Calcareous tubeworms of the Phanerozoic

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Abstract. Morphological similarities indicate that Palaeozoic problematic tubeworms, e.g. tentaculitids, cornulitids, microconchids, trypanoporids, *Anticalyptraea*, and *Tymbochoos*, form a monophyletic group. This group may also include hederelloids. Members of this group share affinities with lophophorates and their evolution could have partly been driven by predation. The extinction of Palaeozoic tubeworms in the Middle Jurassic was possibly at least partly caused by the ecological pressure by serpulid and sabellid polychaetes. The input of Palaeozoic tubeworms to the general ocean biocalcification system may have been smaller in the Ordovician to Jurassic than that of calcareous polychaetes in the Late Triassic to Recent. There seems to have been some correlation between the aragonite–calcite seas and the skeletal mineralogy of Triassic–Recent polychaete tubeworms.

Key words: Phanerozoic, Polychaeta, Lophophorata, tubeworms, problematic fossils, calcification, biomineralization.

INTRODUCTION

In modern oceans hard substrates are often heavily encrusted by serpulid polychaetes. Serpulids were also important encrusting organisms in the geological past (ten Hove & van den Hurk 1993). Serpulids (Family Serpulidae) dwell in calcium carbonate tubes made of aragonite, calcite or a mixture of aragonite and calcite (Bornhold & Milliman 1973; Vinn et al. 2008b). In addition to serpulids, one species of sabellid (Family Sabellidae) – *Glomerula piloseta* – and a few species of cirratulids (Family Cirratulidae), build calcareous tubes (Vinn et al. 2008a, 2008b). Serpulids are globally distributed, whereas calcareous sabellids and cirratulids are known only from tropical and subtropical habitats (Perkins 1991; ten Hove & van den Hurk 1993; Fischer et al. 2000). Serpulids were probably the first polychaete tubeworms to build biomineralized tubes, with the earliest certain representatives of Middle Triassic age (Stiller 2000; Vinn et al. 2008a, 2008c). They were soon followed by calcareous sabellids (e.g. *Glomerula*) in the Early Jurassic (Parsch 1956; Jäger 2004; Vinn et al. 2008a), and later by calcareous cirratulids in the Oligocene (Fischer et al. 2000).

There are reports in the literature of Cambrian and Ordovician serpulids (e.g. Dalvé 1948; Clausen & Álvaro 2002), but none of these records show the presence of unequivocal serpulid or calcareous polychaete skeletal characters (Weedon 1990, 1991, 1994; ten Hove & van den Hurk 1993; Vinn & Mutvei 2005; Vinn 2005a, 2005c, 2006b; Vinn & Furrer 2008; Vinn et al. 2008a,

2008b, 2008c, 2008d). Therefore most likely these fossils belong to various Palaeozoic tubicolous problematica. The Palaeozoic to Middle Jurassic spirorbiform tubeworms, interpreted as the polychaete *Spirorbis* in the older geological literature, have more recently been reinterpreted as microconchids (Weedon 1991, 1994; Taylor & Vinn 2006; Vinn 2006a; Vinn & Taylor 2007). They share affinities with tentaculitids (Weedon 1991, 1994) and more generally with lophophorates (Taylor & Vinn 2006). The other common Palaeozoic tubeworm-like calcitic problematica (tentaculitids, cornulitids, and trypanoporids) have often been affiliated with annelids, but are more recently transferred to lophophorates (Weedon 1990, 1991, 1994; Vinn & Mutvei 2005; Vinn 2005a, 2006b; Vinn & Isakar 2007; Vinn & Mõtus 2008). Some tubeworm-like Early Palaeozoic phosphatic fossils such as *Sphenothallus* (van Iten et al. 1992) and the related hyolithelminth *Torellella* (Vinn 2006c) have been interpreted as cnidarians on the basis of their tube structure. Serpulid-like, chevron-shaped growth lamellae (Weedon 1994; Vinn & Furrer 2008) have been described in the originally calcareous tubes of Cambrian anabaritids (Kouchinsky & Bengtson 2002). However, a convergent development seems to be the most likely explanation because the three radial shell symmetry in anabaritids is alien to serpulids, and there is a long stratigraphic gap to the first record of unequivocal serpulids in the Triassic (Ziegler & Michalík 1980; Stiller 2000; Senowbari-Daryan & Link 2005; Senowbari-Daryan et al. 2007).

In modern oceans lophophorate worms are represented by non-biomineralizing phoronids which dwell in mucus

tubes (Emig 1982). The ichnofossil record of inferred phoronids dates back to the Devonian (as *Talpina*, Bromley 2004). However, some of the Early Palaeozoic questionable polychaete worm borings in brachiopod shells could have been made by phoronids (Vinn 2005b). Enigmatic Palaeozoic tubicolous biomineralized tubeworms such as cornulitids (Vinn & Mutvei 2005; Vinn 2005a; Vinn & Mõtus 2008), microconchids (Taylor & Vinn 2006; Vinn 2006a, Vinn & Taylor 2007), *Tymbochoos* (Vinn 2006b), *Anticalyptraea* (Vinn & Isakar 2007), and tubicolous colonial hederelloids (Taylor & Wilson 2008), could represent calcifying phoronids or phoronid-related lophophorate worms.

