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Original article

Invasion of freshwater and variable marginal marine habitats by microconchid tubeworms – an evolutionary perspective[☆]

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ABSTRACT

Microconchids are an extinct group of *Spirorbis*-like tentaculitoid tubeworms that dwelled in a variety of aquatic environments, ranging from normal marine, through brackish and hypersaline, to freshwater. An analysis of published microconchid occurrences focusing on their ecology and palaeoenvironmental distribution through geological time is conducted in order to establish the timing of microconchid colonization of freshwater and marginal marine habitats. Microconchids originated during the Late Ordovician in shallow shelf, normal marine environments where they thrived until their extinction at the end of the Middle Jurassic (latest Bathonian). Microconchid colonization of marginal marine brackish habitats seems to have started already by the Early Silurian (Wenlock). The freshwater habitats were invaded by microconchids in the Early Devonian, nearly simultaneously in several regions (Germany, Spitsbergen, USA). Since shallow marginal marine and freshwater habitats are more unstable, especially in terms of temperature and salinity fluctuations, as well as prone to desiccation, than normal marine, shelf environments, the drivers of the colonization of these habitats by microconchids are currently incompletely understood. We hypothesize that by colonizing such environments, microconchids gained access to abundant food resources in the form of suspended organic matter delivered from the land by rivers and streams. These, combined with their biology, enabled microconchids to reproduce fast and in large numbers. Microconchids are considered to have gone extinct by the end of the Middle Jurassic (Late Bathonian). Their youngest occurrence in freshwater environments is known from the Late Triassic and it is currently not known whether microconchids continued to occupy such habitats later on in the Jurassic. All the Middle Jurassic records of microconchids come from marine settings. Thus, more focused research on Jurassic brackish and freshwater deposits worldwide is needed to check whether they may have thrived in such environments at some locations, until their hypothesized extinction.

1. Introduction

Microconchids are an extinct group of small, tube-forming encrusting organisms, the fossil record of which extends back to the Late Ordovician and ranges up to nearly the end of the Middle Jurassic (e.g., Taylor and Vinn, 2006; Vinn and Mutvei, 2009; Vinn, 2010a; Zatoń and Vinn, 2011). Due to their millimetric size and calcareous coiled tubes, for decades microconchids were treated as polychaete worms of the genus *Spirorbis* (Taylor and Vinn, 2006; Fig. 1(A, B)), although affinities with vermiform gastropods had also been proposed by some (e.g., Burchette and Riding, 1977).

Because of being equated with spirorbids, microconchids were for a long time excluded from the ranks of interesting fossil material, and it was not until 1990 that they underwent thorough study. In a series of papers, Weedon (1990, 1991, 1994) was the first to address the mystery of these *Spirorbis*-like fossils. He used the microlamellar ultrastructure of the tube wall (Fig. 1(D)), coupled with the presence of punctation and the structure of septa, to show that microconchids are more closely related to extinct tentaculitoids than to polychaetes or vermiform gastropods. The tube structure of true spirorbids, on the other hand, consists of unordered calcitic rods (Weedon, 1994; Taylor and Vinn, 2006; Fig. 1(C)). Based on these conclusions, Weedon (1991) created the new order Microconchida within the class Tentaculita Bouček, 1964. Because the punctate microlamellar structure that characterizes microconchid tubes is also found in brachiopods and bryozoans (Weedon, 1994), it is considered that microconchids could represent an extinct clade of "lophophorates" related to the

