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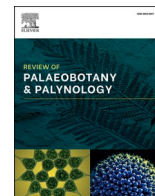
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## Reassessing the Early Devonian flora from Consthun Quarry (Luxembourg)

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### ABSTRACT

The Early Devonian plant fossil record provides evidence of large vegetation turnover events in addition to rapid morphological and anatomical changes among vascular plants. The Ardenno-Rhenish Massif has historically yielded a vast number of these plant fossils allowing us to obtain a nearly unparalleled snapshot of Early Devonian vegetation. Nonetheless, the interest for describing or redescribing fossil floras from this region has waned in recent years despite their inherent value to understand Early Devonian plant diversity dynamics. Here, we describe a newly collected macrofossil flora from the middle Emsian Schuttbourg Formation at Consthun Quarry (Luxembourg). Six different plant macrofossil taxa were identified, including *Drepanophycus spinaeformis* and *Psilophyton* cf. *princeps*, in addition to putative macroalgal and fungal remains. The flora also includes other equivocal specimens resembling *Sawdonia*, *Huvenia* and *Zosterophyllum*. The composition of the assemblage is extremely similar, at generic level, to older Pragian–early Emsian and coeval floras from nearby localities, which indicates that there was no major floral turnover until the latter part of the Emsian in this region. Taxonomic descriptions also highlight many of the underlying issues in identifying Early Devonian sterile specimens. Inconsistencies in plant fossil identifications from this region call for a thorough revision of Belgian and German floras that together could provide a high-resolution picture of plant diversity changes in the Early Devonian.

### 1. Introduction

The Ardenno-Rhenish Massif mainly comprises extensive Devonian sedimentary deposits, and notably thick Early Devonian siliciclastic successions that were historically intensively studied for their fossil faunal and floral content (Hartenfels et al., 2022). Consequently, this region became of prime relevance for paleobotanic research given the significant amount of Early Devonian (mostly late Lochkovian to early Emsian) plant macrofossils that were discovered over the last century or so, in numerous localities across Belgium (e.g., Stockmans, 1940; Fairon-Demaret, 1985; Gerrienne, 1983, 1990, 1993, 1996a, 1996b), Germany (e.g., Kräusel and Weyland, 1930, 1935, 1948; Schweitzer, 1979, 1980a, 1980b, 1983, 1987, 2000; Gossmann et al., 2022), and to a lesser extent northern France (Capel et al., 2022a, 2024) and Luxembourg (Delsate et al., 2003).

Over the years, plant macrofossils were retrieved in two distinct

localities in the northern part of Luxembourg, in the now abandoned Merkholtz, and still actively exploited Consthun ('Rinnen') quarries (Delsate et al., 2003). However, the taxonomic composition of these assemblages has thus far only been preliminarily assessed by P. Gerrienne in Delsate et al. (2003). In contrast, more extensive palynological investigations were undertaken to provide refined age constraints for the sedimentary sequences bearing the macroflora by Steemans et al. (2000) and Delsate et al. (2003), both suggesting a late early to middle Emsian age (ca. 400 Ma). This stratigraphic range is of particular interest as most reliably dated macrofloras from the Ardenno-Rhenish Massif are rarely younger than the early Emsian, i.e., *Emphanisporites annulatus*–*Brochotriteles bellatulus* Oppel Zone (Remy and Hass, 1986; Streel et al., 1987; Gerrienne, 1993). Hence, a taxonomic re-evaluation of the composition of the assemblage provides a rare opportunity to document plant diversity from this time interval in the Ardenno-Rhenish Massif.

In addition, the Emsian represents a decisive transition period from a

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global flora dominated by zosterophylloids (i.e., Early Eophytic Flora) towards a lycophytic and euphyllophyte dominated (i.e., Late Eophytic Flora) world (Capel et al., 2021, 2022b). Major changes in plant morphological and anatomical complexity associated with this vegetation replacement have also recently rekindled and directed paleobotanical interest towards the study of assemblages of similar age (e.g., Bonacorsi et al., 2020; Pfeiler and Tomescu, 2021, 2023; Tomescu and McQueen, 2022; Capel et al., 2022a, 2024; Lalica and Tomescu, 2023).

Here, based on an entirely new set of recently collected plant macrofossils from Consthum Quarry (Luxembourg), we reassess plant fossil identifications in order to provide an updated account of the diversity in this locality. The previously mentioned stratigraphical importance of this flora (middle Emsian) also contributes to further understanding vegetation changes during this interval within the Ardenno-Rhenish Massif, and by extension, the former continent of Laurussia. Lastly, in addition to plant fossil descriptions, discussions are provided on taxonomic concepts, focussing on inconsistencies among previously identified Early Devonian plants from the Ardenno-Rhenish Massif.

## 2. Geological setting and biostratigraphical framework

Plant fossils were originally discovered in two different localities (Delsate et al., 2003) across the northern part of Luxembourg (Fig. 1A), in the Merkholtz (Loc. 2; Fig. 1B), and Consthum quarries (Loc. 1; Fig. 1B). Despite the localities being ca. 4.5 km apart, both belong to the same lithological unit: the Schuttbourg ‘Quartzophyllades’ Formation, reportedly of middle Emsian age (E1b; Fig. 1B). However, the age of the

Schuttbourg Fm. is somewhat controversial (Dejonghe et al., 2017). This stratigraphic unit is inserted between the Stolzembourg (lower Emsian) Formation and the Clervaux Schists Formation, usually attributed to the middle Emsian based on previous analyses of faunal composition (Delsate et al., 2004). Palynological evidence from a section at Merkholtz Quarry by Steemans et al. (2000) originally supported a similar age. Among the poorly diversified palynoflora, biostratigraphically relevant taxa included *Rhabdosporites minutus*, which is an index species characterizing the base of the Min Interval Zone of the *Emphanisporites foveolatus*–*Verruciretusispora dubia* Opperl Zone (middle Emsian; Streel et al., 1987; Gradstein et al., 2020, fig. 22.12), providing a robust maximum age calibration. The co-occurrence of *R. minutus* and *Acinosporites lindlarensis* provided further support for the section to be located within the Min Interval Zone as the *lindlarensis*–*sextantii* Assemblage Zone for North Gondwana - defined at its base by the first occurrence of *A. lindlarensis* - partly correlates with the Western European Min Interval Zone (Streel et al., 1987; Breuer and Steemans, 2013; Wellman et al., 2023).

Nonetheless, in Delsate et al. (2003), newly sampled spores from Consthum and Merkholtz quarries revealed a very poorly preserved spore that might represent the taxon *Acinosporites apiculatus*, characterizing the base of the overlying *apiculatus*–*proteus* Opperl Zone, but given the geological context of the area (Dejonghe et al., 2017), this record can be considered unreliable, especially since the assemblage lacks other typical younger Emsian taxa, which does not support a late Emsian age. Therefore, a middle Emsian age is herein inferred, most likely being within the age range of the Min Interval Zone of the FD Opperl Zone. Our