The aims of the paper are to discuss (1) the zoological affinities and phylogeny of Palaeozoic problematic tubeworm faunas, (2) the biomineralization of calcareous polychaete tubeworms throughout the time, (3) the morphological convergence and similarities in the ecology of Palaeozoic problematic tubeworms and calcareous polychaete tubeworms, (4) the evolutionary replacement of Palaeozoic problematic tubeworms by calcareous polychaete tubeworms, and (5) the comparative input of problematic tubeworms and calcareous polychaete tubeworms to global biocalcification.

SKELETAL STRUCTURES AND BIOMINERALIZATION IN POLYCHAETE TUBEWORMS, AND IMPLICATIOS FOR THE AFFINITIES OF PALAEOZOIC PROBLEMATIC TUBEWORMS

Serpulid tubes have usually chevron-shaped growth lamellae (in longitudinal section), but the lamellae can also be straight in some species (Weedon 1994; Vinn & Furrer 2008; Vinn et al. 2008a, 2008b, 2008c). Most serpulid tubes are single-layered but can also contain up to four, ultrastructurally different, layers (Vinn et al. 2008b). Serpulid tubes can have an unoriented, uniformly oriented, or complex oriented structure. At least thirteen distinct tube ultrastructures have hitherto been described (Vinn et al. 2008b, 2008d). Some particularly interesting evolutionary trends in the development of complex structures in serpulid tubes, such as the lamello-fibrillar structure (Fig. 1A), occur only in genera of the *Crucigera*, *Hydroides*, *Serpula*, *Ditrupa*, *Pseudochitinopoma*, *Ficopomatus*, *Galeolaria*, *Pomatoceros*, *Laminatubus* clade (Vinn et al. 2008b). These complex structures that challenge the traditional carbonate slurry model (Hedley 1958; Neff 1971) of serpulid tube secretion (Vinn 2005c; Vinn et al. 2008a, 2008b, 2008d) probably evolved in the Cretaceous (Vinn & Furrer 2008), but in the Cenozoic at the latest (Vinn 2007, 2008). It is likely that the formation of the complex oriented structures in serpulids is directly controlled by cells or organic matrix

(Vinn et al. 2008a, 2008b, 2008d; Vinn et al. 2009). These structures probably had advanced mechanical properties and evolved from weaker, unoriented structures (Vinn 2008; Vinn et al. 2008b). In contrast, the calcareous tube structures in sabellids (e.g. *Glomerula*) and cirratulids have not changed since their appearance in the Early Jurassic and Oligocene, respectively. Sabellid polychaetes and cirratulids have a less advanced biomineralization system as compared to that of serpulid polychaetes, and have therefore a restricted number of tube ultrastructures (Vinn et al. 2008a, 2008b). The tubes of calcareous sabellids contain a thin, external, spherulitic layer and a thick, inner, spherulitic prismatic layer (Vinn et al. 2008a; Fig. 1B). In cirratulid tubes only the spherulitic prismatic structure and homogeneous structure are known (Vinn et al. 2008a, 2008b; Vinn 2009b; Fig. 1C).

The recent, improved understanding of tube structures and their biomineralization has enabled us to prove serpulid affinities of problematic tubeworms, such as '*Serpula*' *etalensis* from the Early Jurassic of Germany (Vinn et al. 2008c). Polychaete tubes differ from Palaeozoic problematic tubeworm tubes in the following features: (1) polychaete tubes (e.g. Serpulidae, Sabellidae, Cirratulidae) do not have a bulb-like, closed, embryonic chamber that is characteristic of Palaeozoic tubeworms and which resembles the protoconch of mollusks and the protoecium of bryozoans (ten Hove & van den Hurk 1993; Taylor & Vinn 2006; Fig. 1D, E); (2) polychaetes never build calcitic microlamellar shell structures, composed of plate-like crystallites that are oriented parallel to growth layers (Vinn & Mutvei 2005; Vinn 2005a; Taylor & Vinn 2006, Fig. 1F); (3) crystallites of lamellar polychaetes are always oriented perpendicular to growth layers (e.g. *Glomerula*, cirratulids) (Vinn et al. 2008a; Vinn 2009b; Fig. 1B, C); (4) polychaetes have no pseudopunctae and microscopic pores in the tube wall (Vinn 2005c, 2007, 2008; Vinn et al. 2008a, 2008b, 2008c, 2008d; Fig. 1F); (5) polychaetes do not have an external organic tube lining similar to the periostracum of mollusks and the external organic cuticle of bryozoans (Nishi 1993; Vinn et al. 2008b).