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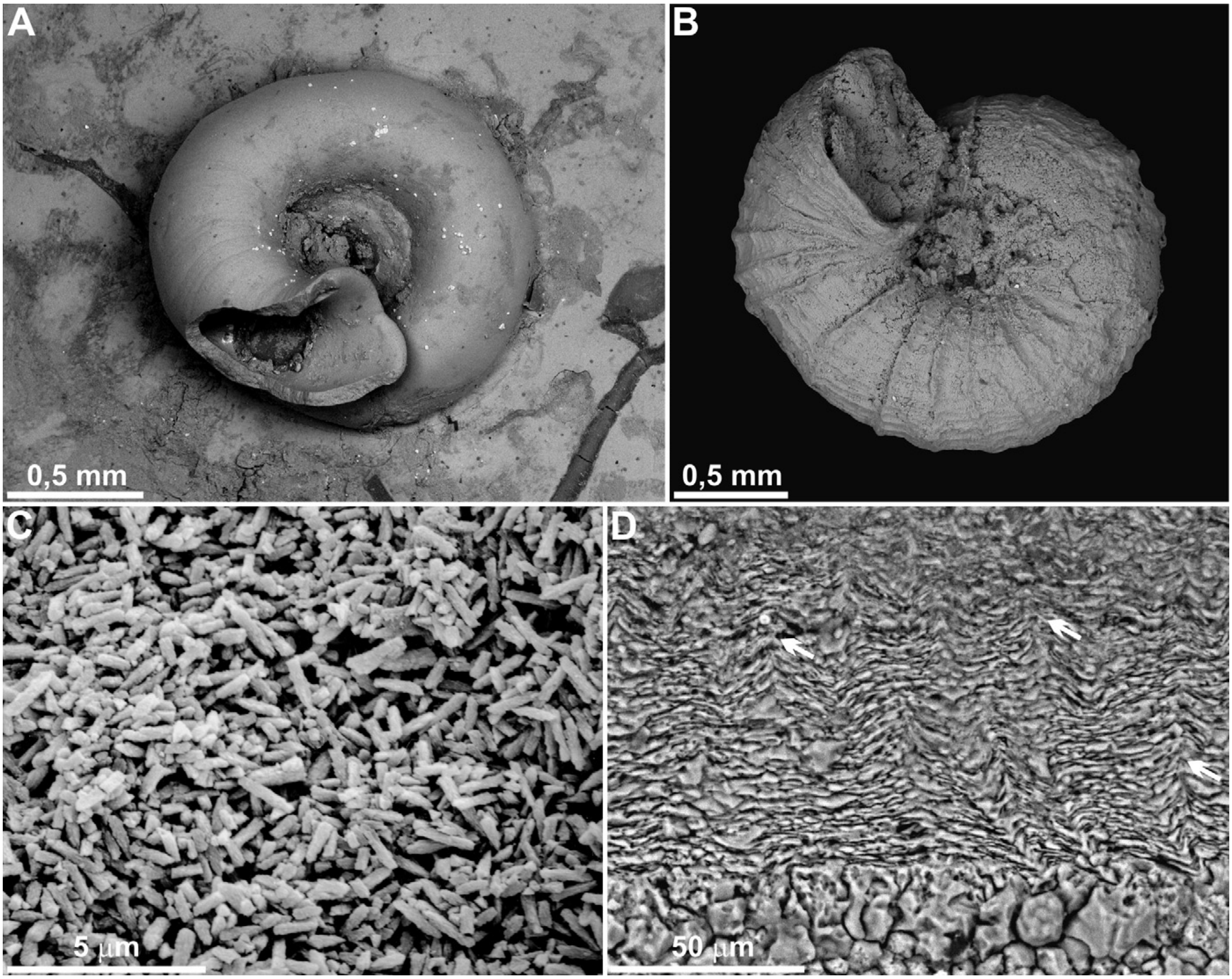

Fig. 1. Morphological and microstructural comparison of the tubes of Recent polychaete *Spirorbis* (**A**) and Middle Devonian (Givetian) microconchid *Microconchus* (**B**). **C**. Tube microstructure of Recent *Spirorbis* consisting of unordered calcitic rods. **D**. Tube microstructure of Late Devonian microconchid *Palaeoconchus*, comprising microlamellar fabric interrupted by cone-like pseudopunctae (arrows).

phoronids (Taylor and Vinn, 2006; Taylor et al., 2010). True polychaete spirorbids, on the other hand, may have evolved as early as the Late Jurassic (Ippolitov, 2010), but did not become widespread before the Late Cretaceous (Jäger, 2004; Vinn and Taylor, 2007).

Microconchids are now recognized as a distinct group of extinct organisms. During their evolutionary history, they not only survived several major and minor mass extinctions but, due to their opportunistic nature, they were exceptionally abundant in the aftermaths of mass extinctions (McGowan et al., 2009; Fraiser, 2011; Zatoń and Krawczyński, 2011a). Their disappearance from the fossil record in the Middle Jurassic, at the end of the Bathonian stage, is attributed to being outcompeted by such efficient encrusting suspension feeders as the serpulid/sabellid polychaetes and cyclostome bryozoans, which thrived and diversified during the Middle Jurassic (Vinn and Mutvei, 2009; Zatoń and Vinn, 2011).

Remarkably, unlike the morphologically similar *Spirorbis*, microconchids occupied a wide array of aquatic environments over the course of their evolutionary history. Having originated in marine environments, they also became adapted to unstable, brackish- and freshwater habitats. Although these environments are characterized by much wider fluctuations of various factors such as oxygenation, salinity, temperature and sedimentation rate, microconchids quickly became as abundant as in marine settings. As a curiosity, it is here worth mentioning that creationists (e.g., Coffin, 1975) have argued for the rapid formation of coal deposits in the sea during the Biblical Flood, on the basis of some "*Spirorbis*" attached to terrestrial plant fragments in Carboniferous Coal Measures. Of course, as we now know that "spirorbiform" microconchids also occupied brackish and freshwater environments, such reasoning is completely faulty.

