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Hemichordata (Pterobranchia, Enteropneusta) and the fossil record

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A B S T R A C T

The Hemichordata are generally interpreted as early deuterostomes, closely related to the chordates, a notion important for modern analyses of the origin of the deuterostomes. Because their fossil record is quite scanty, modern phylogenetic interpretations largely rely on the analysis of DNA of the available extant taxa. The tripartite body plan of the group of worm-like hemichordates, the Enteropneusta, may be traced back in deep time to a few poorly known Middle Cambrian (Series 3, Stage 5) taxa from the Burgess Shale biota. The derived small, colonial or pseudocolonial Pterobranchia (Cephalodiscida and Graptolithina) have a more complete fossil record due to their preservable housing construction, the tubarium. The relationships of fossil taxa, putatively identified as early deuterostomes and possible hemichordates or even as pterobranchs of Lower to Middle Cambrian age (e.g. *Galeaplumosus*, *Herpetogaster*), cannot be substantiated. The Pterobranchia and their housing construction are first seen in the Middle Cambrian Series 3, Stage 5 but a clonal, colonial organization of the tubaria can only be recognized in the basal Drumian. The fossil enteropneust *Mazoglossus ramsdelli* Bardack, 1997 from the Carboniferous Mazon Creek Biota is re-described, its lectotype designated and illustrated for the first time.

1. Introduction

The Hemichordata are a group of variably developed benthic organisms, either living as individuals (Enteropneusta) or in colonies or pseudo-colonies of minute zooids (Pterobranchia) in marine environments from shoreline to deep-sea areas. They can be united by their peculiar body plan, showing an elongated body, differentiated into three parts, the proboscis, collar and trunk regions (Fig. 1). For a long time, the hemichordates attracted little scientific interest, especially as they are inconspicuous faunal elements in most environments. More recently, their phylogenetic position caused them to be considered vital in understanding early chordate origin and evolution. Both, modern taxa, and the relatively poor fossil record attained a highly increased scientific interest as the group is interpreted to be close to the origin of the chordates (e.g. Gerhart et al., 2005). This notion was already implied in the name Hemichordata introduced by Bateson (1885), who included the Enteropneusta in the Chordata. Together with the Echinodermata, the Hemichordata are now interpreted to form the Ambulacraria, a sister group to the Xenacoelomorpha (Philippe et al., 2011). Both groups together can be regarded as early deuterostomes and represent a sister group to the chordates (Fig. 2).

Unfortunately, the fossil record of the Hemichordata is poor and even the extant members are very incompletely known and investigated, leaving many unanswered questions. The modern hemichordates are largely represented by a small group of elongated, worm-like marine organisms, the Enteropneusta (Fig. 1A), ranging from a length of less than 0.6 mm (Worsaae et al., 2012) to more than 2.5 m (Hyman, 1959). A second, even rarer group, the Planctosphaeroidea, is often considered to represent large larval stages of unknown species of Hemichordata (Hyman, 1959; Hadfield and Young, 1983; Cameron, 2002; Cannon et al., 2009) and only a few specimens are known. Hart et al. (1994) were the first to discover the taxon alive. Damas and Stiasny (1961) suggested that the genus *Planctosphaera* simply represents a hypertrophied tornaria larva of an unknown deep-water enteropneust, but actual evidence for this notion is lacking. A third group, the Pterobranchia, recently being re-interpreted as including the extinct Graptolithina (Mitchell et al., 2010, 2012), is found in a small number of extant benthic marine organisms with a colonial or pseudocolonial organization. They secrete a distinct form of housing called the tubarium or coenecium (Fig. 1B, C) or the rhabdosome of the fossil Graptolithina (see Bulman, 1970). The zooids of the Pterobranchia are small and rarely reach more than a few mm in length. They differ from the enteropneusts (Fig. 1A) in the possession of one to several pairs of arms for filter feeding (Fig. 1D–F) on the collar. Pterobranchia occur in most marine environments, from shallow intertidal to shelf, slope and deep-sea regions, both tropical to arctic. They are often difficult to find due to their usually inconspicuous colonies formed from transparent to semi-transparent organic material. The Pterobranchia are usually attached to hardgrounds, corals and other sessile organisms or hidden under stones and empty shells.

As the Planctosphaeroidea are unknown from the fossil record and the Enteropneusta are extremely rare, the origin and early evolution of these two groups are difficult to interpret with paleontological data. The Pterobranchia, the only group of the Hemichordata that includes a reasonable fossil record due to the secretion of the tubaria by its zooids,

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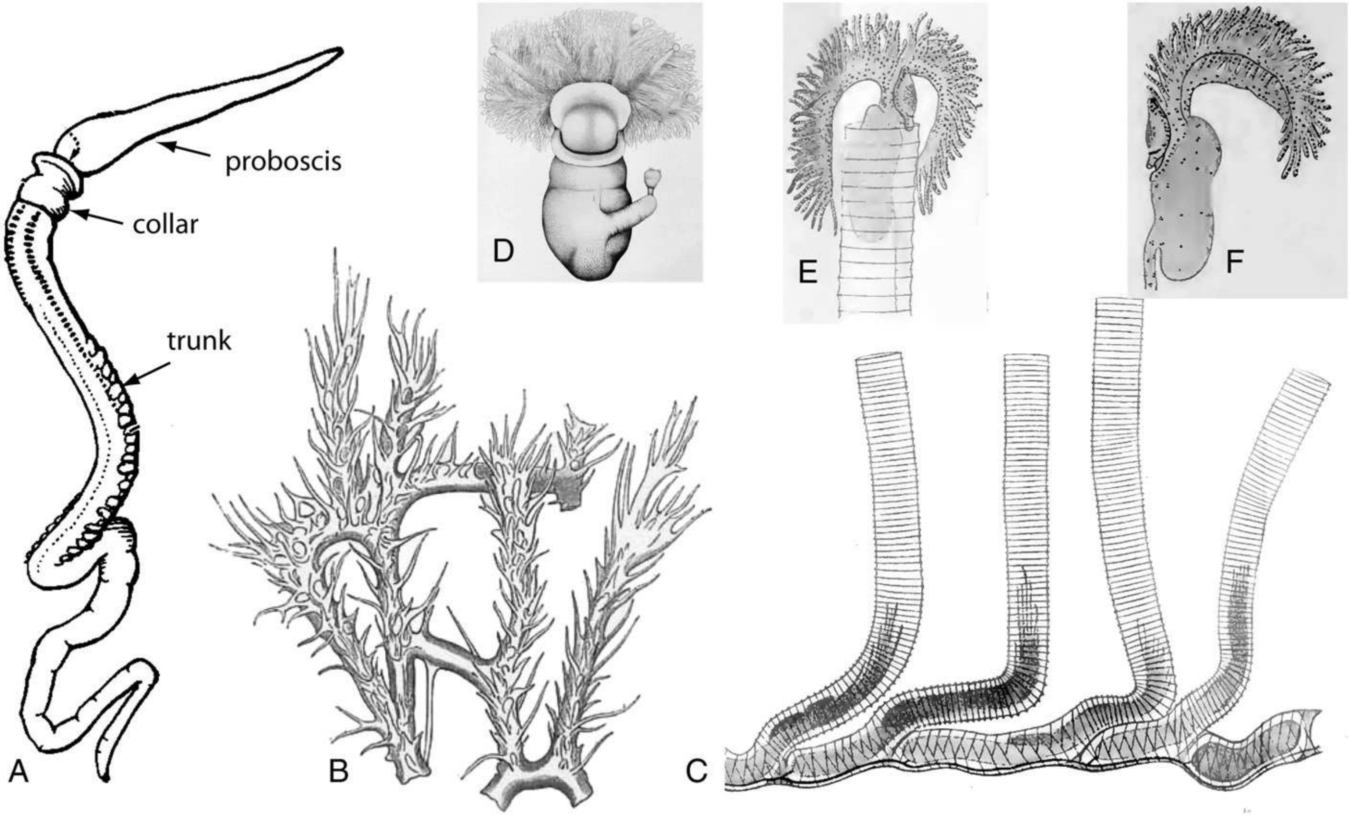

