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Original article

Devonian and Carboniferous dendroid graptolites from Belgium and their significance for the taxonomy of the Dendroidea

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ABSTRACT

Devonian and Carboniferous dendroid graptolites from Belgium are evaluated and partly revised. New finds in two different stratigraphic intervals of the 'Carrière de Lompret', an active quarry exploiting Frasnian limestones and shales east of Frasnes-lez-Couvin, allow the identification of *Callograptus* sp. and *Dictyonema fraiponti*, both belonging to the dendroid family Acanthograptidae. The relatively high diversity of the dendroid graptolite fauna from the Viséan Marbre noir de Denée, one of the few Carboniferous graptolite faunas in the world, can be shown to be based on astogenetic and preservational aspects. Nearly all known specimens can be included in the highly variable *Dictyonema fraiponti*, a fan-shaped large dendroid species with complex stipes formed from tubular thecae, possessing simple to complex bridges connecting adjacent stipes. Some of the graptolite material is well preserved and provides important information on the tubarium construction of Devonian to Carboniferous dendroid graptolites and, thus, is highly significant for a taxonomic and phylogenetic understanding of the youngest dendroid graptolite faunas worldwide. The genera *Callograptus* and *Ptiograptus* are revised based on their type species (*Callograptus elegans* from Quebec, Canada; *Ptiograptus percorrugatus* from the Silurian or Devonian of Kentucky, USA) and referred to the Acanthograptidae.

1. Introduction

Graptolites or the subclass Graptolithina (Class Pterobranchia) are exclusively marine colonial organisms having explored both planktic and benthic modes of life. In the early Paleozoic, the high diversity and abundance of planktic graptolites make them important biostratigraphic tools. However, after the extinction of the planktic graptolites near the end of the early Devonian (Emsian, *Uncinatograptus yukonensis* Biozone; e.g., Jaeger, 1988; Lenz, 2013), only a few records indicate the survival of benthic graptolites up into the Carboniferous (Chapman et al., 1993; Maletz, 2017). These include the famous dendroids from the 'black marble' of Denée, an early Viséan Konservat-Lagerstätte from southern Belgium (Ubaghs, 1941; Mottequin, 2004, 2008), which was reported to be the most diverse Carboniferous dendroid graptolite assemblage known in the world. Interestingly, the record of Devonian benthic graptolites from Belgium contrastingly is fairly poor, with only two unfigured specimens reported by Maillieux (1941). Subsequently, Devonian dendroids have not been mentioned or described from Belgium.

The general rarity of dendroid graptolites in the Devonian and Carboniferous makes the identification of their final extinction also a bit unclear. With no records known from the Pennsylvanian, the extinction most probably took place near the end of the Mississippian. The youngest reported Dendroidea from Europe appear to be the benthic taxa from the Arnsbergian (upper Serpukhovian) of North England and Wales (Hind, 1907; Chapman et al., 1993), considerably younger than the Denée material. Ruedemann and Lochman (1942) described three Mississippian species of *Dictyonema* from the Black Hills of South Dakota and Erdtmann and Adams (1975) described *Callograptus indianensis* from the late Osagian (Early to Middle Mississippian) of Indiana (USA) as the youngest known North American taxa. The record of Permian dendroids from Hainan Island, Guangdong, China (Deng,

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1985) is based on material from the same locality described by Mu et al. (1981) and actually is of Carboniferous age.

After their disappearance from the fossil record in the Late Mississippian, benthic graptolites (Graptolithina) are extinct except for the survival of the encrusting Rhabdopleuridae (Maletz, 2019). These survive all further extinction events in the marine environment and are still around today with a few inconspicuous species of the genus *Rhabdopleura* (Mitchell et al., 2013; Maletz and Beli, 2018). Rhabdopleurids have rarely been found in the fossil record as they are small and may easily be missed, as the accidental recent record of rhabdopleurid stolons on a Jurassic hardground (Keupp et al., 2016) indicates. Beli et al. (2018) even described a new extant rhabdopleurid from the Mediterranean Sea, the first fully documented record for the region and a new species of *Cephalodiscus* has been discovered in the Sagami Bay of Japan (Miyamoto et al., 2020).

New findings made recently in the 'Carrière de Lompret' (see below), west of Frasnes-lez-Couvin (Belgium), the historical type area of the lower Upper Devonian stage, allow the documentation of two new Upper Devonian (Frasnian) records of dendroid graptolites and initiated a revision of all known records of Belgian Devonian and Carboniferous graptolites.

2. The Belgian fossil record of dendroid graptolites

2.1. Pre-Devonian material mistakenly identified as dendroid graptolites

Benthic (dendroid) graptolites are very rare in Belgium and only a few records are available. Often, however, also the early planktic graptolites of the family Anisograptidae were regarded as dendroids until Erdtmann (1982) differentiated the planktic forms into the genus *Rhabdinopora* and regarded only the benthic genus *Dictyonema* as a dendroid. Prior to this, Bulman (1970b), described the *Rhabdinopora flabelliformis* interval with its early planktic taxa from the basal Ordovician from Belgium (see also revisions by Erdtmann, 1986; Wang and Servais, 2015). Subsequently, *Rhabdinopora flabelliformis* and its subspecies were referred to the Anisograptidae, the earliest family of the planktic Graptoloidea (*e.g.*, Maletz, 2014; Maletz et al., 2017).

2.2. Devonian material

Maillieux (1941) reported one Devonian specimen from the 'Couvinien supérieur - Assise de Couvin - Schistes à *Spinocyrtia ostiolata* Co2c' from 'Haies d'Oppagne', near km 5 of the road to Eveux (locality name in Mailleux's unpublished inventory of Belgian fossil localities: pl. Durbuy 30). This is in today's terminology the Jemelle Fm., Eifelian, Middle Devonian. The second specimen is from the 'Assise de Frasnes - zone à *Reticularia pachyrhyncha*', from the railroad section, south of the railroad station of Senzeille. This most probably translates to the Neuville or Les Valisettes Fm. of late Frasnian age. At the end of his paper, Maillieux (1941) indicates that the investigation on these specimens will continue elsewhere, but we are unaware of this study. Possibly WWII intervened and not much later, in 1946, Maillieux passed away (Lecompte, 1946). The material of Maillieux has never been described and has to be regarded as lost, as we were unable to locate the two specimens in the collections at the Royal Belgian Institute of Natural Sciences (RBINS) and at the University of Liège. Several well-preserved, even though fragmentary specimens of Devonian dendroid graptolites recently found in an active quarry near Frasnes-lez-Couvin, Belgium, are described herein. They constitute the single surviving graptolites from the Devonian of Belgium, and can be assigned to the genera *Callograptus* Hall, 1865 and *Dictyonema* Hall, 1851.

The new specimens originate from two collecting spots within an active quarry named 'Carrière de Lompret', located 9 km west of Frasnes-lez-Couvin, the historical type area of the Frasnian stage, in the southwest of Belgium (Fig. 1). The 'old pit' refers to a deep excavation of argillaceous limestones of the Bieumont Mb. (Grands Breux Fm.), ongoing from the 1990s, but ceased in 2013, and almost entirely backfilled by 2018. The stratigraphy and sedimentology of the old pit were subject of studies by Humblet and Boulvain (2000) and Da Silva et al. (2013). The 'new pit' refers to

