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On the occurrence of *Zosterophyllum confertum* in the Lower Devonian of the Lambert quarry near Bertogne, Belgium

Timotheus K.T. Wolterbeek, Anthonie Hellemond, Kevin Nolis, and Sven Van Uytfanghe

ABSTRACT

Zosterophyllopsid specimens are described from the Lower Devonian (Mirwart Formation) of the Lambert quarry near Bertogne, Belgium. The newly discovered fertile material is characterised by the presence of compact, terminally positioned strobili. These strobili correspond closely with those borne by *Zosterophyllum confertum* Gossmann et al., 2022, a zosterophyllopsid species described recently from the Siegenian (Pragian–lower Emsian?) of the central Rhenish Massif, Germany. With the examples of *Z. confertum* from the Ardennes illustrated here, the palaeobiogeographical range of this stratigraphically significant species can be expanded into the Belgian sector of the Rhenohercynian Zone.

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INTRODUCTION

In Early Devonian times, the region encompassing the present-day Ardennes (Belgium), Eisleck (Luxembourg) and Rhenish Slate Mountains (including the Eifel, Bergisches Land, Westerwald and Sauerland – Germany) was located just south of the equator (Ziegler, 1982; Scotese and McKerrow, 1990; Bełka et al., 2010). The area formed a large foreland basin on the southern border of the "Old Red Sandstone" continent of Laurussia, developing in a narrow but elongate extensional mobile belt system (Godefroid and Cravatte, 1999; Pirson et al., 2008; Bełka et al., 2010; Stets and Schäfer, 2011). With sediment being supplied from the north, the German part of the Rhenohercynian basin saw the development of meandering river systems gradually passing into large fluvial-dominated, bird's-feet type siliciclastic delta systems (Stets and Schäfer, 2002, 2009). The clastics-dominated Lower Devonian facies in Belgium are generally similar (Goemaere and Dejonghe, 2005), with marshes, wetlands and fluvial environments occurring towards the London-Brabant Massif in the north and floodplain to nearshore tidal-marine environments occurring towards the Rhenohercynian Ocean in the south (Bultynck and Dejonghe, 2001; Boulvain and Pingot, 2015). The climate was generally humid and warm (Stets and Schäfer, 2002). While fluctuations in eustatic sea level caused occasional flooding of the foreland during most of the Early Devonian (Godefroid and Cravatte, 1999), the regional Pragian strata are characterized by an absence of marine fauna, often referred to as the "Rhenish Gap" (Jansen, 2016, 2019). Given the poor availability of marine index fossils during this interval, there is a need for other markers to help delineate stratigraphic relationships.

The Lambert quarry presents one of the larger outcrops of Lower Devonian rocks in the Ardennes. During a previous study of the locality, Goemaere and Dejonghe (2005) observed several rock units containing abundant plant remains. They reported nude, sometimes dichotomously branching plant axes reaching up to 25 cm in length. These remains were recognised as probably related to the zosterophyllopsids on basis of macroscopic characteristics (Gerrienne in Goemaere and Dejonghe, 2005, p. 42, p. 46). However, since no spines or strobili were observed, closer identification of the plant remains was impossible at the time (Goemaere and Dejonghe, 2005, p. 42). Here, we describe a discovery of fertile specimens at the Lambert quarry, comprising numerous strobili assignable to *Zosterophyllum confertum* Gossmann et al., 2022. Although historically this species has been frequently misidentified as *Zosterophyllum rhenanum* Kräusel and Wayland, 1935, it occurs widespread in Lower Devonian rocks of the central Rhenish Massif, Germany, where it is restricted to – and considered an index fossil for – Siegenian strata (Gossmann et al., 2022). To our knowledge, this is the first time that the species is formally reported from Belgium (Leclercq, 1942; Gerrienne, 1983, 1988). As a potential index fossil, the occurrence of *Z. confertum* at the Lambert quarry may prove valuable for refining stratigraphic correlations between the different subregions of the Ardenno-Rhenohercynian Basin (Dejonghe et al., 2017). In this contribution, we will briefly review the geology of the Lambert quarry and provide an updated record of its Early Devonian vascular plant assemblage, which could also be extended with drepanophycalean lycophyte elements and slender *"Taeniocrada"*-type axes of unknown biological affinity.

