Phenetic phylogenetics of tentaculitoids – extinct, problematic calcareous tube-forming organisms

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Version of record first published: 16 Mar 2012

To cite this article: Olev Vinn & Michał Zatoń (2012): Phenetic phylogenetics of tentaculitoids - extinct, problematic calcareous tube-forming organisms, GFF, 134:2, 145-156

To link to this article: http://dx.doi.org/10.1080/11035897.2012.669788
Phenetic phylogenetics of tentaculitoids – extinct, problematic calcareous tube-forming organisms

OLEV VINN1 and MICHAŁ ZATON2

Abstract: Tentaculitoids have traditionally been assigned to either Mollusca or Annelida. In addition, cnidarian, brachiopod, bryozoan, phoronid and sponge affinities have been proposed. Similarity analyses carried out with tentaculitoid characters place them in a cluster together with Brachiozoa (Brachiopoda+Phoronida). Tentaculitoids are less similar to Mollusca and Bryozoa. No support was found for the annelid, cnidarian and sponge affinities. Thus, tentaculitoids belong to Lophotrochozoa with a high degree of certainty. They are best classified as “lophophorates”, most likely Brachiozoa.

Keywords: biological affinities; Tentaculita; Brachiopoda; Phoronida; tubeworms; Palaeozoic.

Introduction

Tentaculitoid tubeworms are an extinct group of mostly marine invertebrates. They appeared in the Middle Ordovician (Vinn 2006a,b) and became extinct in the Middle Jurassic (Taylor & Vinn 2006; Vinn & Taylor 2007; Zatoń & Vinn 2011). Tentaculitoid tubeworms were an important part of encrusting faunas through parts of the Palaeozoic (Vinn 2010), being mostly benthic in the Silurian, and benthic or pelagic in the Devonian (Boucˇek 1964; Lardeux 1969; Larsson 1979). Tentaculitoids achieved a global distribution in the latest Silurian and have been found on all major continents of the Palaeozoic (Boucˇek 1964; Lardeux 1969; Larsson 1979). Tentaculitoids are less similar to Mollusca and Bryozoa. No support was found for the annelid, cnidarian and sponge affinities. Thus, tentaculitoids belong to Lophotrochozoa with a high degree of certainty. They are best classified as “lophophorates”, most likely Brachiozoa.


Similarities between tentaculitoid groups

There are strong morphological similarities between the substrate-cemented Palaeozoic problematic tubeworms, including microconchids, trypanoporids, cornulitids and Anticalyptraea. These features include calcitic, substrate-cemented tubes, microlamellar tube structure, pseudopunctae (but not in all species), bulb-like embryonic shells and septa, all of which suggest a close relationship (Vinn & Mutvei 2009). One group of Palaeozoic colonial organisms with substrate-cemented tubular calcitic skeletons, the hedereidoids (Silurian to Permian; Taylor & Wilson 2008), resembles the tentaculitoids and may be phylogenetically closely related to them (Taylor et al. 2010).

The morphology of some substrate-cemented Palaeozoic problematic tubeworms (Vinn & Mutvei 2009) and thick-walled tentaculitids (Larsson 1979; Farsan 2005) exhibits several similarities, such as the tube-shaped calcitic shell, microlamellar shell structure, the presence of similarly oriented pseudopunctae, both internal and external annihilations, septae and a bulb-like early shell separated by a constriction from the adult shell. These features suggest a close phylogenetic relationship (Boucˇek 1964; Dzik 1991; Vinn 2005; Vinn & Mutvei 2005). However, these organisms had different lifestyles (cornulitids were substrate-cemented and tentaculitids were free-living) and their shell formation began at different ontogenetic stages. Cornulitids have a bulbous embryonic shell cemented to the substrate (Vinn & Mutvei 2005). In tentaculitids, the bulb-like embryonic shell bears a long conical process (Farsan 2005).
Vinn & Mutvei (2009) hypothesised that tentaculitoids may have had a more prolonged larval stage than cornulitids. In addition, thick-walled tentaculitids may have had a planktotrophic larva, and cornulitids may have had a lecithotrophic larva.