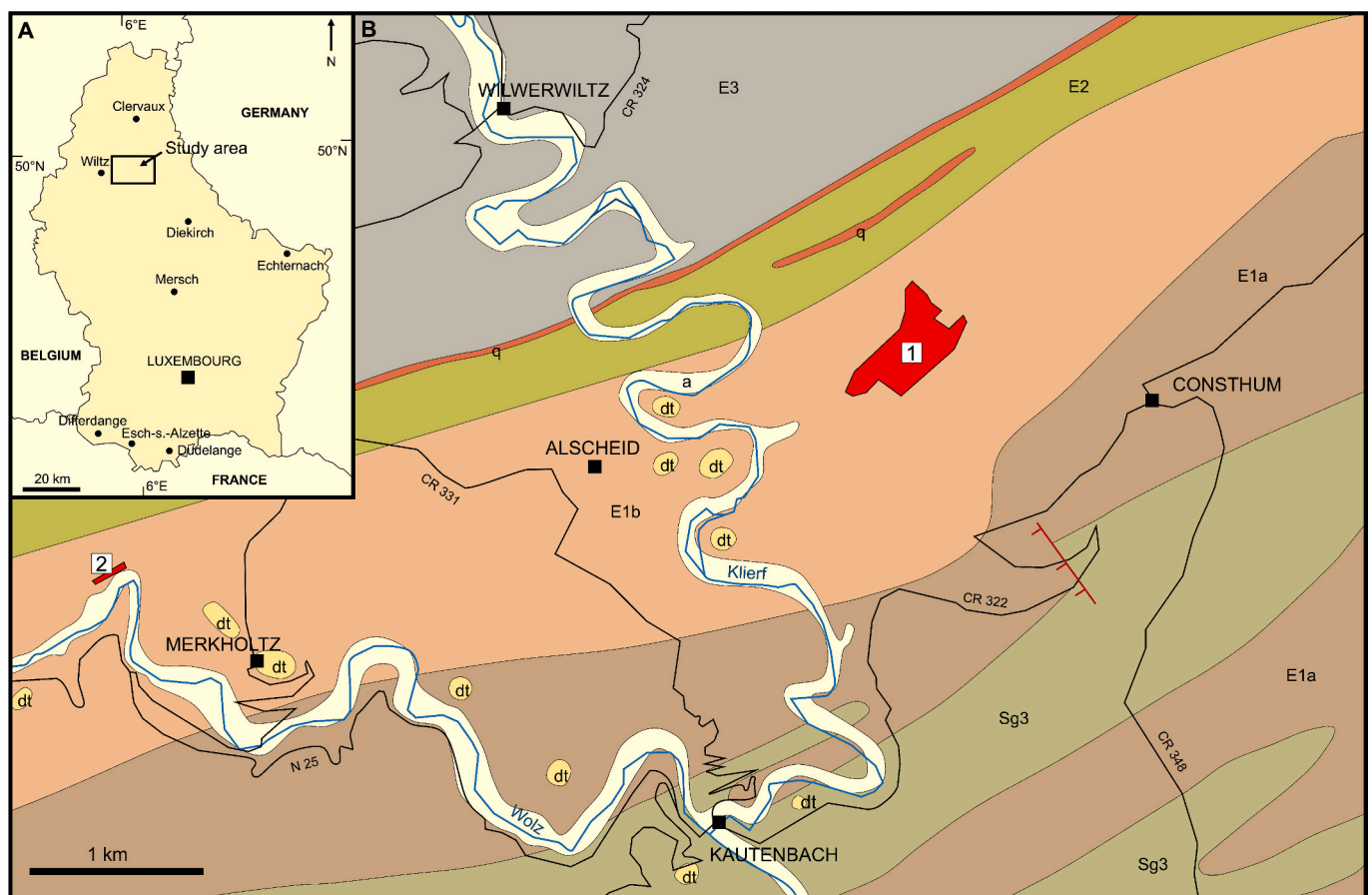


Fig. 1. (A) Map of Luxembourg indicating the location of the study area. (B) Geological map of the study area based on geological maps of northern Luxembourg extracted from (<https://map.geoportail.lu/>). Location of the mentioned plant fossil and palynomorph localities: 1. Consthum Quarry (GPS: 49°58'36.4"N, 6°02'00.5"E); 2. Merkholtz Quarry (GPS: 49°57'53.4"N, 5°58'08.7"E). Abbreviations: Sg3 = Upper Siegenian Schists (Pragian); E1a = Stolzembourg Schists (Lower Emsian); E1b = Schuttbourg Quartzophyllades (Middle Emsian); E2 = Clervaux Schists (Middle–Upper? Emsian); E3 = Wiltz Schists (Upper Emsian); q = Berlé Quartzite (Upper Emsian); dt = fluvial terraces (Pleistocene); a = alluvium (Holocene).

new palynological investigations in levels close to the macrofossil-bearing layers provided limited results, owing to their poor preservation state. Only a few specimens could be identified at the genus level, including *Retusotriletes* spp., *Apiculiretusispora* spp., *Ambitisporites* spp., and a single specimen of the Pragian–Emsian taxon *Dibolisporites* cf. *wetteldorfensis*. Thus, further refinement of the age of the assemblage or additional palaeobotanical implications could not be obtained. However, additional palynological studies are currently in progress.

The studied outcrop at Consthum (‘Rinnen’) quarry represents sub-vertical schist layers of dark partly quartzitic sandstones interlayered with siltstones and mudstones (Fig. 2). The environment of deposition was interpreted by Steemans et al. (2000) to be either continental or nearshore marine, with a significant influx of freshwater from the continent. Ripple marks were also identified indicating neritic or shallower facies (Delsate et al., 2003). The fauna recorded at Consthum Quarry is extensive with previously reported fossils including bivalves, ostracods, tentaculites, eurypterids, trilobites and fish remains (Delsate et al., 2003, 2004; Poschmann and Franke, 2006; Van Viersen and Prescher, 2009; Becker and Franke, 2012). In this section (Consthum I), specimens of the bivalve species *Archanodon ekpempusa* are frequently associated with plant remains (Fig. 2).

Plant macrofossils previously identified at Consthum Quarry by P. Gerrienne in Delsate et al. (2003) include *Drepanophycus spinaeformis*, *Psilophytites* sp., *Dawsonites arcuatus*, ?*Stockmansella langii* and *Taenio-crada*-like fossils. The material collected at Merkholtz Quarry is less abundant and only consists of a few specimens representing an aerial stem of *Drepanophycus spinaeformis* with short truncated leaves (Delsate et al., 2003, pl. 6, figs. 1–2) and other *Taenio-crada*-like plant fossils. The fossil material in Delsate et al. (2003) was not reinvestigated herein. The fossils that are the subject of the present contribution originate from a new thorough sampling in the Consthum Quarry, providing an entirely new collection of past biodiversity within these plant-bearing layers (Fig. 2).

### 3. Materials and methods

The material studied herein was collected during several field works in 2022 at Consthum Quarry (Luxembourg). Around a hundred rock

samples with plant fragments were identified and collected. All plant macrofossils are preserved as adpressions *sensu* Shute and Cleal (1987), although large specimens are at times preserved as partially-compressed casts. Plant macrofossils were prepared through *dégagement* (Fairon-Demaret et al., 1999) and were photographed using a CANON EOS 700D and a macro lens, whilst details were photographed with a Tucson camera mounted on an Olympus SZX FOF microscope. Following taxonomic interpretations, the relative abundance of taxa in the assemblage has been obtained *via* counts of all specimens in the collection that could be reliably attributed to a specific taxon. Selected rock samples were treated using standard HCl-HF-HCl palynological acid macerations techniques at the Evo-Eco-Paléo palynological laboratory at the University of Lille (France). All macrofossil specimens and microscopic slides are housed within the paleontological collections of the Musée National d’Histoire Naturelle de Luxembourg (Luxembourg).

### 4. Taxonomic descriptions

*Taenio-crada* sp. White

Material: EiB677a, EiB677b.

*Description*: Among the diversity of sterile axes found within the assemblage, only a limited number of specimens could be unequivocally attributed to *Taenio-crada* and herein the best-preserved axis (part and counterpart) is illustrated (Plate I, 1–2). This truncated axis is 7.9 cm long and 8.5 mm wide, unbranched, with a smooth surface and a well-centered vascular strand trace, measuring exactly 1/10th of the width of the axis (0.85 mm).

*Interpretation*: *Taenio-crada* is a fossil-taxon for axes with a ribbon-like appearance and a conspicuous central or meandering vascular strand impression. *Taenio-crada*-like axes are frequently occurring in Early Devonian (mostly Pragian–Emsian) plant-bearing localities, especially in northwestern Europe (see e.g., Stockmans, 1940; Croft and Lang, 1942; Capel et al., 2022a, 2024). These types of axes are believed to originate from plants belonging, or closely related to the Rhyniopsida *sensu* Kenrick and Crane (1997), or alternatively Paratracheophyta *sensu* Gerrienne et al. (2006); as fertile and sterile axes originally attributed to *Taenio-crada* were found to be characterized by distinct anatomical features (S-type tracheids) defining rhyniopsids (Fairon-Demaret, 1985,

