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**New morphological and anatomical data derived from a rare Early
Devonian French flora**

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1. Introduction

The Pragian to Emsian time interval (ca. 410–393 Ma) represent a crucial period in the early history of vascular plants. This interval is characterized by the progressive replacement of a zosterophyll-dominated vegetation by early euphyllophyte groups and lycopsids, i.e., the early and late Eophytic Flora (Capel et al., 2021, 2022a). This transition was synchronously reflected in major changes in plant size and architecture, leading to, by the end of the Middle Devonian, of the development of the tree-habit among cladoxyloids and progymnosperms (Meyer-Berthaud and Decombeix, 2007; Stein et al., 2007, 2020). This increased morphological disparity and size is suggested to have had repercussions on the complexity of plant anatomy (predominantly identified in vascular tissues), whilst also concurrently (or alternatively), being the result of a response to constraints to counter embolism spread (Kenrick and Crane, 1997a; Decombeix et al., 2019; Tomescu, 2021; Bouda et al., 2022). Until recently, this anatomical diversification was mostly thought to be rooted in the Middle Devonian, but recent efforts in describing Early Devonian permineralized floras have revealed an earlier appearance of key innovations, such as secondary growth, as well as an increasingly diverse stelar architecture towards the late Emsian, most significantly in the euphyllophyte clade (e.g., Gerrienne et al., 2011; Hoffman and Tomescu, 2013; Strullu-Derrien et al., 2014; Gerrienne and Gensel, 2016; Pfeiler and Tomescu, 2021; Toledo et al., 2011; Durieux et al., 2021; Filipiak et al., 2022).

Nevertheless, evidence documenting early plant anatomical diversification remains scanty linked to the restricted number of localities that have thus far yielded Pragian–Emsian permineralized material. Most of the currently anatomically known taxa have been identified in assemblages from eastern Laurussia, being one of the best sampled areas. However, even in this region, permineralized floras are rare, and only partially document this anatomical diversification, especially since very few early to middle Emsian assemblages were ever

discovered. For instance, the Ardennes-Rhenish Massif, despite being one of the most profuse regions worldwide for Early Devonian plant macrofossils, has very seldom yielded well-enough preserved permineralized remains (i.e., Fairon-Demaret, 1985; Remy and Hass, 1986; Hass and Remy, 1991; Schultka, 1991; Gerrienne, 1996).

Although the bulk of plant macrofossils sampled in this area originates from the extensive exposures of Early Devonian rocks in Germany and Belgium, several more modest Early Devonian outcrops have been located in the Artois region (northern France). These outcrops belong to the same structural unit as other segments of the Ardennes-Rhenish Massif in the Early Devonian, formerly located along the eastern margin of Laurussia and can further contribute to understanding vegetation changes in this region (Blieck et al., 1988; Scotese et al., 2021). French outcrops have yielded macroplant remains in two distinct localities (Matringhem and Rebreuve), described in details in Danzé-Corsin (1956a,b). Whilst the Rebreuve assemblage was revised by Edwards (2006), and more recently, by Capel et al. (2022b), the Matringhem adpression flora remains to be reassessed, especially since the assemblage also includes permineralized material not originally investigated by Danzé-Corsin (1956a).

In this study, we redescribe the original adpression assemblage from Matringhem Quarry, and document, for the first time, the permineralized material, both collected over a century ago. We further present new freshly retrieved specimens from an adjacent locality (La Grande Pièce Quarry) that have allowed a deeper understanding of this flora. Finally, the taxonomic composition is compared to coeval adpression and permineralized assemblages from eastern Laurussia, and a discussion on the timing of the onset of anatomical diversification in this paleoregion is provided.

2. Geological setting and biostratigraphical framework

The Matringhem outcrops represent the westernmost occurrence of a series of sub-aerially exposed Devonian sections in the historical Artois region (northern France), along the Eifel-Midi Thrust fault system (Capel et al., 2022b, fig. 1b; Fig. 1A). More specifically, outcrops are located to the south of the Autun fault line, where Early Devonian sediments were uplifted and subsequently exposed by the erosion provoked by the Lys River (Delattre, 1969; Delattre et al., 1976; Minguely et al., 2010; Capel et al., 2022b; Fig. 1B).

These outcrops in the northernmost part of the Matringhem-Vincly massif (near Dennebroeucq) belong to the Grès de Pernes Formation (d1; Fig. 1B) dated as late Lochkovian based on the presence of ostracoderms such as *Pteraspis crouchi* and *P. rostrata* (Blieck and Janvier, 1989). This formation is overlain to the south by the Pragian–Emsian ‘Grès et Schistes de Matringhem’ Formation exposed over 3 km from the south of Dennebroeucq to Matringhem (d2-3; Fig. 1B). In this formation, layers dip on average 30° south, although northward dips were at time observed (Leclercq, 1975). However, no evidence of any synclinal or anticlinal axis could be identified, and the massif has therefore been resolved as a monoclinical structure (Delattre et al., 1976; Blieck and Janvier, 1989). The sequence is at least 1500 m thick, although it is probably considerably thicker given that the Early Devonian basement is far more extensive than what the sole outcropping area suggests (Delattre, 1969; Minguely et al., 2010).

The ‘Grès et Schistes de Matringhem’ Formation consists of white, green or red sandstones, sometimes interlayered with mudstones (Leclercq, 1975). Previously studied sections are mostly sterile and the fossils –plant macrofossils, possible *Prototaxites*, palynomorphs (spores and acritarchs), crustaceans (ostracods, branchiopods) and fish remains– that have been described over the years, were never found to occur within the same layers (Corsin, 1945; Defretin, 1950; Leclercq, 1975; Blieck and Janvier, 1989). Given the nature of the fossils identified, the environment of deposition was interpreted by Leclercq

(1975) as lagoonal. It is however very likely, that the intensity of the marine influence has periodically varied throughout the time of deposition according to local eustatic sea-level changes.

Spore assemblages were described by M. StreeL (Liège) in two localities near what is now La Malfiance Quarry (Loc. 4, 5; Fig. 1B) in Leclercq (1975). The age of these assemblages was originally identified as possibly late Pragian or early Emsian. The list of spore taxa has been updated (Table S1) and compared with the spore biozonation scheme of the adjacent Ardennes-Rhenish region of StreeL et al. (1987). The revised list confirms earlier estimations of the age of these localities as latest Pragian–earliest Emsian, i.e., Steemans’s (1989) SU biozone, with the shared presence of *Brochotriletes ? foveolatus* Naumova and *Dictyotriletes subgranifer* McGregor. In the immediate vicinity of these localities (Vincly), Blicck and Janvier (1989) identified fish remains belonging to *Rhinopteraspis dunensis* and likewise suggested a Pragian to early Emsian age, which further supports the age obtained via palynological biostratigraphy.

The monoclinical nature of the massif implies that rocks become increasingly younger southward, although thus far, no reliable biostratigraphical indicators apart from plant macrofossils were found in the southernmost part of the formation to provide a minimum age (Locs. 1, 2, 3; Fig. 1B). Nonetheless, the age of the Devonian basement under the Cretaceous layer has been identified as Eifelian, in a borehole about 5 km south of Matringhem. It confirms that rocks continue becoming progressively younger southward, although it remains unclear how these layers were actually dated (Delattre, 1969; Minguely et al., 2010).

3. Historical background

Gosselet and Dollé (1910) first reported plant fossils in this area at a quarry in Matringhem (Loc. 1, Fig. 1B), where lenses of white sandstones rich in ‘*Psilophyton* debris’ were

discovered. In the following years, field excursions were undertaken in that same locality, and Bertrand (1913) provided a first short description, referring these plant fragments as *Psilophyton princeps* Dawson. Danzé-Corsin (1956a) described more thoroughly the fossil flora, concurrently with the Rebreuve assemblage (Danzé-Corsin 1956b) of similar age, located 30 km ESE from Matringhem. The assemblage was shown to be less diverse (7 species) than its Rebreuve counterpart and more fragmentary, but only the adpression assemblage was described (Danzé-Corsin 1956a). Danzé-Corsin (1956a) did mention the existence of permineralized material but never undertook its study. Overall, since the 1950s, there has been almost no interest for these plant fossils due to a combination of factors: quality of preservation, doubtful identifications, and probably the language barrier.

In the meantime, the geological characterization of the Matringhem Devonian massif led Leclercq (1975) to discover three new localities, yielding plant fossils in various preservation states during extensive field works (Locs. 2, 3, 5; Fig. 1B). Best preserved compressed plant fossils (Leclercq, 1975, Delattre et al., 1976) were found in lenses of clay inside a grey sandstone matrix in the now abandoned ‘La Grande Pièce’ Quarry (Loc. 3; Fig. 1B). The adpression assemblage was briefly described, consisting in *Thursophyton vahlbergium* Kräusel et Weyland, *Taenioocrada decheniana* (Goeppert) Kräusel et Weyland and *Hostinella* sp. Barrande ex Stur (Delattre et al., 1976). The current repository of the plants mentioned by Leclercq (1975) is unknown and the very short descriptions and poor illustrations provided does not allow us to confirm this report. Nonetheless, this locality has been revisited and has yielded both new adpression and permineralized material (see Material and methods section).