A growing number of papers have been addressing the taxonomy and palaeoecology of microconchids (Vinn and Taylor, 2007; Zatoń and Taylor, 2009; Vinn, 2010a, 2010b; Wilson et al., 2011; Zatoń and Krawczyński, 2011a, 2011b), yet a synthesis of microconchid ecology across their whole evolutionary history is lacking. Here, we present a compilation of microconchid occurrence data from the literature, and associated information on age and palaeoenvironments. Based on this data set, we discuss microconchid palaeoecology in an evolutionary perspective, addressing several questions:

- When did the microconchid colonization of freshwater environments begin?
- What factors promoted the microconchid colonization of freshwater, brackish and other marginal marine habitats unstable for many other invertebrates?
- What were the advantages and disadvantages associated with colonization of such environments?

2. Material

To detect the earliest stages of colonization of brackish and freshwater habitats by microconchid tubeworms, we searched the published literature focusing on the critical Late Ordovician-Early Devonian time interval. We also corroborated all post-Devonian data points that define the timespan during which microconchids occupied the marginal marine – brackish – freshwater environments. All literature data on microconchid taxonomy, age and locality, patterns of occurrence and inferred palaeoenvironments are included in Table S1 (Appendix A); a simplified synopsis of these data, along with major events of microconchid evolutionary history, is presented in Fig. 2.

The data on fully marine microconchids included in Table S1 is selective rather than comprehensive. This is because microconchids (usually reported under the name "*Spirorbis*") are so often mentioned in the literature concerning marine environments and biotas, that it would be practically impossible to include all of them in a dataset. Additionally, many "*Spirorbis*" or "*Spirorbis*"-like fossils reported without illustration in the literature may not be true microconchids, but different tube-forming organisms, such as the Palaeozoic *Anticalyptraea* (Vinn and Isakar, 2007) or enigmatic "*Serpula*"-like organisms (Beus, 1980). We nevertheless strived to represent in this dataset all the habitat types that microconchids occupied in the marine realm.

3. Patterns of microconchid environmental distribution

3.1. Normal marine environments

The fossil record indicates that since their first appearance in the Late Ordovician (Sandbian; Botting et al., 2011), microconchids occupied normal marine environments, where they resided until their final disappearance in the latest Bathonian (Zatoń and Vinn, 2011; Fig. 2). The fossil record of Late Ordovician microconchids is very sparse, being currently limited to Baltica (Estonia) and Avalonia (Wales) where they have been documented as encrusters of shelly substrates (Vinn, 2006; Botting et al., 2011). Microconchid abundance increased during the Silurian, when they were associated with both skeletal and hard-ground substrates, as documented in Baltoscandia and Laurentia. They are even more frequently reported in the Devonian from many localities scattered throughout Europe and North America, and are especially common on shelly substrates (particularly brachiopods). Some microconchids found detached from their substrate could have originally encrusted seaweeds or aragonitic shells that were dissolved (e.g., Zatoń and Krawczyński, 2011b).

Normal marine forms are not as abundantly known for the Carboniferous as they are for the Devonian; they are recorded primarily in North America and the British Isles (Table S1). Even less frequent are Permian marine microconchids. To date, only two records are known: one from shallow shelf environments in Texas, where aggregated microconchids formed small patch-reefs (Wilson et al., 2011), and one from a deep outer shelf environment (below storm wave base) in Greece (peri-Gondwana; Shen and Clapham, 2009). We nevertheless hypothesize that marine microconchids are more abundant in the Permian fossil record and still await discovery. Normal marine Triassic microconchids are known primarily from North America and Europe (Table S1), where they form dense populations on encrusted shells (e.g., Hagdorn, 2010; Fraiser, 2011). The youngest microconchids are