PALAEOZOIC PROBLEMATIC TUBEWORMS AND THEIR AFFINITIES

Palaeozoic problematic tubeworms comprise (1) thick-walled tentaculitids (Chonioconarida Farsan, 1994), exclusively free-living, (Ordovician?) Silurian to Devonian (Carboniferous?); (2) dacryoconarids (Dacryoconarida Fisher, 1962), exclusively free-living, Devonian; (3) cornulitids (Cornulitidae Fisher, 1962), substrate-cemented, with some secondarily free-living forms, Middle Ordovician to Carboniferous; (4) micro-
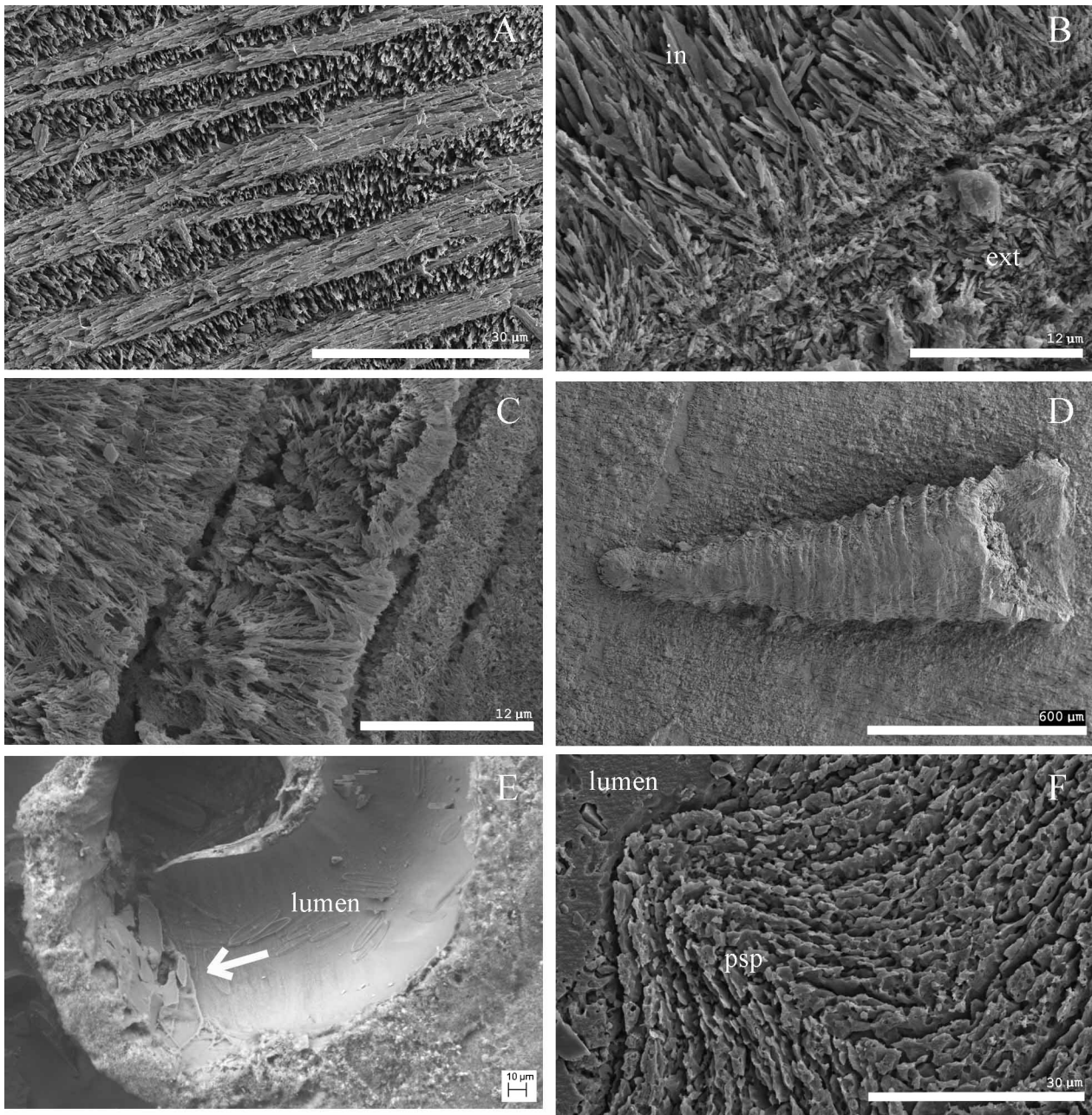
Fig. 1. Morphology and tube structure of Phanerozoic calcareous tubeworms. **A**, serpulid *Spiraserpula* sp., cross section of the lamello-fibrillar structure, Badenian, Miocene, Nussdorf, Austria, NHMW 2006z0233/0007. **B**, sabellid *Glomerula piloseta* (Perkins, 1991), longitudinal section through the inner spherulitic prismatic and outer spherulitic tube layers, Recent, Lizard Island, Australia, ZMA.V.Pol.3744. **C**, cirratulid *Diplochaetetes mexicanus* Wilson, 1986, longitudinal section of the spherulitic prismatic layer, Oligocene, Baja California, ZMA.V.Pol.3808. **D**, cornulitid *Conchicolites* aff. *gregarius*, showing a bulbous, closed, embryonic chamber, Grinstone Member, Ellis Bay Formation, Hirnantian, Ordovician, Anticosti Island, NRMAn 2750. **E**, serpulid *Spirorbis* sp., substrate-cemented side, showing an open tube apex (arrow), Recent, North Sea. **F**, *Anticalyptraea calyptrata* (Eichwald, 1860) longitudinal section of microlamellar tube wall with a pseudopuncta, Ludlow, Silurian, Lau backe, Gotland, NRMMo 36739. **A–C**, **F** polished and treated with 1% acetic acid for 2 min. Abbreviations: ext, external layer; in, inner layer; psp, pseudopuncta.