The Matringhem Quarry (Loc. 1, Fig. 1B) -which was the first locality to be identified- ceased being exploited, and already Leclercq (1975) confirmed that the original plant-bearing beds were submerged and no longer available for further sampling. Consequently, the assemblage presented here solely originates from the Matringhem Quarry, collected over a

century ago, and partly described by Danzé-Corsin (1956a), and newly-collected material from La Grande Pièce Quarry (Loc. 3; Fig. 1B).

4. Materials and methods

Plant macrofossils from the Matringhem Quarry are preserved as: adpressions *sensu* Shute and Cleal (1987), with often only minute amounts of organic matter remaining; impressions, limonitic permineralizations, and even more rarely as casts. Adpressions are occasionally covered fully or partially, by a pyritic/limonitic coating, although not sufficiently to preserve the original anatomy. Fossils are preserved in light to dark gray argillaceous sandstones easily dissolved in contact with water. Around 100 specimens were originally collected, but only a small proportion were herein useful for taxonomic descriptions due to the high-degree of fragmentation and general quality of preservation. Permineralized axes were found scattered across multiple samples with no evident connection with adpression fossils. Attempts to recover palynomorphs from these rock samples have unfortunately failed.

Fossil content from La Grande Pièce Quarry was collected during two separate field sessions in 2022 and 2023. Plant fossils were discovered among loose blocks, dispersed in the eastern part of the quarry, which represents waste material from the extraction used to partially fill up the quarry after exploitation. Thus, the exact layers from which plant fossils originate could not be located as outcrops are nearly entirely covered by this waste material, in addition to the fact that most of the quarry is now submerged. However, most of the fossil content was found near the position of the level mentioned by Leclercq (1975), and the similar lithological aspect suggests that they do indeed originate from the same layer. Adpression material is usually very fragmented, despite being at times quite abundant, in gray to greenish-yellowish argillaceous sandstones. One slab also contained permineralized material.

Permineralized axes from both Locs. 1 and 3 were extracted from the matrix using triangular steel needles and subsequently embedded in epoxy resin. Specimens were then serially sawed at a 1 mm interval. Selected sections were subsequently mounted on glass slides and surfaces were polished using different abrasive sandpapers (800-600 and 2000 grit for finishing). Finally, polished sections were immersed in a solution of hydrochloric acid (5%) during 30 to 60 min to enhance contrast, rinsed with water and dehydrated with ethanol. Specimens were then photographed using a Zeiss Stemi 2000-C microscope using reflected light.

Non-permineralized plant fossils were prepared through *dégagement* (Fairon-Demaret et al., 1999). They were photographed using a CANON EOS 700D and a macro lens. Plant macrofossils and thin-sections are all housed within the paleontological collections of the University of Lille (France).

5. Adpression flora

5.1. Matringhem Quarry

Taeniocrada sp. White

Plate I, 1–2

Material: USTL 3766, 3767.

Description: Two axes are distinguishable from other specimens of the assemblage by their ribbon-like appearance, smooth surface and centered conspicuous vascular strand trace (Plate I, 1–2, at black arrows). The maximum length of the truncated axes reaches 6.6 cm, with a maximum width of 6 mm. Vascular strand trace attains 0.3 mm in diameter (Plate I, 1). Both

the width of axes and the vascular strand trace are relatively constant throughout the entire length of the specimens. No fertile material nor branching was observed.

Interpretation: These axes fit into the taxonomic concept of *Taenioocrada*, a fossil-taxon for smooth stems, with a centered or meandering vascular strand or vascular strand trace, throughout all the length of the axis. The affinities of this likely polyphyletic taxon are believed to be related to the Rhyniopsida *sensu* Kenrick and Crane (1997b), but see e.g., Capel et al. (2022b) for further comments. These types of axes are particularly common in Early Devonian European localities (e.g., Kräusel and Weyland, 1930; Stockmans, 1940; Croft and Lang, 1942; Cascales-Miñana et al., 2011; Capel et al., 2022b). *Taenioocrada*-like axes were not originally described by Danzé-Corsin (1956a).

Psilophyton burnotense (Gilkinet) Kräusel et Weyland

Plate I, 2–7

1956a *Dawsonites* cf. *arcuatus* Halle Danzé-Corsin, pl. X, figs. 13–13a.

1956a *Psilophyton goldschmidtii* Halle, Danzé-Corsin, pl. X, figs. 1–3.

1930 *Psilophyton goldschmidtii* Halle Kräusel et Weyland.

1913 *Psilophyton princeps* Dawson Bertrand.

Material: USTL 3740, USTL 3749, USTL 3757, USTL 3765, USTL 3766.

Description: Fragmented vegetative axes up to 6.6 cm long and 5.8 mm wide displaying anisotomous to pseudomonopodial types of branching (Plate I, 2–4). One specimen with three successive dichotomies demonstrates that branches are alternately arranged on main axis (Plate I, 2). Daughter branches are consistently ca. 1/3 thinner than the parent axis (Plate I, 2–

4). A conspicuous thickened margin can be noticed all along the length of the axes. Spines have a triangular-shaped base tapering into a subulate tip (Plate I, 3). Spines are 0.6–0.9 mm long and spine bases are 0.5–0.8 mm wide. Surface of axes are covered in spine scars (round to oval) in no specific arrangement (Plate I, 2, 4). No fertile structures were found in connection with vegetative axes but isolated pairs of sporangia were identified and are associated to this type of stems (see interpretation section for justification). Pairs of sporangia apparently pendulous and connected to a truncated stalk (Plate I, 5–7). Individual sporangia are strongly elongated fusiform-shaped (Plate I, 5–7). Torsion of sporangia around each other is clearly noticeable (Plate I, 5, 7). Sporangia are 3.3 – (3.7) – 4.2 mm long ($n = 9$) and 0.5 – (0.7) – 0.9 mm wide ($n = 9$). No unequivocal dehiscence line can be noticed. Number of pairs of sporangia per branching unit unknown due to incompleteness of fertile specimens.

Interpretation: Bertrand (1913) briefly described stems found at Matringhem Quarry and identified them as *Psilophyton princeps*, based on Dawson (1871)'s interpretation of this taxon, later clarified by Hueber and Banks (1967). Nonetheless, in an addendum after the printing of his paper, he acknowledged the similarities with specimens found in Rörägen, Norway newly reported by Nathorst (1913), which would subsequently be described by Halle (1916) as *Psilophyton goldschmidtii*. Kräusel and Weyland (1930) likewise argued that these vegetative remains were probably belonging to *P. goldschmidtii*. and in our opinion, rightfully synonymized these vegetative remains with their material from Germany, which is clearly identical (Kräusel and Weyland, 1930, taf. 14, figs 2–5). Danzé-Corsin (1956a) was apparently unaware of Kräusel and Weyland's mention of Matringhem specimens, but provided a more detailed description and confirmed this identification.

The presence of a thickened margin (alternatively called marginal rim), on spiny axes of an anisotomous branching system, allow us to indeed refer these specimens to *Psilophyton*

burnotense (= *P. goldschmidtii*). This type of vegetative axes has been identified recently in the nearby locality of Rebreuve, France (Capel et al., 2022b), and is commonly found in other localities from the Pragian–Emsian of Eastern Laurussia such as in Belgium (Stockmans, 1940; Gerrienne, 1983), Germany (Kräusel and Weyland, 1930; Schweitzer, 1989), UK (Lang, 1932) and Norway (Schweitzer and Heumann, 1993). However, these stems are almost always found without fertile structures, whether in direct connection or dispersed in the same assemblage. Consequently, the assignment of sole vegetative remains to *Psilophyton* has always been equivocal, especially since the findings of identical stems with laterally-inserted sporangia and exarch protosteles (reminiscent of zosterophylls) in the Early Devonian of Siberia (Zakharova, 1981).

Nevertheless, Schweitzer (1989) found terminal pairs of sporangia connected to stems of *Psilophyton burnotense*, and therefore argued that the Russian material was a different plant to the European one (see Schweitzer (1989) or Capel et al. (2022) for a more detailed review of this confusing history). However, aside from this locality, no fertile remains have ever been found elsewhere. Schweitzer (1989) described individual sporangia as “cigar-shaped”, referring here to their elongated aspect and are 4–5 mm long and 1 mm wide. Whilst the French material is slightly smaller in terms of absolute size, the dimensions in proportion remain identical. This is reflected in the peculiar shape of the sporangia in *P. burnotense*, which is slenderer and less fusiform than other species of *Psilophyton* (see e.g., Gerrienne, 1995, fig. 2). Despite the lack of direct connection, the distinctiveness of the pairs of sporangia identified here (Plate, I, 5–7), is in our opinion sufficient to associate the fertile remains with the vegetative specimens. This would be the first time that fertile remains of *P. burnotense* are discovered outside of the early Emsian Klerf Formation at Willwerath Quarry (Schweitzer, 1989).

cf. *Psilophyton* sp. Dawson, emend. Doran

Plate I, 2–7

1956a *Aphylopteris* cf. *robusta* Dawson, Danzé-Corsin, pl. X, figs. 6–7.

