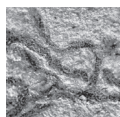


The evolutionary origins of the Hemichordata (Enteropneusta & Pterobranchia) – A review based on fossil evidence and interpretations

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Few fossils demonstrate the presence of the Hemichordata (Enteropneusta, Pterobranchia – excluding benthic and planktic Graptolithina) in the early Palaeozoic. Many of these early records are questionable and are not supported by a reliable fossil record. First definitive fossils are found in the Fortunian (early Cambrian) with the record of *Sokoloviina* representing fragments of the tubarium of the Pterobranchia. Possible Enteropneusta have been described from the Miaolingian (Wuliuan) and the slightly older Cambrian Series 2, Stage 3, but the record is largely based on poor inconclusive material. However, the Fortunian pterobranchs clearly indicate that a differentiation of the Enteropneusta and Pterobranchia must have happened earlier, even though a definitive fossil record is not available. The evolutionary origin of the Hemichordata (Enteropneusta & Pterobranchia), thus is likely to be found in the latest Ediacaran. Fossil burrows of *Gyrolithes* spp. at the Ediacaran–Cambrian GSSP may represent the activity of Enteropneusta, but cannot demonstrate without doubt their presence. Difficult is also the interpretation of meandering deep-water feeding traces or faecal traces in the Cambrian (cf. *Nereites* ichnofacies) that are similar to those produced by extant Enteropneusta (Torquaratoridae). The possible erect housing construction identified as *Margaretia* is unlikely to be built by an enteropneust and is not comparable in any way with the organic-walled tubarium constructions of the Pterobranchia. • Key words: Hemichordata, Enteropneusta, Pterobranchia, fossil record, evolution.

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The fossil record of the Hemichordata, including the Enteropneusta and the Pterobranchia as the main groups, is marred by the difficulty of preserving organic tissues or soft-tissues in fossils. Thus, a strong bias towards the presence of recalcitrant extra-cellular materials like those of the pterobranch tubaria has to be noted. Fossilized remains of the Enteropneusta are extremely rare, while the housing constructions of the Pterobranchia are common and even used frequently for biostratigraphic purposes (cf. Maletz 2020, Maletz *et al.* 2023). Recently, more and more possible fossil enteropneusts are described from middle Cambrian successions, mostly of North America (e.g. Cameron 2018, Foster *et al.* 2022), based on elongated ‘vermiform’ fossils. These often do not show more than a general elongated body and important anatomical details are not available to support the identification due to the poor and fragmentary preservation of the material. A clear tripartite differentiation of the body (as in the Carboniferous *Mazoglossus ramsdelli* Bardack, 1997; see Maletz 2014, fig. 5) (Fig. 1B) is rarely recognizable in the Burgess Shale specimens for example and the possible presence of

gill bars and an enlarged pharynx suggesting an enteropneust may be interpreted otherwise (cf. Walcott 1911).

The Enteropneusta include free-living marine worms with a tripartite body, separated into proboscis, collar and trunk (cf. Cameron 2023). Further anatomical characters are known largely from extant species (Fig. 1C–E) and cannot be recognized in the usually poorly preserved fossil specimens (Fig. 1A, B), except for the presence of possible gill slits in some specimens (e.g. Caron *et al.* 2013). The closely related Pterobranchia, except for their colonial or pseudocolonial organization with the development of clonal reproduction, similarly show a tripartite body differentiation, but have U-shaped intestines with the anus formed close to the base of the collar (Fig. 1F). This development is known only from extant taxa as the soft cellular tissues of the animals are not preserved in the fossil record.

As the early Palaeozoic fossil record is obviously fairly incomplete and fragmentary, all interpretations have to be regarded with caution. This is certainly also true for the Hemichordata and not all published fossils and

interpretations can be taken at face value, but need to be carefully re-evaluated. There are several important points to be considered when discussing the early evolution of the Hemichordata from a palaeontological point of view: a) the available fossil specimens used for the interpretation; b) the preservational aspects of these fossils; and c) the identification or interpretation of the anatomy of these fossils. These aspects in combination are essential for any understanding of the fossils and cannot be used individually and separately as the basis for a sound conclusion.

Fossils generally are the representation of a previously living ancient organism. However, due to modifications during the fossilization process and subsequent metamorphic and tectonic modifications of the rocks in which these fossils are preserved, only parts of the organisms or even only replacements of certain parts of the organisms may be preserved and investigated. Thus, it is easy to misinterpret specimens due to the disappearance or modification of important anatomical details. One of the most intriguing recent examples of misinterpretations may be the case of the Ediacaran *Dickinsonia* from India (Retallack *et al.* 2021). It was described from a single specimen only indirectly investigated as it was seen in the roof of Auditorium Cave near Bhopal, India, apparently out of direct reach to the investigators. Meert *et al.* (2023) and Pandey *et al.* (2023) independently identified the specimen as the impression of an extant beehive and not even representing a fossil. Additional specimens were investigated to demonstrate the identification of the specimens as modern organic material (see also Retallack *et al.* 2023, Kwafo *et al.* 2023 for response).

Maletz (2018, 2020) discussed the preservation of fossil Hemichordata in some detail and explained the problems for the interpretation of the remains of these organisms. He suggested (Maletz 2020, p. 43) to use the term ‘soft-tissue preservation’ only for the preservation of cellular tissues and to differentiate the remains of original organic material of the organisms from any mineral replacement of these to avoid misunderstandings. He also used the term recalcitrant matter or recalcitrant material to describe the more durable, non-cellular or extra-cellular developments like the cuticles of arthropods and plants or the tubaria of the Pterobranchia. This differentiation helps to understand the decay and modification of the various materials of which the organisms are made and to estimate the quality of fossil remains. Soft tissues or cellular tissues are less durable than even thin cuticles of arthropods and especially the highly durable secretions of the pterobranch tubaria. Steiner (2018) discussed the fossil preservation of the Chengjiang fauna and ‘considered most preserved anatomical details as cuticle reinforcements’ and not due to the preservation of soft tissues. Liu *et al.* (2018) explained the supposed preservation of brain tissue

and organic strands identified as nerve cords and other anatomical features in Chengjiang fossils as microbial biofilms following the decomposition of the intestines and other tissues forming halos surrounding the original organic remains, but not forming a genuine replica of the features.

The differentiation of cellular tissues and the preservation of cuticles are often mixed in the investigation of fossils (Maletz 2020). Even delicate, thin cuticles are unfortunately identified as representing soft-body preservation (see the use of the term ‘soft-tissue preservation’ in Saleh *et al.* 2024). Cellular tissues or soft tissues should, however, be clearly differentiated from cuticular (extracellular) material. Naimark *et al.* (2021) for example discussed the ‘soft-bodied’ crustacean organism *Artemia salina*, but the preservation only indicated that cuticular material was preserved (body walls, filter apparatus on antennae, chaetae: Naimark *et al.* 2021, p. 1042), but not cellular features (*e.g.* muscles, brain, organs, *etc.*). Even the delicate chaetae and the outlines of the gut are formed by a cuticular layer and thus, are more resistant to decay than the cellular material.

Maletz (2020, fig. 4) discussed and illustrated the various aspects of the taphonomical changes in pterobranch tubaria and the difficulty in recognizing these. Understanding these taphonomic aspects is enormously important for the subsequent analysis and interpretation of fossils in the light of modern taxonomy and cladistic interpretation of evolutionary patterns. A look into the scientific literature shows that even the interpretation of many genuine and relatively well-preserved fossil specimens has changed considerably through the years. One of the best examples may be that of the lobopod *Hallucigenia*, in which early interpretations reconstructed the animal upside down (see Ramskjöld & Hou 1991). An example from the fossil record of the Pterobranchia is the benthic graptolite *Siberiograptus simplex* Lin, 1985. Song *et al.* (2021, fig. 4) re-interpreted this taxon as a cnidarian and renamed it *Palaeodiphasia simplex* (Lin, 1985), based solely on its type material and providing another highly suggestive reconstruction. The specimens are preserved as flattened, incompletely preserved films of organic material and no new information was available. The interpretation of the fossil as a cnidarian was entirely based on the use of a different terminology for the fossils earlier identified as benthic graptolites. Both interpretations, as a graptolite or a cnidarian, are equally likely, as only the outline of the fossils is available and relevant characters for a definite determination are not present. Thus, there is no verification possible for any of the two interpretations and the identity of this material remains uncertain. The interpretation of Song *et al.* (2021) of this taxon would apparently represent a considerable extension of the mesozoan evolutionary history and cannot be supported