conchids (Microconchida Weedon, 1991), exclusively substrate cemented, Upper Ordovician to Middle Jurassic; and (5) trypanoporids (Trypanoporida Weedon, 1991), exclusively substrate-cemented, Devonian. Other, related 'tubeworms' include *Anticalyptraea* Quenstedt, 1867, exclusively substrate-cemented, Silurian to Middle Devonian (Dzik 1983), and *Tymbochoos* (Okulitch, 1937) exclusively substrate-cemented, Ordovician.

Phylogenetic relationships of substrate-cemented Palaeozoic problematic tubeworms

There are strong morphological similarities between the Palaeozoic problematic tubeworms, including micro-conchids, trypanoporids, cornulitids, and *Anticalyptraea*. These features include calcitic, substrate-cemented tubes, microlamellar tube structure, pseudopunctae (but not in all species), bulb-like embryonic shells part and septae, all of which suggest a monophyletic origin. Unfortunately, the embryonic shell of *Tymbochoos* is not known, but we tentatively assign it to this group because of the microlamellar shell structure and pseudopunctae.

One group of Palaeozoic problematic tubeworms, hederelloids (Silurian to Permian) (Taylor & Wilson 2008), also resembles the substrate-cemented, tubeworm-like problematica described above. Although hederelloids are pseudocolonial and lack microlamellar shell structure, they, too, are substrate-cemented, calcitic, and have a bulb-like embryonic shell and septae (Taylor & Wilson 2008). A ripple mark-like inner tube ornamentation is known both in hederelloids (Taylor & Wilson 2008) and microconchids (Vinn & Taylor 2007).

Phylogenetic relationships of cornulitids and tentaculitids

The morphology of cornulitids (Vinn 2005a; Vinn & Mutvei 2005) and thick-walled tentaculitids (Larsson 1979; Farsan 2005) exhibits several similarities, such as the calcitic shell of a similar shape, similar micro-lamellar shell structure, and the presence of similarly oriented pseudopunctae, both internal and external annulation, septae, and a bulb-like embryonic shell separated by constriction from the adult part of the shell. These features suggest a close phylogenetic relationship, and most likely an ancestor-descendant relationship (Bouček 1964; Dzik 1991; Vinn 2005a; Vinn & Mutvei 2005). However, these fossils had different life styles (substrate-cemented in cornulitids versus free-living in tentaculitids) and their shell formation began at different ontogenetic stages. Cornulitids have a post-larval shell (Vinn & Mutvei 2005) which begins with the initial

bulbous embryonic shell. In tentaculitids the shell first appeared in the larval stage as a long conical process, which was then followed by a bulb-like embryonic shell in the post-larval stage (Farsan 2005). This could mean that tentaculitids may have had a longer larval stage than cornulitids. If that was the case, the thick-walled tentaculitids may have had a planktotrophic larva and cornulitids a lecithotrophic larva. On the basis of the geological age, Dzik (1991) suggested that younger tentaculitids could have been derived from older cornulitids. Indeed, it seems more likely that tentaculitids originated from cornulitids than vice versa, because the substrate-cemented lifestyle does not require loss of the larval shell. In substrate-cemented mollusks, such as vermetid gastropods, the larval shell is preserved. The same could be expected of cornulitids if they had evolved from a tentaculitid ancestor with a larval shell.

Phylogenetic relationships of Palaeozoic problematic tubeworms

Considering on the morphological similarities, we hypo-thesize here that tentaculitids, cornulitids, microconchids, trypanoporids, *Anticalyptraea*, and *Tymbochoos* form a monophyletic group and that their skeletons are homologous (Fig. 2). It is possible that hederelloids also belong to this group. We also hypothesize that the substrate-cemented forms (lacking larval shell) form a sister group to free-living tentaculitids (larval shell present) (Fig. 2). Within the substrate-cemented group, it is possible that spirorbiform microconchids (Upper Ordovician) have been derived from the geologically older, nonspiral cornulitids (first known from the Middle
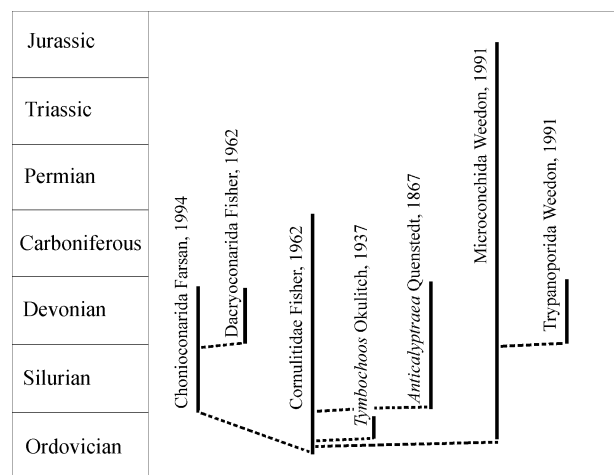

Fig. 2. Stratigraphic ranges and hypothetical phylogenesis of Palaeozoic problematic tubeworms with probable lophophorate affinities.