GEOLOGICAL SETTING

The Lambert quarry is located about 1 km east-southeast of Wigny, a small village in the municipality of Bertogne (Luxembourg province, Wallonia, Belgium). Exploitation of sandstone at the quarry involves intermittent operations by owner "Traveaux et Bétons Lambert Frères SA", which produces aggregates and decorative stone. The region encompassing the quarry forms a transition structure between the Ardenne anticlinorium and the Neufchâteau-Eifel synclinorium (Dejonghe, 2013) in the southwest of the Ardenno-Rhenohercynian Basin (Figure 1A). The Lower Devonian rocks in this part of Belgium and Luxembourg consist of primarily siliciclastic sediments, representing depositional settings ranging from continental to shelf marine environments (Bultynck and Dejonghe, 2001; Dejonghe, 2013; Dejonghe et al., 2017). The strata are generally similar to those of the Northern Facies Belt in the Rhenish Massif (Stets and Schäfer, 2002, 2009, 2011). Nevertheless, detailed stratigraphic correlations across the Belgian and German parts of the Ardenno-Rhenohercynian Basin remain challenging to establish (Bełka et al., 2010; Dejonghe et al., 2017). This difficulty is partly due to the lack of good marine index fossils (Jansen, 2016, 2019) and further complicated by obscuring effects of metamorphism and intense folding in large regions of the High Ardennes Slate Belt (Goemaere and Dejonghe, 2005). In this context, the Lambert quarry offers a

