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RESEARCH PAPER

Oldest known West Gondwanan graptolite: *Ovetograptus*? sp. (lower Agdzian/lowest Wuliuan; basal Middle Cambrian) of the Franconian Forest, Germany, and review of pre-Furongian graptolithoids

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Abstract
The occurrence of a likely graptolite in lowest Wuliuan strata of the Franconian Forest almost certainly records the oldest known graptolithoid hemichordate in West Gondwana and possibly the oldest graptolite presently known. The fossil is a delicate, erect, apparently unbranched rhabdosome with narrow thecae tentatively assigned to the poorly known genus *Ovetograptus* of the Dithecodendridae. This report includes an overview of pre-Furongian graptolithoids with slight corrections on the stratigraphic position of earlier reported species.

Keywords Cambrian · Graptolithoidea · Biostratigraphy · Morphology · West Gondwana

Introduction

Cambrian graptolithoid hemichordates almost certainly were relatively common sessile, benthic faunal elements during the Middle and Late Cambrian (Miaolingian and Furongian), and may have their earliest known appearances in the upper Lower Cambrian (see review in Landing et al. 2018). However, formal reports of these early eucolonial metazoans are fairly rare. The reason for this is that diagenesis and metamorphism often obscure a taxonomically useful preservation. In addition, putative early representatives of graptolithoids, particularly the colonial Graptolithina, appear to have been occasionally assigned to other groups, such as "algae" (e.g., Walcott 1919). Nevertheless, several species of undisputable graptolites have been reported from Middle Cambrian/Miaolingian strata (see Overview and stratigraphic revision of pre-Furongian graptolites).

This report describes a fossil from the lowest Wuliuan Stage and Miaolingian Series of the Franconian Forest, Germany that is almost certainly the oldest known graptolite in West Gondwana. Although the specimen is not very well preserved, there is little doubt about its systematic position as discussed below. Given limited outcrop at a small, overgrown quarry where it was collected, it is unlikely that additional specimens will be collected, so the specimen merits a short characterization.

Taxonomic and chronologic terminology

The suprageneric taxonomy in this report follows Beklemishev (1951) in his definition of the Graptolithoidea Beklemishev (1951) as a class that is identical to and a senior synonym of Maletz' (2014) expanded class "Pterobranchia." The Graptolithoidea (late Early Cambrian?–Recent) include a subclass Graptolithina for all modular colonial animals with organic thecal walls with fusellar structure (i.e., Landing et al. 2018, p. 125). The reptant, sessile modular colonies of

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the rhabdopleurids and dithecoids represent families of the Graptolithina (i.e., Maletz 2014, 2017), while sessile forms with triad budding and bush- or fan-like rhabdosomes are the order Dendroidea (Upper Cambrian–Carboniferous). The remaining pelagic graptolithines are assigned to the order Graptoloidea Lapworth *in* Hopkinson and Lapworth (1875) (Lower Ordovician–Lower Devonian). In this report, the Cambrian is divided into three proposed, formally defined subsystems (Lower, Middle, Upper) and subperiods (Early, Middle, Late) following Landing et al. (2020).

Material, locality, stratigraphy, and geological setting

The graptolite is known from a single incomplete specimen collected from the lower Wildenstein Member of the Tannenknock Formation in the Wildenstein tectonic block of the Franconian Forest (i.e., Frankenwald) of northeastern Bavaria, Germany (Fig. 1). The collection locality is a small abandoned quarry north of Wildenstein (ca. N 50° 12′ 01″, E 11° 33′ 35″) and is locality W9 of Geyer et al. (2019a, Appendix 1; Fig. 2).

The Cambrian succession of the Franconian Forest region is remarkably similar to that of the south Moroccan margin of West Gondwana (Geyer et al. 2019a). Thus, the specimen discussed herein expands the known record of Middle

