



Benthic graptolites (Graptolithina, Pterobranchia) in the Miaolingian (Cambrian Series 3)

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Abstract

Benthic graptolites (Graptolithina) were surprisingly common and diverse in the Miaolingian (Cambrian), but have rarely been described in detail. Encrusting and erect growing colonies already evolved and can be differentiated in early Miaolingian faunas. The Rhabdopleuridae with their encrusting colonies provide few fossils, but members of the erect growing, bushy colonies of the Dithecodendridae are more common, at least as fragments indicating considerable fragmentation and transport. In the Wuliuan, the benthic graptolites reached a considerable diversity at the genus level with at least 6 genera appearing in this interval. The most common taxon is the encrusting genus *Sphenoecium* with its robust colonies, showing a worldwide distribution. Most taxa, however, are known from few records and their biostratigraphical and palaeogeographical distribution cannot be established yet. Erroneously, the widely distributed *Tarnagraptus* with its conical thecae has often been misidentified as the Ordovician *Mastigograptus*, but differs considerably in its tubarium construction and both might not be closely related.

Keywords Graptolites · Cambrian · Miaolingian · Rhabdopleuridae · Dithecodendridae · Evolution · Diversity

Introduction

The Cambrian radiation or explosion introduced numerous organisms to the planet and during this time interval, also the first colonial organisms evolved including those of the Pterobranchia. Landing et al. (2018) discussed potentially colonial metazoans and provided a general overview of the possible evolution of coloniality in several groups. Their interpretation indicates that the best fossil evidence of the presence of colonial metazoans in the Cambrian may be that of the Graptolithina (see Landing et al. 2018, fig. 1), as most other fossil groups provided only unclear and speculative evidence. The fossil record often makes it difficult to understand the remains of these ancient organisms and misinterpretations or controversial interpretations are common. Thus, for example, recently *Protomelission* Brock and Cooper, 1993 from the early Cambrian (Stage 3) of South Australia and China was described and interpreted by Zhang et al. (2021) as an early Cambrian bryozoan, suggesting an early Cambrian evolution

of metazoan coloniality and the Cambrian origin of the Bryozoa. However, Yang et al. (2023) rejected the idea and interpreted *Protomelission* as an early dasyclad alga, showing the difficulty of interpreting even ‘exceptionally’ preserved fossils. Another rejection by Xiang et al. (2023) considered *Protomelission* to be a scleritinous eumetazoan. A similarly complex history of interpretation and re-interpretation exists for the unusual taxon *Pywackia* Landing in Landing et al., 2010, originally identified as a bryozoan (see Hageman and Vinn, 2023). Thus, the hunt for the origin of coloniality in some groups of organisms is still open!

Graptolites (Graptolithina, Pterobranchia) are the first fossil organisms for which a colonial organisation can be proven, even though the organisms are not preserved. They can be recognised as colonial due to the secretion of their housing construction, the tubarium. The real animals inhabiting the tubaria can only be interpreted and understood from the few extant taxa for which we have the organisms and their housing secretions. The tubaria of the fossil members of the Graptolithina show a definite colonial organisation that can be compared and homologized with that of their extant members, the Rhabdopleuridae (Mitchell et al. 2013; Maletz and Beli 2018).

Maletz (2019a) provided the latest overview on the evolution of the Pterobranchia and stated that the earliest forms

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can be traced to the Fortunian (Terreneuvian, Cambrian Series 1) through the record of *Sokoloviina costata* Kirjanov, 1968 in Ukraine (Sokolov 1997). Further fragmentary material of early Pterobranchia is known from the Cambrian Series 2, Stages 2 and 3 (Slater et al. 2018a, b; Slater and Bohlin 2022), but cannot be identified even to family level. All these specimens are based on minute fragments of their tubaria formed from a distinct fusellar construction. They provide little information for the understanding of graptolite evolution in the early Cambrian and a colonial development in the Fortunian cannot be verified.

The first more complete graptolite tubarium showing its colonial organisation is found in the single specimen of *Dalyia annularoides* Resser and Howell, 1938. Resser and Howell (1938) described this fossil from the lower Cambrian *Olenellus* Zone of Pennsylvania, now identified as *Sphenoecium annularoides* by Maletz (2019a, p. 64, fig. 2E). The specimen is poorly preserved, but shows the typical development of the benthic graptolite *Sphenoecium* with its encrusting basal part and the erect, slowly widening thecae. It is the oldest known taxon of the genus and originated from the middle part of Stage 4, Cambrian Series 2 or the regional Dyeran Stage (see Peng et al. 2020; fig. 19.2). Thus, it appears to be the earliest known certain example of a colonial pterobranch. The specimen fits in its shape nicely with other specimens of *Sphenoecium*, but the presence of fusellar construction cannot be verified and the identification as a benthic graptolite remains problematic. Its' graptolitic nature is supported by younger (Miaolingian, Wuliuan)

specimens of *Sphenoecium* for which a fusellar construction has been demonstrated.

The fossil record of graptolites in the uppermost Cambrian (Furongian) is quite poor and is not considered here. Servais and Harper (2018, fig. 1) introduced the term Furongian Gap for an apparent lack of fossil data in a part of the upper Cambrian. Harper et al. (2019) discussed the interval in more detail and indicated that it is unclear whether this gap is apparent or real, while Deng et al. (2023), based on data from China, indicated that there is no gap. A gap in palaeontological knowledge at least is apparent for the graptolite record; the reason of this lack of information is unclear.

The identification of many Cambrian dendroid graptolites is quite difficult and a definitive verification is only possible if fusellar construction can be demonstrated (Fig. 1b, c). However, the general shape of their tubaria is now well understood and helps the identification. Muscente et al. (2016) discussed the recognition and differentiation of fossil hydrozoans and pterobranchs, noting that many putative hydrozoans can be identified as pterobranchs by the recognition of fuselli and other pterobranch features by using scanning electron microscope backscatter method (SEM-BSE) investigations. Earlier, Sdzuy (1974, fig. 5) identified fusellar construction in his material of *Tarnagraptus* and *Sotograptus* from the Cambrian of Spain, verifying their identification as pterobranchs. Maletz et al. (2005, fig. 6C, D) provided additional confirmation from a specimen of *Tarnagraptus palma* based on chemically isolated tubarium fragments. Johnston et al. (2009, fig. 7), LoDuca and Kramer

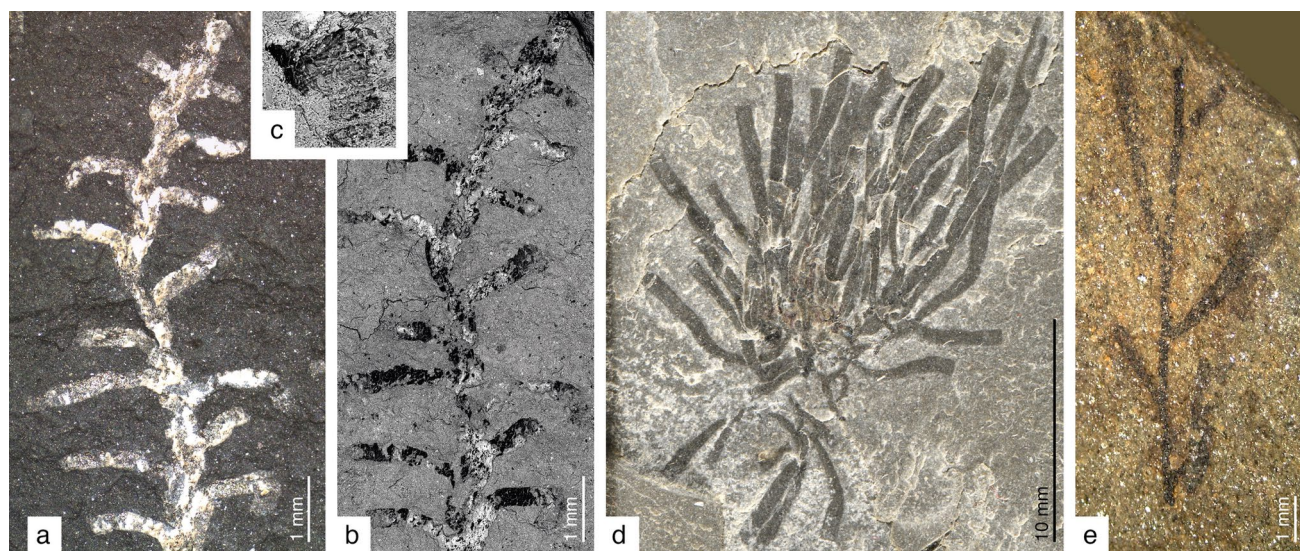


Fig. 1 Cambrian Pterobranchia. **a–c** *Archaeolafoea skeatsi* (Chapman, 1919), NMVP 13114, light photo (**a**), SEM backscatter photo (**b**) of growing end and detail showing fuselli (**c**), organic material in black in (**b**, **c**) (Maletz and Steiner 2015, fig. 4). **d** *Sphenoecium wheelerensis* Maletz and Steiner, 2015, FUBS sample Spe001, complete colony,