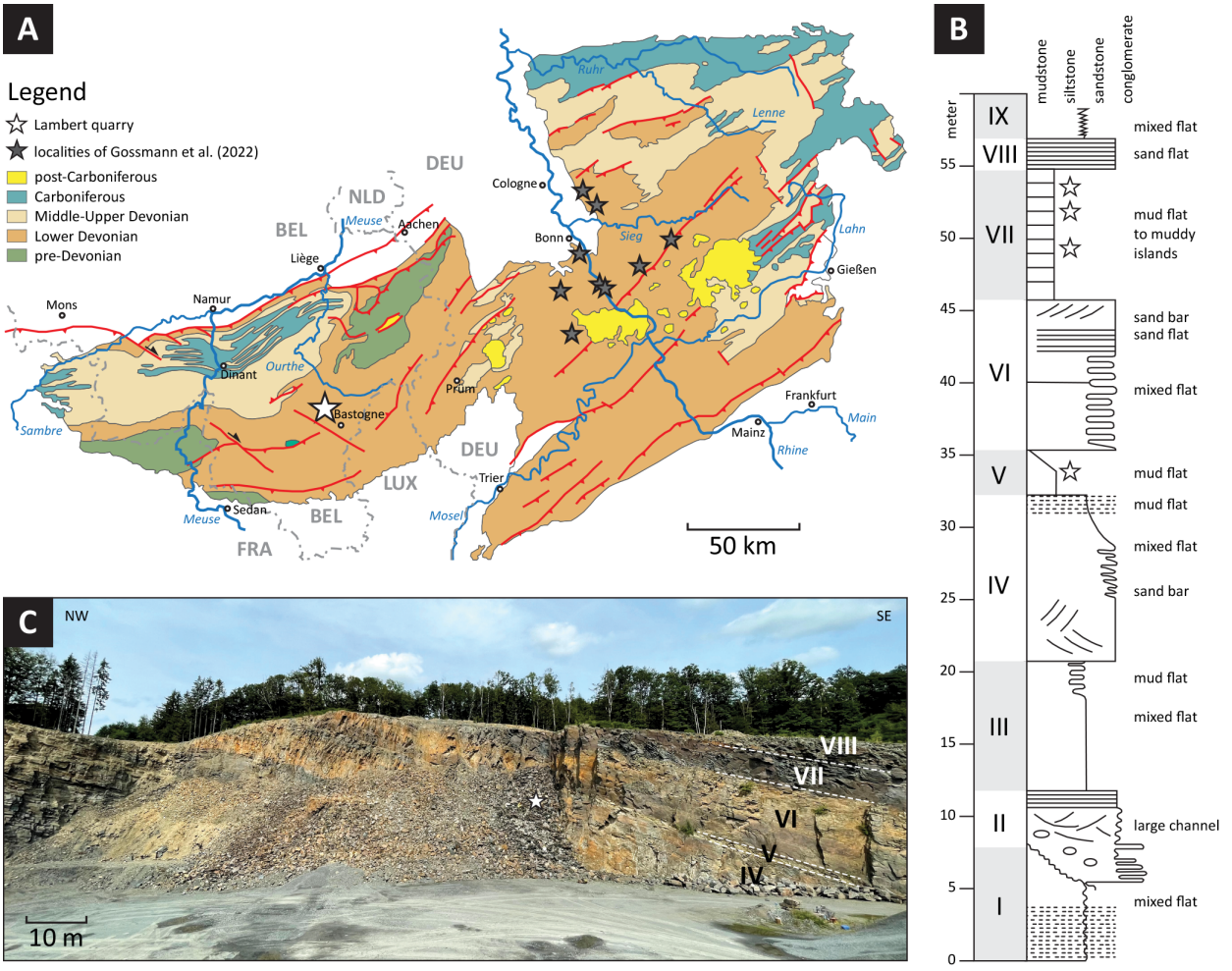

FIGURE 1. Overview of the study area, with A) geological map of the Ardenno-Rhenohercynian Basin (modified after Dittmar et al., 1994; Pirson et al., 2008; Stets and Schäfer, 2009; Barros et al., 2021) showing the location of the Lambert quarry (white star) and occurrences of *Zosterophyllum confertum* in the Rhenish Slate Mountains (grey stars; based on Gossmann et al., 2022, table 1); B) stratigraphic column of Lambert quarry outcrop, with white stars indicating the levels bearing plant remains (modified after Goemaere and Dejonghe, 2005, figure 2); and C) photograph of the main working face of the quarry in August 2021, showing part of the stratigraphy and fossiliferous rock on the quarry tailings (indicated by star).

rare exposure of relatively undisturbed Lower Devonian rocks in Belgium. The site has previously been the subject of a detailed structural, petrological, and sedimentological study by Goemaere and Dejonghe (2005). The following descriptions are based largely on their account.

Structurally, the outcrop accessible at the Lambert quarry corresponds to the northwestern limb of a large syncline (fold axial plane trending N60-75°E, local wavelength 700 m). The rocks suffered only minor tectonic deformation, with weak cleavage development being restricted to specific lithological units. The bedding dips gently (~25°) towards the southeast, showing slight deformation in the form of undulations (Goemaere and Dejonghe, 2005). The rocks consist of a succession of shallow-water siliciclastic deposits, supposedly belonging to the uppermost part of the Mirwart Fm. (Dejonghe, 2013). Goemaere and Dejonghe (2005) recognised nine lithological units in the sedimentary sequence, all representing tidal environments. Here, these units have been assigned Roman numerals I-IX (Figure 1B). The exposed strata can be described as an alternation of mixed flat, mud flat, and sand flat sediments, crosscut by tidal channels and gullies with associated reworking of sediments and lag deposits (Units I-IV, VI and VIII-IX in Figure 1B). Most of the succession consists of brownish, fine-grained sandstones and bluish-grey siltstones. Prevalent sedimentary struc-

tures include current ripples, flute casts, bioturbation, and various forms of tidal bedding (see Goemaere and Dejonghe, 2005, table 2). With the occurrence of abundant plant remains in dark bluish grey to black mud- and siltstones, Units V and VII differ from the main lithological succession. Based on their observations of i) carbonate nodules, interpreted to be pedogenetic in origin, and ii) supposed rooting structures, plus iii) a lack of marine-influenced sedimentary features, Goemaere and Dejonghe (2005) inferred that Units V and VII were deposited under supratidal conditions. Conceivable palaeo-environments include marshlands or temporarily exposed, vegetated muddy islands in the peritidal range of the delta.

It should be noted that the working face at the Lambert quarry has advanced significantly since the study of Goemaere and Dejonghe (2005), to some extent complicating recognition of their lithological units. Rock blasting operations carried out in December, 2020 created large amounts of new material, forming tailings of loose blocks below the eastern working face (Figure 1C). During a subsequent visit in May 2022, it was found that much of the fossiliferous rock previously present on these tailings had been removed and presumably processed to aggregates.

MATERIALS AND METHODS

The specimens used in this study originate from loose blocks derived from the main working face of the quarry and were collected in a number of visits between August 2021 and May 2022. The elevation up to which blocks with plant remains were encountered on the quarry tailings, as well as their mineralogical makeup and overall appearance, lead us to suspect they originate predominantly from Unit VII of the lithological succession as recognised by Goemaere and Dejonghe (2005) (Figure 1B-C). Field collection involved careful splitting of fossiliferous rock and examination of exposed surfaces. While the mud- to siltstone matrix itself tended to break along subconchoidal fractures, concentration and alignment of plant axes provided preferential planes for splitting the shale. Once retrieved and indoors, fossils were uncovered further as needed, carefully removing the enclosing rock using small chisels and preparation needles. The specimens were subsequently studied using optical microscopy and photographed under natural light. The obtained photographs were processed using PhotoScape X to adjust white balance and contrast. Line drawings of selected fossils were prepared using Inkscape 1.3. Since earlier investigations involving bulk-maceration of rock samples from the Lambert quarry proved unsuccessful (Gerrienne and Steemans in Goemaere and Dejonghe, 2005, p. 46), no attempt was made to obtain organic material or associated palynomorphs from the new specimens. The fossil specimens described in this study are stored in the collection of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (catalogue numbers IRSNB b 10028–b 10040 and IRSNB a 14158–a 14159).