1956a *Rhabdophyton striatus* Danzé-Corsin, Danzé-Corsin, pl. X, figs. 9–10.

Material: USTL 3722, USTL 3733, USTL 3742, USTL 3748, USTL 3756, USTL 3822.

Description: Truncated axes up to 11 cm long and 4.5 mm wide. Branching is variable and can be either anisotomous (Plate I, 8–9), isotomous (Plate I, 9–10) or pseudomonopodial (Plate I, 11). The longest axis (Plate I, 8) epitomizes this variability with the three types of branching occurring on the same specimen. Lateral branches arrangement of the main axis is apparently alternate and planar (Plate I, 8). Surface of axes lightly- (Plate I, 8–11) to strongly longitudinally striated (or ridged) (Plate I, 12–13), although this feature may be partly taphonomical (see interpretation section below). No fertile structures were found in connection with vegetative axes.

Interpretation: Danzé-Corsin (1956a) interpreted the specimens illustrated in Plate I, (9, 11) as *Aphylopteris* cf. *robusta*, described by Stockmans (1940), later renamed *Aphylopteris* sp. by Gerrienne (1993) from the late Pragian–Emsian of Belgium. *Aphylopteris* is a fossil-taxon created to accommodate naked stems with pseudomonopodial branching (Gerrienne, 1993) in contrast to *Hostinella* designated for isotomously branching axes (Banks, 1968). Specimens illustrated in Plate I, (12–13) were designated as different from *A. cf. robusta* due to the stronger ridging of the surface of the stem and Danzé-Corsin (1956a) created a new genus and species: *Rhabdophyton striatus* Danzé-Corsin. However, the creation of a new genus for this

type of stem was clearly unjustifiable. Not only because of the lack of fertile structures and/or distinctive branching pattern, but also as it does not have clear and unambiguous distinctive characters, against the artificial genus *Aphylopteris* which is also striated in e.g., Stockmans (1940).

Despite the lack of fertile remains, the branching pattern is quite reminiscent of a basal euphyllophyte taxon like *Psilophyton*, with main axes pseudomonopodially (anisotomously) (Plate I, 8, 11–13) branched and smaller branching systems (probably more distal) being isotomously branched (Plate I, 9–10). Striae are also a feature known to occur in several species of *Psilophyton* i.e., *P. princeps* Dawson, *P. forbesii* Andrews et al., *P. parvulum* Gerrienne and to a lesser extent *P. dapsile* (Kasper et al. 1984). The degree of striations or ribbing has likewise been noted to be somewhat variable, and sometime even unnoticeable, especially on more distal branches (Schweitzer and Heumman, 1993, Gerrienne, 1997). These longitudinal striae or ridges have been interpreted as either the imprint of longitudinal fiber bundles in the outer cortex (Gensel, 1979, Doran, 1980) or as an artifact of compression (Kasper et al., 1984). Interestingly, the most striated specimen appears to be the one preserved as a partially-compressed cast (Plate I, 12–13). The impression of this axis on the part and counterpart shows that striations can be visible or not (Plate I, 12–13). This also showing in Plate I, 11, where the upper part of the specimen is more striated than the counterpart. Previously reported cases and the variability in striations in these specimens suggests that strong ridging (or lack of it), is at least partly a taphonomic feature.

Therefore, upon re-inspection, we argue here that the specimens attributed to *R. striatus* belong to the same morphospecies as *A. cf. robusta* by Danzé-Corsin (1956a) and belong to a plant similar to *Psilophyton*. However, this material is impossible to refer to a single species due to the lack of distinctive characters and are consequently left as *cf. Psilophyton* sp.

Other undetermined remains and excluded taxa

Danzé-Corsin (1956a) differentiated a longitudinally striated axis from the other axes of the assemblage, and identified it as *Calamophyton* sp. (Plate II, 1). *Calamophyton* is a Middle Devonian taxon for branching systems with fertile appendages connected to a trunk named *Duisbergia*, both belonging to the same pseudosporochnalean cladoxylopsid entity (Leclercq and Andrews, 1960; Giesen and Berry, 2013). The taxonomic assignment of this axis to *Calamophyton* is unfounded as it is uniquely grounded on the presence of striae on the surface, which is not a sufficiently diagnostic feature of *Calamophyton*. This axis could in fact potentially represent a stem of the previously documented cf. *Psilophyton* sp. (Plate I, 8–13), but the lack of branching precludes a more precise identification.

Another type of longitudinally striated axis has been recorded in the assemblage (Plate II, 2). This stem differentiates from other specimens of the assemblage by its larger size (10 mm in width) and by being preserved as a partially-compressed cast (diamond-shaped in transverse view). Danzé-Corsin (1956a) compared this fossil with the *Drepanophycus ? crepinii* described by Stockmans (1940, pl. XIII, fig. 3–4a). In this taxon, the surface of the axis is covered by emergences and/or by fusiform punctae that represents emergence bases. The specimen illustrated (Plate II, 2) does not possess emergences and the striae (or punctae) are far slenderer and elongated. Although the Matringhem specimen seems to possess striae, the preservation state does not allow us to assess with certainty if these are continuous or discontinuous. However, interestingly, our specimen arguably resembles more the cf. *Drepanophycus ? crepinii* illustrated in Stockmans (1940, pl. XIII, fig. 5) which represents a specimen with finer, longer and closely packed longitudinal punctae. It is noteworthy to mention that this is a partially-compressed cast similarly to our specimen, whereas *D. ? crepinii* is based on entirely compressed specimens. A possibility is that taphonomic

differences may explain the distinction between cf. *D. ? crepinii* and *D. ? crepinii*.

Taeniocrada dubia Kräusel et Weyland is another taxon that possesses punctae on its surface (Kräusel and Weyland, 1930; Stockmans, 1940). However, punctae on *T. dubia* are oblong and our specimen lacks median vascular strand trace that characterizes *Taeniocrada*-types fossils. Once again, this may also reflect a taphonomic artefact as the preservation as casts would prevent observing a vascular strand trace. Given the lack of well-preserved material in this case, it would be unwise to assign it to any taxon at this time.

Finally, Danzé-Corsin (1956a) described another type of vegetative axis as *Hostinella* sp. (Pl. X, fig. 8–8a). This specimen consists in a smooth anisotomously branching system (Plate II, 3). This stem differentiates from other *Psilophyton* and *Psilophyton*-like axes previously described from the assemblage, due to (1) a more robust appearance and (2) branching occurring at a wider angle and consistently strongly anisotomous. This type of ramification occurs in axes of *Psilophyton burnotense*, but there are no visible spine or spine scars preserved nor a thickened margin, so this axis is here presumed to represent a different plant. *Hostinella* can virtually refer to any isolated vegetative dichotomously branched smooth stems (Hoeg, 1942). The name has been used for describing sterile late Silurian isotomously-branched sporophytes (e.g., Edwards et al., 2004), to Early–Middle Devonian distal branches of basal euphyllophytes and progymnosperms (Lang, 1926; Matten and Schweitzer, 1982; Prestianni et al., 2012). We herein prefer to exclude those remains from *Hostinella* to not add to further confusion into this “artificial” fossil taxon *sensu* Cleal and Thomas (2021), whilst acknowledging the specimen’s difference with other types of vegetative axes from the assemblage.

5.2. La Grande Pièce Quarry

The adpression fossil assemblage in La Grande Pièce Quarry is poorer in diversity compared to the Matringhem Quarry, as few specimens could be identified given the even higher fragmentation degree of plant remains. However, similarly to Matringhem Quarry, several axes attributed to *Taeniocrada* were noticed among several samples. One large and glabrous axis measuring maximum 10 cm in length and 1 cm in width is herein illustrated (Plate II, 4). A meandering vascular strand trace (1 mm in width) along the length of the axis can likewise be noticed (Plate II, 4 at arrow). No branching nor fertile structures were detected after *dégagement*.

One large branching system was recognized without any fertile structures found in connection or in association (Plate II, 5). The main axis is 13.2 cm long with a maximum axis diameter of 4.7 mm. Main axis and branches are glabrous and taper distally. Four successive dichotomies can be noticed (Plate II, 5 at black and white arrows). Branching is planar and mostly anisotomous. However, the most distal dichotomy is isotomous (Plate II, 5 at white arrow) and is reminiscent of ultimate branchlets seen in several species of *Psilophyton* (e.g. *P. forbesii*; Andrews et al., 1968). Nevertheless, it is not possible to claim with certainty these actually represent the most distal dichotomies as the specimen is incomplete. This specimen surely represents a basal euphyllophyte (Trimerophyta) branching system given its complexity/size, and lack of enations or microphylls that are typical of large lycophytic taxa of this time. The absence of anatomy and fertile structures does not allow to go further into the interpretation. Interestingly however, this axis bears a lot of resemblance with the anisotomous branching system described in the Matringhem Quarry (Plate II, 3) in terms of branching pattern, angle of dichotomy and glabrous aspect of the surface.