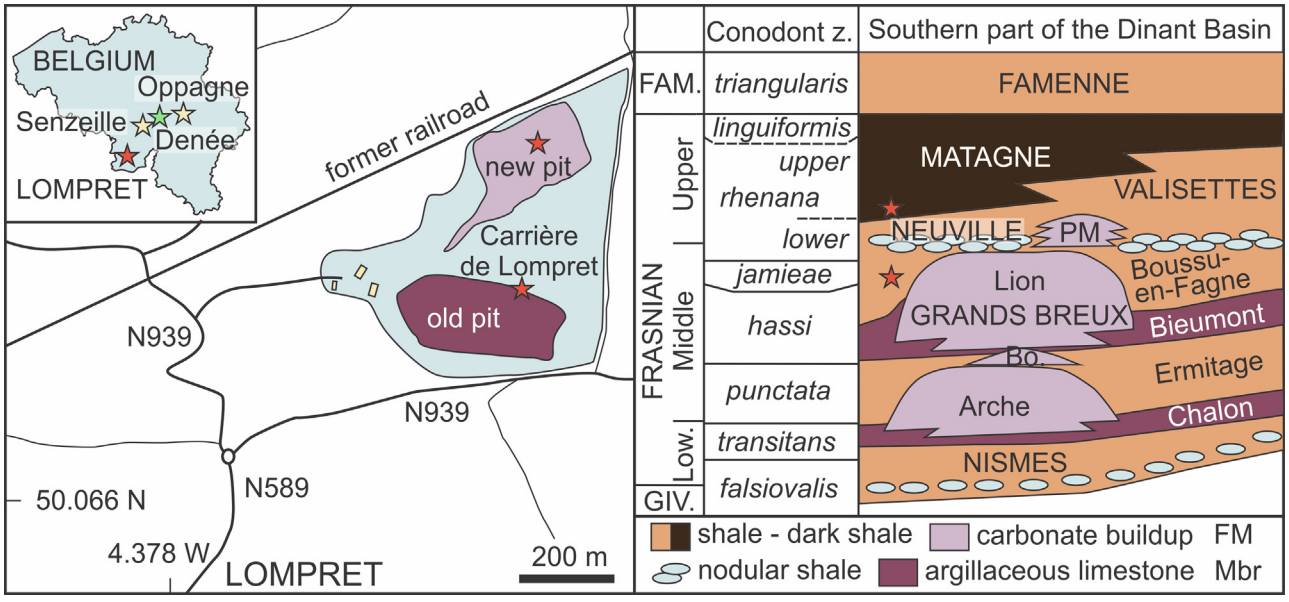

Fig. 1. Location maps of Devonian and Carboniferous graptolite occurrences from Belgium (left). Yellow stars indicate the two localities of Maillieux (1941), the green star the 'black marble' of Denée, red stars the Carrière de Lompret with detailed origin of both collecting spots within the quarry. Generalized stratigraphical architecture of Frasnian deposits in the southern part of the Dinant basin with stratigraphic positioning of the two graptolite collecting spots at Lompret (right), modified after Goolaerts et al. (2017). Abbreviations: Bo.: Boverie Member; Giv.: Givetian; Fam.: Famennian; FM: Formation; Low.: Lower; PM: Petit-Mont Member; Mbr: Member; z: zones. Formation names in upper case, members in lower case letters.

the ongoing excavation of light grey Lion Mb. limestones, for which a multidisciplinary study of the quarried sediments is ongoing (Goolaerts and Gouwy, 2015; Gouwy and Goolaerts, 2015; Ginter et al., 2017; Goolaerts et al., 2018).

Unfortunately, both spots were quarried away shortly after the graptolite discoveries on August 22nd, 2010 and June 30th, 2017 respectively. The first spot, in the 'old pit', exposed greenish grey coloured shales in which small chonetidine brachiopods of the genus *Retichonetes* and trilobites of the genus *Bradocryphaeus* are the most common fossils. It is located stratigraphically within the middle Frasnian Boussu-en-Fagne Mb. of the Grands Breux Fm. (Fig. 1). Only a single slab, displaying three well-preserved fragments was collected at this locality, a few cm below a bentonite horizon.

The second spot, in the 'new pit', exposed dark grey shales of the lower but not lowermost metres of the upper Frasnian Matagne Fm. Here, all collected specimens originate from a single level, in which also juvenile to subadult *Ryocarhynchus tumidus* brachiopods, two lower jaws (anaptychi) of ammonoid cephalopods, some small orthoconic cephalopods and *Glyptohallicardia* bivalves were also found. Pyritic moulds of ammonoids occur in the beds immediately above and below the graptolite level.

2.3. Carboniferous material

While Renier (1925) only mentioned *Dictyonema* from the Viséan (Moliniacian) 'black marble' of Denée, now included within the Molignée Fm., Ubaghs (1941) described and illustrated nine taxa of clearly Carboniferous dendroid graptolites, some left in open nomenclature, and referred the material to the genera *Dendrograptus*, *Desmograptus*, *Dictyonema* and *Ptiograptus*, suggesting a quite high diversity of these Carboniferous dendroid graptolites. The material includes relatively large tubaria with fragments measuring more than 20 cm in length, but most specimens are strongly fragmented and distorted through transport. Little detail on the stipe and thecal construction is available from this poorly preserved, flattened material. Many specimens of the benthic fauna described by Ubaghs (1941) were available for investigation and comparison. A revision of the material indicates that the diversity of many dendroid graptolite faunas may have been overestimated considerably due to lack of understanding of construction and astogenetic changes of the colonies.

3. Preservation

The material of the two small Devonian collections from the 'Carrière de Lompret' is surprisingly well preserved (Fig. 2). The specimens show a robust layer of preserved dark material, representing the organically preserved fusellum of the tubaria (Fig. 2(A–C)). The specimens are in partial or full relief as pyrite filled specimens, but the pyrite is now generally weathered to limonite in weathered specimens. All specimens appear to be fragmented and the full shape of the tubaria can only be estimated. Parallel fractures of the fusellum as seen in some specimens indicate possible distortion by sediment dewatering, compaction or tectonics (Fig. 2(B)). Latex casts have been prepared from several specimens and show the details of the complex thecal development in *Dictyonema fraiponti* Ubaghs, 1941 (Fig. 2(D, G)).

The material provides for the first time insights into the tubarium construction of Devonian dendroid graptolites. Material illustrating this amount of detail has not been described from the Devonian before. A similar preservation is present in the single fragment of *Ophigraptus hercyniae* Jaeger, 1992 from the Emsian/Eifelian boundary beds of the Harz Mountains in Germany, a species showing a much simpler thecal development (Jaeger, 1992). The specimen can be referred to the Dendrograptidae.

4. Systematic palaeontology

The newly collected specimens from the 'Carrière de Lompret' are deposited in the collections of the RBINS, Brussels, Belgium, and can be retraced by number I.G. 33973. Figured specimens bear an additional number with prefix IRSNB a.

The taxonomy of the Dendroidea follows Maletz (2014).

Abbreviations: CGF: Centre Grégoire Fournier, Maredsous Abbey, Maredsous, Belgium; GSC: Geological Survey of Canada, Ottawa, Canada; NYSM: New York State Museum, Albany, New York, USA. ULg: Department of Geology, University of Liège, Liège, Belgium.

Phylum Hemichordata Bateson, 1885
Class Pterobranchia Lankester, 1877
Subclass Graptolithina Bronn, 1849
Order Dendroidea Nicholson, 1872

Diagnosis (Maletz, 2014: p. 492): Benthic graptoloids with variable colony shape; erect, bushy, cone- or fan-shaped tubarium; thecae serially arranged along the stipes with regularly placed bithecae based on a triad budding concept; thecal development variable from tube-shaped to distinctly widening and with ventral rutellum; anastomosis, bridges or dissepiments present in some taxa; sicular and proximal development largely unknown.

Remarks: Maletz (2014) included three families in the Dendroidea. All families include erect growing bushy taxa showing a triad budding system. The proximal end with the sicula is unknown for most taxa and cannot be used for any taxonomic purpose at the moment. He differentiated the family Dendrograptidae with their serially arranged autothecae forming a distinctly widening tube and lacking isolated apertural parts (Fig. 3(C)) from the Acanthograptidae with parallel-sided, tubular thecae and an often non-serial organization of the thecae (Fig. 3(B)). The family Mastigograptidae bears completely isolated autothecae, showing typically thin thecal fusellum with irregular sutures and a robust stem and branches (Fig. 3(A)). The early planktic Anisograptidae (Fig. 3(D)) of the basal Ordovician possess thecae of a similar style to those of the Dendrograptidae with distinctly widening thecae and bithecae on alternating sides of the stipes.

Family Acanthograptidae Bulman, 1938

Diagnosis (Maletz, 2014: p. 493): Benthic graptoloids with variable shape of colonies, from erect, bushy, cone- or fan-shaped; thecae elongated, tube-shaped with a non-serial to serial organization; often complex stipe development of ropy appearance with isolated autothecal apertures or development of twigs; regularly placed bithecae based on a triad budding concept; anastomosis present in some taxa; individual or multiple tubular thecal bridges typical; sicular development largely unknown.