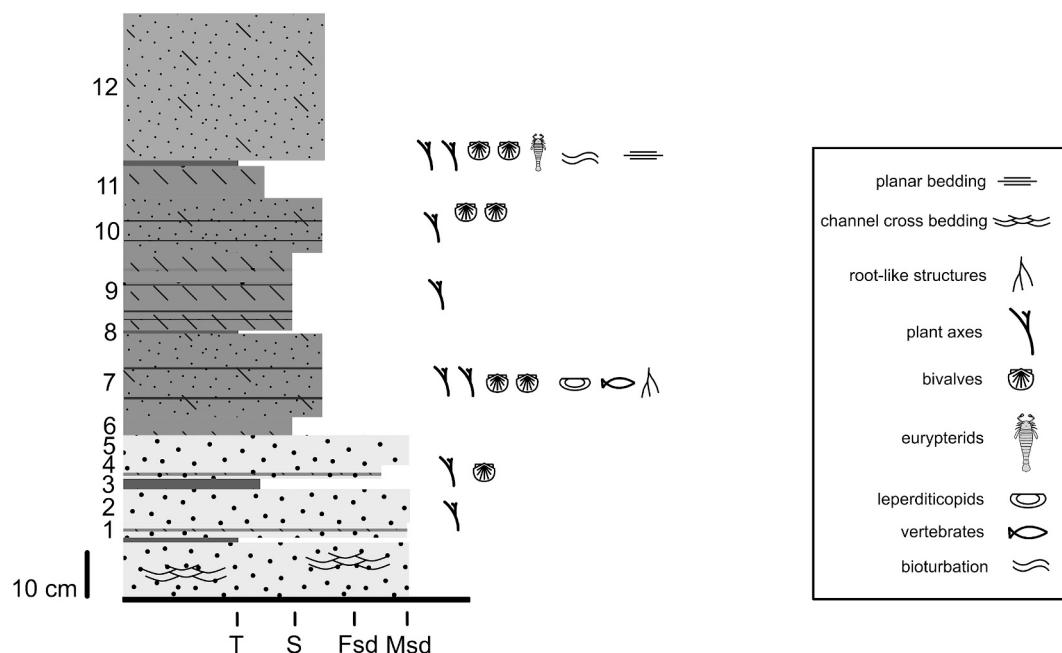
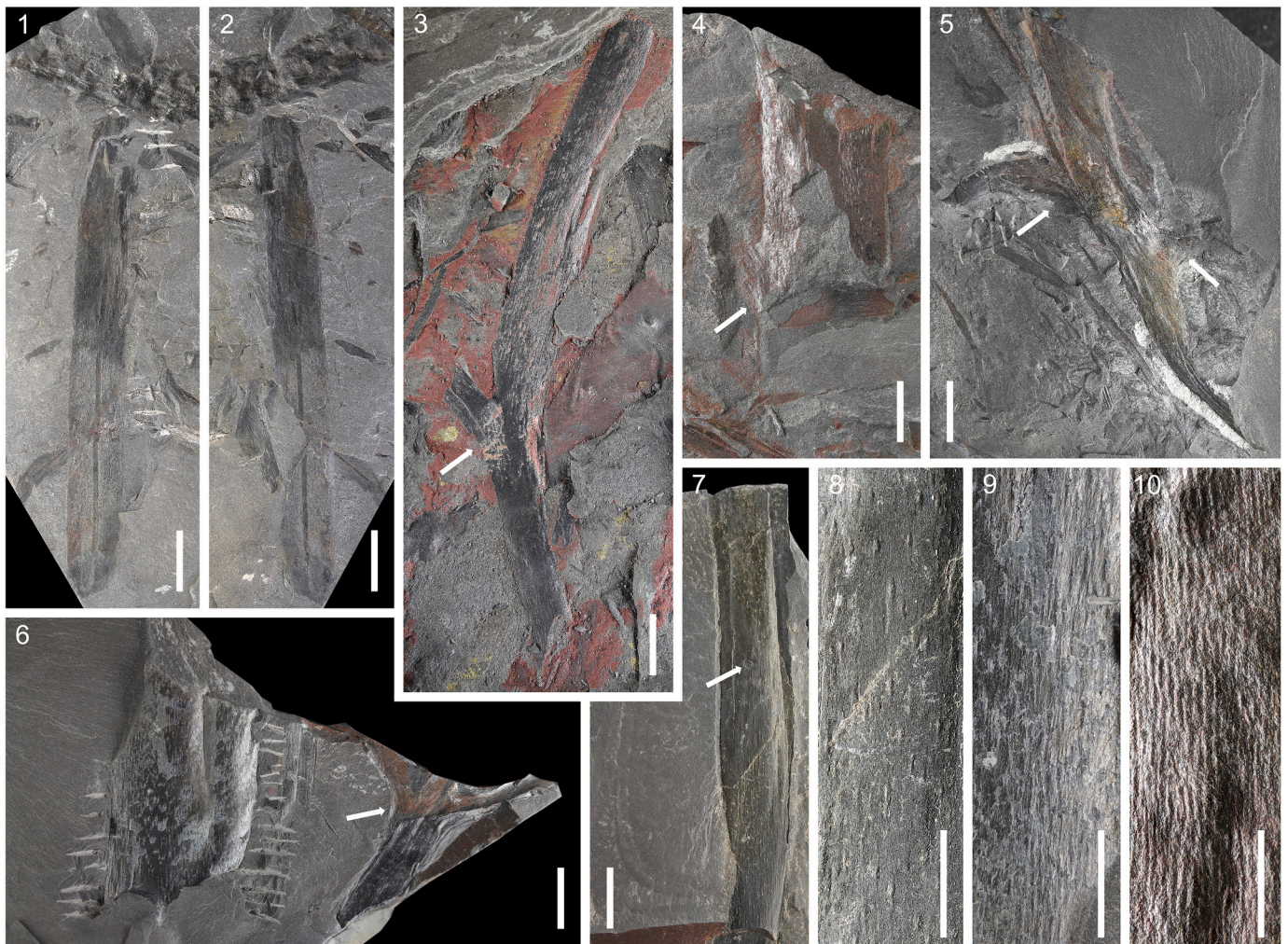


Fig. 2. Stratigraphic log of the studied outcrop at Consthum Quarry showing the occurrence of plant macrofossils and other types of fossil remains within the section. Sedimentological interpretation is tentative. Abbreviations: T = *tonstein* (mudstones); S = *siltstein* (siltstones); Fsd = fine-grained sandstone; Msd = medium-grained sandstone.



**Plate I.** Rhyniopsid macrofossils from Consthum Quarry, Luxembourg. (1–2) *Taenioocrada* sp., part and counterpart of an unbranched axis with a conspicuous central vascular strand imprint, EIB677a, EIB677b. (3) cf. *Huvenia* sp., longest untruncated specimen, displaying an anisotomous dichotomy at arrow, EIB678a. (4) cf. *Huvenia* sp., large superficially-punctuated axis with likewise the occurrence of an anisotomous dichotomy (at arrow), EIB681a. (5) cf. *Huvenia* sp., specimen showing two lateral branches (truncated distally) alternately arranged on the main axis (at arrows), EIB522. (6) cf. *Huvenia* sp., two distinct vegetative axes, the right axis undergoing a trichotomy at arrow, EIB687. (7) cf. *Huvenia* sp., unbranched axis with a circular structure potentially representing a sporangial pad (at arrow), EIB688a. (8) cf. *Huvenia* sp., enlarged view of specimen illustrated in (7) showing a relatively scattered occurrence of longitudinally elongated mounds, EIB688a. (9) cf. *Huvenia* sp., enlarged view of specimen illustrated in (5), with denser and more longitudinally elongated mounds, EIB522. (10) cf. *Huvenia* sp., strongly ridged specimen representing the fusion of individual mounds on axis surface, EIB527. Scale bars: 1–7 = 10 mm, 8–10 = 5 mm.

1986; Kenrick and Crane, 1991). Similarly, several *Taenioocrada*-like axes from Germany were later attributed to another genus (*Huvenia*) with anatomical and morphological features characteristic of the rhyniopsids (Hass and Remy, 1991; Schultka, 1991).

Over the years, *Taenioocrada* has become a ‘catch-all’ taxon with up to 14 different morphospecies described, that are probably not all phylogenetically closely related (Taylor, 1986, tables I, II). The different species differ greatly in terms of anatomy, branching pattern and sporangial insertion on axis, demonstrating that a clarification of the definition of the taxon is long overdue (Gossmann et al., 2008). The confusion in the characterization of this genus originates from the fact that all these taxa were associated based upon likely irrelevant or insufficiently informative features. For instance, a central vascular strand or its imprint is oftentimes found among remains of coeval taxa, despite being relatively phylogenetically distant from rhyniopsids, in addition that the presence of such feature is likely at least partly taphonomic (Rayner, 1984; Li and Edwards, 1995; Gossmann et al., 2008; Capel et al., 2022a). Overall, this taxon is relatively uninformative, but the specimen herein illustrated is nonetheless sufficiently distinct from other axes of this assemblage to interpret it as representing a different

plant.

cf. *Huvenia* sp. Hass et Remy

**Material:** EIB678a, EIB681a, EIB683, EIB687, EIB688a, EIB522, EIB527.

**Description:** Axes between 0.6 cm and 2.2 cm in diameter. Longest truncated axis reaches 10 cm in length (Plate I, 3). Branching is anisotomous, occurring at an angle of 50°, with branches significantly smaller in width than the subtending axis (Plate I, 3–6, at arrows). Alternate branching is illustrated in Plate I, 4 with a subopposite arrangement of daughter axes on the main axis (at arrows). These axes could possibly represent aborted branches, given their appearance of tapering distally shortly after dichotomy, however, distal parts are truncated. One trichotomy is also observed (although incompletely preserved), with both branches likewise branching at a 45–50° angle, whilst the central axis continues in the direction of the main axis (Plate I, 5). No fertile material was found in connection or in association with sterile specimens. Nevertheless, one axis presents a subcircular structure (1.8 × 1.4 mm) with concentric circles that could potentially represent a ‘sporangial pad’, i.e., the zone of attachment of sporangia on the stem

(Plate I, 7, at arrow), but see further comments on the interpretation of this structure below. Axes surfaces are characterized by the presence of distinct oval to fusiform (oblong) mounds, sometimes strongly elongated in the longitudinal direction of the axes and with varying degrees of density (Plate I, 8–10). On ‘low-density’ specimens, the length of structures ranges from 0.4 to 1.6 mm (Plate I, 8). In subsequent illustrated specimens (Plate I, 9–10), the density of individual structures becomes so significant that it is difficult to distinguish them individually. Nonetheless, the variation in density of structures (Plate I, 8–10) demonstrates that specimens that appear longitudinally striated with elongated grooves and ridges, result from the longitudinal fusion of individual mounds (Plate I, 10).

