Citation: Gutiérrez-Marco, J.C., Maletz, J., 2024. Mass occurrence of planktic dendroid graptolite synrhabdosomes (*Calyxdendrum*) from the Early Ordovician Fezouata biota of Morocco. Geologica Acta, 22.4, 1-19.
DOI: 10.1344/GeologicaAct2024.22.4

geologicaacta

Mass occurrence of planktic dendroid graptolite synrhabdosomes (*Calyxdendrum*) from the Early Ordovician Fezouata biota of Morocco

Juan Carlos Gutiérrez-Marco[1] and **Jörg Maletz**[2]

[1]**Instituto de Geociencias CSIC-UCM, and Área de Paleontología, Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas UCM**
José Antonio Novais 12, 28040 Madrid, Spain. E-mail: jcgrapto@ucm.es ORCID ID: 0000-0003-4213-6144

[2]**Institut für Geologische Wissenschaften, Freie Universität Berlin**
Malteser Str. 74-100, Haus C, Raum 105, D-12249 Berlin, Germany. E-mail: yorge@zedat.fu-berlin.de ORCID ID: 0000-0001-7986-0617

ABSTRACT

The genus *Calyxdendrum* is here revised to include planktic dendroid graptolites from the Ordovician (Tremadocian to Sandbian). The mass occurrence of *Calyxdendrum amicabilis* n. sp. from the Fezouata biota represents one of the few occurrences of synrhabdosomes of dendroid morphology that have ever been discovered. Composite structures, formed from about four to six slender, conical tubaria of the species appear as umbrella-shaped synrhabdosomes. In these, the individual tubaria are connected by their short nemata forming an irregularly shaped proximal membrane. The species is found in the late Tremadocian *Sagenograptus murrayi* Biozone of the Bou Izargane section in the Ternata plain north of Zagora, Morocco. The mass occurrence is interpreted to represent planktic dendroid colonies transported by low velocity currents or moving actively into different water regions on a wide shallow shelf region. They settled in the "soupy" soft sediment, where they were subsequently compacted in the now lithified mudstone. Planktic dendroids of the genus *Calyxdendrum* are so far known exclusively from the peri-Gondwana region, but may prove to show a wider biogeographical distribution when better known

KEYWORDS **Ordovician. Konservat-Lagerstätte. Morocco. Planktic dendroids. Synrhabdosomes.**

INTRODUCTION

Synrhabdosomes are radially arrayed associations of graptoloid tubaria, normally attached by the distal extremities of their nemata and mostly monospecific. These enigmatic assemblages are rare and are known only in about thirty of the few thousands planktic graptolite species, having received various paleobiological interpretations and others that include a merely taphonomic origin (references in Cooper *et al.,* 2023). In any case, it seems clear that synrhabdosomes were not part of the life history and ecology of most graptolites (Cooper *et al.,* 2012; Maletz, 2015), in spite of the fact that they have long appeared in the artistic reconstructions of many museums and paleontology books as a common lifestyle for planktic graptolites. In this sense, the review of the original material with which Ruedemann (1895, 1904) described the chambered structures in the center of the synrhabdosomes –the "float" called *pneumatophore* and the "reproductive vesicles" or *gonangia*– resulted in these structures being purely imaginary (Gutiérrez-Marco and Lenz, 1998).

The scarce record of synrhabdosomes mainly involves biserial and uniserial axonophoran genera from the Middle Ordovician to the Lower Devonian, being extremely rare among anisograptids and Dichograptina from the Early and Middle Ordovician (Gutiérrez-Marco and Lenz, 1998).

In the present paper we describe the first evidence of synrhabdosomes in the oldest planktic representatives of the graptolite order Dendroidea NICHOLSON, 1872, belonging to a genus (*Calyxdendrum* KOZŁOWSKI, 1960) whose scarce species were until now known from the Middle-Late Ordovician of Bohemia, Poland and Iran (see below). The new material comes from upper Tremadocian strata of the central Anti-Atlas, Morocco, where perhaps millions of synrhabdosomes of a new species of *Calyxdendrum* occur in a massive accumulation horizon intercalated within the stratigraphic interval of the so-called Fezouata biota in its type area, one of the most famous fossil-Lagerstätten of the Ordovician system of the world (El Hariri *et al.*, 2022; Lefebvre *et al.*, 2016, 2020; Van Roy *et al.*, 2010, 2015a). The good preservation conditions prevailing in this interval allowed us to advance details to the knowledge of synrhabdosomes, regardless of its interpretation, to make general statements about mass occurrences of other early planktic graptolites with conical tubaria, as well as to document cases of exceptional preservation of some of internal structures present in the tubarium of this unusual dendroid graptolite.

GEOLOGICAL SETTING

The Fezouata Formation (=Fezouata Shale) is a Lower Ordovician unit mainly composed of argillites and siltstones, that unconformably overlies diverse Cambrian formations and reach a maximum thickness of 900–1000 meters in the Zagora–Foum Zguid depocentre of the central Moroccan Anti-Atlas (Lefebvre *et al.*, 2016; Vaucher *et al.*, 2016, 2017), the type area where the Fezouata biota has been documented. Sediments were deposited in the southern Gondwanan margin near the South Pole, at a high paleolatitude of ca. 65ºS –up to 80ºS according to the maps of Torsvik and Cocks (2017, figs 6.2a, 6.3) and involve almost exclusively environments developed between the fair-weather wave base and just below the storm wave base (Martin *et al.*, 2016a; Saleh *et al.*, 2018; Vaucher *et al.*, 2017).

The Fezouata biota is composed by an abundant and diverse assemblage of marine organisms which include many non-biomineralized animals showing exceptional preservation, and typical Paleozoic groups like trilobites, echinoderms, mollusks, brachiopods, etc. It is a Burgess Shale-type Lagerstätte of late Tremadocian to Floian (Early Ordovician) age, which is providing many keys to understand the transition between the Cambrian Explosion and the Great Ordovician Biodiversification Event (GOBE) (Lefebvre *et al.*, 2016; Martin *et al.*, 2016a; Saleh *et al.*, 2021a, 2022b; Servais *et al.*, 2016, 2023). In this sense, the Fezouata fauna includes a number of typical Burgess Shale or Chengjiang biota taxa, extending the ranges of many iconic groups into the Ordovician, such as radiodonts, lobopodians, highly diversified non-trilobite arthropods (aglaspidids, nektaspids, and others), palaeoscolecid and selkirkiimorph priapulid worms, protomonaxonid sponges, etc. (Botting, 2007; Drage *et al.*, 2023; Laibl *et al.*, 2023; Lefebvre *et al.*, 2016, 2020; Legg, 2016; Lustri *et al.*, 2024; Nanglu and Ortega-Hernández, 2024; Ortega-Hernández *et al.*, 2016; Pérez-Peris *et al.*, 2021; Potin *et al.*, 2023; Saleh *et al.*, 2022b; Van Roy and Briggs, 2011; Van Roy *et al.*, 2010, 2015a, b).

The main outcrops of the Fezouata Shale Formation yielding the Fezouata biota occur near the city of Zagora (Fig. 1), especially in the Ternata plain to the north, where its most representative paleontological place is located and was recently designated among *The First 100 IUGS Geological Heritage Sites* (El Hariri *et al.*, 2022). This Early Ordovician Konservat-Lagerstätte includes several modes of preservation of non-biomineralized, cuticularized or lightly sclerotized fossils occurring mainly in shales, but also within silica-chlorite concretions (Gaines *et al.*, 2012; Saleh *et al.*, 2020a, c, 2021a, b, 2022b). There are two main intervals of exceptional preservation within the Fezouata Shale, dated to the late Tremadocian and middle Floian (Lefebvre *et al.*, 2016, 2018). The lower interval ranges from 250 to 360m above the base of the Formation, and corresponds essentially to the *Sagenograptus murrayi* graptolite Biozone (previously called *"Araneograptus" murrayi*) of the upper Tremadocian. The upper (but not the uppermost) main interval with soft-bodied biota is located between 575 and 675m above the base of the Formation, always measured in the northern Zagora depocentre, and is assigned to the *Baltograptus jacksoni* graptolite Biozone of the middle Floian (Akodad *et al.*, 2018; Gutiérrez-Marco and Martin, 2016; Lefebvre *et al.*, 2018; Martin *et al.*, 2016a). In addition, there is a third interval in the uppermost part of the formation, ranging probably from the upper Floian *Baltograptus minutus* graptolite Biozone upwards (Saleh *et al.*, 2022b).

The record of late Tremadocian dendroid graptolites in the Fezouata biota has been related to taxa interpreted as benthic and sessile organisms. Martin et al. (2016a, figs. 5C, J) identified and illustrated two specimens of

Koremagraptus sp. and *Dictyonema?* sp. and referred to them as “rooted benthic dendroids”. Their original material has been reviewed and partially prepared by us, recognizing both specimens as belonging to the planktic genus *Calyxdendrum* due to the sicular morphology and by the frequent presence of oblique thecal bridges instead of true anastomosis among adjacent stipes.

Likewise, other problematic organisms of the Fezouata biota deserve re-interpretation. *Webbyites felix* MUIR AND GUTIÉRREZ-MARCO, 2023, originally described as a benthic graptolite of uncertain affinity, may represent a hydrozoan (Cnidaria), because its’ supposed “stolonal system” could have been confused with preservational variants of a chitinous hydrorhiza with thickened perisarcal features (Maletz and Gutiérrez-Marco, in press work in progress). We must also mention the record of two rare benthic hemichordates: the first is a specimen illustrated as a “tuboid graptolite” or an “undescribed benthic graptolite” by Van Roy (2006, fig. 3.10), Van Roy *et al.* (2010, fig. S2i) and