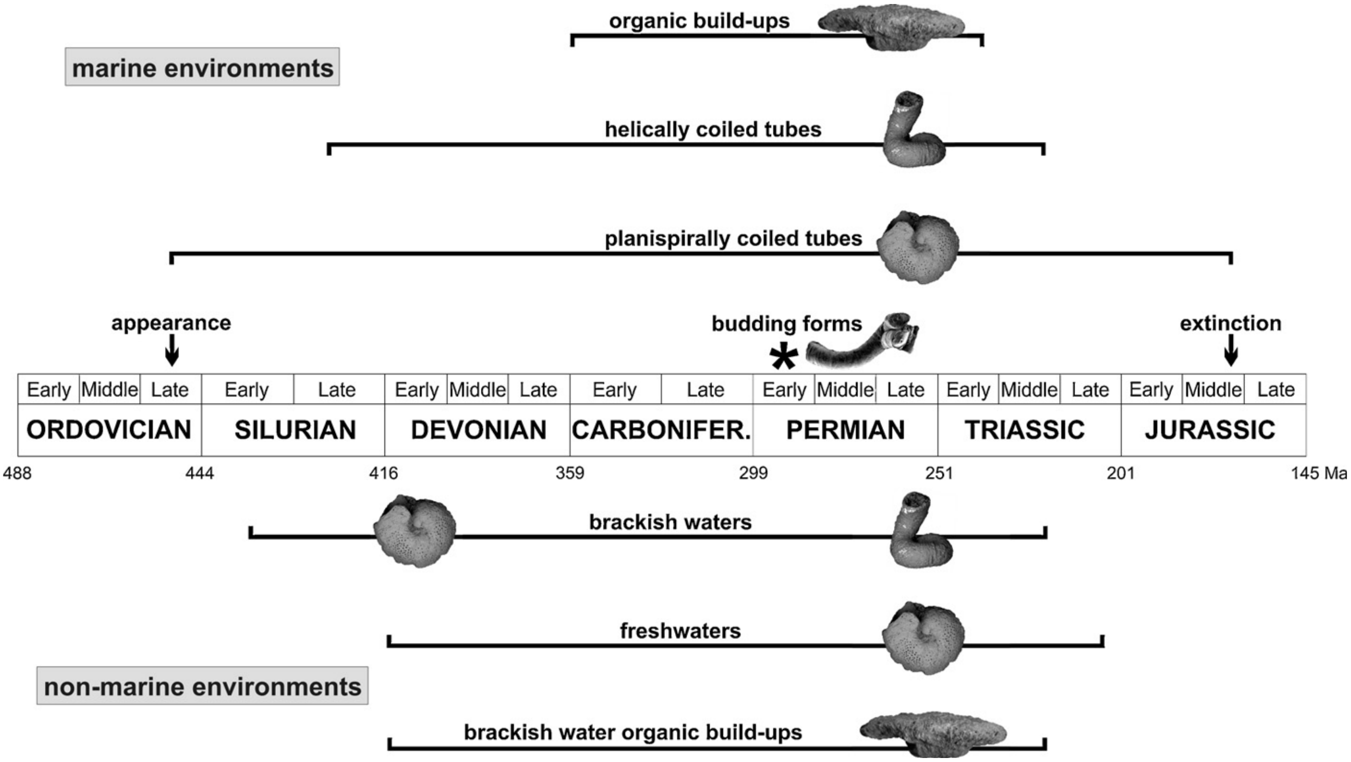

Fig. 2. Major events in microconchid evolutionary history. Carbonifer.: Carboniferous. Time scale after Gradstein et al. (2004).

currently known from the Middle Jurassic, only in Europe (England, France and Poland) where they are associated with sponge patch-reefs (Palmer and Fürsich, 1981), shells (Vinn and Taylor, 2007; Taylor, 2009) and oncoids (Zatoń and Taylor, 2009; Zatoń et al., 2012).

Generally, in normal-marine settings microconchids occur in shallower environments (Table S1). In these environments, on both lithic and biogenic substrates, microconchids were able to respond to changing sedimentation rates and competition by associated encrusters, by elevating their tubes through vertical growth (e.g., Burchette and Riding, 1977; Vinn, 2010a; Vinn and Wilson, 2010; Zatoń and Krawczyński, 2011b). In contrast, when they occur in deeper settings, such as the Upper Devonian condensed deposits of the Holy Cross Mountains in Poland, they seem to be significantly outnumbered by other encrusters (e.g., crinoids; Rakociński, 2011). Additionally, unlike other encrusters (serpulids, bryozoans) which may be abundant on unstable substrates, microconchids are absent from those substrates; such is the case of the Middle Jurassic hiatus concretions from siliciclastic subtidal environments (Zatoń et al., 2011). These observations imply that both depth and substrate stability may have been important factors influencing microconchid distribution. Nevertheless, it is important to note that even in shallower settings microconchid abundance varied. Whereas in some localities microconchids are among the dominant taxa (Hurst, 1974; Palmer and Fürsich, 1981; Liddell and Brett, 1982; Alvarez and Taylor, 1987; Bordeaux and Brett, 1990; Lescinsky, 1997; Vinn and Wilson, 2010), in others they are represented by a few specimens (Rodriguez and Gutschick, 1975; Kesling et al., 1980; Sando, 1984; Lescinsky, 1997; Zatoń and Taylor, 2009). Their distribution and relative abundance were, thus, governed at least in part by other environmental factors.