**Interpretation:** Large creeping axes that appear longitudinally striated or punctuated with oval to elongated fusiform pits or mounds, have been identified in numerous European and North American Early Devonian localities. These types of axes have been described as different taxa based oftentimes on minute or dubious differences, when in fact, these fossils potentially represent closely related, if not identical plants, which will be discussed here thoroughly to highlight taxonomic inconsistencies.

The most comparable taxa to the Consthum specimens are *Huvenia kleui* and *H. elongata*, respectively from the late Pragian and early to middle Emsian of Germany (Hass and Remy, 1991; Schultka, 1991; Poschmann and Gossmann, 2013). Anatomically preserved remains of *H. kleui* were concurrently studied by Kenrick et al. (1991) showing water-conducting cells (S-type) comparable to well-known rhyniopsids (e.g., *Sennicaulis hippocrepiformis*), thereby confirming its affinities with this early plant group. Our specimens share many characteristics with these two species, including similar ornamentation on the surface of axes, branching pattern (including trichotomies), aborted branches (truncated cone-shaped axes), and potentially ‘sporangial pads’. It is noteworthy that these latter structures herein interpreted as sporangial pads may originate from the impression left behind by the growth of the small, coiled, calcareous tube of a lophophorate (Taylor and Vinn, 2006). Microconchids are indeed present in samples from Consthum Quarry, but are extremely rare. However, most of the following discussion revolves around differences in plant vegetative morphology, therefore, one or the other possibilities does not particularly undermine the interpretation of these specimens.

Axes of *H. kleui* and *H. elongata* are narrower (up to 6–8 mm and 8–9 mm respectively), although this still falls within the lower range of axes from Consthum Quarry. Another difference is that half of specimens of *H. kleui* possess a smooth surface, whereas all our specimens are ornamented. Interestingly however, it appears that axes of *H. elongata* all bear ‘emergences’, reaching a length of 1.6 mm in the longitudinal direction of axes, and likewise, strongly longitudinally grooved axes, similarly to some of our axes (Plate I, 8–10). The lack of fertile morphology and anatomy among specimens from Consthum precludes further comparison with these taxa, although vegetative morphology is evidently similar. The lack of fertile material can probably be attributed to its rarity in comparison to vegetative remains. 1000 specimens of *H. kleui* were examined in previous studies, of which only about 100 were fertile. Finding fertile material among the 10 specimens that could be reliably identified at Consthum is therefore unlikely. *Huvenia* is also reported from the Canadian middle to late Emsian Battery Point Fm. in Hottton et al. (2000). However, comparison is hindered by a very limited description and no general illustration of specimens, with only very detailed SEMs of sporangial bases, sporangia and *in situ* spores.

Another strongly comparable taxon to the specimens from Consthum is *Taeniocrada dubia*, which was likewise reported from several coeval plant-bearing localities in Belgium and Germany (Stockmans, 1940; Kräusel and Weyland, 1930; Schweitzer, 1980a, 1987; Gerrienne, 1993). *T. dubia* was curiously not compared with *Huvenia* spp. in neither Hass and Remy (1991) nor Schultka (1991), despite the obvious similarities in vegetative and fertile morphology. Specimens are mostly unbranched, although isotomously-dichotomizing axes are recorded with similar

ornamentation to our specimens, and also bearing a conspicuous vascular strand imprint (Kräusel and Weyland, 1930; Stockmans, 1940). Fertile remains of *T. dubia*, although not found in direct connection but associated with sterile axes similar to those of *Huvenia* and *Stockmansella*, were also illustrated in Kräusel and Weyland (1930, taf. 6, fig. 1–2). *T. dubia* was more recently identified in the Battery Point Fm. at Gaspé Bay (Canada) in Hottton et al. (2000), but these authors informally referred to it as ‘New genus D’, given that this plant should be re-described. Sporangial pads (1 × 2 mm) were likewise noticed on several axes (Hottton et al., 2000, fig. 11.13F). Interestingly, oval pits on the axis surface were interpreted as stomata. It is not clear how this interpretation arose, as no cuticular material seems to have been extracted and studied. Regardless, some of these ‘oval pits’ are overly elongated to represent stomata or stomatal traces (Hottton et al., 2000, fig. 11.13C). Furthermore, stomata do not typically leave such a strong imprint on the rock matrix. The nature of these oval pits remains quite uncertain. Hass and Remy (1991) illustrated specimens of *H. kleui* that displayed, on the side of the axis, semi-circular elevations, similarly to Schultka (1991) with *H. elongata*. A possible emergence was identified but is poorly preserved and no other examples were found (Hass and Remy, 1991, taf. 52, fig. 5).

Another specimen of *T. dubia* from the Battery Point Fm. presents a permineralized central vascular strand that, after preparation, confirmed its rhyniopsid affinities, further supporting the interpretation that *T. dubia* represents a very similar plant to *Huvenia* (Hottton et al., 2000). The only remaining difference between the two taxa almost solely rests on the presence of a more conspicuous vascular strand. Nonetheless, as discussed previously in the section on *Taeniocrada* sp., the preservation of a vascular strand is probably not a reliable discriminating factor in Early Devonian plant identifications and is likely to some extent taphonomic. The attribution herein of our axes to cf. *Huvenia* sp. and not *T. dubia* is grounded on the fact that comparison with *Huvenia* could be more thorough as it is based on more complete specimens than *Taeniocrada*, but also because our specimens are differentiated from *T. dubia* by the lack of conspicuous vascular strand imprint and isotomous type of branching.

Another comparable taxon was described by Stockmans (1940) under the name *Drepanophycus? crepinii*. On *D.? crepinii*, mounds or punctae are observed on the surface of axes but without any vascular strand imprint. It was provisionally assigned to *Drepanophycus* based on apparent emergences on one compressed specimen (Stockmans, 1940; pl. XIII, fig. 3–3a). However, its assignment to *Drepanophycus* is unwarranted as these emergences have no indication of vascularization, along with the fact that the axis poorly compares to the general vegetative morphology of *Drepanophycus*. The cf. *Drepanophycus? crepinii* from Grimbiémont-Roy (Stockmans, 1940, pl. XIII, fig. 5) and from Rouveroy (Stockmans, 1940, pl. II, fig. 4), partially preserved as a cast, displays similar features to the specimen illustrated at Plate I, 10 with strong ridging on the surface of the axis and anisotomous branching. A similar vegetative axis recently re-described in Capel et al. (2024, pl. II, fig. 2) from the Emsian of France, is also preserved as partially-compressed cast with what appears to be longitudinal ridging and grooves and was previously attributed to *Drepanophycus? crepinii* by Danzé-Corsin (1956). This specimen was also compared to *T. dubia*, and the absence of a vascular strand imprint was attributed to taphonomy. It is noteworthy that most specimens from Consthum are preserved as partially-compressed casts, which probably also did not allow the preservation of the vascular strand nor its imprint.

Given the available evidence, it is possible that all the previously mentioned taxa and undetermined axes belong to a similar rhyniopsid entity with a creeping habit. The nature of the ‘ornamentation’ remains to be defined, but these structures probably do not represent emergences (i.e., spines or spine-like structures), nor stomatal traces. It is possible that this feature, more or less densely occurring, may vary depending on the original position of the axis in the plant, e.g., creeping vs. aerial stems, similarly to *Drepanophycus*, although no correlation between size

and ridging of axis is observed. This feature could also potentially represent a trait that was more or less expressed according to a particular environmental factor.