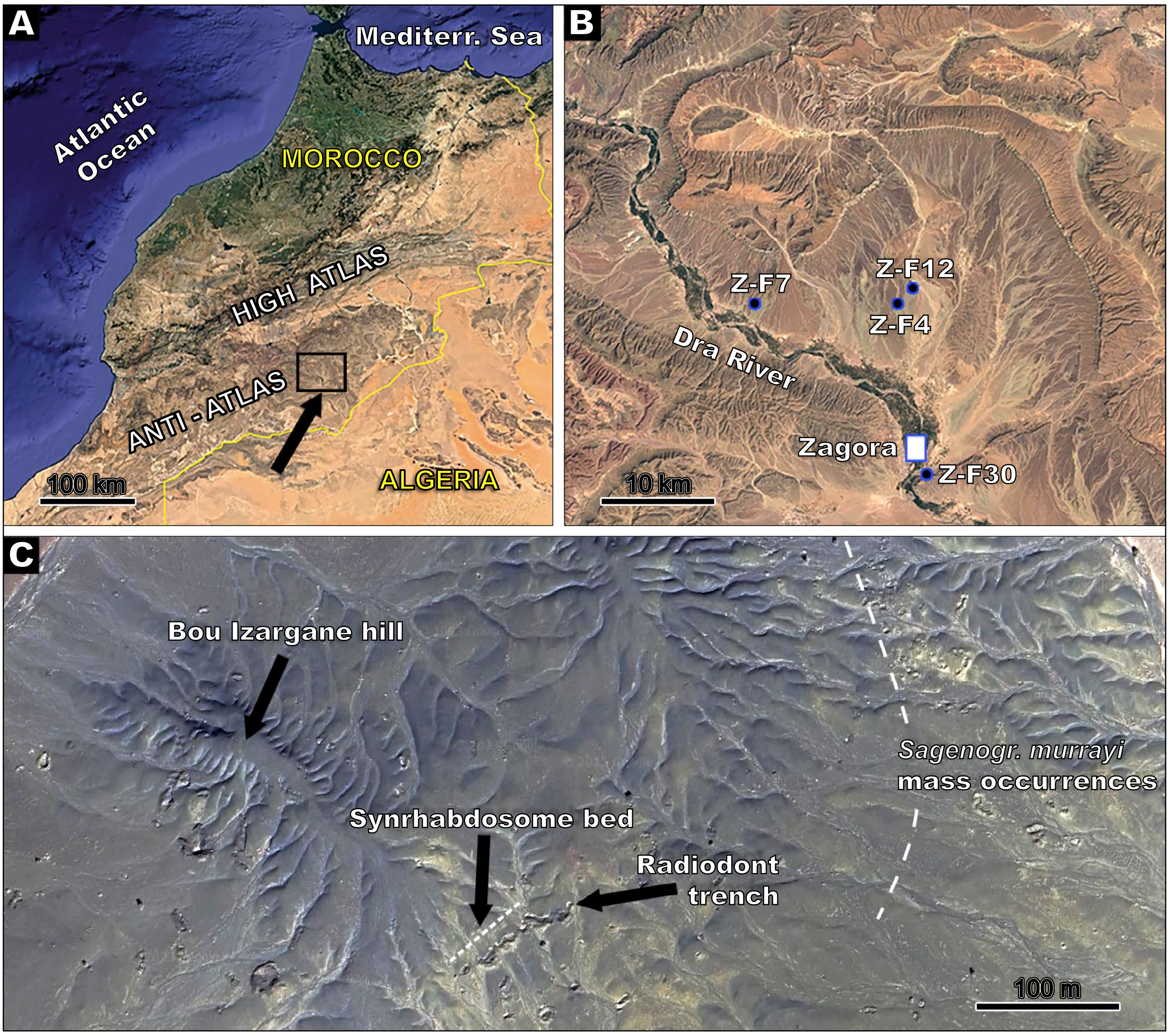

FIGURE 1. Satellite images showing the location of the studied localities in the Anti-Atlas region of Morocco (square and arrow in A) and enlargement of the area (B) showing the placement of the sections bearing records of the late Tremadocian graptolite *Calyxdendrum amicabilis* n. sp. From west to east they are: Bou Zargouan (Z-F7), Bou Izargane (Z-F4, type section for the species), Jbel Tizagzaouine (Z-F2), and Jbel Zagora (Z-F30). The localities Z-F4 and Z-F2 are situated in the center of the Ternata plain to the north of the city of Zagora. C) A detailed view (dated April 12th, 2022), of the outcrops of the Fezouata Formation at the upper part of the section of Bou Izargane (Z-F4 in B), showing the position of the main excavations corresponding to the three fossiliferous beds cited in text, including the stratotype (Synrhabdosome bed) of the new species. Landsat/Copernicus images, adapted from Google Earth ©2023.

Nanglu *et al.* (2023, fig. 5C, D); the second was described in detail as an "epibiontic rhabdopleurid hemichordate" (Nanglu *et al.*, 2023, figs. 1–4). However, these two specimens may alternatively represent the pseudocolonial tubaria of cephalodiscid-like pterobranchs and were definitely benthic (but non "epibiontic") forms (Maletz and Gutiérrez-Marco, work in progress). Present on calcareous shell fragments, the material indicates that transportation was responsible for the specimens to be preserved in these "soupy" soft-bottom sediments, where an epibenthic, sessile life style was impossible to be maintained.

In the present paper we describe a new species of the planktic dendroid *Calyxdendrum* that was previously recorded, although incorrectly identified as *Koremagraptus* sp. (Martin *et al.*, 2016a), in several sections of the Fezouata Formation within the *S. murrayi* Biozone (Fig. 1B). They include four localities near Zagora: Bou Izargane (Z-F4), Jbel Tizagzaouine (Z-F2), Bou Zargouan (Z-F7) and Jbel Zagora (Z-F30), according to the abbreviations for fossil localities used in previous studies (see compilation in Lebrun, 2017; Lefebvre *et al.*, 2016). Previous collections from Bou Izargane deposited at the University of Lyon (France) includes a sample, FSL 712 407, that was collected by the amateur paleontologists Roland and Véronique Reboul in 2013 at coordinates N30°29'59", W5°51'00". It is a thin slab that bears the evidence of a mass concentration horizon of large tubaria of *Calyxdendrum*, not grouped into synrhabdosomes, and that has not been recovered again in situ. Other material from the remaining localities consists of single tubaria of *Calyxdendrum amicabilis* n. sp. in variable states of preservation, with the exception of the isolated central part of a broken synrhabdosome that preserves the apical fragments of 5–6 tubaria and comes from the level Z-F2(3)5 of the Jbel Tizagzaouine section (see below).

The new research period, leading to the discovery of a mass occurrence of planktic dendroid graptolites in the Fezouata Biota, started in March 2017 in the shop of fossil collector Mohamed Ben Moula in Taichoute (Alnif region, Morocco), who was the discoverer of the Fezouata biota and received the Mary Anning Award of the Palaeontological Association. "Ou Saïd" Ben Moula is a renowned Moroccan excavator, who has provided most of the exceptional fossils described in international studies. Among the graptolite slabs for sale (almost all *S. murrayi*) there was one with an enigmatic accumulation of dendroids, of poor aspect and little value relative to the others. The problem was that M. Ben Moula had forgotten the place of provenance of this graptolite and only remembered that it originated from one of the dozens of hole surveys in the Ternata plain where, as there was nothing but graptolites, they recovered the slab knowing that the first author could be the only person interested in their study. Together with his sons, he then abandoned what they described as "a small hole". Once the sample was obtained by us (Fig. 2A–C), and with vague indication that its origin could be located in the plain south of either Bou Izargane or Jbel Tizagzaouine, we finally managed to find its place of origin (Fig. 2D–E) and fixed the position of the mass concentration horizon of dendroid synrhabdosomes described in this article. This goal was achieved after spending two weeks of field work in consecutive annual campaigns, completed successfully and with good luck.

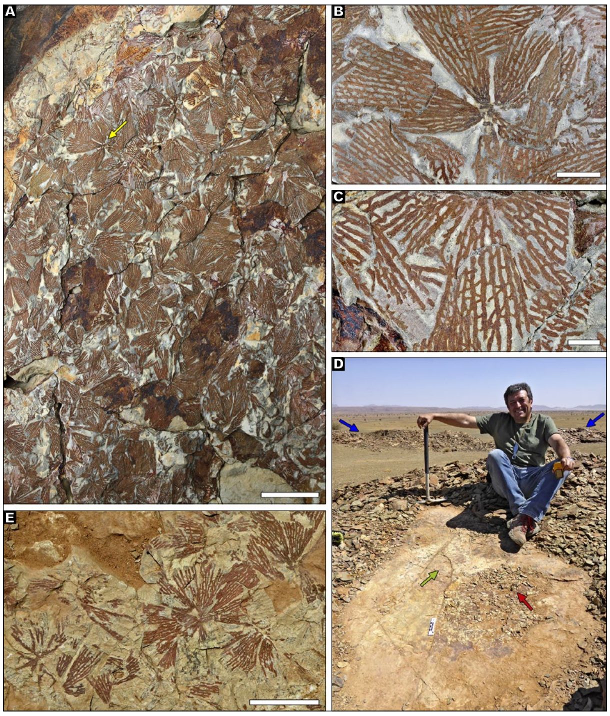

FIGURE 2. Massive occurrence of synrhabdosomes of *Calyxdendrum amicabilis* n. sp. at the type locality, Bou Izargane section in the Ternata plain north of Zagora. A) Partial aspect of the slab MGM-7775X showing numerous synrhabdosomes stacked on top of each other. B) Detail of the synrhabdosome MGM-7775X-1, indicated with a yellow arrow in the previous picture. C) A view of some tubaria on the same slab, MGM-7775X-2 (center), showing details of the mesh and autothecae in the lateral stipes. D) Excavation of the synrhabdosome bed, with indication of the area detailed in Figure 2E (green arrow) and the place of origin of the slab in Figure 2A (red arrow). The blue arrows indicate the accumulation bed of large radiodonts placed stratigraphically 3.4m below the graptolite horizon. E) field photograph of a small part of the synrhabdosome bed during excavation (unnumbered specimens, broken during extraction). Scale bars, A: 50mm, B: 10mm, C: 5mm, E: 30mm.

Fossil locality and horizon

The studied locality consists of a small fossil pit (Fig. 2D, geographic coordinates N30°29'57.8", W5°50'52.6") situated in the southeastern slope of the Bou Izargane hill, ca. 19.5km north of the city of Zagora (for detailed position see Fig. 1B, C). From a stratigraphic perspective, and with reference to the three excavation sites opened by the French paleontologist team in 2014 in the interval between 257 and 280m above the base of the Fezouata Formation, the new graptolite horizon can be found in the non-quarried interval between the lower and intermediate Z-F4 excavation sites of these authors (Martin *et al.,* 2016b; Vaucher *et al.,* 2016). This interval belongs to the late Tremadocian *Sagenograptus murrayi* graptolite Biozone (Gutiérrez-Marco and Martin, 2016; Martin *et al.,* 2016a). The single sample of planktic dendroids collected during these formal excavations was a fragment of tubaria found at the top of the lower excavation site, in the sample Z-F4/10. In the two or three years following the completion of these excavations, the Ben Moula family carried out new surveys in the area, which resulted in the discovery of a bed extraordinarily rich in remains of giant radiodonts, which was intensively trenched between 2017 and 2018 (Fig. 1C). This fossiliferous horizon is about 60cm thick, and the first author noticed up to five cephalic shields of *Aegirocassis benmoulai* VAN ROY, DALEY AND BRIGGS, 2015b concentrated on a small bedding plane, as well as lateral accumulations of various radiodonts arranged horizontally one above the other. In the same bed, complete trilobites (*Platypeltoides*) and sporadic concentrations of large tubaria of the planktic dendroid *Calyxdendrum* also appeared, but without forming synrhabdosomes. This impressive fossil horizon was succeeded by 40cm of brown siltstones that produce some relief, on top of which the typical blue-green shales that constitute the majority of the outcrops of the Fezouata Formation in the area continue. About 3m stratigraphically above the preceding siltstones, the shales include the mass concentration of synrhabdosomes of the new species *Calyxdendrum amicabilis* n. sp. here studied, which together constitute a thin level (10–20mm) internally formed by the superposition of several graptolite accumulation planes (Fig. 2A, 3E, 4G–H). Between 2–4cm above the top of the graptolite horizon, the lithology becomes siltier and a bed rich in horizontal trace fossils and some large cuticular fragments (12x17cm) of marine arthropods is also recorded. These unidentified trace fossils developed in the horizontal plane as dm-long winding burrows of 2–4mm in diameter, branching laterally from one of its sides at irregular intervals (angle of branching: 45–90°). Eventually, a short oblique shaft can connect the burrow system with a level placed only 2–3cm above it. The burrows are apparently unlined and are filled with a lighter (oxidized?) material than the silty rock.

Most of the specimens of *Calyxdendrum amicabilis* n. sp. discovered in the mass concentration horizon of the Bou Izargane section form synrhabdosomes (Figs. 2–6) in which the tubaria are connected to each other by the tips of their siculae. Due to the preservation as largely flattened specimens, little detail of the precise construction of the tubaria and synrhabdosomes is available. The specimens

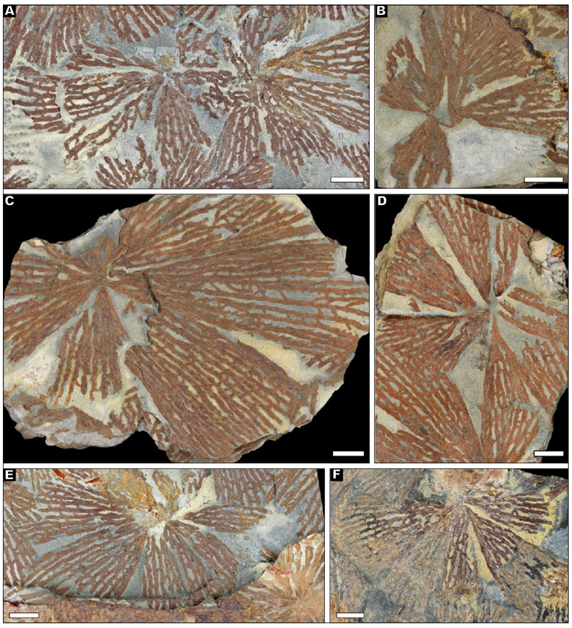

FIGURE 3. Some relatively well preserved synrhabdosomes of *Calyxdendrum amicabilis* n. sp., showing variations in the mesh of some of their integrating tubaria. A) two adjacent synrhabdosomes, MGM-7776X-1 (left) and MGM-7776X-2 (right) preserved on the same slab. B) MGM-7777X (see apical detail on Fig. 6A). C) MGM-7778X. D) MGM-7779X. E) Part of a slab preserving synrhabdosomes in three stacked layers: MGM-7780X-1 (centre), MGM-7780X-2 (lower right). F) MGM-7781X. Scale bars: 5mm.