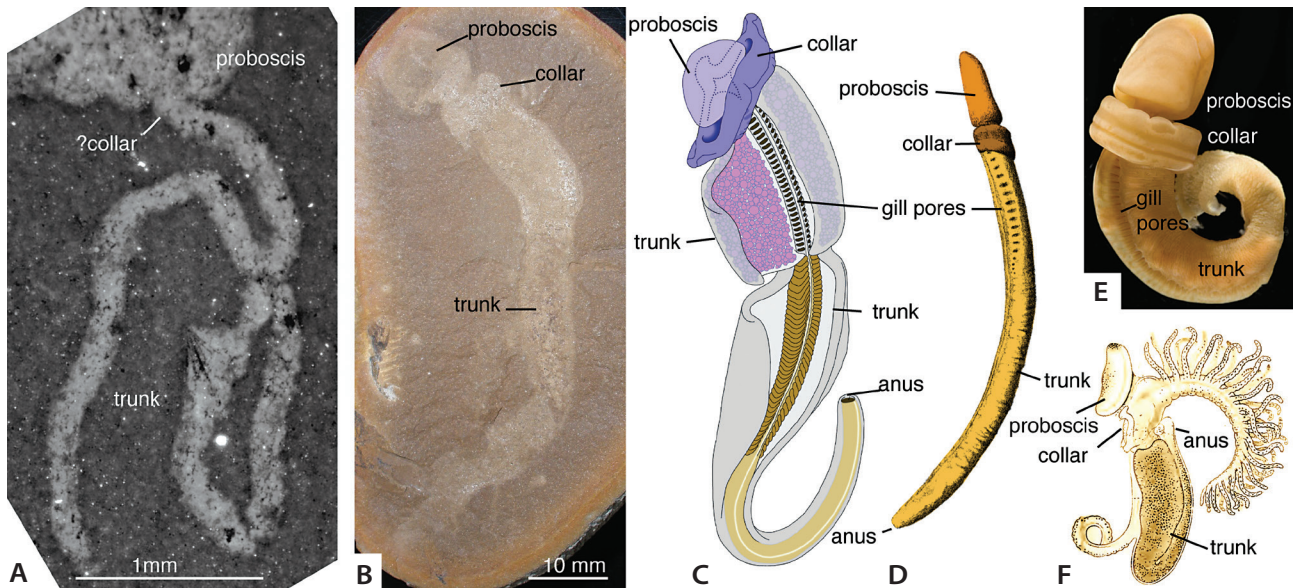


Figure 1. Hemichordata. • A – *Cambrobranchus pelagobenthos* Yang *et al.*, 2024 (after Yang *et al.* 2024, fig. 1e). • B – *Mazoglossus ramsdelli* Bardack, 1997, PE 23053, nearly complete specimen. • C – *Quattuoralisia malakovi* Ezhova *et al.*, 2021, showing morphology, Torquatoridae (after Ezhova *et al.* 2023, fig. 1). • D, E – *Protoglossus bocki* Cedhagen & Hansson, 2013, drawing (D) and photo (E) of the species, Harrimaniidae (after Cedhagen & Hansson 2013). • F – *Rhabdopleura normani* Sars, 1874, reconstruction of zooid (after Sars 1874, pl. 1, fig. 1).

by the available data. The interpretation of the specimens as a benthic graptolite species would fit nicely with the knowledge on graptolite distribution and evolution.

The Hemichordata

The Hemichordata include two main clades, the Enteropneusta Gegenbaur, 1870 and the Pterobranchia Lankester, 1877, but also the poorly known Planctosphaeroidea Spengel, 1932 may have to be included (Maletz & Cameron 2021). The Planctosphaeroidea have been described from a few large, possible larval forms (Spengel 1932), comparable to the tornaria larva of certain enteropneusts. It is now speculated upon their connection to deep-sea enteropneusts (*cf.* Damas & Stiasny 1961, Scheltema 1970, Hadfield & Young 1983), but due to their rare occurrence and the poor knowledge of their development, a definitive identification is impossible. There is no fossil record of this group.

The monophyly of the Hemichordata Bateson, 1885 is supported by morphological and molecular data (*e.g.* Cameron *et al.* 2000, Winchell *et al.* 2002, Cameron 2005) and does not seem in doubt. Caron *et al.* (2013) considered *Ottoia tenuis* Walcott, 1911 (now *Spartobranchus tenuis*: see Caron *et al.* 2013) as a possible stem-group deuterostome that may characterize the entire stem group of the deuterostomes, but not necessarily demonstrating strict enteropneust affinities. Conway Morris (1986, pp. 436, 437) discussed *Ottoia tenuis* as reminiscent to en-

teropneusts based on the bulbous anterior, the elongate trunk and the narrow stalk. Budd & Jensen (2000, p. 263), however, considered the hemichordates not to be a monophyletic group and that there may be no ‘hemichordate body plan’ as the characters uniting the pterobranchs and enteropneusts may be plesiomorphic.

The Hemichordata together with the Echinodermata form the Ambulacraria among the Deuterostomia (*e.g.* Halanych 1995, Cameron *et al.* 2000, Philippe *et al.* 2011, Cannon *et al.* 2014, fig. 1) and all these taxa can be identified as Bilateria. Martynov & Korshunova (2022), in their discussion of the bilaterian origins, elaborated in some detail the phylogenetic connection of the Pterobranchia with the Enteropneusta and used these to suggest a sedentary-pelagic last common bilaterian ancestor. They provided an interesting overview on the current knowledge to understand the origin of the Bilateria, based on the published fossil record and on theoretical considerations. Martynov & Korshunova’s (2022) discussions, however, also point at some of the problems with the largely theoretical considerations and urge a more critical view on some recent fossil descriptions and interpretations. The authors voiced their opinion that “It is dangerous to provide artistic reconstructions without support from actual material” (Martynov & Korshunova 2022, p. 298). One of their examples was the description of the putative bilaterian *Ikaria* Evans *et al.*, 2020, a taxon based on highly speculative interpretations of small casts and moulds of possible organisms and a highly suggestive artistic reconstruction (Evans *et al.* 2020, fig. 3) without

reasonable palaeontological support. From the available fossil record, we can only learn that the evolutionary origin and early evolution of the Deuterostomia is still shrouded in mystery due to the poor fossil record and the enormous distance of the largely incomplete fossil data to information available from extant organisms.

Cameron *et al.* (2000) suggested that the common ancestor to the deuterostomes was an enteropneust-like worm with chordate-like gills, further elaborated by Cameron (2002, 2005), who stated that the ancestral deuterostome was a benthic vermiform organism with a terminal mouth and anus and a pharynx perforated with gill slits bordered by gill bars of collagen used in filter feeding.

The interpretation of *Yunnanozoon lividum* Hou *et al.*, 1991 may also be a warning here. The species has been referred to various fossil groups in the past. Originally, Hou *et al.* (1991) identified it as of unknown affinity, a worm-like organism with distinctly segmented cuticle, showing early phosphatization. Chen *et al.* (1995) identified it as a possible early Cambrian chordate. Shu *et al.* (1996) even interpreted it as the earliest hemichordate, closely comparable to living balanoglossid hemichordates, and referred to the ‘typical tripartite body plan’ of the taxon.

To get a closer look at the evolutionary origins of the Hemichordata, we have to look at the available fossil record, try to figure out how much information we can get there and then compare this record with the evidence from extant organisms. Here we see that there are numerous problems in the interpretation and homologization of morphological features and with the possibilities of the phylogenetic interpretations of these features.

Maletz & Cameron (2016) discussed a number of taxa recently identified as possible early pterobranchs, including *Herpetogaster* Caron *et al.*, 2010 and *Galeaplumosus* Hou *et al.*, 2011, based largely on the presumed presence of their tentaculated arms. The highly unusual *Herpetogaster* is now referred to the Cambroernida, a heterogeneous combination of taxa interpreted as primitive deuterostomes. The group includes *Eldonia* from the Burgess Shale and its supposed relatives (see Caron *et al.* 2010, MacGabhann & Murray 2010, Yang, X. *et al.* 2020). Nanglu *et al.* (2022, fig. 1) referred to these taxa (the cambroernids) and also the vetulicystids and *Yanjiahella* as possible stem-group ambulacrarians. *Herpetogaster* bears dendritic oral tentacles (Caron *et al.* 2010, fig.4; reconstruction), quite different to the paired arms of the Pterobranchia. Thus, their constructions are unlikely to be homologous or showing any closer phylogenetic relationships. The stolon in the middle of its segmented body is known from the holotype specimen of *Herpetogaster* only (but see also Yang *et al.* 2023 for a new record from China), and might easily be interpreted

as a fossil fragment not related to the specimen at all. Interestingly O’Brian & Caron (2012, fig. 18a) illustrated *Herpetogaster collinsi* as a stalked ambulacrarian in a specimen showing an elongated body with the stalk at the end.

Recently, Botting *et al.* (2023) described “an animal possessing a conical tube with fusellar-like banding and tentacles” as a possible hemichordate resembling the Cambrian *Herpetogaster* from the Darriwilian of Wales. The record of this single, poorly preserved, flattened specimen would extend the record of the unusual *Herpetogaster* into the Middle Ordovician if verifiable. This Middle Ordovician fauna was interpreted as a typical Burgess Shale-type fauna yielding numerous organically preserved fossils. The authors indicate a rich graptolite fauna (benthic and planktic ones) from the succession. Most of the faunal elements, however, were not illustrated, except for a ‘multibranched benthic graptolite’ (Botting *et al.* 2023, extended data fig. 4d: probably identifiable as an alga) and a specimen referred to the genus *Dictyonema* possibly bearing the remains of zooids. The illustrations of the *Herpetogaster*-like fossil show a poorly preserved remain and a considerable over-interpretation of the specimen. Most of the features shown in the interpretative drawing cannot be verified from the available photographs of the specimen.

Ou *et al.* (2017) identified *Galeaplumosus abilis* Hou *et al.*, 2011, the supposed early Cambrian hemichordate zooid, as a fragment of the possible stem-group cnidarian *Xianguangia sinica* Chen & Erdtmann, 1991 and included also *Chengjiangopenna wangii* Shu & Conway Morris, 2006 in this taxon, highlighting the problems for a reasonable interpretation of these early metazoan fossils, often based on incomplete and fragmentary specimens. However, Zhao *et al.* (2023, p. 10) preferred to keep *Galeaplumosus* as a separate taxon and transferred *Xianguangia sinica* Chen & Erdtmann, 1991 to the Dinomischidae Conway Morris, 1977. The fossil record of ancestral forms related to the Hemichordata, thus, is quite poor and inconclusive.

Pterobranchia & Enteropneusta

The precise connection of the Pterobranchia and the Enteropneusta is still debated and somewhat different interpretations exist that are referred to here in short.

a) A sister group relationship for the Enteropneusta and Pterobranchia (Fig. 2A, C) was shown by a number of authors based on the investigation of extant taxa (*e.g.* Cameron 2005; Cannon *et al.* 2009, 2013, 2014; Osborn *et al.* 2012; Worsaae *et al.* 2012; Simakov *et al.* 2015; Tassia *et al.* 2016, 2018). The Enteropneusta and the Pterobranchia, thus, were regarded as monophyletic clades.