aff. *Zosterophyllum* sp. Penhallow

Plate II, 1–2

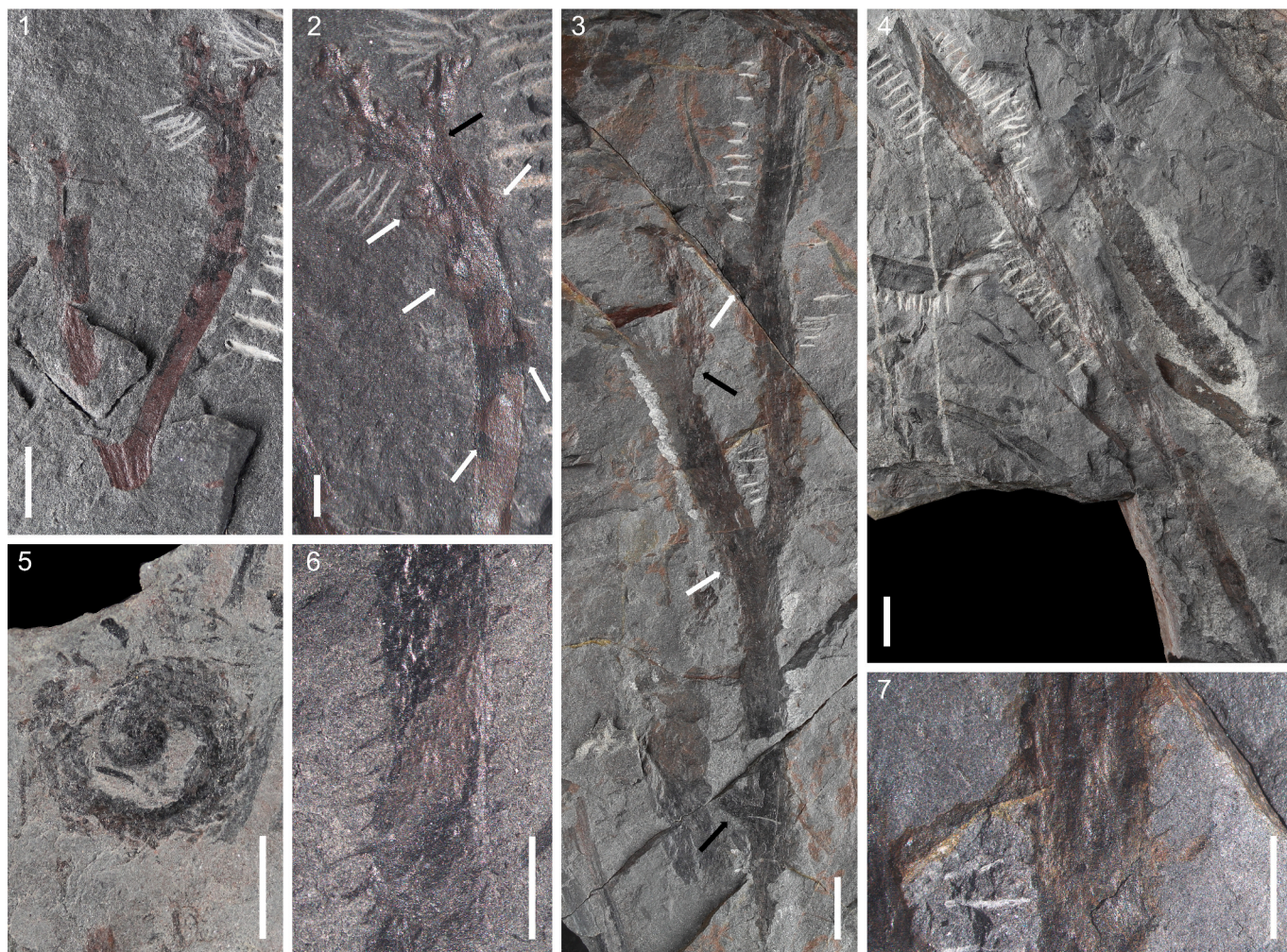
Material: EiB517.

**Description:** A single smooth isotomously-branched specimen was identified (Plate II, 1). The main axis below the dichotomy reaches 3.5 mm in diameter. The two branches are 2.5 and 2.1 mm wide respectively. The branch on the right bears sporangia-like structures, seemingly helically arranged (Plate II, 1–2). Sporangia-like structures are loosely inserted onto the axis, nonetheless increasingly tightly clustered towards the apex (Plate II, 2, at arrows). Individual structures are oval in frontal view ( $3.1 \times 1.5$  mm), whilst distalmost structures appear sub-circular and reach between 1 and 2.5 mm in maximum diameter. The axis bears small globose structures near the apex and seems to branch once again, but this time anisotomously, although this remains ambiguous as this part is likely truncated.

**Interpretation:** The general morphology of this specimen is

reminiscent of the architecture found within the speciose genus *Zosterophyllum*. Similar types of branching pattern and axial morphology are documented in e.g., *Z. ramosum* from the Pragian–Emsian of South China (Hao and Wang, 2000; Hao and Xue, 2013, fig. 4.15) or the recently described *Z. confertum* from the Pragian–Emsian of Germany (Gossmann et al., 2022). However, in both species, sporangia are larger, more reniform and feature a conspicuous thickened rim. In addition, sporangia are tightly clustered towards the apex and not loosely inserted on the axis. Nevertheless, it remains unclear to what extent the specimen illustrated herein is complete, especially near the apex, so the presence of another segment with increasingly clustered sporangia cannot be ruled out. On the other hand, numerous other species do display this type of sporangial organization on fertile axes: e.g., *Z. tenerum* (Hao and Xue, 2013), *Z. ovatum* (Edwards and Li, 2018), *Z. shengfengense* (Hao et al., 2010) or even other zosterophylls such as *Wenshania zhichangensis* (Zhu and Kenrick, 1999). *Z. myretonianum*, in addition to presenting loosely inserted sporangia on fertile axes, also exhibits, at times, smaller, and less clearly defined sporangia towards the base of the axis, similarly to this Consthum plant (Edwards, 1975, pl. I, figs. 1–4).

Independently of sporangial arrangement on the axis, most species of



**Plate II.** Zosterophylloids macrofossils from Consthum Quarry, Luxembourg. (1) aff. *Zosterophyllum* sp., general view of the smooth isotomously-branched specimen; note the truncated left axis and the round to oval structures potentially representing fertile structures on the right axis, EiB517. (2) aff. *Zosterophyllum* sp., enlarged view of the putative fertile axis; note the helical arrangement of sporangia-like structures (at white arrows) and a potential ultimate anisotomous dichotomy (at black arrow) with unclear small globose structures towards the apex, EiB517. (3) cf. *Sawdonia* sp., vegetative specimen displaying multiple anisotomous (at black arrows) and pseudomonopodial (at white arrows) dichotomies, EiB520. (4) cf. *Sawdonia* sp., multiple sterile spiny axes with one particularly long unbranched specimen, EiB532. (5) cf. *Sawdonia* sp., isolated axis showing circinate vernation with numerous densely packed emergences, EiB689. (6) cf. *Sawdonia* sp., specimen with well-preserved untruncated acicular emergences, EiB685. (7) cf. *Sawdonia* sp., enlarged view of a portion of an axis illustrated in (3) showing conspicuous emergences with stout triangular bases than an acicular tip, EiB520. Scale bars: 1, 5–7 = 5 mm; 2 = 2 mm; 3–4 = 10 mm.

*Zosterophyllum*, including *Z. myretonianum*, possess larger sporangia in proportion to subtending axes width, casting further doubts on the interpretation that these structures represent in fact sporangia. In addition to the small size of purported sporangia, the absence of conspicuous stalks and thickened rim—which are features oftentimes present in zosterophyll taxa—likewise undermines this interpretation. One possibility worth considering is that these structures represent immature sporangia. However, in *Ramopheris analia* (Hao and Xue, 2011), a closely allied plant to *Zosterophyllum*, immature sporangia are located at the apex, not towards the basalmost portion of the axis (Hao and Xue, 2013, fig. 4.11b), whilst all potential fertile structures on our specimen appear immature. To conclude, the equivocal nature of the helically arranged round to oval structures hinders a more precise identification and the specimen herein illustrated can only be shown to have affinities with the genus *Zosterophyllum*.

cf. *Sawdonia* sp. Hueber emend Gensel et Berry

Plate II, 3–8

Material: EiB520, EiB532, EiB685, EiB689.

**Description:** Vegetative axes reaching 0.8 cm in width and 14.6 cm in length (Plate II, 3–4). The best-preserved specimen frequently branches (Plate II, 3, at arrows), whilst other large axes are completely unbranched (Plate II, 4). Branching is planar and alternate. Branching pattern is either anisotomous or pseudomonopodial (Plate II, 3 at white and black arrows respectively). Axes branch at a 60° wide angle before recurving and growing more closely parallel to the main axis. An isolated axis is interpreted to represent a circinate tip with numerous small adaxially recurved emergences (Plate II, 5). Emergences observed on the side of mature axes are separated by a distance ranging from 0.9 to 1.4 mm (Plate II, 6–7). Emergences often appear truncated and surface texture of axes suggests emergences are even more densely packed (Plate II, 6). No specific arrangement of emergences on axes surfaces can be reliably identified. Emergences have a triangular base (at times relatively stout), that first rapidly, then slowly tapers, terminating in an acicular tip (Plate II, 6–7). Measurements on best preserved specimens show that bases are 0.7–1.3 mm wide, whilst emergences reach a maximum length of 1.5–2.5 mm. Several emergences appear abaxially or adaxially recurved (Plate II, 6–7). No fertile structures were detected after preparation of specimens.

**Interpretation:** As no fertile structures were identified, comparisons will be herein strictly limited to vegetative morphology. Vegetative axes covered with emergences, branching anisotomously firstly at a wide angle then recurving to grow closely parallel to the other axis, are features characteristic of the zosterophyll genus *Sawdonia* and other *Sawdonia*-like plants. In addition, emergences shape and size solely compare accurately with those found in *Sawdonia* (Jensen and Gensel, 2013, table 1). Lastly, despite being a defining feature of zosterophylls, the presence of circinate axes, associated with the same type of emergences, likewise suggests a zosterophyll such as *Sawdonia*.