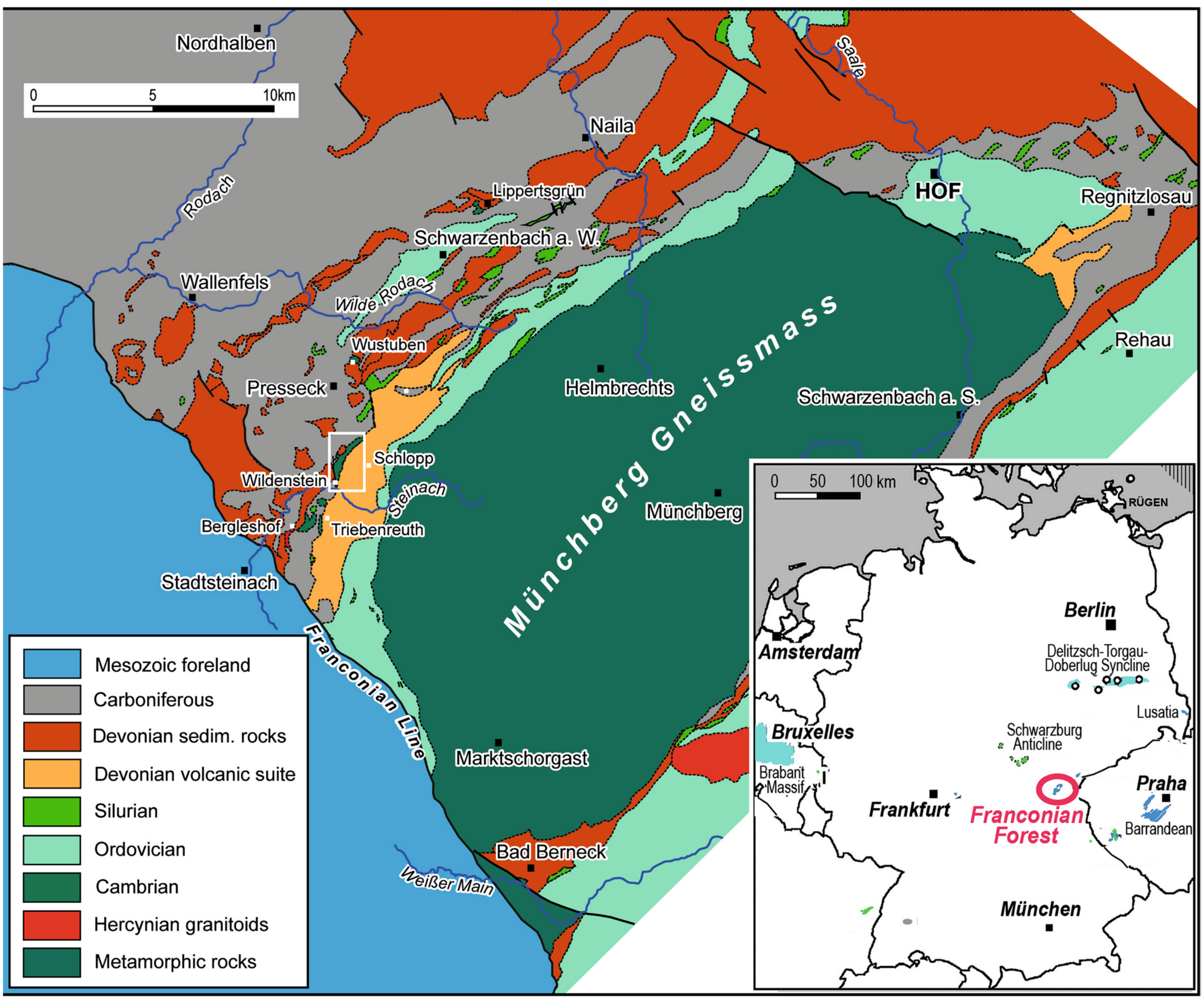


Fig. 1 Generalized geological map of the Saxothuringian Zone in northeastern Bavaria, southern Germany; insert map shows boundaries of Germany and adjacent countries with Cambrian rocks (blue: surface outcrops; green: rocks with Cambrian portions or suspect Cambrian rocks; turquois: subsurface Cambrian rocks) and location of Franconian Forest region. White rectangle outlines map area shown in Fig. 2

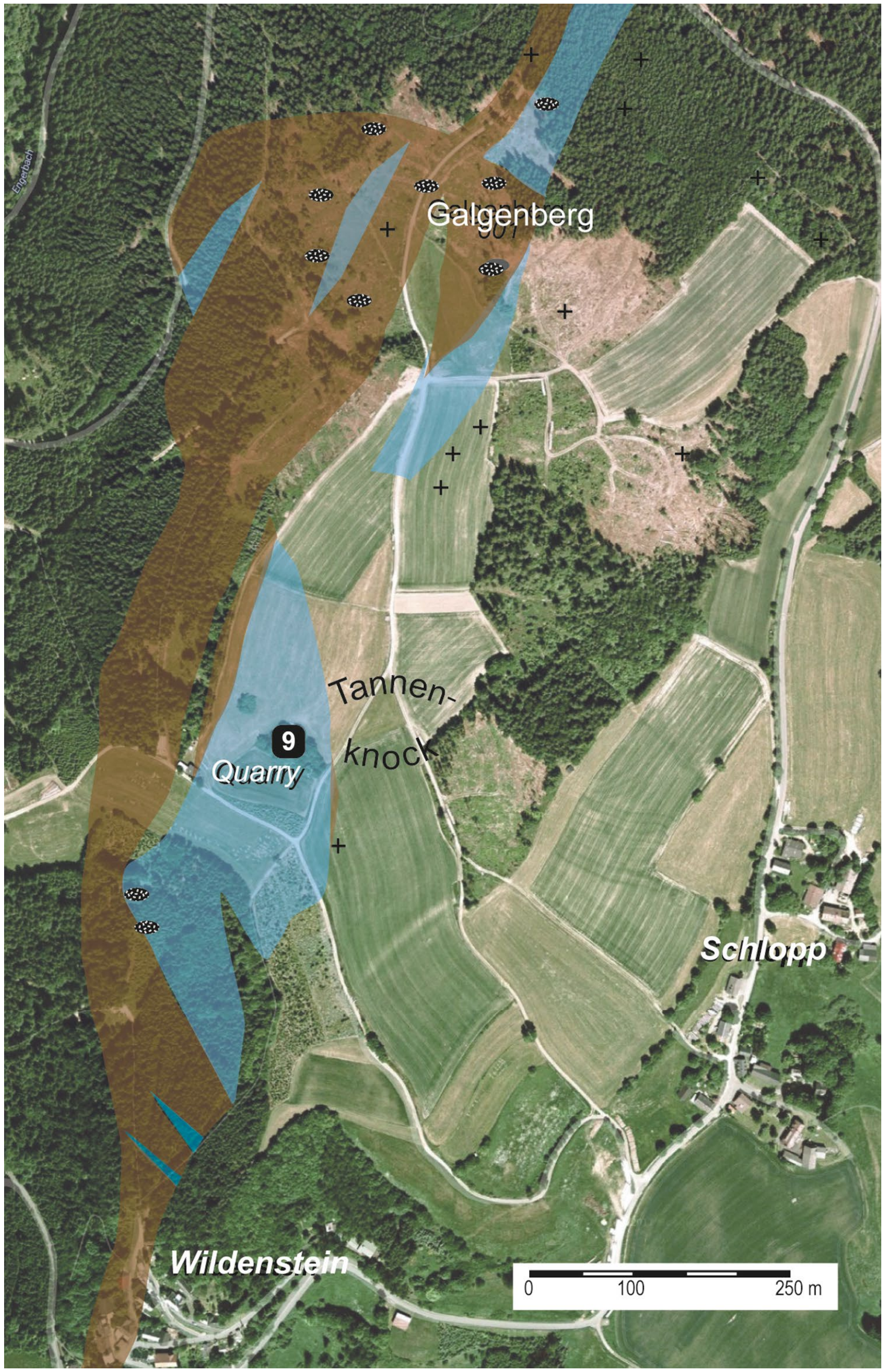
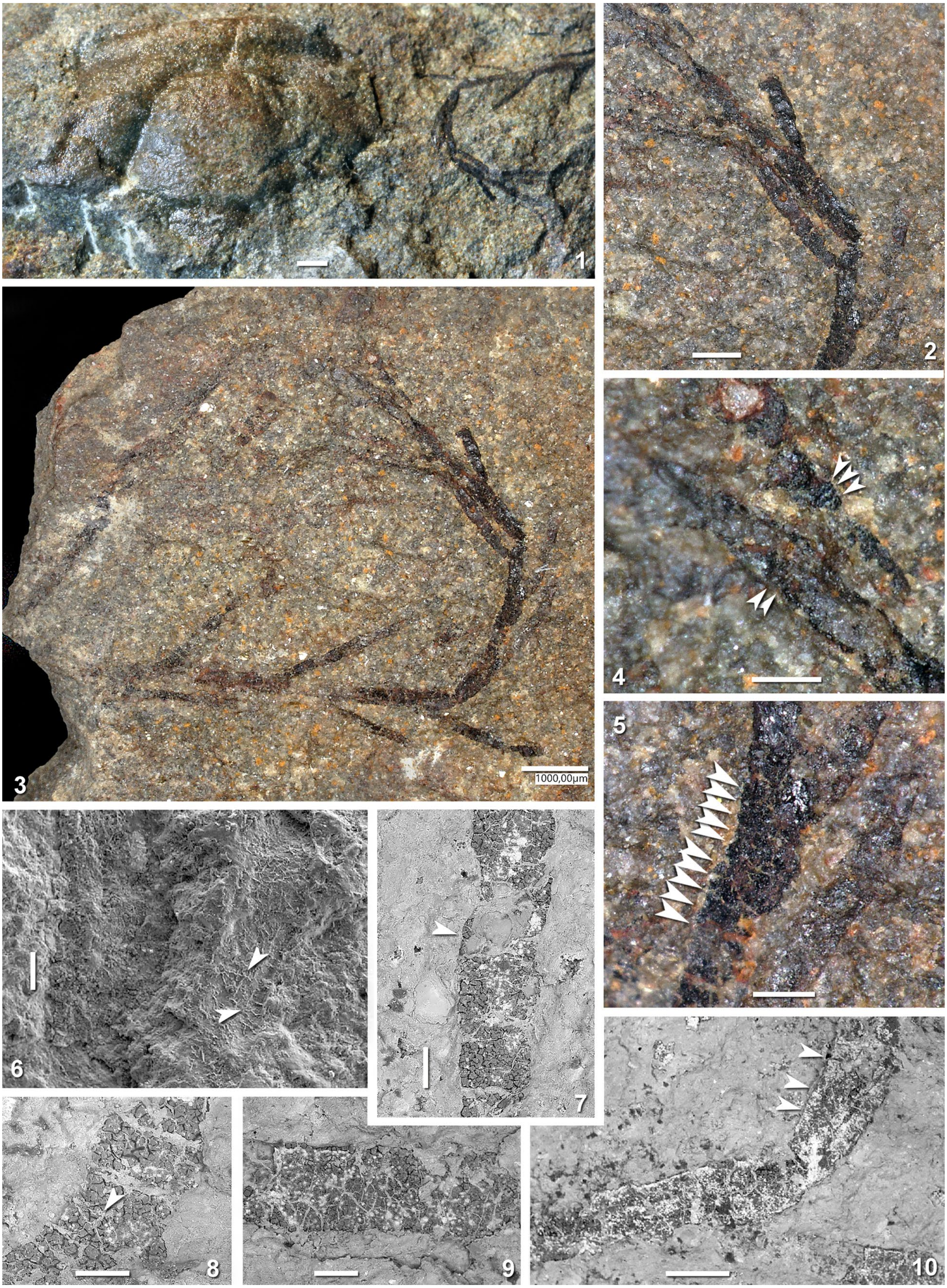