Fig. 1. A. Acorn worm (enteropneust) *Saccoglossus pusillus* (based on Bulman, 1970: Fig. 1). B, D. Pterobranch *Cephalodiscus dodecalophus* (based on M'Intosh, 1887: text — Fig. 1; pl. 2), tubarium (B) and single zooid with bud (D). Pterobranch *Rhabdopleura normanni*, tubarium (C), based on Schepotieff (1907: pl. 22) and zooids (E, F), based on Schepotieff (1906: pl. 23).

provide us with some of the most important paleontological and geological objects, the Graptolithina (Bulman, 1970). The Graptolithina undoubtedly possess one of the best and most complete records of any Paleozoic fossil group. They are quite important for dating rock sequences, to calibrate and understand deep time, to provide a tool for biostratigraphy and further geological application, most notably in structural geology, plate tectonics and paleogeography (see Bulman, 1955, 1970). Graptolites are used to define 13 out of 16 GSSP's for the Ordovician to Lower Devonian time intervals (see www.stratigraphy.org). Their common occurrence forms the basis to a biological understanding of long-term macro- and micro-evolutionary patterns of this peculiar group of marine organisms in the Paleozoic Era (e.g. Mitchell, 1990; Fortey et al., 2005; Maletz et al., 2009; Urbanek et al., 2012) and provides insight into tempo and mode of evolutionary change of life in the Paleozoic oceans (Cooper and Sadler, 2010; Sadler et al., 2011). This is possible only due to the preservation of their rhabdosomes, secreted by the individual zooids from an organic, scleroproteic material, most probably collagen (Towe and Urbanek, 1972; Bustin et al., 1989; Gupta et al., 2006). The homologous housing structure of extant Pterobranchia (*Cephalodiscus*, *Rhabdopleura*) has been termed the coenecium or tubarium in the past, leading to unwarranted misunderstanding. The used terminology indicates a difference, that does not exist (see Mitchell et al., 2012) and the term tubarium is here used for all pterobranch secretions.

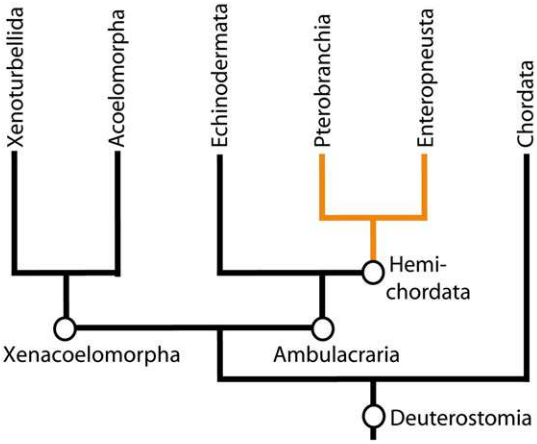

Fig. 2. Cladistic diagram (based on Swalla and Smith, 2008: Fig. 1; Philippe et al., 2011).

2. Evolutionary relationships

Little is known of the origin and early evolution of the Hemichordata and, in fact, of their origination, as the fossil record is largely restricted to the preservation of the organic housing constructions or tubaria of the colonial Pterobranchia. Entirely soft-bodied organisms are less likely to be preserved in the fossil record and it was shown that the zooids of modern *Rhabdopleura* decay to an unidentifiable organic mass within few days after death (Briggs et al., 1995). It is evident from the investigation of extant rhabdopleurids and cephalodiscids, that the tubarium construction cannot be used to infer or understand the detailed morphology of the zooids. The high variation of the tubaria in *Cephalodiscus* led to the introduction of a number of extant subgenera (see Bulman, 1970), while the variability of their zooids (Fig. 1D–F) is minimal and is largely restricted to the number of arms.

Recent biological investigations of extant hemichordates and related taxa provide a general picture (Fig. 2) of the taxonomic and evolutionary relationships of the relevant clades (see discussion in Winchell et al., 2002; Gerhart et al., 2005; Swalla and Smith, 2008; Kaul-Strehlow, 2011; Perseke et al., 2011; Stach and Kaul, 2011), but their exact origins remain a mystery. It is sufficiently well established from molecular data that the hemichordates are a sister group to the echinoderms, with which they form the Ambulacraria (Halanych, 1996; Bromham and Degnan, 1999; Cameron et al., 2000; Halanych, 2004; Peterson, 2004; Cameron, 2005; Bourlat et al., 2006; Sato et al., 2008b; Perseke et al., 2011). The Xenoturbellida are regarded as a sister group of the Ambulacraria, but the latter phylogenetic interpretation is not yet settled and the Xenoturbellida may alternatively represent an out-group to the deuterostomes (Swalla and Smith, 2008). However, Philippe et al. (2011) used microRNAs and additional evidence to support their new taxon Xenacoelomorpha, including the Acoelomorpha and *Xenoturbella*, as sister group to Ambulacraria.

The detailed evolutionary relationships within the extant Hemichordata are still in a state of flux and various competing concepts exist. Some authors consider the Hemichordata to include two monophyletic groups, the Pterobranchia and the Enteropneusta (e.g. Winchell et al., 2002). Others suggest that the Enteropneusta are a paraphyletic group with the family Harrimaniidae as a sister group to the Pterobranchia, thus implying that the hemichordate ancestor was a solitary enteropneust-like organism (Halanych, 1995; Cameron et al., 2000; Bourlat et al., 2006; Cannon et al., 2009). Studies on 18S rDNA (Cannon et al., 2009; Worsaae et al., 2012) provide good evidence of an origin of the Pterobranchia from within the Enteropneusta. It would, thus indicate that miniaturization of the individuals led to the loss of many anatomical details and ultimately to a colonial life style in the Pterobranchia as a derived state. Coloniality, thus, may not be the primary condition of the life style of the Pterobranchia. This statement may be supported by the record of *Atubaria* (Sato, 1936), a possibly non-colonial cephalodiscid for which, unfortunately, information is not available on the reproduction cycle and life style.

Worsaae et al. (2012) recently described *Meioglossus*, a miniaturized harrimaniid enteropneust with the ability of asexual reproduction through paratomy (regeneration perpendicular to an anterior–posterior plane). Asexual reproduction through architomy (fragmentation and regeneration) has been recognized in enteropneusts before (e.g. Petersen and Ditadi, 1971), but appears to be restricted to a small number of ptychoderid species. Paratomy, however, has not been recognized before, but may be important for a comparison with the pterobranch *Cephalodiscus*, in which the budding may be regarded as a special form of paratomy (Worsaae et al., 2012: p. 2).

The emerging picture is still quite incomplete and even Cannon et al. (2009: p. 22) stated the need of a modern investigation of extant Hemichordata. This is understandable considering the amount of recent discoveries among the Enteropneusta (e.g. Cameron, 2002; Holland et al., 2005; Miyamoto and Saito, 2007; Holland et al., 2009; Cameron et al., 2010; Deland et al., 2010). Especially deep-water enteropneusts have not been explored in much detail and many new finding may have to be expected, not to mention the lack of information on the phylogenetic relationships of the Planctosphaeroidea with the rest of the Hemichordata. The more speculative concept of the lophenteropneusts (Lemche et al., 1976; Tendal, 1998), based solely on photography of otherwise unknown deep-sea enteropneusts has been rejected (Holland et al., 2005) as more enteropneust specimens were collected or photographed from deep-sea regions (Holland et al., 2009). The record led to the introduction of a new family, the Torquaratoridae, recognized through a special development of the collar with two lateral projecting lips (Holland et al., 2005), a feature not known from any of the shallow water representatives of the Enteropneusta. New discoveries appear constantly, changing our understanding of the enteropneusts (see Osborn et al., 2011; Holland et al., 2012a,b; Priede et al., 2012; Worsaae et al., 2012). Their record may also be important as it provides clues to the nature of the producer of trace fossils in deeper water environments found in many ancient sediments.