Among currently accepted and well circumscribed *Sawdonia* species, emergences of the Consthumb specimens bear the most resemblance to those of *S. ornata* and *S. deblondii*, with their triangular base and acicular point, whilst emergences in *Sawdonia hippotheca* are longer (3–5 mm), widely spaced, and decurrent at their base (Gerrienne, 1996a; Gensel and Berry, 2016; Berry and Gensel, 2019). In *Sawdonia ornata*, the bases of the emergences are smaller and generally less triangular than those of our specimens, although the intraspecific variability is important and at times, emergences closely resemble ours in terms of size and shape (Gensel and Berry, 2016). Emergences are most similar to those found in *S. deblondii* which are more triangular at their base and thinner in their distal part, alongside a very similar size range. Nevertheless, emergences in both species do not appear as tightly packed as the specimens from Consthumb.

Other *Sawdonia*-like plants described as *Psilophyton princeps* in Stockmans (1940, pl. VIII, fig. 6–9) from Belgium display more densely packed emergences. The axes surface in terms of emergence density also

bears a lot of resemblance with the taxon *Thursophyton vahlbergium* (Kräusel and Weyland, 1930; taf. 9, fig. 6, taf. 11, fig. 1) created for 5–10 mm wide axes covered by 0.4–0.6 mm long spines (although probably mostly truncated), and apical circination. *T. vahlbergium* probably represents sterile isolated axes of *Sawdonia* or other *Sawdonia*-like plants. Gensel and Berry (2016) argued that in the absence of fertile attributes and unequivocal vegetative morphology, *Sawdonia*-like axes are better referred to as cf. *Sawdonia*, which is the designation applied herein.

*Drepanophycus spinaeformis* Göppert emend Li et al.

Plate III, 1–7

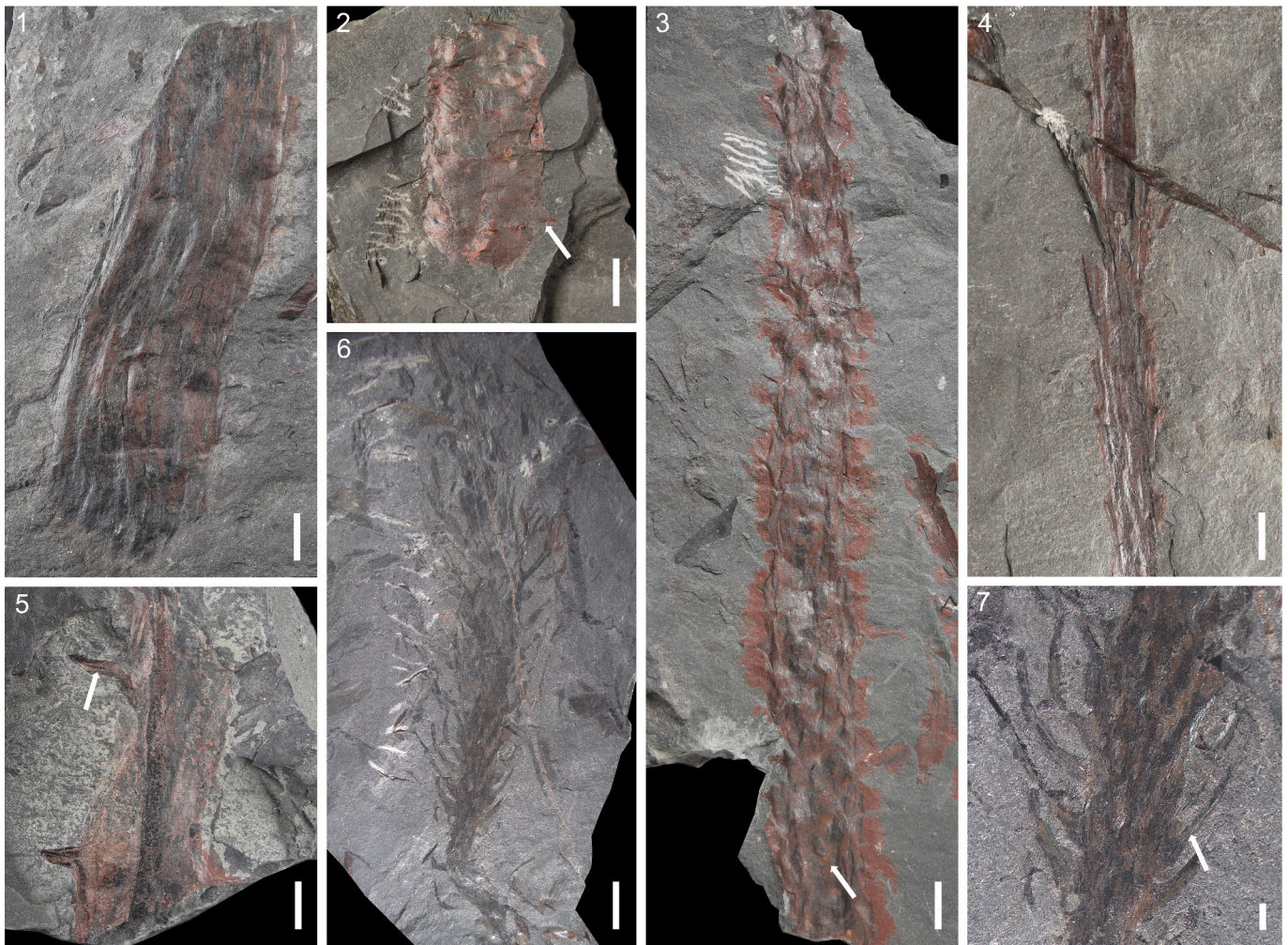
Material: EiB531a, EiB533a, EiB686a, EiB680, EiB682a, EiB679a.

**Description:** Largest vegetative axis reaches 3.4 cm in width (Plate III, 1). Large axes surface smoother (ribbon-like texture) than thinner axes and are generally rarely covered by, or devoid of, conspicuous leaves or leaf bases (Plate III, 1–4). All specimens are unbranched despite certain stems reaching up to 19 cm in length (Plate III, 3). One specimen shows a meandering vascular strand within the axis (2.2 mm wide) that also bears large leaves (4–5 mm), with a conspicuous vascular strand imprint in its center from base to apex (Plate III, 5, at arrow). One smaller, particularly leafy shoot has been identified (Plate III, 6–7). Largest leaves on this shoot are thinner than the specimen illustrated in Plate III, 5, but also longer with a length reaching 5–7.5 mm. A vascular strand imprint can be observed at their center confirming their vascularized nature (Plate III, 7, at arrow). Leaves are separated by a distance of 1.7–2.1 mm on the leafy shoot and are recurved adaxially. The arrangement of leaves is not clearly distinguishable owing to the preservation, and at times, density of leaves on axes, although one specimen with large leaf bases suggests a helical arrangement of these features on axes (Plate III, 3, at arrow). No fertile specimens were identified.

**Interpretation:** Large creeping axes covered with microphylls and/or microphyll bases suggests the widespread Early Devonian taxon *Drepanophycus* and more specifically *D. spinaeformis* (Li et al., 2000). The only other well circumscribed species of *Drepanophycus* (*D. qujingensis*), is differentiated from *D. spinaeformis* mostly over divergence in branching pattern, sporangial morphology, and vegetative anatomy; features that were not preserved in the material from Luxembourg rendering difficult to assign to either species. Nonetheless, leaves in *D. qujingensis* tend to be abaxially recurved, a feature argued by Li and Edwards (1995) to not originate from taphonomy. The leafy shoot illustrated in Plate III, 6 bears the most resemblance to leafy shoots reported from the neotype locality of *D. spinaeformis*, likewise displaying adaxially recurved microphylls (Li et al., 2000), a feature which has also been observed in material from the original type area (Poschmann, 2012). Overall, vegetative morphology is sufficiently distinct to assign the specimen from Consthumb to *D. spinaeformis*.

Nevertheless, another genus was recently created to accommodate material previously assigned to *Drepanophycus* (Matsunaga and Tomescu, 2017), which also closely resembles the Consthumb specimens. This genus represents plants with a similar grade of organization to *Drepanophycus*, being likewise characterized by large creeping axes with vascularized emergences interpreted as leaves. Vegetative specimens of *Sengelia* however differ from *D. spinaeformis* by their specific branching pattern (mostly or even exclusively K-branching). Unfortunately, the absence of branching in our material herein precludes a more thorough comparison with the different species of *Sengelia*, in addition to the absence of sporangia. However, leaves in *Sengelia radicans* are usually stouter than our specimens and more deltoid-shaped, even at time showing a convex border (Matsunaga and Tomescu, 2017, fig. 2). Additionally, shoots are not as densely covered of leaves compared to *D. spinaeformis*. Slenderer and slightly more densely packed leaves are observed on axes of *Sengelia (Drepanophycus) minor* (Xu et al., 2013), but this time leaves are thinner than what is observed on our specimens. Therefore, our interpretation favors the attribution of these specimens to *D. spinaeformis* over any species of *Sengelia*.