### Previous concepts on the phylogenetic relationships of tentaculitoids

Considering their morphological similarities, Vinn and Mutvei (2009) hypothesised that tentaculitids, cornulitids, microconchids, trypanoporids, Anticalyptraea and Tymbochaos form a monophyletic group and that their skeletons are homologous (Tourneur et al. 1994). They also hypothesised that the substrate-cemented forms (lacking larval shells) form a sister group to free-living tentaculitids (with larval shells present; Fig. 1). Within the substrate-cemented group, it is possible that spiroribiform microconchids (Late Ordovician) were derived from the geologically older, non-spiral cornulitids (first known from the Middle Ordovician; Fig. 1). Similarly, spirally coiled trypanoporids (Devonian) were most likely derived from the considerably older microconchids (Late Ordovician; Fig. 1). The reef-forming Tymbochaos most probably originated from a cornulitid ancestor (Fig. 1) because it has similar inwardly pointed pseudopunctae and constrictions resembling the annulation in the tube interior of Cornulites. Anticalyptraea either evolved directly from cornulitids, as suggested by similar inwardly pointed pseudopunctae and a vesicular tube wall, or from spiral microconchids. If the latter case were true, Anticalyptraea must have changed the direction of the pseudopunctation and evolved a vesicular tube wall.

### Possible zoological affinities of tentaculitoids

**Annelida.** – In his original description of Cornulites, Schlotheim (1820) found it to be most similar to recent tubiculous annelids based on their general shape. In 1839, Murchison came to similar conclusions for Microconchus and found it to be closely related to the recent spirorbine serpulid genus Spirorbis. Gürich (1899) found Chonioconarida to be most similar to tubiculous annelids. The general shape of the tube played an important role in the classification of Anticalyptraea (Horny 1965), Trypanopora (Tourney et al. 1994) and Conchicollies (Blind 1972) within the serpulid annelids. Brachiopoda. – The discovery of cross-bladed lamellar structure in Tentaculites led Towe (1978) to propose brachiopod affinities for the tentaculitids. The occurrence of pseudopunctae in the tube wall further supported the hypothesis of brachiopod affinities for the Chonioconarida (Larsson 1979).

**Bryozoa.** – Bryozoan affinities of cornulitoids were proposed by Dzik (1991) based on the presence of a protoecium-like embryonic chamber in cornulitids.

**Cnidaria.** – Knight (1937) suggested that the slender conical shape of the tentaculitid shell indicate either Hydrozoa or Scyphozoa affinities for the group. Fisher (1962) compared cornulitids with calcareous hydroids based on their vesicular wall structure. Later, Herringshaw (2007) also found similarities between Cornulites and the Cnidaria: “cellulae” and “tabulae” are comparable with both the dissepiments and tabulae of corals; cornulitid shell symmetry is clearly radial, suggesting also a closer affinity to cnidarians, although the initial chamber of Cornulites resembles that of bryozaons. Its morphology is also similar to that of some corals (e.g. Stolarski 2000; Fig. 2D); lamellar calcite skeletons, which have been argued could have been low-magnesian (e.g. Sorauf 1977), occur in rugose corals.

**Foraminifera.** – Fisher (1962) compared cornulitids with fusulinids because of similarities in the vesicular shell structure.

**Mollusca.** – Molluscan affinities were first suggested by Austin (1845) who found that dacryoconaridans are morphologically similar to pteropods. This became the standard view on the biological affinities of tentaculitoids (sensu stricto; Ljashenko 1955; Farsan 1994). Ljashenko (1955) also included hyolithids with tentaculitids and assigned them to molluscs. Blind (1972) suggested that the shell structure and bulbous shape of the early growth stages of Cornulites indicate a molluscan affinity. Similarly, microconchids were interpreted as vermetid-like gastropods by Burchette & Riding (1977) and Weedon (1990) based on the occurrence of a protoconch-like initial shell. Quenstedt (1867) assigned Anticalyptraea to gastropods because of the generally similar shape of the shell.

**Phoronida.** – Towe (1978) identified cross-bladed microstructure in Tentaculites, which is known to occur in brachiopods, but also in bryozoans and molluscs. He suggested that because of their cross-bladed shell structure tentaculitids could be close relatives of brachiopods – phoronids. Vinn (2005) and Vinn and Mutvei (2005) found that the biomineralisation of cornulitids (Cornulites) most closely...
resembles that of lophophorates, and they hypothesised that cornulitids could be closely related to phoronids. A similar hypothesis was formulated for the microconchids by Taylor and Vinn (2006) and for *Anticalyptraea* by Vinn and Isakar (2007). Vinn and Mutvei (2009) expanded the biomineralised phoronid hypothesis for all tentaculitoid tubeworms. Recently, Taylor et al. (2010) suggested that the lophophorate-style biomineralisation of tentaculitoid tubeworms and hederelloids allows them to be classified as stem-group phoronids.