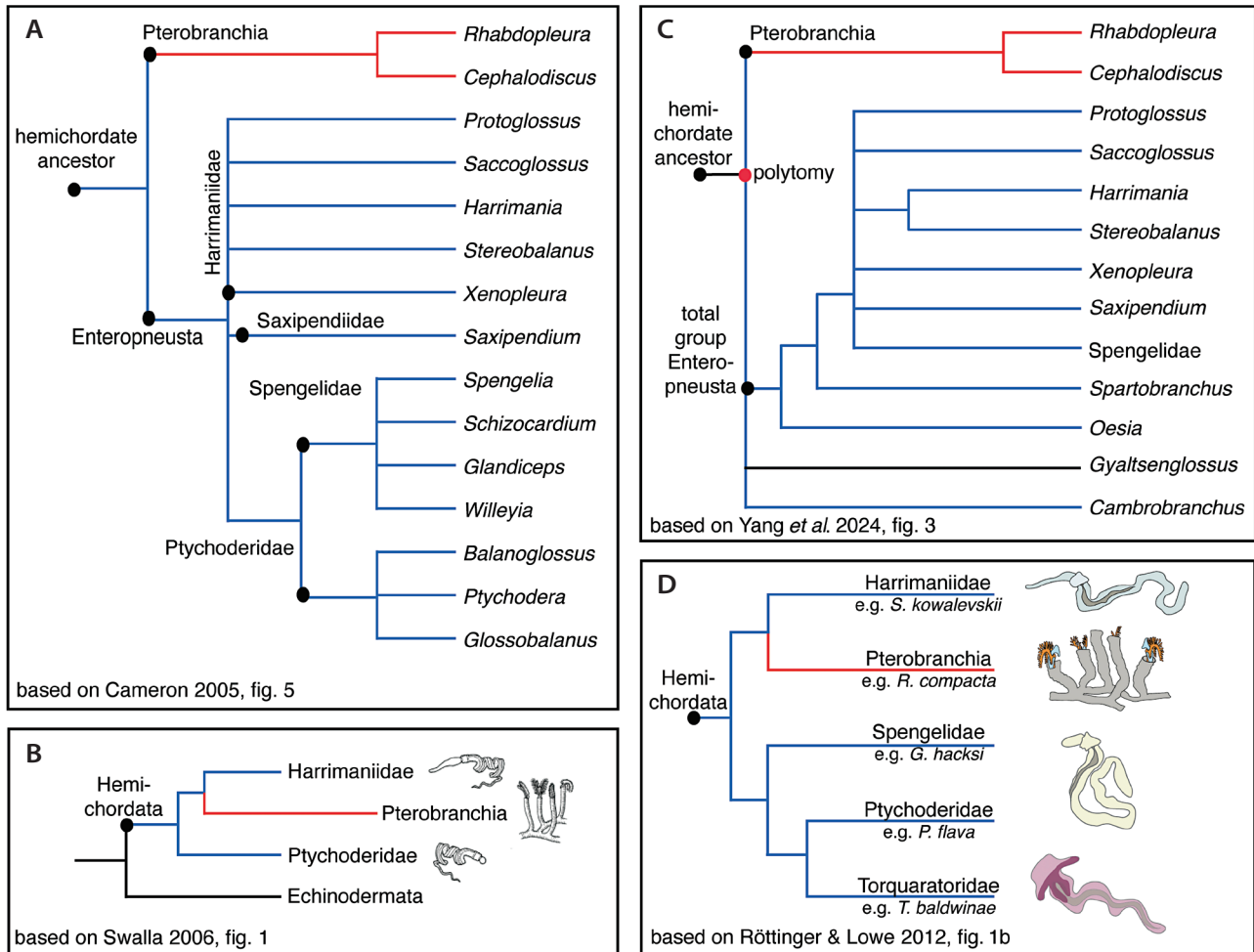


Figure 2. Monophyletic (A, C) and paraphyletic (B, D) interpretation of the Enteropneusta.

Both clades together are seen as a sister taxon to the Echinodermata among the Ambulacraria.

b) Zeng & Swalla (2005, fig. 1), Swalla (2006, fig. 1), Röttinger & Martindale (2006, fig. 1), Swalla & Smith (2008) and Röttinger & Lowe (2012, fig. 1b) indicated a sister relationship between the Pterobranchia and the Harrimaniidae of the Enteropneusta (Fig. 2B, D) and a sister relationship of this group to the remaining Enteropneusta, creating a paraphyletic clade Enteropneusta in which the Pterobranchia were nested. A similar interpretation can be found in Osborn *et al.* (2012, fig. 4), in which pterobranchs, harrimaniids and a moderately supported clade consisting of spengelids, ptychoderids and torquaratorids form a basal polytomy. In these interpretations, the pseudo-colonial and colonial life style of the Pterobranchia and the formation of the pterobranch tubarium evolved from within the Enteropneusta. The ancestral state of development, therefore, must have been an elongated worm-like organism, that eventually produced the pterobranch style tubarium (*cf.* Cameron 2005).

c) Budd & Jensen (2000) added another angle to the discussion by suggesting that the Hemichordata are not monophyletic and that important characters uniting the Pterobranchia and Enteropneusta may be plesiomorphic, but did not discuss the details of this claim.

Even though understanding the Enteropneusta and Pterobranchia as sister groups seems to be the current consensus, the origin of the Hemichordata still poses problems and leads to considerable recent speculation. Nanglu *et al.* (2020) described *Gyaltsenglossus senis* as a stem group hemichordate with an enteropneust-like elongated body and a tentacle crown like the arms and tentacles of the Pterobranchia (see zooidal anatomy in Maletz & Cameron 2016). Their reconstruction shows six arms with tentacles originating from a single point (Fig. 3E), very unlike the tentacle crown of *Cephalodiscus* (Lester 1985, figs 1–3), in which the arms are arranged in pairs on the dorsal side of the collar. Nanglu *et al.* (2020) stated that the feeding arms in *Gyaltsenglossus* originate from the collar, but this detail is not visible

in the illustrated specimens. The suggestion from the interpretation of Nanglu *et al.* (2020) must be that the origin of the U-shaped intestine of the Pterobranchia is a derived character, most probably the result of the secretion of the tubarium tubes with a single distal opening to extrude the excrements. The tentacled arms, however, originated earlier in their stem-group hemichordates and unites the Pterobranchia with the Enteropneusta, in which the arms got lost.

Yang *et al.* (2024, fig. 6) indicated a polytomy at the base of the Hemichordata with the Pterobranchia, the ‘total group of the Enteropneusta’, *Cambrobranchus* and the tentaculate *Gyaltsenglossus* (Fig. 2C). Thus, their analysis does not necessarily support the inclusion of *Cambrobranchus pelagobenthos* in the Enteropneusta, even though the authors described the taxon as an enteropneust. The analysis also does not support the recognition of *Gyaltsenglossus* as a stem-group hemichordate, excluded from the Enteropneusta and thus, probably ancestral to the Enteropneusta and Pterobranchia (see Nanglu *et al.* 2020, fig. 3). Nanglu *et al.* (2022, fig. 1, tab. 1) identified *Gyaltsenglossus* as a stem group enteropneust without additional data and regarded Enteropneusta and Pterobranchia as sister groups.

Identifying the Pterobranchia and Enteropneusta as sister groups does not answer the question about the ancestral state of development in the Hemichordata unless the genus *Gyaltsenglossus* of Nanglu *et al.* (2020) is interpreted as a stem-group hemichordate and the evolution of the feeding arms preceded the tubarium secreted from organic material. Thus, it is not clear whether the ancestral development could either be a worm-like organism like an enteropneust worm or a tentaculate organism living in a tube secreted from organic material. This question will certainly be important when the origin and early evolution of the hemichordates is of interest. Therefore, the recognition of a larval form in *Cambrobranchus* (cf. Yang *et al.* 2024) could potentially be important as it would indicate that early hemichordates possessed a larval stage as found in some, but not all extant enteropneusts. It does not answer the question to the origin and early differentiation of the Enteropneusta and Pterobranchia or the origin of the coloniality in the Graptolithina.

The fossil record of the Enteropneusta

The fossil record of the Enteropneusta has to be differentiated into body fossils and their imprints and the trace fossils that represent their activity and life style. Erect tubular constructions in which the specimens possibly lived have been separated here into a third group. These are probably made from recalcitrant material and do not

represent trace fossils, but also do not represent the animal bodies. The trace fossils and tubular erect fossils are difficult to relate to the animal itself, as Enteropneusta are rarely found in association with their traces in the fossil record. However, traces and burrows associated with Enteropneusta are frequent in extant taxa.

Body fossils

Until quite recently there was little evidence for a fossil record and fossil material has rarely been referred to the Enteropneusta (see Bulman 1970; Caron *et al.* 2013; Nanglu *et al.* 2016; Cameron 2018; Maletz 2019, 2020; Maletz & Cameron 2021). Cameron (2018) listed a few specimens from the Jurassic and Carboniferous as crown group taxa of the Enteropneusta. He identified the Cambrian *Spartobranchus tenuis* (Walcott, 1911) and *Oesia disjuncta* Walcott, 1911 as the oldest enteropneust fossils, originating from the middle Cambrian (Miaolingian, Wuliuan) Burgess Shale of North America. They cannot be referred to any of the extant families and were identified as stem-group enteropneusts. Recent re-interpretations and descriptions of additional taxa (Nanglu *et al.* 2020, Yang *et al.* 2024) added new dimensions to this record (Figs 3, 4).

Spartobranchus tenuis (Walcott, 1911)

Spartobranchus tenuis has a difficult taxonomic history. Walcott (1911) described the species as *Ottoia tenuis*, but did not figure it. Boulter (2003) presented the taxon as a ‘new enteropneust-like hemichordate’ but her investigation was never published. The first illustrations of the taxon are by Caron *et al.* (2013; and supplementary material), who designated USNM 108494 as the lectotype of the species, a poor fragment lacking the proboscis and probably the terminal portion of the trunk (Fig. 4A), thus lacking all indications of a possible assignment to the Enteropneusta. Two additional specimens from Walcott’s material were identified as paralectotypes (Caron *et al.* 2013; supplementary material, USNM 553526) and are equally incomplete. According to Caron *et al.* (2013) the specimens are preserved as carbonaceous compressions and the associated supposed tubes of *Spartobranchus tenuis* are organic. However, there are no geochemical analyses verifying the composition of the material. Thus, the identification of *Spartobranchus tenuis* (Figs 3A, B; 4A, B) as an enteropneust (Caron *et al.* 2013) leaves a number of questions in the light of the poor type material and the low preservational potential of the Enteropneusta in the fossil record (see Maletz 2020), especially as better-preserved specimens have not been illustrated.