A molecular clock approach has been used more recently to determine evolutionary events in earth history. The published data are still difficult to interpret (Welch et al., 2005) as 'large discrepancies have been found in the dates of evolutionary events' (Pulquério and Nichols, 2007). Among others, Ayala et al. (1998) and Aris-Brosou and Yang (2003) discussed a late Precambrian diversification of the metazoans. Aris-Brosou and Yang (2003) dated the protostome–deuterostome divergence at 582 ± 112 MYA, fitting in general with the paleontological record. While Blair and Hedges (2005a, b) estimated the divergence of the echinoderms and the hemichordates at 876 MYA (725–1.074 MYA) and, thus, provided data not supporting the Cambrian Explosion. More conservative estimates by Peterson et al. (2004) and Swalla and Smith (2008) discussed a time interval of 526–567 MYA for the divergence of the two groups. Paleontological data indicate that the oldest fossil hemichordates are from the Burgess Shale (ca. 505 MYA) (Boulter, 2003), but the record of pterobranchs from the Kaili Formation (Harvey et al., 2012) appears to be slightly older. The fossil data support the data of Peterson et al. (2004) and Swalla and Smith (2008).

3. Preservation potential of Hemichordata

As soft-bodied organisms do not preserve easily in the fossil record, the fossil representation of the Hemichordata is difficult to interpret. Only the colonial, benthic and planktic Graptolithina are common in marine environments as they secrete a relatively durable organic housing structure that can easily be preserved in many sediment types under dysoxic and anoxic bottom conditions or when quickly covered and protected by sediment. The fossil preservation of enteropneust hemichordates is restricted to a number of exceptional Lagerstätten like the Cambrian Burgess Shale (Conway Morris, 1979) or the Carboniferous Mazon Creek Biota (Bardack, 1997), but even here these organisms in general appear to be uncommon. Their fossil remains usually lack many details of the body construction that would be important for a taxonomic understanding (see *Mazaglossus* description). The preservation of body fossils under these exceptional circumstances is poor. Specimens are preserved either as thin films of organic material or as replacements of these original films by pyrite or a number of other minerals as the result of oxidation of the pyrite or weathering of the organic components. Little is preserved of the original organism and many taxonomically important features may not be accessible for scrutiny (e.g. Donoghue and Purnell, 2009; Sansom et al., 2010). Very often, fossil remains cannot be identified and related to modern organisms, as too many details are lacking. This, however, should not be used as an argument to ignore the material, but to caution interpretations.

Even for some famous Lagerstätten like the Hunsrück Shale of Germany, a clear and unanimous understanding of the aspects of fossil preservation has not been achieved. Otto (2002), for example, argues strongly for a re-interpretation of much of the so-called 'soft tissue preservation', as it is often based on a superficial investigation of the material and misinterpretations of taxa are common. Truly soft tissue like muscle fibers, epithelial and nervous tissue may not be pyritized and preservable. A similar case can be seen in the preservation of the Burgess Shale faunas. Page et al. (2008) discussed the preservation of Burgess Shale fossils as consisting of organic films associated with phyllosilicate compression films, identical to the silicate pressure shadows known from fossil graptolites (Underwood, 1992), aiding the preservation and recognition of organically preserved fossils. As the original organic material of the organisms may be destroyed easily through later modifications of the sediments (diagenesis, metamorphosis, tectonics, even recent weathering), the silicate pressure shadow films may be the only remaining indication of the former presence of the specimens. Pyritization, or better replacement by pyrite, is not present in graptolites and all cases of 'pyritized' graptolites (see Underwood, 1992; Underwood and Bottrell, 1994) turn out to represent a pyrite filling or later overgrowth of the organic tubaria. Replacement of tissues or the organic secretions of the graptolite colonies by pyrite cannot be recognized. Localized pyrite halos or concretions around thecal apertures have been interpreted as decaying remains of zooids (e.g. Bjerreskov, 1978), but do not show anatomical details.

The Graptolithina (Fig. 3) with their organic housing structures (rhabdosome or tubarium), have been recorded from numerous localities around the world and are common in many sediments. This is true only for the planktic taxa, while the benthic taxa are rarely preserved and their taxonomy and evolution are more poorly constrained. Planktic Graptolithina (Fig. 3E) are widely distributed in the Ordovician to Lower Devonian time interval (Bulman, 1970) and their earliest record is close to the base of the Ordovician System (Cooper et al., 1998, 2001). Benthic graptolites (Fig. 3A–D) are, as most benthic, sessile organisms, rarely found in situ in their living environment. They are often only recognized as transported fragments in deep water sediments, but in these cases are rarely identifiable even to genus level. Their taxonomy and evolution is much less well known due to this highly fragmentary record.

4. Possible early Hemichordata

The age of the earliest Hemichordata is still not settled and new interpretations, based on recent fossil discoveries have challenged the emerging picture. What is clear is that in the upper part of the Lower Cambrian a differentiation of the deuterostomes had already been taken place. Early hemichordates may already be present, even though not yet recognized unequivocally in the fossil record. Harvey et al. (2012) recently illustrated fragments of pterobranch tubaria from the Cambrian Kaili Formation; the oldest evidence of the presence of pterobranchs in the Paleozoic (Fig. 4B). The discussion of early hemichordates and the differentiation of the deuterostomes, however, are still in its infancy as the discussion of the cambroernids (Caron et al., 2010) and the uncertainty of the identification of many of the earliest fossils interpreted as deuterostomes shows (Aldridge et al., 2007; Shu et al., 2009). It leads to the notion that early soft-bodied fossils already lost most of their definitive characters through the fossilization process and an assignment to any group is marred with problems (Donoghue and Purnell, 2009; Sansom et al., 2010). The well-known *Yunannozoon* from the Lower Cambrian of the Chenjiang biota, Yunnan (China), for example, has been interpreted in various ways (Mallatt and Chen, 2003; Shu et al., 2003). Originally described as a problematic animal of unknown affinity (Hou et al., 1991), it was later identified as a possible early Cambrian vertebrate (Chen et al., 1995; Dzik, 1995). Shu et al. (1996, 2001a, 2001b) interpreted the taxon as the earliest known hemichordate, a view that has been challenged subsequently. A consensus has not yet been achieved (see Chen and Huang, 2008; Swalla and Xavier-Neto, 2008), but considerable differences to extant enteropneusts have been quoted making a close relationship unlikely. A similar complex situation of variable and diametrically different interpretations exists for many other early metazoan fossils.

Very few Cambrian hemichordates or taxa related to hemichordates have been described and can be verified as such. A Lower Cambrian age can be attributed to *Galeaplumosus abilus* (Hou et al., 2010) from the Chengjiang Konservat-Lagerstätte of southern China. The single specimen from the *Eoredlichia-Wutingaspis* Biozone of the Mafang section (Yunnan, China) of Atdabanian or early Botomian age is relatively incomplete and is poorly preserved. It shows a feather-like structure with a central strand and paired, lateral structures, interpreted by the authors as the feeding arm of a zooid (Fig. 4A). A second, more incomplete, but possibly identical structure is associated. Both seem to be connected to a conical feature, interpreted as a cone-shaped tube which shows parallel lines, interpreted as fuselli, and thus, providing the evidence to identify the fossil as a pterobranch hemichordate. Hou et al. (2010: p. 1) also state that a helical line is not visible in the cone-shaped tube, an odd statement as the helical line is a special

