Discussion


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A B S T R A C T

Gierlowski-Kordesch and Cassle (2015, Earth-Science Reviews 148, 209–227) interpreted microconchids (extinct tentaculitoid encrusters) as strictly marine, rejecting the previous conclusions that these organisms occupied a variety of habitats ranging from marine to non-marine. We argue that due to misunderstanding of previous statements concerning the affinity of microconchids, the authors used an actualistic approach and incorrectly compared microconchids with modern phoronids, which led to oversimplifications and misinterpretations. Also their idea that microconchids, as supposedly strictly marine organisms, were preserved in non-marine settings only because of transport by storm surges and tsunamis is unsupported on paleontological grounds. These errors led to mistaken conclusions about microconchid paleoecology that must be discussed in order to avoid an erroneous interpretation of microconchid paleoenvironments.

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1. Introduction

In their recent paper, Gierlowski-Kordesch and Cassle (2015) discussed the paleoecology of microconchids, an extinct group of tubeworms that for decades were known under the generic name Spirorbis (Taylor and Vinn, 2006). The superficial similarity of microconchids to the spirally-coiled, Recent polychaete genus Spirorbis has confused researchers on many occasions, resulting in erroneous interpretation of microconchid-inhabited paleoenvironments as purely marine (see discussions in Taylor and Vinn, 2006; Zatoń et al., 2012). Weedon (1990, 1991, 1994) was the first to demonstrate on the basis of microstructural evidence that Paleozoic ‘spirobords’ are in fact tentaculitoid tubeworms and not polychaetes. This discovery moved the microconchids to a completely different place on the phylogenetic tree. The ‘Spirorbis’ problem received close attention by Taylor and Vinn (2006) with respect to microconchid paleoecology. Analyzing specimens from Paleozoic and Mesozoic sections, as well as the literature, these authors showed that in fact these organisms not only inhabited marine settings, but were also able to live in a variety of other paleoenvironments ranging from brackish to freshwater and sometimes even in hypersaline waters. Later, Zatoń et al. (2012) showed possible scenarios of when microconchids colonized particular non-marine paleoenvironments and what the potential benefits were for colonizing such unstable habitats. However, Gierlowski-Kordesch and Cassle (2015) tried to show that during their long evolutionary history microconchids lived only in marine paleoenvironments, and that their occurrences in deposits interpreted as brackish or freshwater resulted from transportation out of their original marine settings by storm surges or even tsunamis.

As we are actively interested in various problems concerning this fascinating group of extinct tubeworms, and knowing that they still need a thorough investigation in order to address many unsolved problems, we are pleased that microconchids received additional attention. However, we found that the thorough review of Gierlowski-Kordesch and Cassle (2015) contains many oversimplifications and misunderstandings that strongly influenced their final conclusions. Therefore, we would like to comment on the most important issues raised by Gierlowski-Kordesch and Cassle (2015).

2. Affinity of microconchids

In order to discuss the potential biology and thus paleoecological requirements of an extinct group such as the microconchids, we must first assess their phylogenetic affinity. Gierlowski-Kordesch and Cassle (2015) stated that microconchids (Order Microconchida, Class...
Tentaculitina) are interpreted as phoronids (Phylum Phoronida), and this interpretation was used to support their statements about the strictly marine nature of microconchids. Microconchids, however, are not phoronids. Taking into account the microstructural features of the microconchid tube, such as its lamellar and punctate microstructure, as well as its bulbous, protoconch-like origin (e.g., Taylor and Vinn, 2006; Taylor et al., 2010; Vinn and Mutvei, 2009) and even budding (Wilson et al., 2011), it is evident that microconchids were also not serpulid polychaetes to which they were previously compared. Microconchids were instead closely related to such lophophorates as brachiopods, bryozoans and phoronids (e.g., Taylor and Waeenschbach, 2015). Having both solitary and colonial (thus far one species only, see Wilson et al., 2011) modes of life, microconchids were hypothesized to be related to such suspension-feeding lophophorates as phoronids (Vinn and Mutvei, 2009; Taylor et al., 2010). However, this is only a hypothesis, as microconchids went extinct at the end of the Middle Jurassic (e.g., Taylor and Vinn, 2006; Zatoń and Vinn, 2011), leaving no living descendants. This is also only a statement about relationships, not that microconchids actually were phoronids. The origin of microconchids remains enigmatic. We know that they appeared in the Late Ordovician but whether they really derived from solitary, straight-shelled cornulitids as has been postulated (e.g., Vinn and Mutvei, 2009; Taylor et al., 2010) is also uncertain. In summary, microconchids may be considered to be extinct lophophorates of uncertain phylogenetic affinity. Thus, there are no extant descendants of microconchids as Gierlowski-Kordesch and Cassle (2015, p. 213) stated. In order to decipher their true affinity, finding microconchid soft-parts preserved would be important. Therefore, contrary to the assumption of Gierlowski-Kordesch and Cassle (2015, p. 210), we should not use any actualistic inferences from the biology and ecology of phoronids and other extant species in interpretations of microconchid paleoecology.