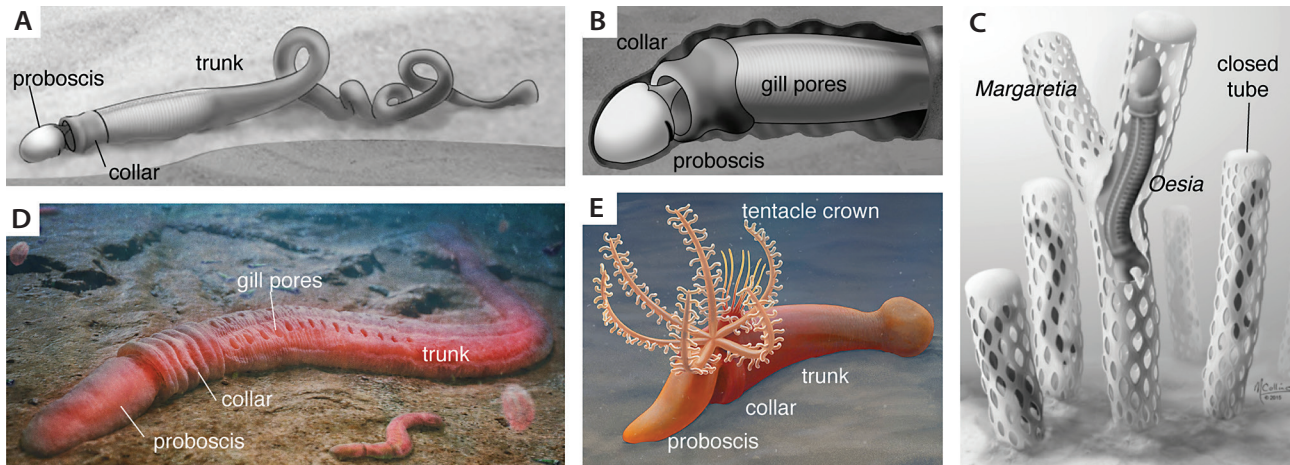


Figure 3. Reconstructions of specimens interpreted as early Enteropneusta. • A, B – *Spartobranchus tenuis* (Walcott, 1911), complete specimen (A) and anterior end of specimen in tube (B), after Caron *et al.* (2013, supplementary information fig. 6). • C – *Oesia disjuncta*, worm in tube previously identified as the alga *Margaretia dorus* Walcott, 1931 (after Nanglu *et al.* 2016, fig. 5a). • D – *Cambrobranchus pelagobenthos* Yang *et al.*, 2024 from Chengjiang fauna (after Yang *et al.* 2024, fig. 5). • E – *Gyaltseoglossus senis* Nanglu *et al.*, 2020, showing the star-shaped tentacle crown (after Nanglu *et al.* 2020, fig. 4). Illustrations not to scale.

Holland *et al.* (2012, 2013) and Cameron & Ostiguy (2013) indicated that extant enteropneusts are quite fragile and often break during recovery. The differentiation into the proboscis, collar and trunk appears easy to recognize in some of the illustrated material identified as *Spartobranchus tenuis*, but additional details are questionable and difficult to verify. The ‘posterior trunk’ with its bulbous structure (see Caron *et al.* 2013, fig. 1a) does not show any details and its formation with a circular gut and a ‘post-anal tail’ (Caron *et al.* 2013, fig. 2d, e) is hard to understand in an anatomical context. None of these details are shown in the type specimen where the trunk has a pointed end and the anterior part of the body is lacking (Fig. 4A). The specimen is actually not identifiable as an enteropneust.

Even though a number of specimens referred to *Spartobranchus tenuis* have been found in sometimes branched ‘tubes’ (Caron *et al.* 2013), this association of *Spartobranchus* also is not entirely clear. Due to the preservation, details of the originally three-dimensional construction are not available and the vaguely visible specimens identified as *Spartobranchus* within these ‘tubes’ may represent other generally worm-shaped organisms instead.

Foster *et al.* (2022) tentatively identified a few fossils from the Wheeler Formation as *Spartobranchus?* sp. They indicated an anterior expansion of the body diameter, but in the material a clear front and back end cannot be identified. One specimen is tentatively interpreted as a possible tube of *Spartobranchus?* sp. (Foster *et al.* 2022, fig. 3c), but represents a fragment of a featureless fossil of unknown affinity as do several further ‘vermiform’ specimens identified as possible enteropneusts.

Nanglu & Caron (2021, p. 3) discussed another enteropneust from the Burgess Shale as ‘*Spartobranchus*-like’ and recognized it ‘tentatively’ as an ‘undescribed species of *Spartobranchus*’. The species was interpreted as apparently living in large organic tubes in association with possible (undescribed) polychaetes in what they interpreted as symbiosis (uncritically accepted by Osawa *et al.* 2023). As several specimens of the enteropneust were found in a single tube, their life style was considered as possibly pseudo-colonial and even a connection to the pseudo-colonial life style of the Cephalodiscida was considered. According to Nanglu & Caron (2021), these enteropneusts are too poorly preserved for a proper identification and the authors also had to admit that the tube maker may have been a different organism, but quickly jumped to the conclusion that ‘these kinds of tubes were thought to be restricted to the coenicia of the hemichordate class Pterobranchia, which includes the tubaria of the Graptolithina’. However, there is no evidence on the particular way of the construction of these tubes to relate them to the Pterobranchia and the precise development and the possible organic composition of the tubes is not demonstrated. The possibly mucous-lined tubes may represent burrows of other organisms and may not be related to the robust organic tubes of the Pterobranchia. Thus, the story has to be regarded with caution and probably misleading for the interpretation of hemichordate evolution. Also the associated commensal polychaetes have not been described. Unfortunately, the idea of enteropneusts (acorn worms) living in tubes in the Cambrian has been incorporated as a fact in modern biology compendia (e.g. Tagawa 2019, pp. 7, 21), even though verification is not available and the connection remains a mere fiction.

Oesia disjuncta Walcott, 1911

Walcott (1911, p. 133) described this organism as a polychaete worm with an enlarged head region and numerous segments, apparently living in a translucent tube ('an irregular tube that was so thin the annelid shows through it'). He did not mention the 'bulbous' posterior end, sometimes terminating in a 'bilobed structure' as discussed by Nanglu *et al.* (2016, p. 2). This bilobed posterior structure has been recognized in few specimens (Fig. 4C) and appears to be more strongly sclerotized as it is shown as a dark and compact feature (see Nanglu *et al.* 2016, fig. 2a, f). The general outline of the specimens suggests an enteropneust, except for this unusual posterior part. The best illustrations of this taxon are not in the main paper of Nanglu *et al.* (2016), but in the additional information. Nanglu *et al.* (2016) interpreted *Oesia disjuncta* as a tubicolous enteropneust and identified the putative alga *Margaretia dorus* Walcott, 1931 as its tube (Fig. 3C), but did not mention the opinion of Walcott (1911) that *Oesia disjuncta* lived in a translucent tube. Thus, two quite different styles of 'tubes' have been associated with this species in the past. Nanglu *et al.* (2016, fig. 2) understood the segmentation indicated by Walcott (1911) as the remains of the gill bars and gill pores of the enteropneust body. A definitive identification of these features is not possible and the identification of *Oesia disjuncta* as an enteropneust remains tentative, but cannot be excluded. The differentiation into proboscis, collar and trunk is easily recognized only in the reconstruction and in some of the additional illustrations of the species in Nanglu *et al.* (2016, fig. 5a; additional files 1, 2).

Gyaltsenglossus senis Nanglu et al., 2020

Nanglu *et al.* (2020) introduced *Gyaltsenglossus senis* from the upper part of the Odayay Shale Member of the Stephen Formation ('Burgess Shale') of British Columbia bearing six feeding arms with tentacles (Fig. 4E). The type material is flattened and most additional specimens are fragmentary, not showing much detail. The species is supposed to possess a long proboscis and six thin arms with about 15 pairs of short tentacles radiating from the dorsal side of the body, but a clear differentiation into a proboscis, collar and trunk cannot be recognized. The shape and number of the arms and tentacles is nowhere seen clearly in the original illustrations (Nanglu *et al.* 2020, p. 4239: 'these tentacles are not clearly observable in most specimens'). The additional 'thin appendages' present in the holotype (Nanglu *et al.* 2020, fig. 1b, d) have not been recognized in other specimens. They supposedly project from a small platform posteriorly to the crown of feeding arms and have no counterpart in extant

enteropneusts. The rounded posterior structure with its internal features is unclear, but Nanglu *et al.* (2020, fig. 4) seem to suggest an attachment in upright orientation, which is not supported by their own interpretations (Fig. 3E). A relationship to the Enteropneusta may be possible, but other options need to be explored (see Yang, X. *et al.* 2020; tentaculate *Herpetogaster* and related taxa).

Nanglu *et al.* (2020) identified the species as a stem-group hemichordate, not referred to the Enteropneusta, even though the genus name suggested this relationship and Nanglu *et al.* (2022) in the next step identified it as a stem group enteropneust. Nanglu *et al.* (2020) discussed their analysis to be consistent with the hypothesis of the vermiform body plan preceding the tube building and colonial development of the Pterobranchia. Thus, they argued that an enteropneust-like body plan might be the ancestral type of the hemichordate and the pterobranch-type U-shaped body within an organic tube and the pseudo-colonial to colonial life style is the derived condition.

