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A new microconchid tubeworm from the Artinskian (Lower Permian) of central Texas, USA

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Calcareous tubeworms are common in the Artinskian (Lower Permian) shale and limestone rocks of the Wichita-Albany Group in central Texas. In some units they form small reefs of budding tubes spreading outward from a common origin. These tubular fossils have been traditionally referred to as serpulids, but here we identify them as microconchids (*Helicoconchus elongatus* gen. et sp. nov.) These microconchids are unusual because of their greatly elongated impunctate tubes with centrally pitted diaphragms. They also show two types of budding: lateral with small daughter tubes that begin as small coils, and binary fission that produced two daughter tubes of equal diameters. These microconchids flourished in shallow marine environments with a fauna dominated by mollusks, echinoids, and foraminifera.

Key words: Tentaculita, Microconchida, reefs, Permian, Texas.

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Introduction

Calcareous tubeworms are common fossils throughout the Phanerozoic, but only recently have their systematics been addressed in detail (Vinn and Mutvei 2009). Studies of skeletal microstructure were used in the early 1990s to begin sorting out the serpulids, tentaculitids, cornulitids, trypanoporids, and other fossil tubeworms (Weedon 1990, 1991, 1994). The Order Microconchida Weedon, 1991, in particular has emerged as a diverse group found from the Upper Ordovician to the Middle Jurassic around the world (Vinn 2006, 2010a; Vinn and Mutvei 2009; Zatoń and Taylor 2009). Long misidentified as serpulid worms (especially "Spirorbis") (Taylor and Vinn 2006), the microconchids are now seen as likely lophophorates (Taylor et al. 2010). In addition to normal marine environments, microconchids also colonized freshwater, brackish and hypersaline environments during the Devonian to Triassic (Taylor and Vinn 2006). However, in general, microconchids occupy a similar niche in the Upper Paleozoic to that of the oyster/serpulids association of the Mesozoic and Cenozoic (Burchette and Riding 1977; Wright and Wright 1981; Weedon 1990). This paper describes an unusual microconchid (Helicoconchus elongatus gen. et sp. nov.) from the Lower Permian of Texas that provides significant new information on the morphology and paleoecology of the order.

These microconchids from the Wichita-Albany Group had previously been described as "Serpula" and "serpulid worm colonies" (Walsh 2002). They are locally known as "spaghetti corals" (Peter Holterhoff, personal communica-

tion 2010). Late Paleozoic to Triassic microconchids often occur as secondary frame builders in algal/microconchid buildups (Peryt 1974; Burchette and Riding 1977; Toomey and Cys 1977; Wright and Wright 1981). In contrast, Helicoconchus forms relatively large independent buildups (Fig. 1), which is also less common in microconchids than solitary growth, biostromes or small aggregations (a few cm in diameter). Serpulid buildups of similar size (fossil and modern) have commonly been termed "reefs" (e.g., Leeder 1973; Hove and Hurk 1993; Bianchi and Morri 2001; Moore et al. 2009), so we prefer to use this term for the aggregations of Helicoconchus as well because it emphasizes their large size for microconchids and their integrated skeletons. The earliest known microconchid reefs are probably Early Devonian (Vinn 2010a). In contrast to the Carboniferous (Barrois 1904; Leeder 1973; Burchette and Riding 1977; Wright and Wright 1981; Weedon 1990) and Triassic (Brönnimann and Zaninetti 1972; Peryt 1974; Ball 1980; Warth 1982; Weedon 1990) microconchid faunas, little attention has paid to Permian microconchids (Toomey and Cys 1977). Permian microconchids are important for reconstructing the evolutionary history of Microconchida, especially for understanding the survival strategies of microconchids in the end-Permian mass extinction.

Institutional abbreviations.—C/W, The College of Wooster Geology Department, Wooster, USA; NHM, Natural History Museum, London, UK; NPL, Non-vertebrate Paleontology Laboratory, Texas Natural Science Center, The University of Texas at Austin, USA.