TAPHONOMY AND PRESERVATION

The macrofloral remains encountered in the Lambert quarry generally displayed a certain degree of preferred alignment, probably corresponding to some paleocurrent or -flow direction. The ex-situ nature of the collected specimens prevents correlation to any specific (inter)cardinal direction. The only in situ plant remains observed at the quarry were located on a heavily weathered bedding plane exposed in a small gully atop the eastern working face (presumably corresponding to the upper part of Unit VII of Goemaere and Dejonghe, 2005). Most of the slabs collected from loose blocks on the tailings below displayed a subparallel orientation of vegetative axes. Variation in the intensity and direction of alignment of the plant axes, from one level to another within Unit VII, was previously noted by Goemaere and Dejonghe (2005, p. 42). Unfortunately, steepness and instability of the quarry working face prohibited more detailed in situ observation of individual rock layers.

The collected fossils consist of yellow-golden to pale green-silverish pseudomorphic compressions in a matrix of deep bluish-grey to black mud- or siltstone. No organic matter has been preserved. The fossils show only the external morphology of the plant remains, preserved in the form of flaky mineral films previously identified to consist mainly of the chlorite group mineral chamosite (Goemaere and Dejonghe, 2005, p. 46). Some of the fossil imprints seem to have developed a weak tectonic cleavage, while the host rock generally showed no such signs. The appearance of the strobili varies due to differences in their orientation with respect to the main direction of compaction and flattening during burial, as well as orientation with respect to the plane of splitting of the shale matrix.

SYSTEMATIC PALAEOBOTANY

Order: ZOSTEROPHYLLALES Banks, 1968
Family: ZOSTEROPHYLLACEAE Banks, 1968
Genus: *Zosterophyllum* Penhallow, 1892

Type species. *Zosterophyllum myretonianum* Penhallow, 1892

Zosterophyllum confertum
Gossmann, Poschmann, Giesen and Schultka, 2022
Figure 2A–F

2022 *Zosterophyllum confertum*; Gossmann, Poschmann, Giesen and Schultka, p. 506–513, figs. 1–7.

Description of the Lambert Quarry Specimens

The zosterophyllopsid remains from the Lambert quarry consist of dichotomously branching axes bearing compact terminal strobili (Figure 2). Most of the vegetative axes are smooth, some show faint longitudinal striation. Others appear slightly grainy, but this is likely related to the coarseness of the sediments in which these remains are preserved. The collected axes are generally flattened, up to 5 mm wide, and up to 9 cm long. Dichotomous branching of the axes is marked by asymmetric bifurcations, where the laterals have a similar to slightly smaller width than their parent axes (Figure 2C). Apparent bifurcation angles vary between 60° and 90° at the point of attachment, but shortly after most of the laterals tend to curve up and adopt a more subparallel orientation (Figure 2C, 2E). No remains of vascular strands or other preserved anatomical features could be identified in the Lambert quarry specimens. The strobili are 10-20 mm long, 5-9 mm wide, and borne terminally on 2-5 mm wide axes (Figure 2A–F). The overall shape of the strobili varies from oval to oblong (Figure 2F), to subtriangular (Figure 2B), with many of the specimens showing some degree of distortion due to lateral compression. The number of sporangia visible on the exposed sections of the strobili ranges from 5 to 15, with lower numbers corresponding to smaller or partially preserved strobili. The sporangia are overlapping one another in their strobilar arrangement, creating a compact helical structure. Individual sporangia measure up to 5 mm in width and length. They vary in outline from transverse-oval to kidney-shaped when observed in face view (Figure 2F), to apparently elongate or even subtriangular in side view (Figure 2D).