3.2. Brackish and freshwater environments

Having originated in normal marine settings, microconchids subsequently started to expand into marginal marine brackish environments during the Silurian, where they are associated with fish and plant remains in the Wenlock deposits of Scotland (Brower, 1975). The freshwater environments were invaded by microconchids during the Early Devonian, and they thrived in these habitats until at least the Triassic (Taylor and Vinn, 2006; Fig. 2). However, because Silurian non-marine deposits have received comparatively less attention than Devonian ones in this respect, it is possible that microconchids may have colonized strictly freshwater habitats prior to the Early Devonian.

Documented microconchid abundances are especially high in brackish and freshwater environments during the Carboniferous (Table S1), when they are found with high densities and forming buildups such as patch-reefs, bioherms or biostromes; often associated with algae, they formed algal-microconchid stromatolites (Leeder, 1973; Burchette and Riding, 1977) in peritidal and lagoonal environments. During the Carboniferous expansion of the terrestrial vegetation onto land masses and into terrestrial aquatic basins (Park and Gierlowski-Kordesch, 2007), microconchids commonly used terrestrial plants and bivalves as hard substrates in fresh and brackish water environments (Fig. 3(C–F)). The data on Permian microconchids inhabiting restricted environments are as rare as for the normal marine settings. That is because Permian hard substrate communities are generally poorly known (Taylor and Wilson, 2003). However, it is possible that they were common globally and lack of data represents only a sampling bias. For example, Shikama and Hirano (1969) described ‘‘spirorbids’’ associated with land plants from Korea, and Toomey and Cys (1977) reported microconchids encrusting stromatolites in marginal marine environments of New Mexico (Table S1).

Triassic examples are more numerous (Table S1); microconchids are known to have thrived in fresh, brackish and hypersaline waters in different habitats, ranging from supratidal to limnic environments of North America and Europe. By contrast, no occurrences of microconchids in fresh, brackish or hypersaline waters have been documented in the Jurassic. Since microconchids are present in marine settings in the Jurassic, more non-marine deposits from this period should be investigated for microconchids in order to eliminate potential biases. At the moment we are not sure whether the last occurrence of microconchids in fresh and brackish habitats during the Late Triassic is a fact, or maybe an artifact caused by insufficient sampling of Jurassic deposits originated in such facies.

As in the case of microconchids occupying normal marine environments, those inhabiting hypersaline, brackish settings and freshwaters also tended to live in aggregations. However, unlike marine forms, those from restricted environments usually were the most abundant, if not the only encrusters in their habitats. Whether there are structural features that distinguish freshwater microconchids from marine forms is currently unknown. Freshwater forms are generally poorly preserved; for example, microconchids from the Lower Devonian of Wyoming and Upper Carboniferous of Poland (Fig. 3) have diagenetically altered (dolomitised) tubes (Zatoń and Mazurek, 2011; Caruso and Tomescu, 2012). In these cases, such important primary features as tube mineralogy (calcitic or even aragonitic) and tube microstructure (presence/absence of punctation or pseudopuntaction), which would help distinguish them from marine forms, could not be documented.

4. Colonization of brackish and freshwater habitats: a discussion

Although the fossil record of microconchids is currently biased geographically toward Europe and North America (Table S1), some ecological and evolutionary patterns are nevertheless emerging. Immediately after their first appearance in the Late Ordovician, microconchids seem to have dwelled exclusively in marine environments, as they are known only from marine deposits representing both shallow marine and deep water shelf habitats in Europe and North America.

As indicated by the fossil record, the colonization of marginal marine brackish environments occurred during the Silurian, and the invasion of freshwater habitats by microconchids started during the Early Devonian (Fig. 2). Thus, the current available data show that microconchids colonized such settings in a stepwise manner, from normal marine in the Late Ordovician, through brackish in the Silurian, to freshwater environments during the Early Devonian. It seems that during the Early Devonian freshwater environments were, at a geological time scale, invaded quasi-simultaneously in different part of the world. This is reflected in the near-synchronous occurrences of microconchids in freshwater deposits of Wyoming (USA), Germany and Spitsbergen (Table S1). In Wyoming, microconchids occur in Lochkovian to Emsian deposits of the Beartooth Butte Formation (Caruso and Tomescu, 2012). This unit has been interpreted as brackish and freshwater deposits of estuarine to fluvial environments (Dorf, 1934; Sandberg, 1961; Fiorillo, 2000); its fossil content includes fish, eurypterid, and terrestrial plant fragments. The microconchids are associated here with the lycopsid *Drepanophycus* and other early land plants (Fig. 3(A, B)). In slightly younger deposits (Pragian-Emsian) of Germany, microconchids have also been found associated with land plants in fresh to brackish water environments (Schweitzer, 1983). Similarly, in Spitsbergen they have been found associated with agnathan fish scales, ostracods and charophytes in Pragian-Emsian strata (Ilyes, 1995; Table S1).