**Porifera.** – Fisher (1962) compared cornulitids with stromatoporoids (demosponges with calcareous basal skeleton) and found similarities in their vesicular wall structures.

### Material and methods

In this study, tentaculitoid characters were weighted *a priori* based on their presumed biological value and inferred non-homoplastic, apomorphic characters. It is generally accepted that early ontogenetic stages are most conservative in invertebrates. In addition, all characters that should have had important biological function were also selected (Table 2). The characters were coded according to their presence or absence.

The symmetry of the tentaculitoid soft body was most likely bilateral, a conclusion supported by the morphology of muscle attachment scars in the *Volynites velaini* (see Lardeux 1969: p. 12; Fig. 2). Bilateral soft body symmetry is also supported by the bilateral symmetry of the late larval–early juvenile part of the shell in the Trompetocoenarida (Farsan 2005). However, soft body symmetry is not included in the table of comparison because it is based on indirect evidence (morphology of the shell). The external transverse sculpture was also excluded from the analysis because it is likely that all the animal phyla studied have analogies in character states of the sculpture.

The following tentaculitoid characters were included in our analysis:

1. **Calcitic cross-bladed structure.** – Within each lamina, blades form parallel aggregations oriented in more or less random directions in vertically adjacent laminae and in laterally adjacent portions of the same lamina (Carter et al. 1990).

2. **Calcitic regular foliated structure.** – More or less mutually parallel blades or laths arranged in laminae dipping at a generally uniform angle and in the same

![Fig. 1. Phylogenetic relationships of the tentaculitoids, modified after Vinn & Mutvei (2009) and Vinn (2010).](image-url)
Fig. 2. **A.** Euclidean similarity measure performed for tentaculitoids together with Annelida, Brachiopoda, Bryozoa, Cnidaria, Mollusca and Porifera. **B.** Jaccard similarity measure performed for tentaculitoids together with Annelida, Brachiopoda, Bryozoa, Cnidaria, Mollusca and Porifera.

Table 2. Distribution of analogous characters of tentaculitoids among the discussed phyla and higher groupings.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Annelida</th>
<th>Mollusca</th>
<th>Brachiopoda</th>
<th>Phoronida</th>
<th>Bryozoa</th>
<th>Cnidaria</th>
<th>Porifera</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Calcitic cross-bladed structure</td>
<td></td>
<td>–</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
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<tr>
<td>2. Calcitic regular foliated structure</td>
<td></td>
<td>–</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>3. Calcitic fibrous prismatic structure</td>
<td></td>
<td>–</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>4. Pseudopunctae point in the opposite direction as skeletal accretion</td>
<td></td>
<td>–</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>5. Pseudopunctae point in the same direction as skeletal accretion</td>
<td></td>
<td>–</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
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<tr>
<td>6. Punctae</td>
<td></td>
<td>Moll.</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>9. Occurrence of fission</td>
<td></td>
<td>Ann.</td>
<td>–</td>
<td>Phor.</td>
<td>–</td>
<td>Cnid.</td>
<td>Por.</td>
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<tr>
<td>10. Larval shell</td>
<td></td>
<td>Ann.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>11. Apertural constriction between bulbous embryonic shell and adult shell</td>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>12. Free bulbous initial tube part</td>
<td></td>
<td>–</td>
<td>–</td>
<td>Phor.</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>14. Planispiral initial substrate-cemented growth</td>
<td></td>
<td>Ann.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>16. Hollow spines</td>
<td></td>
<td>–</td>
<td>Moll.</td>
<td>Brach.</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>19. Adult pelagic life mode (with shell)</td>
<td></td>
<td>–</td>
<td>Moll.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>21. Muscle attachment scars on the skeleton</td>
<td></td>
<td>–</td>
<td>Moll.</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
</tr>
<tr>
<td>22. Periostracum-like external organic layer</td>
<td></td>
<td>–</td>
<td>Moll.</td>
<td>Brach.</td>
<td>–</td>
<td>Bryo.</td>
<td>–</td>
</tr>
</tbody>
</table>

Note: Number of common characters is indicated in the parenthesis. Abbreviation of phyla denotes presence of the character, (–) denotes absence of the character. Only certain occurrences are counted.
general direction over large portions of the depositional surface (Carter et al. 1990).

(3) Calcitic fibrous prismatic structure. – Mutually parallel, elongate, adjacent structural units that do not interdigitate (Carter et al. 1990).