The interpretation of the Cambrian *Gyaltsenglossus senis* reminds of the interpretation of the 'Lophenteropneusta' of Lemche *et al.* (1976, pls 25, 26) based on photos of deep-sea enteropneusts. This interpretation from photos was based on the idea of a pterobranch relationship of these worm-like creatures with the 'rhabdopleuran head' and a 'ring of well-developed tentacles' (Lemche *et al.* 1976, p. 291), even though an illustration by Bourne & Heezen (1965) already suggested a 'normal' enteropneust type anatomy for these deep-sea critters. Pawson (2003) and Holland *et al.* (2005) refuted the lophenteropneust interpretation after the first detailed color photos and collections of specimens were available. In this respect, it is quite strange that Martynov & Korshunova (2022, p. 308) stated that the 'lophenteropneust' hypothesis has strong support based on the description of *Gyaltsenglossus senis*. A number of genus and species level taxa have now been included in the deep-water Torquaratoridae (Holland *et al.* 2005, 2009, 2012; Osborn *et al.* 2013; Jabr *et al.* 2018; Ezhova *et al.* 2021) and the interpretation of the Lophenteropneusta is clearly a misinterpretation of early photos of these organisms and not a reasonable interpretation.

Cambrobranchus pelagobenthos Yang et al., 2024

Yang *et al.* (2024) described *Cambrobranchus pelagobenthos* from the early Cambrian Chengjiang fauna of China (Series 2, Stage 3) as the oldest fossil enteropneust, based on supposedly excellent material. The description indicates a preservation of the specimens as flattened film(?) of mineral replacement without any traces of

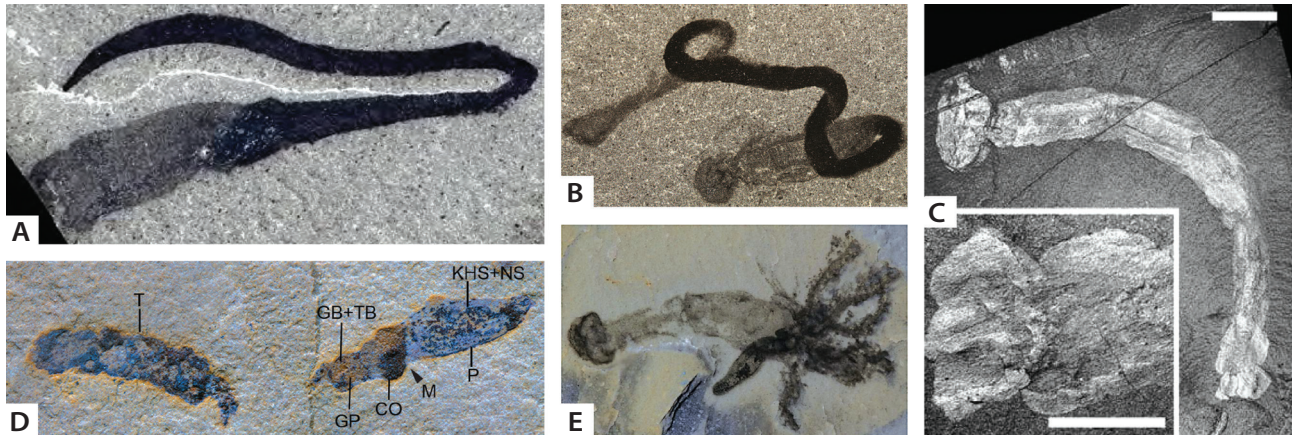


Figure 4. Specimens interpreted as early Enteropneusta. • A, B – *Spartobranchus tenuis* (Walcott, 1911), Burgess Shale; A – USNM 1084494, counterpart of lectotype (after Caron *et al.* 2013, supplementary information, fig. 1d); B – ROM 62123, complete specimen (after Caron *et al.* 2013, fig. 1a). • C – *Oesia disjuncta* Walcott, 1911, USNM 57630, lectotype (after Conway Morris 2009, fig. 1a). • D – *Cambrobranchus pelagobenthos* Yang *et al.*, 2024, part of holotype, Chengjiang fauna (after Yang *et al.* 2024, fig. 1a). • E – *Gyaltsenglossus senis* Nanglu *et al.*, 2020, holotype (after Nanglu *et al.* 2020, fig. 1b). Illustrations not to scale.

organic material. The holotype was apparently only illustrated in part and does not show any details that are reasonable to identify it as an enteropneust (Fig. 4D). The main problem is the interpretation of the species shown here by one example (Fig. 5A–C: based on Yang *et al.* 2024, fig. 1d–f). The interpretative drawing (Fig. 5B) shows many features not recognizable in the photos (Figs 1A; 5A, C) and, thus, suggesting an interpretation of characters not present. The ‘uncertain sclerite’ to which it is attached, is a mass of unidentifiable material, apparently of the same composition as the described fossil specimen. The specimen could easily be identified as faecal string or coprolite, or as unidentifiable algal remains. There is no preservation of organic material (see Yang *et al.* 2024, fig. 4) and the outline is largely recognizable due to the presence of pyrite crystals, possibly a secondary replacement or mineral growth on the surface of the decaying specimen. The preservation, thus compares well with the discussion of Chengjiang fossil preservation in Liu *et al.* (2018), stating that organic material within arthropods may be interpreted as the remains of microbial films formed during decomposition and thus may not faithfully represent original organic components (*e.g.* organs, soft tissues).

The specimens described as *Cambrobranchus pelagobenthos* may alternately be identified as fragments of *Fuxianospira gyrata* Chen & Zhou, 1997 (see Hou & Bergström 2003, Hou *et al.* 2017, Qiao *et al.* 2023, fig. 1g). LoDuca *et al.* (2015b) re-described this species as an alga, but the authors were unable to rule out a coprolite affinity! Steiner *et al.* (2005, figs 4, 7k) illustrated a number of examples of faecal strings, some with (Fig. 5E) and some without enclosed sediment pellets (Fig. 5D) and indicated that most specimens previously identified as algal remains from the Chengjiang Biota may actually be faecal strings.

A faecal origin of the illustrated *Cambrobranchus* fossils is thus reasonable and the idea of their identification as a fossil enteropneust is unlikely.

The artistic reconstruction of *Cambrobranchus pelagobenthos* (Fig. 3D) shows a general enteropneust of a probably harrimaniid type without any specific characteristics. It appears to be made for the purpose of convincing scientists of the warranted identification of the material, but does not show the actual details visible in the described and illustrated specimens (Figs 1A, 4D, 5A–C).

Yang *et al.* (2024, fig. 3a–d) described and illustrated also two specimens as tornaria larvae of *Cambrobranchus pelagobenthos*. These are about 1.5 mm long and show little detail for an interpretation. These specimens would be the first and only tornaria larvae ever found in the fossil record. This interpretation, however, might have to be questioned due to the poor preservation and the excessive interpretation of unrecognizable features even in the mature specimens. The material might be identified as coprolites or unidentifiable fragments, probably of organic origin. Such small and unidentifiable pieces of possible fossil remains are extremely common in the Chengjiang Biota.

Trace fossils

Traces of the Enteropneusta include burrowing–housing (within the sediment) and feeding traces (on sediment surface), well known from a number of extant taxa, but the identification and comparison with possible trace fossils of Enteropneusta is difficult. Housing (burrowing) and feeding traces are formed for different purposes and thus should be kept separate in the interpretation.

Burrows or housing traces

Housing traces or burrows are a special development and include the variously shaped burrows of enteropneusts in soft sediments and are permanently inhabited by the producer. Burrows may also be produced for feeding and are not necessarily only housing constructions. Burrows extend variously deep into the sediment and may be simple or complex. Cameron (2018) discussed the burrows of extant enteropneusts and illustrated the spiral or helical mucous-lined burrow of *Saccoglossus bromophenolophus*, a type of construction already demonstrated for *Saccoglossus inhaensis* by Van der Horst (1934, 1940). Laing *et al.* (2018) considered it likely that the Cambrian spiral burrow *Gyrolithes* from the Ediacaran–Cambrian boundary stratotype section and point (GSSP) in eastern Newfoundland was formed by an enteropneust and regarded it as the earliest vertical burrow recorded so far. Even though this is a possible interpretation, it cannot prove the presence of enteropneusts in the latest Ediacaran to earliest Cambrian without doubt as similar burrows can theoretically be formed by quite different organisms (see Gingras *et al.* 2008, Moosavizadeh & Knaust 2022) or may not even represent burrows (McIlroy 2022). Bertling *et al.* (2006, fig. 15) illustrated the compound structure of a malacostracean crustacean comprising a number of different ichnogenera, including *Gyrolithes*. Still, the shallow water origin of *Gyrolithes* sp. in the GSSP section would fit with the shallow water occurrence of extant enteropneusts forming spiral burrows. Seilacher (2007, p. 54) considered the spiral burrow *Gyrolithes* as a farming burrow, a behavior that is unknown from enteropneusts.

Faecal castings can be found at the entrance or exit of the U-shaped burrows of other extant enteropneusts. Stiasny (1910, p. 563) illustrated schematically the burrow of *Balanoglossus clavigerus* and explained in detail the formation with the faecal coils at the exit. The U-shaped main burrow can be up to 60 cm deep in this species and may bear several entrances (Stiasny 1910, p. 633). Cameron (2018, fig. 4.2) illustrated the characteristic faecal cast at the exit of *Saccoglossus pusillus* Ritter, 1902. Bromley (1996) noted that some U-shaped traces identified in the past as *Arenicolites* may be produced by enteropneusts.

Mägdefrau (1932) suggested that branched burrows from the Triassic of Germany may be formed by enteropneusts and described them as *Balanoglossites*. He also noted that some *Balanoglossites* traces may be produced by polychaetes. Kaźmierczak & Pszczółkowski (1969) discussed more complex, possible enteropneust burrows from the Muschelkalk (Triassic) of Poland. These constructions in extant taxa are often lined by mucus to gain some stability and are by some researchers considered as

the precursors of the erect tubular constructions supposed to be related to certain enteropneusts in the Cambrian (*cf.* Nanglu *et al.* 2016). Knaust (2021) revised the genus *Balanoglossites* and considered that the origin of these trace fossils is manifold with enteropneusts, but also various polychaetes as reasonable producers. Altogether, the burrows of burrowing enteropneusts can be quite variable and it may be impossible to relate any fossil burrows reliably to the Enteropneusta.