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Ordovician) (Fig. 2). Similarly, spirally coiled trypano-porids (Devonian) have most likely been derived from the geologically older microconchids (Upper Ordovician) (Fig. 2). The reef-forming *Tymbochoos* most probably originates from a cornulitid ancestor (Fig. 2), because it has similar, inwardly pointed pseudopunctae and constrictions resembling the annulation in the tube interior of *Cornulites*. The position of the spirally coiled *Anticalyptraea* remains controversial in the phylogeny of the problematic tubeworms and needs further study (Fig. 2). *Anticalyptraea* has either evolved directly from cornulitids, because of similar inwardly pointed pseudo-punctae and vesicular tube wall, or from spiral micro-conchids. In the latter case it must have changed the direction of the pseudopunctation and evolved a vesicular tube wall. On the basis of the occurrence of the micro-lamellar shell structure, cross-bladed lamellar structure, regularly foliated structure, pseudopunctae (both out-wardly and inwardly pointed), pores, and possible periostracum-like external organic layer (Vinn & Taylor 2007; Filipiak & Jarzynka 2009) we suggest that the problematic tubeworms with tentaculitid affinities were phylogenetically closely linked to lophophorates (e.g. bryozoans and brachiopods), but probably most closely to phoronids.

Diversity and evolution of Palaeozoic problematic tubeworms

Lophophorate (e.g. brachiopods and bryozoans) diversity during the Phanerozoic was highest in the Palaeozoic. However, if we add Palaeozoic tubeworms of lopho-phorate affinities to this record, the shelly faunas of the Palaeozoic era may have been even more dominated by lophophorates than previously thought. The diversity of Palaeozoic problematic tubeworms was highest in the Silurian and Devonian (Bouček 1964; Richards 1974; Larsson 1979; Vinn 2004, 2005a, 2006a; Taylor & Wilson 2008; Vinn & Mõtus 2008) and decreased markedly in the Carboniferous. Hitherto reported shell repair indicates attempted predation on the problematic tubeworms in the Late Ordovician (Vinn 2009a), Silurian (Larsson 1979; Vinn & Mutvei 2005; Vinn & Isakar 2007; Vinn 2009a), and Devonian (Wilson & Taylor 2006). Thus, predation pressure may have had some role in shaping the evolution of Palaeozoic problematic tubeworms. Taxa with large soft-body volumes, such as some Late Ordovician to Silurian *Cornulites* and tentaculitids, are lacking in the Late Palaeozoic, supporting, at least partially, predation-driven evolution. The occurrence of numerous endosymbiotic tubeworms in the Silurian (Vinn & Mõtus 2008; Vinn & Wilson 2009) and Devonian (Weedon 1991; Tapanila 2005) also reflects the pressure by predators.

MORPHOLOGICAL CONVERGENCE AND ECOLOGY

A remarkable morphological convergence exists between Palaeozoic problematic tubeworms and calcareous poly-chaete tubeworms, including (1) encrusting, substrate-cemented, nonspiral tubes, e.g. in cornulitids (Vinn & Mutvei 2005) and Triassic to Recent serpulids (ten Hove & Kupriyanova 2009); (2) substrate-cemented, erect tubes, e.g. in the Ordovician *Tymbochoos* (Vinn 2006b), Silurian to Triassic microconchids and Triassic to Recent serpulids (ten Hove & Kupriyanova 2009), and Oligocene to Recent cirratulids (Fischer et al. 2000); (3) planispiral tubes, e.g. in Ordovician to Jurassic microconchids, and Jurassic to Recent serpulids (Serpulidae, Spirorbidae) (Taylor & Vinn 2006); (4) substrate-cemented, spiral, erect, conical shells, e.g. in Silurian to Devonian *Anticalyptraea* (Vinn & Isakar 2007), and Cretaceous *Orthoconorca* (Jäger 1983); (5) pseudocolonial branching tubes, e.g. in Silurian to Permian hederelloids (Taylor & Wilson 2008) and Triassic to Recent filogranids (Serpulidae) (Senowbari-Daryan & Link 2005; ten Hove & Kupriyanova 2009). This morphological convergence presumably resulted from similarities in the common tubicolous bauplan of the skeleton.