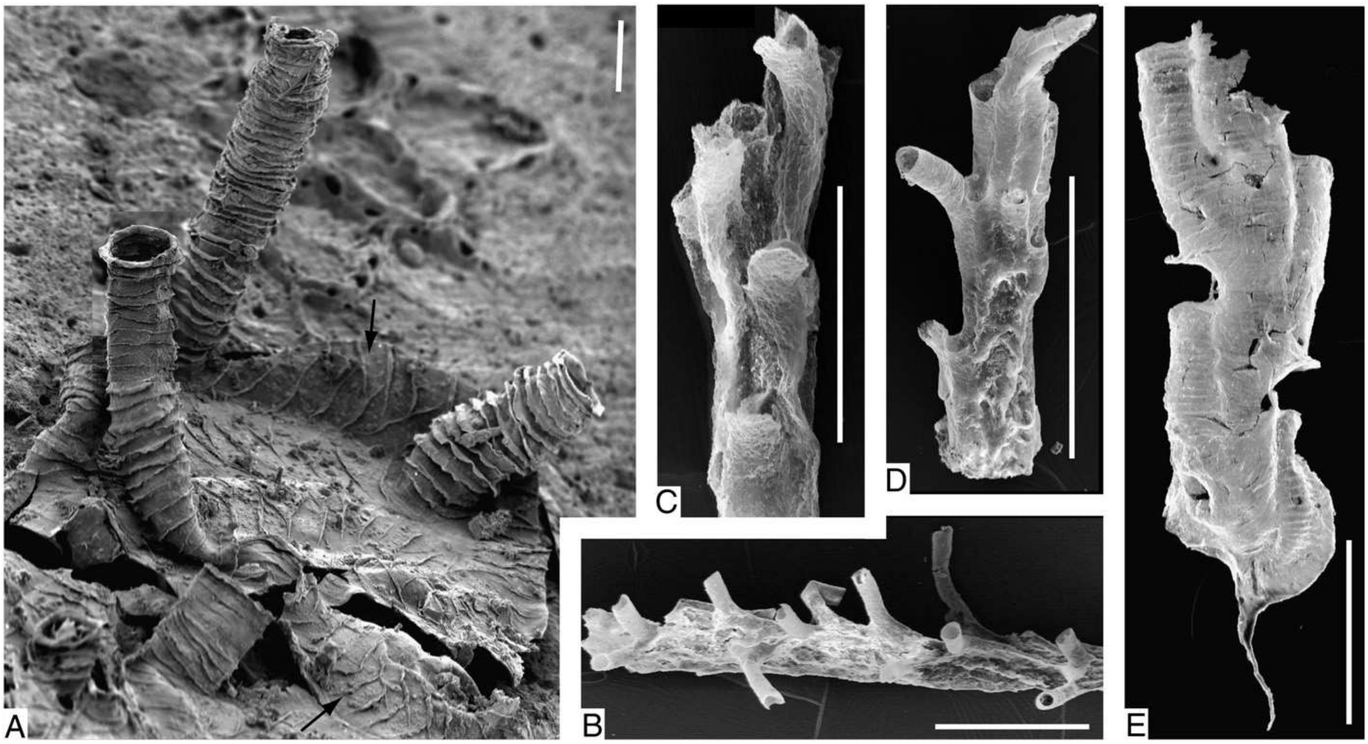

Fig. 3. Graptolithina, SEM photographs. A. *Rhabdopleura compacta*, extant, small dried and fractured colony showing three erect thecal tubes, fuselli visible, zigzag suture on creeping tubes indicated by arrow, colony was growing on the inside on an empty *Glycimeris* shell, North Sea near Plymouth, Britain, SMF 75727. B–D, *Acanthograptus divergens*, showing thecal tubes and complex colony development, Öland, Sweden, Darriwilian (Upper Middle Ordovician), LO 11412t (JM 39.5), LO 11413t (JM 39.2), LO 11414t (JM 39.4). E. *Geniculograptus typicalis*, axonophoran (biserial) colony with distinct fuselli visible on thecae, Katian (Upper Ordovician), Viola Limestone, Oklahoma, SMF 75726, SEM stub JM 25.8. Magnification: scale represents 0.1 mm in A; 1 mm in B–E.

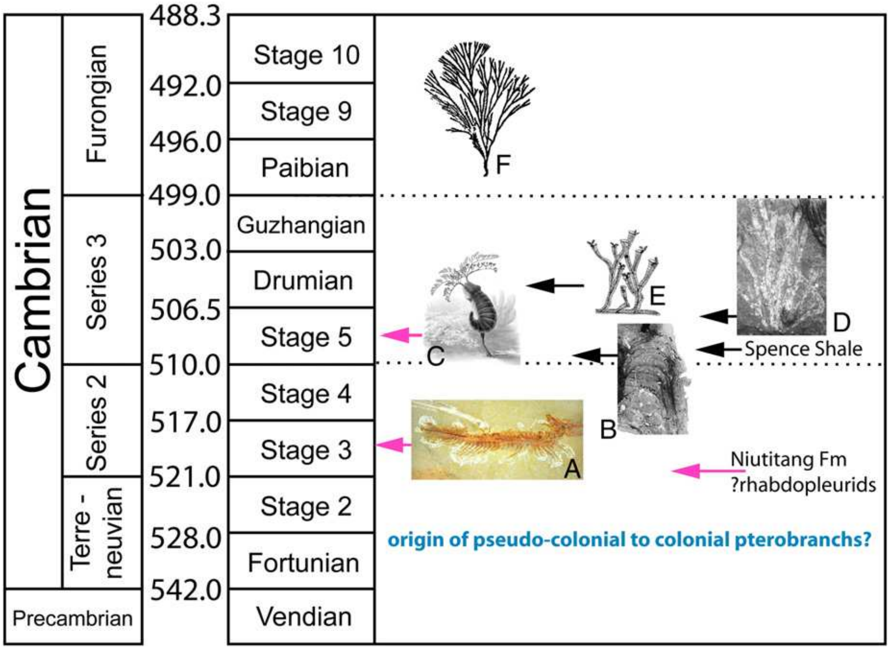

Fig. 4. Cambrian chronostratigraphy and record of putative Hemichordata. Numerical ages from www.stratigraphy.org. Ages of Chengjiang and Niutitang lagerstätten based on Zhu et al. (2006: Fig. 1). A. *Galeaplumosus*, Chengjiang (Hou et al., 2010). B. Pterobranch fragment, Kaili Formation (Harvey et al., 2012). C. *Herpetogaster*, Burgess Shale (Caron et al., 2010). D. ?*Cephalodiscus* sp. (Maletz et al., 2005). E. *'Rhabdopleura' obuti* (Durman and Sennikov, 1993). F. *Dendrograptus hallianus* (Bulman, 1970) as representative of early diverse benthic Dendroidea (Graptolithina).

feature of the prosicula of Lower Ordovician benthic dendrograptids (*Dendrograptus*: Kozlowski, 1949) and all subsequently evolved planktic graptolites (see Bulman, 1970). This feature may not be expected in any earlier Cambrian members of the Pterobranchia. The evidence of the presence of fuselli in the illustrations is not very convincing, as they are not recognizable in the provided photos. Fuselli are formed from 'durable' organic secretions of the zooids (e.g. graptolite tubaria) and should be better preserved than the zooids themselves, which here is not the case. The 'arms' of the zooid are directly adjacent to the remains of the 'cone-shaped zooid tube', without any traces of the body of a zooid being preserved. The conical zooidal tube – compared with the dimensions of a modern pterobranch – would be either a small fragment of a tube or the zooid might not be able to retract into the tube, facts that are questioning the original interpretation. The specimen of *Galeaplumosus*, if indeed a pterobranch hemichordate, represents the oldest known and only record of a recognizable fossil zooid of any pterobranch. From the original description and illustrations, however, it is not possible to confirm that the 'arm' and the 'tube' even belong to a single organism. They may actually represent unrelated fossil fragments and the association of these may be accidental.

Caron et al. (2010) introduced the genus *Herpetogaster* from the Middle Cambrian Burgess Shale of British Columbia as a sessile organism with a muscular stalk with attachment disk and prominent, elongate dendritic oral tentacles (Fig. 4C). The authors interpreted the taxon as a possible primitive deuterostome and made specific comparisons to the pterobranch hemichordates. The genus was included with the eldoniids in the stem group cambroernids as possible basal ambulacrarians. However, the comparison of a number of characters with the pterobranchs may be misleading as it is based on superficial evidence. The whole interpretation depends on the acceptance of the suggested homologies.