Remarks: The Acanthograptidae have tubarium shapes very similar to the Dendrograptidae, but differ considerably in the construction of their stipes from complexly overlapping tubular thecae. A differentiation is impossible in many cases as the thecal style is rarely discernible in flattened material. The thecae of the Acanthograptidae are parallel-sided tubes with isolated apertures. The thecae are arranged in a serial succession generally, based on the triad budding system. However, due to the increased thecal overlap the stipes appear as ropy bundles of thecae and look less regular than they actually are. All thecal apertures are directed to the ventral side of the stipe, or, in complex stipes, show thecal

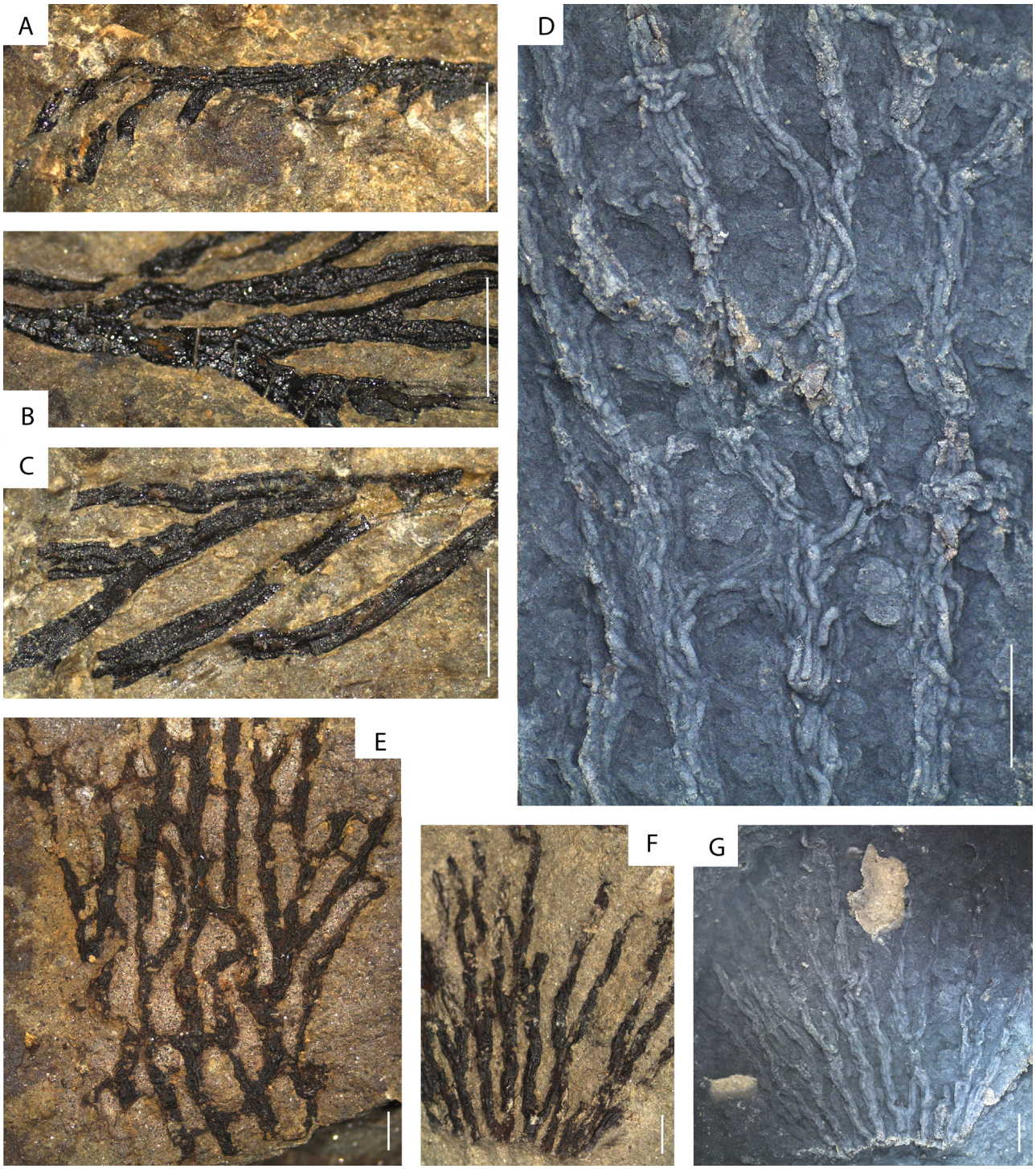

Fig. 2. Details of dendroid graptolites from the Carrière de Lompret. **A–C.** *Callograptus* sp., IRSNB a13391, details of specimen from old pit, middle Frasnian Grands Breux Formation (Boussu-en-Fagne Member). A: detail showing isolated, tubular thecal apertures; B: specimen showing branching and possible fractures due to tectonic distortion; C: fragment showing dorsal view of stipes. **D–G.** *Dictyonema fraiponti* Ubaghs, 1941, new pit, upper Frasnian Matagne Formation (upper Frasnian). D: IRSNB a13388, Den 1b, latex cast, coated, showing thecal style; E: IRSNB a13392, Den 4a, fragment showing considerable growth irregularities; F: IRSNB a13393, Den 2a, relief specimen showing fusellum in black; G: IRSNB a13393, Den 2b, latex cast after preparation of proximal part, coated. Scale bars: 1 mm.

apertures also regularly directed sideways. Imprints of laterally preserved specimens may show the seriality of the thecal apertures more clearly. The bithecae are difficult to separate as they do not differ in size from the autothecae and their presence can only be estimated through the presence of the triad budding. Maletz (2014) included a number of taxa in this family. These are largely erect growing taxa with compound stipes.

The genera *Callodendrograptus* Decker, 1945 and *Alternograptus* Bouček, 1957 are included here in the Acanthograptidae due to the presence of tubular, aperturally isolated thecae. Maletz (2014) provisionally included these genera in the family Cyclograptidae Bulman, 1938, as the detailed tubarium construction was unknown. The genus *Callograptus* Hall, 1865 is transferred to the Acanthograptidae based on the tubular thecae with isolated

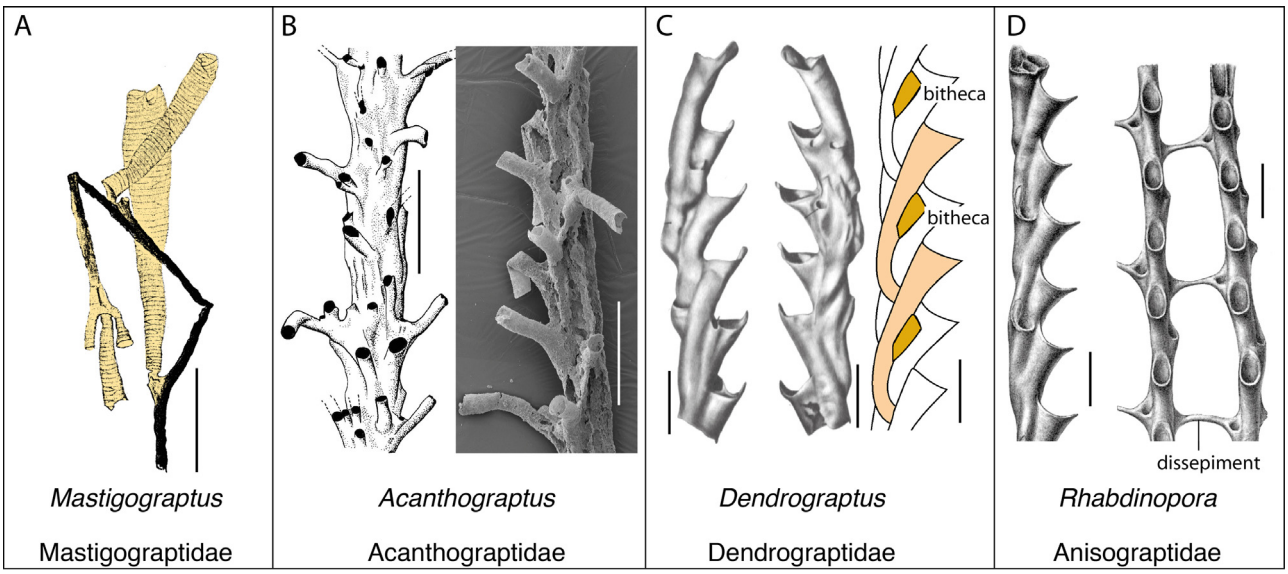

Fig. 3. Thecal styles in the three families of the Dendroidea (**A–C**), and the thecal style of the anisograptid *Rhabdinopora* (**D**) for comparison. Scale bars: 1 mm.

apertures in the type species *Callograptus elegans* Hall, 1865 as redescribed herein.

Many taxa of the Acanthograptidae show the development of lateral connections between stipes, previously interpreted or identified as dissepiments from flattened material. At least three types of stipe connections can be differentiated in the Dendroidea. These represent considerable constructional differences and cannot be regarded as homologous. They are characterized from relief material and chemically isolated specimens. The distribution of the three types within the Dendroidea is unclear, as in the past all have been identified under the terms dissepiments and anastomosis.

Dissepiments (Fig. 3(D)) are generally understood as connecting strips of cortical material between adjacent stipes (*cf.* Bulman, 1970a; Maletz et al., 2014), but Urbanek and Mierzejewski (2009) demonstrated that the dissepiments of *Dictyonema* s.l. from the Ordovician of Estonia and *Dictyonema* cf. *cervicorne* from glacial boulders possess an internal fusellar component, covered by cortical material.