Fig. 2 Area with outcrops of the Cambrian Tannenknock Formation in the Wildenstein slice, Franconian Forest (white rectangle in Fig. 1). Brown colour marks outcrop areas dominated by Galgenberg Member; blue colour shows outcrop areas dominated by Wildenstein Member. "W9" indicates collecting site of *Ovetograptus*? sp. in abandoned small quarry. Modified from Geyer (2017, fig. 4) and Geyer et al. (2019a, fig. 10)

Cambrian West Gondwanan graptolites known from Iberia, as well as the Barrandian region ("Perunica") of Gondwana and East Gondwana (Victoria and Tasmania, Australia) (discussed below).

The lower Wildenstein Member is typically composed of fine-grained, shallow-marine sandstones of variable thicknesses. Its fauna consists of a moderately diverse assemblage dominated by trilobites with locally abundant articulate and acrothelid brachiopods, hyoliths and relatively rare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◂**Fig. 3** Specimen SSMM 10,357, from Wildenstein Member, Tannenknock Formation, sample locality W 9. **1**, *Parasolenopleura* sp. cranidium and *Ovetograptus*? sp. rhabdosome. **2–10**, *Ovetograptus*? sp., strongly curved rhabdosome; **2**, detail showing carbon coat and mode of branching as well as typical deformation features; **3**, entire specimen; **4**, **5**, details showing bulging of carbonaceous coats suspicious to indicate fusellar structures; **6**, SEM micrograph with secondarily filled shrinkage cracks; **7–10**, BSE photos of stolon, with bulging margin at close to narrow transverse filament of organic matter (arrow) in **7**; irregular shrinkage cracks (arrow) in **8**; degraded organic coats and transverse lines in **9**; and transverse organic filaments (arrows) in **10**. Scale bars 1 mm in 1 and 3; 0.5 mm in 2; 300 µm in 10; 250 µm in 4, 5; 100 µm in 6–9

helcionelloids, echinoderm ossicles from different systematic groups, bradoriids, sponge spicules, and remains of other fossil groups (e.g., Geyer 2010, 2017; Geyer et al. 2019a, 2019b; Streng and Geyer 2019).

The graptolite comes from a relatively hard, slightly feldspathic sandstone in a facies recording agitated waters. It is associated with a cranidium of the trilobite *Parasolenopleura* sp. (Fig. 3.1). Associated fossils are fairly large and commonly unfractured sclerites of other trilobites and hyoliths.