Spartobranchus tenuis sometimes appears to produce branched tubular constructions within the sediment that should be identified as burrows as they extend into the soft sediment (see Caron *et al.* 2013). The precise construction and overall form of the burrows is unknown, as entrance or exit places have not been noted. The burrows are described as outlined by fibrous material showing regular constrictions, but the fibers have not been illustrated. Apparently thickened parts (darker color; composition unknown) can be seen in the provided illustrations (Caron *et al.* 2013, fig. 2). There is no information of the involvement of mucus in these constructions, but mucus would not be preservable in the fossil record. Little evidence of transport of the worm-type specimens and the associated tubes can be shown. The tubes appear to be too fragile to be formed on the surface of the sediment or even form erect constructions. Boulter (2003) suggested that secreted mucus and organo-bromides may have played a role in the preservation of the non-cuticular nature of the soft-bodied hemichordate fossils from the Burgess Shale.

Nanglu & Caron (2021) described possible symbiosis between undescribed enteropneust and polychaete worms from the Burgess Shale and claimed that these tubes are collagenous, but evidence of the presence of any organic compounds in these tubes was not provided. They may have been mucous-lined burrows as generally formed by extant enteropneusts. Alternately, they did not even relate to the enteropneusts, a hypothesis that was not ruled out by the authors. It is also unclear, whether these tubes are formed on the sediment surface or within the sediment, but Nanglu & Caron (2021, fig. 3), in their reconstruction, obviously favoured a surface position of these tubes, where mucous lined tubes would be especially unstable and unlikely to have existed.

Feeding or faecal traces

Bourne & Heezen (1965) already discussed and illustrated the spiral faecal traces of deep-sea enteropneusts, comparing them to the fossil tracks of *Taphrhelminthopsis* at a time when the deep-sea enteropneusts of the family Torquaratoridae were not yet described. Halanych *et al.* (2013) discussed the mucous tubes surrounding the faecal traces or trails of deep-water enteropneusts, now referred

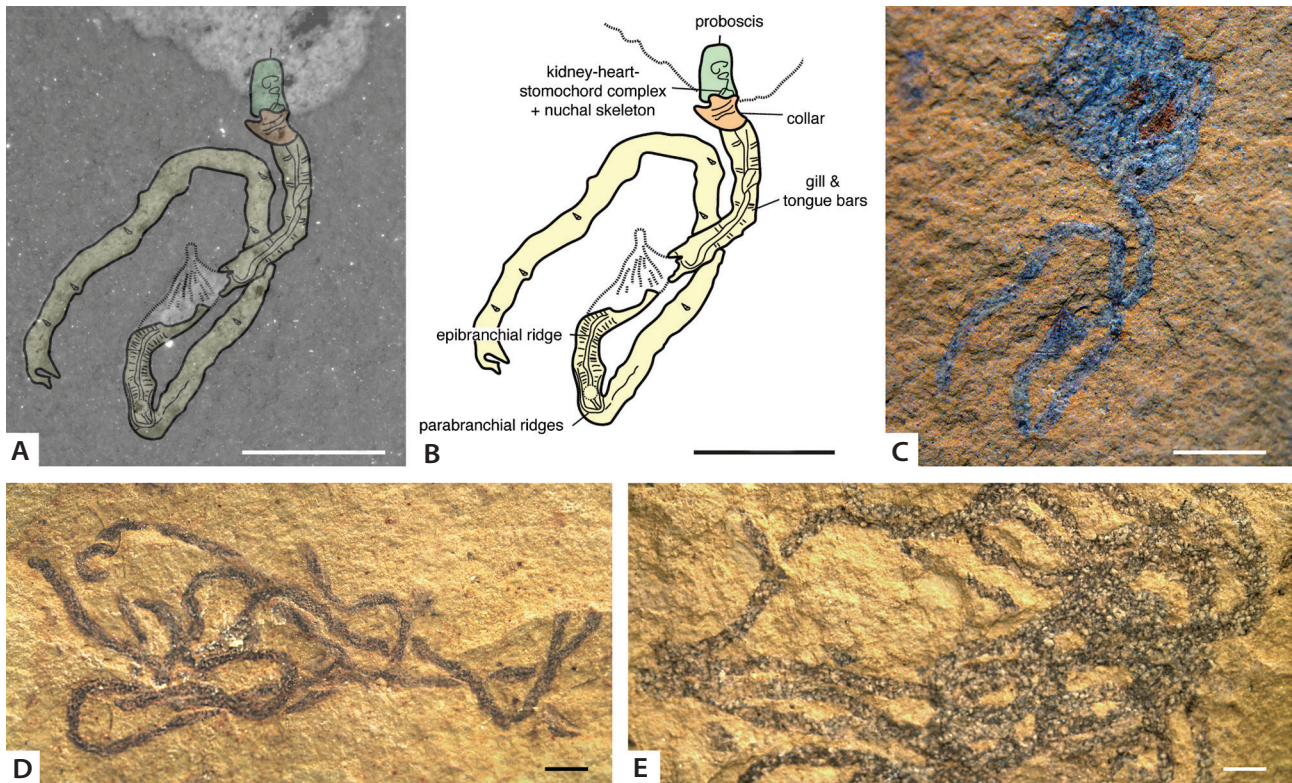


Figure 5. *Cambrobranchus pelagobenthos* Yang *et al.*, 2024, comparison. • A–C – *Cambrobranchus pelagobenthos* after Yang *et al.* (2024, fig. 1d–f); A – fluorescent microscopy image with overlay of interpretive drawing (see also Fig. 1A); B – interpretive drawing; C – normal photograph; D, E – faecal strings, NIGP 203937A, B and NIGP 203938, Maotianshan, China, coll. Michael Steiner.

to the Torquaratoridae. These are short-lived (up to about 60 hours were demonstrated), formed apparently by mucus secretion from the posterior region of the collar of the worms, surrounding the faecal traces. There is no information on the chemical composition of the ‘tubes’, but these mucous tubes are certainly not long-lived and cannot be compared with mucous-lined burrows formed within the sediment. Inside the ‘tubes’, the faecal trails of indigestible, presumably mineralized material’ (*cf.* Holland *et al.* 2009, Jones *et al.* 2013) can be seen expelled from the organism after the digestion of the organic material. Illustrations show that mucous tubes cover meandering faecal trails, while more distally they disintegrate and only the faecal trails remain (Halanych *et al.* 2013, fig. 1). These faecal trails remain preserved in the fossil record and could represent certain deep-water trace fossils of the *Nereites* ichnofacies, formed on soft sediment surfaces. Thus, *Nereites* facies type trace fossils may indicate the presence of deep-water enteropneusts, but it is not possible to prove this origin in the fossil record as other organisms may produce similar traces. The faecal traces formed on the surface of the sediment layer during feeding activities cannot be compared with the housing tubes or burrows of other extant enteropneusts like *Balanoglossus* or *Saccoglossus* discussed earlier.

Resting traces

Resting traces of Enteropneusta could theoretically be present in species living on the surface of soft sediments. Twitchett (1996) illustrated a single example of a resting trace of an enteropneust from the Lower Triassic of the Dolomites, northern Italy. The specimen shows the characteristic lateral collar lips of a torquaratorid enteropneust and thus, is quite convincing (see Cameron 2018, fig. 4). Other resting traces of enteropneusts are unknown from the fossil record and from extant specimens.

Erect housing tubes

Erect housing constructions cannot be regarded as body fossils of the organisms, but are also not truly trace fossils. They represent body fossils as secretions of the organisms that are difficult to relate to certain taxa. Thus, they are here separated from both, the body fossils of the animals and their trace fossils. The tubaria of the extant and extinct Pterobranchia are one of the most easily recognizable type of housing constructions, formed from organic secretions of the animals.

Erect housing constructions have been inferred for the Cambrian *Oesia disjuncta*, but are unknown for extant

enteropneusts. They must have been secreted from durable material to be preservable and certainly not from mucus alone. Thus, if they existed, they may provide a reasonable connection to the tubaria of the Pterobranchia. A mucous lining was enough to stabilize the enteropneust tubes within the soft sediment and also the faecal traces on the sediment surface, at least for short time. Erect constructions, however, need a much more durable material for stability reasons. Thus, a considerable change in the composition and a different way of production of the material forming these housing constructions must have evolved.

Margaretia, the peculiar ‘tube’ referred to *Oesia disjuncta* by Nanglu *et al.* (2016) is a strange construction and its relationship to *Oesia* is not fully established. Foster *et al.* (2022, p. 274) described a number of specimens of *Margaretia dorus* from the Wheeler Formation and the Spence Shale of the western United States and kept the material as a separate enteropneust taxon, thus taxonomically separating the enteropneust *Oesia disjuncta* and its supposed tube. Originally, Walcott (1931) described the fossil *Margaretia dorus* as a Cambrian alga. Nanglu *et al.* (2016) and Cameron (2018) interpreted this construction of woven fibers to form a tube anchored to the sediment and projecting into the water column. Nanglu *et al.* (2016, fig. 5a) reconstructed this tube as a short(?) tube, filled out largely by the inhabiting worm *Oesia disjuncta* and closed at the upper end (Fig. 3C), thus apparently imprisoning its inhabitant. It is unclear on what evidence the “hypothetical closed terminal ends of the tube” (Nanglu *et al.* 2016, fig. 5; explanation) is based. The claw-like posterior end of *Oesia disjuncta* was interpreted to have had an active role in the up and down movement of the animal in its tube. Nanglu *et al.* (2016, p. 2) considered *Margaretia* to be unlike any known Palaeozoic alga with its fibrous construction and elaborate pore architecture and thus unlikely to represent algal origin. Their interpretation is questionable through their own remark that “there is no evidence the worm could enter or leave the tube at either end” (Nanglu *et al.* 2016, p. 5). Why should a worm – or any organism – imprison itself in this way, especially if it is a suspension feeder, thus needs to at least extend its body partly from the tube into the water column? The numerous known specimens of *Margaretia* are highly variable in length and several branchings are present in a number of specimens. Conway Morris & Robison (1988) measured a length of 40 cm (more than 50 cm in Nanglu *et al.* 2016) and considered entire specimens to be much longer. The meandering path and multiple branching of these (Nanglu *et al.* 2016, fig. 4) strongly suggest that these are not upright extending tubes, but more flexible constructions, probably attached to the sea-floor and moving with the water current. In any way, the relationship to *Oesia disjuncta* is hard to

retain for a flexible, long and slender tube like that of the fossils identified as *Margaretia*. The enteropneust worm-like body of *Oesia disjuncta* is up to 12 cm long with an average length of 53 mm (Nanglu *et al.* 2016, pp. 1, 2), thus in longer tubes would fill out only *ca.* 10% of the tube, considerable waste of energy for the production of the tube as a housing construction by this worm.