In addition to morphological convergence, similarities are observed in the ecology of Palaeozoic problematic tubeworms and calcareous polychaete tubeworms. Both groups were exclusively suspension feeders, with a probable exception of pelagic tentaculitids. Secondarily free-living forms occurred among problematic tube-worms (e.g. *Cornulites*, see Richards 1974, probably also tentaculitids) and among calcareous polychaetes (e.g. *Ditrupa*, ten Hove & Smith 1990; *Rotularia*, *Glomerula*, Seilacher et al. 2008). Endosymbiotic forms evolved among problematic tubeworms, e.g. in Silurian cornulitids (Vinn & Mõtus 2008; Vinn & Wilson 2009), Devonian trypanoporids (Weedon 1991), and Jurassic to Recent polychaete serpulids (O. Vinn pers. obs. 2007; ten Hove & Kupriyanova 2009). Reef-forming gregarious forms occurred among problematic tubeworms, e.g. in the Ordovician *Tymbochoos*, Devonian to Carboniferous microconchids (Dreesen & Jux 1995), Upper Triassic to Recent polychaete serpulids (ten Hove & van den Hurk 1993), and Oligocene to Recent polychaete cirratulids (Fischer et al. 2000). Freshwater environments were colonized from the Carboniferous to Triassic by micro-conchids (Taylor & Vinn 2006), which were widely distributed and more successful in colonization of fresh water than calcareous polychaetes. The only Recent species of freshwater calcareous polychaetes, the serpulid *Marifugia cavatina*, lives in caves in Herzegovina (ten Hove & Kupriyanova 2009). However, there is a difference in the ecology between the members of

Palaeozoic problematic tubeworms and calcareous poly-chaetes which should be mentioned – pelagic lifestyle in tentaculitids (Larsson 1979) has no analogue in calcareous polychaetes.

MESOZOIC TURNOVER FROM PALAEOZOIC PROBLEMATIC TUBEWORMS TO CALCAREOUS POLYCHAETE TUBEWORM FAUNAS

Microconchids are the only problematic tubeworms in the Permian. Microconchids survived the P/T mass extinction (Taylor & Vinn 2006), and opportunistic micro-conchids are present in extinction recovery faunas from the Early Triassic of North America (Taylor et al. 2006). Microconchids are relatively common encrusters on biogenic substrates of the Early Triassic in Europe (O. Vinn pers. obs. 2007). The extinction of micro-conchids was probably gradual and lasted from the Early Jurassic until their final extinction at the end of the Middle Jurassic (Taylor & Vinn 2006; Vinn & Taylor 2007). The earliest calcareous polychaete tubeworms were serpulids, which appeared in the Triassic (Vinn et al. 2008a, 2008c), whereas their oldest unequivocal representatives are known from the Middle Triassic of China (Stiller 2000). The diversification of serpulids in the Late Triassic (Ziegler & Michalík 1980; Stiller 2000; Senowbari-Daryan & Link 2005; Senowbari-Daryan et al. 2007) and Early Jurassic (Parsch 1956; Jäger & Schubert 2008) coincides with the decrease in the abundance of microconchids. The extinction of microconchids in the Jurassic was possibly driven by the ecological pressure by serpulids if serpulids were more rapidly growing and more efficient suspension feeders than microconchids. The abundance and diversity of Mesozoic hard substrate encrusters increased in the Jurassic (Taylor & Wilson 2003), which could have added additional competition pressure into the hard substrate communities. In the latter case, the extinction of microconchids may have also been driven by the increase in the abundance and diversity of the other Mesozoic efficient suspension feeders such as Bivalvia.

The biomineralization systems of Palaeozoic problematic tubeworms and calcareous polychaete tube-worms are comparable in respect of their ability to produce advanced skeletal ultrastructures. The foliated structures (e.g. *Cornulites*, Vinn & Mutvei 2005) and cross-bladed lamellar structures (e.g. *Tentaculites*, Towe 1978) of problematic tubeworms are as advanced and complex as the lamello-fibrillar structures of some serpulids (Vinn et al. 2008a, 2008b, 2008d). However, the spherulitic prismatic structures of the Cirratulidae and Sabellidae (Vinn et al. 2008a, 2008b) are less advanced and probably inferior with respect to material properties than the structures of problematic tubeworms. The advanced, complex oriented structures, such as lamello-fibrillar structures, may have appeared late in the evolution of serpulids (Late Cretaceous to Early Cenozoic). Primitive Triassic and Jurassic serpulids may have possessed only simple, unoriented structures (Vinn & Furrer 2008). Thus, the complexity of skeletal ultra-structures was presumably not related to the evolutionary replacement of problematic tubeworms by calcareous polychaete tubeworms in the Middle Mesozoic.

PHANEROZOIC HISTORY OF CALCIUM CARBONATE ACCUMULATION BY PALAEOZOIC PROBLEMATIC TUBEWORMS AND POLYCHAETE TUBEWORMS

Reefs formed by Palaeozoic problematic tubeworms

Only a few studies have been published on reefs formed by problematic tubeworms in the Palaeozoic. The oldest are reefs formed by *Tymbochoos* in the Upper Ordovician of North America (Steele-Petrovich & Bolton 1998; Vinn 2006b). The earliest microconchid bioherms occur in the Upper Devonian of Arizona (Beus 1980) and Upper Devonian of Belgium (Dreesen & Jux 1995). Microconchid patch reefs, bioherms, and biostromes are known from the Lower Carboniferous (Tournaisian) of Cumberland and Roxburghshire (Leeder 1973). Although upper Ordovician and Silurian cornulitids (e.g. *Cornulites*) may occur in aggregations (Hall 1888; Richards 1974), they have never been found to form structures larger than a few centimetres in diameter (Hall 1888; Fisher 1962; Richards 1974; Vinn 2005a).