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Geological setting

Sedimentary deposits containing microconchid tubeworm aggregates of *Helicoconchus* occur in strata of Artinskian– Kungurian (Early Permian) age on the Eastern Shelf of the Midland Basin in central Texas, within an outcrop trend extending north from the Colorado River Valley to the Brazos River Valley. Helicoconchus occurs in strata of the Elm Creek, Valera, Bead Mountain and Leuders Formations of the Wichita-Albany Group, an interval of thick limestone and shale, with some beds of evaporite sediments present near the top of the Valera Formation (Moore 1949). These sediments were deposited on a flat shelf surface, gently tilted to the west and located between highlands to the east and the deep center of the Midland Basin (Brown et al. 1987). Clastic sediments in this area were derived from mountainous highlands of the Ouachita trend, a upland region that was eroding during the Permian and later subsided to great depths during late Triassic rifting and opening of the Gulf of Mexico by detachment of the Yucatan block (Bird et al. 2005). Artinskian sedimentation on the Eastern Shelf is the beginning of dominantly autochthonous carbonate deposition in an area formerly dominated by siliciclastic sediments derived from the eastern uplands.

Strata of the Wichita-Albany Group are characterized by low diversity, mollusk-dominated marine biotas, in contrast to the high diversity marine biotas present in the underlying siliciclastic-dominated Cisco Group. This biotic change is associated with a change to drier climates and occurrence of intermittent evaporite sediment deposition (Moore 1949). In the Colorado River Valley exposures, microconchid tubeworm aggregates are common in the base of the Bead Mountain Formation within an interval at the top of a transition from deposits of bedded gypsum evaporites (top of Valera Formation) to beds of argillaceous-to-silty limestone (base of Bead Mountain Formation) This interval of common *Helicoconchus* aggregates is traceable to the Brazos River Valley (Peter Holterhoff, personal communication 2010).

The common occurrence of *Helicoconchus* in the late stages of a transition from evaporite sediment deposition suggests it was tolerant of fluctuating salinities in a shallow marine environment. Strata in this interval have nearly planar bedding, consistent with deposition on a shallow gently sloping surface with minor seafloor relief. Bioclastic strata contain fragmental fossils and indicate episodic higher energy conditions, but these beds also contain substantial amounts of siliciclastic silt and mud and are poorly winnowed.

Material and methods

This material was studied with both light microscopes (dissecting and petrographic) and an environmental scanning electron microscope in the Department of Geology at the University of Akron. A micrometer system was used in the

light microscopes for the measurements. All of the figured specimens, holotypes, and paratypes have been registered into the fossil worm collections of NHM. Additional topotype material is deposited in NPL.

Microconchids and polychaete tubeworms

The order Microconchida is distinguished from tubicolous polychaetes by its lamellar skeletal microstructure and bulblike (rather than open) tube origin (Weedon 1991; Taylor and Vinn 2006). It is these features that have been used to classify all pre-Cretaceous specimens of the ubiquitous encruster "Spirorbis" as microconchids and not serpulids like the Cretaceous to Recent Spirorbis (Taylor and Vinn 2006).

Systematic paleontology

Class Tentaculita Bouček, 1964 Order Microconchida Weedon, 1991 Genus *Helicoconchus* nov.

Type species: Helicoconchus elongatus sp. nov.; by monotypy, see below.

Etymology: Combination of helico, spiral and conch, tubicolous shell.

Diagnosis.—Small calcitic tube with planispiral, dextrallycoiling attachment surface, tube diameter increasing rapidly; after one to two whorls the tube becomes erect, helical, very long and its diameter remains relatively constant. Well-developed umbilicus absent in planispiral portion of juvenile attached tube. Tube wall microlamellar with no punctae or pseudopunctae. Tube interior with diaphragms, many of which have central pits; spacing of diaphragms changes with growth from infrequent to an average of one every two mm in erect portion of tubes; tube interior walls smooth. Tube exterior with very fine growth lines. Tubes show lateral budding and binary fission budding with the interior connections between parent and daughter tubes apparently repaired by secretion of new wall. Gregarious habits, some forming small reefs up to two meters in diameter of radial, tightly packed, branching tubes and others remaining as isolated tubes.