Spence Shale, Wellsville Mountains, Utah, specimen preserved as a clay template, no organic matter present (Maletz and Steiner 2015, fig. 17C). **e** *Tarnagraptus robustus* Sdzuy, 1974, SMF 30005, small fragment showing thecal style, part of fusellum preserved. NMVP: Museums Victoria, Melbourne, Australia, Paleontology

(2014, fig. 3) and Ramírez-Guerrero and Cameron (2021, fig. 4) added further information on fusellar construction of Cambrian benthic graptolites, helping to understand the general tubarium construction of these organisms. Thus, a variety of tubarium shapes (Fig. 1) have been recognised in these taxa and a first glimpse on their construction was achieved. Both, encrusting (Fig. 1a-d) and erect growing, bushy colonies (Fig. 1e) are already present, but the differentiation is difficult due to the highly fragmentary preservation of the material. The SEM-BSE method (Fig. 1c) helps to identify the presence of organic material of the tubaria and can detect fusellar construction (Maletz et al. 2005; Maletz and Steiner 2015). The preservation of the specimens is quite variable and even visually well-preserved specimens (cf. Fig. 1d) may represent clay templates and do not even preserve any of the original organic material (see Maletz and Steiner 2015). Maletz (2020a) discussed the general preservation of fossil graptolites and used a number of Cambrian examples.

Miaolingian Pterobranchia

Miaolingian graptolites (Pterobranchia) have rarely been described in detail, but are found widely scattered over the Cambrian world. Due to their preservation largely as small fragments, the colony shape of these taxa is incompletely known (Fig. 1); identification and comparison has been difficult in the past. The flattening of the material in the sediments often precludes an understanding of their three-dimensional construction and leads to further problems. It is, however, clear that benthic graptolites have been common and diverse in the Miaolingian and that we are only starting to understand their importance in the Cambrian marine benthic ecosystem. Descriptions of genera and species from small fragments also led to over-splitting of the material and masked the biological connection of faunas from different regions.

North America

Miaolingian dendroid graptolites in North America are mainly described from British Columbia (Burgess Shale faunas) and from a number of formations in Utah, including the Spence Shale, Wheeler Shale and Marjum Formation (Fig. 2). The preservation of the material is often poor, even though the material originates from lagerstätten for which excellent preservation has been suggested. The Burgess Shale region of British Columbia is extensively metamorphosed and tectonically deformed, even though the Burgess Shale itself was somewhat sheltered from deformation and the mudstones were only weakly deformed (cf. Powell 2003). The Burgess Shale fossils are definitely deformed

as can be shown from surrounding pressure shadows (cf. Powell 2003, fig. 4) and was stated by Mángano et al. (2019, p. 5; ‘late brittle deformation related to tectonic processes is evident in some specimens’), but fossil deformation has not been investigated in any detail (see also remarks in Maletz and Steiner 2015, p. 1083–1084). Butterfield et al. (2007; text-fig. 1B) discussed the fossil diagenesis of the Burgess Shale and illustrated a specimen clearly showing parallel fractures in the organic material that indicate tectonic deformation. The Utah material in addition includes deeply weathered material and original organic films often disappeared. Secondary minerals have outlined the specimens and made them more visible on the shale surfaces (Fig. 1d).

A comparison of these faunas with those from other regions has never been attempted and only a few specimens have been illustrated in the past. Species of the genera *Sphenoecium* and *Tarnagraptus* are widely distributed, but species differentiation is unclear due to the low number of mostly fragmentary specimens available for the identification, making the understanding of intraspecific variation difficult. Except for the record of *Sphenoecium annularoides* (Fig. 2) from the Dyeran, the fossil record of Cambrian benthic graptolites preserved on bedding planes starts only in the mid-Wuliuan Spence Shale (Fig. 2), while chemically isolated pterobranch fragments are known from older records (see later discussion). Several species of the encrusting *Sphenoecium* and *Yuknessia* have been described, of which the colonial organisation is only verified for *Sphenoecium*.

British Columbia, Canada: The Burgess Shale of British Columbia includes the most famous early Cambrian graptolite faunas, based on a small number of fragmentary specimens. Ramírez-Guerrero and Cameron (2021) provided a much needed overview of the known taxa. The authors indicated that the earliest species form bushy, erect growing colonies, but included also two supposedly encrusting taxa (*Chaunograptus*, *Yuknessia*). Especially *Chaunograptus* Hall, 1882 may be of interest, a taxon that includes tubaria with slender, branching tubes showing little differentiation of the thecal tubes. Maletz and Beli (2018) included the genus in the Rhabdopleuridae and re-illustrated the type species *Chaunograptus novellus* Hall, 1882. This species from the Silurian Waldron Shale of Indiana, USA clearly shows an encrusting tubarium with a main, meandering stem from which short tubes grow to both sides. These lateral tubes appear quite irregular in shape and indicate to be erect growing in their distal (apertural) parts at least. Maletz and Steiner (2015) did not consider the Burgess Shale *Chaunograptus scandens* Ruedemann, 1931 to be related to this form. Ramírez-Guerrero and Cameron (2021) revised *Chaunograptus scandens* as showing short, aperturally widening thecae growing to alternate sides from the stem. The fairly straight to somewhat undulating stem with the short thecal tubes

MIAOLINGIAN	North America		Australasia		Czech Republic		Iberia		Siberia		Baltica	
	FURONGIAN		FURONGIAN		FURONGIAN		FURONGIAN		AYUSOKKANIAN		FURONGIAN	
500.5	Guzhan-Gian	Proagnostus bulbosus	Lejopyge laevigata	Protohalecium	?		Langue-ducian		Lejopyge laevigata	A. pisiformis	Lejopyge laevigata	Guzhan-Gian
		Lejopyge laevigata	Goniagnostus nathorsti	Tasmania	Ptychagnostus punctuosus equivalent	Langue-ducian	Solenopleurospis	Anomocarioidea	Goniagnostus nathorsti	Goniagnostus nathorsti		
504.5	Drumian	Ptychagnostus punctuosus	Ptychagnostus punctuosus	Archaeolafoea	Ptychagnostus punctuosus equivalent	Caeser-augustian	Caeser-augustian	A. henrici	A. henrici	Pt. punctuosus	Pt. punctuosus	Drumian
		Pt. atavus	E. optimus	Heathcote	?	Caeser-augustian	Pardalhanina	C. perforatus	C. perforatus	Pt. atavus	Pt. atavus	
509.0	Wulluan	Ptychagnostus gibbus	Pt. gibbus	Sphenoeicum discoidalis	?	Agdzian	Badulesia	Pt. gibbus	Pt. gibbus	Pt. gibbus	Pt. gibbus	Wulluan
		Ptychagnostus praecurrens	Pt. praecurrens	Sphenoeicum discoidalis	Eccaparaoxides pinus	Agdzian	Eccaparaoxides asturianus	Kounamites	Kounamites	Pt. praecurrens	Pt. praecurrens	
509.0	Delamarian	Albertella	P. anabensis		Eccaparaoxides insularis	Agdzian	Eccaparaoxides szczyli		Ovatoryctocara/Schistocaphalus	Eccap. insularis	Eccap. insularis	Wulluan
		Oryctoc. iridicus	Pentagn. krusel		?	Agdzian	Acadoparaoxides mureoensis					
509.0	Stage 4	Amecephalus amojosensis	Redlichia forresti		?	Agdzian						Stage 4
		Ekochaspis nodosa	?			Agdzian						
509.0	Dyerran	Olenellus	Pararaia janeae			Agdzian						Stage 4
						Agdzian						