Discussion

Features used for distinguishing the various species of *Zosterophyllum* include the i) size and ii) shape of the sporangia, as well as their iii) arrangement and iv) mode of attachment on the main axis of the fructification (Edwards, 1975; Gerrienne, 1988; Gossmann et al., 2022). Species of *Zosterophyllum* hitherto known to occur in the Devonian of Belgium include *Z. fertile* Leclercq, 1942 and *Z. deciduum* Gerrienne, 1988, as well as forms comparable to *Z. myretonianum* Penhallow, 1892 and *Z. rhenanum* Kräusel and Weyland, 1935 (Leclercq, 1942; Gerrienne, 1983, 1988). Of these species, *Z. fertile* differs from the Lambert quarry material in bearing bilaterally arranged sporangia, i.e. showing *"Platyzosterophyllum*-type" sporangial insertion on the main axis (Edwards, 1972; Gerrienne, 1988). Considering species with spirally inserted sporangia, i.e., *"Zosterophyllum*-type" sporangial arrangement, *Z. deciduum*, and *Z. myretonianum* differ from the Lambert quarry zosterophyllopsid in having much more widely spaced sporangia, forming loosely inserted spikes rather than compact strobili (Edwards, 1975; Gerrienne, 1988; Gossmann et al., 2022). Compared to typical examples of *Z. rhenanum* (Kräusel and Weyland, 1935; Schweitzer, 1979), specimens recovered from the Lambert quarry possess considerably smaller and more conically shaped strobili. While the newly discovered Lambert quarry specimens differ from previously known Belgian species, their characteristics closely correspond to those of *Z. confertum* Gossmann et al., 2022, a species which occurs widespread in Siegenian strata of the Rhenish Slate Mountains in neighbouring Germany.

ASSOCIATED FLORA AND FAUNA

Zosterophyllopsids seem to have dominated the vascular plant assemblage at the Lambert quarry. Most vegetative axes recovered look morphologically similar to those bearing the strobili described above. No other types of fertile structures were recovered. Although uncommon, a few specimens of other plants have been found in association with the zosterophyllopsid material. Of these, the most abundant are dense masses of roughly parallel-oriented, relatively slender axes. These slender, naked stems are up to 2.5 mm wide and often show quite prominent midribs (Figure 3A), which suggests they may be related to certain plants within the form genus *"Taeniocrada"* (e.g., Kräusel and Weyland, 1930; Taylor, 1986). Some