Lastly, one spherical structure with a radius of 1.3 mm (Plate II, 6) referable to *Pachytheca* was noticed in a sample where the permineralized material was discovered (see section 6). It is likewise partly permineralized, allowing to distinguish the original structure with for

instance, the radial alignment of tubes interpreted as the cortical region (0.45 mm wide) (Niklas, 1976; Gerrienne, 1990). The central area, which is poorly preserved, is here interpreted as the medullary region, with the notable absence of outward extending tubes (Plate II, 6). Further assignment to a particular species is hindered by its incomplete preservation. *Pachytheca* has been interpreted as a likely alga (although fungal affinities are not excluded), and is a commonly found element in Lower Devonian deposits (Abbott et al., 1998; Gerrienne et al., 1999). It is also noteworthy to mention that this is the first discovery of *Pachytheca* in the Emsian of the Artois region beyond the Lochkovian where it is abundant and extensively documented by Corsin (1945).

6. Permineralized flora

Among transverse polished sections yielding sufficiently well-preserved anatomy, cell walls are recognizable as a darker boundary whilst lumens are translucent, or *vice versa* depending on the amount of time the specimen was immersed into acid and its inherent reaction to it. Coalified material seems either absent or fused with pyrite which hindered the possibility to observe secondary wall thickening patterns in transverse view. All studied specimens are characterized by an unlobed protostele with an exarch maturation of the xylem which together indicates zosterophyll affinities. Three different morphotypes were identified and are herein described below.

Zosterophyllopsida (Taxon I)

Plate III, 1–2

Material: USTL 3749-1; USTL 3817-A.

Occurrence: Matringhem Quarry, Matringhem, Pas-de-Calais, France.

Description: Two specimens possess a terete to sub-terete xylem strand (0.52–0.65 mm of maximum width), in an otherwise slightly elliptically-shaped axis in transverse view (Plate III, 1–2). Tracheid outline is polygonal (5–8 sides). Smaller elements (interpreted as protoxylem cells) are found at the periphery of the stele without any signs of concentration in one specific area. Protoxylem cell diameter ranges between 8 – (13) – 19 μm ($n=8$) and the maximum observed metaxylem cell diameter reaches 64 μm . The cortex and epidermis are not well preserved or completely absent (Plate III, 1–2). However, a layer of one to two cells can be observed in specimen illustrated in Plate III, 1. These cells (20–40 μm in diameter) are thick-walled, rounded to elliptical and some elongated horizontally (e.g., at arrows). The latter could represent cells of the epidermis but the incompleteness of the specimen precludes further support to this assertion.

Interpretation: Given the lack of well-preserved extraxylary tissues, the comparison and discussion of possible affinities is here strictly limited to the morphology and size of xylem cells and strand. A terete strand with an exarch maturation of the xylem is typical of several basal grade zosterophylls *sensu* Nibbelink and Tomescu (2021). Most comparable taxa are the two anatomically known species of *Zosterophyllum* and two zosterophylls from the Rhynie and Windyfield Chert (i.e., *Trichopherophyton*, *Ventarura*). Our specimens differ from *Zosterophyllum llanoverum* and *Z. cf. fertile* (Edwards, 1969a,b) by a significantly larger xylem strand and metaxylem elements. *Ventarura lyonii* (Powell et al., 2000), on the other hand, is characterized by a larger xylem strand size (0.64–1.9 mm). *Trichopherophyton teuchansii* (Lyon and Edwards, 1991) likewise possesses a terete to subterete xylem strand (0.45–0.7 mm) with a 40–50 μm maximum width of tracheids, which broadly corresponds to

size ranges found in these Matringhem axes. However, any further comparison with this taxon is hindered by the lack of vegetative and fertile morphology/anatomy. Therefore, we argue that we are in the presence of larger plant than *Zosterophyllum* and closer in terms of size and xylem strand morphology to Rhynie Chert zosterophylls, especially *Trichopherophyton*.

Zosterophyllopsida (Taxon II)

Plate III, 3–5

Material: USTL 3759-2; USTL 3808-19B.

Occurrence: Matringhem Quarry, Matringhem, Pas-de-Calais, France.

Description: The xylem strand in both specimens is elliptical and relatively large, both reaching 1.9 mm in maximum diameter (Plate III, 3–5). Tracheids are polygonal-shaped (5–8 sides). Distribution of the protoxylem appears diffuse (Plate III, 3–4 at arrows). Protoxylem cell diameter range is 15 – (26) – 34 μm ($n=8$). Maximum diameter of metaxylem cells reaches 98 μm . The cortex preserved in specimen USTL 3808-19B (Plate III, 4) is seemingly stratified into an inner (poorly preserved) and outer unit. The inner cortex (0.32 mm) is as thick as the outer cortex (0.31 mm). Cells of the inner cortex are thin-walled and rounded to elliptical in outline, with occasionally thicker-walled angular cells ranging from 15 to 68 μm in diameter (Plate III, 4–5). Cells of the outer cortex are thicker-walled and more angular, especially in the outermost layers of cells (Plate III, 4–5). Their diameter varies between 22 to 100 μm . The epidermis is not preserved in both specimens.

Interpretation: These specimens differ from the previously-described morphotype mainly by the larger size and shape of axes and xylem strands. Metaxylem cells diameter in cross-sections is also substantially wider. An elliptical stele with an exarch maturation of the xylem and unconcentrated protoxylem suggests an affinity with more derived taxa of zosterophylls such as *Gosslingia*, *Sawdonia* and *Deheubarthia*. *Gosslingia breconensis* is one of the best-known Early Devonian zosterophyll, being both preserved in adpression and permineralized forms, originally found in the Anglo-Welsh Basin (Heard, 1927; Edwards, 1970; Kenrick and Edwards, 1988a). Matringhem specimens closely resemble this plant in terms of stele morphology, with similarly, a distinct inner and outer cortex, the latter being characterized by well-preserved thicker-walled cells. The stratification into an inner and outer cortex occurs among all anatomically-preserved zosterophylls except *Nothia* (El-Saadawy and Lacey, 1979), and is therefore not a particularly informative character in this case. Regardless, *Gosslingia* has smaller metaxylem elements (30–50 μm) and a significantly smaller (0.6 mm), and less elongated xylem strand than our specimens, suggesting that these axes belong to a different, yet potentially closely related plant.

The anatomy of *Sawdonia* has also been documented and although the xylem strand in *S. ornata* (Rayner, 1983) and *S. hipbotheca* (Berry and Gensel, 2019) is far more elongated (strap-shaped) than our specimens; *S. deblondii* (Gerrienne, 1996; Gensel and Berry, 2016) possesses a less elongated (elliptical) xylem strand resembling the present specimens. Large metaxylem cell diameter (up to 60 μm) and large protoxylem elements (8–26 μm) also characterize this taxon. However, the size of the xylem stand is again significantly smaller (0.55 mm) than our specimens. To our knowledge, these axes potentially represent one of the largest Early Devonian anatomically-known zosterophyll, exception of *Deheubarthia splendens* (Edwards et al., 1989). *D. splendens* is however likewise characterized by a strap-shaped stele, distinctly different from the Matringhem material. Our interpretation is that

these specimens probably originally belonged to a large zosterophyll, but its assignation to any taxon at this time is unwarranted. Nevertheless, in terms of general morphology, these axes are most similar to axes of *Gosslingia* and *Sawdonia deblondii*.

Zosterophyllopsida (Taxon III)

Plate III, 6–7

Material: LGP-2.

Occurrence: La Grande Pièce Quarry, Matringhem, Pas-de-Calais, France.

Description: The xylem strand in this specimen is elliptical and reaches 0.98 mm in maximum diameter (Plate III, 6). Tracheids are polygonal shaped (5–8 sides) in transverse view.

Distribution of the protoxylem diffuse. Protoxylem cell diameter ranges from 12 to 18 μm , whilst maximum diameter of metaxylem cells is 55 μm . One transverse section illustrated in Plate III, 7 displays an ongoing anisotomous dichotomy, with the presence of a smaller elliptical xylem strand (0.35 mm) not yet fully detached from the main xylem strand. The inner and outer cortex are not clearly delimited, but a group of small (26–38 μm), rounded to slightly angular and thinner walled cells can be noticed in Plate III, 6, in the immediate vicinity of the stele. Outermost cells of the cortex are larger (26–71 μm), more angular, thicker-walled, and some horizontally elongated. The epidermis is not preserved.

