



EARLY TRIASSIC (SPATHIAN) POST-EXTINCTION MICROCONCHIDS FROM WESTERN PANGEA

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ABSTRACT—A new microconchid tentaculitoid, *Microconchus utahensis* new species, is described from the Lower Triassic (Spathian) Virgin Formation of two localities (Hurricane Cliffs and Beaver Dam Mountains) near St George, Utah. This small encrusting tubeworm, previously referred to erroneously as *Spirorbis*, has a laminated shell microstructure containing minute pores (punctae). The population from deeper water facies of the Beaver Dam Mountains is more abundant than that from Hurricane Cliffs and the tubes are significantly larger in size. Although represented by only one species (*M. utahensis*), microconchids are by far the most dominant component of the otherwise impoverished sclerobiont assemblage of the Virgin Formation, which also includes rare cemented bivalves and probable foraminifers. Whereas the remainder of the Virgin fauna is quite diverse, the low diversity of encrusters suggests a slow recovery from end-Permian mass extinctions. Indeed, more typically Mesozoic sclerobiont assemblages dominated by cyclostome bryozoans and serpulid polychaetes did not appear until the Late Triassic, probably Rhaetian.

INTRODUCTION

MICROCONCHIDS ARE small tubeworms known in the fossil record from the Late Ordovician to the Middle Jurassic (e.g., Vinn, 2006; Taylor and Vinn, 2006; Vinn and Mutvei, 2009; Zatoń and Vinn, 2011a, 2011b). Their calcitic spirally coiled tubes were mistaken for the polychaete genus *Spirorbis* in the older literature (see Taylor and Vinn, 2006). However, they differ from true *Spirorbis* in several important respects (Weedon, 1990, 1991, 1994; see also Taylor and Vinn, 2006) and are more allied to tentaculitids than tube-forming spirorbid polychaetes. Weedon (1991) classified them within the new Order Microconchida of the Class Tentaculita Bouček, 1964. Microconchids are believed to have evolved from cornulitids, another group of sessile tentaculitoids. Tentaculitoids were possibly lophophorates in the stem-group of the phoronids (Taylor et al., 2010). Thus, microconchids are interpreted as more closely related to brachiopods, bryozoans and phoronids than to mollusks or annelids (for details see Vinn and Mutvei, 2009; Taylor and Vinn, 2006; Taylor et al., 2010; Wilson et al., 2011).

Despite high local abundances of microconchids throughout their stratigraphical range, they are a poorly known fossil group. The few modern taxonomic investigations undertaken on Ordovician–Silurian (Vinn, 2006), Devonian (Zatoń and Krawczyński, 2011a, 2011b), Permian (Wilson et al., 2011) and Middle Jurassic (Vinn and Taylor, 2007; Zatoń and Taylor, 2009a) microconchids have revealed the existence of six genera and not many more species from just a handful of localities. Therefore, much remains to be done on their taxonomic composition, paleobiogeography and paleoecology. As microconchids survived many major and minor extinction events, it is especially interesting to investigate their taxonomic composition and paleoecology in the aftermath of these important biotic turnovers.

Triassic microconchids were common constituents of several paleoenvironments, from freshwater lakes and pools, through marginal marine to various shallow and deeper marine settings. Traditionally they have been identified either as *Spirorbis* (e.g., Ball, 1980; Brönnimann and Zaninetti, 1972; Peryt, 1974) or *Microconchus* (e.g., McGowan et al., 2009; Hagdorn, 2010). The only modern taxonomic study of a Triassic microconchid

concerns the Muschelkalk species *Microconchus aberrans* from Germany (Vinn, 2010).

In the present paper, Early Triassic microconchids are described from the early Spathian (Olenekian) Virgin Limestone of southwestern Utah, U.S.A. Microconchids of this age from the U.S. have never been taxonomically investigated, although they were mentioned (as ‘*Spirorbis*’) and illustrated by Nützel and Schulbert (2005) from the Smithian Sinbad Formation, Spathian. In addition, Griesbachian–Spathian microconchids were investigated with respect to recovery patterns after the end-Permian mass extinction by McGowan et al. (2009) and Fraiser (2011).

GEOLOGICAL SETTING

Comprising limestones and siltstones, the Virgin Limestone is the middle member of the Moenkopi Formation of southeastern Nevada and southwestern Utah, underlain by the Timpoweap Limestone and overlain by the Schnabkaib Limestone (e.g., Bottjer and Schubert, 1997). Recently, Hofmann et al. (2012) have raised the Virgin Limestone to formation status, as the Virgin Formation of the Moenkopi Group, a practice which will be followed here.