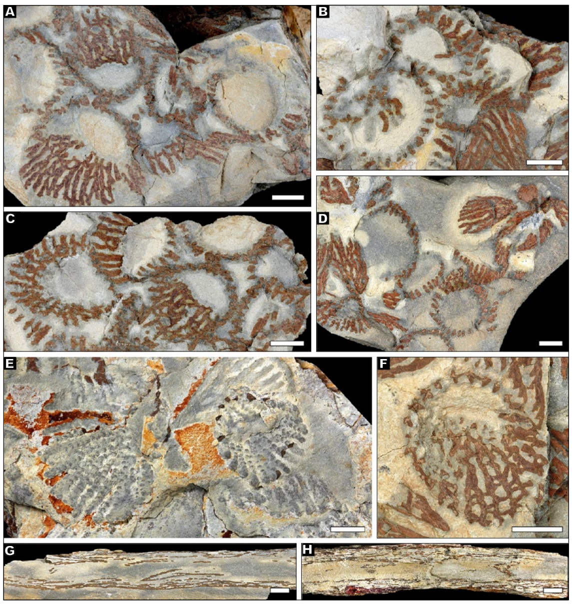

FIGURE 4. A–F) Sections of diverse tubaria of *Calyxdendrum amicabilis* n. sp. in the horizontal plane, partly grouped in synrhabdosomes, showing oblique orientation to the bedding plane and complete infilling of synrhabdosome structures and individual tubaria by "soupy" ground sediment before compaction. Most sections are seen from the lower side, and in E autothecae are preserved with some relief indicating a very early phase of pyritization. A) MGM-7782X; B) MGM-7783X; C) MGM-7784X; D) MGM-7785X; E) MGM-7786X; F) MGM-7787X-1. G–H) transverse sections through the massive graptolite bed, MGM-7788X and MGM-7789X, showing two pulses of synrhabdosome accumulation separated by one with predominance of sediment decantation and 3-D infilling of tubaria. Scale bars: 5mm..

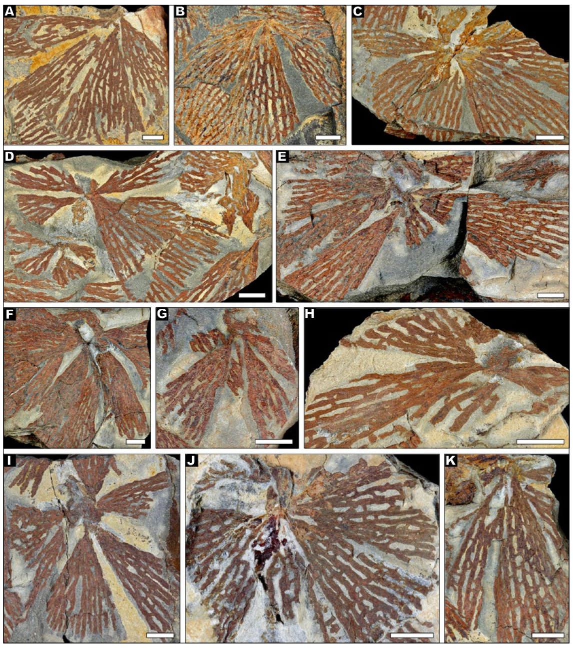

FIGURE 5. Relatively well preserved synrhabdosomes of *Calyxdendrum amicabilis* n. sp., showing the central attachment area and taphonomic variations in the number of preserved radiating tubaria. A) MGM-7790X; B) MGM-7791X; C) MGM-7792X; D) MGM-7793X; E) MGM-7794X; F) MGM-7795X; G) MGM-7796X; H) MGM-7797X; I) MGM-7798X; J) MGM-7799X; K) MGM-7800X. Scale bars: 5mm.

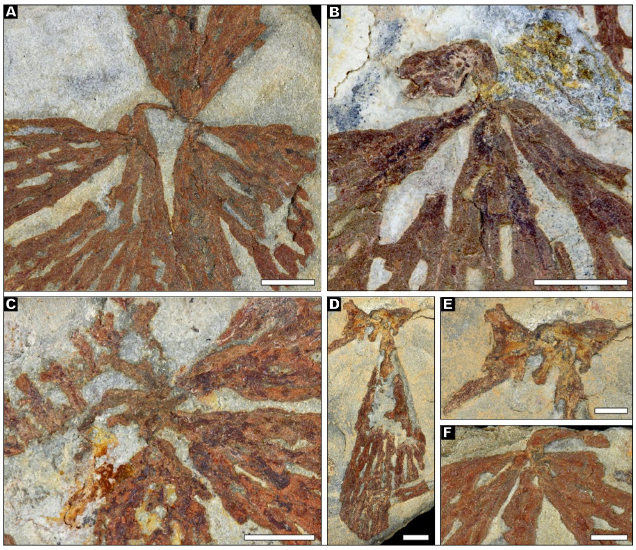

FIGURE 6. Enlargement of the central part of some synrhabdosomes of *Calyxdendrum amicabilis* n. sp. showing details of the attachment of the individual tubaria. A) Proximal end of Figure 3B, showing five tubaria, MGM-7777X. B) Synrhabdosome with possible membrane, MGM-7801X. C) Synrhabdosome with three tubaria attached to a central membrane which shows (left-hand) remnants of apical attachments of possibly three other tubaria, MGM-7802X. D–E) Isolated tubarium possibly belonging to a degraded synrhabdosome, still attached to the central membrane after the detachment of the remaining tubaria, and magnification, MGM-7803X. F) Detail of the center of a synrhabdosome in slightly oblique-lateral preservation, with at least four tubaria, MGM-7804X. Scale bars, A-D: 3mm, E-F: 2mm.

must be regarded as planktic as will be discussed and, thus, are unusual for the benthic dendroid graptolites of the order Dendroidea, that characteristically comprises erect growing benthic graptolites ranging in age from the Miaolingian (middle Cambrian) to the late Mississippian (early Carboniferous).

MASS OCCURRENCES AND SYNRHABDOSOMES OF PLANKTIC DENDROIDS

Three aspects of general interest to the understanding of graptolites come together in the here presented discovery. These need to be commented upon in a first step to properly understand our conclusions of the taphonomic analysis and the taxonomic characterization of the new species.

Mass occurrences

Mass occurrences appear to be common in graptolites (Fig. 2A), but have rarely been mentioned or discussed. They are invariably found in planktic graptolites, as environments in which benthic graptolites flourished, are not preserved in situ in the fossil record and most fossil benthic graptolites are described from fragmented and transported material. The mass occurrence found in Victoria (Australia) shows that numerous specimens and species of planktic graptolites are associated in dense masses of tubaria on few bedding planes (*cf.* Cooper *et al.*, 2017, figs. 5-6), either showing diverse faunal assemblages or near monospecific ones. A similar situation, however, may be present in many assemblages worldwide, but these details are generally not listed in taxonomic descriptions and usually only individual specimens are illustrated for identification purposes. A good example of a possibly overlooked mass occurrence is shown by Maletz and VandenBerg (2021, fig. 2) and Maletz *et al.* (2023a, fig. 86); a small slab bearing a number of current aligned biserial graptolites, that may have covered a much larger area of the sediment. However, only a small slab was collected/illustrated as it was sufficient to identify the specimens.

Mass occurrences of monospecific faunas have been noted in few species and the example of *Sagenograptus murrayi* (see Aceñolaza *et al.*, 1996; Gutiérrez-Marco and Aceñolaza, 1987; Lindholm, 1991; Martin *et al.*, 2016a) is especially notable as it represents a species with an enormously large tubarium in mature specimens. However, early planktic graptolites of the genus *Rhabdinopora* are commonly found in extremely large numbers on shale surfaces (Cooper *et al.*, 1998; Erdtmann, 1982a; Gutiérrez-Marco and Esteban, 2005; and others). This is also noted for the Xiaoyanggqiao ASSP section for the base of the Ordovician System in Jilin Province (China) where the earliest *Rhabdinopora* species is found only in a less than 5cm thick interval in the succession (*Rhabdinopora proparabola* (LIN, 1986): Wang *et al.,* 2021; Maletz *et al.,* 2023b), where the sediment surfaces are crowded with specimens, including all sizes from juveniles to mature and gerontic ones. The exact distribution of these mass occurrences cannot be investigated in most cases, as exposure sizes are limited and outcrops are widely separated from each other. They may, however, cover larger areas, hundreds of square meters in some areas or even more.

Monospecific assemblages of graptolites cover larger areas and may be compared to modern plankton/algal blooms (*cf.* Hallegraeff *et al.,* 2004) and blooms of jellyfish (*cf.* Hamner and Dawson, 2009; Lilley *et al.,* 2011) that cover huge regions of the marine realms. However, details on their preservation are difficult to access.

Planktic dendroid graptolites?

The identification of "planktic dendroids" goes back to Kozłowski (1960) and his description of *Calyxdendrum graptoloides*, a species considered to be intermediate between Dendroidea and Graptoloidea. The species was included in the family Anisograptidae by Bulman (1970), but referred to the Dendrograptidae by Maletz et al. (2023a) in the revision of the Graptolite Treatise. *Calyxdendrum* KOZŁOWSKI, 1960 was based on chemically isolated material found as a few specimens in a glacial boulder from the Sandbian *Nemagraptus gracilis* Biozone of Poland.

Kraft and Kraft (2006, 2007, 2008) discussed a number of Ordovician graptolites as planktic dendroids, based on the presence of a nema on the sicula of these specimens, and asked the question whether these represent "fiction or reality". Certainly, the interpretation of species as planktic dendroids appears to be strange and is probably misleading to most researchers, especially as Fortey and Cooper (1986) defined the order Graptoloidea as planktic by the presence of a free nema. From this definition it follows that the "planktic dendroids" listed by Kraft and Kraft (2006, 2007, 2008) may have to be considered as independent lineages of graptoloid graptolites, thus the order Graptoloidea would have to be identified as polyphyletic (see Kraft and Kraft, 2007, p. 73). This, however, is not necessary if we accept that the family Dendrograptidae provides additional instances of the evolution of planktic graptolites that are not included in the Graptoloidea, but represent independently evolved clades. The Graptoloidea as a monophyletic clade (in the sense of Fortey and Cooper, 1986; Maletz *et al.,* 2023a) can be maintained by this interpretation.

All fossil evidence indicates that the origin of planktic graptolites happened more than once in the late Cambrian to Middle Ordovician, but only one group was successful on the long run. The origin of the planktic Graptoloidea around the base of the Ordovician appears to be well established (Cooper *et al.,* 1998; Erdtmann, 1982a, b; Fortey and Cooper, 1986; Maletz *et al.,* 2023b), even though the precise origin and evolutionary changes involved are still uncertain since the genus *Dictyonema* HALL, 1851 with its type species *Dictyonema retiformis* (HALL, 1843) was identified as a benthic callograptid (see Maletz, 2019; Maletz *et al.,* 2023a). The origin of the Graptoloidea, however, may be traced back to a species with simple thecal style, triad budding and the presence of dissepiments to connect the stipes laterally, thus most similar in construction to the early planktic *Rhabdinopora* EICHWALD, 1855 of Erdtmann (1982a, b).