This part of the succession belongs to the *Ornamentaspis frequens* Zone in the regional biostratigraphic scheme, which corresponds to the *O. frequens* Zone of the Moroccan Anti-Atlas and characterizes the middle Agdzian Stage (see Geyer and Landing 2004) (Fig. 5). Unfortunately, this West Gondwanan biostratigraphy cannot be correlated precisely with the internationally applied chronostratigraphy, but the *O. frequens* Zone is thought to correspond to the lowest Wuliuan Stage and Miaolingian Series (e.g., Geyer 2019).

Systematic palaeontology

Class **Graptolithoidea** Beklemishev, 1951
Subclass **Graptolithina** Bronn, 1849
Incertae sedis
Family **Dithecodendridae** Obut, 1964
(Senior synonym of Dithecoidea Rickards and Durham, 2006).

Discussion. For genera assigned to the Dithecodendridae, see discussion in Maletz (2014, p. 490, 491).

Several graptolite taxa were described by Sdzuy (1974) from shales of the lower Oville Formation in the Oviedo and León provinces of the Cantabrian Mountains, northern Spain. Sdzuy (1974) recognized 11 different species and forms in open nomenclature, which he assigned to the four genera *Tarnagraptus* Sdzuy, 1974; *Sotograptus* Sdzuy, 1974; *Ovetograptus* Sdzuy, 1974; and *Archaeolafoea* Chapman, 1919. The specimens come from upper Agdzian–Caesaraugustan (upper Wuliuan–lower Drumian) strata. Mierzejewski (1986) suggested that most of the taxa are colonial scyphopolyps. However, based on recognizable fusellar rings, Maletz et al. (2005) considered them to be early graptolites.

The species from the Cantabrian Mountains are all erect colonies with limited branching. Taxa with comparable morphology are rare but include material (unnamed genus and species) from Drumian strata of the Chancellor Basin, British Columbia (Johnston et al. 2009); material assigned to *Archaeolafoea* and *Mastigiograptus* from the Middle Cambrian Wheeler and Marjum formations of Utah (LoDuca and Kramer 2014); and in the upper Wuliuan/Floran Heathcote fauna of the Monegeetta Shale Formation of Victoria, Australia (Chapman 1919; Chapman and Thomas 1936).

Genus ***Ovetograptus*** Sdzuy, 1974

Type species. *Ovetograptus gracilis* Sdzuy, 1974, from the lower Oville Formation of the Cantabrian Mountains, Spain (by original designation).

Discussion. Ovetograptus is characterized and distinguished from the closely related genera *Tarnagraptus* Sdzuy, 1974, and *Sotograptus* Sdzuy, 1974, by its long and very slender thecae, which are barely wider than the axis to which they are attached. In the only described species, *O. gracilis*, the thecae are distant from each other and the rhabdosome has a loose habit as emphasized by Sdzuy (1974).

Ovetograptus? sp.
Figures 3, 4.

Material. Single specimen from locality W9 of the Tannenknock Formation, Wildenstein Member (see Geyer et al. 2019a, b, fig. 10, for additional information on sample location). Reposited in the Mineralienkabinett S. Meier collection, Marktredwitz, SSMM 10357b.

Description. The specimen is a curved, almost horseshoe-shaped, unbranched rhabdosome more than 20 mm in length and 11 mm wide. Stolonal axis ca. 0.25–0.35 mm wide, slightly deformed during deposition and burial. The thecae appear to be arranged along the axis in a relatively unordered, pseudo-verticillate manner. Thecae ca. 2.0–2.4 mm long and ca. 0.2–2.5 mm wide, branch from axis at angles of generally ca. 25–40°; thecae nearly straight tubes with subparallel margins, but slightly broadened in the middle part in some of the thecae probably due to dorsoventral compression.

Preservation and suprageneric taxonomy. The Franconian Forest region underwent tectonic deformation during the

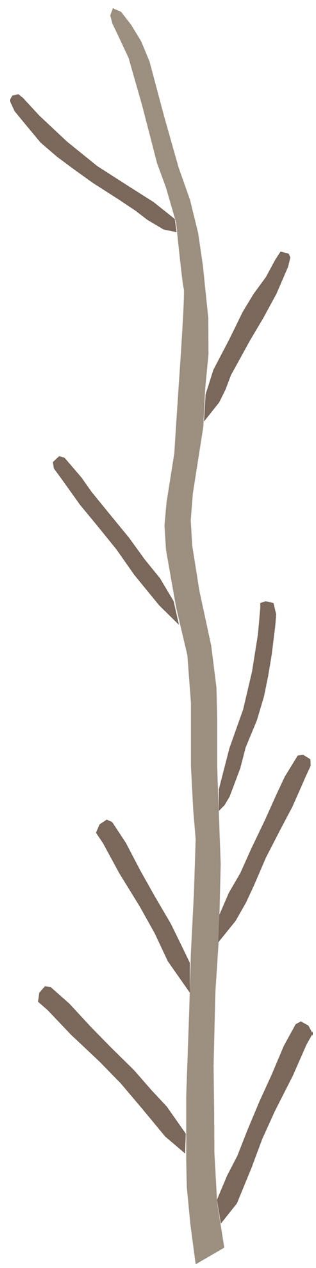

Fig. 4 Reconstruction of *Ovetograptus*? sp. with axis in light brown, thecae in dark brown-grey

Variscan/Hercynian Orogeny. The Cambrian is preserved as large blocks in a Lower Carboniferous melange and recognizable Cambrian fossils are limited in abundance. This means that the preservation of this specimen likely would not include preservation of such fine structures as the fusellar rings characteristic of graptolites. However, despite the imperfect preservation, fine details indicate the presence of transverse elements composing the stolonal axis, which appear to be intensified and amplified by compression and secondary transverse cracks, but represent primary structures (e.g., Fig. 3.4, .5, .10, arrowed). Examination under Backscatter SEM imaging did not reveal details which prove the presence of unequivocal fusellar sutures, but show rhythmic transverse lines created by residual organic material (e.g., Fig. 3.7, .9, .10) which suggest a primary compartmental composition. These "units" are subequal in size and broader (along the axis of the stolon) than the usual fuselli of younger/later graptolites (e.g., in *Archaeolafoea longicornis*; Maletz and Steiner 2015, fig. 3C).