A supposed specimen of *Margaretia* was recently recognized in the Floian (Lower Ordovician) Cabrières Biota of France (Saleh *et al.* 2024, fig. 2g). This specimen and other remains illustrated as sponges (*e.g.* Saleh *et al.* 2024, fig. 2b, c) more likely represent poorly preserved trace fossils and can be recognized as *Tomaculum problematicum* (= Groom, 1902) as revised by Eiserhardt *et al.* (2001).

A similar or possibly identical organism to *Margaretia* can be seen in the Siberian *Aldanophyton* Krishtofovich, 1953 and possibly in the much younger *Krejciella* Obrhel, 1968 from the Czech Republic, lately discussed by Fatka & Vodička (2022) as an enteropneust tube. In the type of *Krejciella* there is no preservation of organic material and the full relief shows the form of the ‘tube’ clearly as an internal cast. The outside is ornamented with distinct papillae (*cf.* Conway Morris & Robison 1988: *Margaretia*), not pores (*cf.* Nanglu *et al.* 2016: *Margaretia*). In flattened material these papillae are difficult to see, but ‘pores’ or ‘holes’ can be interpreted as preservational aspects, as material was sheared off through transport/splitting of shale pieces, *etc.* It is clear, that the outer surface of the ‘tube’ of *Krejciella* is not smooth and the interpretation as a worm tube, thus, is unlikely. Why should *Oesia* use its energy to produce this very obvious ornamentation (see type of *Krejciella*)? Thus, the material of *Krejciella* could more easily be used to reject the enteropneust relationship of *Margaretia* and related taxa. It should also be noted here that Havlíček *et al.* (1993) provided a completely different discussion on *Krejciella* as an alga, suggesting (but not illustrating) a rhizome with erect tubes showing branching and the presence of distinct papillae instead of holes.

The fossil record of the Pterobranchia

The fossil record of the Pterobranchia, especially the planktic taxa, is well documented in numerous publications as these organisms include important biostratigraphic marker species from the Ordovician to early Devonian (*cf.* Maletz 2017a, b, 2020; Maletz *et al.* 2023). Thus, it is not necessary here, to repeat the information in detail. Maletz (2019) discussed the known fossil record of the Hemichordata, showing the quite uneven distribution of fossils during the Phanerozoic. Much of this uneven distribution is based on the preservational potential of

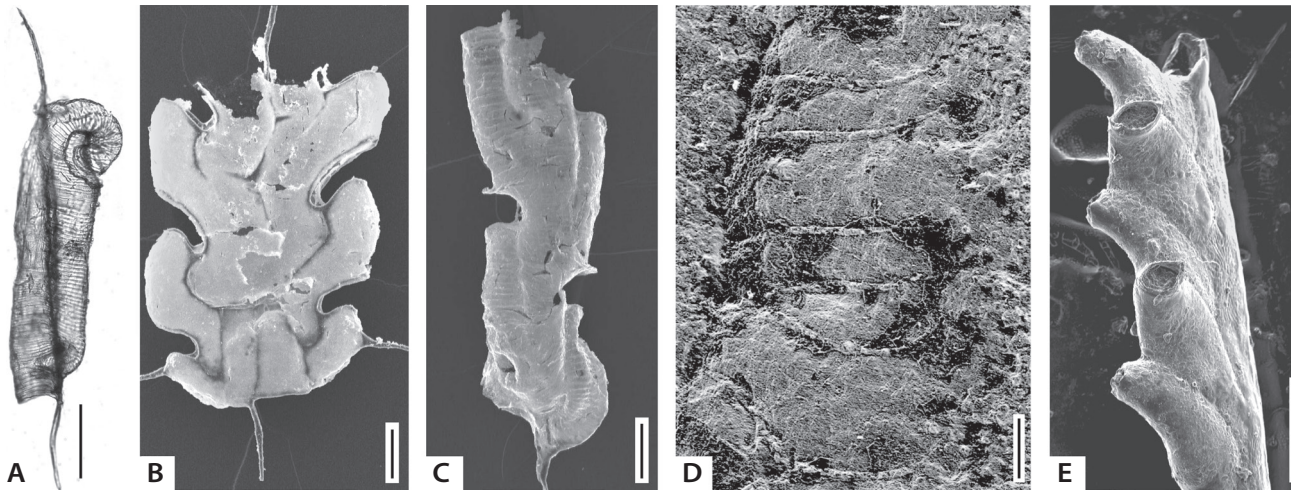


Figure 6. Fusellar recognition. • A – *Streptograptus sartorius* (Törnquist, 1881), PMU 100 003, Dalarna, Sweden, IR-photo showing densely spaced fuselli (see Maletz *et al.* 2019, fig. 31). • B – *Archiclimacograptus* sp., JM 24/5, SEM photo, showing smooth surface, fusellar construction not recognizable. • C – *Gencilograptus typicalis* (Hall, 1865), SMF 75726, SEM photo, showing fusellar construction. • D – *Rotacirca superbus* Briggs & Mongiardino Koch, 2023, tube wall showing supposed fusellar construction (see Briggs & Mongiardino Koch 2023, fig. 3e). • E – *Hydrallmania falcata* (Linnaeus, 1758), JM27-2, North Sea at Portsmouth, UK, small fragment of colony showing serial arrangement of hydrothecae with alternate orientation of apertures, surface covered by diatoms. Scale bar is 200 µm in each photo.

the various materials involved in the animal bodies and their housing constructions in the environments (Maletz 2020), but also due to their life style as benthic or planktic organisms. While the Pterobranchia are relatively well documented in the fossil record from their organic housing construction, the tubarium (extracellular secretions), there is basically no record of the pterobranch zooids (cellular tissues). Considerable differences can be seen in the numbers of benthic and planktic pterobranchs found in the fossil record. While the planktic ones are fairly common in many marine sediments, benthic faunas are usually seen only in few fragmented and transported specimens. One of the best examples is Kozłowski (1949), who described numerous benthic graptolites from the Tremadocian of Poland. This record is based on chemically isolated material and most of these taxa have never been reported again, showing the difficulty of the interpretation of the dendroid graptolite record.

A recent description also provides an idea on the difficulty of interpreting potential fossil pterobranchs. Briggs & Mongiardino Koch (2023) described a problematic late Silurian (Pridolian) fossil as the planktic cephalodiscid *Rotacirca superbus* and referred it to the new family Ezekielidae. The material would represent the first and only known planktic cephalodiscid and one of the extremely rare fossil records of the Cephalodiscida (Maletz & Gonzalez 2017), but a definite identification of the fusellar construction was not provided. The recognizable ‘segmentation’ shows an unusual central rib (Briggs & Mongiardino Koch 2023, fig. 3) that cannot indicate the fusellar construction of a pterobranch (*cf.*

Fig. 6D). The circular construction of *Rotacirca superbus* reminds more of the unusual paropsonemid fossils from the Devonian of New York (see Hagadorn & Allmon 2019 for a detailed discussion of comparable taxa), but the taxon should be left unassigned to any group of organisms, as long as there is no better evidence about its construction and phylogenetic relationships.

The recent record of possible rhabdopleurid specimens from the Fezouata biota of Morocco (Nanglu *et al.* 2023) again shows the difficult of identification of early pterobranchs. Maletz & Gutiérrez-Marco (unpublished data) reinterpreted the specimens as possible cephalodiscids and rejected their understanding as epibiontic rhabdopleurids based on the misunderstanding of certain preservational aspects of the material. The specimens appear to show genuine fusellar construction to identify them as pterobranch remains.