The phylogenetic relationships of the Ordovician species recognized as planktic dendroids (pendent taxa with bithecae(?) and a free nema; excluding the Anisograptidae) is unclear, as nearly all material is preserved as flattened films of organic material or even lacks the preservation of organic material and thus, details of their tubarium construction are unknown. Therefore, all these taxa are here referred to the genus *Calyxdendrum*. This genus appears to show a fairly long biostratigraphic range from the late Tremadocian (*Sagenograptus murrayi* Biozone) to the Sandbian (*Nemagraptus gracilis* Biozone), but has been described so far from few specimens and species found in widely separated biostratigraphic horizons.

Synrhabdosomes

Maletz *et al.* (2023a, p. 97) discussed the term synrhabdosome as "monospecific assemblages of radially arrayed tubaria attached by the distal extremities of their nemata", occurring in various groups of graptolites. They were in the past interpreted as reproductive adaptations, chance entanglements and as adaptations for a variety of further purposes, but a verification of any of these alternative interpretations was not possible. As synrhabdosomes are still recognized in only few species, we here use the term in a purely descriptive way as a morphological character and will not speculate on any possible biological interpretation.

Ruedemann (1895; 1904, p. 483) introduced the term synrhabdosome for a certain association of graptolite tubaria (at the time identified as rhabdosomes) of compound colonies or "colonies of colonies", suggesting that these represent living associations of tubaria. Ruedemann's (1895, 1904) reconstructions are clearly influenced by the reconstruction of *Retiograptus eucharis* by Hall (1865, pl. 14, fig. 9) as was demonstrated by Maletz (2015, fig. 7). This reconstruction based on a combination of observations from several only loosely related graptolites cannot be accepted now and new directions for the interpretation of graptolite synrhabdosomes may have to be explored.

Subsequently, only Buss and Rice (2012) and Gutiérrez-Marco and Lenz (1998) discussed the synrhabdosomes in some detail and interpreted them as biological entities. Gutiérrez-Marco and Lenz (1998, table 1) provided an almost complete list of published descriptions and illustrations of synrhabdosomes in graptolites. Thus, a discussion of these records is not necessary here. The synrhabdosomes of *Calyxdendrum amicabilis* n. sp. (Figs. 2–6) represent some of the oldest synrhabdosomes found in the fossil record and the only ones reported for a dendroid graptolite, as these normally do not show a free nema. In the type locality of the new species near Zagora, Morocco, *Calyxdendrum amicabilis* n. sp. forms a very unusual mass occurrence with millions of synrhabdosomes in a very small area crowded on a number of closely spaced shale surfaces. Older synrhabdosomes are known from a single specimen with a few juvenile tubaria of *Anisograptus monseni* BULMAN (1941, fig. 5a) and a small number of tubaria of *Rhabdinopora* spp. (listed in Gutiérrez-Marco and Lenz, 1998, table 1); both taxa included in the Anisograptidae. While specimens of the genus *Rhabdinopora* are extremely common (see below: mass occurrences), synrhabdosomes of the genus have been illustrated in a few rare cases only (*e.g.* Bulman, 1927, text-fig. 15; Erdtmann, 1982a, pl. 2, fig. 2; Hahn, 1912, fig. 2) and it is not clear whether they represent rare exceptions or general developments. It appears, however, that most *Rhabdinopora* specimens which show a tendency to radial grouping are separate conical colonies and did not form synrhabdosomes (*cf.* Cooper *et al.,* 1998, fig. 15m; Gutiérrez-Marco and Esteban, 2005, fig. 15d).

TAPHONOMIC ANALYSIS

Various studies have shown that entirely soft non-cuticularized organisms are absent from any of the intervals of exceptional preservation in the Fezouata Shale, which represents a clear pre-burial difference when compared to the Cambrian Burgess Shale and Chengjiang biotas (Saleh *et al.,* 2020a, 2021b). However, the Fezouata fossils share with these Cambrian biotas a rather similar mode of preservation as defined by carbonaceous compressions and accessory authigenic mineralization (Saleh *et al.,* 2021b).

The most common fossilization mode in the Fezouata lagerstätte is the preservation as two-dimensional iron oxide compressions within mudstone (Van Roy *et al.,* 2010; Martin *et al.,* 2016a), both of exoskeletal remains as well as lightly biomineralized or sclerotized carapaces and scleritomes and cuticularized tissues. Strata with exceptional preservation represent a specific sedimentary facies related to calm sea-bottoms, sporadically smothered by distal storm deposits (Lefebvre *et al.,* 2018; Saleh *et al.,* 2018; Vaucher *et al.,* 2016). Most organisms of the Fezouata biota that were buried in situ were already dead and decaying on the seafloor (Vaucher *et al.,* 2017; Saleh *et al.,* 2020c, 2021a, b). According to previous studies, pre-burial degradation was slowed by the deposition of a favorable clay mineralogy (Saleh *et al.,* 2020a) and the carbonaceous films resulting from compaction were replicated in rapidly forming authigenic pyrite (Saleh *et al.,* 2020c, 2021b; Vaucher *et al.,* 2016). However, the recent weathering of surface deposits yielding the Fezouata biota resulted in the leaching of organic materials from fossils originally preserved as carbonaceous compressions and the transformation of pyrite into iron oxides (Saleh *et al.,* 2020c).

Graptolites in this study derive from the lower Tremadocian interval of exceptional preservation in the general form of two-dimensional iron oxide compressions. Their uniqueness is that they appear on a mass concentration horizon, 10–20mm thick, formed almost entirely by synrhabdosomes of the new species *Calyxdendrum amicabilis* n. sp. Within this bed they occur in superposed layers (Fig. 2A; 3E), both in the form of synrhabdosomes stacked on top of each other and flattened in a single plane, or as in a single layer covered with synrhabdosomes with little lateral overlap. Also they can occur as synrhabdosomes partially preserved in relief (Fig. 4A–E), generally because its tubaria were partially infilled with the "soupy" interstitial sediment before compaction. The transverse sections through the massive graptolite bed (Fig. 4G, H), usually show two to three pulses of synrhabdosome accumulation (each with 1–3 consecutive layers) separated by one or two 5–6mm thick intervals in which rapid sediment decantation and 3D fossilization of inclined tubaria predominate.

The analysis of the orientation of the synrhabdosomes in the sediment was addressed in the counterpart slab (50x40cm) of Figure 2A, where 14 synrhabdosomes retaining some relief were recorded on different surfaces. Of these 14 specimens, 10 point with the center of the synrhabdosome downwards (ca. 71%) and 4 pointed upwards (28.5%).

In addition to synrhabdosomes, this monospecific mass occurrence of *Calyxdendrum amicabilis* n. sp. includes some juvenile to mature tubaria of all sizes except of gerontic ones, which are not seen among the synrhabdosomes. The largest gerontic specimens constitute single occurrences in the succession, or they formed other thin mass occurrences –apart from those of synrhabdosomes of the same species–, as is the case of the horizon represented by the sample FSL 712 407 (Bou Izargane) mentioned above.

The record of graptolites other than planktic dendroids is limited to a discontinuous level located just below the synrhabdosome horizon, which contains fragmentary tubaria of the multiramous horizontal genus

Paradelograptus and the two-stiped *Kiaerograptus*; both previously indicated in the *Sagenograptus murrayi* Biozone of the studied succession (Martin *et al.,* 2016a). A large trilobite pygidium (*Platypeltoides* sp.) was also recognized in the same bed.

The preservation of a vast amount of specimens of *Calyxdendrum* in the Fezouata biota provides some interesting aspects for the accumulation of this material, but is not easy to explain. While the synrhabdosomes cover large surfaces of the sediment in the field, they appear not to show any distortion that may be attributed to current transport. The synrhabdosomes are spread out more or less horizontally on the shale surfaces in their original umbrella-shape (Fig. 4), sometimes overlapping with associated synrhabdosomes and oriented with their proximal part pointing up or down. All synrhabdosomes are loosely spread out with the individual tubaria clearly separated from each other laterally. Thus, the number of tubaria in a certain synrhabdosome can easily be recognized unless a fragmentation of the slabs is seen.

The stipes usually are pointing with the thecal apertures downwards and lateral thecal outlines are only seen at the sides of the individual tubaria or in rarely twisted distal stipes. In some specimens the thecal apertures are visible on the underside of the tubarium showing the regular succession of autothecal apertures, but providing no information on a possible presence of bithecae (Fig. 4E). The lateral separation of the stipes is easily kept by the strong thecal bridges.

A case of exceptional preservation recorded in our material refers to certain structures occurring within the stipes, and originally made up of cuticularized extra-cellular material (see Maletz, 2020, fig. 2). They have been interpreted as organic stolons linked to the budding and growth of new zooids, as well as to possible diaphragms in relation with the stolonal system (see below). The occurrence of these structures inside the stipes follows the general model of preservation of the Fezouata biota, in which internal organic features are rarely preserved only in cases where resistant skeletal parts and cuticular external surfaces created isolated environments within the skeletons (here the tubaria) that maintained a chemical equilibrium conductive to the preservation of soft tissues (Saleh *et al.,* 2020a). Moreover, according to the hypothesis of Saleh et al. (2020b, 2022a), the selective replication of cuticularized extra-cellular structures in pyrite may have initialized by its content in ferritin, a globular protein that contains ferrihydrite minerals, extremely reactive under anoxic environmental conditions.

For *Calyxdendrum amicabilis* n. sp. (Figs. 2–4), the preservation on a soft-bottom, “soupy” sediment indicates that the specimens may have been transported by very gentle currents or active swimming into this region, where they were unable to get out again. They thus probably slowly settled on the ground when the current speed decreased and sank into the muddy sediment where they are preserved now.

However, the predominant downwards orientation of both the isolated tubaria and the center of synrhabdosomes that are preserved with some relief in the accumulation horizon, reveals that sinking in the water column perhaps occurred when the zooids were no longer active and could not swim to stabilize their colonies, falling passively to the bottom in the most efficient hydrodynamic position. The record of a small percentage of synrhabdosomes upwardly oriented, could be due to the interaction between adjacent structures during a massive drop of the colonies at the time of accumulation at the sea-bottom.

Altogether, there is no evidence of a current direction or moving directions for the synrhabdosomes, indicating transport through water currents. The current velocity was already quite low when the colonies settled into the sediment, thus a current orientation is not recognizable. It is impossible to estimate the distance the colonies were transported as the point of origin of the specimens in a shallow or deeper water region is unknown.

The fact that this dense mass of monospecific synrhabdosomes may occur in a presumably large area, being still difficult to locate due to its millimetric thickness, can also be related to a living planktic community affected by certain unfavorable factors. Among them we cannot exclude a death in masse, perhaps induced by rapid changes in environmental circumstances (*e.g.* seawater chemistry) or either by biological facts, such as the (local) appearance of toxins in the micro- or picoplankton that served as food for the graptolites. In this sense, it should be noted that some Tremadocian taxa with conical planktic tubaria (*Rhabdinopora*, *Sagenograptus*) are among the graptolites more commonly recorded in mass accumulation horizons, perhaps indicating a greater sensibility than other coeval graptolites to these presumed subtle changes during the first stages of the so-called “Ordovician Planktic Revolution” (Servais *et al.,* 2016).

METHODOLOGICAL SUMMARY

To cause minimal impact on natural outcrops of the Fezouata Formation, the excavation of the thin synrhabdosome bed was reduced to the small extension shown in Figure 2D. This also included the central area already affected by the professional Moroccan diggers, who extracted from there the slab illustrated in Figure 2A. In addition to the main excavation, a second small pit

(60x60cm) was opened about 12m west-southwest of the first, in order to check the continuity of the fossiliferous layer, with a positive result.

A selection of the specimens derived from the excavation were cleaned and partially consolidated at the Laboratory of restauration of the Museo Geominero, Madrid. The non-exposed parts of some tubaria were mechanically prepared with a Micro-Jack 6 compressed-air vibration tool equipped with a fine MJ 6 stylus.