(4) Pseudopunctae point in the opposite direction as skeletal accretion. – Conical deflections of the shell laminae, without the hollow core, continue through the whole shell wall or a large portion of it.

(5) Pseudopunctae point in the same direction as the skeletal accretion.

(6) Punctae. – Continuous microscopic pores through the shell wall, usually associated with the conical deflection of the shell laminae at their edges.

(7) Vesicular wall structure. – Chambers between the lamina of the shell that are multiangular to subcircular in a horizontal plane. Vesicles were probably formed by periodic uplifting of the secretory epithelium inside the living chamber (Vinn & Mutvei 2005; Vinn & Isakar 2007).

(8) Occurrence of budding. – The daughter tubes with much smaller diameters than the parent tube.

(9) Occurrence of fission. – The large parent tube dividing into two daughter tubes of almost equal diameter at its aperture.

(10) Larval shell. – Mineralised shell secreted during the larval growth stage.

(11) Aperture constriction between bulbous embryonic shell and adult shell.

(12) Free bulbous initial tube. – The bulbous initial tube is not cemented to the substrate.

(13) Substrate-cemented initial shell. – Biomineralisation began after attachment to the substrate, resulting in a substrate-cemented initial shell.

(14) Planispiral initial substrate-cemented growth. – Initial substrate-cemented shell is planispirally coiled.

(15) Tabulae. – Horizontal floors in the shell cavity.

(16) Hollow spines. – Edge of shell folded to form a spine.

(17) External longitudinal sculpture. – In the form of longitudinal ridges.

(18) Slender body shape. – Low divergence of angle in the living chamber.

(19) Adult pelagic life mode (with shell). – Adults have pelagic life mode, floating or active swimming.

(20) Monovalve, tubicolous. – Tubular shell with or without operculum.

(21) Muscle attachment scars on the skeleton. – Skeleton has a specific morphology at the place of muscle attachment.

(22) Periostracum-like external organic layer. – The mineral skeleton is externally covered with a non-living organic layer, which was identified in exceptionally preserved material (Wood et al. 2004; Filipiak & Jarzynka 2009).

We conducted a cluster analysis with respect to all characters of tentaculitoids that are shared by at least one invertebrate phylum (Table 2), using the PAST software package (Hammer et al. 2001). At first, we compared tentaculitoids using an Euclidean similarity measure and a Jaccard similarity measure with Annelida, Brachiopoda, Bryozoa, Cnidaria, Mollusca and Porifera (Fig. 2). Then we carried out similar analyses for tentaculitoids using the monophyletic group Brachiopoda (Brachiopoda+Phoronida) instead of Brachiopoda (Fig. 3).

One could ask why a cladistic analysis has not been carried out to solve the problem of tentaculitoid affinities. The precondition for cladistics is the presence of homologies among all the taxa analysed. It is not certain whether the tentaculitoids share homologous skeletons with any members of extant biomineralising animal phyla. Under such conditions, cladistic analyses would result in an unreliable tree. The current comparison and discussion are based on the assumption that animals within the same phylogenetic lineage are more likely to reach similar constructional and functional solutions than the members of the remotely linked phyla.

Discussion of characters

Tube structure. – Both the calcitic cross-bladed structure of Tentaculites (Toye 1978; Fig. 4A) and the calcitic regular foliated structure of Cornulites (Vinn & Mutvei 2005; Fig. 4B) occur in brachiopods, bryozoans and molluscs (Carter et al. 1990). Although extant phoronids do not build calcareous tubes, their mucous tubes have a lamellar structure (Emig 1982).

Both outwards (as in Microonchida and Trypanoporida; Fig. 5A) and inwards pointed pseudopunctae (as in Choniocnida; Cornulitidae, Anticalyptraea, Tymbocochinos; Fig. 5B) occur in brachiopods (Williams 1997). In bryozoans, there are similar structures termed styles that are always pointed in the same direction as the skeleton accretion (P. D. Taylor, pers. info. 2010; Table 2). Pores in the microconchid tubes (Fig. 5C) are analogous to brachiopod punctae and cyclostome byozoan pseudopores (Taylor & Vinn 2006). There are large alveoli in the tube wall of some spiroberine serpulids (Rzhavsky 1994), but these structures are not analogous to pores (cacea) in tentaculitoids. Similarly, various pores occur in the walls of corals, but these porous structures are not comparable to the long and sub-parallel ceca that result from epithelial extensions through mineralised skeletons (J.-P. Cuif, pers. info. 2010). The vesicular structure of the shell wall of tentaculitoids (e.g. Cornulites, Trypanopora and Anticalyptraea; Fig. 5D) is similar to that of brachiopods, bryozoans and corals. Cavities in the tube wall of serpulids are formed only at the tube’s contact with the substrate (ten Hove & Kupriyanova 2009), and their formation differs from the vesicles of tentaculitoids (Vinn & Mutvei 2005). The vesicular shell structure of tentaculitoids also somewhat resembles the chambered shell structure in oysters (Okoshi & Sato-Okoshi 1996: p. 153; Figs. 1, 2), but chambers of the latter do not have the spongy architecture of tentaculitoids and are more similar to the cavities in the tube wall of serpulids.

