1 for most of the other taxa could be related to the fact that when charred remains reach a mass of water, the larger the fragment, the longer it takes for it to waterlog. Therefore, it can be transported longer distances (Nichols et al., 2000). Larger fragments would be carried further from the lake during a more turbulent deposition. This suggests lithofacies 1 is associated with a calmer deposition. In contrast, lithofacies 2 is associated with flooding events where there could be a more active size selection by transport and that entail the arrival of plant fragments that were produced at a more considerable distance from the lake as well as those produced at the margin. This is also supported by the presence of “algae” exclusively in lithofacies 1, and the higher species richness observed in lithofacies 2.

5.2. Palaeoecological reconstruction

Based on the taphonomic results, we suggest that all the elements of the flora are parautochthonous or allochthonous, except

for the “algae”, which are autochthonous. All the specimens recovered are fragmented and seem to have undergone some transport. The differences in relative abundance and size distribution of the fragments of each taxon in the two lithologies lead to the interpretation of at least four distinct communities:

- (1) A flora of “algae” submerged in the lake.
- (2) The ferns *Weichselia* and *Phlebopteris* would have lived closest to the lake margin, as they are generally found in association and are very frequent in both lithofacies. *Ruffordia* most probably lived near the margin, too, although it would have been less frequent. All these taxa have a higher mean and variance in fragment size in lithofacies 1, being significantly different in the case of *Weichselia*, and suggesting proximity to the area of production and little transport.
- (3) The rest of the ferns were probably further away and were washed into the lake in greater numbers during flooding events. It is particularly the case of *Hausmannia* and *Ornichiopsis*, where larger mean and variance in the fragment size suggest a limited selection of the fragments in lithofacies 2.
- (4) *Matoniaceae* indet., conifers, and *Taeniopteris* are very scarce elements that only appear in lithofacies 2 and generally

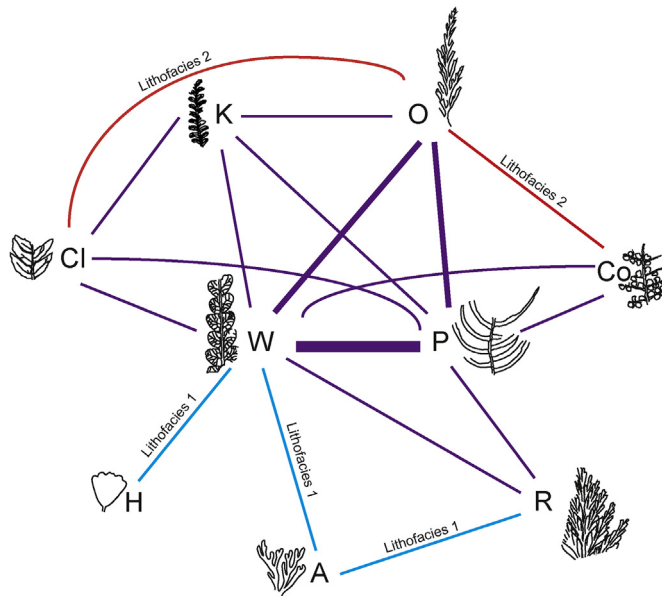


Fig. 10. Diagram of the association between taxa. A, “Algae”; Cl, *Cladophlebis* sp.; Co, *Coniopteris* sp.; H, *Hausmannia* sp.; K, *Korallipteris* sp.; O, *Onychiopsis psilotoides*; P, *Phlebopteris dunkeri*; R, *Ruffordia goeppertii*; W, *Weichselia reticulata*. Lines with no label for the type of lithofacies represent associations present in both lithofacies.

consist of large charred fragments, suggesting these plants lived even further away from the depositional site. Although the results suggest Matoniaceae indet. belongs to this group of plants that were probably living further away from the depositional site, the entire frond that has been recovered indicates it would have been living closer. Its presence might have been punctual in a very restricted moment in time, based on the small number of remains from this plant in the locality. However, due to the small sample, a more detailed analysis is not possible.