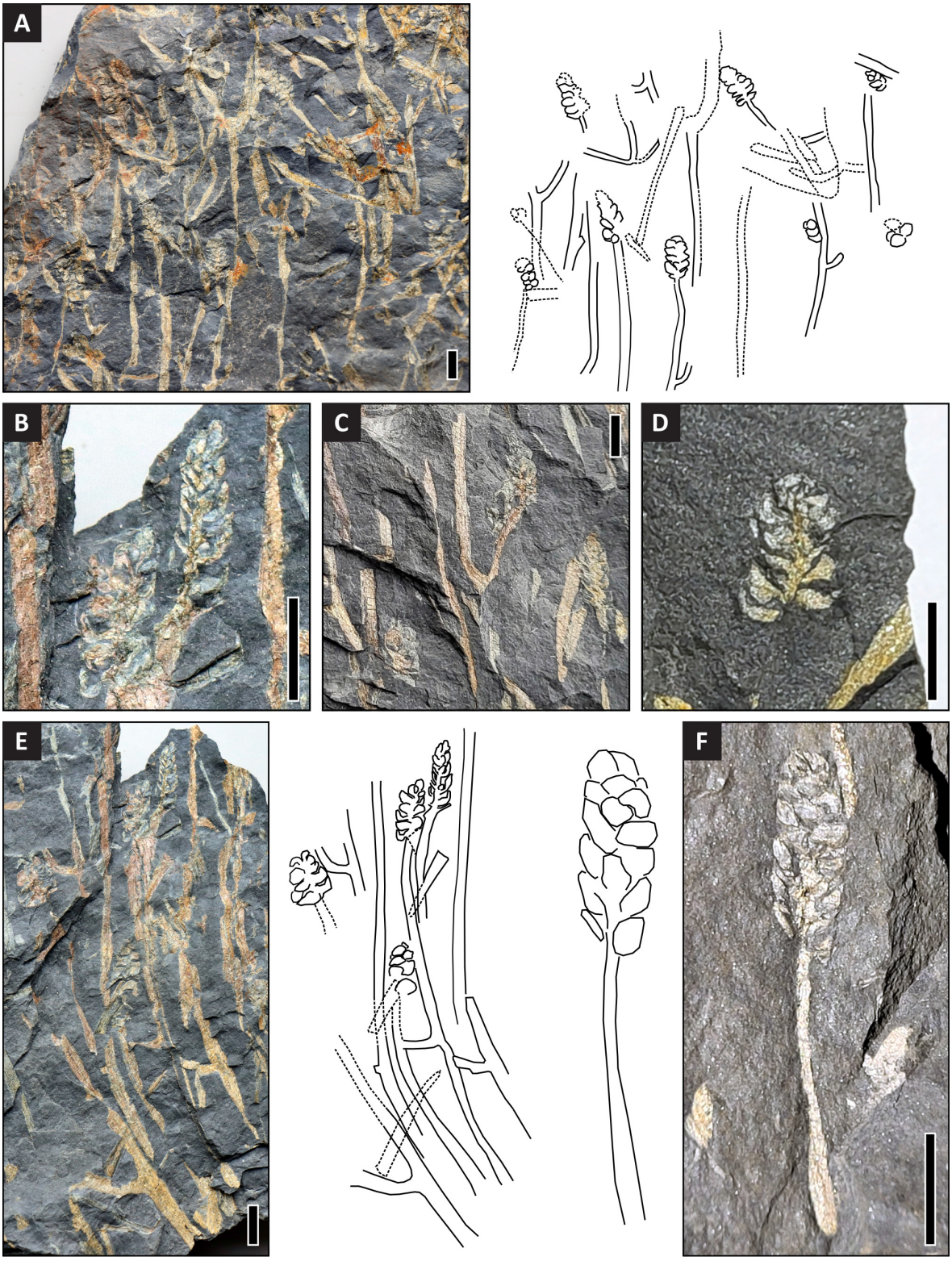

FIGURE 2. Photographs of *Zosterophyllum confertum* from the Lambert quarry, with interpretative sketches: A) dense mat of subparallel axes bearing numerous strobili, specimen IRSNB b 10028 (TKTW0808); B) subtriangular-shaped strobilus, specimen IRSNB b 10029 (TKTW0802); C) dichotomous branching with strobili, specimen IRSNB b 10030 (TKTW0803); D) detached oval-shaped strobilus, specimen IRSNB b 10031 (TKTW1013); E) subparallel axes bearing several strobili, specimen IRSNB b 10029 (TKTW0802); and F) oblong-shaped strobilus, specimen IRSNB b 10032 (TKTW0806). All scale bars are 1 cm.

of the slender axes display circinate tips (Figure 3B). However, a lack of fertile material among the collected specimens prevents closer assignment at this stage (Gensel and Andrews, 1984, p. 340; Fairon-Demaret, 1985).

The vascular plant assemblage further included vegetative axes that have an uneven, nodose (rhomboidal?) surface pattern and bear thorn-shaped microphylls (Figure 3C–D). The collected specimens measure up to 20 mm in width and 20 cm in length and sometimes show anisotomous branching (Figure 3E). Based on their gross morphology and size, the stems likely represent a drepanophycalean lycophyte (e.g., Kräusel and Weyland, 1930; Stockmans, 1940). The surface pattern of the stems is reminiscent of that produced by the rhomboidal 'leaf' bases covering *Drepanophycus gaspianus* (Dawson) Kräusel and Wayland, 1948 (Stockmans, 1939, 1940; Fairon-Demaret, 1977), as characterised and figured from various other Lower Devonian localities in Belgium by Stockmans (1940). One specimen consisting of a 17 mm long oval-shaped body, covered in rhomboidal scales bearing curved, spine-like protrusions, superficially resembles the drepanophycalean axes but is set apart by its markedly rounded shape (Figure 3F).

We also recovered a few blocks containing substantially wider vegetative axes of an otherwise unidentified nature. These axes measure up to at least 15 mm in width and 15 cm in length and sometimes show faint longitudinal striation (Figure 3G–H).

In direct association with the slender *"Taeniocrada"*-type axes, a putative bivalve was found (white arrow, Figure 4A). Unfortunately, no original shell material has been preserved and, apart from concentric growth lines, the partial imprint provided insufficient features to enable further identification. We also found decalcified internal moulds of spiriferids and bivalves together with poorly preserved plant remains (Figure 4B). The occurrence of spiriferids, some with both valves preserved held together, strongly hints at deposition under (shallow) marine conditions. Given the deteriorated appearance of the associated vegetative debris, it is likely the plant remains got swept out during a storm or were otherwise transported into deeper water. The loose blocks on the quarry tailings additionally contained various ichnofossils, including both *Diplichnites*-type and *Cruziana*-type trackways, but these were not encountered in association with plant remains and likely originated from lithological units other than V and VII (Figure 1B). A future study on the sedimentary structures of the Lambert quarry is planned to address these aspects in more detail.