Tube morphology of the early growth stages. – The ontogenetically earliest growth stage of tentaculitoid shell has been interpreted as larval shell (Farsan 2005; Fig. 6). Among tentaculitoids, the larval shell occurs in Chonioconarida (Farsan 1994). Similarly to tentaculitoids, larval shells also
occur in molluscs (Weiss et al. 2002) and brachiopods (Freeman & Lundelius 2005; Table 2). The bulbous larval shell of Chonioconarida bears a long slender conical process. If secretion of the process preceded formation of the bulbous chamber, no similar larval shell morphology is known in the animal world. However, there are some similarities between the bulbous part of the tentaculitoid larval shell and the protoconch of pteropod gastropods and hyoliths, as well as with the initial part of the Calceola rugose coral corallite (J. Dzik, pers. info. 2011). The ontogeny of substrate-cemented tentaculitoids begins with a bulbous initial chamber (Fig. 7) that could be homologous with the bulbous embryonic shell of Dacryoconarida Fisher, 1962. Similar bulbous initial substrate-cemented shell occurs in Bryozoa (Dzik 1991; Table 2). This means that larvae settled down and each secreted a dome-like skeletal structure before metamorphosis – the mode of early development previously recognised in bryozoans (but also in pterobranch hemichordates, constructing skeletal tubes in completely different ways; J. Dzik, pers. info. 2011). Phoronid tubes also have a bulbous initial part, but they are not biomineralised (Emig 1982). It has also been argued that the morphology of some corals is similar to the bulbous embryonic shell of tentaculitoids (Herringshaw et al. 2007). However, these corals lack a real bulb-shaped initial shell with apertural constriction; they just have a rounded beginning of a conical shell (see Stolarski 2000: p. 16; Fig. 2D). Thus, we think that the morphology of the initial shell of corals and substrate-cemented tentaculitoids is different.

Planispiral initial substrate-cemented growth. – Microconchid shells grew initially planispirally (either dextrally or sinistrally) cemented to the substrate (Fig. 8). Similar spiral substrate-cemented growth occurs in anellids (e.g. spirobrine serpulids; Table 2) and in substrate-cementing gastropods and rudist bivalves. Some juvenile substrate-cemented rugose corals also have a spiral morphology (Ausich & Smith 1982), but these specimens are not planispiral, instead they grew spirally (helically) around various stems.

Fig. 3. A. Euclidean similarity measure performed for tentaculitoids together with Annelida, Brachiopoda (Brachiopoda+Phoronida), Bryozoa, Cnidaria, Mollusca and Porifera. B. Jaccard similarity measure performed for tentaculitoids together with Annelida, Brachiopoda (Brachiopoda+Phoronida), Bryozoa, Cnidaria, Mollusca and Porifera.
Muscle attachment scars. – Up to four longitudinal long, narrow, shallow, furrow-like muscle attachment scars have been found in the tube lumen of *Cornulites* (Cornulitidae; Vinn & Mutvei 2005). Muscle attachment scars have also been found in *Volynites* (Chonioconarida; Lardeux 1969). These scars were used to show that the tentaculitid body plan was bilaterally symmetrical, not radial. In addition to tentaculitoids, serially distributed muscle attachment scars of various forms occur in molluscs (Ponder & Lindberg 2008), brachiopods (Mackinnon 1977) and bryozoans (P.D. Taylor, pers. info. 2010; Table 2).

Reproduction. – Asexual reproduction by budding (Fig. 9) occurs in all the phyla that have been compared to tentaculitoids. In corals (Barnes & Hughes 1999), sponges (Ruppert et al. 2004) and annelids (Bely & Wray 2001; Pernet 2001), both budding and fission occur. In bryozoans, only budding occurs (P.D. Taylor, pers. info. 2010). In phoronids, asexual reproduction occurs by budding and fission (Harmer 1917; Marcus 1949; Figs. 10, 11, Table 2) similar to the way that asexual reproduction is inferred to occur in microconchid tentaculitoids (Wilson et al. 2011).