The results presented here are consistent with those of the palynological study of the locality (Dejax et al., 2007). Both palynomorphs and macroremains are of continental origin only. Dejax et al. (2007) suggest a zonation where conifers, cycads and bennettitales would be living further away from the lake. It is coherent with the few collected macroremains of these groups (i.e. *Pinites* and *Taeniopteris*), and the fact that they are only found in lithofacies 2. Dejax et al. (2007) further suggest that “algae”, ferns and taxodiaceae inhabited the banks of the lake (Dejax et al., 2007). The macroremain results do not agree so closely with this interpretation, as no taxodiaceae macroremains were found. Furthermore, as discussed earlier, ferns lived at different distances of the lake. Finally, Dejax et al. (2007) concluded on the very likely occurrence of angiosperms in Bernissart based on the rare occurrence of the biorecord superret-croton (less than 1% of the palynomorphs). There is, however, no evidence of the presence of angiosperms in the macroremains. If early angiosperms inhabited disturbed environments (Felid et al., 2004) or freshwater ecosystems (Gomez et al., 2015), macroremains of this group should have been found together with the charred fern remains or with the “algae”. The low proportion of palynomorphs of this group could indicate these plants were not frequent in the flora, or inhabited areas further away from the depositional area. Both possibilities could explain the absence of angiosperm macroremains.

Hautrage (Mons Basin, Belgium) is another Barremian locality in the vicinity of Bernissart. Very different, its depositional environment corresponds to a floodplain with meandering channels

interspersed with marshy and swampy sub-environments (Spagna et al., 2012). More diverse in terms of depositional settings, it provides information ranging from a relatively local scale up to a broader regional level due to the fluvial conditions that record remains transported from the whole drainage system. The Hautrage flora has been studied in detail, using mostly the meso-remains (Gomez et al., 2012; Barral et al., 2016). The reconstruction of the community structure by Barral et al. (2016) for Hautrage is temporal as well as spatial. These authors describe several alternating communities representing different ecological stages. Mature vegetation stages consist mainly of *Frenelopsis* and some specimens of *Brachyphyllum*, with a very low taxonomic diversity. Plant communities in early or medium successional stages, on the other hand, are dominated by *Weichselia reticulata*, *Phlebopteris dunkeri*, *Cladophlebis* sp., *Onychiopsis* and *Gleichenites nordenskoeldi* with a high species richness (Barral et al., 2016). The latter communities conform to open vegetation types. Another approach was undertaken by Gerards et al. (2008), who based its study on the analysis of the burned remains of large logs of wood in the same quarry. This work led to the identification of 7 wood taxa occurring in high energy deposits and interpreted as recording a more distal environment.

When compared to Hautrage, Bernissart records the flora at a more local scale. Nevertheless, the high proportion of burnt remains, together with the absence of taxodiaceae and cheir-lepidaceae remains, suggests the plant community at Bernissart represents open vegetation at a relatively immature ecological stage that was frequently disturbed (burnt).

6. Conclusion

The revision of the Bernissart flora has provided the first updated taxonomical list of the plants since their first description in 1900. Although no new species have been identified, taxonomic assignments have been updated and corrected. The specimens have been described in more detail, increasing considerably the sample studied in comparison with the previous work (Seward, 1900). Moreover, the species diversity and taphonomical analysis provide an idea of the vegetation of the area, where four distinct communities have been identified. This work demonstrates the necessity to update and revise floras that have been published in the past to obtain new information and depict bigger pictures of the floras and vegetation. Although some historical collections do not preserve information on the extraction of the material, some taphonomical and quantitative analyses are possible if the sample is numerous, and there is no suspected bias in the collection. This work will contribute to a more comprehensive study of the Early Cretaceous floras in Europe, where substantial palaeontological evidence has been recovered, some of which must be thoroughly revised, and others must be studied for the first time.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.104814>.