The term anastomosis is usually used for graptolites in which two adjacent stipes touch temporarily with their sides (Bulman, 1970a; Maletz et al., 2014). Bulman (1945) recognized the mere touching as true anastomosis, while anastomosis with thecal transfer has been identified as pseudanastomosis (Rickards and Lane, 1997). The differentiation of both types of anastomosis is impossible in the usual flattened preservation of most graptolites. In many instances, lateral touching of stipes may be accidental and preservational (Fig. 2(E)). A clear identification can only be achieved when chemically isolated material is available (see Bulman, 1945).

Maletz (2019) redescribed the type species of *Dictyonema*, *Dictyonema retiforme* (Hall, 1843) as an acanthograptid taxon based on the thecal development and the presence of bridges as lateral connections of the stipes. Bridges are connections between two stipes in which the stipes keep their distance, but one or more tubular thecae, either auto- or bitheca, grows across the gap to connect the two stipes (Fig. 2(D)). This development can easily be mistaken as dissepiment formation and has been as the case of *Dictyonema fraiponti* Ubaghs, 1941 shows. Bridges can easily be formed from twigs (Maletz et al., 2014) in the Acanthograptidae, but details of these developments are unknown due to the lack of well-preserved material.

Genus ***Callograptus*** Hall, 1865

Type species: *Callograptus elegans* Hall, 1865 (subsequently designated by Miller, 1889: p. 175)

Distribution: The genus might be distributed worldwide from the upper Cambrian to the Carboniferous. However, many species attributed to the genus need re-evaluation and the precise biostratigraphic distribution remains uncertain.

Revised diagnosis: Tubarium conical, flabellate or irregular with or without a thecate stem; stipes branching dichotomously, attaining a subparallel to parallel orientation quickly; autothecae tubular, slightly to strongly isolate aperturally; bithecae indistinct, tubular; pseudanastomosis common; proximal development unknown.

Remarks: The genus *Callograptus* was previously included in the Dendrograptidae due to the supposed presence of aperturally widening, denticulate thecae (Bulman, 1970a; Maletz, 2014). Ruedemann (1947: p. 205) noted that a specimen of *Callograptus elegans* Hall, 1865 from Point Levis at the U.S. National Museum shows tubular thecae. These are verified from the lectotype of this species herein (Fig. 4). The genus *Callograptus* is therefore included in the Acanthograptidae. Bulman (1970a) indicated the presence of denticulate autothecae in *Callograptus*, but these have never been illustrated from any specimens referred to this genus.

Callograptus elegans Hall, 1865
Fig. 4

1865. *Callograptus elegans*, Hall (n. s.) – Hall, p. 134, pl. 18, fig. 4; pl. 19, figs. 1–4.

Type material: Specimen GSC 956a (Hall, 1865: pl. 19, fig. 2) is here designated as the lectotype (Fig. 4(A, B)). It was incompletely illustrated by Bulman (1970a: fig. 16.3), to show the colony shape. Details of its construction and thecal shape have not previously been shown. The lectotype is associated on the slab with a specimen of *Callograptus salteri* (Hall, 1865: pl. 19, fig. 6; GSC 955a). The remaining specimens of Hall (1865; GSC 956, 956c) are regarded as paralectotypes. The material originates from Gros Maule, Québec, Canada. Unfortunately, no additional specimens are available from the slabs to determine the precise age of the material. Hall (1865: p. 134) indicated an association with *Expansograptus nitidus* (Hall, 1865), *Expansograptus constrictus* (Hall, 1865), *Tetragraptus bryonoides* and *Dichograptus octobrachiatus* (Hall, 1865), suggesting an Early Ordovician (Floian) age.

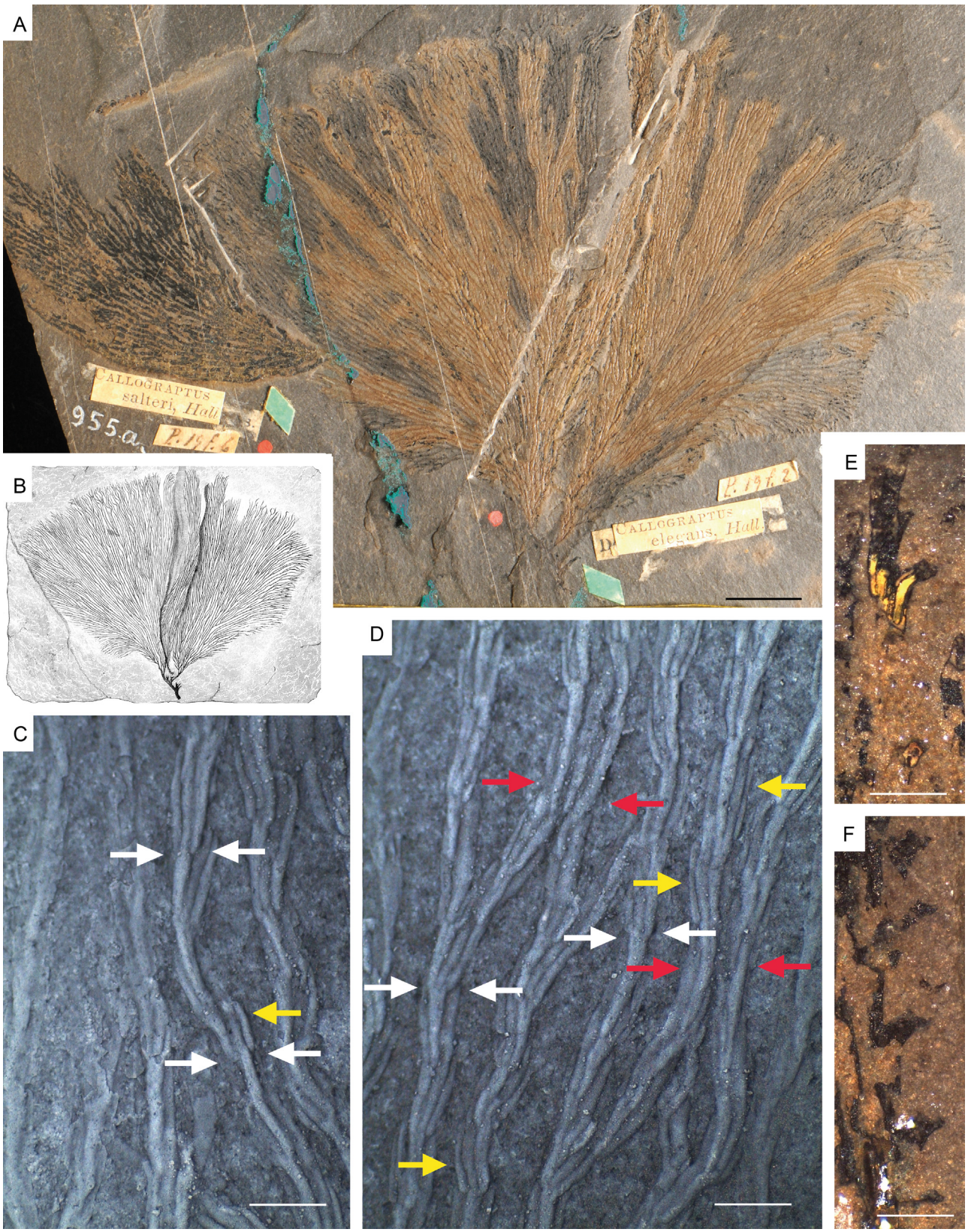

Fig. 4. Type species of *Callograptus*: *Callograptus elegans* Hall, 1865, GSC 956a, lectotype. **A.** Complete specimen associated with *Callograptus salteri*, GSC 955a (Hall, 1865: pl. 19, fig. 6). **B.** Original illustration of Hall (1865). **C, D.** Latex casts of stipe details, showing triad budding (white arrows), possible anastomosis (red arrows) and a few possible bithecae (yellow arrows). **E, F.** Laterally preserved stipes showing isolated tubular thecal apertures. Scale bars: 10 mm (A), 1 mm (C–F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Description: The material is well-preserved in partial relief, either as a mould or a relief specimen, probably originally filled with pyrite. Considerable remains are found as the organic fusellum, while the moulds show thin layers of light coloured probable diagenetic or metamorphic mineralizations (Fig. 4(A)). In dorsal view (Fig. 4(C, D)) the typical triad budding of a dendroid graptolite can be seen. The thecae are slender, largely parallel-sided and show considerable overlap. Only at the apertures they bend outwards and are, thus, isolated. The presence of a rutellum at the thecal apertures cannot be verified, as the thecae do not show any apertural widening (Fig. 4(E, F)). Possible bithecae are difficult to verify, as they show the same width as the autothecae, but appear to be considerably shorter (Fig. 4(C, D): yellow arrows). The presence of triad budding, however, indicates that bithecae are present in the material.