Fig. 2 Distribution of Miaolingian (Cambrian) benthic graptolites. Chronostratigraphy largely based on Geyer (2019) and Peng et al. (2020). **a** *Sphenoeicum annularoides* (reconstruction from Maletz 2019a, fig. 2E). **b** *Sphenoeicum wheelerensis* (KUMIP 204381). **c** *Chaunograptus scandens* (drawn after Ramirez-Guerrero and Cameron, 2021, fig. 2C). **d** *Sphenoeicum wheelerensis* (from Foster and Gaines 2016, fig. 8F; Yuknessia spissa). **e** *Sphenoeicum discoidalis* (modified from Maletz and Steiner 2015, fig. 13D). **f** *Archaeolafoea longicornis* (after Maletz and Steiner 2015, fig. 3F). **g** *Protohalecium hallitanum* (from Quilty 1971, fig. 3.10). **h** *Sphenoeicum robustus* (from Maletz et al. 2005, fig. 8E). **i** *Sphenoeicum robustus* (from Maletz et al. 2005, fig. 7B). **j** *Ovetograptus* sp. (SSMM 10,357, photo JM). **k** *Tarnagraptus palma* (from Sdzuy 1974, fig. 2). **l** *Sotograptus flexilis* (from Sdzuy 1974, fig. 2). **m** *Ovetograptus gracilis* (from Sdzuy 1974, fig. 2). **n** *Archaeolafoea longicornis* (from Sennikov 2016, pl. 1, fig. 1). **o** *Sphenoeicum mesocambrius* (after Bengtson and Urbanek 1986, fig. 2D). **p** *Sphenoeicum mesocambrius* (after Wolvers and Maletz 2016, fig. 3A). KUMIP: Kansas University Invertebrate Paleontology collection, Lawrence, Kansas, USA

(Fig. 2c) may suggest an erect growth of the colonies, thus a possible relationship to the Dithecodendridae and especially to *Tarnagraptus*. Thus, only the genus *Yuknessia* remains as an encrusting taxon in the Burgess Shale. Maletz and Steiner (2015) discussed the species *Yuknessia simplex* Walcott, 1919 and *Yuknessia stephenensis* LoDuca et al., 2015 in some detail and referred them to the Pterobranchia *incertae sedis*, as a colonial organisation was not verifiable from the type specimens. Therefore they could easily be referred to the non-colonial Cephalodiscida (see Maletz and Gonzalez 2017). Alternately, they may be closely related to or represent specimens identified as the colonial *Sphenoecium*.

Ramírez-Guerrero and Cameron (2021) described for the first time *Protohalecium hallianum* from the Burgess Shale, showing the characteristic spiraled stem (Fig. 2g) from which the thecal tubes grow. The genus appears to be closely related to *Tarnagraptus* (identified as *Mastigograptus* sp. sensu Ruedemann, 1947 by Ramírez-Guerrero and Cameron 2021). A number of relatively large colonies of *Tarnagraptus* have been illustrated in recent years showing a wider biogeographic distribution of the genus (Johnston et al. 2009; LoDuca and Kramer 2014; Ramírez-Guerrero and Cameron 2021). Johnston et al. (2009) described specimens here referred to *Tarnagraptus* with bundled stems ('stolothecal bundles') and 'conical pedunculate' thecae as Graptolithina, gen. et sp. nov., recognising the complex construction of the *Tarnagraptus* tubaria. The species identification may be difficult as can be seen from the small and fragmented specimens described from Spain and referred to several distinct species (Sdzuy 1974).

The problematic erect growing *Dalyia racemata* Walcott, 1919 from the Burgess Shale bears characters possibly relating the species with the Graptolithina, but a verification is not possible. Maletz and Steiner (2015) and Maletz and Beli (2018) only tentatively referred the species to the Graptolithina. A morphological connection to known early Cambrian graptolites is not possible as thecal tubes are not recognisable in the specimens. The material clearly shows a bushy, erect growth, but may belong to another type of organism, probably indicating algal or hydroid relationships.

A slightly younger Burgess Shale-type fauna from the Chancellor Basin of British Columbia bears a common species of *Tarnagraptus* (Johnston et al. 2009, fig. 7: Graptolithina gen. et sp. nov.), but no further graptolites.

Utah, USA: The Spence Shale of NE Utah and SE Idaho, one of the central North American lagerstätten, is famous for its 'soft-body' preservation, but also for the abundance of trilobites and hyoliths (e.g. Kimmig et al. 2019). Graptolites have recently been described from this unit, that bear specimens identified as *Yuknessia stephenensis* LoDuca et al., 2015 and *Sphenoecium wheelerensis* Maletz and Steiner, 2015 (Fig. 2b) (see Kimmig et al. 2019, fig. 5F),

but specimens of *Tarnagraptus* have not been mentioned. LoDuca et al. (2015, fig. 5.8) also illustrated *Yuknessia stephenensis* from the Pierson Cove Formation of Drum Mountains in Utah (Drumian Stage).

Encrusting *Sphenoecium* and erect *Tarnagraptus* appear to be not uncommon in the Wheeler Shale (Maletz et al. 2005; LoDuca and Kramer 2014; Maletz and Steiner 2015). Foster and Gaines (2016, fig. 8F) illustrated a specimen of *Sphenoecium wheelerensis* (Fig. 2d) as 'pterobranch hemichordate *Yuknessia spissa*', accidentally mixing the species with the unrelated Cambrian alga *Marpolia spissa* Walcott, 1919 (see Steiner and Fatka 1996). LoDuca and Kramer (2014, fig. 2, 3) described and illustrated erect growing specimens of *Tarnagraptus* as *Archaeolafoea monegettae* (Chapman, 1919). The specimens show fairly long thecae (6–9 mm) and are quite similar to *Tarnagraptus robustus* Sdzuy, 1974 from the Cambrian of Spain. The specimens clearly show the fusellar construction of the tubarium.

Early benthic graptolites are not uncommon in the Marjum Formation, but have only recently been collected and described in more detail. Maletz and Steiner (2015, fig. 7) illustrated a complete specimen of the encrusting *Sphenoecium wheelerensis* showing the poor preservation of the organic material in specimens from the Marjum Formation. LoDuca and Kramer (2014, fig. 2) described a specimen of *Tarnagraptus* sp. as *Mastigograptus* sp. from the Marjum Formation and indicated the presence of apparently paired thecae. The authors also indicated multiple tubes in the stem of this specimen.

The graptolites from the Spence Shale, Wheeler Shale and Marjum Formation are quite similar and may represent largely the same species. As the graptolites from these units have rarely been collected, their taxonomy has been neglected. Also the specimens have often been misidentified as poorly preserved and useless algae in the past and thus have been ignored in the field. Only in recent years, after being identified as pterobranchs (cf. Maletz et al. 2005; Maletz and Steiner 2015), material has been collected more frequently.

Australasia

The Cambrian benthic graptolites from Victoria, Australia (Fig. 3) (Chapman 1917, 1919; Chapman and Skeats 1919; Chapman and Thomas 1936) were originally identified as hydroids, but Maletz and Steiner (2015) revised several taxa and recognised fusellar construction verifying their identity as graptolites. The material largely consists of small fragments and their tubarium shape is hard to estimate. Thomas and Singleton (1956, p. 161) considered the Heathcote Fauna to be approximately of *Ptychagnostus gibbus* Biozone age (Fig. 2), but were unable to provide an age estimate for the Monegetta Fauna. The composition of both faunas is