Discussion.—Helicoconchus, like all microconchids, can be distinguished from serpulid and spirorbid polychaetes by its microlamellar shell structure and the closed proximal end of the tube (Vinn and Mutvei 2009). This new genus differs from Punctaconchus Vinn and Taylor, 2007; Microconchus Murchison, 1839; and Pseudobrachidium Grupe, 1907; by its lack of punctae, budding origin of daughter tubes, and greatly extended late growth erect tube. Species of Microconchus with an erect helical adult tube part, such as M. advena (Salter, 1863) (Late Devonian—Carboniferous) and M. aberrans (Hohenstein, 1913) (Middle Triassic), are normally less extended than the tubes of new genus. Helicoconchus also lacks

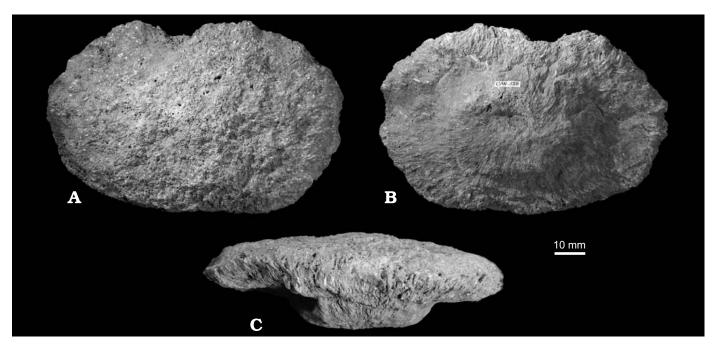


Fig. 1. Microconchid tubeworm Helicoconchus elongatus gen. et sp. nov. aggregation, NHM PI AN 1183 (holotype) in top (A), basal (B), and side (C) views.

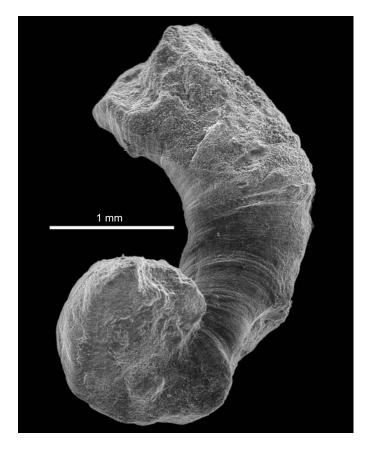


Fig. 2. Isolated origin of microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov. (scanning electron micrograph), NHM PI AN 1184.

the annulated shell of *Annuliconchus* Vinn, 2006, and the pseudopunctae of *Palaeoconchus* Vinn, 2006. These latter two microconchid genera also do not have the extended, budding helical tube that distinguishes *Helicoconchus*.

Helicoconchus aggregations superficially resemble the "serpulid" Serpula helicalis Beus, 1980, found in the Upper Devonian (Frasnian) of Arizona, USA, with their narrow helical tubes and distinct exterior growth lines. S. helicalis, however, appears to have no internal features, no known budding, nor a planispiral attachment surface. The only known specimens are silicified, so its shell microstructure remains unknown. The "tabulate coral" Spirapora Copper, 1981, of the Upper Ordovician (Ashgill) of Ontario, Canada, looks even more like Helicoconchus as a colony of helical, budding tubes of the same general size and shape. Spirapora, though, has no internal structures or a planispiral attachment surface. Serpula helicalis and Spirapora are almost certainly not serpulids or corals, and they deserve further study. They are not apparently related to Helicoconchus.

Stratigraphic and geographic range.—Helicoconchus is thus far known only from the Wichita-Albany Group (Lower Permian, Artinskian–Kungurian, of central Texas), beginning with occurrences through an interval of Artinskian restricted marine strata including the Elm Creek Limestone (Walsh 2002: fig. 5.9), Valera Shale and basal Bead Mountain Formation and at a higher level of Kungurian age restricted marine deposits in the Leuders Limestone and Lytle Limestone of the lower Clear Fork Group (Peter Holterhoff, personal communication 2010). Age assignments of north-central Texas formations are from Wardlaw (2005).

Helicoconchus elongatus sp. nov.

Figs. 1-8.

Etymology: Refers to the elongated nature of the late growth tube.

Holotype: NHM PI AN 1183, aggregation of tubes.

Type locality: Roadcut on Farm-to-Market Road 1929 (Ray Stoker Jr.

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Fig. 3. Microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov. reef in the lower portion of the E unit of the Bead Mountain Formation (Lellis and Holterhoff, 2010) and more specifically the 3B cycle set of Lellis (2010) at location N latitude 32° 41' 39.31", W longitude 99° 22' 58.37". Viewed from above. The radiating surficial pattern is due to weathering. The scale is numbered in tenths of meters. Photograph courtesy of Peter Holterhoff.

Highway) on the south side of Ivie Reservoir on the Colorado River, Concho County, Texas (coordinates: N 31.48454°, W 99.69368°).