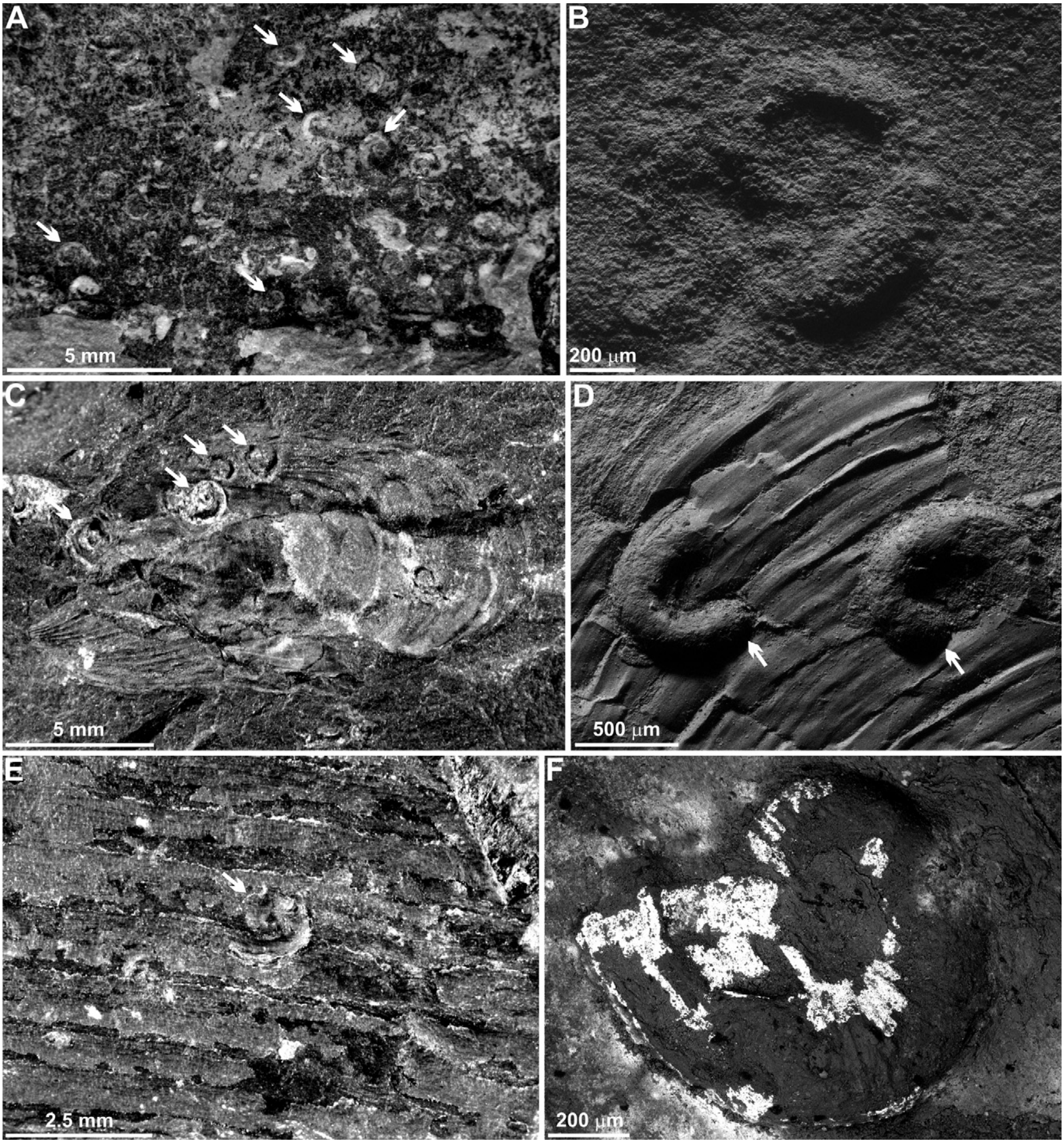

Fig. 3. Examples of freshwater microconchids. **A, B**. The earliest record of freshwater microconchids encrusting terrestrial plants (*Drepanophycus*) from the Lower Devonian (Lochkovian-Emsian) of Wyoming, USA; A: Mass aggregation of microconchids on plant remains. Despite poor preservation, the spiral coiling of some of the tubes is conspicuous (arrowed); B: Single tube with only the last whorl preserved. **C–F**. Microconchids from the Upper Carboniferous Coal Measures of southern Poland (see Zatoń and Mazurek, 2011); C, D, F: Microconchids encrusting freshwater bivalve shells; C: Small aggregation (arrowed) of poorly preserved specimens; D: ESEM photomicrograph of two juvenile individuals with tube origin indicated (arrows); E: Poorly preserved specimen encrusting conspicuous plant shoot; F: ESEM photomicrograph of better preserved tube with some remnants of primary ornamentation still visible. The tubes of both the Lower Devonian and Upper Carboniferous specimens were diagenetically dolomitized.