INFERRED AGE AND STRATIGRAPHIC RELATIONS

On their detailed geological map of the Amberloup–La Roche-en-Ardenne–Houffaize sector, Dejonghe (2013) assigns the Lambert quarry to the Mirwart Fm. This lithological unit corresponds largely with the former "Assisse d'Anor" and is known to be diachronous from east to west, with ages ranging from the Lochkovian to Pragian (Bultynck and Dejonghe, 2001). According to Goemaere and Dejonghe (2005), the succession exposed at the Lambert quarry belongs to the uppermost part of the Mirwart Fm., suggesting an early Pragian age. Though our findings can provide only limited constraints, they are at least consistent with this assessment. The occurrences of *Z. confertum* reported by Gossmann et al. (2022) all pertain to strata of Pragian, to possibly early Emsian age. The occurrence of this plant at the Lambert quarry (Figure 2) suggests the exposed succession likely is of a similar age. Note Bultynck and Dejonghe (2001) mention that the top 100 m of the Mirwart Fm. may contain rare shells, which also fits with our findings at the Lambert quarry (Figure 4).

CONCLUSIONS

Newly discovered fertile zosterophyllopsid material is presented from the Lower Devonian of the Lambert quarry, in the municipality of Bertogne, Belgium. The specimens display compact, terminally borne strobili, which can be assigned to *Zosterophyllum confertum* Gossmann et al., 2022. This species is considered an index fossil for Siegenian (Pragian-early Emsian?) strata within the central Rhenish Massif, Germany. With the observation of *Z. confertum* at the Lambert quarry, the palaeobiogeographical range of this species can now be increased to include the Belgian Ardennes. Its occurrence here offers corroborating evidence for the inferred Pragian age of the upper part of the Mirwart Fm. In addition, this paper provides a first account of drepanophycalean lycophytes and *"Taeniocrada"*-like elements occurring in the Early Devonian vascular plant assemblage of the Lambert quarry.

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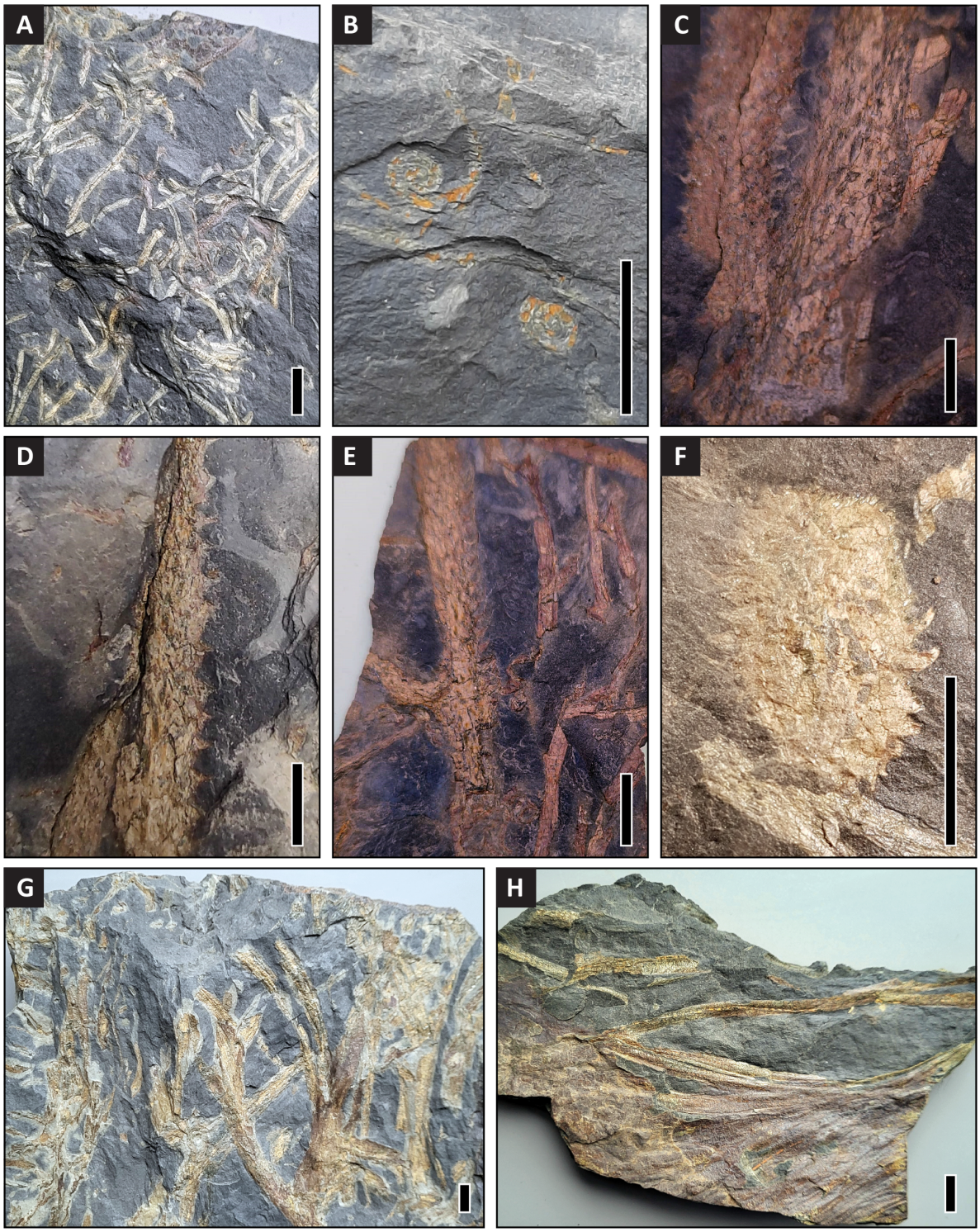