Photographs were taken with a digital camera Canon EOS 5D with a Canon Compact-Macro 100mm EF. All specimens were photographed either with circular or low-angle NW lighting, both dry and immersed in water or alcohol, in order to increase contrast between rock and specimen. The images were subsequently processed and assembled in figures using Adobe Photoshop CS6 Extended, to enrich focus, brightness, contrast, shadows, highlights and saturation. All illustrated specimens are housed in the paleontological collection of the Museo Geominero (prefix MGM) of the Spanish Geological Survey (IGME-CSIC, Madrid). Other unpublished material belonging to French (FSL) and Moroccan (AA) collections, as well of the originals from Martin *et al.* (2016a) were accessioned in the University of Lyon 1 (LyonTech-la Doua, Villeurbanne, France).

The systematics and taxonomy used for the Graptolithina herein follows the latest version of the "Graptolite Treatise" (Maletz *et al.*, 2023a).

SYSTEMATIC PALEONTOLOGY

Class: Pterobranchia LANKESTER, 1877
Subclass: Graptolithina BRONN, 1849
Order: Dendroidea NICHOLSON, 1872
Family: Dendrograptidae ROEMER in FRECH, 1897

GENUS *Calyxdendrum* KOZŁOWSKI, 1960

Type species: *Calyxdendrum graptoloides* KOZŁOWSKI, 1960, from Sandbian (Upper Ordovician, *Nemagraptus gracilis* Biozone) glacial erratic boulders of Poland.

Diagnosis. (Maletz *et al.*, 2023a, p. 239). Possibly biradiate, multiramous dendrograptid with thick free nema; autothecae conical, bithecae opening into autothecal cavities.

Included species. *Calyxdendrum graptoloides* KOZŁOWSKI, 1960; *Dictyonema rokycanense* KRAFT, 1972; *Reticulograptus? inusitatus* KRAFT, 1973; *Dendrograptus titanus* KRAFT, 1990; *Dictyonema ghodsiae* RICKARDS, HAMEDI AND WRIGHT, 1994; *Calyxdendrum amicabilis* n. sp.

Remarks. We include here provisionally all 'planktic dendroids', even though for most taxa the detailed tubarium construction is unknown. The proximal development and thecal style has been described only for *Calyxdendrum graptoloides* KOZŁOWSKI, 1960 from the Sandbian of Poland, based on chemically isolated fragments preserved in full relief.

Calyxdendrum amicabilis n. sp.
(Figs. 2–9)

v2016a *Koremagraptus* sp. – Martin *et al.*, figs. 4 and 5C (not described).
v2023 rooted dendroid *Didymograptus* (sic) – Nanglu *et al.*, pp. 1 and 8 (three citations in text).

Type material. Individual tubarium MGM-7808X (Fig. 7E) is here selected as holotype of the species, belonging to the paleontological collection of the Museo Geominero, Madrid. Among the abundant material from the type locality, 52 paratypes were selected and figured, both considering

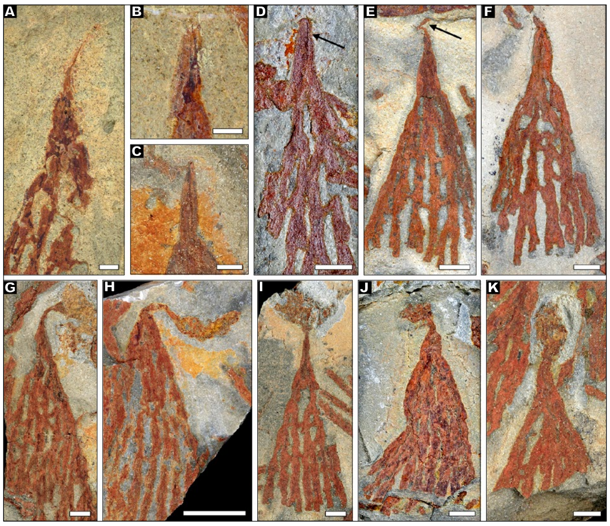

FIGURE 7. Proximal ends and variable development of nematularia in *Calyxdendrum amicabilis* n. sp. A) specimen with relatively long nema, MGM-7805X-1. B–D) specimens with traces of nema (arrowed in D) and possibly showing first theca, MGM-7805X-2, MGM-7806X, and MGM-7807X, respectively. E) Holotype, MGM-7808X, with thickened nema (arrow). F) MGM-7809X, with strong cortical overgrowth around sicula and first thecae (like in specimens B and D). G–K) proximal ends showing the proximal membrane or floating device at the tip of the nema: G) MGM-7810X-1; H) MGM-7810X-2; I) MGM-7811X; J) MGM-7812X; K) MGM-7813X. Scale bars, A-C: 1mm, D-G, I-K: 2mm, H: 5mm.

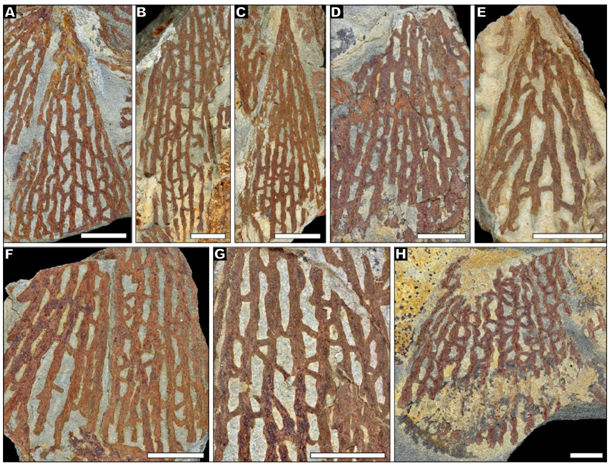

FIGURE 8. Details of mesh on individual tubaria of *Calyxdendrum amicabilis* n. sp. A) MGM-7776X-2; B) MGM-7814X; C) MGM-7815X, a narrow tubarium; D) MGM-7816X; E) MGM-7817X, proximal region; F) MGM-7818X, with some incomplete thecal bridges; G) MGM-7787X-2; H) MGM-7819X, oblique flattened tubarium with deformed stipes and thecal bridges. Scale bars: 5mm.

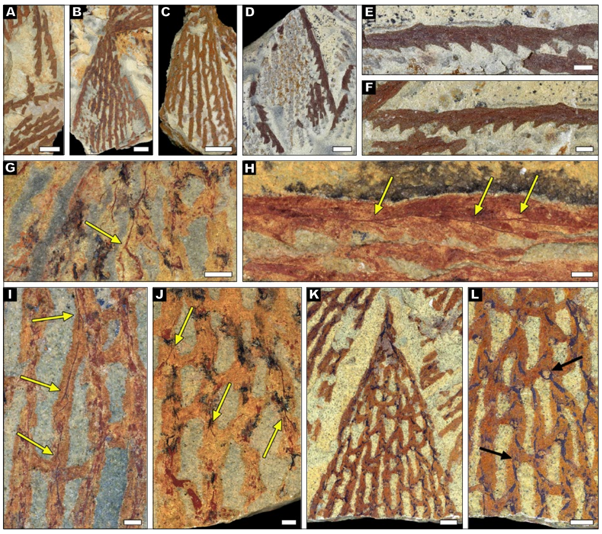

FIGURE 9. *Calyxdendrum amicabilis* n. sp. A to F, Details of autothecal morphology in lateral view: A) MGM-7820X; B) MGM-7821X; C) MGM-7822X; D–E) MGM-7776X-3, inner view of a conical tubarium and detail of the right lateral stipe, respectively; F) MGM-7823X.G to J and L, details of structures preserved internally to stipes. Yellow arrows in G to J indicate some points of bifurcation of the exceptionally fossilized organic stolon; black arrows in L point some of the annular structures possibly representing a diaphragm complex (?) which was described in some benthic dendroids as related to the stolon system. G) MGM-7824X; H) MGM-7825X; I) MGM-7826X; J) MGM-7827X; K–L) MGM-7805X-3, general view of the tubarium and detail of the stipes on its lower right part. Scale bars, A-D: 3mm, E-L: 1mm.

synrhabdosomes and individual tubaria: MGM-7775X to MGM-7807X and MGM-7809X to MGM-7775X (Figs. 2–9). Additional paratypes are MGM-7776X-1 and MGM-7776X-2 (not figured), corresponding to the largest tubaria recorded for the species, coming from a slab from slightly lower bed in the type area, as well as MGM-7777X, a synrhabdosome (not figured) derived from an unknown horizon in the Jbel Tizagzaouine section. The study is complemented with the review of other material corresponding to the paper of Martin *et al.* (2016a), coming from the localities Z-F4, Z-F2, Z-F7 and Z-F30 (see Fig. 1B and stratigraphic distribution below), which is deposited in the collections of the University of Lyon, and include a single figured tubarium (Martin *et al.*, 2016a, fig. 5C).

Type locality and horizon. Small fossil pit in the southeastern slope of the Bou Izargane hill, ca. 19.5km north of the city of Zagora. Geographic coordinates N 30°29'57.8", W 5°50'52.6". Thin (10–20mm) graptolite horizon occurring in shales ca. 270m above the base of the Fezouata Formation. Upper Tremadocian, *Sagenograptus murrayi* graptolite Biozone.

Derivation of name. From lat. *amicabilis*, friendly (adjective), because of the tendency of the colonies to join others of the same species to form synrhabdosomes.

Diagnosis. Narrow cone with pointed proximal end and a relatively long sicula; stipes connected by often obliquely oriented thecal bridges; thecal apertures of simple "dichograptid" type; thecae widening aperturally and with a short ventral rutellum; tubaria show the tendency to form synrhabdosomes.

Description. Numerous tubaria and synrhabdosomes are available for this species, showing a slender, conical tubarium often connected to others by the proximal end with a short nema and forming a membrane (Fig. 3; 5; 6). The individual tubaria in the synrhabdosomes are up to 50mm long and reach a width of ca. 40mm, but often less. Individual tubaria from the "radiodont bed" (3.4m below the synrhabdosome bed) reach the maximum dimensions known for the species: 70mm in length and 38mm in distal width. The values may be modified considerably through preservational artefacts of the flattening in the sediment layer (Figs. 2–5). Individual tubaria show a distinctly pointed proximal end with a very narrow cone showing the long sicula in the center. Often a short nema can be recognized on the tip of the sicula, or a possible membrane of unclear shape and development.

There are 3–6 tubaria connected at the nemata to form a synrhabdosome (Figs. 3; 5–6). These invariably form a circular synrhabdosome of tubaria of generally the same size. Indications are that the tubaria in a synrhabdosome are not arranged in a horizontal plane, but point with their proximal ends upwards at a low angle. This can be seen most clearly in some specimens in which most parts of the synrhabdosome are covered in the sediment and the visible parts are represented by cross sections through the distal parts of the colonies (Fig. 4) showing that the mature tubaria appear to possess a diameter of ca. 30mm.

The individual tubaria of a synrhabdosome are connected at the proximal end, probably through the modified nema that is sometimes recognizable (Figs. 3B; 6A). In most synrhabdosomes, however, the attachment site is covered by additional, secondary cortical(?) material forming a wide, irregularly developed feature, a disc or float of unknown development (Figs. 5; 6). The details of this development as a two- or three-dimensional feature are not available, as all specimens are completely flattened.

The interpretation of the proximal end is based on flattened specimens and some details have to be estimated only. The proximal end is narrow and pointed (Fig. 7) and the tubarium widens slowly towards the distal end. There appears to be a relatively long sicula, that might be more than 2.5mm long, before the first branching can be seen, but its aperture is usually not visible as it is covered by the initial stipes. The origin of the first theca and the possible presence of bithecae cannot be verified in the flattened material. A short and wide nema may be recognized at the tip of the sicula (Fig. 7A, E). More common, however, is a distinct irregular feature that may be identified as a floating device or membrane (Fig. 7G–K). It is impossible to state whether this is a three-dimensional construction or a planar membrane. None of the specimens show the number of first order stipes, but after a growth of about 5mm, usually four stipes can be recognized. The initial branchings, thus appear to be quite close to each other. There are about 5–6 stipes per 5mm in well-preserved specimens. The dorso-ventral width of the stipes is about 0.8–1.0mm, while the lateral width, in which the thecal apertures are visible, is 1.5–1.8mm.