Microconchids were far more common as secondary frame builders in the Late Palaeozoic and Triassic, forming microconchid (= 'spirorbid')-algal stromatolites in the Devonian of France (Mistiaen & Poncet 1983), Lower Carboniferous of Wales, UK (Wright & Wright 1981), Carboniferous of Belgium (Barrois 1904; Hance & Hennebert 1980), Lower Permian of New Mexico, USA (Toomey & Cys 1977), Lower Permian of Germany (Stapf 1971), Triassic of Germany (Haack 1921), Lower Triassic of western Poland (Peryt 1974), and Upper Triassic of southwest Britain (Wright & Mayall 1981).

Rocks formed by Palaeozoic problematic tubeworms

Palaeozoic sedimentary rocks contain problematic tube-worms, especially tentaculitids, often in large numbers, but only microconchids (such as '*Serpula* spp.') are reported to form rocks (banks) in the Upper Silurian of

Austria (Suttner & Lukeneder 2004). Notable tentaculitid concentrations may occur on bedding planes in Silurian and Devonian limestones (Bouček 1964; Lindemann & Melycher 1997), but they do not form thick biogenic layers.

Reefs formed by calcareous polychaetes

Among Recent calcareous polychaete tubeworms, serpulids and cirratulids may form reefs (ten Hove & van den Hurk 1993; Fischer et al. 2000). The earliest serpulid build-ups are known from the Late Triassic (Norian) of Europe (ten Hove & van den Hurk 1993; Berra & Jadoul 1996; Cirilli et al. 1999), and cirratulid reefs from the Oligocene of Mexico (Fischer et al. 2000). Serpulid build-ups occur also at the Triassic–Liassic boundary in Spain (Braga & López-López 1989), in the Middle Jurassic of SE Spain (Navarro et al. 2008), in the Miocene and Pliocene of Spain (ten Hove & van den Hurk 1993), and in the Mid-Holocene of Argentina (Ferreroa et al. 2005). Serpulid build-ups are relatively common in modern oceans and are found in all climatic zones in shallow-water environments (ten Hove & van den Hurk 1993; Ramos & San Martín 1999; Smith et al. 2005). The earliest cirratulid reefs occur in the Oligocene of Mexico (Fischer et al. 2000), with later examples from the Plio-Pleistocene of Oregon and California (ten Hove & van den Hurk 1993). Recent cirratulid patch-reefs occur in the Caribbean of Yucatan, Mexico (ten Hove & van den Hurk 1993).

Rocks formed by calcareous polychaetes

Serpulids are the only rock-forming calcareous polychaetes in the Middle Jurassic to Recent (ten Hove & van den Hurk 1993). From the Middle Jurassic to Danian, *Glomerula* (Sabellidae) is the most common calcareous tubeworm, at least among European tubeworm associations (M. Jäger, pers. comm. 2009). Serpulid limestones became more common from the Late Jurassic–Early Cretaceous onwards on various continents (Palma & Angeleri 1992; ten Hove & van den Hurk 1993; Kiessling et al. 2006). In modern oceans serpulids, especially *Ditrupa*, form banks or shell concentrations that have been reported from continental shelves in temperate to tropical seas all over the world (ten Hove & van den Hurk 1993).

Comparison of Phanerozoic calcium carbonate accumulation by polychaete tubeworms and by Palaeozoic problematic tubeworms

Among Mesozoic encrusters, mollusks and serpulids grew to a much larger size than their Palaeozoic counterparts, and thick biogenic layers of shelly material were often built on tops of original hardground surfaces (Palmer & Fürsich 1974; Taylor & Wilson 2003). Such biogenic layers are rare on Palaeozoic hardgrounds (Palmer 1982; Wilson & Palmer 1992). A possible explanation is that the main Palaeozoic encrusters (trepostomes, cryptostomes, echinoderms, corals) had scour-susceptible soft tissue covering their skeletons, whereas the dominant Mesozoic encrusters (serpulids, bivalves, most cyclostomes) had true exoskeletons into which soft parts of the living animals could withdraw completely (Palmer 1982). However, Palaeozoic problematic tubeworms also had true exoskeletons offering similar protection as calcareous polychaete tubes. Thus, the inability of problematic tubeworms to form thick biogenic layers on Palaeozoic to Jurassic hard substrates can be explained by their general slower calcification rate in ocean ecosystems as compared to Mesozoic to Recent calcareous polychaetes.