In the fossil record there are other examples of colonization of brackish and freshwater environments by originally marine animals. The most interesting group for comparisons are the serpulid polychaetes, suspension feeding worms that build calcareous tubes similar in many ways to those of microconchids. Among serpulids only one species, *Marifugia cavatica*, lives in freshwater (ten Hove and van den Hurk, 1993; Kupriyanova et al., 2009), namely in ground waters of the Dinaric Karst of northeastern Italy, Slovenia, Croatia, and Bosnia and Herzegovina. Shallow water marine serpulids presumably colonized freshwater similarly to microconchids, via a brackish water intermediate stage. In support of this idea, *Marifugia cavatica* is phylogenetically most closely related to five species of the brackish water serpulid genus *Ficopomatus* (Kupriyanova et al., 2009). The transition to the freshwater subterranean environment in serpulids may have occurred via ancestral marine shallow water to intertidal or estuarine species (like *Ficopomatus*) that evolved the physiological mechanisms needed to withstand low salinity. Thereafter, they could have penetrated the hypogeal freshwater environments via surface rivers and lakes (Kupriyanova et al., 2009). Fossilized tubes of *M. cavatica* have been discovered in a collapsed cave in Slovenia and are dated to 3.6 Ma (Bośak et al., 2004). The Eastern Paratethys, fringed by brackish to palustrine environments and persisting throughout the Miocene and Pliocene (Popov et al., 2004), is the most likely ancestral habitat of *Marifugia*.

In contrast to freshwater microconchids, *Marifugia* can occur as agglomerating masses that form encrustations over 10 cm-thick. Similarly to microconchids in marginal marine environments, *Ficopomatus enigmaticus* may form small reefs. In Argentina's Mar Chiquita coastal lagoon, large masses of *Ficopomatus enigmaticus* form reefs up to 7 m in diameter and 0.5 m-thick, as circular patches scattered over hundreds of hectares (Obenat and Pezzani, 1994). The lagoon El Bahira (Lac de Tunis, Tunisia) hosts similar aggregations of *Ficopomatus* (ten Hove and van den Hurk, 1993). Normal marine serpulids are also known to form large aggregations and small reefs (ten Hove and van den Hurk, 1993).

Aside from serpulids, ostracods also show a similar evolutionary pattern of invasion of freshwater habitats via brackish habitats. According to Bennett (2008), the first putative brackish water ostracods are known from the middle Silurian (with unequivocal evidence from the Devonian) and the first putative freshwater forms are known from the early Carboniferous, becoming common in the late Carboniferous. Bennett (2008) hypothesised that ostracods could have colonized the freshwater habitats in two different ways (after Gray, 1988):

- Passive invasion, occurring in coastal subtidal marine environments exposed due to regression-driven processes, such as the formation of isolated bodies of saltwater that became increasingly less saline due to freshwater input from land;
- Active invasion by migration up estuaries and into coastal lakes or rivers during periods of high sea-levels.

In the Early Devonian, an interval during which microconchids are considered to have invaded freshwater habitats, sea-levels fluctuated following a marked sea-level fall near the Silurian-Devonian boundary (Johnson et al., 1985; Haq and Schutter, 2008; Stets and Schäfer, 2009). During such eustatic fluctuations, microconchids may have colonized freshwater habitats repeatedly through both passive and active invasions.

Living in freshwater and marginal marine, brackish to hypersaline environments entails potential exposure and adaptation to a number of associated factors. Unlike open marine environments, marginal marine settings are unstable. They may witness episodic (seasonal) changes in many parameters, such as salinity (reduced salinity by freshwater input, or salinity increase due to evaporation in closed lagoons and ponds), atmospheric exposure and desiccation during low tides, seasonal temperature changes, periodic anoxia, or changes in sedimentation rates. All these stressing factors can have profound effects on organisms. What, then, could have been the gains for microconchids in colonizing such environments?