The stipes form a meshwork through a lateral connection of the stipes through thecal bridges (*cf.* Maletz, 2019). All lateral connections have the same width of ca. 0.8–1.0mm and are parallel-sided (Fig. 8). The interpretation of the lateral connections of the stipes as bridges can be supported by their constant width, also seen in the most distal parts of the colonies, where dissepiments would have been quite slender with a considerable widening as they approach the side of the stipes (*cf.* Urbanek and Mierzejewski, 2009). Therefore, it is unlikely that they represent dissepiments. The bridges may be perpendicular to the stipes, but are commonly also oblique (Figs. 2C; 8G) and a number of specimens show incomplete development in which they do not reach the neighboring stipe (Figs. 2C; 8F). Due to the compaction of the sediment and the flattening of the fossil specimens, it may be possible that these “unconnected” bridges represent places where the bridges are broken though the flattening process, instead. It is unclear whether the bridges are formed by autothecae or bithecae.

Irregular development and wavy development can be seen in some stipes, indicating the compaction of the material in the fine-grained soft sediment, when the stipes were embedded in the sediment at high angles (Fig. 8H). In these cases, the bridges are more closely spaced than in undeformed specimens.

The thecal bridges are distributed very irregularly in the tubaria (Figs. 2C; 3; 8) and distances between 1 and 8mm have been measured, but more commonly the distances are 2–4mm. There are no differences between the proximal and distal parts of the colonies.

There are 6–7 thecae in 5mm on the stipes. The thecae are simple, slowly widening tubes with a short rutellum (Fig. 9E, F). There is no evidence of the presence of bithecae in the material, but all specimens are flattened. Low relief specimens in ventral view show the parallel orientation of the autothecal apertures (Fig. 4E), but again no evidence of bithecal development. A number of specimens show slender dark lines inside the tubarium that are here interpreted as the remains of the stolon system (Fig. 9G–J). Dichotomous branchings can be recognized, but no indication of triad budding –the usual development in dendroid graptolites– has been found. The development of wider tube-like features in a single specimen may indicate the presence of a diaphragm complex in *Calyxdendrum amicabilis* n. sp. (Fig. 9K, L), similar to that in extant *Rhabdopleura* (*cf.* Urbanek and Dilly, 2000). Saunders *et al.* (2009) described the stolon system of the benthic graptolite *Desmograptus* based on relief material, in which also a complex initial stolon system is shown that may include a diaphragm complex. The presence of a diaphragm complex would add important new information on the construction and interconnection of the graptolite tubarium and its zooids. A more detailed investigation would be needed to demonstrate the presence of a diaphragm complex in this species.

Remarks. Numerous specimens are available, often found in complexly organized synrhabdosomes, but also separate individual, conical tubaria occur. While the tubaria may still show some relief (*cf.* Fig. 4G, H), as seen in sections, the stipes of the colonies are completely flattened. The original organic material appears to be lost and the outlines are shown by mineral staining, probably at least in part through weathering. Due to the preservation, details of the tubarium construction (*e.g.* prosicula, metasicula, thecae, bithecae, thecal bridges, etc.) are not available and, thus, limit the interpretation.

Geographic and stratigraphic distribution. *Calyxdendrum amicabilis* n. sp. is known from four different sections in the Zagora area (Fig. 1B), all of them within the *Sagenograptus murrayi* graptolite Biozone (late Tremadocian) and stratigraphically between 258 and 325m above the base of the Fezouata Formation. Martin *et al.* (2016a, fig. 4) noted the presence of "*Koremagraptus* sp." (= *C. amicabilis* n. sp.) in five horizons of these sections, based on isolated, often fragmentary tubaria. From stratigraphically older to younger, these horizons correspond to the localities Z-F7, Z-F4/10, Z-F2(3)10, Z-F2(3)5 y Z-F2(3)8, respectively. The last three cover a stratigraphic interval of 55m for the species in the Jbel Tizgzaouine section. The locality Z-F30(D) in the Jbel Zagora was not represented in this column but is situated in an imprecise range equivalent to the localities Z-F7 and Z-F2(3)10. To date, *C. amicabilis* n. sp. always occurs above the mass accumulation horizons of *Sagenograptus murrayi*, as seen in the Jbel Tizgzaouine and Bou Izargane sections in the interval between 235–250m above the base of the Fezouata Formation (Fig. 1C). Nanglu *et al.* (2023) cited *Didymograptus* as a rooted dendroid in the Fezouata biota, most probably meaning the specimens identified as *Koremagraptus* sp. in Martin *et al.* (2016a). The genus name *Didymograptus* is reserved for pendent, two-stiped dichograptids of Darriwilian age, not closely related to the dendroids (Maletz *et al.*, 2023a) and not even comparable in their tubarium shape to the multiramous, bushy dendroids.

Life style. It is highly likely that *Calyxdendrum amicabilis* n. sp. is a planktic graptolite, not just because of the presence of a short nema in many specimens, but also due to the presence of numerous synrhabdosomes, attached to each other by their nemata. A benthic lifestyle makes no sense for this synrhabdosome development, even though the reason for the creation of synrhabdosomes is uncertain and speculative. All benthic graptolites are attached to the ground, may it be a hardground, a rock fragment or a fossil shell with their sicula. Only planktic graptolites have definitively developed a nematophorous sicula, even though early planktic *Rhabdinopora proparabola* does not possess a nema, but bears three proximal lobes at the tip of the prosicula (Maletz *et al.*, 2023b). This development reminds that of the membranes found in the center of some synrhabdosomes of *Calyxdendrum amicabilis* n. sp., but may not be strictly homologous. It is interesting to note that the invariably slender conical development of the individual tubaria of *Calyxdendrum amicabilis* n. sp. may indicate a dendroid benthic development. However, the invariable presence of a short nema could negate the interpretation. The irregular development of a float or membrane in the species also could theoretically indicate an attachment of the colonies to the floor, but here also the attachment to another colony to form a synrhabdosome has to be considered. Thus, the mode of attachment of benthic graptolite colonies may be the key to the interpretation of synrhabdosomes and the construction of "attachment discs" in these needs to be investigated in detail to verify its use.

Calyxdendrum graptoloides KOZŁOWSKI, 1960 from the Sandbian of Poland is the only representative of the genus for which chemically isolated material has been described. The species is known from a few small specimens, most likely representing juveniles of a taxon with much larger colonies. The species shows triad budding with distinct bithecae that open into the autothecal tubes, thus are difficult to see without the investigation of three-dimensionally preserved material. It bears a robust, but short nema indicating a planktic life style as suggested already by Kozłowski (1960). All specimens are broken and show only a very short part of the nema, thus could potentially have had a larger attachment disc at the tip of the nema. A true planktic life style may not be verified for the taxon. In this aspect, *C. amicabilis* n. sp. differs from *C. graptoloides*, as a planktic life style can be verified from the tubarium or synrhabdosome development and the preservational aspects known from numerous specimens. *Calyxdendrum graptoloides* bears bithecae that open inside the autothecal apertures, thus are not visible from the outside. If *Calyxdendrum amicabilis* n. sp. shows the same development, the bithecae will not be recognizable in the usual flattened preservation of the material.

Kraft and Kraft (2006) discussed the Bohemian planktic dendroids as occurring in the Floian to late Dapingian time interval (*Corymbograptus v-similis* to *Azygograptus ellesi-Tetragraptus reclinatus abbreviatus* biozones: Kraft *et al.*, 2023, fig. 4). The material, is thus much younger than the specimens from the Fezouata biota. The type material of *Calyxdendrum rokycanense* (KRAFT, 1972) includes a few fragmentary specimens (Kraft, 1972, 1975) and only later a single specimen with a complete proximal end was illustrated as a planktic dendroid (Kraft and Kraft, 2006, fig. 3). The specimen does not a show a nema. Its robust meshwork shows irregularly placed dissepiments of a variable width and wide bases, forming round holes, but further thecal details are not available. The complete specimen shows a slender cone with a prominent sicula. The robustness of the tubarium is comparable to specimens of *C. amicabilis* n. sp., but the dissepiments show clear differences.

Calyxdendrum titanus (KRAFT, 1990) is based on one small specimen and a few fragments (Kraft, 1990). Kraft and Kraft (2007, fig. 1) illustrated the only known specimen to show a distinct nema, a small tubarium with a narrow cone and probably six stipes, about 12mm long. Thecal details are not available and dissepiments or thecal bridges are not present in the specimen. The species *Calyxdendrum inusitatus*, originally identified as *Reticulograptus? inusitatus* KRAFT, 1973 and later related with *Pseudoreticulograptus*, shows a much wider cone of the tubarium with slender stipes, apparently connected through dissepiments and anastomosis and low inclined thecae (Kraft and Kraft, 1990). The species differs considerably from all other members of the genus *Calyxdendrum* from the Czech Republic through the delicate tubarium and may not be closely related.

Calyxdendrum ghodsiae (RICKARDS, HAMEDI AND WRIGHT, 1994) was found in a single complete specimen of possible late Arenig age in the Kerman District of Iran. The species was described as a planktic dendroid due to the presence of a possible nema and the attached vesicles. The tubarium has a pointed proximal end with a slender cone, distinctly widening after a few mm forming a wide umbrella type shape. The number of thecae was estimated at 24–26 in 10mm. Thus, an unusually dense thecal spacing can be recognized. The species was described to bear "rather sparsely distributed" dissepiments, but these are not indicated in the reconstruction (Rickards *et al.*, 1994, fig. 5) at all. The tubarium with its distally widening umbrella-shape is very distinctive and differs from all other species of the genus *Calyxdendrum*.

CONCLUSIONS

Planktic dendroids are known from the late Tremadocian to the Sandbian of the Peri-Gondwanan regions, but have rarely been recognized as such. They are here preliminarily referred to the not necessarily monophyletic genus *Calyxdendrum*.

Calyxdendrum amicabilis n. sp. from the Fezouata biota represents the oldest known planktic dendroid. It can, but not necessarily does produce synrhabdosomes and may be extremely common at certain levels in the *Sagenograptus murrayi* Biozone of Morocco.

The *Calyxdendrum* specimens from the Fezouata biota may have been transported by gentle currents or active swimming from their living environment on the Tremadocian shelf into the environments where they are fossilized and preserved.

The genus *Calyxdendrum* may be widely distributed at least in the Gondwana region, but is difficult to separate from other dendroids when proximal ends are not available. A wider (world-wide?) biogeographical distribution may have to be expected due to the planktic life style of the species of this genus.

ACKNOWLEDGMENTS

We are grateful for careful reviews and constructive comments by Nexxys C. Herrera-Sánchez (Córdoba, Argentina) and Petr Štorch (Prague, Czech Republic). Carlos Alonso (Madrid) took the photographs and composed the Figures 2–9. Gema García Martín (Universidad Complutense de Madrid, Spain) also contributed detailed photographs to Figure 8. Sara Romero (Universidad Complutense de Madrid, Spain) make the Figure 1. Eleuterio Baeza and Silvia Menéndez (Museo Geominero, Madrid) are thanked by the consolidation of specimens and curation in the collection, respectively. Julio Cabo (Navas de Estena, Ciudad Real) and Julio Martín (Mataelpino, Madrid) are grateful from the help provided in the field research and excavations along the years. Emmanuel Martin and Bertrand Lefebvre (Lyon) allowed us to consult the collections of the Moroccan material deposited in France. This research is a contribution to projects PDI2021-125585NB-I00 of the Spanish Ministry of Science, Innovation and Universities (funding to JCG-M) and IGCP 735 (Rocks 'n' ROL) of the IUGS-UNESCO.

REFERENCES

Aceñolaza, F.G., Aceñolaza, G.F., Esteban, S.B., Gutiérrez-Marco, J.C., 1996. Estructuras nemales de *Araneograptus murrayi* (J. Hall) (graptolito del Ordovícico Inferior) y actualización del registro perigondwánico de la especie. Tarija, Memorias del XII Congreso Geológico de Bolivia, 2, 681-689.