3. Paleoecology of microconchids

What is known from the literature on microconchids is that these extinct tubeworms occurred in a variety of aquatic paleoenvironments, ranging from marine, through brackish, to freshwater and even hypersaline (e.g., Taylor and Vinn, 2006; Caruso and Tomescu, 2012; Zatoń et al., 2012, 2014a; Zatoń and Peck, 2013). Thus, during their long history from the Late Ordovician into the Middle Jurassic, microconchids, unlike the superficially similar spirorbid polychaetes, occupied a wide range of habitats (see Zatoń et al., 2012). Their presence in different unstable habitats (e.g., Taylor and Vinn, 2006; Zatoń et al., 2012), as well as their abundance following mass extinctions (e.g., Fraser, 2011; Zatoń and Krawczyński, 2011; Zatoń et al., 2013; He et al., 2012; Yang et al., 2015), indicates that they were opportunistic organisms well adapted to a variety of settings. In contrast to the above, Gierlowski-Kordesch and Cassle (2015) presented microconchids as strictly marine organisms. Such a hypothesis is primarily based on their erroneous assumption that microconchids were phoronids. Considering microconchids as phoronids has a serious impact on the paleoecological interpretation of their habitats. Another misunderstanding is the statement that “No invertebrate organism today is able to tolerate all salinities from fresh to saline” (p. 211). First, it must be mentioned that genetically closely related invertebrate taxa can live in different salinities. For example, freshwater polychaete species can be closely related to marine species (Kupriyanova et al., 2009). Second, and most important, we are here concerned with a higher taxonomic rank — the Order Microconchia. No one has claimed that the same individual microconchid or a single microconchid species could have lived in both fresh and marine waters. Even Zatoń et al. (2012, p. 609) indicated that the salinity ranges that Individual species could tolerate is as yet unknown but worth investigating. It is reasonable and probable that a given, single microconchid species was not able to live in both marine and freshwater habitats. Zatoń et al. (2012) hypothesized, based on a literature survey, that the microconchids inhabiting freshwaters disappeared long before the marine species went extinct.

Gierlowski-Kordesch and Cassle (2015) stated that all occurrences of microconchids in distal floodplain deposits within low-gradient coastal areas were results of landward transportation of marine forms by storm surges and even tsunamis. However, in the deposits interpreted as representing brackish or even freshwater habitats (e.g., Zatoń and Peck, 2013; Zatoń et al., 2014a), microconchids are not only associated with terrestrial plants, but also with freshwater oysters, bivalves and even charophyte gyrogonites (Zatoń and Peck, 2013). Moreover, if the presence of microconchids in such deposits was due to storms or tsunamis, why were not other marine organisms transported as well? It is known from modern studies that tsunamis can transport exclusively marine organisms far onshore (Khare et al., 2009; Scicchitano et al., 2010). The presence of fossils of such stenohaline organisms as echiuromorpha, brachiopods or ammonoids would be excellent and conclusive evidence for microconchid transportation landward from marine settings. The lack of such evidence, however, significantly weakens the hypothesis of Gierlowski-Kordesch and Cassle (2015) that microconchids were strictly marine organisms. Isotopic analyses of the calcitic microconchid tubes could help determine whether they grew in marine waters or in freshwater conditions (Ingram and Sloan, 1992), but no such analyses have been performed. Gierlowski-Kordesch and Cassle (2015, p. 213) went further and stated that the “odd” preservation of microconchids in the form of loose tubes detached from the substrates is additional evidence of their transportation from marine to terrestrial settings. It must be noted, however, that microconchids, as encrusting organisms, used a variety of hard or firm substrates for attachment. If they attached to a hard substrate such as a cobble or shell (e.g., Vinn and Taylor, 2007; Zatoń and Krawczyński, 2011; Zatoń et al., 2014b), they would have been transported together with that substrate. However, if they originally attached to an epipodically firm substrate, such as the thallus of a nonmineralized alga, they most commonly would be preserved as detached, scattered specimens. Such detached specimens have been encountered in both marine (e.g., Peryt, 1974; Vinn and Taylor, 2007) and non-marine deposits (Zatoń and Peck, 2013). In the latter, microconchids may have detached from terrestrial plants and freshwater algae (charophytes) following their decomposition in aquatic environments. Therefore such loosely scattered microconchid tubes likely resulted from purely taphonomic factors and were not related to any transportation agents. Also the statement that the presence of juvenile specimens attached to plants in Carboniferous deposits, as described by Zatoń and Mazurek (2011), attests to “the quick demise of these worms as they settled during storm surges and quickly died as the marine conditions receded” is misunderstood by Gierlowski-Kordesch and Cassle (2015, p. 219). First, Zatoń and Mazurek (2011) not only detected juveniles, but also well-developed adult specimens. Second, the abundance of juveniles is explained by their deaths from either quick burial due to an increase of sediment input and/or the onset of unfavorable, oxygen-deficient conditions that may have occurred due to decomposition of organic matter in such brackish or even freshwater environments.