There are a number of important differences in the anatomy of the body between the known (extant) pterobranch zooids and the Cambrian *Herpetogaster* that may question the assumed homologies and make a closer phylogenetic relationship unlikely. The paired (*Rhabdopleura*) to multiple (*Cephalodiscus*) arms of modern pterobranchs are developed as an extension of the mesosoma or collar region of the organism, not as anterior developments on the head (prosoma or proboscis in Hemichordata) as in *Herpetogaster*. The oral tentacles of *Herpetogaster* are dendritic or fractal (see Caron et al., 2010) and not bilaterally symmetrical as in all known Pterobranchia (Fig. 1E, F), thus are unlikely to be homologous features. Even though it may be tempting to see the 'stolon' or 'stalk' with attachment disk as homologous to the stolon of the Pterobranchia, this may be a far fetched interpretation. It is based only on the suggestive labeling of the characters in both taxa. Donoghue and Purnell (2009, p. 187) state, that anatomical interpretations should not 'leap directly to a particular clade of living organisms […] as an interpretative model', meaning that we need to be more careful when we compare extinct and extant taxa and use the same terminology. We may limit our understanding through inadvertently forcing an interpretation through the choice of comparison. The features discussed in *Herpetogaster* may not be phylogenetically related to those of the Pterobranchia (e.g. synapomorphies), but of separate and independent origin and are similarly due to the purpose for their evolution as attachments for a benthic, sessile organism. Any closer relationships to the Pterobranchia cannot be supported at the moment and any body features of *Herpetogaster* that may show a resemblance to pterobranchs may have to be interpreted as convergence. The relationships of other taxa included in the cambroernids by Caron et al. (2010) cannot be explored here.

5. Fossil Enteropneusta

Modern enteropneusts can be found in almost all marine environments, from the tidal zone of the shallow water regions to the deep-sea environments and from tropical to arctic regions. In the past, they were largely regarded as infaunal inhabitants of mainly shallow shelf regions (Hyman, 1959). Recent evidence of common epibenthic enteropneust populations in deep-water environments is mounting, however (e.g. Holland et al., 2005, 2009). A single species, *Saxipendium coronatum*, is even restricted to hydrothermal vents (see Woodwick and Sensenbaugh, 1985; Tunnicliffe, 1992), indicating quite diverse life styles of the extant enteropneusts.

Due to the fragility of the enderopneust body (see remarks in Mauviel et al., 1987; Cameron, 2002) and the lack of any preservable hard parts, the fossil record of body fossils is extremely poor. Body fossils of enteropneusts can be formed only under very special conditions in the marine environment. These have never been explored and the known specimens are found in anoxic sediments. Conway Morris (1979) discussed the possibly oldest-known enteropneusts from the Burgess Shale of British Columbia. Boulter (2003) claimed that an undescribed enteropneust is one of the most common taxa of the Burgess Shale, possessing already the tripartite body plan with a proboscis, collar and trunk regions. However, the material has never been published and, thus, further information is not available at the moment.

Conway Morris (2009: p. 178) suggested that *Oesia disjuncta*, originally described as an annelid (Walcott, 1911), may belong to the hemichordates, as it shows vague similarities to a balanoglossid hemichordate. The taxon has been identified previously as a chaetognath (Szaniawski, 2005) and an appendicularian tunicate (Lohmann, 1922). Unfortunately, a complete redescription of *Oesia* is not available to support the suggestion. Caron and Jackson (2008) described the paleoecology of the Greater Phyllopod bed of the Burgess Shale and tabulated the fauna including three hemichordates; the possible benthic pterobranch *Chaunograptus scandens* (Ruedemann, 1931), the possible enteropneust *O. disjuncta* (= *Ottoia tenuis*) and a species only identified as Hemichordata A. None of these taxa has been described recently and their identity remains unclear.

Mazoglossus ramsdelli Bardack, 1997 from the Mazon Creek concretions of Illinois is currently the oldest fossil clearly identifiable as an enteropneust hemichordate, even though not much more than the general outline of the body is available for this taxon (Fig. 5). The concretions in the Francis Creek Shale have long been known and have extensively been explored (Shabica and Hay, 1997). The Mazon Creek Biota of northeastern Illinois provides a spectacular insight into the shallow marine to terrestrial life of the Upper Carboniferous (Pennsylvanian), ca. 280 MA ago, but is already more than 200 Ma younger than the next oldest possible enteropneust record, providing ample evidence for the highly patchy fossil record of the enteropneusts at least.

A number of occurrences of enteropneusts have been documented from Jurassic strata of western Europe. Of these, *Megaderaion sinemuriense* Arduini Pinna and Teruzzi, 1981 from the Sinemurian (Lower Jurassic) of Osteno (Lake Lugano) in northern Italy is the oldest. The small specimen (less than 20 mm long) is poorly preserved in coarse-grained sediment and preserves only the outline, but it clearly shows the tri-partite body of an enteropneust. The authors included the genus and species in the extant Harrimaniidae based on the body outline. Slightly younger is *Megaderaion callovianum* Alessandrello, Bracchi and Riou, 2004 from the Lower Callovian (Middle Jurassic) of La Voulte-sur-Rhône (Ardèche, France). The single specimen is preserved in three dimensions as a pyritic relief specimen, clearly showing the tri-partite body. The specimen is the best-preserved fossil enteropneust ever found.

Mesobalanoglossus buergeri Bechly and Frickhinger, 1999 (in Frickhinger, 1999) from the famous Solnhofen Limestones of Lower Tithonian (Upper Jurassic) age is the youngest of the Jurassic records of enteropneusts. *M. buergeri* is a slender worm, 68.8 cm long and 2.1 cm wide at the collar and, thus, differs considerably from the older *Megaderaion* species. The taxon was assigned to the Ptychoderidae due to the size and the enlarged genital region (genital wings) of the specimen. If the assignments of the Jurassic taxa to modern families can be substantiated, it may show a considerable conservativism of the enteropneusts.

6. Enteropneusta trace fossils

It is obviously impossible to recognize the maker of a certain trace in the fossil record without finding the producer in its tracks, or to have a modern counterpart that may provide a reasonable interpretation. Thus, speculations on trace fossils made by enteropneusts are difficult to verify, but a number of trace fossils have been suggested to be produced by enteropneusts or are similar to modern enteropneust traces. Traces of modern enteropneusts have been described numerous times and are quite variable (see van der Horst, 1934; Mauviel et al., 1987), based on their life styles as infaunal or epifaunal elements. The traces may be specific for certain species of enteropneusts (Duncan, 1987), but much more needs to be learned from modern taxa. Other modern marine trace fossils have been questionably assigned to the enteropneusts (e.g. Tuck and Atkinson, 1995), but have not been verified. Resting traces more easily show the shape of the producing organism and, thus, can verify the identity of the trace maker. A good example is the presumed resting trace of an enteropneust from the Lower Triassic (Twitchett, 1996), showing a shape very similar to that of a modern deep-sea member of the Torquaratoridae.

Various trace fossils have been suggested as being produced by enteropneusts (e.g. Mägdefrau, 1932: *Balanoglossites*; van der Horst, 1940: *Gyrolithus*) and have even been named, but the evidence is circumstantial as the producer of all these traces has never been identified definitively. Sörgel (1923) considered the U-shaped burrows with irregular lateral branching in the Thuringian Muschelkalk as being similar to the burrows of the modern enteropneust *Balanoglossus*. Mägdefrau (1932) discussed some trace fossils from the Muschelkalk of the Jena Region, Thuringia and described the trace fossil genus *Balanoglossites* with two species, *Balanoglossites eurystomus* (possibly produced by an enteropneust) and *Balanoglossites triadicus* (possibly produced by a polychaete). Kazmierczak and Psczikowski (1969) described burrow systems of possible enteropneusts from the equivalent Lower Muschelkalk (Triassic) of the Holy Cross Mountains of Poland. These infaunal burrow systems consist of a number of U-shaped tunnels connected by horizontal branches and are similar to the *Balanoglossites* traces described earlier by Mägdefrau (1932). Knaust (2008) revised the genus *Balanoglossites* and interpreted it as a complex burrowing and boring system. The author suggested a polychaete as the producer, based on the 'fingerprints' (scratches and striations) of the organism inside the burrows and borings, synonymizing both species erected by Mägdefrau (1932) and rejecting the notion of a possible enteropneust producer for the Thuringian and Polish Muschelkalk records.