The lectotype shows a short thick stem or early branch on which thecae are not visible (Fig. 4(A, B)). This might be due to cortical overgrowth and the 'stem' might be an earlier branch, but not necessarily indicating a position close to the attachment of the tubarium. Thus, the specimen has to be regarded as a fragment. More complete material with a clear site of attachment has not been discovered so far. A differentiation of cortical overgrowth from the thecate stipes is not possible.

The lectotype may indicate the presence of anastomosis (Fig. 4(D)), but this is difficult to verify as the touching of adjacent stipes could also be due to preservational aspects. There is no indication for dissepiments in this material, even though dissepiments were noted – at least for the genus – by Hall (1865) in his introduction of the genus *Callograptus*.

The lectotype is *ca.* 75 mm long and 100 mm wide, but represents a fragment of a larger colony. The stipes are *ca.* 0.5 mm wide with lateral distances between stipes measuring 0.5–1.0 mm. Values are, however, approximate due to distortion of the flexible stipes. The thecal tubes are *ca.* 0.1–0.15 mm wide and largely parallel sided. The length is difficult to measure as usually only parts of the thecae are visible in dorsal view. The individual autothecae may be *ca.* 3.3 mm long, probably even longer. The apertural parts of the autothecae are isolated as can be seen in a few distal ends where stipes are laterally twisted. This isolated part of the autotheca is 0.2–0.3 mm long (Fig. 4(E, F)). Shorter thecal tubes have preliminarily been identified as bithecae (Fig. 4(C, D)). The dorsal view of the stipes shows distinct triad budding with two thecae originating at both sides of the mother theca (Fig. 4(D)). It is impossible to differentiate which one of the two daughter thecae will become an autotheca or a bitheca.

Callograptus sp.

Figs. 2(A–C), 5, 6(C)

Localities: Carrière de Lompret, old pit, Grands Breux Fm. (Boussu-en-Fagne Mb.), middle Frasnian. Three fragments on a single slab of shale (IRSNB a 13391). One specimen from Carrière de Lompret, new pit, upper Frasnian Matagne Fm. (IRSNB a 13389).

Description: The material from the old pit consists of three small stipe fragments on a single slab of brown shale and its counterpart, bearing imprints of brachiopods of the genus *Retichonetes* (Fig. 6(C)). The specimen is preserved in partial relief as black organic material, supposedly representing the original fusellum of the colony. The largest fragment is 15 mm long and shows at least six consecutive branching divisions. The dorso-ventral stipe width is 0.3–0.4 mm and decreases slightly towards the distal portion of the fragment. There is no evidence of anastomosis and dissepiments have not been found. The stipes show a ropy appearance due to the long, parallel-sided thecae with high thecal overlap. A triad budding is vaguely recognizable in places, indicating a differentiation into autothecae and bithecae, but these are impossible to separate in the fragments.

The autothecae are parallel-sided, *ca.* 0.1 mm wide and at least 2–3 mm long. They show a distinctly isolated apertural part with a straight aperture curving downwards ventrally (Fig. 2(A)). In a dorso-ventral preservation the thecal apertures would be directed downwards into the sediment and would not be visible. The 2TRD (two thecae repeat distance; Howe, 1983) is *ca.* 1.2 mm, but could be measured at a single place only, as the thecal apertures are rarely visible.

The specimen from the new pit (Fig. 5) is larger, but less complete. In some parts of the fan-shaped tubarium the weathered fusellum is preserved and the counterpart provides low relief information on the dorsal development of the stipes (Fig. 5(A, B)). Vague indications of triad branching can be seen in the tubarium. Dissepiments are not observed.

Remarks: The specimen from the new pit indicates a largely fan-shaped tubarium with irregular branching of the stipes. The fragmentary material from the old pit may belong to a single specimen. The fusellum appears to be fractured and possible secondary fractures are filled with some minerals (Fig. 2(B)). All specimens are here included in the genus *Callograptus* based upon the branched tubarium without dissepiments and anastomosis. The parallel-sided, tubular thecae with their characteristic isolated apertures are very similar to those of *Callograptus elegans* Hall, 1865. The development of the thecae differs considerably from the one in *Dictyonema fraiponti* (Fig. 2(D)), which shows a more complex overlap and irregular growth of the thecal tubes.

Genus ***Dictyonema*** Hall, 1851

Type species: *Gorgonia*? *retiformis* Hall, 1843 (subsequently designated by Miller, 1889: p. 185)

Remarks: Maletz (2019) revised the type species of the genus *Dictyonema* and referred the genus to the family Acanthograptidae based on the complex overlapping, tubular thecae.

Dictyonema fraiponti Ubaghs, 1941

Figs. 2(D–G), 6(A, D, E), 7

1941. *Dictyonema fraiponti* nov. sp. – Ubaghs, p. 7, pl. 4, figs. 15–17.

1941. *Dictyonema fraiponti* var. 1 – Ubaghs, p. 9, pl. 1, fig. 1; pl. 3, fig. 13.

1941. *Dictyonema fraiponti* Ubaghs var. 2 – Ubaghs, p. 9, (unfigured).

1941. *Ptiograptus fournieri* nov. sp. – Ubaghs, p. 9, pl. 1, fig. 2; pl. 2, figs. 7–8; pl. 5, figs. 18–19.

1941. *Ptiograptus fournieri* var. – Ubaghs, p. 15, pl. 1, fig. 3.

1941. *Dendrograptus* sp. 1 – Ubaghs, p. 16, pl. 2, fig. 9.

1941. *Dendrograptus* sp. 2 – Ubaghs, p. 17, pl. 1, fig. 4.

1941. *Desmograptus crassus* nov. sp. – Ubaghs, p. 18, pl. 3, fig. 14.

1941. *Desmograptus* sp. – Ubaghs, p. 20, pl. 5, fig. 20.

1951. *Dictyonema fraiponti* Ubaghs – Henrard, p. 26.

1951. *Ptiograptus fournieri* Ubaghs – Henrard, p. 26, unnumbered figure.

1993. *Ptiograptus fournieri* Ubaghs – Chapman et al., p. 316, figs. 27, 28, 29.

1993. *Dictyonema fraiponti* Ubaghs – Groessens (in Dupuis et al.), p. 32, fig. 19.5.

1993. *Ptiograptus fournieri* Ubaghs – Groessens (in Dupuis et al.), p. 32, fig. 19.6.

1994. *Ptiograptus fournieri* – Groessens, p. 114, fig. 1.

2009. *Ptiograptus fournieri* Ubaghs – Mottequin, fig. 7G.

2009. *Dictyonema fraiponti* Ubaghs – Mottequin, fig. 7H.

2015. *Ptiograptus fournieri* Ubaghs, 1941 – Mottequin et al., p. 12, fig. 13.

2015. *Dictyonema fraiponti* Ubaghs, 1941 – Mottequin et al., p. 12.

2017. *Ptiograptus fournieri* Ubaghs, 1941 – Maletz, fig. 8.12.