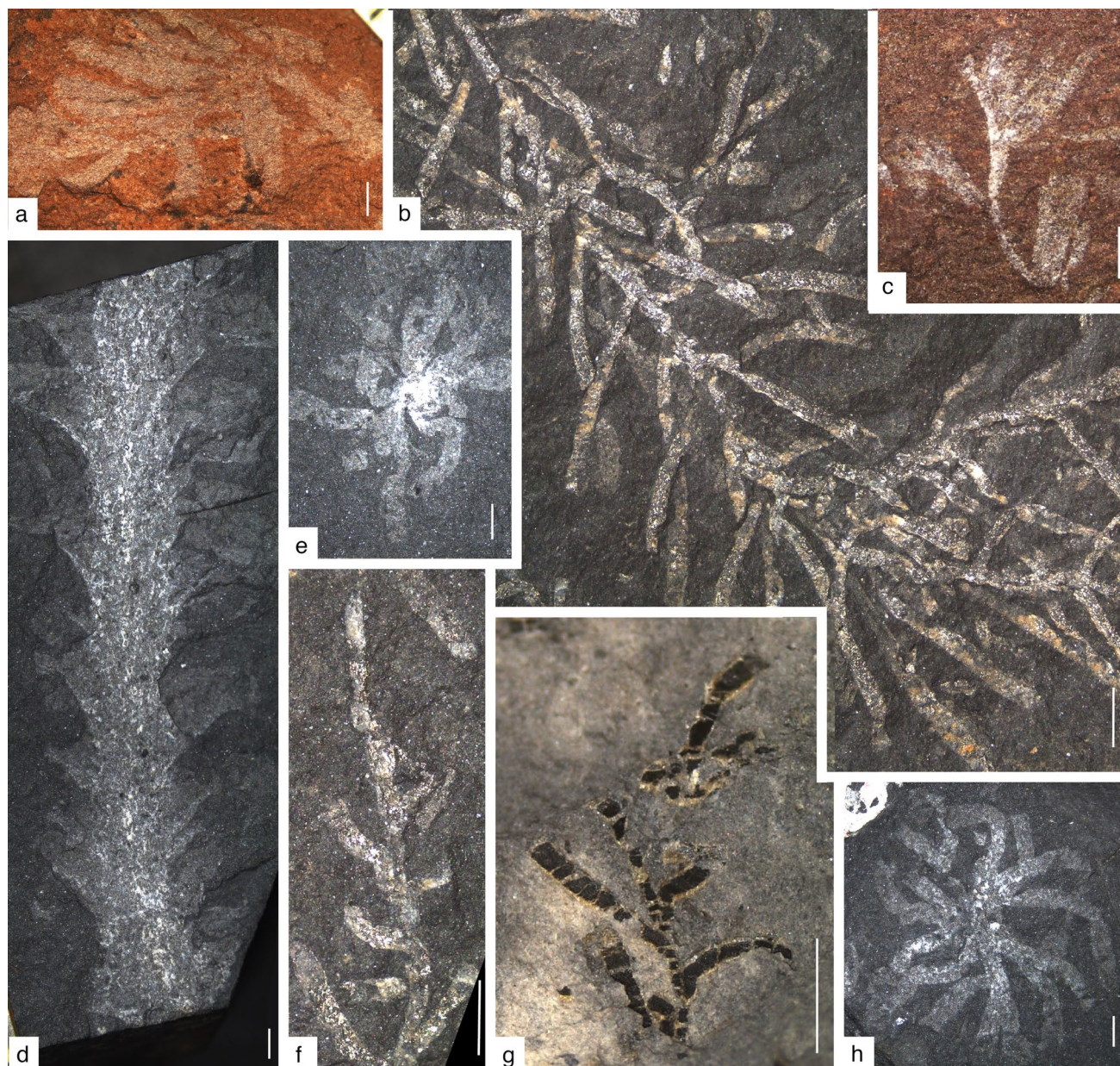


Fig. 3 Miaolingian graptolites of Australasia. **a** NMVP 14305, *Sphenoecium filicoides* Chapman, 1919, holotype. **b, f** NMVP 13112, *Archaeolafoea longicornis* Chapman, 1919, holotype (pars) (**b**) and growing end (**f**). **c** NMVP 47748, *Protohalecium hallianum* Chapman and Thomas, 1936, holotype. **d** NMVP 47751, *Cactograptus flexispinosus* Chapman and Thomas, 1936, paratype. **e** NMVP 134657,

Sphenoecium discoidalis Chapman and Thomas, 1936, paratype, on slab with NMVP 47751 (*Cactograptus flexispinosus*). **g** NMVP 47738, *Archaeolafoea longicornis* (see Chapman and Thomas 1936, pl. 14, fig. 5). **h** NMVP 47734, *Sphenoecium discoidalis* Chapman, 1919, counterpart of holotype. Scale bars are 1 mm

largely identical, however (cf. Thomas and Singleton 1956; tabel on p. 153-154). The most common forms are small specimens of *Sphenoecium*, of which probably more than one species is present (Figs. 3a, e, h) and specimens identified as *Archaeolafoea* and *Mastigograptus*, among a few other, less well-known species.

Maletz and Steiner (2015) revised *Archaeolafoea longicornis* Chapman, 1919 and recognised the species as

a possible rhabdopleurid, with a creeping colony form (Fig. 3b, f). The interpretation is largely based on the irregular growth of the stems in this taxon, differing considerably from the straight stems of the otherwise similar *Sotograptus*, indicating an erect growth of the colonies. The tubarium shows the monopodial development characteristic of *Rhabdopleura* (cf. Bulman 1955, p. 23) (Fig. 3f), but not described from the taxon so far.

The Heathcote and Monegeeta faunas are quite diverse and include about 20 described species, most of which are in need of revision. The material is strongly fragmented and also tectonized. Thus, many details of their tubarium and thecal construction are not available. Encrusting taxa (Fig. 2f, 3b, g: *Archaeolafoea longicornis*) and erect growing ones (*Sotograptus monegettae*; *Cactograptus* species: Fig. 3d) can be recognised, indicating the evolution of ecologically diverse faunal elements in the Cambrian. These faunas represent the most diverse benthic graptolites of Wuliuan age and are difficult to compare with benthic graptolite faunas from other regions.

Mastigograptus monegettae Chapman, 1919 with its straight stem and the long and nearly parallel-sided thecae is similar in its tubarium style to *Sotograptus flexilis* Sdzuy, 1974 from Spain, but has much longer thecae. The species is here referred to the genus *Sotograptus* as is *Archaeolafoea fruticosa* Chapman and Thomas, 1936. Both taxa show the straight, inflexible stem with long and slender thecae typical of the erect growing dithecodendrid *Sotograptus* and differ considerably from the encrusting runner-type colonies of *Archaeolafoea longicornis* (Fig. 3b, f). These runner-type colonies may often be difficult to separate from fragments of the erect growing *Sotograptus*.

Protohalecium hallianum Chapman and Thomas, 1936 with its coiled stem and the apparently bundled thecae was originally described and illustrated by a single poorly preserved specimen (Fig. 3c). Larger specimens have subsequently been reported from Tasmania (Quilty 1971) (Fig. 2g) and from the Burgess Shale of British Columbia (Ramírez-Guerrero and Cameron, 2021), supporting it as a genuine, widely distributed taxon, probably closely related to *Tarnagraptus*. *Tarnagraptus* and *Protohalecium* share the conical, aperturally widening thecae on an erect growing stem. As *Protohalecium* is known from single stipes only, a comparison with the complex stems of mature *Tarnagraptus* cannot be made.

Comparable benthic graptolite faunas are known from Tasmania (e.g. Thomas and Henderson 1945; Quilty 1971; Rickards et al. 1990), but appear to be slightly younger. Quilty (1971) described faunas from several localities indicating a Drumian age and ranging from the *Ptychagnostus atavus* Biozone to the *Goniagnostus nathorsti* Biozone. Thomas and Henderson (1945) provided the first illustration of some of this material. The fauna shows already a number of quite different taxa, ranging from encrusting *Sphenoecium discoidalis* (Fig. 2e) and *Sphenoecium filicoides* (Fig. 3a) to erect forms identified as *Cactograptus flexispinosus* (Fig. 3d) and *Protohalecium hallianum*. Also specimens probably referable to *Sotograptus* (identified as *Archaeolafoea monegettae*) are present. The faunas range through the Drumian (Miaolingian) (Fig. 2), but the precise age of most faunas cannot be determined.

The faunas of Rickards et al. (1990) are younger, originating from the Idamean (lower Furongian, Paibian: Peng et al. 2020, fig. 19.11). They are not discussed here in detail, but may be important as they still bear a number of earlier taxa like the *Tarnagraptus*-type specimens (identified as *Mastigograptus serialis*, *Archaeolafoea monegettae*), but is largely composed of bushy, dendroid taxa of unknown relationship as there is no information on their thecal construction. These taxa appear to show originally a conical shape, but are flattened and strongly tectonized. Thus, their original shape is difficult to estimate due to the overlapping stipes. Anastomosis may be common in the material. Rickards et al. (1990) described a number of genus level and species level taxa referred to the Dendrograptidae and Acanthograptidae. The specimens of *Thallograptus* sp. (Rickards et al. 1990, fig. 11C-D) show compound stipes of a possible callograptid. The fauna may show that a distinct change in faunal composition happened between the late Miaolingian and the Furongian, where supposedly the Dendrograptidae and Callograptidae originated (cf. Maletz et al. 2022).

Gondwana and peri-Gondwanan terranes

Cambrian graptolites have occasionally been reported from several regions generally regarded as Gondwana/peri-Gondwana. The material is usually poorly preserved and consists of few fragments and only occasionally of larger specimens.

A few specimens from the Czech Republic have been described as *Rhabdotubus robustus* Maletz et al., 2005, but are now identified as *Sphenoecium robustus* (see Maletz and Steiner 2015). They show a creeping, sometimes branching axis and erect growing thecal tubes (Fig. 2h, i). The holotype specimen from Koníček shows fusellar construction and also possible traces of a stolon system. It was found in the *Ellipsocephalus hoffi* – *Rejkocephalus* Assemblage zone of the middle Cambrian Jince Formation (cf. Fatka and Szabad 2014), roughly correlating with the *Ptychagnostus punctuosus* Biozone of other regions. The material from the Luh locality of the Skryje-Tysovice basin is less precisely dated to the lower part of the Wuliuan based on the trilobite association (Fig. 2). Erect growing bushy forms have not been detected in the Czech Republic. The few specimens at hand do not provide any information on the diversity of the benthic graptolites in this peri-Gondwanan terrane.