Interpretation: This third morphotype is most comparable to the Taxon II, but is differentiated based on a few features: (1) the strand is slightly less elongated, (2) the tracheids and the xylem strand are smaller, and (3) the presence of an anisotomous dichotomy. The size of the

stele being to some extent dependent on the original diameter of the axes, hence, potentially may vary according to the order of branching within the plant the cross-section is located; this feature alone cannot be accounted as an unequivocally reliable difference for comparison. However, the diameter of metaxylem cells does not seem to be strictly correlated with the original size of the xylem strand. As observed in dichotomizing axes in Edwards (1970, fig. 44-47) and noticeable in Plate III, 7, a smaller xylem strand seems to only result in a lower number of individual larger tracheids interpreted as metaxylem elements, but not significantly their size. The smaller size of metaxylem and protoxylem tracheids here further supports that this is indeed a different plant compared to Taxon II.

The most distinctive feature of this specimen is the presence of anisotomous branching, even though this is a common trait among zosterophylls especially in large, more derived and stratigraphically younger taxa. Branching in anatomically-preserved zosterophylls has solely been recorded in *Gosslingia* (Edwards, 1970), which likewise possesses an elliptically-shaped xylem strand and metaxylem elements of comparable size (30–50 μm). However, dichotomies in this plant are always associated with a third vascularized strand representing axillary tubercles (or branches). In fact, most taxa comparable to this specimen developed axillary tubercles, although not documented anatomically, and are therefore only presumed vascularized. There are here no signs of a third vascularized strand, but the presence of axillary tubercles cannot be totally excluded as the dichotomy is at a relatively early stage.

Thrinakophyton formosum Kenrick et Edwards is a closely related taxon to *Gosslingia* which also shares with our specimens an elliptically-shaped stele, with however smaller metaxylem cells and xylem strand and lacks preserved extraxylary tissues, precluding further comparison (Kenrick and Edwards, 1988b). *Crenaticaulis verruculosus* (Banks and Davis, 1969) from the mid- to late Emsian Battery Point Formation is also characterized by an elliptical stele but the size of metaxylem tracheids is far smaller and the inner cortex appears

significantly thicker. We therefore argue that this specimen represents a plant with a similar grade of organization to *Gosslingia*, *Thrinakophyton* and *Crenaticaulis*, and resembles the most to *Gosslingia*. However, the lack of vegetative and fertile morphology and the equivocal absence of axillary tubercles, cannot allow a definitive assignation of this specimen to this taxon.

7. Discussion

7.1. Implications of the revision of Early Devonian assemblages from northern France

This work completes the revision process initiated by Edwards (2006) and continued in Capel et al. (2022b) of relatively modest, yet interesting, fossil floras from northernmost France originally described over 60 years ago. The novelty regarding this assemblage was the rare occurrence of permineralized material, demonstrating the potential of this region in bringing new insights into the diversity of Early Devonian plants from the Ardenno-Rhenish Massif, and by extension the former continent of Laurussia. The newly-found interest for this area has resulted in additional sampling in nearly forgotten localities, which have not yet been all revisited, but might provide supplementary fossil material in the future.

The revision herein provided revealed an originally artificially augmented number of adpression taxa in the Matringhem Quarry locality. Indeed, Danzé-Corsin (1956a) assigned some material to different taxa that either, did not correspond to the taxonomic concept, or were simply far too fragmented to be reliably identified. The more conservative approach adopted here (especially regarding fragmented vegetative axes), has drastically reduced the number of identified taxa (Table 1), although diversity might be higher as some specimens may indeed belong to different plants (see section 5.1.4.). Despite the fact that sample size and quality of preservation was lower at the La Grande Pièce Quarry, both floras have a

similar composition being mostly represented by basal euphyllophytes and share the occurrence of one putative rhynopsid (*Taenioocrada*).

The most important discovery within the adpression record at Matringhem Quarry is the identification of isolated pairs of sporangia, comparable to those produced by *Psilophyton burnotense* (Schweitzer, 1989), in association with vegetative stems. This finding further supports the basal euphyllophyte affinities of European occurrences of vegetative stems either attributed to *Psilophyton burnotense* or *Margophyton goldschmidtii* Zakharova (Cascales-Minana and Meyer-Berthaud, 2015; Edwards and Li, 2018). We here also argue that the material from Northwestern Europe was not originally a zosterophyll as: (1) thousands of specimens in Germany alone, were devoid of laterally-inserted sporangia, and it would be extremely unlikely that not at least one fertile unit be found (Schweitzer, 1989); (2) it is more logical that distal branches bearing sporangia (as in basal euphyllophytes), being the most fragile part of the plant, be the first to sever (especially when transport has been substantial), explaining the lack of attached fertile material (Hotton et al., 2001). A reinvestigation of *M. goldschmidtii* (Zakharova, 1981) would be nonetheless commendable to resolve this contentious issue.

The Matringhem assemblage displays significant similarities with the other northern French locality yielding Early Devonian plant fossils (i.e., Rebreuve), sharing the occurrence of *Taenioocrada* and vegetative axes of *Psilophyton burnotense* (Capel et al., 2022b). Nonetheless, it is somewhat delicate to compare the fossil content between both localities as the Matringhem assemblage consists in more fragmented specimens and is therefore presumably more allochthonous than Rebreuve. Similarly to Rebreuve however, the assemblage bears notable resemblance to other early Emsian floras from the Ardenno-Rhenish Massif (Stockmans, 1940; Schweitzer, 1983, 1989; Gerrienne, 1993), suggesting a

close proximity of these different localities ca. 400 Ma, which all belonged to the Equatorial to mid-latitudes phytochorion in the late Early Devonian (Capel et al., 2023).

7.2. Discrepancy between the adpression and permineralized record

The Matringhem permineralized flora, in contrast to the adpression assemblage, is entirely constituted of plants with terete to elliptical haplosteles with an exarch maturation of the xylem, indicative of zosterophylls. The lack of significant anatomical disparity between different zosterophyll taxa has rendered arduous the comparison of isolated permineralized axes with nearly complete taxa, known in both compressed and permineralized forms. Nonetheless, the identification of several morphotypes suggests that zosterophylls were omnipresent and diversified in this area, which would have been overlooked based on the adpression record alone (Table 1). Indeed, all adpression fossils were identified as rhyniopsids or basal euphyllophytes, either defined by a centrarch or a mesarch maturation of the xylem (Edwards, 1993), a feature absent from our permineralized material.

Differences between the content of the permineralized and adpression plant fossil record in a single locality or formation is common in the Early Devonian (e.g., Fanning et al, 1992; Filipiak et al., 2022). An excellent, nearly coeval analogue is the Battery Point Formation (Canada), where among the 19 adpression and (currently) 15 permineralized genera described, only a select few are known from both records (Mihai Tomescu, pers. comm.). Several explanations can be tentatively put forward to justify this discrepancy among Matringhem assemblages:

(1) The permineralized record does not provide a representative sample of the original plant diversity. Considering that only a handful of specimens were sufficiently well-enough preserved to be identified, a larger amount of anatomically-preserved material could have possibly revealed the presence of other plant groups.

(2) Morphological convergence between vegetative axes of zosterophylls and basal euphyllophytes during the Pragian-Emsian interval. For example, zosterophyll taxa such as *Deheubarthia*, *Gosslingia* or *Thrinakophyton*, similarly to basal euphyllophytes, developed anisotomously-branched main axes with oftentimes distal isotomously-branched stems (Kenrick and Edwards, 1988a,b; Edwards et al., 1989). Emergences are also known to occur on axes of taxa from both groups, making isolated stems without fertile material potentially difficult to differentiate, exemplified herein in the previously discussed *Margophyton/Psilophyton* issue. It is therefore possible that among unidentifiable axes, some could belong to zosterophylls that could not be discriminated against other fragmented *Psilophyton*-like axes.

(3) The permineralized and adpression material are coming from different sources but were deposited in the same location. Emsian vegetation in the Battery Point Fm. was shown to organize itself in monospecific or monodominant stands, with zosterophylls possibly occupying different ecological niches to basal euphyllophytes (Hotton et al., 2001). Since the assemblages are assumed to be allochthonous, it is not implausible that these plants were originally growing in different habitats and therefore experienced distinct pre-diagenetic histories.

Regardless of the cause of this discrepancy, the permineralized flora still arguably reflects, to a large extent, the vegetation of the time as permineralized axes in both localities belong to different morphotypes of zosterophylls, and therefore probably different plants, showing that they remained an important component of the local flora.

7.3. Timing of the onset of anatomical diversification in eastern Laurussia

Permineralized material is virtually inexistent in the earliest Devonian (Lochkovian) period, and plant anatomical features have almost been entirely recovered from charcoalfied

fragments (Morris et al., 2018). It is only during the Pragian-Emsian interval that this mode of preservation becomes increasingly common and that complexification in stelar morphology and tracheid ultrastructure becomes more widely documented (Edwards, 2003; Decombeix et al., 2019). Nevertheless, permineralized material from this time period remains rare, understudied, and unevenly distributed geographically (Fig. 2). The patchiness of this record through time and space complicates our understanding of the timing of plant anatomical complexification. The Matringhem flora (1, Fig. 2) provides here additional information toward this objective of identifying centers of diversification and reconstruct patterns of dispersion of key anatomical traits.