External periostracum-like organic cover. – Direct evidence for an external periostracum-like covering has been found for dacryoconarids from the Devonian of Poland (Wood et al. 2004; Filipiak & Jarzynka 2009). Similarly, large pores in microconchs have been interpreted as evidence of an external periostracum-like organic cover (Vinn & Taylor 2007). External skeletal organic covers of such type occur in molluscs (Taylor & Kennedy 1969), brachiopods (Williams & Mackay 1978) and bryozoans (Banta 1968; Table 2). Such disparity between the external organic skeleton and internal mineral means that their secretion is separated spatially in a mantle-like organ, the organic periostracum being secreted at the mantle margin and the mineral wall by the body surface.

**Tubicolous shell (monovalve).** – Tubicolous shell occurs in most of calcified skeleton-bearing invertebrate phyla compared to tentaculitoids (Fig. 11), except for brachiopods (but note the Permian richthofenids). However, the closest relatives of the brachiopods, the phoronids, have a tubicolous shell that is organic (Emig 1982; Table 2).

**Results**

We found 22 characters (Table 2) in tentaculitoids that are likely to be of phylogenetic importance and can be used for comparison with the phyla traditionally affiliated with tentaculitoids. In initial analyses, both an Euclidean similarity
measure (Fig. 2A) and a Jaccard similarity measure (Fig. 2B) were used to cluster tentaculitoids together with Annelida, Brachiopoda, Bryozoa, Cnidaria, Mollusca and Porifera. Results show that the Lophotrochozoan phyla (Brachiopoda, Bryozoa and Mollusca) cluster with tentaculitoids. In analyses using the Euclidean similarity measure, the Brachiopoda and Mollusca formed a pair with tentaculitoids, followed by Bryozoa, supporting brachiopod–molluscan affinities instead of bryozoan affinities (Fig. 2). In analyses using the Jaccard similarity measure, tentaculitoids formed a pair with the Mollusca, followed by Brachiopoda and finally the Bryozoa.

In the second group of analyses, in which monophyletic group Brachiozoa (Brachiopoda+Phoronida) substituted for the Brachiopoda, both the Euclidean similarity measure (Fig. 3A) and the Jaccard similarity measure (Fig. 3B) resulted in grouping of the lophotrochozoan Brachiopoda, Bryozoa and Brachiozoa (Brachiopoda+Phoronida) with tentaculitoids. In this case, the

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**Fig. 6.** Larval and juvenile parts of a chonioconarid shell. Modified after Farsan (2005).

**Fig. 7.** Conulites aff. flexuosus, general view of an embryonic shell, Anticosti (Canada), Ellis Bay Formation, Upper Ordovician (Hirnantian). Note the constriction between embryonic shell and juvenile shell.

**Fig. 8.** Substrate-cemented initial planispiral shell of Punctaconchus ampliporus Vinn & Taylor, 2007. Scanning electron micrographs (back-scattered electron images) of uncoated specimens from the Jurassic (Bathonian, White Limestone, Foss Cross Quarry, Gloucestershire, UK).

**Fig. 9.** Coiled bud on a parent tube of a microconchid Helicoconchus from the Permian of Texas. From Wilson et al. (2011).
Mollusca was found to be more similar to tentaculitoids than to the Bryozoa (Fig. 3). Both analyses strongly support “lophophorate” (Brachiopoda, Bryozoa and Phoronida) affinities of the tentaculitoids. They strongly support Brachiozoa (Brachiopoda + Phoronida) affinities. However, there is also a strong similarity with molluscs. These analyses do not support the traditional annelid hypotheses, nor do they support cnidarian or poriferan affinities.