Geyer et al. (2022) regarded a single specimen of *Ovetograptus?* sp. from the Frankonian Forest (Germany) as the oldest benthic graptolite from West Gondwana and one of the oldest known graptolites (Fig. 2j, 4f), but it is clearly younger than *Sphenoecium annularoides* from the Dyeran of North America (Fig. 2a). The specimen is similar to the material of *Ovetograptus gracilis* Szuy, 1974 from Spain (Fig. 2m, 4a, b) with the nearly parallel-sided thecae, but these are

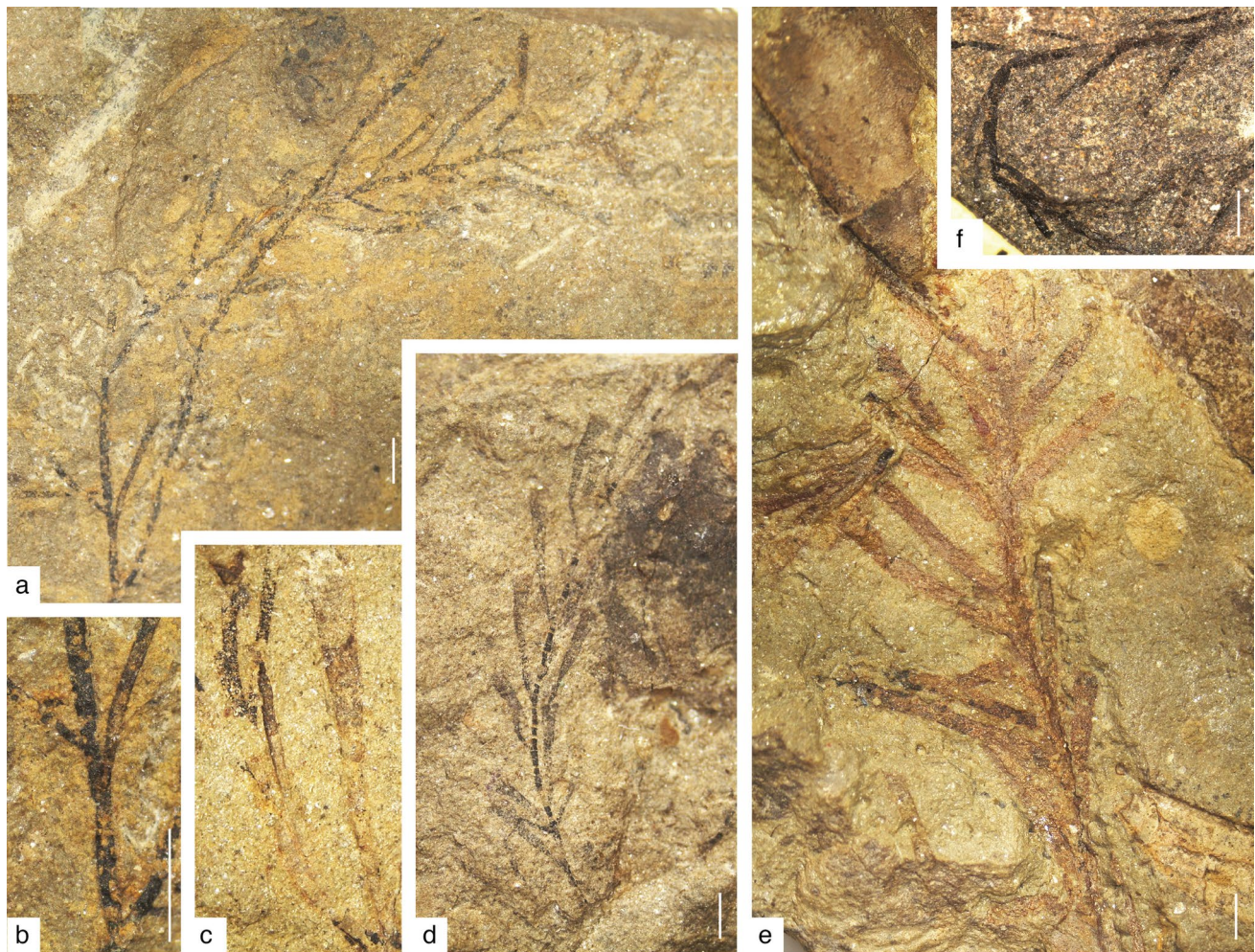


Fig. 4 Dithecodendridae from the Cantabrian Mountains, Spain. **a, b** *Ovetograptus gracilis* Sdzuy, 1974, SMF 30026, holotype (**a**) and detail (**b**) showing poor preservation of organic material. **c** *Tarnagraptus robustus* Sdzuy, 1974, SMF 30003, stem (left) and theca

(right) showing little remains of organic material. **d** *Tarnagraptus palma* Sduzy, 1974, SMF 30000, holotype. **e** *Sotograptus flexilis* Sdzuy, 1974, SMF 30026, holotype. **f** *Ovetograptus* sp., SSMM 10,357, Frankonian Forest. Scale bars indicate 1 mm

shorter than those in *Ovetograptus gracilis*. It clearly represents an erect growing taxon with a relatively thick stem and narrow, parallel-sided thecae. There are no details about the precise construction available. The specimen originated from the *Ornamentaspis frequens* trilobite zone of early Wuliuan age (see Geyer 2019; Geyer et al. 2019).

Material described by Sdzuy (1974) from the Cantabrian region of Spain originated from a considerable biostratigraphic interval, ranging from the upper Wuliuan to the upper Drumian (Fig. 2). The original illustrations of the material in Sdzuy (1974) appear to be retouched as can be seen from new photos of the material (Fig. 4). This is especially obvious in *Ovetograptus gracilis* (Fig. 4a). The Sdzuy (1974, pl. 23, fig. 4) photo shows black stipes, while the specimen shows only partly the remains of the organic material and some parts of the colony are barely recognisable on the sediment surface.

Sdzuy (1974) described eleven taxa, some in open nomenclature, indicating a diverse fauna of erect growing bushy forms (Fig. 4). All specimens are small fragments suggesting a considerable transport before they were embedded in the sediment, where they are often associated with shelly faunas. There are no encrusting species described from the region. The genus *Tarnagraptus* (Fig. 2k, 4c, d) with a number of species is the most common and diverse form in the Cantabrian Mountains. Its slowly widening thecae are characteristically found also in other regions discussed herein and can easily be misidentified for the Ordovician *Mastigograptus* with its typical triad budding (see Bates and Urbanek 2002). A biostratigraphic differentiation is not possible for the material due to the poor and fragmentary record. The robust *Sotograptus flexilis* Sdzuy, 1974 (Fig. 2l, 4e) can easily be compared to the Australia *Sotograptus fruticosus*