Kern (1978: p. 255) described ?*Spirophycus* from the Cretaceous to Eocene flysch deposits of the Vienna Woods as possibly produced by an enteropneust. Mangano et al. (2000: p. 152) speculated that the trace fossil *Nereites* may have been produced by a worm-like sediment-feeder, probably an enteropneust, but no definite evidence is provided in these cases.

Recent records of deep-sea traces and their producers provide some important new insight into the production of fossil traces and their origins. Bourne and Heezen (1965) showed the first strong evidence for the identification of certain deep-water traces as the evidence of activities of enteropneusts. Meandering and spiral traces may be the mucus-coated fecal casts of deep-water enteropneusts and have been recorded commonly in modern deep-sea environments (e.g. Ewing and Davis, 1967; Heezen and Hollister, 1971; Foell and Pawson, 1986; Gaillard, 1991; Gage, 2005; Holland et al., 2005; Osborn et al., 2011). A number of specimens of a deep-sea enteropneust were observed and photographed during the production of their trails (Smith et al., 2005), showing that trails can be variably clockwise, anticlockwise or meandering in the same specimen. Thus, the individual species of deep-sea enteropneusts may not produce highly specific traces. A single specimen was observed to produce a trail of ca. four complete whorls in 39 h, before swimming away (Smith et al., 2005).

7. Pterobranchia

The Pterobranchia can be differentiated into the colonial Graptolithina, including the single extant genus *Rhabdopleura*, and

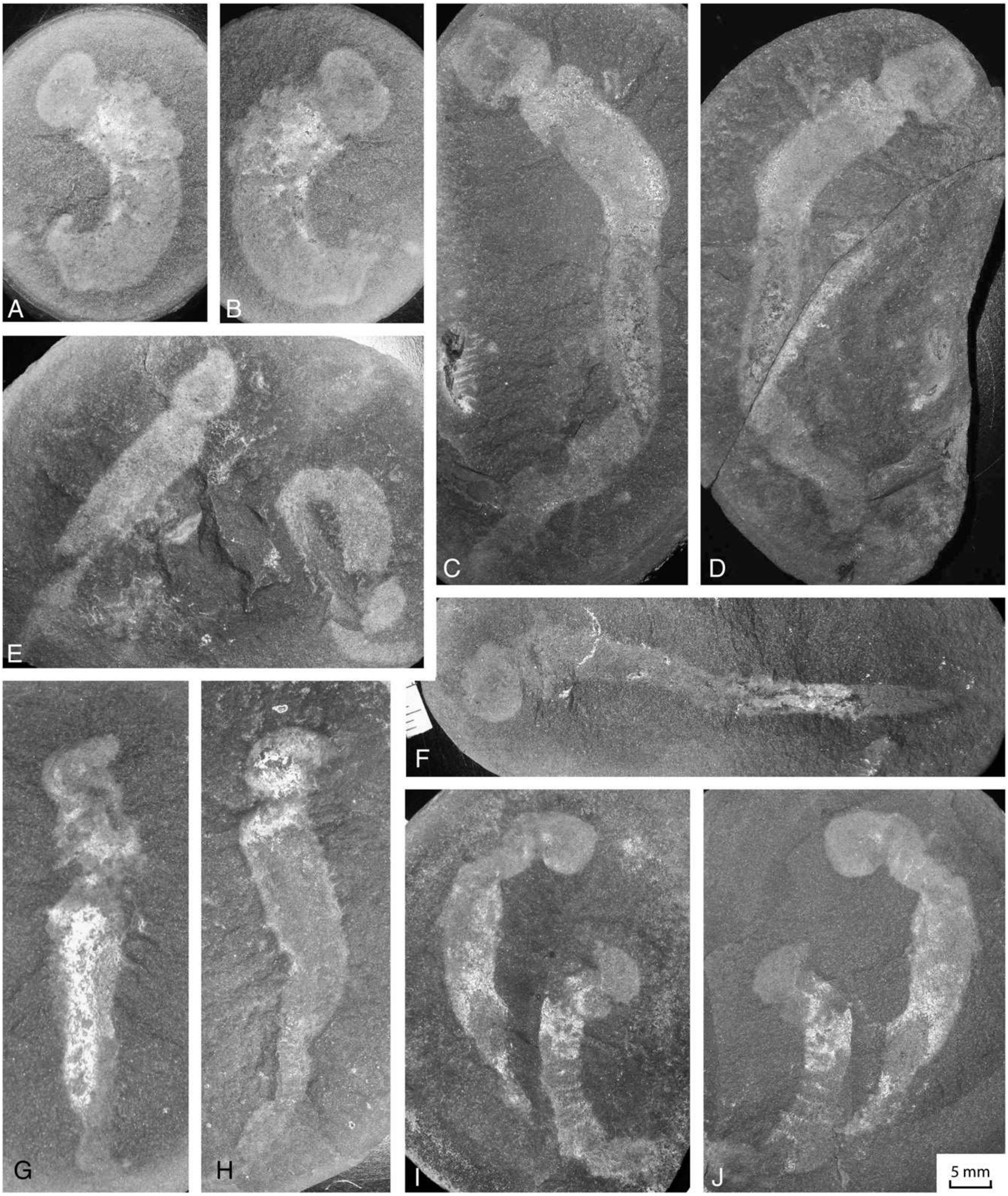

Fig. 5. *Mazoglossus ramsdelli* Bardack, 1997. A, B. PE 45 214, counterparts, frontal fragment of specimen. C, D. PE 23 053, counterparts, complete specimen. E. 47 806, two fragments. F. PE 56 605, complete specimen. G. PE 32 746, incomplete specimen. H. PE 57 104, nearly complete specimen with dark rim. I, J. PE 45 207, part and counterpart, holotype. Magnifications for all specimens shown by 5 mm long bar in J.

the non-colonial or pseudo-colonial Cephalodiscida (Mitchell et al., 2012). Even though both groups possess a complex life cycle with sexual and asexual (budding) reproduction, only the Graptolithina can be called truly colonial as their zooids stay in physical contact through their entire life, connected by the stolon system (gymnocaulus/pectocaulus) (Bulman, 1970). The sexually produced cephalodiscid zooids develop additional zooids on the basal disk of their stalks (Lester, 1985), but these separate as soon as they are mature and lead their individual lives, but staying closely together in the form of large pseudo-colonies or aggregations (e.g. Harmer, 1905; Hadfield, 1975). Dilly (2013), however, doubted the separation and interpreted the zooidal associations to be truly colonial.

The Pterobranchia have barely any credible fossil record of their zooids and are largely known by their tubaria or rhabdosomes. Briggs et al. (1995) showed that modern pterobranch zooids were unrecognizable after only a few days of decay, while the tubarium and the stolon system may be preservable for several months, providing an idea on how difficult it would be to preserve zooids in the fossil record. The most reliable record of fossil zooids is by Durman and Sennikov (1993: Figs. 3–2), who described zooids from a Middle Cambrian (Drumian) rhabdopleurid including even faint indications of the lophophore (=arm). Other records of possible zooidal fossils include Bjerreskov (1978), Rickards and Stait (1984) and Loydell et al. (2004), but in none of these cases are any details of the body construction visible and the fossils consist of elongated bodies of darker material or pyrite within the thecal tubes or extending outside of these.