Discussion of the biological affinities of tentaculitoids

Traditionally, substrate-cemented tentaculitoid tubeworms have most often been affiliated with tubicolous annelids, especially with serpulids (Schlotheim 1820; Murchison 1839; Horný 1965; Blind 1972; Tourneur et al. 1994). Alternatively, a molluscan affinity has been the mainstream hypothesis for free-living tentaculitoids (Austin 1845; Ljashenko 1955, 1957; Blind 1969, 1970; Farsan 1994). However, recently, the hypothesis of “lophophorate” and phoronid affinities of tentaculitoids has been supported by a number of studies (Vinn 2005; Vinn & Mutvei 2005; Taylor & Vinn 2006; Vinn & Isakar 2007; Vinn & Taylor 2007; Vinn & Mutvei 2009; Taylor et al. 2010; Vinn 2010; Wilson et al. 2011). The results of similarity analyses carried out with tentaculitoid characters (Table 2) point strongly towards an affinity with the Lophotrochozoa (Fig. 12). Especially, important characters are the presence of larval shell (in tentaculitids) and advanced skeletal microstructure (tentaculitids, cornulitids and microconchids). Most likely, tentaculitoids had a bilateral body symmetry, a conclusion supported by the morphology of muscle attachment scars in tentaculitids (Lardeux 1969). Among the Lophotrochozoa, tentaculitoids share the greatest number of similarities with the “lophophorates” and molluscs (Figs. 2, 3). “Lophophorates” originally embracing the Brachiopoda, Phoronida and Bryozoa are now considered to be polyphyletic (Paps et al. 2009). Phoronida and Brachiopoda form the monophyletic group “Brachiozoa”, which is not genetically closely related to Bryozoa (Fig. 12).
Brachiopoda (Phoronida+Brachiopoda). – Our similarity analyses found strong support for brachiopod affinities of tentaculitoids (Fig. 3). This is in accord with the calcifying stem-group phoronid hypothesis. In a series of papers, Bernie Cohen and colleagues (Cohen 2000; Cohen & Weydmann 2005; Santagata & Cohen 2009) suggested that phoronids were derived from brachiopods (nesting within the phylum Brachiopoda in cladistic terms) (see also Balthasar & Butterfield 2009). Phoronids have also played a part in discussions of the evolution of brachiopods from tommotiids in the Cambrian. Skovsted et al. (2008, 2011) suggested that the tubular Eccentrotheca is a stem-group phoronid. The tentaculitoids share skeletal structures with brachiopods and presumably had a similar biomineralisation system. They both have calcitic shells. There are also other similarities between brachiopods and tentaculitoids such as the presence of larval shell, substrate-cemented initial shell growth, muscle attachment scars and an external organic layer (periostracum; Wood et al. 2004; Filipiak & Jarzynka 2009). On the other hand, the worm-shaped body plan (tubicolous shell), bulbous beginning of the tube and asexual reproduction link tentaculitoids to phoronids (Table 2, Figs. 10, 11). If calcification in the Brachiozoa is a plesiomorphic condition, it is possible that tentaculitoids represent the stem group of the calcifying phoronids (Taylor et al. 2010). A lophophore-based feeding system of phoronids has been argued (Larsson 1979; Herringshaw et al. 2007; Emig 2010) to be incompatible with the supposed planktic lifestyle of Darcyocoradina although these authors did not explain the reasons for incompatibility. Discinacean and lingulacean brachiopods larvae are thought to both swim and feed with their lophophores (Strathmann 1993).

Bryozoa. – Our similarity analyses found moderate support for an affinity between Bryozoa and tentaculitoids (Fig. 3). Bryozoans have a number of common characters with the tentaculitoids, especially in biomineralisation and skeletal structures (see Table 2). Other similarities include a worm-shaped body plan, a bulbous tube origin, muscle attachment scars and an external organic layer. However, asexual reproduction via fission does not occur in bryozoans (Fig. 10). In bryozoans, the pseudopunctae never point in the opposite direction from fission accretion (P.D. Taylor, pers. info. 2010; Fig. 5A). The main difficulty with a bryozoan affinity for the tentaculitoids is their non-cementing larval shell with an apical process, which indicates significant differences in their life histories compared to the cornulitids and bryozoans (Table 2, Fig. 6).

Mollusca. – In our similarity analysis, the molluscs were found in the cluster together with Brachiopoda, Bryozoa and tentaculitoids or in the cluster together with Brachiopoda (Brachiopoda+Phoronida), Bryozoa and tentaculitoids. They were found to be more similar to tentaculitoids than to bryozoans (Fig. 3). The biomineralisation and skeletal structures of molluscs closely resemble that of tentaculitoids. However, the aragonitic mineralogy typical for molluscs is not known in tentaculitoids. Molluscs also do not have pseudopunctae (Larsson 1979; Vinn & Mutvei 2009; Fig. 5A–B). Molluscs have larval shells (protoconchs), planktic lifestyles, muscle attachment scars, bulbous protoconchs and a periostracum that link them to tentaculitoids. On the other hand, molluscs have never been found to cement their initial shells to the substrate (Vinn & Mutvei 2009; Figs. 7, 12). The occurrence of asexual reproduction in some tentaculitoids in the form of budding and fission (Wilson et al. 2011) argues against molluscan affinities (Figs. 10, 11, Table 2). In contrast to calcitic tentaculitoids, molluscs were originally aragonitic biomineralisers.