The specimen is preserved as a thick black carbon film which indicates original organic walls (Fig. 3.2, .4, .9, .10). This suggests that the form cannot be assigned to the morphologically similar, colonial cnidarian *Sphenothallus* Hall, 1847, which has phosphatic wall structure (i.e., Landing et al. 2018). Organic wall structure is obviously consistent with assignment of the specimen to non-mineralized hydrozoans [as indicated by minor shrinkage cracks (e.g., Fig. 3.6, .7, .8, arrowed)]. However, hydrozoans are often characterized by paired thecae and hydrocladia (i.e., Song et al. 2021), and the Franconian Forest specimen has superficially alternating (but in fact pseudo-verticillate) thecae. There is no evidence of hydrocladia and not a regular alternation in arrangement of thecae as in some extant hydrozoans.

Discussion. The specimen resembles the only known species of *Ovetograptus*, *O. gracilis*, in the morphology of the rhabdosome as well as the size of the thecae. *Ovetograptus gracilis* has slender, straight-to-slightly curved thecae with a width comparable to or slightly narrower than the axis. However, *O. gracilis* is distinguished from the form represented by the specimen from the Franconian Forest. The latter has distinctly more elongate and more widely spaced thecae that branch from the axis at a higher angle and more delicate thecae and rhabdosome. Nevertheless, more and better preserved material would be needed to provide a well-defined characterization of the species represented by the described specimen.

Overview and stratigraphic revision of pre-Furongian graptolites

Undisputed graptolites from Middle Cambrian/Miaolingian strata include specimens from most of the Cambrian continents. The following list compliments the reviews in Maletz and Steiner (2015, fig. 11) and Ramírez-Guerrero and Cameron (2021, fig. 1), but also corrects or adjusts the stratigraphic information on the provenance of the Middle Cambrian taxa.

In general, three distinctly different morphological types of rhabdosomes can be distinguished. Several genera such as the Iberian *Tarnagraptus*, *Ovetograptus,* and *Sotograptus* and the Siberian and North China genus *Siberiodendrum* are erect colonies with limited branching or are unbranched and have relatively narrow tubes.

A distinctly different morphology is exhibited by *Sphenoecium* Chapman and Thomas, 1936, a genus which in its revised concept suggested by Maletz and Steiner (2015) includes several Miaolingian species from different Cambrian continents. The species of this genus are colonies with encrusting thecorhizae and numerous erect, tubular thecae that are usually relatively broad. This genus was tentatively assigned to the family Rhabdopleuridae (along with the morphologically distinct genus *Archaeolafoea*; see Maletz 2014; Maletz and Steiner 2015).

A third group is represented by *Mastigograptus* Ruedemann, 1908. This genus, characterized by trifid budding and erect rhabsosomes with widely separated autothecae, comprises the family Mastigograptidae.

The West Gondwana margin of the giant Gondwana continent has yielded Middle Cambrian graptolites from shales of the Oville Formation in the Cantabrian Mountains, northern Spain (Sdzuy 1974). These graptolites have a fairly long stratigraphical range from the upper Agdzian through the middle Caesaraugustan (= upper Wuliuan–middle Drumian). All known specimens are erect rhabdosomes of the Dithecodendridae. The form described by Sdzuy (1974) as *Archaeolafoea* sp. A is regarded herein as a probable new dithecodendrid closely related to the three other genera known from the Oville Formation (i.e., *Tarnagraptus*, *Ovetograptus*, *Sotograptus*).

East Gondwana has a number of probable upper Wuliuan/Floran graptolites in the Heathcote fauna of the Monegeetta Shale Formation of Victoria, Australia (Chapman 1919; Chapman and Thomas 1936), and the Dundas Group of Tasmania, Australia (Thomas and Henderson 1945; Quilty 1971). Two species from the Monegeetta Shale, *Sphenoecium filicoides* (Chapman, 1919) and *S. discoidalis* Chapman and Thomas, 1936, are congeneric with several species of *Sphenoecium* described from Bohemia, Norway, the western United States, and the Canadian Cordillera. Other species identified from the formation are *Archaeolafoea longicornis* Chapman, 1919; *A. monegeetae* Chapman, 1919; and *Archaeocryptolaria skeatsi* Chapman, 1919, with the latter considered to be a synonym of *Archaeolafoea longicornis* (i.e., Maletz and Steiner 2015). *Protohalecium* Chapman and Thomas, 1936, is another graptolite with a sinuously branching rhabdosome with increasing thecae separation proximally (Rickards and Durman 2006; Ramírez-Guerrero and Cameron 2021). The material from the Dundas Group has been described as *Mastigograptus serialis* Chapman and Thomas, 1936; *M. simplex* (Walcott, 1919); and *Archaeolafoea monegeetae* (Quilty, 1971). However, the specimens are poorly preserved and need careful revision.

Maletz et al. (2005) reported a graptolite species characterized by encrusting thecorhiza and erect tubes from the Perunica/Barrandian region of Gondwana. This is *Rhabdotubus robustus* Maletz et al. 2005, from the upper Jince Formation of the Barrandian region of the Czech Republic. The species was subsequently revised to *Sphenoecium robustum* by Maletz and Steiner (2015; erroneously spelled "*Sphenoecium robustus*"). Its known range corresponds to the middle Caesaraugustan Stage (=middle Drumian). This species has also been recorded from distinctly older strata of the lower Jince Formation from Luh, Bohemia, which belong to the middle Agdzian (=lower, but not lowest Wuliuan) (Maletz and Steiner 2015).

From the Avalonian microcontinent (e.g., Landing 1996; Landing et al. 2022), Howell (1963) described a specimen under the name *Archaeolafoea terranovaensis* from black shales of the Manuels River Formation on Conception Bay, southeastern Newfoundland (his "Kelligrews Brook Formation" in Howell 1963). This form was regarded as a hydrozoan. The specimen is difficult to assess. The strata from which it originates belong to the Guzhangian *Paradoxides davidis* Zone.