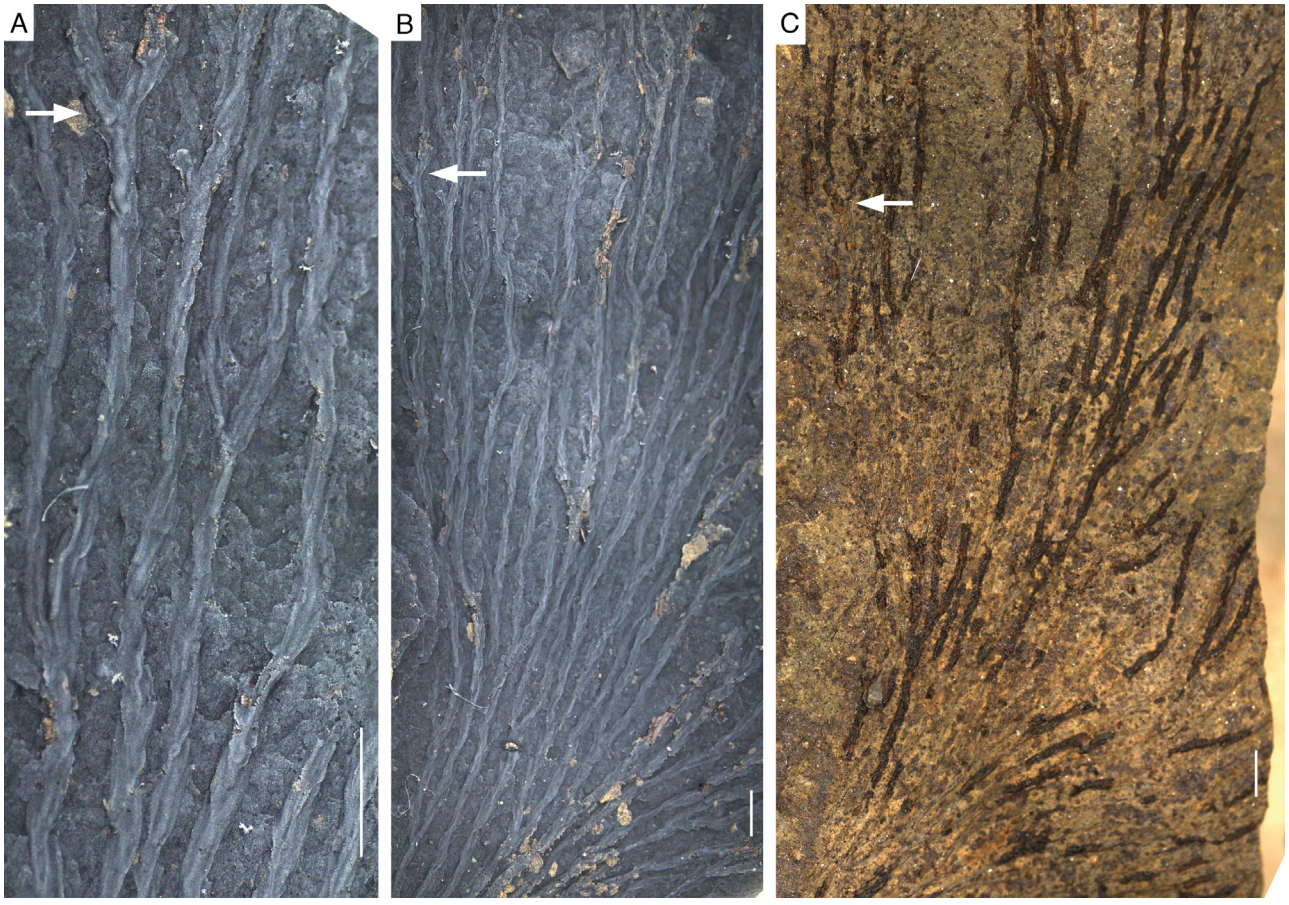

Fig. 5. *Callograptus* sp., largest specimen. Carrière de Lompret, new pit, upper Frasnian Matagne Formation (IRSNB a13389). **A, B.** latex casts showing dorsal preservation of stipes with vague expression of triad budding and dichotomous branching. **C.** Counterpart of specimen showing some preservation of fusellum (dark matter). White arrows point to a single branching point to allow comparison of specimen on the photos. Scale bars: 1 mm.

2019. *Dictyonema fournieri* (Ubaghs, 1941) – Maletz, p. 157, fig. 4b-c; ?4a.

Holotype: The holotype of *Dictyonema fraiponti* Ubaghs, 1941 is CGF 724 (Ubaghs, 1941: pl. 4, fig. 16) from the Piette quarry in Denée (Mottequin et al., 2015), Molignée Fm. (quarried level known as La Veine), a large and nearly complete specimen in which parts of the fan-shaped tubarium were folded over to cover the central portion. The holotype of *Ptiograptus fournieri* Ubaghs, 1941 is CGF 702. It was illustrated by Mottequin et al. (2015: fig. 13C) and Maletz (2017: fig. 8.12) and shows the typical wide fan of the tubarium of *Dictyonema fraiponti* Ubaghs, 1941.

Ubaghs' material: The specimens of all taxa of Ubaghs (1941), as listed above, originated from several quarries around the village of Denée exploiting the 'black marble' of Denée, now included within the Molignée Fm. of Moliniacian age (Viséan) (see Mottequin et al., 2015 for an overview). The specimens were included into the genera *Dendrograptus*, *Desmograptus*, *Dictyonema* and *Ptiograptus*, including also a few specimens not referred to a defined species. The described specimens can be shown to belong to a single species, here identified as *Dictyonema fraiponti* Ubaghs, 1941. The most juvenile specimens have originally been identified as *Dendrograptus* sp. 1 and *Dendrograptus* sp. 2 by Ubaghs (1941) and differences can only be seen in the size of the specimens and the length of the possible stem. Ubaghs (1941) also noted that the material may be referred to *Ptiograptus* instead. Both taxa bear a number of bridges in their small colonies (Fig. 7(A, B)). The stipes grow slowly and the typical fan-shape of the mature colonies is not yet developed. The illustrated specimen of *Dendrograptus* sp. 1 is distorted and shows the lateral overlap and bending of stipes, most probably due to transport and current action. If the stipes would be spread out, the specimen would look like *Ptiograptus fournieri* var. of Ubaghs (1941) (Fig. 7(C)), showing an increasing number of bridges closer to the proximal part of the colony. The distal end of the colony is somewhat irregular as some regions grow faster than others. In the mature colony, the distal rim is more precisely defined (Fig. 7(E)). Specimens identified by Ubaghs (1941) as *Dictyonema fraiponti* appear to be more strongly distorted through transport with the lateral parts of the fan-shaped colonies flapped over the central parts (Fig. 7(D)). They may easily be identified as cone-shaped, even though they are fan-shaped. Some distal fragments may easily be misidentified as *Desmograptus*, as the tubarium bridges are as wide as the main stipes, and stipes and bridges are difficult to differentiate in these specimens.

Devonian material: Carrière de Lompret, new pit, Matagne Fm., upper Frasnian, from a single level within the Matagne Fm. (upper Frasnian) (max. 50 cm of interval, most probably of a single, <1 cm interval; Fig. 6(A, D, E)).

Description: The material consists of several specimens on seven small slabs of shale, some with counterparts. All graptolites are preserved as fragments with the largest piece *ca.* 60 × 30 mm^2 in size. Some of the slabs are strongly weathered. The general shape of the colonies is difficult if not impossible to establish. Evidence indicates that the colonies may be fan-shaped as indications for a conical shape are not found. The smaller fragments which originated probably more proximally, already show a fan shape, but appear to have the stipes initially closer

Fig. 6. Devonian dendroids of the Carrière de Lompret, Belgium. **A, D, E.** *Dictyonema fraiponti* Ubaghs, 1941, new pit, upper Frasnian Matagne Formation. A: IRSNB a13388, large fragment in partial relief; D, E: IRSNB a13390, counterparts, poorly preserved and weathered specimen showing general colony shape. **B, C.** *Callograptus* sp. B: IRSNB a13389, new pit, laterally preserved specimen showing fan-shaped tubarium; C: IRSNB a13391, old pit, middle Frasnian Grands Breux Formation (Boussu-en-Fagne Member), three fragments on slab, largely flattened, two fragments on right side largely overlapping. Scale bar: 10 mm.