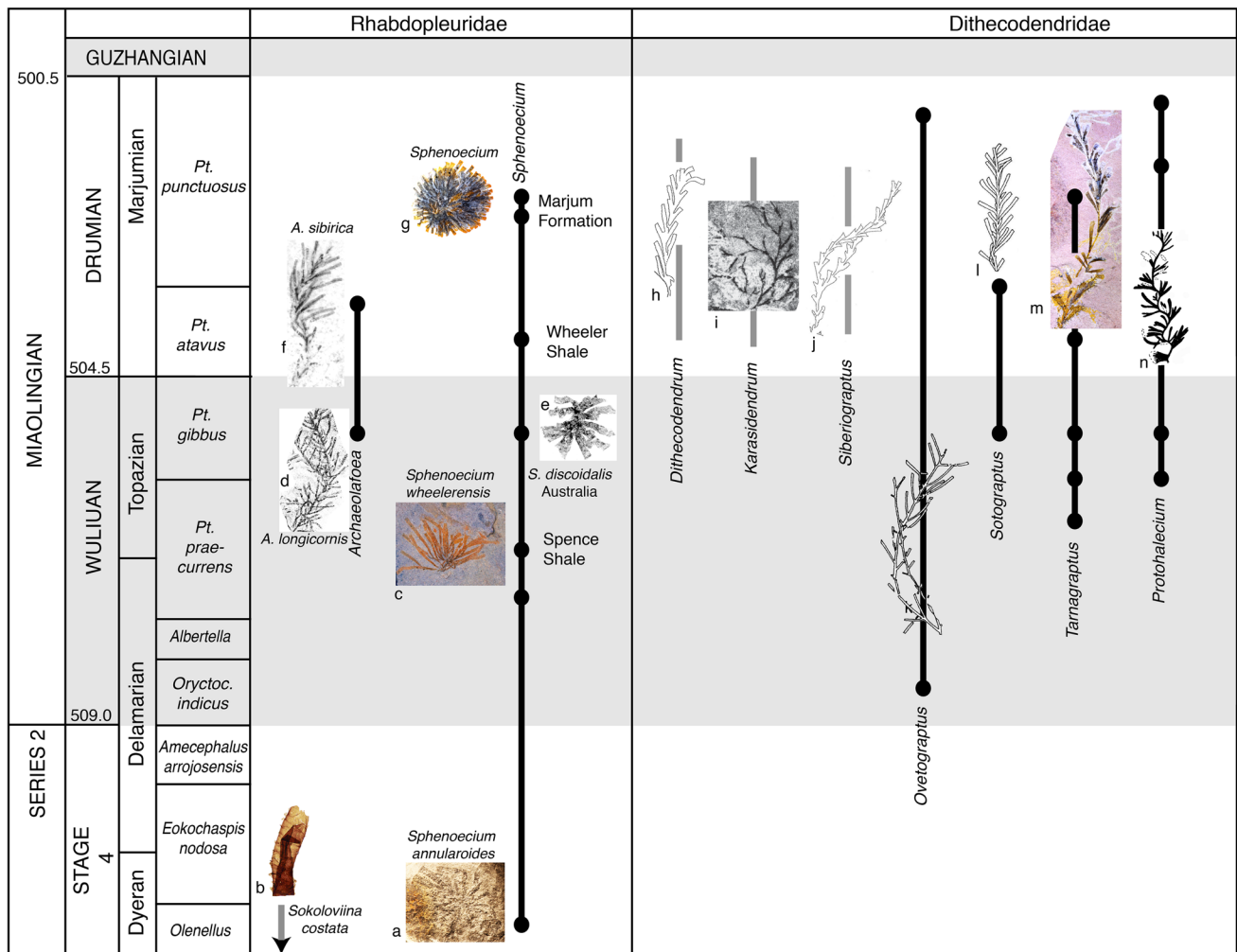


Fig. 5 Miaolingian (Cambrian) graptolite biostratigraphy showing all genera. **a** *Sokoloviina costata* (from Slater et al. 2018a, fig. 5H). **b** *Sphenocium annularoides* (from Maletz 2019a, fig. 2E). **c** *Sphenocium wheelerensis* (KUMIP 514266, from Kimmig, Twitter, 2020-04-17). **d** *Archaeolafoea longicornis* (after Maletz and Steiner 2015, fig. 3F). **e** *Sphenocium discoidalis* (modified from Maletz and Steiner 2015, fig. 13D). **f** *Archaeolafoea longicornis* (originally *Rhabdopleura sibirica*; Sennikov 2016, pl. 1, fig. 1). **g** *Sphenocium*

sp. (MCZ.IP.199806, Marjum Formation, coll. R. Lerosey-Aubril). **h** *Dithecodendrium sibiricum* (from Maletz 2019b, fig. 10.2). **i** *Karasidendrum aspidograptoides* (from Maletz 2019b, fig. 10.6). **j** *Siberiograptus kotujensis* (from Maletz 2019b, fig. 10.3). **k** *Ovetograptus gracilis* (from Maletz 2019b, fig. 10.7). **l** *Sotograptus flexilis* (from Maletz 2019b, fig. 10.8). **m** *Tarnagraptus palma* (MCZ. IP.199870, Marjum Formation). **n** *Protohalecium hallianum* (from Quilty 1971, fig. 3.10)

(Chapman and Thomas, 1936) and *Sotograptus monegettae* (Chapman, 1919), based on the tubarium construction, but differs in the length of the thecae.

Siberia

A number of dithecodendrids and rhabdopleurids have been described from the Siberian Platform (Obut 1964, 1974; Durman and Sennikov 1993; Sennikov 1998, 2016). *Archaeodendrum bulmani* Obut, 1974 was found in the middle part of the *Anomocarioides* Biozone, thus, the upper Drumian international stage or the lower Mayan regional stage. This taxon was regarded as a hydroid by Rickards and

Durman (2006, p. 58) and Maletz and Steiner (2021, p. 7). It is here identified as a synonym of *Protohalecium*.

Durman and Sennikov (1993) described *Rhabdopleura obuti* from the Mayan Stage (Drumian) of Siberia and noted a stolon system and the possible preservation of zooids. The robust tubarium shows dimensions that suggest it may represent a member of the genus *Sphenocium* with a runner-type tubarium or a member of the genus *Archaeolafoea*, but does not belong to the delicate genus *Rhabdopleura*. Sennikov (2016) described *Rhabdopleura sibirica* (Fig. 2n) as a new rhabdopleurid with densely spaced thecal tubes from the lower Mayan Stage (upper Drumian) of Siberia. The species may be identical to *Archaeolafoea longicornis* Chapman,

1919, but only a single small fragment is available for the interpretation of this taxon. It may alternately represent a fragment of the erect *Tarnagraptus robustus* Sdzuy, 1974 as it is not entirely clear whether the small, fragmentary specimen is encrusting or erect growing.

All further benthic graptolites from Siberia were reported from the Drumian or Mayan stages. There are no precise ages available, but all forms can be considered to be of late Miaolingian age (Fig. 5). The material is somewhat younger than the material from Western Gondwana and Baltica (Fig. 2). Even though based on few specimens, the material indicates a quite high diversity of tubarium shapes of the Dithecodendridae in the late Drumian of Siberia. Due to the poor preservation and the few available fragments, details of their tubarium construction are not available.

South China

As the early record of pterobranchs dates back to the Fortunian (Maletz 2019a), it may be expected that the Chengjiang lagerstätte from the Cambrian Series 2, Stage 3 (see Peng et al. 2020) of China bear members of the Pterobranchia. Definite pterobranchs have, however, not been discovered in these deposits. The record of *Yuknessia* from China (LoDuca et al. 2016, p. 899) appears to be based on poorly preserved fossil material and the specimens were referred to the Cambrian alga *Fuxianospira* or may even represent fecal trails.

Malongitubus kuangshanensis Hu, 2005 from the Yuanshan Formation (Cambrian Stage 3) of South China has been considered an alga or a potential pterobranch (Wang et al. 2012; Hu et al. 2018), but verification is wanted. The available specimens show a possibly branching stem, but there is no evidence of any thecal tubes and internal remains are interpreted as a possible stolon system. Maletz and Steiner (2015, p. 1096) considered *Malongitubus* as a possible synonym of *Dalyia* Walcott, 1919. Hu et al. (2018) were unable to unanimously demonstrate fusellar construction in their material, but considered the taxon to be the best indication that hemichordates were present in the Cambrian Stage 3.

Babcock et al. (2011, fig. 1A, B) illustrated a single fragment of *Archaeocryptolaria furongguoia* as a possible cnidarian from the *Ptychagnostus atavus* Biozone (lower Drumian) of the Huaqiao Formation of Hunan Province. The poor, small fragment shows at least 12 conical thecae connected to a slender stem, indicating its identity as *Tarnagraptus*. It is the only record of the genus *Tarnagraptus* from China so far. The description of a new species based on the small fragment may be questionable, but a revision is not possible here.

Maletz et al. (2022) described a number of benthic graptolites from the Guole biota of mid-Furongian age (Guangxi Province, South China), including specimens referred to *Rhabdopleura* sp. These would be the oldest known specimens of *Rhabdopleura*. They were found encrusting on

fossil shells of possible *Sphenothallus* specimens. Specimens referred to *Siberiograptus kotujensis* Obut, 1964 are also present and extend the biostratigraphic and palaeogeographic range of the species. There is no evidence of *Tarnagraptus* and *Sphenoecium* from the Guole fauna.

Biostratigraphic ranges

The compilation of the biostratigraphic ranges of the Miaolingian benthic graptolites (Fig. 5) indicates that we know very little about these faunas. During this about 9 MA long interval (500.5–509.0 MA) the presence of a number of genera has been documented, but a useful picture does not yet appear. It is obvious, that encrusting and erect growing taxa are present in the interval, but there is no evidence of the emergence of any of the derived dendroids (cf. Dendrograptidae, Callograptidae: Maletz et al. 2022). The compilation provides a first insight into the diversity of these early graptolites in the Miaolingian. The diversity seen here is based on the identification at genus level, as most species are known from a single record and the total diversity may be overestimated if counting these separately.

The oldest recognisable form is the encrusting rhabdopleurid *Sphenoecium annularoides* (Fig. 5a) from the Dyeran Stage of North America. It is a robust form with a dense spacing of the origin of the thecal tubes, as can be expected from this early form. Details of the construction and fusellar development are not visible. The next younger form is the erect growing *Ovetograptus* sp. (Fig. 4f) from the Frankonian Forest of Germany, found in the lower Wuliuan. Thus, at least from the Wuliuan onwards, a differentiation of encrusting and erect growing taxa was established, even though the fossil record is quite inconclusive otherwise.

In the upper Wuliuan, the record gets a bit better when a number of new erect growing taxa appear. These are largely found as transported small fragments and, thus, difficult to identify to species level. However, Sdzuy (1974) differentiated four genera of the Dithecodendridae based on the development of the thecae from his material found in the Cantabrian Mountains of Spain. As the tubarium shape is unknown from these taxa, the thecal style is the main character to differentiate species and genera. At least six genera of benthic graptolites can be differentiated in the upper Wuliuan (Fig. 5). All of these genera are also present in the Drumian, where further taxa have been described, including the genus *Karasidendrum* (Fig. 5i) showing dicalycal branching of the stipes. Unfortunately, thecal details are not available for the genus.