Two species have been described from the Baltica palaeocontinent. One of these is *Dendrograptus mesocambricus* from the Guzhangian part of the Alum Shale Formation of southern Norway (Öpik 1933). The other described by Bengtson and Urbanek (1986) is *Rhabdotubus johanssoni* from the upper Wuliuan part of the currently distinguished Borgholm Formation of southern Sweden. Both species have been synonymized and dealt with as *Sphenoecium mesocambricum* (Öpik, 1933) (erroneously spelled "*Sphenoecium mesocambricus*" by Maletz and Steiner (2015).

The Sibiria palaeocontinent has yielded an exceptionally well-preserved rhabdopleurid from the Zelenotsvet Formation of the southeastern Prianabar region on the Siberian Platform. The occurrence is in the *Anomocarioides limbataeformis–Lejopyge laevigata*/*Aldanaspis truncata* zones of the Bulunian Substage of the Mayan Stage (Guzhangian). It was first described as *Rhabdopleura obuti* by Durman and Sennikov (1993) and later revised to *Sphenoecium obuti* by Maletz and Steiner (2015). Associated taxa include *Archaeolafoea* sp. and *Siberiodendrum robustum* Obut, 1964 (Durman and Sennikov 1993).

Reports of graptolites from South China/the Yangtze Platform refer to specimens from the Kaili fauna of the Kaili Formation in Guizhou Province (Harvey et al. 2012). The early Wuliuan age of this material is more or less coeval with *Ovetograptus*? sp. described herein from the Franconian Forest. Unfortunately, the specimens from the Kaili Formation are only preserved as fragments of periderm with a distinctive banded microstructure. Harvey et al. (2012) suggested that they most likely represent rhabdopleurids. *Malongitubus* Hu, 2005, from the older (late Early Cambrian) Chengjiang Lagerstätte of South China has been interpreted as a possible pterobranch (and, thus, as a graptolite; Hu et al. 2018), but an unequivocal taxonomic assignment should be regarded as not possible based on the available material.

Siberiograptus Obut, 1964, is also recorded from the upper Furongian Fengshan Formation of Shandong Province, North China Platform (Lin 1985). Lin (1985) proposed two new species of the genus, *S. simplex* and *S. polycladus*. The first species is now termed *Palaeodiphasia simplex*, the type species of a new genus assigned to the Hydrozoa (Song et al. 2021). The latter species is poorly preserved and should be regarded as systematically problematical.

Laurentian graptolites are known from the Topazian–Marjuman (= uppermost Wuliuan–lower Guzhangian) Spence, Marjum and Wheeler formations of the western U.S., and from the Drumian Burgess Shale of Alberta, Canada (Ruedemann 1931, 1947). These include the cephalodiscid graptolithoid *Cephalodiscus*? sp. (see discussions in Maletz et al. 2005, and Maletz and Steiner 2015) and *Sphenoecium wheelerensis* Maletz and Steiner, 2015, from the Spence Shale of Idaho and the Wheeler and Marjum formations of Utah (Conway Morris and Robison 1988). The systematic position of *Chaunograptus* Hall, 1879, from the Burgess Shale has been disputed, but recent analyses suggest that it very likely is a rhabdopleurid graptolite (Maletz and Beli 2018; Ramírez-Guerrero and Cameron 2021). Furthermore, genera such as *Yuknessia* Walcott, 1919, and *Dalyia* Walcott, 1919, from the Drumian Burgess Shale of the Canadian Cordillera and Marjum and Wheeler formations of are regarded as Graptolithina (Maletz and Steiner 2015; LoDuca et al. 2015; Maletz and Beli 2018; Ramírez-Guerrero and Cameron 2021) and specimens from the Wheeler Formation previously identified as *Yuknessia simplex* Walcott, 1919, were considered as the new species *S. wheelerensis* (Maletz and Steiner, 2015).

Another possible graptolite from the middle Dyerian Forteau Formation of Laurentian western Newfoundland (Cambrian Stage 4) has been mentioned in Maletz and Steiner (2015, fig. 11) and would be the oldest known graptolithoid. However, it has not been figured or elsewise described.

Conclusions

The end of the Cambrian Evolutionary Radiation included the appearance of undoubted modular colonies of eumetazoans in the late Early Cambrian. These include rare specimens of coralomorphs, the likely cnidarian *Sphenothallus*, and the problematicum *Torellella* (see Landing et al. 2018). Tiny colonies of sessile graptolites may have appeared by the late Early Cambrian in tropical carbonate platform facies in NE Laurentia, and relatively abruptly have a world-wide distribution in Middle Cambrian shelf and marginal successions (Baltica, East and West Gondwana, Sibiria, western