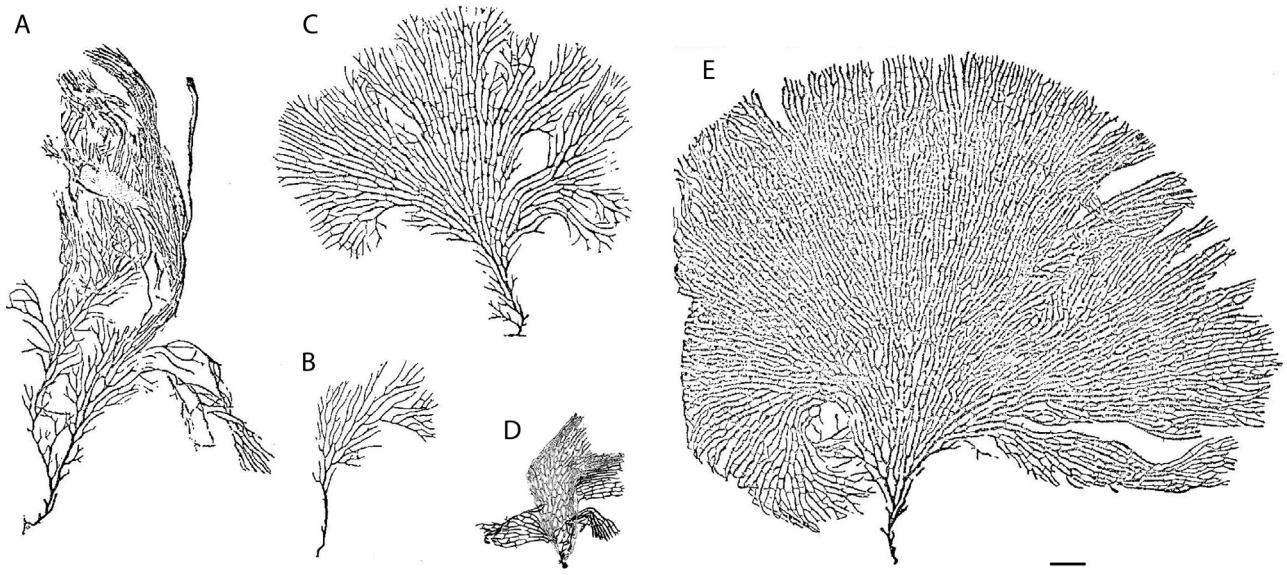

Fig. 7. The astogeny of *Dictyonema fraiponti* Ubaghs, 1941 from the Molignée Formation ('black marble' of Denée), Viséan. All specimens are identified by their original (Ubaghs, 1941) names and drawings. **A.** *Dendrograptus* sp. 1, CGF 701. **B.** *Dendrograptus* sp. 2, CGF 704. **C.** *Ptiograptus fournieri* var., ULg 11,282. **D.** *Dictyonema fraiponti* var. 1, CGF 714. **E.** *Ptiograptus fournieri*, ULg 11,281. All specimens based on Ubaghs (1941) to show the intraspecific variation of the taxon. Scale bar: 10 mm.

together (Fig. 2(F, G)). The material shows a stipe width of 0.35–0.45 mm and a stipe count of *ca*. 8–12 stipes in 10 mm. However, due to transport, folding or bending over, this count may be misleading and inaccurate. Thecal transfer can be found at irregular distances between 1.5 and more than 6 mm. The thecal connections between the stipes are *ca*. 0.1–0.15 mm wide. They keep the adjacent stipes at fairly constant distances. Anastomosis has not been recognized in this species, but the thecal transfer through thecal bridges may have been misidentified as anastomosis or in flattened material as representing dissepiments (Maletz, 2019). The bridges of the thecal transfer often include more than one theca, and up to four thecae have been counted. The bridges are often not perpendicular to the stipes but form oblique features. The thecae are long and slender, parallel-sided with simple straight apertures which bend downwards from the dorsal side of the stipes. They are several mm long, but exact measurements are impossible for this material. Thecal apertures are very difficult to find in the few collected fossils and there is no evidence of lateral growth of thecal tubes, except at positions with bridge building. The number of thecae at each point of a stipe is probably about 4–6 and appears to be quite consistent as the stipe width shows little variation. Quite a number of irregularities of stipe development can be seen in the few available fragments (Fig. 2(E)). Stipes branch, but after a short distance join again. In other places stipes are aborted as they get too close to adjacent stipes on the sides and then join one of the side stipes. At the distal ends of growing stipes, sometimes a single theca can be seen. Thus, not all thecae at the end of a stipe grow at the same time and same velocity.

Remarks: The problem was that the here described Devonian material is highly fragmentary and it was difficult to compare with the more complete and in most cases quite large specimens of Ubaghs (1941). It turned out, that most specimens described by Ubaghs (1941) from the Carboniferous can be included in a single species. The species varies considerably through its astogeny (Fig. 7). Small and medium sized specimens show fewer bridges and a less dense development of the stipes of the tubarium and were referred by Ubaghs (1941) to the genus *Dendrograptus*. The inclusion in the Carboniferous taxon *Dictyonema fraiponti* may indicate that dendroid graptolite species may be quite conservative and long ranging in the Devonian and Carboniferous. The tubarium shape with its characteristic bridges may easily be mistaken for the dendroid genus *Desmograptus* when thecal details are not available. *Desmograptus* has non-compound stipes and shows anastomosis without thecal transfer (Rickards et al., 1990; Saunders et al., 2009).

Genus Ptiograptus Ruedemann, 1908

Type species: *Ptiograptus percorrugatus* Ruedemann, 1908, by original designation.

Revised diagnosis: Fan-shaped tubarium with compound stipes; stipes formed through triad budding(?) of long, tubular thecae; stipes are connected at irregular distances by thecal transfer of single or multiple thecae (bridges); anastomosis is not found; thecae tubular, aperturally isolated and often laterally oriented to the stipes; bithecae may be present, but are impossible to recognize; proximal development unknown.

Remarks: The original inclusion of *Ptiograptus fournieri* Ubaghs, 1941 in the genus *Ptiograptus* was initially the reason to revise this genus and to re-describe its type species. The type material of *Ptiograptus percorrugatus* Ruedemann, 1908 probably originated from the Middle Devonian Waterlime of Louisville, Kentucky, USA. It consists of a single specimen showing what could be interpreted as part of an attachment. The type specimen has been illustrated only from a line drawing and details of the development are unknown. *Ptiograptus* is here interpreted to show thecal transfer at irregular distances (bridges), but the stipes do not connect laterally and join for instance, as would be seen if anastomosis was present (Maletz et al., 2014). The thecal transfer cannot be identified as pseudanastomosis sensu Rickards and Lane (1997) either. Therefore, the term bridge has been used to describe the thecal transfer in *Ptiograptus* and related taxa following Maletz (2019).

Specimens of the genus *Ptiograptus* have rarely been described. Ruedemann (1947) listed the three species *P. percorrugatus*, *P. coloradoensis* Ruedemann, 1947, and *P. multispinus* (Gurley, in Bassler, 1909) from the Silurian to Middle Devonian of North America. The material is poorly preserved and the identity is uncertain.

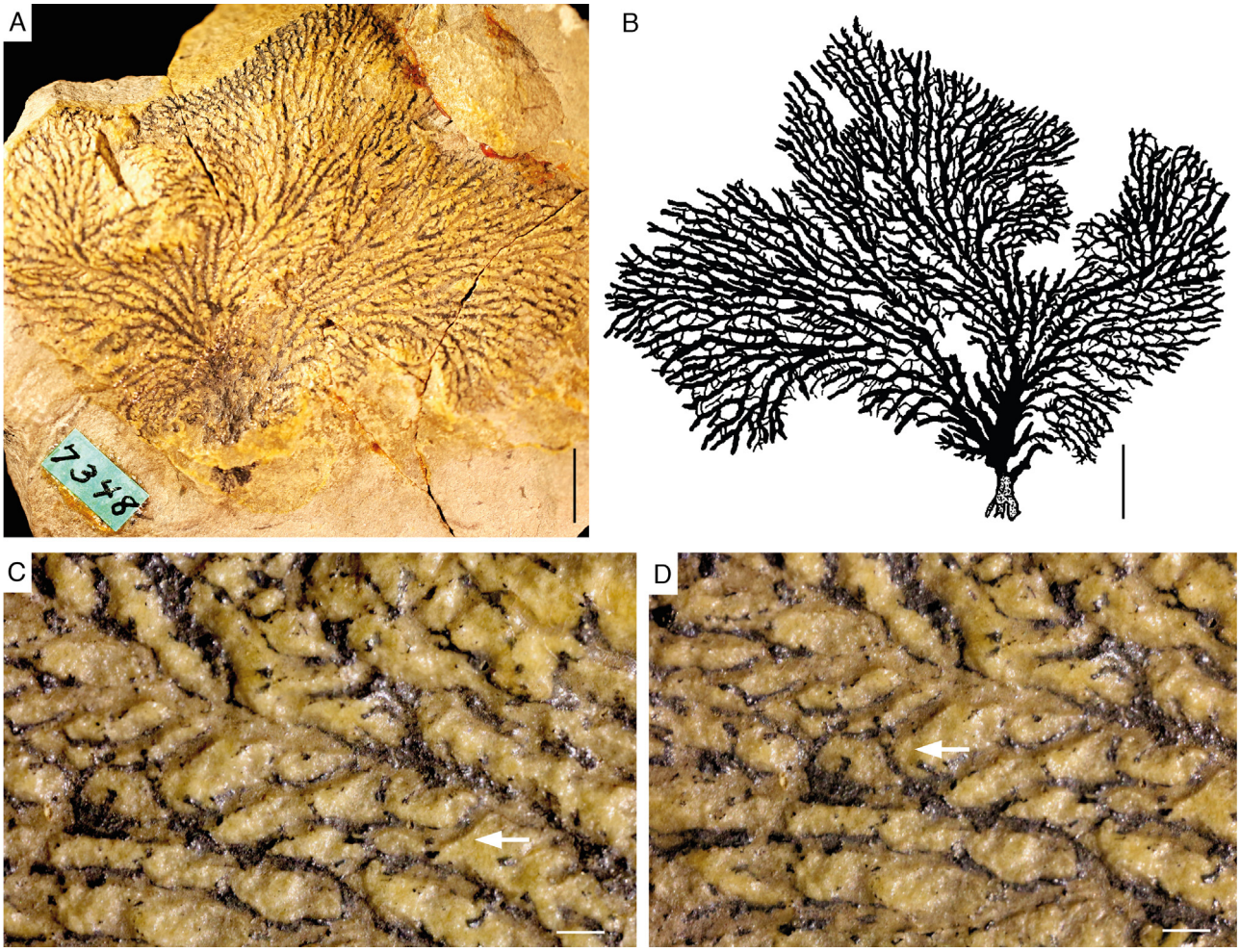

Fig. 8. Holotype of *Ptiograptus perrugatus* Ruedemann, 1908, NYSM 7348. **A.** Overview of the specimen. **B.** Illustration from Bulman (1970a: fig. 16.6), based on Ruedemann (1908) showing the mirror image of the specimen. **C, D.** Details of tubarium, showing isolated thecal tubes on stipes. Scale bars: 10 mm (A, B), 1 mm (C, D).