Interestingly, the encrusting taxa of the Rhabdopleuridae are less well known from the fossil record than the erect growing Dithecodendridae. Only the robust *Sphenoecium* (Fig. 5c, e, g) can be seen as a widely distributed taxon of the Rhabdopleuridae, but even these are found in few regions

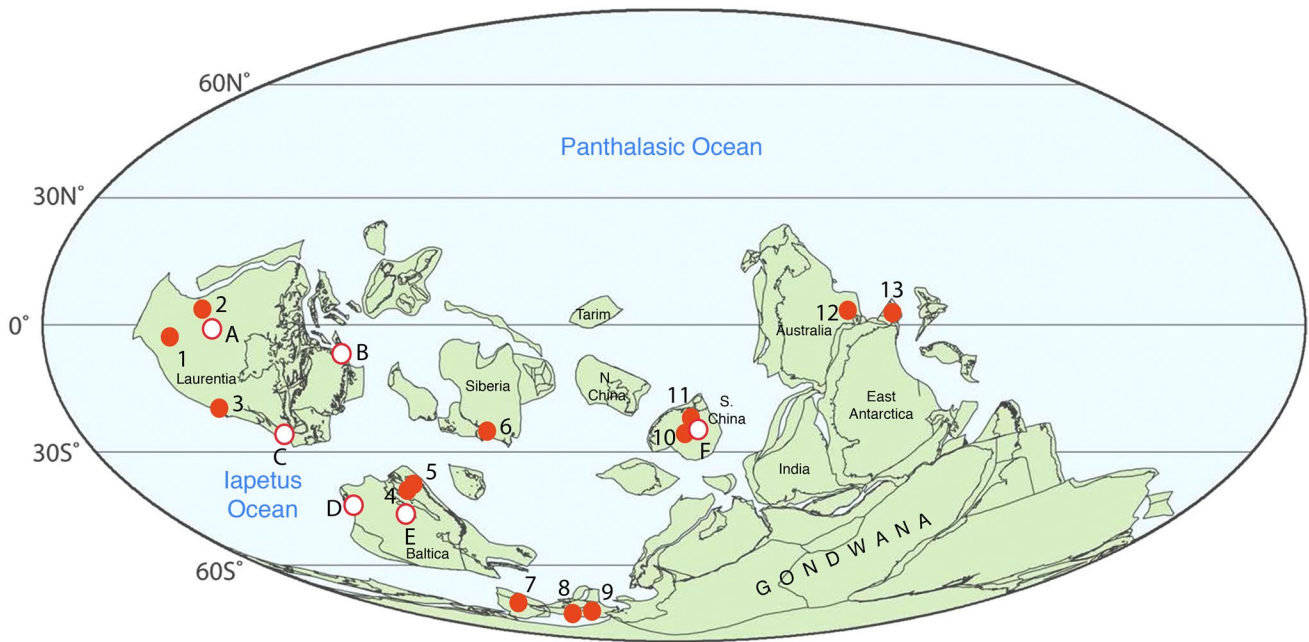


Fig. 6 Palaeogeographic distribution. Red dots, shale material: 1 Utah, USA. 2 British Columbia, Burgess Shale. 3 Pennsylvania. 4 Örebro, Närke, Sweden. 5 Krekling, Norway. 6 Siberian Platform. 7 Iberia. 8 Perunica (Czech Republic). 9 Germany, Frankonian Forest. 10 South China, Hunnan Province. 11 South China, Guangxi Prov-

ince, Guole Biota. 12 Australia, Victoria. 13 Tasmania. White dots, chemically isolated material: A Saskatchewan, Canada. B North Greenland, Peary Land (Pearya terrane). C western Newfoundland, Forteau Formation. D western Ukraine. E Estonia. F South China, Kaili Formation

and are most common in the Cambrian of North America, where they have been reported in recent years from special lagerstätten bearing ‘soft-body preservation’ of fossils, a reason for a detailed search for unusual fossils.

Palaeogeographical distribution

A biogeographic differentiation of planktic graptolite faunas has been recognised (e.g. Goldman et al. 2013; Maletz 2020c), but little is known about the biogeographic differentiation of benthic graptolite faunas. Thus, it appears to be useful to provide an overview on the known distribution of benthic graptolites in the Cambrian (Fig. 6). Quite a number of somewhat differing palaeogeographic maps have been published over the years. The most commonly used ones are the maps produced by Torsvik and co-workers in various publications. Here the map for the Late Cambrian (Furongian) at 500 Ma from Torsvik and Cocks (2013, fig. 2.9) is used to plot the biogeographic distribution of Miaolingian graptolites. According to Peng et al. (2020; fig. 19.1), the 500 Ma level would be in the lower Guzhangian (upper Miaolingian) now.

Our understanding of the biogeographic distribution of the Miaolingian graptolites (Fig. 6) is still quite spotty and restricted to areas with thorough palaeontological investigation, during which generally only few fragmentary specimens have been detected. Thus, a number of

localities yielding benthic graptolites of Miaolingian age have been reported from Laurentia and Baltica, as well as from some ‘European’ terranes of the peri-Gondwana terrane assemblage.

Some of the oldest records are based on few chemically isolated specimens (Fig. 6A-E), but these include only small fragments of uncertain relationship. They can invariably be identified as pterobranch remains through the presence of fusellar construction, but it is impossible to assign them to a family or genus level taxon. Their record from three main plates, the Laurentia (Harvey et al. 2012a; Slater et al. 2018b), Baltica (Sokolov 2007; Slater et al. 2018a; Slater and Bohlin 2022) and South China (Harvey et al. 2012b) plates, indicates a worldwide distribution of the benthic graptolites already in the late Fortunian (Terreneuvian, lower Cambrian). It does not provide indications for a certain area of origin of the pterobranchs.

A better fossil record appears with the discovery of larger and more complete colonies from shale successions (Fig. 6; loc. 1-14). The genus *Sphenoecium* is already found worldwide in the Miaolingian. Specimens are found in the tropical to subtropical regions of Laurentia (Resser and Howell 1938; Maletz and Steiner 2015) and Australasia (Chapman 1917, 1919; Chapman and Thomas 1936; Thomas and Henderson 1945; Quilty 1971), but also in intermediate latitudes of Baltica (Bengtson and Urbanek 1986; Wolvers and Maletz 2016) and on the peri-Gondwana terranes (Sdzuy 1974; Maletz and

Steiner 2015; Geyer et al. 2022). The distribution of some other taxa could be considered endemic (cf. *Dithecodendrum*, *Karasidendrum*, *Siberiograptus* from Siberia), but as these taxa are only found once, they may not provide firm evidence for a local distribution. A wider distribution may be expected for these genera and species. The rarity of descriptions and illustrations of Miaolingian benthic graptolites may be the main reason for the lack of biogeographical information and differentiation.

Taxonomic notes

A taxonomic revision of all faunas is not possible here, but notes on important identifications are provided for all recognised genera.

Rhabdopleuridae

Sokoloviina Kirjanov, 1968: The genus is known from the Fortunian of Ukraine. It has recently been reported from the Lontova Formation of Baltica (Slater et al. 2018a) (Fig. 5b). It is not further considered here, as it is based on small fragments of pterobranch origin showing fusellar construction. The tubarium shape and development is unknown (Maletz 2019a, p. 63).

Archaeolafaea Chapman, 1919: According to Maletz and Beli (2018, p. 7), the genus includes only creeping, encrusting taxa (Fig. 5d), similar to those of *Rhabdopleura*. The genus is only known from fossil material. The distinct collars of the erect tubes of *Rhabdopleura* have not been recognised in *Archaeolafaea*. All described material from Australasia originated from the Wuliuan (Miaolingian, Cambrian). While fusellar construction has been reported for the genus (Maletz and Steiner 2015), further details are not available. The characteristic monopodial growth with a permanent terminal zooid on the stem (cf. Bulman 1955, p. 23) can be seen in the genus (Fig. 1a, b, 3f). The record of *Archaeolafaea sibirica* (Sennikov, 2016) from Siberia (Fig. 5f) extends its range from the upper Wuliuan into the Drumian.