Type horizon: Base of the Bead Mountain Formation (Lower Permian, Artinskian), Wichita-Albany Group; 3.9 meters above the top of a massive gypsum unit.

Material.—Holotype NHM PI AN 1183. Paratypes NHM PI AN 1184–1189. Topotypes also deposited at The University of Texas, Texas Natural Science Center.

Diagnosis.—As for genus, by monotypy.

Description.—Tube small, dextrally coiled and attached at its base and then extended as an erect, free helical tube, elongated many times its attachment diameter. Attachment portion consists of one to two slightly overlapping whorls, circular to elliptical in outline. Well-developed umbilicus absent in planispiral portion of juvenile attached tube. Tube origin is closed, bulb-like; tube diameter increases rapidly through whorls to erect portion, where it then maintains a consistent diameter (Figs. 1–5). Two types of budding present. Erect portion of the tube has frequent lateral budding, producing daughter tubes that grew parallel to the parent tube and at least started as helical (Fig. 6). Tubes also show budding by distal fission that produced daughter tubes of equal diameter (Fig. 7). When tubes become closely packed in mature colonies their helical nature is lost and they are more or less straight.

Tube interior walls are smooth. Diaphragms are common in the erect portion of the tubes, roughly one every two mm of length, and planar, convex or concave toward the distal end. The diaphragms are microlamellar like the tube walls, with about half their thickness. The diaphragms have small open-

ings in their centers formed by invaginated diaphragm shell structure. The living chamber (portion of the tube from the last diaphragm to its aperture) is between 5 and 7 mm long.

Tube exteriors have fine growth lines, about 4 per 0.1 mm. They often form incomplete rings and merge on parts of the tube.

Tube walls are thin (0.03–0.05 mm) and microlamellar with no punctae or pseudopunctae (Fig. 8). There are roughly 4–5 microlamellae in the walls of erect tubes. The junction between a parent tube and a daughter tube shows no internal connection (no pore or other canal).

Often forming an integrated colony of tubes with a radial growth habit of spreading laterally over substrate and growing upward in closely packed array of tubes. Large colonies have closely packed tubes; loose arrangement of tubes allows helical coiling to develop (Figs. 1, 2).

Dimensions.—The planispiral coiled attachment base of *H. elongatus* ranges from 0.8 to 1.9 mm in outline diameter; the proximal bulb within it is about 0.6 mm at its widest. The erect portion of the tube ranges from 0.9 mm (where it

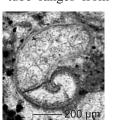


Fig. 4. Thin-section of tube origin in microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov., NHM PI AN 1185.

emerges from the coiled attachment) to 1.5 mm in diameter and up to 5.0 cm in length and probably extended much longer. (Individual tube length is difficult to estimate because of the budding and closely packed nature of mature aggregations.) Mature aggregations form small reefs up to 2.0 meter in diameter and at least 0.5 meters high.

Stratigraphic and geographic range.—As for the genus.

Discussion

Helicoconchus elongatus extends our knowledge of microconchid morphology and paleoecology, and hence what we can deduce about the evolution of the group. The initially helical and greatly extended erect impunctate tube, centrally pitted diaphragms, and two styles of budding of *H. elongatus* are distinctive in the order. Its lateral style of budding, shell structure and growth lines show similarities with the hederelloids (Taylor and Wilson 2008), and its centrally pitted diaphragms resemble those of some microconchids and other tentaculitoids (Weedon 1990).

The *H. elongatus* reefs are in the "loosely coiled helical aggregative tubes" tentaculitoid morphotype of Vinn (2010a: 214), which he interpreted as an adaptation to limited hard substrates and as a protection against burial by sediment. As such, these microconchid reefs are in the same ecological niche space as serpulid reefs and bioherms of the Upper Jurassic and above (Palma and Angeleri 1992; Hove and Hurk 1993; Kiessling et al. 2006).

Reef building.—Because of its asexual reproduction of daughter tubes, Helicoconchus could be the most advanced reef builder among microconchids. Forming a colony by budding is probably energetically cheaper than forming a colony via larvae with gregarious behavior. It could also offer better control of the growth of the "colony", increasing its mechanical strength and probably offering more effective feeding opportunities for individuals. Helicoconchus aggregations probably evolved from helical gregarious (not budding) reef-building microconchids that first appeared in Early Devonian (Vinn 2010a). Budding could be considered the last innovation in the evolution of microconchids, which otherwise had not changed much since the Early Devonian (Vinn 2010b). Microconchid aggregations and reefs are not known from the earliest Triassic, probably due to the end-Permian ecosystem collapse and extinction of Helicoconchus-like forms. Microconchid aggregations and small reefs evolved in the Middle Triassic, but they did not have asexual reproduction (budding), and were similar to the microconchid buildups of their earliest evolutionary stage (Devonian-Carboniferous).