The tubaria of fossil Pterobranchia are found commonly only after the taxa attained a planktic lifestyle in the Ordovician. However, a few possible benthic ones are known from the Cambrian. Recognition of the typical fusellar construction is difficult, but is the only way to ascertain their taxonomic relationships. Maletz et al. (2005) recognized the fusellar structure in ?*Cephalodiscus* sp. from the Cambrian Wheeler Shale only through an investigation with BSE-SEM-microscopy (back scatter electron investigation) of a specimen initially identified as a Cambrian algae. Steiner and Maletz (2012) suggested that many taxa originally described as Cambrian algae may actually represent early pterobranchs. The findings indicate that additional pterobranch fossils may be hidden in the fossil record of Cambrian 'algae'.

7.1. Cephalodiscida

The non-colonial cephalodiscids are represented in the fossil record from the Middle Cambrian (Maletz et al., 2005; Rickards and Durman, 2006) and Ordovician (Kozlowski, 1949), but lacks any further credible fossil record. Bengtson and Urbanek (1986) described *Rhabdotubus johanssoni* from the *Eccaparadoxides pinus* Biozone of Närke, Sweden, as a rhabdopleurid pterobranch, but Maletz et al. (2005) placed the taxon to the cephalodiscids due to the lack of a stolon, the typical rhabdopleurid suture patterns and any evidence of connections between the individual tubes. The age of this material can now be assessed as to be Series 3, Stage 5 of the Cambrian System (see Babcock and Peng, 2007). A small number of sixteen extant species referred to four subgenera of *Cephalodiscus* (*Acoelothecia*, *Demiothecia*, *Idiothecia*, *Orthoecus*) have been described from marine regions worldwide (Markham, 1971). The non-colonial genus *Atubaria* (Sato, 1936; Komai, 1949) is considered a cephalodiscid, but does not secrete a tubarium.

7.2. Graptolithina

The fossil record of benthic Rhabdopleurida, including the extant *Rhabdopleura* (Fig. 3A) and related taxa, is largely restricted to fragmentary material found mostly in acid dissolutions (e.g. Kozlowski, 1956; Kulicki, 1969, 1971; Mierzejewski, 1986). Sato et al. (2008b: p. 312) suggested a divergence of the pterobranchs slightly before 530 Ma in the earliest Middle Cambrian, but first fossil records are considerably younger (Fig. 4). Questionable rhabdopleurids are mentioned from the Niutitang Formation of Guizhou Province, China (Zhao et al., 1999; Peng et al., 2005), but illustrations are inconclusive to verify the affinities of these fossils.

First recognizable tubarium secreting and colonial pterobranchs can be found in the basal stage 5 (Harvey et al., 2012) as tubarium fragments. It is, however, unclear whether these fragments originate from a colonial (graptolitic) or non-colonial (cephalodiscid) member of the Pterobranchia. More complete forms can be found in upper stage 5 or in the basal Drumian (Stage 6) with the Scandinavian *Rhabdotubus* (Bengtson and Urbanek, 1986; Maletz et al., 2005) and the slightly younger possible dithecoids of Johnston et al. (2009). Especially *Rhabdotubus* clearly shows the development of the typical pterobranch tubes, secreted presumably by a gland on the preoral disk of a zooid, similar to the modern rhabdopleurids and cephalodiscids and showing fusellar structures. By then, the colonial or pseudocolonial pterobranchs must have been safely established, indicating an origin in some earlier time interval. The single ?*Cephalodiscus* sp. specimen of Maletz et al. (2005) from the Wheeler Shale of North America also belongs to this group.

The genus *Chaunograptus* from the Middle Cambrian Burgess Shale (Ruedemann, 1931) may represent the oldest known colonial pterobranch, if fusellar construction and the presence of a stolon system can be established for the genus. Bulman (1970: V54) listed *Chaunograptus* as a graptolite with uncertain position. The shape of *C. scandens* indicates a possible colonial organism, but the taxon could also represent a colonial hydroid.

One of the oldest known, clearly colonial pterobranchs is '*Rhabdopleura*' *obuti* (Durman and Sennikov, 1993) from the Mayan (Middle Cambrian) of the Sukhan Depression of Siberia. The specimens show well-preserved tubaria with fusellar structures, indicating a fairly regular development of the tubarium. However, a differentiation of the creeping part with dorsal a zigzag suture and an erect part with fusellar full rings and distinct collars as in modern *Rhabdopleura* is apparently not developed, or at least is not recognizable from the illustrations despite being described. Other differences to *Rhabdopleura* include the obvious widening of the robust, erect tubes and their branching patterns, which has never been recognized in erect tubes of extant and extinct *Rhabdopleura* species. The species, thus, may not be referred to the genus *Rhabdopleura*. The taxon undoubtedly represents one of the oldest colonial pterobranchs on record.

The typical development of the *Rhabdopleura* tubarium is first recorded from the Middle Ordovician (Kozlowski, 1961: *Rhabdopleuroides*; Skevington, 1965: graptovermids; Mierzejewski, 1986) and indicates little change during a long time of evolution of the taxon. The few records from the Middle Cambrian (Durman and Sennikov, 1993; Rickards and Durman, 2006) onwards to the Eocene (Thomas and Davis, 1949; Bulman, 1970) show little change in their tubarium construction. Chapman et al. (1995) provided a complete record of previously described fossil rhabdopleurids, but did not discuss the record of extant species.

The Middle Cambrian is the first occurrence for a number of poorly known erect graptoloids (see Rickards and Durman, 2006). These may conveniently be included in the Dithecoidea of Obut (1964) at the moment, even though little is known on their exact structure and phylogenetic relationships. The group includes species described as *Archaocryptolaria*, *Archaeolafoea*, *Tarnagraptus*, *Ovetograptus* and *Sotograptus* among others (see Sdzuy, 1974). The only morphologically similar taxon described from isolated material is a Middle Ordovician species of *Mastigograptus* (see Andres, 1977; Bates and Urbanek, 2002), showing the typical triad budding system of derived graptoloids. Johnston et al. (2009) illustrated a number of erect 'dithecoid'-like, bushy graptolites from a Burgess Shale-type biota on Haiduk and Tangle Peaks, British Columbia, which may represent the oldest taxa of this group. The material originates from the *Bolaspidella* trilobite zone of Drumian age (see Babcock et al., 2007) and is thus slightly younger than the Burgess Shale. The material from the *Paradoxides oelandicus* to *Paradoxides paradoxissimus* trilobite zones of the Cantabrian Mountains of Spain (Szuy, 1974) is much more fragmented and may be slightly older. Younger faunas with dithecoid graptolites are common in the Furongian, Upper Cambrian (review in Rickards and Durman, 2006).

Bushy dendroid graptolites of the genera *Dendrograptus*, *Desmograptus*, *Dictyonema* and others probably appear around the base of the upper Cambrian (Paibian), but are rarely found. Rickards et al. (1990) described one of the richest faunas of this age from the Idamean of Tasmania, indicating a quite remarkable diversity of taxa.

8. Conclusions

The Hemichordata can be regarded as a sister-group of the echinoderms and have their roots in the Lower Cambrian, but apart from this, little is known. Their earliest occurrence is still shrouded in uncertainty, as the affinities of fossil hemichordates from the Lower Cambrian are called into question. Earliest hemichordate fossils are probably found in the Burgess Shale of Stage 5 (Series 3) of the Cambrian System and are represented by undescribed enteropneust-like organisms as well as pseudocolonial to colonial pterobranchs.

The oldest reliable fossil enteropneust remains *Mazoglossus* from the Mazon Creek Biota of Carboniferous age, more than 200 Million years younger than the Burgess Shale faunas. It is related to the extant enteropneusts only through a few Mesozoic (Jurassic) taxa found as individual well-preserved specimens, but again not offering much detail of their body construction and closer phylogenetic relationships. The youngest of these records from the Tithonian Solnhofen Limestone of Germany is about 150 Ma old and represents the youngest fossil record of any enteropneust. These fossil enteropneusts cannot be reliably assigned to any modern enteropneust clades or families, unfortunately.