The only other known Early Devonian French permineralized flora is late Pragian to possibly earliest Emsian in age (2, Fig. 2). It is quite distinct from the Matringhem assemblage with the presence of centrarch protosteles characteristic of basal euphyllophytes and most importantly *Armoricaphyton*, the earliest known wood-producing plant (Gerrienne et al., 2011; Strullu-Derrien et al., 2010, 2014). The Armorican Massif is posited to have been located on the northern Gondwanan margin, whilst northernmost France was situated on the eastern Laurussian margin during the Early Devonian (Fig. 2), separated by a closing Rheic Ocean (Scotese, 2021). Consequently, the observed disparities between these assemblages may reflect a geographically diachronous complexification of plant anatomy as plants with secondary growth only begin to appear in the middle to late Emsian in Laurussia (Hoffman and Tomescu, 2013; Durieux et al., 2021; Toledo et al., 2021; Pfeiler and Tomescu, 2021, 2023). Other examples of Gondwanan Early Devonian permineralized floras would be nonetheless necessary to conclusively identify this region as one of the centers of origin of more anatomically-complex plants.

The Laurussian record, on the other hand, is more complete, and consequently provides a more continuous timeline of anatomical diversification (Fig. 2). Interestingly, the Matringhem

permineralized flora presents strong similarities with the zosterophyll-dominated record from the Anglo-Welsh Basin (3, Fig. 2), which is dated as Pragian and possibly extends into the earliest Emsian (Edwards, 1970; Kenrick and Edwards, 1988a,b; Edwards et al., 1989; Wellman et al., 1998). Some of our specimens are indeed comparable to Welsh taxa like *Gosslingia* or *Thrinakophyton*, whilst another morphotype corresponds most closely to the late Pragian-early Emsian Scottish Rhynie Chert zosterophylls (Lyon and Edwards, 1991). In contrast, plants from the Canadian mid- to late Emsian Battery Point Fm. (4, Fig. 2), or from the preliminary described latest Emsian Polish flora (5, Fig. 2), are far more complex and diversified anatomically, especially among euphyllophytes, with the occurrence of early cladoxyloids (ribbed or dissected steles) and numerous plants with secondary growth (Hoffman and Tomescu, 2013; Durieux et al., 2021; Filipiak et al., 2022). The increased resemblance of the Matringhem flora with the Welsh plant fossil record further indicates that the assemblages presented herein are not younger than the early Emsian.

The content of this new anatomically preserved flora is also consistent with the other few scattered permineralized remains found in the early Emsian Ardenno-Rhenish Massif localities, either identified as zosterophylls or rhyniopsids (Hass and Remy, 1991; Schultka, 1991; Gerrienne, 1996). Although the middle to late Emsian is as poor as the early Emsian in terms of anatomically preserved material in this region, the presence of a more derived basal euphyllophyte with a deeply lobed actinostele (*Gothanophyton*) in the late Emsian of Germany (Remy and Hass, 1986), tends to suggest that plants with this type of anatomical complexity was not present, or at least predominant, before the middle to late Emsian in this region. Nevertheless, this remains a preliminary assumption as the fossil record is at this stage excessively poor, but this scenario would be compatible with the timeline of anatomical diversification in eastern Laurussia reconstructed based on these few other floras. Further

sampling in this region and outside Laurussia will be critical to better understand this part of plant evolutionary history.

8. Conclusions

- The revision of the adpression flora has drastically reduced the number of taxa occurring at Matringhem Quarry, but allowed the identification of stems of *Psilophyton burnotense* and likely isolated pairs of sporangia of this species, thereby further arguing in favor of European vegetative remains to belong to a basal euphyllophyte.
- Additional sampling in a nearby quarry provided a few other compressed macroalgal and macroplant remains, which similarly to the other locality, is composed of a putative rhyniopsid and basal euphyllophytes.
- The permineralized floras were found to be exclusively composed of zosterophyll-like plants with three different morphotypes identified, even though assignation to any specific taxon was deemed premature given the paucity of distinctive characters in the anatomy of these primitive plants.
- The discrepancy observed between the basal euphyllophyte-dominated adpression record and the zosterophyll-dominated permineralized record, could be the product of either: an insufficient number of specimens, an incapacity to reliably discriminate between isolated vegetative zosterophyll and basal euphyllophyte axes, or different taphonomic histories.
- This assemblage represents a rare occurrence of a permineralized flora from the Ardenno-Rhenish Massif, and by extension, eastern Laurussia. It was found most similar to the Pragian-earliest Emsian welsh record, as younger assemblages are more anatomically diverse and complex.

- Based on previous palynological analyses and considering the content of both the adpression and permineralized floras, an early Emsian age is inferred for these assemblages.

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Supporting information

Table S1. Updated spore taxa list originally identified in Leclercq (1975) and associated biostratigraphical range in the Ardenno-Rhenish region.

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Figure legends

Fig. 1. (A) Map of northern France indicating the location of the study area and (B) geological map of the study area (Matringhem-Vincly) based on geological maps of northern France at a 1/50000 scale (<https://infoterre.brgm.fr/>). Location of the mentioned plant fossil and palynomorphs localities: 1. Matringhem Quarry (GPS: 50°32'40.23"N, 2° 9'50.02"E); 2. North Matringhem Quarry (GPS: 50°32'51.08"N, 2°10'3.76"E); 3. La Grande Pièce Quarry (GPS: 50°32'58.53"N, 2°10'10.40"E); 4. Outcrop n°24 in Leclercq (1975) (GPS : 50°33'24.28"N, 2°9'48.27"E); 5. La Malfiance Quarry (GPS: 50°33'48.63"N, 2°9'14.21"E). Colors: white = Quaternary; green = Upper Cretaceous; grey = Upper Pennsylvanian (Carboniferous); light brown = Lower Devonian. Abbreviations: d1 = Lochkovian ‘Grès de Pernes’ Formation; d2 = Pragian–Emsian ‘Grès de Matringhem-Vincly’ Formation.

Fig. 2. Position of the main regions in Laurussia and Gondwana with the most relevant Pragian-Emsian permineralized floras, plotted onto the paleogeographic map of the Early Devonian (Emsian). Paleogeographic map modified from Scotese et al. (2021). 1. Ardenno-Rhenish Massif (including Matringhem); 2. Armorican Massif (France); 3. Anglo-Welsh Basin (UK); 4. Gaspé Bay (Canada); 5. Holy Cross Mountains (Poland).

Plate I. Plant fossils from Matringhem Quarry, northern France. (1) *Taeniochrada* sp., smooth axis with a distinguishable vascular strand trace (at arrow) throughout its entire length, USTL 3767. (2) Axis of *Taeniochrada* sp. with a vascular strand trace at black arrow; to the right is a vegetative axis of *Psilophyton burnotense*; note the successive dichotomies at white arrows, showing an alternate pattern of branching, USTL 3766. (3) *Psilophyton burnotense*, vegetative specimen with pseudomonopodial branching; note the presence of spines on the abaxial side of the axis immediately before, and after the dichotomy, USTL 3740. (4) *Psilophyton burnotense*, anisotomously-branched axis with conspicuous spine scars on the surface, as well as a thickened margin throughout the entire length of the axis, USTL 3757. (5) *Psilophyton burnotense*. isolated pairs of elongated and fusiform sporangia showing slight torsion; note the presence of an insufficiently well-preserved permineralized axis not connected to the pair of sporangia,, USTL 3765. (6) *Psilophyton burnotense*, isolated pairs of sporangia connected to a truncated stalk, USTL 3749. (7) *Psilophyton burnotense*, other incompletely preserved isolated pairs of sporangia found in the sample as (6), USTL 3749. (8) cf. *Psilophyton* sp., long axis displaying various types of branching (pseudomonopodial, anisotomous and isotomous), USTL 3822. (9) cf. *Psilophyton* sp., two stems with isotomous branching on the left and anisotomous branching on the right, USTL 3733. (10) cf. *Psilophyton* sp., probable distal branches with two successive isotomous dichotomies, USTL 3742. (11) cf. *Psilophyton* sp., striated stem with pseudomonopodial type of branching, USTL

3722. (12) cf. *Psilophyton* sp., cast and imprints remain of a more strongly striated surface, USTL 3748. (13) cf. *Psilophyton* sp., counterpart of axis in (12), showing that the degree of striations and ridging is partly related to taphonomy, USTL 3756. Scale bars: 1–4, 8–13 = 10 mm, 5–7 = 5 mm.