Akodad, M., El Hariri, K., Gutiérrez-Marco, J.C., Lefebvre, B., Lehnert, O., Martin, E.L.O., Nowak, H., Servais, T., 2018. The precise age of the Fezouata Lagerstätte, Lower Ordovician, Morocco. In: Zhang, Y., Zhan, R., Fan, J., Muir, L. (eds.). Filling the gap between Cambrian Explosion and the GOBE. Zhejiang, Zhejiang University Press, 3-7.

Botting, J.P., 2007. "Cambrian" demosponges in the Ordovician of Morocco: insights into the early evolution of sponges. Geobios, 40, 737-748.

Bronn, H.G., 1849. Handbuch der Geschichte der Natur. Dritter Band, Zweite Abtheilung. II. Theil: Organisches Leben (Schluβ). Index Palaeontologicus oder Ueberblick der bis jetzt bekannten fossilen Organismen. Stuttgart, Schweizerbart, 1106pp.

Bulman, O.M.B., 1927. A monograph of British dendroid graptolites. Part 1. Palaeontographical Society Monograph, 79(367), 1-28.

Bulman, O.M.B., 1941. Some dichograptids of the Tremadocian and Lower Ordovician. Annals and Magazine of Natural History, series 2(7), 100-121. DOI: 10.1080/03745481.1941.9727905

Bulman, O.M.B., 1970. Graptolithina with sections on Enteropneusta and Pterobranchia. In: Teichert, C. (ed.). Treatise on Invertebrate Paleontology. Part V, second edition (revised and enlarged). Boulder & Lawrence, Geological Society of America & University of Kansas Press, 163pp.

Buss, L.W., Rice, M.G., 2012. Synrhabdosome life cycles. Evolutionary Ecology, 26, 259-263. DOI: 10.1007/s10682-011-9535-1

Cooper, R.A., Maletz, J., Wang, H.F., Erdtmann, B.-D., 1998. Taxonomy and evolution of earliest Ordovician graptoloids. Norsk Geologisk Tidsskrift, 78(1), 3-32.

Cooper, R.A., Rigby, S., Loydell, D.K., Bates, D.E.B., 2012. Palaeoecology of the Graptoloidea. Earth Science Reviews, 112, 23-41. DOI: 10.1016/j.earscirev.202.01.001

Cooper, R.A., Rigby, S., Bates, D.E.B., Maletz, J., 2017. Part V, Second Revision, Chapter 6: Paleoecology of the Pterobranchia (Cephalodiscida and Graptolithina). Treatise Online, 86, 1–16.

Cooper, R.A., Rigby, S., Bates, D.E.B., Maletz, J., 2023. Paleoecology of the Pterobranchia (Cephalodiscida and Graptolithina). In: Maletz, J. (coord.). Treatise on Invertebrate Paleontology, Part V, Hemichordata, Second Revision, including Enteropneusta, Pterobranchia (Graptolithina). Lawrence (Kansas, USA), The University of Kansas, Paleontological Institute, 91-126.

Drage, H.B., Legg, D.A., Daley, A.C., 2024. Novel marrellomorph moulting behaviour preserved in the Lower Ordovician Fezouata Shale, Morocco. Frontiers in Ecology and Evolution, 11, 1226924, 10pp. DOI: 10.3389/fevo.2023.1226924

Eichwald, E.J., 1855. Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. Alte Periode. Bulletin de la Société des Naturalistes de Moscou, 28(4), 433-466.

El Hariri, K., Lefebvre, B., Van Roy, P., Soulaimani, A., Hafid, A., Bachnou, A., Botting, J.P., Daley, A., Gutiérrez-Marco, J.C., Saleh, F., 2022. Ordovician Fezouata Shale fossil site at Jbel Tizagzaouine, Morocco. The First 100 IUGS Geological Heritage Sites. Zumaia (Spain), International Union of Geological Sciences, 88-89, 275 .

Erdtmann, B.-D., 1982a. A reorganization and proposed phylogenetic classification of planktic Tremadoc (early Ordovician) dendroid graptolites. Norsk Geologisk Tidsskrift, 62(2), 121-145.

Erdtmann, B.-D., 1982b. Palaeobiogeography and environments of planktic dictyonemid graptolites during the earliest Ordovician. In: Bassett, M.G., Dean, W.T. (eds.). The Cambrian–Ordovician Boundary: Sections, Fossil Distributions, and Correlations. Cardiff, National Museum of Wales, Geological Series 3, 9-27.

Fortey, R.A., Cooper, R.A., 1986. A phylogenetic classification of the graptoloids. Palaeontology, 29(4), 631-654.

Frech, F., 1897. Lethaea geognostica oder Beschreibung und Abbildung für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Stuttgart, Herausgegeben von einer Vereinigung von Palaeontologen, 1. Teil – Lethaea Palaeozoica. E. Schweizerbart'sche Verlagshandlung, 544-684.

Gaines, R.R., Briggs, D.E.G., Orr, P.J., Van Roy, P., 2012. Preservation of giant anomalocaridids in silica-chlorite concretions from the Early Ordovician of Morocco. Palaios, 27(5), 317-325. DOI: 10.2110/palo.2011.p11-093r

Gutiérrez-Marco, J.C., Aceñolaza, F.G., 1987. *Araneograptus murrayi* (Hall) (Graptoloidea, Anisograptidae): su identidad con *D. yaconense* Turner y distribución en España y Sudamérica. Tucumán, Actas X Congreso Geológico Argentino, 1, 321-334.

Gutiérrez-Marco, J.C., Lenz, A.C., 1998. Graptolite synrhabdosomes: biological or taphonomic entities? Paleobiology, 24(1), 37-48.

Gutiérrez-Marco, J.C., Esteban, S.B., 2005. Graptolitos del Tremadociense (Ordovícico Inferior) de la Formación Volcancito, Sistema de Famatina (La Rioja, Argentina). Revista Española de Paleontología, 20(1), 65-118.

Gutiérrez-Marco, J.C., Martin, E.L.O., 2016. Biostratigraphy and palaeoecology of Lower Ordovician graptolites from the Fezouata Shale (Moroccan Anti-Atlas). Palaeogeography, Palaeoclimatology, Palaeoecology, 460, 35-49. DOI: 10.1016/j.palaeo.2016.07.026

Hahn, F.F., 1912. On the *Dictyonema*-Fauna of Navy Island, New Brunswick. Annals of the New York Academy of Science, 22, 135-160, pls. 20-22.

Hall, J., 1843. Geology of New York. Part IV. Comprising the survey of the Fourth Geological District. Albany, Carroll & Cook, 683pp., 19pls.

Hall, J., 1851. New genera of fossil corals from the report by James Hall, on the palaeontology of New York. The American Journal of Science and Arts (series 2), 11, 398-401.

Hall, J., 1865. Figures and descriptions of Canadian organic remains. Decade 2, Graptolites of the Quebec Group. Montreal, Geological Survey of Canada, Dawson Brothers, 154pp.

Hallegraeff, G.M., Anderson, D.M., Cembella, A.D., Enevoldsen, H.O. (eds.), 2004. Manual on Harmful Marine Microalgae. 2nd revised edition. UNESCO, Paris. Monographs on Oceanographic Methodology, 11, 793pp. DOI: 10.25607/OBP-1370

Hamner, W.M., Dawson, M.N., 2009. A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. Hydrobiologia, 616(1), 161-191. DOI: 10.1007/978-1-4020-9749-2_12

Kozłowski, R., 1960. *Calyxdendrum graptoloides* n. gen. n. sp. – a graptolite intermediate between the Dendroidea and the Graptoloidea. Acta Palaeontologica Polonica, 5(2), 107-125.

Kraft, J., 1972. *Dictyonema rokycanense* sp. n. from the Klabava Formation (Arenig) of the Ordovician of the Barrandian. Věstník Ústředního ústavu geologického, 47, 39-40, 2pls.

Kraft, J., 1973. New graptolites from the Klabava Formation (Arenig) of the Barrandian Ordovician. Časopis pro mineralogii a geologii, 18(1), 25-30, 2pls.

Kraft, J., 1975. Dendroid graptolites of the Ordovician of Bohemia. Sborník Národního Muzea v Praze, 31B(3-5), 211-238, 14pls.

Kraft, P., 1990. Dendroid graptolites of the *Tetragraptus abbreviatus* Biozone (Klabava Formation, Barrandian Ordovician). Věstník Ústředního ústavu geologického, 65(4), 249-253, 2pls.

Kraft, J., Kraft, P., 1990. Some new and lesser-known Ordovician localities in the western part of the Prague Basin. Folia Musei Rerum naturalium Bohemia occidentalis, Geologica, 31, 1-24.

Kraft, P., Kraft, J., 2006. Planktoničtí dendroidi – podvratné živly graptolitové taxonomie. Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology, 33/34, 48-50.

Kraft, P., Kraft, J., 2007. Planktic dendroids – subversives of graptolite taxonomy. Wissenschaftliche Mitteilungen des Institutes für Geologie der TU Bergakademie Freiberg, 36, 72-73.

Kraft, P., Kraft, J., 2008. Planktic dendroids – fiction or reality? In: Štorch, P., Kraft, P. (eds.). Workshop on Graptolite volume of Treatise on Invertebrate Paleontology and IPA Graptolite working group meeting. Abstract book and Excursion guide. Prague, Geologický ústav AV ČR, 10.

Kraft, P., Linnemann, U., Mergl, M., Bruthansová, J., Laibl, L., Geyer, G., 2023. Ordovician of the Bohemian Massif. In: Harper, D.A.T., Lefebvre, B., Percival, I.G., Servais, T. (eds.). A Global Synthesis of the Ordovician System: Part 1. London, The Geological Society, 532 (Special Publications), 433-464. DOI: 10.1144/SP532-2022-191

Laibl, L., Gueriau, P., Saleh, F., Pérez-Peris, F., Lustri, L., Drage, H.B., Bath Enright, O.G., Potin, G.J.-M., Daley, A.C., 2023. Early developmental stages of a Lower Ordovician marrellid from Morocco suggest simple ontogenetic niche differentiation in early euarthropods. Frontiers in Ecology and Evolution, 11, 1232612, 16pp. DOI: 10.3389/fevo.2023.1232612

Lankester, E.R., 1877. Notes on the embryology and classification of the animal kingdom: Comprising a revision of speculations relative to the origin and significance of the germ-layers. Quarterly Journal of Microscopical Science, 17, 399-454.

Lebrun, P., 2017. Le biotope des Fezouata: un gisement fossilifère d’exception de l’Ordovicien Inférieur au Maroc. Fossiles, 31, 5–30.

Lefebvre, B., Lerosey-Aubril, R., Servais, T., Van Roy, P. (eds.), 2016. The Fezouata Biota: an exceptional window on the Cambro–Ordovician faunal transition. Palaeogeography, Palaeoclimatology, Palaeoecology, 460, 1-178. DOI: 10.1016/j.palaeo.2016.06.041

Lefebvre, B., Gutiérrez-Marco, J.C., Lehnert, O., Martin, E.L.O., Nowak, H., Akodad, M., El Hariri, K., Servais, T., 2018. Age calibration of the Lower Ordovician Fezouata Lagerstätte, Morocco. Lethaia, 51(2), 296-311. DOI: 10.1111/let.12240

Lefebvre, B., Akodad, M., El Hariri, K., Gutiérrez-Marco, J.C., Kouraïss, K., Pittet, B., Saleh, F., Servais, T., Vidal, M., 2020. Les Fezouata: le *Burgess Shale* ordovicien du Maroc. Géochronique, 153, 37-44.

Legg, D.A., 2016. An acercostracan marrellomorph (Euarthropoda) from the Lower Ordovician of Morocco. The Science of Nature, 103(3-4), 1-7. DOI: 10.1007/s00114-016-1352-5

Lilley, M.K.S., Beggs, S.E., Doyle, T.K., Hobson, V.J., Stromberg, K.H.P., Hays, G.C., 2011. Global patterns of epipelagic gelatinous zooplankton biomass. Marine Biology, 158(11), 2429-2436. DOI: 10.1007/s00227-011-1744-1

Lin, Y.K., 1986. A new planktonic graptolite fauna. In: Chen, J.Y. (ed.). Aspects of Cambrian–Ordovician Boundary in Dayangcha, China. Beijing, Prospect Publishing House, 224-254.