The scant record of fossil hemichordates might support the idea expressed by Cameron et al. (2000) of an origin of the pterobranchs from a mobile, benthic enteropneust ancestor within the Enteropneusta and not as a sister group to the enteropneusts. However, there is little evidence in the fossil record to suggest a reliable date of origin of any of the involved groups. If the notion of the origin of the pterobranchs from within the Enteropneusta can be confirmed, it is clear that the evolution of the Pterobranchia led to a reduction in size and complexity of the organization of the organisms to a clonal, colonial organism. However, other aspects of extant pterobranchs and enteropneusts like the feeding strategy, reproduction, ontogeny and developmental biology (Sato et al., 2008a), even morphological traits (asymmetry: Sato and Holland, 2008) may provide important information to the origin of the hemichordates. Thus, information not available from the fossil record of the graptolite tubaria would be essential for the understanding of the phylogenetic relationships of the group, even though direct data for the transition may not be available.

The subsequent evolution of the Pterobranchia (Cephalodiscida and Graptolithina: Mitchell et al., 2012) from the Middle Cambrian onwards can be followed through the fossil record in some detail, showing a stepwise change from a creeping to an erect mode of colony growth. A modification of thecal styles and colony shape is obvious, but the record is sketchy for benthic taxa. Sato et al. (2008b) claimed that *Rhabdopleura* is one of the most long-ranging living fossils, spanning an interval of more than 500 Million years. This might be exaggerated, as we know only the tubarium construction, but not the soft body anatomy of the inhabiting organism. Even the precise tubarium design seen in extant *Rhabdopleura* species is first found in Ordovician strata.

While there is very little evidence of body fossils of fossil Hemichordata and the actual construction of their bodies remains unexplained, putative trace fossils of enteropneusts may at least be able to provide us with a suggestion of the life style and distribution of this group of animals in the geological past.

9. Systematic paleontology

Repositories. The illustrated material is preserved in the following collections: FMNH PE (Field Museum, Chicago, Illinois, USA), MBx (Museum für Naturkunde, Berlin, Germany), LO (Lund Original, Department of Geology, Lund University, Sweden), SMF (Forschungsinstitut Senckenberg, Frankfurt/Main, Germany).

Phylum HEMICHORDATA Bateson, 1885 (emend. Fowler, 1892)

Class ENTEROPNEUSTA Gegenbaur, 1870, p. 158

Remarks: Cameron (2002, p. 191) provided a very useful key to the extant families and genera of the Enteropneusta. A number of recent discoveries need to be added to the record, however (Holland et al., 2009; Osborn et al., 2012; Priede et al., 2012; Worsaae et al., 2012).

Genus **Mazoglossus** Bardack, 1997

Type species: *Mazoglossus ramsdelli* Bardack, 1997; original designation.

Diagnosis (Bardack, 1997: p. 89): Small specimens (less than 10 cm total length) enteropneusts, recognizable by outline shape of proboscis, collar, trunk and small, circular branchial pores(?).

Remarks: The genus is based on the outline of the type species only, as further details are not available. Even though the shape of *Mazoglossus ramsdelli* indicates its enteropneust relationships, no further taxonomic and evolutionary interpretations should be based upon it. Therefore, the genus is not assigned to any of the modern enteropneust families.

Mazoglossus ramsdelli Bardack, 1997.
(Fig. 5A–J)

1997 *Mazaglossus ramsdelli* n. sp., n. gen. — Bardack, p. 89, Figs. 7C1–C8.

Diagnosis: Slender worm-like body with the distinct tripartite body of an enteropneust, proboscis short, often vaguely triangular and wider than long; trunk initially parallel-sided, distinctly narrowing distally into a slender tail.

Type material: Bardack (1997) selected FNMH PE 45207 as the holotype of the species, but did not figure this specimen in his paper. He also referred to numerous specimens in various collections, both public museums and private. The concretion with the number PE 45207 is preserved in both counterparts and a third piece, which is the counterpart to a fragment possibly also belonging to *M. ramsdelli* in the same concretion (not illustrated herein). Unfortunately, the type concretion includes two incomplete specimens of *M. ramsdelli* (Fig. 5I, J), both of which lack the tail. The upper specimen in Fig. 5I, J is here designated the lectotype, while the second specimen is recognized as a paralectotype. Both specimens are illustrated here for the first time. The concretion originates from the Francis Creek Shale, of Carbondale, Will, Kanakee or Grundy Co., Illinois, USA.

Description: The lectotype and lectoparatype (Fig. 5I, J) are incomplete, showing a rounded proboscis, a collar that is difficult to differentiate from the initial part of the trunk and a partly preserved trunk without the more slender distal part. The lectotype is more than 55 mm long and gently curled. The proboscis is 8 mm wide and 6 mm long. A constriction is present but the collar is difficult to recognize and is incompletely preserved. The preserved trunk region is 7 mm wide, but the distal part is lacking and the complete length and width of the trunk and tail regions cannot be seen. The lectoparatype is slightly smaller, but is equally incomplete.

Other investigated specimens are quite variable in length and also completeness of the body. Thus, exact dimensions are difficult to provide for the species. The specimens are ca. 30–80 mm long and 5 to 11 mm wide at the collar. A single most complete specimen, used here for the detailed description (Fig. 5C, D), is about 70 mm long including a possibly complete tail and providing information on the relations of the body parts. It has a proboscis about 15 mm long and 10 mm wide, which tapers only slightly to the front. Details are not preserved in the proboscis. A distinct constriction separates the proboscis from the collar, a features observable in nearly all available specimens. The collar is 10 mm wide and 5–7 mm long, thus clearly wider than long, but is often difficult to differentiate from the trunk region. The trunk starts at a width of 8–9 mm, slightly more slender than proboscis and collar and is parallel-sided for about 15 mm. Then a pronounced restriction follows, separating a tail region of about 6 mm wide and 45–50 mm long, that tapers slowly only in the last 10 mm.

Remarks: Most available specimens are incomplete and can only be recognized as enteropneusts in cases in which the frontal part of the animal with the constriction behind the proboscis is preserved (Fig. 5A, B). A number of specimens suggest the differentiation of the internal alimentary tract through slight differences in the preservation (Fig. 5C, D, F), but this may also be taphonomic and should not be over-interpreted. The specimens are either straight or coiled in the concretions and commonly more than one specimen is present. Bardack (1997) described more or less regular transverse patterns of epidermal grooves, but these are not recognizable with certainty, as also the recognition of branchial pores has to be questioned. These have not been verified in any of the investigated specimens.

Preservation: The Mazon Creek fossils are invariably found in siderite concretions formed around organic remains (Baird, 1997a), and a differentiation is made between the marine “Essex Fauna” and the non-marine to brackish “Braidwood” Fauna (Baird, 1997b). All investigated enteropneust specimens originate from the “Essex” fauna. They are completely flattened and can be recognized only due to the lighter color of the sediment outlining the specimens, not due to the preservation of any organic material. Surrounding sediment does not differ in grain size and composition, but in its slightly darker color. Light gray to whitish parts of the specimens (e.g. Fig. 5G, H) are due to mineralizations, possibly secondary or even representing modern weathering effects. They are irregularly distributed on the specimens, but do not penetrate into the surrounding sediment. The outlines of specimens are often distorted and unclear, possibly an effect of decay of the organic material (Bardack, 1997). This is clearly visible when comparing the proboscis of a number of specimens. Rounded and short proboscis shapes (Fig. 5A) occur together with more square ones (Fig. 5I, J) and also elongated ones (Fig. 5C, D). These details are regarded as preservational aspects of a soft-bodied organism in which shapes can be changed considerably, and also modified by the decay of the material (Bardack, 1997). All specimens are found in concretions without evidence of burrowing or any indications of traces, even though trace fossils are sometimes present in the concretions and the surrounding sediments (Shabica, 1997). Therefore, it is difficult to conclude whether they were infaunal or epifaunal.

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