In the Late Palaeozoic microconchids become more common as secondary frame builders in microconchid-algal build-ups, but they never contributed to reef formation like calcareous polychaetes from the Mesozoic to Recent. There is no analogue to the Jurassic and Cretaceous serpulite (formed by serpulids) in the Palaeozoic and Triassic. It seems that calcareous polychaetes contributed to sedimentary rock formation of their time (Triassic to Recent) notably more than problematic tubeworms did in the Palaeozoic and Triassic. Thus, it is possible that Palaeozoic to Early Mesozoic problematic tubeworms never reached the level (quantity) of calcification carried out by polychaete annelids in the Late Mesozoic to Recent oceans.

Much of the Middle Mesozoic polychaete calcification was performed by sabellids, which play a minor role among calcifying annelids of the Recent oceans. Their primitive biomineralization system, as compared to that of serpulids, could be among the reasons why their abundance has decreased in the long term. However, changing seawater chemistry could also have affected calcification by sabellids.

Influence of seawater chemistry on biomineralization of calcareous polychaetes and Palaeozoic problematic tubeworms

Sandberg (1983, 1985) found that the composition of nonskeletal carbonate precipitates (early marine cements and ooliths) has undergone oscillations during Phanerozoic time: there have been three intervals of aragonite seas (Early Cambrian, Late Carboniferous–Early Jurassic, Oligocene–Recent), and two intervals of calcite seas (Middle Cambrian–Early Carboniferous, Middle Jurassic–Eocene) (Stanley 2006). Although some organisms

exercise considerable control over their biomineralization, seawater chemistry has affected skeletal secretion by many Phanerozoic animal taxa (Stanley 2006; Taylor 2008). There are no records of an aragonitic mineralogy in Palaeozoic to Middle Jurassic problematic tube-worms. They appeared in the Ordovician calcite seas and seem to have remained exclusively calcitic throughout their evolution, even in Late Carboniferous to Early Jurassic aragonitic seas. Thus, they may have exercised a considerable control over their biomineralization. The primitive mineralogy of serpulids was presumably aragonitic (Vinn et al. 2008c), and they began to calcify in the aragonitic seas of the Triassic. Recent sabellids (e.g. *Glomerula*) are aragonitic, and they also appeared in the aragonitic seas of the Early Jurassic (Vinn et al. 2008a). However, in the Middle Jurassic to Eocene calcite seas sabellids may have had a calcitic or pre-dominantly calcitic mineralogy, as they are usually very well preserved compared to co-occurring aragonitic mollusks in the Mesozoic of Europe (M. Jäger, pers. comm. 2009). Sabellid abundance peaked in Mesozoic calcite seas (M. Jäger, pers. comm. 2009). If sabellids were calcitic in the Middle Jurassic to Eocene calcite seas, they may have favoured the calcite sea conditions over aragonite sea conditions. Thus, there could have been some correlation between the aragonite-calcite seas and skeletal mineralogy of polychaetes, but further studies are needed, especially on the mineralogical history of sabellids (e.g. *Glomerula*). The mineralogy of probable aragonitic cirratulids (O. Vinn pers. obs. 2007) also needs further study.

CONCLUSIONS

1. Morphological similarities indicate that Palaeozoic problematic tubeworms – tentaculitids, cornulitids, microconchids, trypanoporids, *Anticalyptraea*, and *Tymbochoos* – form a monophyletic group and their skeletons are homologous. It is possible that hederelloids also belong to this group. The group likely shares affinities with lophophorates.

2. The complexity of skeletal ultrastructures was presumably not related to the evolutionary replace-ment of Palaeozoic problematic tubeworms by calcareous polychaete tubeworms in the Middle Mesozoic.

3. The extinction of Palaeozoic problematic tubeworms in the Middle Jurassic could have been at least partly driven by the ecological pressure from serpulids and sabellids because calcareous polychaete tubeworms probably grew more rapidly and were more efficient suspension feeders.

4. The input of Palaeozoic problematic tubeworms to the general ocean biocalcification system may have been smaller in the Ordovician to Jurassic than that of calcareous polychaetes in the Late Triassic to Recent. Palaeozoic problematic tubeworms may have been less efficient calcifiers than calcareous poly-chaete tubeworms.

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Fanerosoikumi lubikojaga ussid

Olev Vinn ja Harry Mutvei

Problemaatiliste Paleosoikumi lubikojaga usside (tentakuliidid, kornuliidid, mikrokonhiidid, trüpanoporiidid, *Anticalyptraea* ja *Tymbochoos*) morfoloogilise sarnasuse alusel võib arvata, et nad moodustavad monofüleetilise rühma. Sinna rühma kuuluvad tõenäoliselt ka hederelloidid. See rühm seisab evolutsiooniliselt kõige lähemal lofoforaatidele ja nende evolutsioon võis olla kiskjate poolt mõjutatud. Paleosoikumi lubikojaga usside väljasuremist Juura ajastul võis soodustada serpuliidide ja sabelliidide ökoloogiline surve. Paleosoikumi lubikojaga usside (Ordoviitsium–Juura) panus ookeani biokaltsifitseerimise süsteemi võis olla väiksem kui lubikojaga hulkharjasussidel (Triias–tänapäev). Aragoniidi- ja kaltsiidimerede ning lubikojaga hulkharjasusside skeleti mineraloogia vahel võib olla mõningane korrelatsioon.