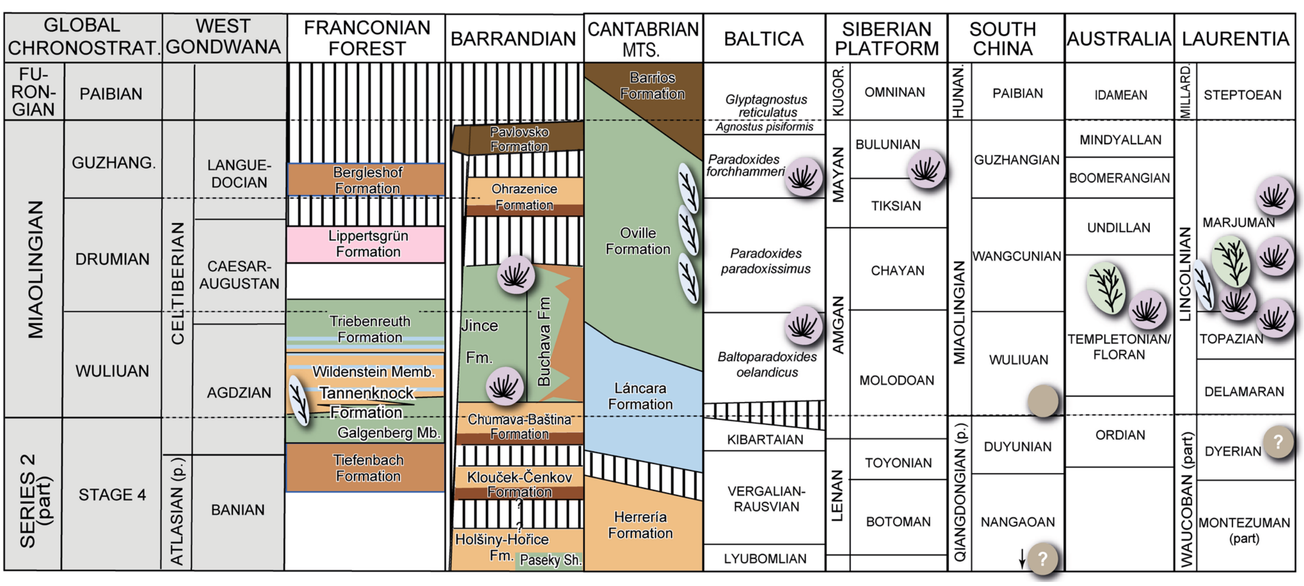

Fig. 5 Stratigraphic occurrences of graptolites in pre-Furongian Cambrian strata. West Gondwanan regions with lithofacies by colour (dark and medium brown: coarse or dominantly coarse-grained, shallow-marine siliciclastics; light brown: fine-grained shallow-marine siliciclastics; green: shale-dominated, shallow-marine rocks; pink: red-to-purple shales; blue: shallow-marine carbonates). Columns for other Cambrian continents with regional series and stages. Symbols for graptolites distinguish erect colonies with limited branching or unbranched rhabdosomes and relatively narrow stolons (*Tarnagraptus*-type Dithecodendridae; on light grey oval), moderately branching, erect rhabdosomes of Mastigograptidae (light green oval), and colonies with encrusting thecorhizae and multiple autothecae (*Sphenoecium*-type Rhabdinopleuridae; purple circle). Light brown circles indicate occurrences of rhabdopleurids or supposed rhabdopleurids/pterobranchs (with question mark) of uncertain taxonomic affinity

Laurentia, South China platform, possibly Avalonia). The occurrence of *Ovetograptus*? sp. appears to expand the lower Middle Cambrian range of early graptolites in West Gondwana from Iberia to the Franconian Forest of Germany (Fig. 5).

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References

Beklemishev, V.N. 1951. K postroeniyu sistemy zhivotnykh. Vtorichnorotye (Deuterostomia), ikh proizkhozdenie i sostav (Toward the building system of animals. Deuterostomia, their origin and composition). *Uspekhi Sovremennoy Biologii* 32: 256–270.

Chapman, F. 1919. On some hydroid remains of lower Palaeozoic age from Monegetta, near Lancefield. *Proceedings of the Royal Society of Victoria, New Series* 2 (31): 388–393.

Chapman, F., and D.E. Thomas. 1936. The Cambrian hydroidea of the Heathcote and Monegeeta districts. *Proceedings of the Royal Society of Victoria, New Series* 48: 193–212.

Conway Morris, S., and R.A. Robison. 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. *University of Kansas Paleontological Contributions, Paper* 12: 1–48.

Durman, P.N., and N.V. Sennikov. 1993. A new rhabdopleurid hemichordate from the Middle Cambrian of Siberia. *Palaeontology* 36: 283–296.

Geyer, G. 2010. Cambrian and lowermost Ordovician of the Franconian Forest. In *Prague 2010 – The 15th Field Conference of the Cambrian Stage subdivision Working Group, International Subcommission on Cambrian Stratigraphy, 4–11 June 2010, Abstracts and Excursion Guide*, eds. Fatka, O., and P. Budil. Czech Geological Survey, Prague: 78–92.

Geyer, G. 2017. Trilobites of the Galgenberg Member (Tannenknock Formation), middle Cambrian Stage 5, Franconian Forest, Germany: A paradigmatic lowermost middle Cambrian West Gondwanan fauna. *Paläontologische Zeitschrift* 91: 5–70.

Geyer, G. 2019. A comprehensive Cambrian correlation chart. *Episodes* 42: 321–332. https://doi.org/10.18814/epiiugs/2019/019026.

Geyer, G., and E. Landing. 2004. A unified Lower–Middle Cambrian chronostratigraphy for West Gondwana. *Acta Geologica Polonica* 54: 179–218.

Geyer, G., E. Landing, S. Höhn, U. Linnemann, S. Meier, T. Servais, T. Wotte, and H.-G. Herbig. 2019a. Revised Cambrian stratigraphy in the Franconian Forest (Frankenwald), Germany, reveals typical West Gondwana succession in the Saxothuringian Belt. *Newsletters on Stratigraphy* 54 (2): 377–433. https://doi.org/10.1127/nos/2019/0495.

Geyer, G., M. Valent, and S. Meier. 2019b. Helcionelloids, stenothecoids and hyoliths from the Tannenknock Formation (traditional lower middle Stage 4/Wuliuan boundary interval) of the Franconian Forest, Germany. *PalZ* 93: 207–253. https://doi.org/10.1007/s12542-018-0433-5.

Hall, J. 1847. *Palaeontology of New York. Containing descriptions of the organic remains of the lower division of the New York System. Vol. 1*. 338 pp. Albany: C. Van Benthuysen.

Harvey, T.H.P., J. Ortega-Hernandez, J.-P. Lin, Y.L. Zhao, and N.J. Butterfield. 2012. Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China. *Acta Palaeontologica Polonica* 57: 423–436.

Hopkinson, J., and C. Lapworth. 1875. Description of the graptolites of the Arenig and Llandeilo rocks of St. Davidh's. *Quarterly Journal of the Geological Society of London* 31: 631–672.

Howell, B.F. 1963. New Cambrian conchostracans from Wyoming and Newfoundland, brachiopods from Vermont, and worm, hydrozoan and problematicum from Newfoundland. *Journal of Paleontology* 37: 164–167.