**Plate III.** Vegetative remains of *Drepanophycus spinaeformis* from Consthum Quarry, Luxembourg. (1) Large unbranched smooth stem with a ribbon-like aspect, EIB533a. (2) Relatively smooth axis with nonetheless a conspicuous leaf (at arrow) and leaf bases, EIB679a. (3) Longest untruncated stem from the assemblage, note the higher density of leaf bases compared to previously-illustrated specimens and evidence of helical arrangement (at arrow), EIB682a. (4) Thinner stem with an increased density of leaves on axis (although truncated), EIB680. (5) Axis displaying a meandering vascular strand imprint and two well-preserved leaves, including a conspicuous vascular strand imprint at their center (at arrow), EIB531a. (6) Leafy shoot with numerous densely-packed and well-preserved leaves, EIB686a. (7) Enlarged view of (6), showing in further details the leaves; note the thin central vascular strand imprint at arrow, EIB686a. Scale bars: 1–3 = 10 mm; 4–6 = 5 mm; 7 = 1 mm.

Despite all the specimens from Consthum being unbranched and sterile, vegetative morphology is quite variable with the larger axes usually devoid of leaves and leaf bases, or only occasionally bearing stout leaves or leaf bases, and thinner axes being increasingly densely covered in leaves (Plate III, 1–6). These have been interpreted to respectively represent rhizomatous and aerial stems leading to this wide intraspecific variation (Li et al., 2000). Not unlike several common taxa from coeval deposits, *Drepanophycus* is rarely fertile, and most findings were of sterile vegetative axes, indicating that the plant mainly reproduces vegetatively (Hueber, 1992; Li et al., 2000; Hotton et al., 2000). For instance, axes of *D. spinaeformis* have been identified in nine different Early Devonian localities in Belgium and none were found to be fertile (Stockmans, 1940; Gerrienne, 1993). This discrepancy may also arise due to a greater quantity of vegetative axes produced, reflecting resources being primarily allocated to photosynthetic as opposed to reproductive functions within the individual.

*Psilophyton* cf. *princeps* Dawson emend Hueber

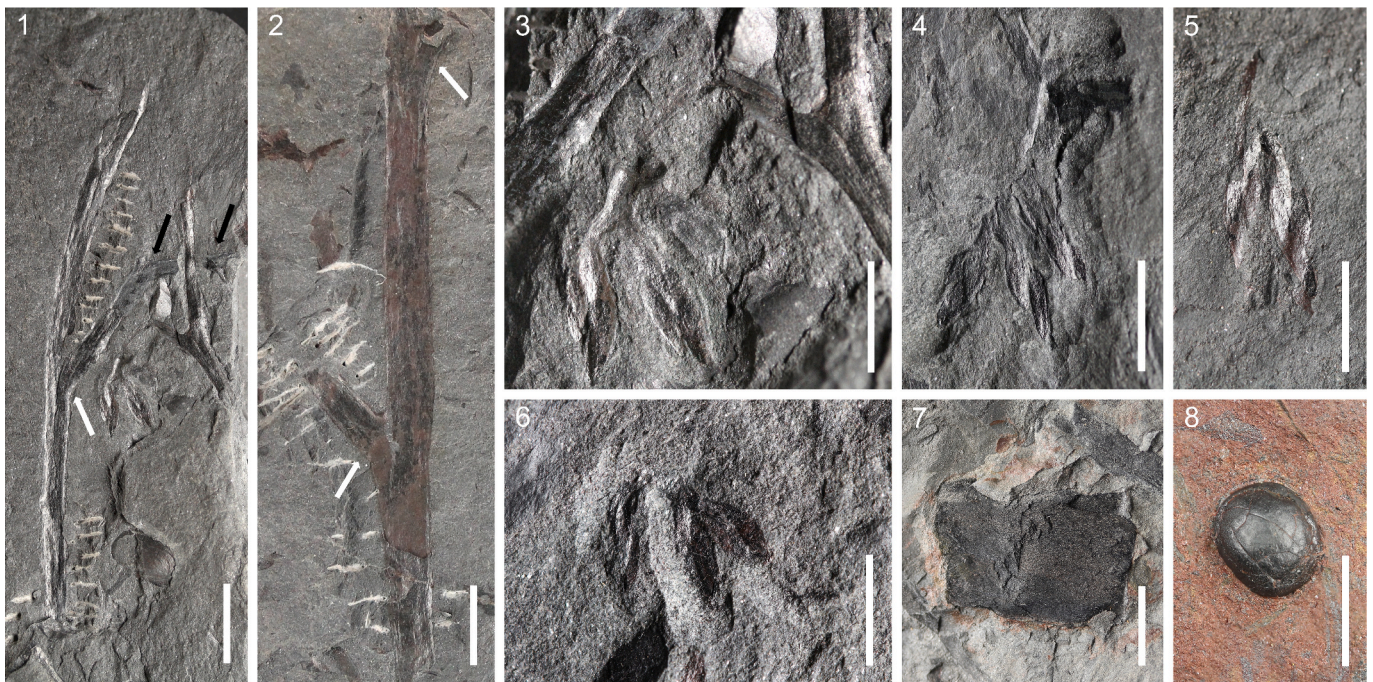
Plate IV, 1–6

**Material:** EIB513a, EIB684, EIB506, EIB509a, EIB508a.

**Description:** Vegetative axes were identified as such, based on their

association with fertile remains unequivocally assignable to *Psilophyton* (Plate IV, 1). Main axes maximum width reaches 6 mm (Plate IV, 2). Axes surfaces are smooth or slightly striated (Plate IV, 1–3). Branching is pseudomonopodial on main axes and isotomous among distal branches (Plate IV, 1, 2, at arrows). One isolated vegetative axis, interpreted to belong to the same taxon, shows an alternate type of branching (Plate IV, 2, at arrows). In addition to vegetative remains, multiple pairs of sporangia were found either in association or isolated across rock samples (Plate IV, 3–6). Pairs of sporangia are pendulous with a clear torsion of the sporangia around each other. The number of pairs of sporangia per fertile unit is unknown given the degree of incompleteness of fertile specimens. Sporangia are elongated, fusiform and connected to thick - in proportion to sporangial width - stalks (Plate IV, 3). Individual sporangia are between 6.2–7.4 mm long and 0.9–1.2 mm wide.

**Interpretation:** Pairs of fusiform sporangia borne terminally on stalks along with a torsion of sporangia around each other indicates that this material belongs to the genus *Psilophyton* (Hueber and Banks, 1967; Gerrienne, 1997). Regarding vegetative morphology, a pseudomonopodial branching pattern of the main axes and isotomous branching in distal parts is also a defining feature of *Psilophyton*. A conspicuous feature of fertile specimens from Consthum Quarry is the large size of the



**Plate IV.** Basal euphyllphyte and putative algal and fungal macrofossil remains from Consthum Quarry, Luxembourg. (1) *Psilophyton* cf. *princeps*, pseudomonopodially-branched axis (at white arrow) followed by two successive isotomous dichotomies (at black arrows); note another isotomously-branched axis to the right as well as pairs of sporangia, associated, but not directly connected to vegetative axes, EIB513a. (2) *Psilophyton* cf. *princeps*, large vegetative alternately- and pseudomonopodially-branched axis (dichotomies at arrows), EIB684. (3) *Psilophyton* cf. *princeps*, detailed view of pairs of sporangia connected to a wide stalk illustrated in (1), EIB513a. (4–6) *Psilophyton* cf. *princeps*, other isolated pairs of twisted fusiform sporangia; (4) EIB506; (5) EIB509a; (6) EIB508a. (7) Possible specimen of *Prototaxites*, EIB534. (8) *Pachythea* sp., EIB505a. Scale bars: 1–2, 7 = 10 mm; 2–6, 8 = 5 mm.

sporangia. The only currently described species of *Psilophyton* bearing such large fertile organs is *P. princeps* (Dawson, 1871; Hueber and Banks, 1967), with sporangia up 7.5 to 8 mm long and 1 to 2 mm wide (Gerrienne, 1995, fig. 2). Sporangia illustrated herein are slightly smaller and less fusiform than those produced by *P. princeps* but are also borne on wide stalks (Hueber and Banks, 1967, fig. 6). However, whereas the surfaces of vegetative and fertile axes in *P. princeps* are occasionally covered with 1.5 to 2.5 mm long peg-like enations, none of the Luxembourg material presents this feature. Consequently, the plant described herein is probably closely related to *P. princeps*, but since sporangial morphology and size is slightly different, in addition to the absence of peg-like enations, specimens cannot be conclusively attributed to this species and are designated as *Psilophyton* cf. *princeps*.