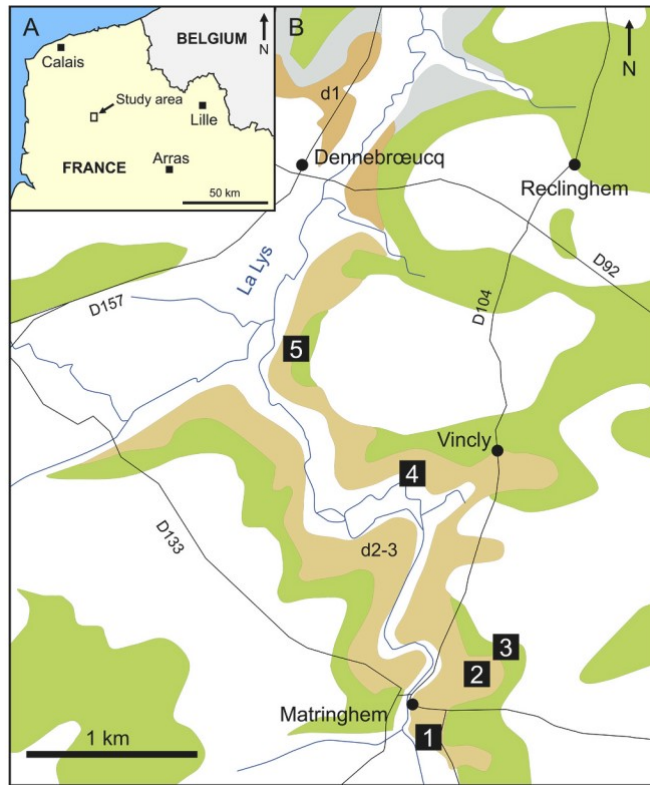
Plate II. Plant fossils from Matringhem Quarry (1–3) and La Grande Pièce Quarry (4–6), northern France. (1) Unbranched longitudinally-striated stem referred to as *Calamophyton* sp. in Danzé-Corsin (1956a), USTL 3727. (2) Partially-compressed cast of a large longitudinally (but not continuously) striated axis identified as *Drepanophycus ? crepinii* in Danzé-Corsin (1956a), USTL 3758. 3) Anisotomously-branched glabrous axis identified as *Hostinella* sp. in Danzé-Corsin (1956a), USTL 3721. 4) *Taeniocrada* sp., unbranched axis with meandering vascular strand trace, USTL 3841. 5) Large glabrous branching system; note the isotomous dichotomy at arrow close to previous branching point, USTL 3842. 6) *Pachythea* sp., spherical structure with radially-arranged tubes at the periphery, USTL 3843. Scale bars: 1–5 = 10 mm, 6 = 1 mm.

Plate III. Transverse sections of anatomically-preserved zosterophylls from Matringhem (1–5) and La Grande Pièce Quarries (6–7), northern France. (1) Taxon I, terete xylem strand with outermost cells possibly representing either the outer cortex or the epidermis. Arrows point to horizontally elongated smaller cells possibly representing epidermal cells, USTL 3749-1. (2) Taxon I, sub-terete stele unequivocally displaying an exarch maturation of the xylem with smallest tracheids in the outermost part of the stele, USTL 3817-A. (3) Taxon II, specimen lacking preserved extraxillary tissues, showing an elliptically-shaped xylem strand. Protoxylem cells at black arrows, USTL 3759-2. (4) Taxon II, specimen showing a large elliptical protostele, surrounded by an incompletely preserved inner cortex followed by an

outer cortex of equivalent size. Protoxylem cells at white arrows, USTL 3808-19B. (5) Taxon II, other polished section of specimen USTL 3808-19B with enhanced contrast showing more distinctly cell wall outline in the primary xylem and cortex. (6) Taxon III, specimen with preserved elliptical xylem strand and cortex, note the larger and thicker walled cells in the outermost part of the cortex, whilst inner cortex cells are smaller and more rounded, LGP-2. (7) Taxon III, polished section originating from the same axis as (6) with a conspicuous anisotomous dichotomy, as evidenced in the primary xylem strand shape, LGP-2. Scale bars = 50 μm .

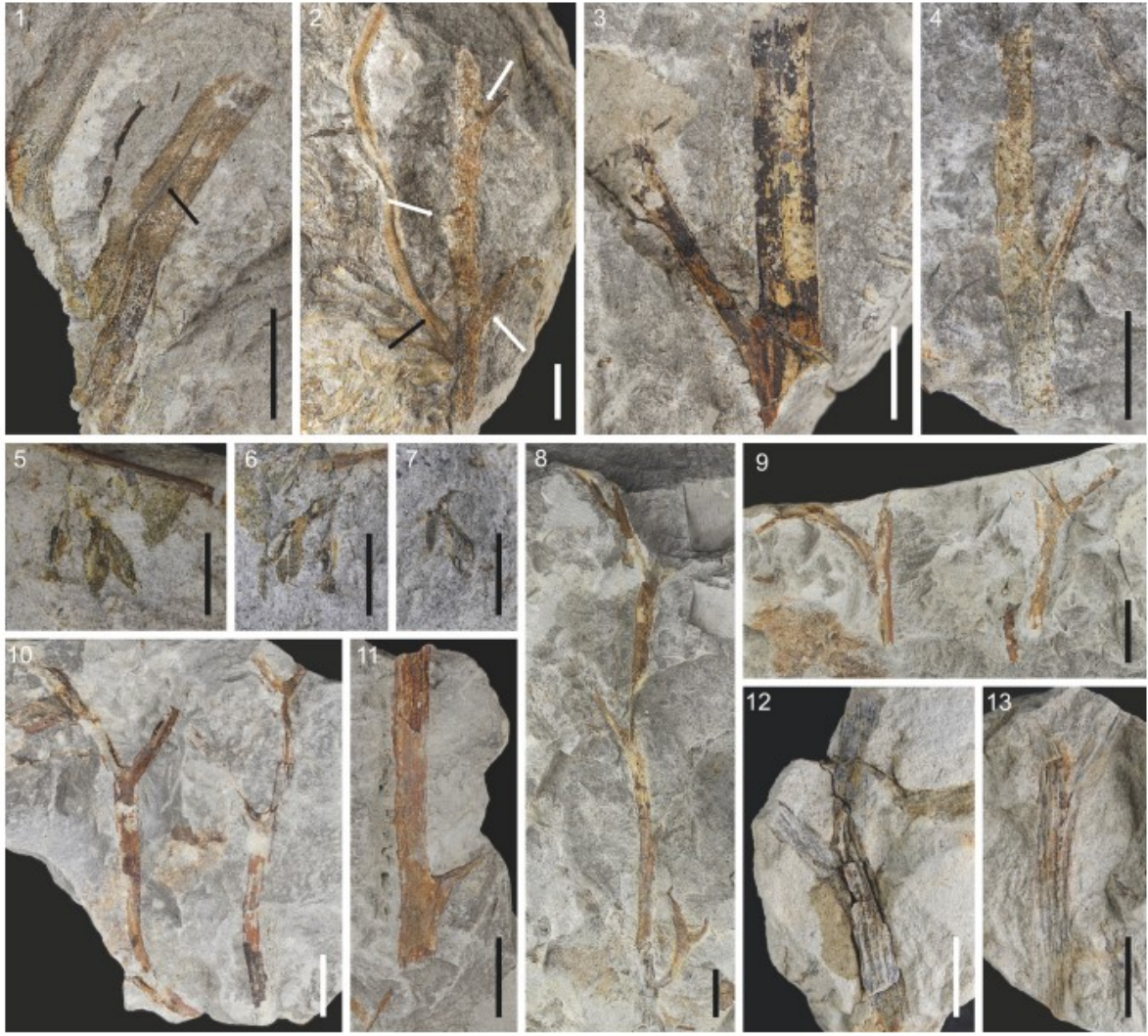
Table captions

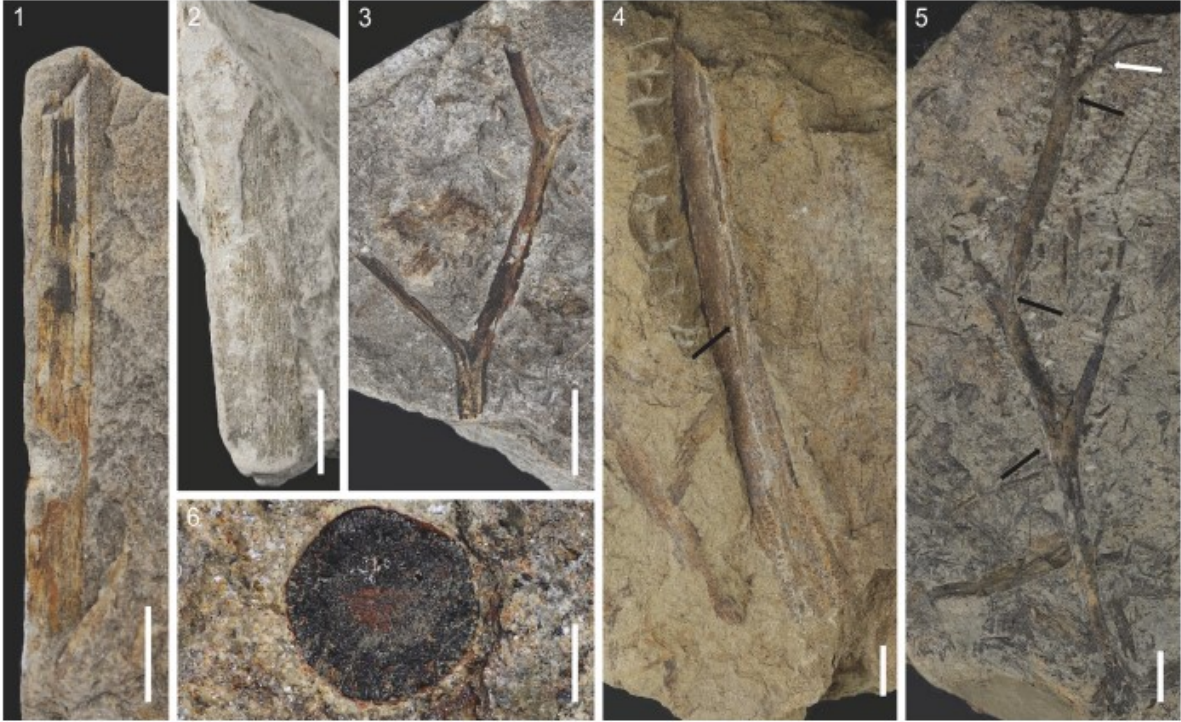
Table 1. Original and updated list of Matringhem plant taxa.