Chaunograptus Hall, 1882: The type species *Chaunograptus novellus* Hall, 1882 (see Maletz and Steiner 2015, fig. 5B) is clearly an encrusting species from the Silurian Waldron Shale of North America. *Chaunograptus scandens* Ruedemann, 1931 from the Burgess Shale of British Columbia is based on a few specimens with a slender stem (ca. 0.1 mm) wide and short, conical thecae (up to 0.7 mm long) (Ramírez-Guerrero and Cameron 2021, fig. 2). The tubarium appears to be erect growing and is similar to that of *Tarnagraptus*, but the thecae are much shorter (Fig. 2c). Thus, the species is here preliminarily referred to the genus *Tarnagraptus*. It differs from other species of the genus by its short, but distinctly widening conical thecae. *Chaunograptus* has not been discovered in the Cambrian.

Sphenoecium Chapman and Thomas, 1936: The genus *Sphenoecium* is the genus most widely known from the Miaolingian (Fig. 5) and includes the oldest pterobranch taxon known from a more or less complete tubarium. A number of species have been included in the genus. *Sphenoecium annularoides* (Resser and Howell, 1938) is the oldest species of this genus (Fig. 5a), known from a single poorly preserved specimen found in the *Olenellus* Biozone of the Kinzers Formation of Pennsylvania (see Maletz 2019a, fig. 2E). Harvey et al. (2012a, fig. 2G) illustrated a single chemically isolated theca from middle Cambrian of Saskatchewan that may belong to this genus. It shows clearly the fusellar construction of the specimen, apparently forming irregular fusellar full rings. At least a zigzag suture is not recognisable in the specimen. Specimens of *Sphenoecium* are known from Baltica (Öpik 1933; Wolvers and Maletz 2016), the Czech Republic (Maletz et al. 2005), North America (Maletz et al. 2005; Maletz and Steiner 2015) and Australasia (Chapman and Thomas 1936). Species differences appear to be based on the rate of widening of the thecal tubes and the length of the thecae. Further differences may be seen in the development of the rhizome, either forming compact tubaria (Fig. 5g) or runner-type (Fig. 5c) colonies. Unfortunately, too few specimens are known from most localities to estimate the intraspecific and ecological variation of the described species. Maletz and Beli (2018) indicated a range into the Ordovician, which, however, may be based on a misinformation, as specimens have only been described from the Miaolingian (Cambrian). It may be of interest to note that the colony of *Chaunograptus confertus* Bouček, 1957 from the Pridoli (Silurian) of the Czech Republic reminds of *Sphenoecium*, but may be more delicate (see Bouček 1957; p. 150, fig. 7).

Dithecodendridae

Bulmanidendrum Obut, 1974: The genus is known from a single specimen found in the Drumian of Siberia. Maletz (2019a) included it in the Dithecodendridae, but Rickards and Durman (2006, p. 65) suggested that it is not a graptolite as fusellar construction was not recognisable. The taxon is here excluded from the Dithecodendridae and not further considered.

Dithecodendrum Obut, 1964: Obut (1964, 1974) described three species of *Dithecodendrum* from the Drumian of Russia (Fig. 5h). Rickards and Durman (2006) discussed and re-illustrated the material. They indicated that a differentiation of the species is difficult. The species are clearly erect in growth with the thecae apparently partly attached to the stem, but details are not available. The thecae are parallel-sided and as wide as the stems. Branching of the stems has not been described from the fragmented material. Thecae

are formed on alternate sides on the stem. The genus may be closely related to *Sotograptus* or even represent a senior synonym.

***Karasidendrum* Sennikov, 1998:** The genus is known from a single specimen found in the Drumian of Siberia (Fig. 5i). It shows the distinct dichotomous branching of a multiramous colony. Details of the thecal construction and even the presence of fusellar development are not available. There is no evidence of the typical monopodial growth of the Rhabdopleuridae and Dithecodendridae in *Karasidendrum*. Thus, the phylogenetic relationship of the genus is uncertain.

***Protodendrum* Sennikov, 1998:** The genus is known from a few specimens found in the Drumian of Siberia. The material does not show much detail and may represent poorly preserved members of *Tarnagraptus*. Thus, the genus is not shown in Fig. 5.

***Protohalecium* Chapman and Thomas, 1936:** The genus *Protohalecium* was first described from the middle Cambrian of Tasmania, based on a single poor and small specimen (Fig. 3c). Quilty (1971) added a more complete specimen (Fig. 5n) with a single long, spiraled stem or axis and slender, slowly widening thecae (see also Rickards and Durman 2006) and referred *Archaeocryptolaria recta flexilis* Chapman and Thomas, 1936 to *Protohalecium*. Ramírez Guerrero and Cameron (2021) reported a single longer fragment of *Protohalecium hallianum* from the Burgess Shale of British Columbia and demonstrated the presence of fusellar construction of the species, identified earlier as a possible alga by Maletz and Steiner (2021). The genus *Archaeodendrum* (Obut, 1974) is here regarded as a synonym of *Protohalecium*. The type species *Archaeodendrum bulmani* Obut, 1974 is from the middle part of the *Anomocaroides* Zone, directly below the *Lejopyge laevigata*-*Majaspis mirabilis* Zone (uppermost Drumian, Miaolingian). The precise development of the tubarium of this genus is uncertain, but most stems show a spiral shape and also a spiral arrangement of the densely spaced thecae. Branching of the stipes has not been recognised, but this may be due to the fragmentary material.

***Siberiograptus* Obut, 1964:** The species *Siberiograptus kotujensis* Obut, 1964 (Fig. 5j) is known from few fragments, some branched. The material indicates an erect growing colony. Lin (1985) described two additional species from China, of which one was interpreted as a Hydrozoa and identified as *Palaeodiphasia simplex* (Lin, 1985) by Song et al. (2021). The thecae are parallel-sided and grow to alternate sides from the stem. Fusellar construction has not been demonstrated for the genus. Maletz et al. (2022) found a few specimens of *Siberiograptus kotujensis* in the Furongian Guole fauna.

***Siberiodendrum* Obut, 1964:** The genus is known from a few specimens found in the middle to upper Cambrian of Siberia. The precise age and locality are unknown. Thus, it should not be considered herein. The small fragments show a wide stem with thecae growing to alternate sides as in *Siberiograptus* and *Dithecodendrum*.

***Ovetograptus* Sdzuy, 1974:** Sdzuy (1974) described *Ovetograptus gracilis* from his locality Gorias d. A. (Oviedo, Spain) (Fig. 4a, b, 5k). The specimens represent the youngest dithecodendrids from Spain, originating from the *Solenopleuropsis* trilobite zone (latest Drumian). Geyer et al. (2022) illustrated a single small fragment as *Ovetograptus?* sp. (Fig. 4f) from the Frankenwald (Franconian Forrest) of Germany. The specimen originated from lower Agdzian (lowest Wuliuan) strata as determined by associated trilobites. It is, thus, one of the oldest benthic graptolites known so far.

***Sotograptus* Sdzuy, 1974:** *Sotograptus flexilis* Sdzuy, 1974 (Fig. 4e) is known only from one locality in Spain. It shows stems with densely spaced, nearly parallel-sided thecal tubes. *Archaeolafoea fruticosa* Chapman and Thomas, 1936 from the Wuliuan of Australia may belong to this genus, indicating a longer biostratigraphic range for the taxon (Fig. 5l).

***Tarnagraptus* Sdzuy, 1974:** The genus *Tarnagraptus* with its typically widening conical thecae on slender stems (Fig. 5m) is widely distributed, but often described from small fragments. Thus, the differentiation of individual species is difficult. The Spanish material ranges from the upper Wuliuan (Leonian Stage, *Eccaparadoxides asturianus* trilobite zone) through most of the Drumian (Caesaraugustian Stage, *Pardaihanian* trilobite zone).

In North America *Tarnagraptus* was found in the Wheeler Shale and Marjum Formation of Utah, sometimes identified as *Mastigograptus* (cf. LoDuca and Kramer 2014). Johnston et al. (2009) identified their material from the *Bolaspidella* trilobite zone of the Chancellor Basin of British Columbia (Canada) as a dithecod or mastigograptid graptolite.

The differentiation of *Tarnagraptus* and *Mastigograptus* is quite important as many specimens from the Cambrian have in the past been identified as *Mastigograptus*, but belong to the Dithecodendridae. The taxa in both families have delicate conical thecae with irregular fusellar development. The concept of *Mastigograptus* has been unsettled and quite a number of species were included based on slender branching stems only as the thecal style was unknown (cf. Ruedemann, 1947). Bates and Urbanek (1986) established the family Mastigograptidae based on the tubarium construction with a clear triad budding system of the stolon previously described by Andres (1977) from Ordovician glacial

boulders. Rickards and Durman (2006) included *Mastigograptus* in the Dithecodendridae based on the investigation of Cambrian material. Maletz (2020b) included the Ordovician genera *Mastigograptus* and *Micrograptus* in the Mastigograptidae, a family of the Dendroidea, but the Dithecodendridae were not included.

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Declarations

Conflict of Interest The author declares that he has no conflict of interest.

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