It is noteworthy that specimens attributed to *Taeniocrada longisporangiata* or “*T.*” *longisporangiata* from the Klerf and Nellenköpfchen Formations in Germany, also display similar features in terms of sporangial morphology (Poschmann et al., 2012; Poschmann and Gossmann, 2013). Nonetheless, their sporangia measure between 4.1 to 6.7 mm in length, which is notably smaller than the Consthum specimens. Some of these sporangia also appear significantly wider. Further reinvestigation of the material will be necessary to better assess the degree of similarity of these specimens with the ones from Consthum. These German fossils likely belong to a basal euphyllphyte such as *Psilophyton* and should therefore be revised.

#### Putative fungal and macroalgal remains

##### Plate IV, 7–8

An enigmatic specimen noticed within the assemblage could potentially represent the taxon *Prototaxites* (Plate IV, 7), an organism with presumed fungal affinities from the Silurian–Devonian interval (Hueber, 2001; Morris and Edwards, 2014; Honegger et al., 2018). The specimen is 4.2 cm long and 1.5 cm wide, longitudinally striated with seemingly several superimposed layers of this material, that impart to it a different surface texture than the other plant macrofossils. Since the primary

focus of this study are plant macrofossils, the specimen was not further prepared and studied, but is nonetheless mentioned.

Another specimen is interpreted to represent *Pachythea*, a putative macroalga, also very common among Early Devonian assemblages (Corsin, 1945; Gerrienne et al., 1999). This specimen is subcircular (5.3 mm long and 4.8 mm wide) and superficially cracked (Plate IV, 8). This cracked appearance of the surface is illustrated in another *Pachythea* specimen from England in Croft and Lang (1942, pl. 11, fig. 71). For similar reasons to *Prototaxites*-like remains, this specimen was not thin-sectioned and consequently not studied in detail anatomically.

## 5. Discussion

This new collection provides an updated and critical account of plant fossil diversity at Consthum Quarry, which is higher than previously thought. Compared to the original plant fossil collection (Delsate et al., 2003), the taxonomic composition of the new assemblage is somewhat similar, with the shared occurrence of *Drepanophycus spinaeformis*, and ? *Stockmansella langii*/*Taeniocrada*-like plant fossils (herein identified as *Taeniocrada* sp.). Furthermore, isolated pairs of sporangia originally attributed to *Dawsonites arcuatus* in Delsate et al. (2003) - *Dawsonites* being a genus created to accommodate isolated pairs of twisted sporangia likely produced by *Psilophyton* - could be similar if not identical to the material identified as *Psilophyton* cf. *princeps*, where sporangia are likewise borne terminally on robust stalks. On the other hand, axes bearing stout spines identified as *Psilophytites* sp. in Delsate et al. (2003) were not recorded in our new collection. These types of isolated vegetative axes are notoriously difficult to identify as they can equally belong to a basal euphyllphyte such as *Psilophyton* or a zosterophyll. Regardless, this specimen seems to represent a different plant to any identified herein. Lastly, specimens assignable to cf. *Huvenia* sp. were apparently absent from the original collection in Delsate et al. (2003), although probably *Huvenia* remains were not differentiated from *Taeniocrada* or ?*Stockmansella*.

The taxonomic composition at higher taxonomic levels reveals that all major clades of early land plants (i.e., rhyniopsids, zosterophylls, lycopsids and basal euphyllophytes) were present and in relatively equal abundance, even though remains of the lycopsid *Drepanophycus spinaeformis* are most abundant (Fig. 3). Unfortunately, since most remains were found to be sterile, the specific affinities of several taxa identified remain conjectural, but nonetheless supported by vegetative morphology. The only notable difference is *Psilophyton cf. princeps* as several isolated pairs of sporangia were found within the assemblage. The discrepancy observed between the number of fertile specimens of *P. cf. princeps* and other taxa in the Consthum assemblage is linked to the fact that *Sawdonia*, *Drepanophycus* and *Huvenia* are known to produce very few sporangia (Hass and Remy, 1991; Hotton et al., 2000; Gensel and Berry, 2016). Similar reproductive strategies, despite their phylogenetic distance, are probably the consequence of an adaptation to a particular ecological niche. It is noteworthy that all these plants are also interpreted to possess a creeping habit further suggesting an occupation of similar ecological niches. *Psilophyton* on the other hand, is interpreted to represent a plant that sexually reproduced profusely, with the aerial part of the plant more significantly developed than the rhizomatous system (Hotton et al., 2000). The ecology of early land plants remains poorly understood, so further ecological interpretations always remain speculative.

Overall, the Consthum flora is closely comparable to other Emsian floras from the paleocontinent of Laurussia and especially with other localities from the Ardenno-Rhenish Massif (e.g., Kräusel and Weyland, 1930; Stockmans, 1940; Hass and Remy, 1991) and the Battery Point Fm. in Canada (e.g., Li et al., 2000; Hotton et al., 2000). A good analogue of this flora comes from a coeval assemblage (Oppel Zone AB to FD) of the Klerf Fm. at Waxweiler (Eifel, Germany), shows similar composition with the co-occurrence of *Drepanophycus*, *Psilophyton*, *Sawdonia*, *Taeniochrada*, and *Zosterophyllum*. (Schweitzer, 1983, 2000; Poschmann and Franke, 2006; Steemans et al., 2023). Such associations of plants are legion among classic Belgian and German Pragian-early Emsian floras, and in this way, the Consthum assemblage does not particularly stand out (Capel et al., 2023). However, a distinct feature of this assemblage is the identification of plant remains that resemble *Psilophyton princeps*, a taxon only thus far found in the late Emsian of Gaspé Bay, Canada (Hueber and Banks, 1967; Gerrienne, 1995). The absence of this taxon from the Ardenno-Rhenish massif may be related to the fact that Emsian floras are oftentimes early Emsian in age. Nonetheless, even though the flora herein is younger than many Pragian–Emsian localities from Belgium and Germany, taxonomic composition, at the generic level remains identical showing a relatively slow vegetational turnover. This is corroborated by the preliminary description of a paleogeographically close flora from the latest Emsian of Poland also showing that this type of vegetation - at least according to the adpression record - in this area remains dominant throughout the Emsian (Filipiak et al., 2022).

Finally, the Consthum fossil flora also exemplifies in many instances the taxonomic inconsistencies encountered when identifying Early Devonian plants, especially regarding isolated sterile remains. For instance, sterile axes attributed herein to *cf. Huvenia* sp. may be similar to several specimens previously attributed to *Taeniochrada* and *Drepanophycus*, although a reinvestigation of that fossil material itself from several localities in Europe and North America would be required to assert with certainty that they represent the same plant. Many taxonomic descriptions of plants from the Ardenno-Rhenish Massif are usually rather outdated and were, until very recently, written in two different languages (i.e., German and French). A harmonization of plant identifications from this region - by virtue of containing some of the best biostratigraphically constrained Early Devonian successions - could provide, for the first time, an accurate high-resolution depiction of plant diversity changes during this key period of the plant terrestrialization process. The work undertaken herein is a first step towards the completion of this objective.

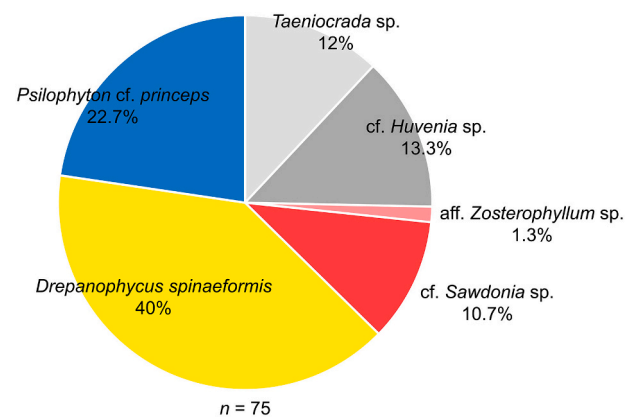


Fig. 3. Relative abundance of each identified plant macrofossil species within the Consthum Quarry assemblage. Colors: gray = rhyniopsids; red = zosterophylls; yellow = lycopsids; blue = basal euphyllophytes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

## 6. Conclusions

- The newly collected macroflora from Consthum Quarry is moderately diverse and consists of typical taxa found among numerous coeval assemblages across the paleocontinent Laurussia, both at genus and at higher taxonomic levels.
- The taxonomic composition of this new collection is relatively similar to the previous assemblage collected in the early 2000s from this locality, although *Sawdonia*- and *Huvenia*-like remains were not originally identified and the new collection lacks *Psilophytites*.
- This middle Emsian flora is extremely similar in composition to coeval or older floras from this region, further suggesting an absence of major floral turnovers throughout this time interval.
- Numerous inconsistencies in previous identifications of plant fossils from the Ardenno-Rhenish Massif highlight the need for a deep and thorough revision of collections located in Belgium and Germany.

## Declaration of competing interest

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

## Data availability

Data will be made available on request.

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