Phylogenetic affinities.—Asexual reproduction is widespread among many tubicolous members of various invertebrate phyla (i.e., cnidarians, bryozoans, annelids, phoronids) and so does not on its own support any particular suggested biological affinity of microconchids (i.e., tentaculitoid tube-



Fig. 5. Eroded side view of microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov. aggregation, NHM PI AN 1186.

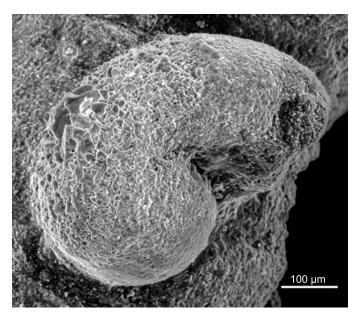


Fig. 6. Coiled lateral bud on the side of a tube of microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov., NHM PI AN 1187.

worms). However, this type of asexual reproduction (budding) in order to form an aggregation is alien to mollusks and thus supports the non-molluscan affinities of microconchids. The occurrence of two types of asexual reproduction is a peculiar feature of *Helicoconchus*, and its adaptational meaning is unclear.

Central pits.—Common central pits in the diaphragms of *Helicoconchus* (Fig. 7) are atypical for microconchids. Usually microconchids have simple slightly concave diaphragms without pits. However, Weedon (1990) has reported domelike central projections in some diaphragms of Devonian to Lower Triassic microconchids. He interpreted the folding of posterior micro-lamellar sheets of the diaphragms as perforations. We believe these unusual structures were not related to real perforations, but are the result of a folding process comparable to that in *Helicoconchus*. In spite of the different orienta-

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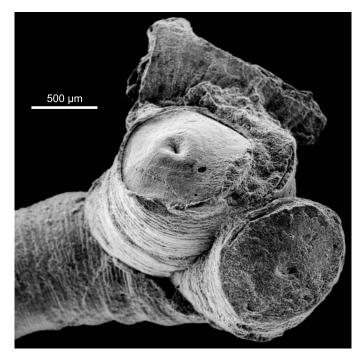


Fig. 7. Binary fission budding and diaphragms in microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov., NHM PI AN 1188.

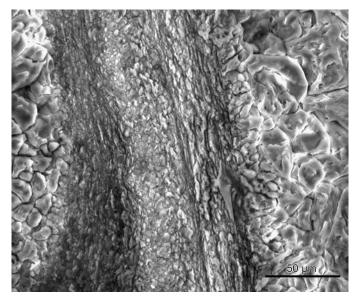


Fig. 8. Scanning electron image of two microlamellar walls of microconchid tubeworm *Helicoconchus elongatus* gen. et sp. nov. abutting each other in a polished and etched cross-section, NHM PI AN 1189.

tion of the central deflections of diaphragms described by Weedon (1990) from those in *Helicoconchus*, it could indicate that microconchid diaphragms had a certain degree of plasticity during the early phase of their formation. Alternatively, the central pits of *Helicoconchus* could reflect soft body characteristics, but in this case one would expect to find central pits in all the diaphragms. This probable early plasticity of diaphragms in microconchids is different from the other encrusting members of tentaculitoid tubeworms such as cornulitids

and trypanoporids. Similar deflections could be present in some tentaculitids, interpreted as the perforations by Blind (1969). Most likely the diaphragms were not strongly calcified during secretion and were deformed by body movements (causing the pits and the mix of concave, planar and convex cross-sections) before final calcification.

Shell structure.—Helicoconchus has no pseudopunctae or pores (Fig. 8), which have been interpreted as shell strengthening structures in microconchids (Vinn and Taylor 2007). However, there is probably not a direct correlation between the presence of pseudopunctae and the erect growth of the tube (a mechanically more demanding growth form than a planispiral shell) in microconchids. The helically coiled microconchid M. aberrans from the Middle Triassic had fewer pseudopunctae (if any at all) than its contemporary the planispiral microconchid species M. valvatus (Vinn 2010b).

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