Problems with the identification of fossil pterobranchs can often be solved through the recognition of fusellar construction of their tubaria (Fig. 6), for example through the SEM backscatter method in well-preserved material today (*cf.* Maletz *et al.* 2005, LoDuca & Kramer 2014, LoDuca *et al.* 2015a, Maletz 2020, 2023a), but does not invariably provide sufficient evidence. Fusellar construction can also be identified in chemically isolated material through IR-photography (Fig. 6A) or in many cases through SEM investigations (Fig. 6C). However, as the surface of the graptolite tubaria are often covered by cortical bandages, the fusellar construction may not be recognizable (Fig. 6B). Unrelated organically preserved fossil organisms may be quite difficult to separate from

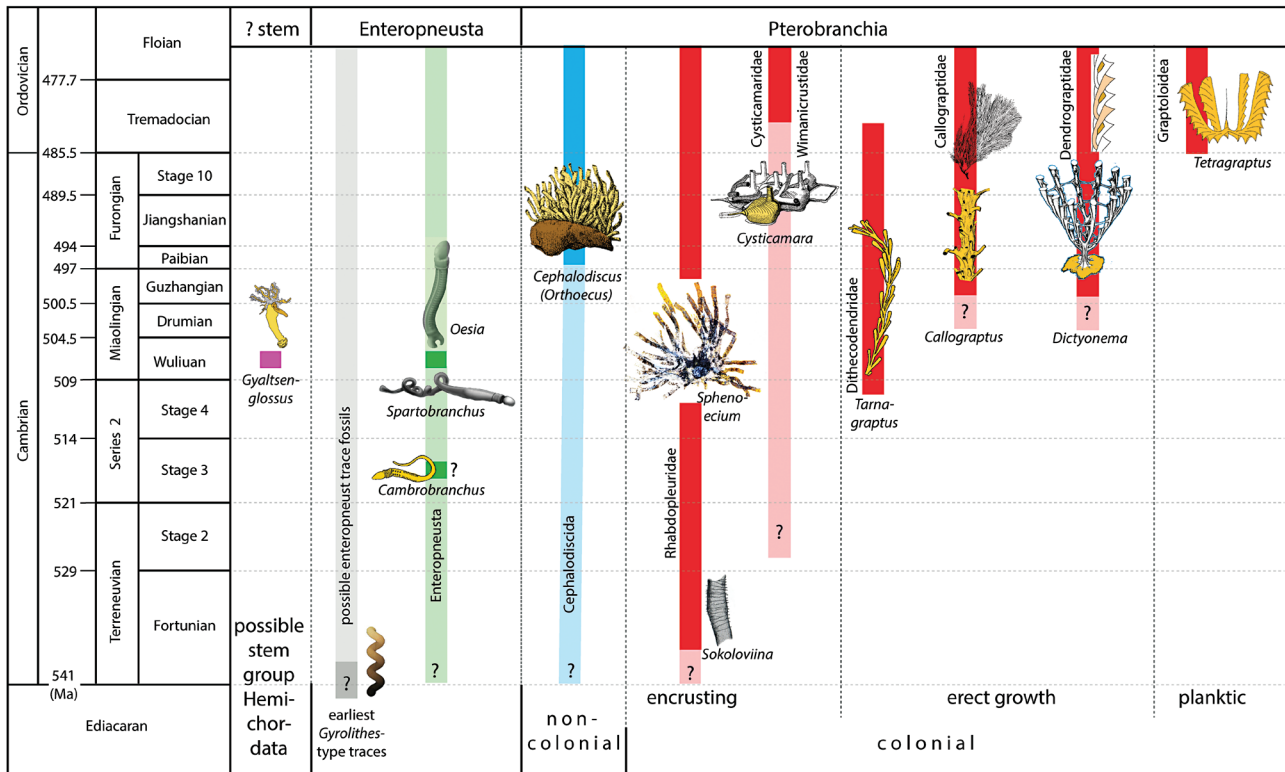


Figure 7. Known fossil record of the Hemichordata (Enteropneusta & Pterobranchia) in the Cambrian to early Ordovician (revised from Maletz 2019, fig. 3). Dark color indicates known presence, lighter colors indicate estimated ranges.

the graptolites (see Muscente *et al.* 2016), especially those of the colonial hydroids, when formed as possessing a serial organization and apertural openings (*cf.* Fig. 6E: *Hydrallmania falcata*; see Kosevich 2006 for a detailed description).

The pterobranch tubaria are formed from highly durable organic material (Maletz *et al.* 2023), probably a chitin polysaccharide, not comparable to the mucous tubes of the Enteropneusta. The biochemical composition and the phylogenetic origin of this secretion is still uncertain. The earliest tubarium remains of pterobranchs include *Sokoloviina costata* Kirjanov, 1968 from the Lower Palaeozoic of Podolia (Fig. 7). Sokolov (1997, pl. 8, fig. 2) illustrated a small fragment clearly showing the distinct fusellar construction from the Rovno Horizon of basal Cambrian (Fortunian) age of Ukraine under this name. Further material has been described from the Cambrian (Terreneuvian), Fortunian Stage 2 (Slater *et al.* 2017, 2018; Slater & Bohlin 2022), but is also relatively incomplete. Hu *et al.* (2018) first indicated the phylogenetic relationship of *Sokoloviina* to the hemichordates based on the presence of fusellar construction. As the transverse ‘flanges’ of *Sokoloviina* (*e.g.* Slater *et al.* 2018, fig. 5) strongly suggest a rhabdopleurid relationship, Maletz & Beli (2018) referred the genus to the Rhabdopleuridae

and regarded the taxon as the oldest rhabdopleurid on record. While Maletz (2019) considered an age of the Rhabdopleuridae older than Cambrian Series 2, stage 4 as uncertain, the range is now considerably extended into the Fortunian (Fig. 7).

Ramírez-Guerrero & Cameron (2021) discussed the pterobranch record from the Burgess Shale of British Columbia, verifying the presence of erect growing colonies in the interval, but not of encrusting forms. The material shows the erect growing *Protohalecium hallianum* with its dense whorls of numerous long and isolated, tubular thecae. While Maletz & Steiner (2021, p. 7) listed *Protohalecium* as a possible hydroid, Ramírez-Guerrero & Cameron (2021) were able to demonstrate the presence of fusellar construction and referred the taxon to the Graptolithina. Ramírez-Guerrero & Cameron (2021, p. 11) referred material identified from the Burgess Shale (Johnston *et al.* 2009) as *Mastigograptus* sp. and suggested, but did not proof triad budding in the material, extending the range of the Mastigograptidae into the Miaolingian (Wuliuan). Maletz (2023b) identified the material as a species of the dithecodendrid *Tarnagraptus*. The record of the large, bushy colonies of the Dithecodendridae shows the advancement of the evolution of the Pterobranchia in the early Cambrian. The encrusting rhabdopleurid-type

taxa might have to be regarded as the basal group of the colonial Graptolithina (cf. Maletz, 2023b, fig. 2), only preceded by the non-colonial Cephalodiscida (Fig. 7). Erect growing Graptolithina then are the derived forms (cf. Mitchell *et al.* 2013), of which extant members do not exist any more. It is quite obvious, that the fossil record of the benthic Graptolithina in the Cambrian is highly incomplete and based on few available fragments (Maletz 2023b). Kozłowski (1949) described with the benthic, encrusting graptolites from the Tremadocian of Poland the only diverse benthic graptolite fauna ever documented (Fig. 7: Cysticamaridae, Wimanicrustidae). The material indicates that the benthic graptolites might have been an important faunal group in the early Palaeozoic, of which we have an extremely limited knowledge. The evolution of the benthic, encrusting graptolites might have originated much earlier and may be traced back to the early Cambrian if these faunas could be secured.

Martynov & Korshunova (2022) in their review on the possible last common ancestor of the Bilateria compared the tube-building of the Cloudinidae with that of the Pterobranchia, which is certainly interesting and valuable at first sight. However, it is not acceptable if we look at the details of the tube construction. The Pterobranchia form their tubes from glands on the cephalic shield, secreting fusellar full rings with a single suture or half rings with a dorsal and ventral suture. The details are quite well known from extant *Rhabdopleura* and fossil pterobranchs and are unmistakable. The organic fusellar half-rings are secreted one after another upon the rim of the previous one in the encrusting parts of the colonies (see Kozłowski 1938, Maletz *et al.* 2016), but erect tubes show fusellar full rings with a single suture instead. The development of the Cloudinidae differs considerably in its full rings without sutures, either of organic material or as a mineralic (carbonate?) development (see Selly *et al.* 2020). The easily visible ‘segmentation’ cannot be taken as an argument to compare and homologize the construction of the Cloudinidae and Pterobranchia, even though they might look very similar at first sight. The ‘funnel in funnel’ (stacked) construction of the Cloudinidae (nicely shown in Selly *et al.* 2020, fig. 2: *Saarina hagadorni*) is quite different to the construction of the tubes in the Pterobranchia. Hua *et al.* (2005) and Cai *et al.* (2014, 2017) illustrated and discussed the development in some cloudinids from SEM photos that are quite informative showing the ‘funnel inside funnel’ construction. Yang, B. *et al.* (2020) provided a somewhat different interpretation of the tubes of cloudinids and suggested that the tubes were originally organic in composition. There are similarities, but not homologies in the tube construction of the Pterobranchia and the Cloudinidae and thus, cannot indicate any closer evolutionary relationships as may be suggested by Martynov & Korshunova (2022).

Conclusions

- 1) The earliest most likely Enteropneusta (stem group taxa; *Oesia*, *Spartobranchus*) are from the Miaolingian (Wuliuan). Older taxa from Series 2, Stage 3 (Yang *et al.* 2024, *Cambrobranchus*) are even more questionable.
- 2) The presence of *Gyrolithes* spp. in the Ediacaran–Cambrian boundary GSSP section (Laing *et al.* 2018) could potentially indicate the presence of burrowing activity of early enteropneusts, but there is not definitive proof available. Spiral burrows are known from extant enteropneusts, but this type of construction is not restricted to the Enteropneusta.
- 3) Possible stem group hemichordates (cf. *Gyaltsenglossus* Nanglu *et al.* 2020) are known from the Miaolingian (Wuliuan) and thus, from the same interval as early Enteropneusta. However, main details of the anatomy of *Gyaltsenglossus* are uncertain and the relationship to the Enteropneusta is questionable.
- 4) The fossil record of Enteropneusta and of stem group hemichordates is extremely poor and therefore unreliable. There is no evidence of any early taxa in ‘organic preservation’ showing more than a general outline of the animal body. The interpretation of gill bars and a gut needs verification.
- 5) The interpretation of *Margaretia dorus* as the erect growing housing construction of *Oesia disjuncta* is unlikely due to constructional concerns. An enteropneust imprisoned in its tubes is unlikely to be realistic.
- 6) The evolutionary separation of the Enteropneusta and Pterobranchia within the Hemichordata can be expected in late Ediacaran to early Cambrian times based on the presence of the colonial, tubicolous Pterobranchia (Rhabdopleuridae) in the Fortunian, early Cambrian (Maletz 2019).
- 7) Highly diverse pterobranch faunas in the Tremadocian of Poland (Kozłowski 1949) indicate that there must have been successful lineages of benthic, encrusting Pterobranchia in the Cambrian of which very little paleontological evidence is available.

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