Hu, S., B.-D. Erdtmann, M. Steiner, Y. Zhang, F. Zhao, Z. Zhang, and J. Han. 2018. *Malongitubus*: A possible pterobranch hemichordate from the early Cambrian of South China. *Journal of Paleontology* 92: 26–32. https://doi.org/10.1017/jpa.2017.134.

Johnston, K.J., P.A. Johnston, and W.G. Powell. 2009. A new, Middle Cambrian, Burgess Shale-type biota, *Bolaspidella* Zone, Chancellor Basin, southeastern British Columbia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 277: 106–126.

Landing, E. 1996. Avalon—insular continent by the latest Precambrian, In *Avalonian and related peri-Gondwanan terranes of the circum-North Atlantic*, eds. Nance, R.D., and M. Thompson. Geological Society of America, Special Paper 304: 27–64.

Landing, E., J. Antcliffe, G. Geyer, A. Kouchinsky, A. Andreas, and S.S. Bowser. 2018. Early evolution of colonial animals (Ediacaran evolutionary revolution-Cambrian evolutionary radiation-great Ordovician diversification interval). *Earth-Science Reviews* 178: 105–135.

Landing, E., G. Geyer, M.D. Schmitz, T. Wotte, and A. Kouchinsky. 2020. (Re)proposal of three Cambrian subsystems and their geochronology. *Episodes* 44: 273–283. https://doi.org/10.18814/epiiugs/2020/020088.

Landing, E., J.D. Keppie, D.F. Keppie, G. Geyer, and S.R. Westrop. 2022. Greater Avalonia—latest Ediacaran-Ordovician “peribaltic” terrane bounded by continental margin prisms (“Ganderia”, Harlech Dome, Meguma): Review, tectonic implications, and paleogeography. *Earth-Science Reviews* 224: 1–49. https://doi.org/10.1016/j.earscirev.2021.103863.

Lin, Y.K. 1985. On the discovery of *Siberiograptus* from North China. *Acta Palaeontologica Sinica* 24: 237–242, 290 (In Chinese with English Abstract).

LoDuca, S.T., and A. Kramer. 2014. Graptolites from the wheeler and Marjum formations (Cambrian, Series 3) of Utah. *Journal of Paleontology* 88: 403–410. https://doi.org/10.1666/12-096.

LoDuca, S.T., J.B. Caron, J.D. Schiffbauer, S. Xiao, and A. Kramer. 2015. A reexamination of *Yuknessia* from the Cambrian of British Columbia and Utah. *Journal of Paleontology* 89: 82–95. https://doi.org/10.1017/jpa.2014.7.

Maletz, J. 2014. The classification of the Pterobranchia (Cephalodiscida and Graptolithina). *Bulletin of Geosciences* 89: 477–540.

Maletz, J. 2017. Graptolite Palaeobiology. In *Topics in Geobiology*. New York: Wiley Blackwell, 366 pp.

Maletz, J., and E. Beli. 2018. Part V, Second Revision, Chapter 15: Subclass Graptolithina and incertae sedis Family Rhabdopleuridae: Introduction and Systematic Descriptions. *Treatise Online* 101: 1–14. https://doi.org/10.17161/to.v0i0.7053.

Maletz, J., and M. Steiner. 2015. Graptolite (Hemichordata, Pterobranchia) preservation and identification in the Cambrian Series 3. *Palaeontology* 58: 1073–1107.

Maletz, J., M. Steiner, and O. Fatka. 2005. Middle Cambrian pterobranchs and the question: What is a graptolite? *Lethaia* 38: 73–85.

Mierzejewski, P. 1986. Ultrastructure, taxonomy and affinities of some Ordovician and Silurian organic microfossils. *Palaeontologia Polonica* 47: 129–220.

Obut, A.M. 1964. Podtip Stomochordata. Stomokhordovye, p. 279–337. In *Osnovy paleontogii: Echinodermata, Hemichordata, Pogonophora, Chaetognatha*, ed. Orlov, Yu.A. Nedra, Moscow, 379 pp (In Russian).

Öpik, A. 1933. Über einen kambrischen Graptolithen aus Norwegen. *Norsk Geologisk Tidsskrift* 13: 8–10.

Quilty, P.G. 1971. Cambrian and Ordovician dendroids and hydroids of Tasmania. *Journal of the Geological Society of Australia* 17: 171–189.

Ramírez-Guerrero, G.M., and C.B. Cameron. 2021. Systematics of pterobranchs from the Cambrian Period Burgess Shales of Canada and the early evolution of graptolites. *Bulletin of Geosciences* 96: 1–18.

Rickards, R.B., and P. Durman. 2006. Evolution of the earliest graptolites and other hemichordates. *National Museum of Wales, Geological Series* 25: 5–92.

Ruedemann, R. 1931. Some new Middle Cambrian fossils from British Columbia. *Proceedings of the United States National Museum* 79: 1–25.

Ruedemann, R. 1947. Graptolites of North America. *Geological Society of America, Memoir* 19: 1–652.

Sdzuy, K. 1974. Mittelkambrische Graptolithen aus NW-Spanien. *Paläontologische Zeitschrift* 48: 110–139.

Song, X., B. Ruthensteiner, M. Lyu, X. Liu, J. Wang, and J. Han. 2021. Advanced Cambrian hydroid fossils (Cnidaria: Hydrozoa) extend the medusozoan evolutionary history. *Proceedings of the Royal Society, B (Biological Sciences)* 288 (1944): 20202939.

Streng, M., and G. Geyer. 2019. Middle Cambrian Bradoriida (Arthropoda) from the Franconian Forest, Germany, with a review of the bradoriids described from West Gondwana and a revision of material from Baltica. *PalZ* 93: 567–591. https://doi.org/10.1007/s12542-019-00448-z.

Thomas, D.E., and Q.J. Henderson. 1945. Some fossils from the Dundas series, Dundas. *Papers and Proceedings of the Royal Society of Tasmania* 1944: 1–8.

Walcott, C.D. 1919. Middle Cambrian Algae. Cambrian Geology and Paleontology, IV. *Smithsonian Miscellaneous Collections* 67: 217–260.