Annelida. – Our similarity analyses found no support for annelid affinities of tentaculitoids. Annelids always formed clusters with more distantly related phyla (Figs. 2, 3). Similarity of tentaculitoids to the tubicolous annelids is essentially restricted to the overall shape of the shell and its initial substrate-cemented growth in some taxa. Asexual reproduction is also similar in annelids and tentaculitoids (Table 2). The skeletal structures of calcareous polychaete tubeworms (e.g. serpulids, sabellids and cirratulids) are mostly different from those of tentaculitoids. Calcareous polychaete tubeworms never have laminar structures, such as cross-bladed or regular foliated structures (Vinn et al. 2008a,b,c; Vinn 2009; Vinn & Mutvei 2009; Fig. 4). In addition, pseudopunctae and pores are not known in calcareous polychaete (Vinn & Mutvei 2009; Fig. 5A–C). Calcareous polychaetes are not attached to their tubes, but tentaculitoids were attached to them by muscles. The proximal opening of calcareous polychaete tubes separates them easily from the tentaculitoids (Figs. 6, 7, 12). Polychaetes do not have an external organic cover of the shell. Thus, there is a long list of fundamental differences between calcareous polychaete tubeworms and tentaculitoids, making any close phylogenetic relationships unlikely.

Cnidaria. – Our analyses found no support for cnidian affinities of tentaculitoids. Cnidarians always formed a cluster with more distantly related phyla (Figs. 2, 3). The resemblance of tentaculitoids to cnidarians is based on the similarities of their tubular shell, substrate-cemented initial growth and vesicular shell walls (Table 2). The remaining characters in common also occur in other analysed phyla. The major difference between cnidarians and tentaculitoids lies in the complexity of their biomineralisation systems. The cnidarians are not known to form laminar structures such as the cross-bladed form of Tentaculites or the regular foliated structure of Cornulites (Carter et al. 1990; Fig. 4). Cnidarians lack pseudopunctae, punctae and an external periostracum-like cover of their skeleton, and they never have larval shells (Figs. 5A–C). The differences in biologically important characters rule out cnidian affinities of the tentaculitoids (Table 2).

Sponges. – Our analyses revealed no similarity between sponges and tentaculitoids (Figs. 2, 3). The similarity of sponges and tentaculitoids is in the initial substrate-cemented growth and asexual reproduction, and probably also in the analogous vesicular wall structure. The lack of any other biologically important common characters rule out sponge affinities (Table 2).

Foraminifera. – Fisher (1962) compared cornulitids with fusulinids because of the similarities in the vesicular shell structure, but it is not clear whether this structure was formed in the same way in fusulinids and tentaculitoids. The rest of the biologically important characters indicate that tentaculitoids and fusulinids are not closely related, so fusulinid affinities of tentaculitoids can be ruled out.

Conclusions

1. Tentaculitoids belong to Lophotrochozoa with a high degree of certainty.

2. They are best classified as “lophophorzoa”, most likely close to Brachiopoda (Phoronida+Brachiopoda). It is possible that tentaculitoids are calcifying
stem-group phoronids as suggested by Taylor et al. (2010).

(3) There are many similarities between tentaculitoids and molluscs. The hypothesis of molluscan affinity cannot be ruled out. However, it is unlikely that molluscs were capable of asexual reproduction via budding and fission. In contrast to some tentaculitoids, their larvae did not cement to the substrate before metamorphosis. Unlike tentaculitoids with calcitic tubes, molluscs were originally aragonitic bioamineralisers.

(4) Traditional annelid affinities can be refuted as based on the differences in bioamineralisation and skeletal growth.

(5) Interpretations of tentaculitoids as calcareous sponges, cnidarians or even fusulinids cannot be supported by data on their biology.

Acknowledgements. — We are grateful to J.P. Cuf and J. Stolarski for comments on coral skeletal structure; P.D. Taylor for comments on the morphology of Bryozoa and to J. Dzik for comments on the earlier version of the manuscript. O.V. is grateful to The College of Wooster, M.A. Wilson, The College of Wooster, (Ohio) for constructive review. This research is a contribution to three International Geoscience Programme projects: IGCP 591, IGCP 596 and IGCP 572.

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