As putative lophophorate (phoronid-related) suspension feeding organisms (Vinn and Mutvei, 2009; Taylor et al., 2010), microconchids relied on a variety of particles occurring in the water. Like phoronids, they also may have fed on detritus dispersed in the water column (Emig, 2003). For these organisms, the colonization of, and further diversification in marginal marine and freshwater environments certainly benefited from location in close proximity of virtually unlimited sources of food. In such environments, nutrients are delivered from the land by rivers and streams in the form of terrestrial organic matter that decomposes in the water. Supplied by such a vast source of food and facing no ecological competitors throughout their Paleozoic history (the serpulids as potential competitors diversified during the Late Triassic; Stiller, 2000; Vinn and Mutvei, 2009), microconchids could have thrived in this wide array of habitats.

Ecologically speaking, microconchids behaved as opportunists (as defined by Levinton, 1970; Fraiser and Bottjer, 2004). Although in stable open marine habitats they represented a normal component (that is, neither significantly dominant nor subordinate) of encrusting communities, in unstable marginal marine and freshwater environments microconchids were numerically very abundant, often forming dense and presumably monospecific communities. This is indicated by their abundant occurrence in organic buildups of marginal marine habitats and on submerged plant remains in brackish to freshwater settings (Table S1). Such prolific colonization reflects biology – they probably developed fast, attained maturity early, and were reproductively fecund. The density of assemblages suggests that they may have been gregarious like the Recent *Spirorbis* (e.g., Knight-Jones, 1951). The high levels of food in suspension were a necessary factor for this kind of ecology. It is also very probable that the first non-marine environments occupied by microconchids on the way to freshwater settings, were influenced by marine waters and so had variable salinity (e.g., Bennett, 2008). Thus, like ostracods at the beginning of their invasion of freshwater environments (Bennett, 2008), microconchids may have become adapted to euryhaline conditions through changes in osmoregulation which allowed them to live in a range of water salinities. All these would also explain how microconchids coped with the environmental fluctuations characteristic of the unstable environments (e.g., salinity changes), being able to recover fast in the wake of events that episodically wiped out the greatest part of established populations. It is therefore not surprising that microconchids are reported as a dominant encrusting taxon in the immediate aftermath of the end-Permian mass extinction (McGowan et al., 2009; Fraiser, 2011). Zatoń and Krawczyński (2011a) also reported microconchids as a dominant taxon in the recovery interval following the Frasnian-Famennian mass extinction. These data lend further support to the opportunistic nature of microconchid ecology, and their ability for rapid colonization of habitats vacated as a result of biotic crises.

5. Conclusions and future directions

Review of the fossil record indicates that microconchid tubeworms originated in normal marine environments during the Late Ordovician, and that by the Early Devonian they had spread into freshwater habitats via brackish environments. It also appears that the colonization of freshwater environments proceeded, on geologic time scales, nearly synchronously in several geographic regions.

For microconchids, the colonization of marginal marine and freshwater environments had important advantages, which counter-balanced the disadvantages associated with these habitats that included fluctuations in water salinity, temperature and oxygenation, episodic desiccation or episodic burial by sediments derived from the land. Living in such environments, on the fringe of land masses, microconchids gained access to vast food resources in the form of suspended organic matter delivered from land by rivers and streams. These rich food resources, along with the biology of microconchids, enabled them to reproduce quickly and to recruit in large numbers. As opportunistic organisms, they were also able to spread quickly and dominate the encrusting assemblages in the aftermaths of mass extinctions. Considering these characteristics of microconchid ecology, their extinction at the end of the Middle Jurassic is somewhat of an enigma.

Although knowledge about microconchids is currently accumulating, we still know little about this extinct group of organisms. Especially interesting, but so far unproved and worth investigating, are the salinity ranges that individual species could tolerate; could the same species live in both normal marine and brackish/freshwater habitats? Another interesting question is whether just before their disappearance in the Middle Jurassic, microconchids lived only in fully marine settings, or they were still found in brackish and freshwater habitats as well? Here, data are needed to check whether any Middle Jurassic microconchids could have survived beyond the latest Bathonian in brackish and freshwater environments. Serpulid polychaetes that are ecologically similar to microconchids in many respects are capable of living in all oceanic depth zones, including hadal trenches (Kupriyanova et al., 2011). They also inhabit all climatic zones. Thus, it will be important to find out whether microconchids were also capable of living in deeper parts of the ocean than the continental shelf, or they had a depth distribution more similar to that of modern phoronids (i.e., down to ca. 400 m of depth; Emig, 2003).

To answer these and other questions, the fossil record needs to be carefully investigated, and all microconchid occurrences documented and assessed in terms of living and depositional environments. Quantitative treatments of these records in terms of age, geographical position and environments will then refine their patterns of evolution, colonization and extinction.

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Appendix A. Supplementary material

Supplementary material (Table S1) associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2011.12.003.

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