FIGURE 3. Examples of other vascular plant fossils collected at the Lambert quarry: A) slender axes showing a quite prominent midrib, morphologically resembling "*Taeniocrada*", biological affinity unknown, specimen IRSNB b 10033 (TKTW1015); B) slender axes with circinate tips, specimen IRSNB b 10034 (TKTW0805); C) drepanophycalean axes with indistinctly rhomboidal surface pattern, specimen IRSNB b 10035; D) drepanophycalean axis showing spine-like microphylls, specimen IRSNB b 10036; E) drepanophycalean axis showing anisotomous branching, specimen IRSNB b 10037; F) oval body with similar spine-like protrusions, specimen IRSNB b 10038 (TKTW0807); G) wide vegetative axes of unknown biological affinity, specimen IRSNB b 10039 (TKTW1018); and H) wide vegetative axes, specimen IRSNB b 10040 (TKTW1017). All scale bars are 1 cm.

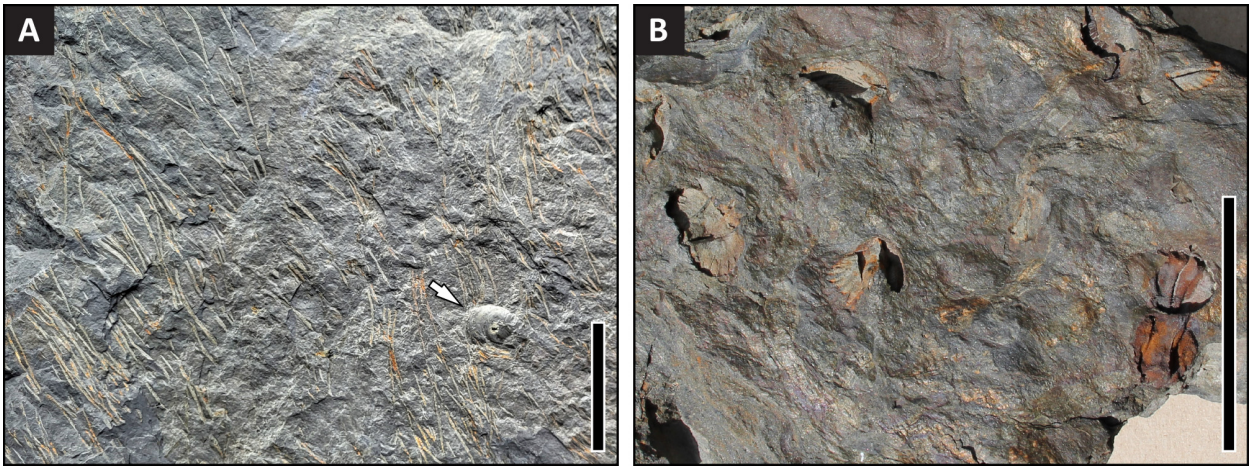

FIGURE 4. Fauna collected in association with plant remains at the Lambert quarry: A) unidentified bivalve (white arrow) having a relatively smooth shell surface showing concentric growth lines, found in a mass of subparallel slender vegetative axes, specimen IRSNB a 14158 (TKTW1019); and B) spiriferids and bivalves, some articulated, found in association with poorly preserved vegetative axes, specimen IRSNB b 14159. All scale bars are 5 cm.

sion to visit and collect rock specimens at the Lambert quarry. This manuscript benefitted from anonymous feedback during peer review, for which we are thankful. We also like to express our sincere gratitude to the editorial office of *Palaeontologia Electronica,* and handling editor Dr. M. Pole in particular, for their considerate approach and allowing us the time needed to find a suitable public repository for the fossil specimens after peer review. We are equally thankful to the Royal Belgian Institute for Natural Sciences, and curator of palaeontology Dr. A. Folie and collections assistant J. Lalanne, for their kind support and willingness to give the figured specimens a good new home.

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