Lindholm, K., 1991. Ordovician graptolites from the early Hunneberg of southern Scandinavia. Palaeontology, 34(2), 283-327.

Lustri, L., Gueriau, P., Daley, A.C., 2024. Lower Ordovician synziphosurine reveals early euchelicerate diversity and evolution. Nature Communications, (2024)15, 3808, 12pp. DOI: 10.1038/s41467-024-48013-w

Maletz, J., 2015. Graptolite reconstructions and interpretations. Paläontologische Zeitschrift, 89, 271-286. DOI: 10.1007/s12542-014-0234-4

Maletz, J., 2019. *Dictyonema* Hall and its importance for the evolutionary history of the Graptoloidea. Palaeontology, 62(1), 151-161. DOI: 10.1111/papa.12394

Maletz, J., 2020. Hemichordata (Enteropneusta & Pterobranchia, incl. Graptolithina): A review of their fossil preservation as organic material. Bulletin of Geosciences, 95(1), 41-80. DOI: 10.3140/bull.geosci.1776

Maletz, J., VandenBerg, A.H.M., 2021. Part V, Second revision, Chapter 9: Geological applications. Treatise Online, 155, 1-12.

Maletz, J., Gutiérrez-Marco, J.C., inpress. The purported record of an epibiontic(?) rhabdopleurid in the Early Ordovician Fezouata biota of Morocco, with a discussion about benthic pterobranchs (Hemichordata) in the Lagerstätte. Geobios.

Maletz, J. (coord.), Bates, D.E.B., Beli, E., Brussa, D.E., Cameron, C.B., Cooper, R.A., Gonzalez, P., Kozłowska, A., Lenz, A.C., Loydell, D.K., Maletz, J., Rigby, S., Riva, J.F., Steiner, M., Toro, B.A., VandenBerg, A.H.M., Zalasiewicz, J.A., Zhang Y.D., 2023a. Treatise on invertebrate paleontology, Part V, Hemichordata, Second Revision, including Enteropneusta, Pterobranchia (Graptolithina). Lawrence (Kansas), The University of Kansas, Paleontological Institute, 548pp.

Maletz, J., Wang, X.-F., Wang, C.-S., 2023b. Early Tremadocian (Ordovician) graptolite biostratigraphy and correlation. Palaeoworld, 32, 44-62. DOI: 10.1016/j.palwor.2022.03.010

Martin, E.L.O., Pittet, B., Gutiérrez‐Marco, J.C., Vannier, J., El Hariri, K., Lerosey-Aubril, R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R.A., Van Roy, P., Vaucher, R., Lefebvre, B., 2016a. The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: Age, environment and evolutionary perspective. Gondwana Research, 34, 274-283. DOI: 10.1016/j.gr.2015.03.009

Martin, E.L.O., Vidal, M., Vizcaïno, D., Vaucher, R., Sansjofre, P., Lefebvre, B., Destombes, J., 2016b. Biostratigraphic and palaeoenvironmental controls of the trilobite associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology, 460, 142-154. DOI: 10.1016/j.palaeo.2016.06.003

Muir, L.A., Gutiérrez-Marco, J.C., 2023. A new species of the problematic organism *Webbyites* from the early Ordovician Fezouata biota of Morocco. Estonian Journal of Earth Sciences, 72(1), 74-77. DOI: 10.3176/earth.2023.24

Nanglu, K., Ortega-Hernández, J., 2024. Post-Cambrian survival of the tubicolous scalidophoran *Selkirkia*. Biology Letters, 20, 20240042, 8pp. DOI: 10.1098/rslb.2024.0042

Nanglu, K., Waskom, M.E., Richards, J.C., Ortega-Hernández, J., 2023. Rhabdopleurid epibionts from the Ordovician Fezouata Shale biota and the longevity of cross-phylum interactions. Communications Biology, 6, 1002, 10pp. DOI: 10.1038/s42003-023-05377-x

Nicholson, H.A., 1872. A Monograph of the British Graptolitidae. Part 1. Edinburgh and London, Blackwood & Sons, x+133pp.

Ortega-Hernández, J., Van Roy, P., Lerosey-Aubril, R., 2016. A new aglaspidid euarthropod with a six-segmented trunk from the Lower Ordovician Fezouata Konservat-Lagerstätte, Morocco. Geological Magazine, 153(3), 524-536. DOI: 10.1017/S0016756815000710

Pérez-Peris, F., Laibl, L., Lustri, L., Gueriau, P., Antcliffe, J.B., Bath Enright, O.G., Daley, A.C., 2021. A new nektaspid euarthropod from the Lower Ordovician strata of Morocco. Geological Magazine, 158(3), 509-517. DOI: 10.1017/S001675682000062X

Potin, G.J.-M, Gueriau, P., Daley, A.C., 2023. Radiodont frontal appendages from the Fezouata Biota (Morocco) reveal high diversity and ecological adaptations to suspension feeding during the Early Ordovician. Frontiers in Ecology and Evolution, 11, 1214109, 22pp. DOI: 10.3389/fevo.2023.1214109

Rickards, R.B., Hamedi, M.A., Wright, A.J., 1994. A new Arenig (Ordovician) graptolite fauna from the Kerman District, east-central Iran. Geological Magazine, 131(1), 35-42.

Ruedemann, R., 1895. Development and the mode of growth of *Diplograptus* M'Coy. New York State Geological Survey, Annual Report for 1894, 219-249.

Ruedemann, R., 1904. Graptolites of New York, part I. Graptolites of the lower beds. New York State Museum Memoir, 7, 455-807.

Saleh, F., Candela, Y., Harper, D.A.T., Polechová, M., Lefebvre, B., Pittet, B., 2018. Storm-induced community dynamics in the Fezouata Biota (Lower Ordovician, Morocco). Palaios, 33(12), 535-541. DOI: 10.2110/palo.2018.055

Saleh, F., Antcliffe, J.B., Lefebvre, B., Pittet, B., Laibl, L., Pérez-Peris, F., Lustri, L., Gueriau, P., Daley, A.C., 2020a. Taphonomic bias in exceptionally preserved biotas. Earth and Planetary Science Letters, 529, 115873, 6pp. DOI: 10.1016/j.epsl.2019.115873

Saleh, F., Daley, A.C., Lefebvre, B., Pittet, B., Perrillat, J.P., 2020b. Biogenic iron preserves structures during fossilization: A hypothesis. BioEssays, 42, 1900243, 6 pp. DOI: 10.1002/BIES.201900243

Saleh, F., Pittet, B., Sansjofre, P., Gueriau, P., Lalonde, S., Perrillat, J.-P., Vidal, M., Lucas, V., El Hariri, K., Kouraiss, K., Lefebvre, B., 2020c. Taphonomic pathway of exceptionally preserved fossils in the Lower Ordovician of Morocco. Geobios, 60, 99-115. DOI: 10.1016/j.geobios.2020.04.001

Saleh, F., Bath-Enright, O.G., Daley, A.C., Lefebvre, B., Pittet, B., Vite, A., Ma, X., Mángano, M.G., Buatois, L., Antcliffe, J.B., 2021a. A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas. Earth and Planetary Science Letters, 569, 117061, 9 pp. DOI: 10.1016/j.epsl.2021.11706

Saleh, F., Vaucher, R., Antcliffe, J.B., Daley, A.C., El Hariri, K., Kouraiss, K., Lefebvre, B., Martin, E.L.O., Perrillat, J.P., Sansjofre, P., Vidal, M., Pittet, B., 2021b. Insights into soft-part preservation from the Early Ordovician Fezouata Biota. Earth-Science Reviews, 213, 103464, 12 pp. DOI: 10.1016/j.earscirev.2020.103464

Saleh, F., Lucas, V., Pittet, B., Lefebvre, B., Lalonde, S.V., Sansjofre, P., 2022a. Iron from continental weathering dictated soft-part preservation during the Early Ordovician. Terra Nova, 34(3), 163-168. DOI: 10.1111/ter.12572

Saleh, F., Vaucher, R., Vidal, M., El Hariri, K., Laibl, L., Daley, A.C., Gutiérrez-Marco, J.C., Candela, Y., Harper, D.A.T., Ortega-Hernández, J., Ma, X., Rida, A., Vizcaïno, D., Lefebvre, B., 2022b. New fossil assemblages from the Early Ordovician Fezouata Biota. Scientific Reports, 12(1), 20773, 10pp. DOI: 10.1038/s41598-022-25000-z

Saunders, K.M., Bates, D.E.B., Kluessendorf, J., Loydell, D.K., Mikulic, D.G., 2009. *Desmograptus micronematodes*, a Silurian dendroid graptolite, and its ultrastructure. Palaeontology, 52(3), 541-559. DOI: 10.1111/j.1475-4983.2009.00859.x

Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R., Munnecke, A., Nowak, H., Nützel, A., Vandenbroucke, T.R., Williams, M., Rasmussen, C.M., 2016. The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. Palaeogeography, Palaeoclimatology, Palaeoecology, 458, 12-28. DOI: 10.1016/j.palaeo.2015.11.003

Servais, T., Cascales-Miñana, B., Harper, D.A.T., Lefebvre, B., Munnecke, A., Wang, W., Zhang, Y., 2023. No (Cambrian) explosion and no (Ordovician) event: A single long-term radiation in the early Palaeozoic. Palaeogeography, Palaeoclimatology, Palaeoecology, 623, 111592, 20 pp. DOI: 10.1016/j.palaeo.2023.111592

Torsvik, T., Cocks, L.R.M., 2017. Earth History and Palaeogeography. Cambridge, Cambridge University Press, 317pp.

Urbanek, A., Dilly, P.N., 2000. The stolon system in *Rhabdopleura compacta* (Hemichordata) and its phylogenetic implications. Acta Palaeontologica Polonica, 45(3), 201-226.

Urbanek, A., Mierzejewski, P., 2009. The ultrastructure and building of graptolite dissepiments. Acta Palaeontologica Polonica, 54(2), 243-252. DOI: 10.4202/app.2006.0020

Van Roy, P., 2006. Non-trilobite arthropods from the Ordovician of Morocco. Ph.D. dissertation. Ghent, Ghent University, Unpublished, xxviii+230pp.

Van Roy, P., Briggs, D.E.G., 2011. A giant Ordovician anomalocaridid. Nature, 473(7348), 510-513. DOI: 10.1038/nature09920

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., El Hariri, K., Briggs, D.E.G., 2010. Ordovician faunas of Burgess Shale type. Nature, 465(7295), 215-218. DOI: 10.1038/nature09038

Van Roy, P., Briggs, D.E.G., Gaines, R.R., 2015a. The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. Journal of the Geological Society, 172, 541-549. DOI: 10.1144/jgs2015-017

Van Roy, P., Daley, A.C., Briggs, D.E.G., 2015b. Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. Nature, 522(7554), 77-80. DOI: 10.1038/nature14256

Vaucher, R., Martin, E.L.O., Hormière, H., Pittet, B., 2016. A genetic link between *Konzentrat-* and *Konservat-Lagerstȯtten* in the Fezouata Shale (Lower Ordovician, Morocco). Palaeogeography, Palaeoclimatology, Palaeoecology, 460, 24-34.

Vaucher, R., Pittet, B., Hormière, H., Martin, E.L.O., Lefebvre, B., 2017. A wave-dominated, tide-modulated model for the Lower Ordovician of the Anti-Atlas, Morocco. Sedimentology, 64(3), 777-807. DOI: 10.1111/sed.12327

Wang, X.-F., Stouge, S., Maletz, J., Bagnoli, G., Qi, J., Raevskaya, E.G., Wang, C.-S., Yan, C., 2021. The Xiaoyangqiao section, Dayangcha, North China: the new global Auxiliary Boundary Stratotype Section and Point (ASSP) for the base of the Ordovician System. Episodes, 44(4), 359-383. DOI: 10.18814/epiiugs/2020/020091

Manuscript received January 2024;
revision accepted May 2024;
published Online July 2024.