Ptiograptus percorrugatus Ruedemann, 1908
Fig. 8

1908. *Ptiograptus percorrugatus* n. s. – Ruedemann, p. 176, pl. 5, fig. 6; text-figs. 82–83.

1947. *Ptiograptus percorrugatus* Ruedemann – Ruedemann, p. 201, pl. 15, figs. 4–6.

Holotype: NYSM 7348, Middle Devonian(?) Waterlime, Louisville, Kentucky, USA.

Age: Ruedemann (1908, 1947) stated that the type and only specimen of *Ptiograptus percorrugatus* originated from the 'waterlime at Louisville, Kentucky' and referred the specimen to the Middle Devonian. The matrix of the limestone appears to match the dolomitic Louisville Limestone of late Silurian age (Ludlow; Ettensohn et al., 2013), however (Alan Goldstein, Park Palaeontologist, Falls of the Ohio State Park, 2019; pers. com.; see also http://louisvillefossils.blogspot.com/2011/03/silurian-graptolite.html for a similar specimen that might belong to *Ptiograptus percorrugatus*), and it is likely that the specimen is of Silurian age. Both Silurian and Devonian lithological units of the region have been termed 'waterlime' in the past.

Diagnosis: As for the genus, by monotypy.

Description: The original illustration of *Ptiograptus percorrugatus* Ruedemann, 1908 is a mirror image of the preserved specimen (Fig. 8(A, B)). The only available specimen shows a fan-shaped tubarium with the robust stipes showing multiple branching and attain a parallel orientation quickly. The colony appears to possess at least a part of an attachment, but details are not available. It is preserved on a yellowish piece of limestone, but only small pieces of organic(?) material are preserved. As the specimen has been coated with glue(?) for protection, some details cannot be investigated.

The robust stipes are *ca.* 0.6–0.7 mm wide in the proximal end, but thinner in distal, growing parts of the colony. Isolated thecal tubes are *ca.* 0.15–0.2 mm wide and at least 0. 2–0.3 mm long. They grow towards the sides of the stipes at various angles. The lateral distance between stipes is *ca.* 1.2–1.5 mm. Branching distances are highly variable in the specimen and have not been measured. In some places elongated thecal tubes curve distally and merge, apparently producing new stipes or joining to form long tubular thecae between two adjacent stipes (Fig. 8(C, D), white arrows). Anastomosis has not been observed in the specimen and there is no development of twigs either.

Remarks: *Ptiograptus* is characterized by a fan-shaped tubarium with compound stipes. The isolated thecal apertures are oriented sideways. Ventrally orientation of thecal tubes cannot be excluded, but is not possible to observe in the flattened specimen. The construction of the tubarium is in many ways similar to those of *Acanthograptus, Koremagraptus* and *Palaeodictyota*, but there is no anastomosis or development of twigs in *Ptiograptus*. In these taxa also lateral extending thecal tubes are present, which lack in the equally complex stipes of *Dictyonema*. The specimens identified as *Ptiograptus fournieri* by Ubaghs (1941) from the Carboniferous of Belgium are not comparable with the concept of the genus *Ptiograptus* and are now referred to *Dictyonema fraiponti*.

5. The sparsely known record of mid Devonian to early Carboniferous dendroid graptolites

Dendroid graptolites have rarely been documented from sediments post-dating the extinction of the planktic graptolites near the end of the early Devonian, and, thus, these faunas cannot easily be compared and correlated.

From Germany, Devonian dendroid graptolites are known from only four localities. From both Gees (Eifelian) and Gerolstein (Givetian), Kowalski (1987) reported a single indeterminable fragment, and from the Paffrath Syncline of the Rheinisches Schiefergebirge (upper Frasnian), Jux (1967) described a single fragment of ?*Palaeodictyota montana* (Maletz, 2006). From the Givetian of Burgberg (Rheinisches Schiefergebirge), a larger number of relatively poorly preserved specimens were recorded, which can be assigned to the genera *Dictyonema* and *Ruedemannograptus* Termier and Termier, 1948 (Maletz, 2006). The material is poorly preserved and details of the development of thecae and stipes are not available.

From the Czech Republic, a small number of fragmentary and poorly preserved specimens are known from the Eifelian and Givetian (Kraft, 1984), allowing to document the presence of *Dictyonema* in the Eifelian, and *Thallograptus*, *Desmograptus* and *Dictyonema* in the Givetian (Maletz, 2006).

Ruedemann (1947) described and illustrated a number of dendroid graptolites from the Eifelian Onondaga Limestone of eastern North America, including at least four species, *Dictyonema hamiltoniae, Dictyonema leroyense, Dictyonema megadictyon,* and *Dictyonema perradiatum* (Cassa and Kissling, 1982; Maletz, 2008). Berry (1969) found specimens of the genera *Desmograptus* and *Dictyonema* in the Givetian of Iowa, Illinois and Michigan. Most of the specimens could be considered as indeterminable, as they are based on poorly preserved(?) fragments. The age of *Ptiograptus percorrugatus* Ruedemann, 1908 is uncertain, as it may have originated from the mid-Silurian Louisville Limestone (see remarks for this species).

Berry (1972) described a single fragment from the Lower Devonian Humevale Fm. of Victoria, Australia. The thecae are tubular and the tubarium shows a typical anastomosis of the stipes. The details of the thecal development, the shape of the thecal apertures and the development of the anastomosis are, however, unclear. He compared the material also to the genus *Reticulograptus* and suggested that certain specimens assigned to *Desmograptus* may alternately be referred to *Reticulograptus*. Rickards and Wright (2000) illustrated a very poor, small fragment as *Dendrograptus* sp. from the Lower Devonian of Limekilns, New South Wales and regarded it as the stratigraphically highest dendroid reported from Australia. Thecal details are not available in this specimen. From many other parts of the world, middle to upper Devonian dendroid graptolites are completely unknown.

Ruedemann (1947) listed five possible Carboniferous dendroid graptolite species from North America and provided illustrations of these. Three of them belong to *Dictyonema* from the Englewood Fm. of North Dakota, of which thecal details are not available.

The best known Carboniferous dendroids are from Britain and Ireland (Chapman et al., 1993). The material shows a considerable diversity and demonstrates that at least taxa of the Dendrograptidae and Acanthograptidae are still present. The authors also described a specimen of *Dictyonema fraiponti* under the name *Dictyonema fournieri* from the Asbian (Viséan), supporting a considerably longer biostratigraphic range than known from the Ubaghs (1941) record.

Summed up, most of the Devonian and Carboniferous dendroid species and specimens are described from small fragments or are poorly illustrated and details of their development are unknown. For most taxa only the general outline, branching pattern and presence of lateral connections, either dissepiments or bridges, are recognizable. Thecal details, presence of bithecae or compound stipes cannot be verified in this flattened material. Thus, a thorough revision is needed for each taxon to understand the real diversity of the younger dendroid graptolite faunas. As dendroids are generally considered useless for any biostratigraphic purpose, they are not well investigated and a recent comprehensive revision is not available.

The newly discovered material from the Belgian Frasnian thus constitutes an important addition to the knowledge of Devonian dendroid graptolites by adding two new localities to their sparsely known record. It allows to state the presence of representatives of the genus *Callograptus* in the middle Frasnian, and the presence of *Dictyonema fraiponti* in the late Frasnian, greatly enlarging the stratigraphic range of the latter, until previously, only from the Carboniferous recorded, species. Being very well-preserved, for the very first time, the details of the tubarium construction of Devonian dendroid graptolites can be revealed, being highly important for a taxonomic and phylogenetic understanding of the youngest dendroid graptolite faunas worldwide.

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