Emsian (400 Ma)







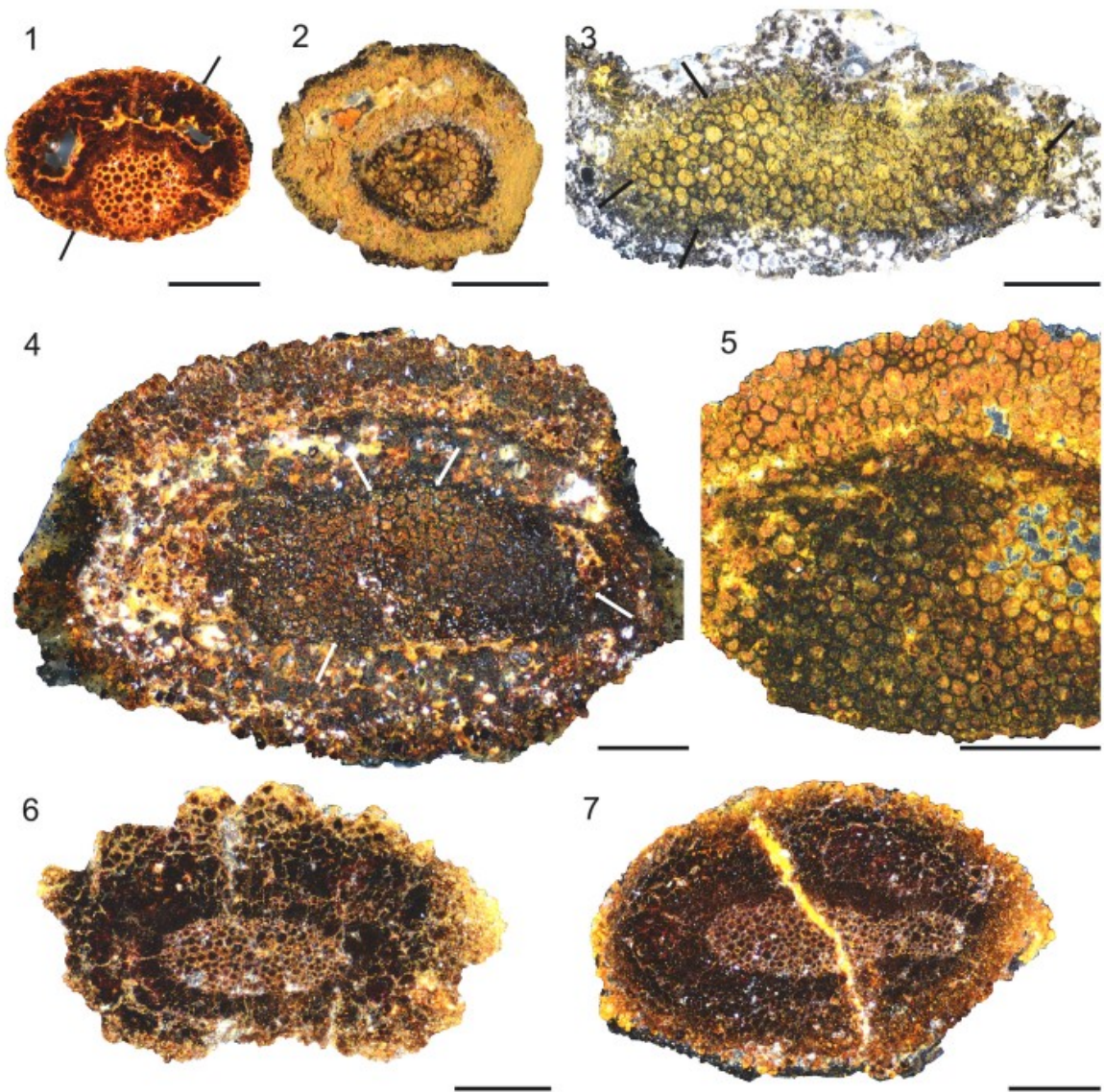


Table 1. Original and updated list of Matringhem plant taxa.

| Matringhem quarry | |
|---|-------------------------------------|
| Danzé-Corsin (1956a) | This study |
| - | <i>Taeniocrada</i> sp. |
| <i>Psilophyton goldschmidtii</i> | <i>Psilophyton burnotense</i> |
| <i>Dawsonites</i> cf. <i>arcuatus</i> | |
| <i>Aphylopteris</i> cf. <i>robusta</i> | cf. <i>Psilophyton</i> sp. |
| <i>Rhabdophyton striatus</i> gen. et sp. nov. | |
| <i>Calamophyton</i> sp. | Undet. axis |
| <i>Drepanophycus</i> ? <i>crepini</i> | Undet. axis |
| <i>Hostinella</i> sp. | Undet. axis |
| - | Zosterophyllopsida (Morphotype I) |
| - | Zosterophyllopsida (Morphotype II) |
| La Grande Pièce quarry | |
| Leclercq (1975) | This study |
| <i>Hostinella</i> sp. | - |
| <i>Taeniocrada decheniana</i> | - |
| <i>Thursophyton vahlbergium</i> | - |
| - | <i>Taeniocrada</i> sp. |
| - | Basal euphyllophyte ? |
| - | <i>Pachythea</i> sp. (alga ?) |
| - | Zosterophyllopsida (Morphotype III) |

Table S1. Updated spore taxa list originally identified in Leclercq (1975) and associated biostratigraphical range in the Ardennes-Rhenish region

| Spore taxa identified by M. Streeel in Leclercq (1975) | Updated spore taxa list | Biostratigraphical range |
|--|--|--------------------------|
| <i>Anapiculatisporites</i> sp. | <i>Anapiculatisporites</i> sp. | - |
| <i>Aneurospora</i> (<i>Retusotriletes</i>) <i>semizonalis</i> | <i>Retusotriletes semizonalis</i> | - |
| <i>Aneurospora</i> sp. | <i>Aneurospora</i> sp. | - |
| <i>Apiculiretusispora</i> (<i>Cyclogranisporites</i>) <i>plicata</i> | <i>Apiculiretusispora</i> (<i>Cyclogranisporites</i>) <i>plicata</i> | N β -AB |
| <i>A. cf. brandtii</i> | <i>A. cf. brandtii</i> | - |
| <i>Archaeozonotriletes cf. chulus</i> | <i>Archaeozonotriletes cf. chulus</i> | - |
| <i>Brochotriletes</i> sp. A | <i>Brochotriletes?</i> <i>foveolatus</i> | Si β -Su |
| <i>Cirratricadites</i> sp. F | <i>Breconisporites breconensis</i> | Z-AB |
| <i>Dictyotriletes subgranifer</i> | <i>Dictyotriletes subgranifer</i> | Su-AB |
| <i>Emphanisporites verrucatus</i> | <i>Emphanisporites verrucatus</i> | - |
| <i>Emphanisporites rotatus</i> | <i>Emphanisporites rotatus</i> | N β -AB |
| cf. <i>Hyemenozonotriletes</i> sp. | cf. <i>Hyemenozonotriletes</i> sp. | - |
| <i>Punctatisporites</i> aff. <i>limbatus</i> | <i>Punctatisporites</i> aff. <i>limbatus</i> | - |
| <i>Retusotriletes rotundus</i> | <i>Retusotriletes rotundus</i> | - |
| <i>Retusotriletes</i> sp. | <i>Retusotriletes</i> sp. | - |

Miospore biozones according to Steemans (1989). Opper zone: AB, *annulatus*-*bellatulus*. Interval zones: N, *newportensis*-*retorrida*; Su, *subgranifer*-*annulatus*. Phylogenic zones: Si, *sinuosus*-*gedinniensis*; Z, *zavallatus*-*emsiensis*.