Clear examples of the transport of marine organisms into terrestrial setting were provided by Maeda et al. (2003) from the Lower Permian of Texas. The authors described the presence of damaged cephalopod (ammonoid and nautiloid) shells within deposits containing terrestrial plants and non-marine gastropods, but lacking such stenohaline organisms as echiuromorpha or brachiopods. The authors interpreted the cephalopod shells as transported from an off-shore environment to a brackish water or muddy beach environment. Interestingly, the preserved plants are also encrusted by microconchids (see Maeda et al., 2003, Fig. 4C). Thus, in this case the cephalopods provided good evidence for their transportation to the terrestrial setting. Their floating shells could have been carried by strong surface currents rather than storm surges or tsunami, as in the latter case some stenohaline fauna would also have had
the chance to be transported. Microconchids, however, were unlikely to have been transported from the sea as they originally encrusted the three-dimensional, well-preserved plants which underwent minimal transport from their living habitat on land. These plant-encrusting microconchids lived in a terrestrial, brackish-water habitat.

Thus, the lack of evidence (such as stenohaline taxa preserved together with microconchids in terrestrial settings) makes the Gierlowski-Kordesch and Cassle (2015) hypothesis about microconchid landward transportation by storms or tsunamis completely unsupported. We know that sedimentological analysis is very important in order to interpret a given palaeoenvironment (Gierlowski-Kordesch and Cassle, 2015, e.g., Section 6); however, we think that fossils are equal, or even more important, paleoenvironmental indicators.

We agree with Gierlowski-Kordesch and Cassle (2015) that brachiopods (a likely sister group to microconchids) never adapted to freshwaters because of the barrier of osmoregulation. We also agree that another probable microconchid sister taxon, Bryozoa, probably adapted to freshwaters because they lack excretory systems (and thus have no need for osmoregulation). There is no evidence that microconchids possessed excretory systems; their small body sizes have no need for osmoregulation. We also agree with Gierlowski-Kordesch and Cassle (2015) that microconchids were solitary organisms living in aggregations on a given hard or substrate (e.g., Zato et al., 2012). Strictly colonial microconchids are currently known only from one species in the Permian of Texas (Wilson et al., 2011).

4. Conclusions and final remarks

All the known data about microconchids indicate that they were enigmatic, extinct suspension-feeding organisms of lophophorate affinity, placed somewhere close to such taxa as Brachiopoda, Bryozoa and Phoronida. However, their true taxonomic status is still a mystery. Therefore, we cannot apply strictly actualistic approaches in order to decipher their biology and then ecology, as Gierlowski-Kordesch and Cassle (2015) did when they considered microconchids to be phoronids. No matter what the extinct fossil group is, such oversimplification leads to false conclusions. To decipher the ecological requirements of microconchids, we should look not only at the sedimentology of the deposits containing the fossils, but also the associated fossil assemblages. We should follow ‘Occam’s razor’ when interpreting microconchid aquatic habitats. To postulate that microconchids were strictly marine and occurred in non-marine settings only because of transportation by storm surges or tsunamis requires evidence in the form of other stenohaline organisms similarly transported. Such evidence is lacking. Storm deposits preserved within a ria-type rocky coastal setting (Siracusa, SE Sicily), would follow

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