Unlike the underlying Timpoweap Limestone and overlying Schnabkaib Limestone, the Virgin Formation is richly fossiliferous. Among the fossils present is the ammonoid *Columbites* cf. *parisianus* Hyatt and Smith, 1905, indicating a late early Spathian (Olenekian) age (Hautmann et al., 2011). Other fossils recorded from the Virgin Formation include 27 species of bivalve mollusks (Hautmann et al., 2011), at least five species of gastropods and five of brachiopods (McGowan et al., 2009), the sponge *Cypellospongia* (Hofmann et al., 2012), echinoids (Kier, 1968), ophiuroids (Twitchett et al., 2005), articulate crinoids (Schubert et al., 1992) and more than 12 ichnotaxa (Hofmann et al., 2012, table 1), as well as the new species of microconchid tubeworm described in this paper. For a unit deposited only about 2 myr after the end-Permian mass extinction, the Virgin Formation contains an impressive diversity of invertebrate fossils.

The abundant benthic fauna is distributed almost throughout the Virgin Formation and points to a shallow water environment with good oxygenation. Based on faunal associations, Hofmann

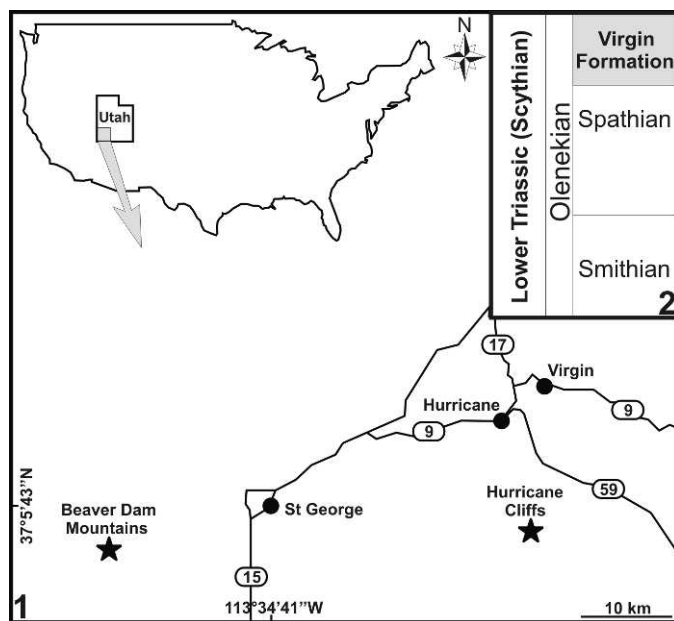


FIGURE 1—1, sketch map showing field localities (stars) of Beaver Dam Mountains and Hurricane Cliffs in south-western Utah; 2, stratigraphic position of the Spathian Virgin Formation of the Moenkopi Group.

et al. (2012) were able to recognize a range of environments, encompassing marginal marine, tidal inlet, shallow subtidal to offshore transition zones.

In a regional context, the Virgin Formation was deposited in a mixed carbonate–siliciclastic depositional system (Poborski, 1953, 1954; Stewart et al., 1972; Pruss and Bottjer, 2004) formed by a marine transgression from Panthalassa into the western interior of North America. The transgression occurred over a land surface with considerable relief (Hofmann et al., 2012), which is reflected in the rapid variations in lateral facies characteristic of the Virgin. The more westerly sections were deposited in somewhat deeper water than those in the east (Blakey, 1972). Consequently, in the area around St. George, Utah, sections in the Beaver Dam Mountains represent deeper water facies than those at Hurricane Cliffs some 50 km to the east. Approximately 34 m of Virgin Formation has been recorded in the Beaver Dam Mountains compared with up to 20 m at Hurricane Cliffs (Hofmann et al., 2012).

MATERIAL AND METHODS

Material provenance and preservation.—Material was collected during fieldwork in May 2006 by Al McGowan, Andrew Smith and one of us (PDT). The samples, including type and figured material deposited in the NMNH, Smithsonian Institution, Washington, D. C. (abbreviated USNM), were obtained from two areas near St George, southwestern Utah: Hurricane Cliffs and Beaver Dam Mountains where deposits of the Virgin Formation are outcropped (Fig. 1). The total collection contains hundreds of specimens from numerous outcrops (see McGowan et al., 2009 for details). Their preservation varies, from a minority of well-preserved tubes showing ornamentation, through lightly worn tubes in which the ornamentation is partially preserved, to severely abraded tubes without any visible ornamentation. Very often only the attached basal walls are preserved on bivalve shells. However, internal microstructures are well preserved regardless of the preservational condition of the tube exterior.

For comparative purposes we also studied the similarly coiled Middle Triassic species *Microconchus valvatus* (Goldfuss) from Germany, using samples kindly provided by Dr. Hans Hagdorn (Muschelkalkmuseum, Ingelfingen, registration number 2080/2).

Methods.—After gentle washing, the specimens were first inspected under a binocular microscope and the best-preserved microconchids were selected for further study. They were cleaned ultrasonically and studied in an uncoated condition using a Philips XL 30 environmental scanning electron microscope (ESEM) in back-scattered mode. Some specimens were embedded in epoxy resin, polished and etched in weak HCl for a few seconds in order to observe microstructural details. For the population study, tube diameters were measured in 100 randomly selected microconchids from Hurricane Cliffs and 100 from the Beaver Dam Mountains. Such features as umbilical width and apertural diameter were measured directly from ESEM microphotographs of selected specimens.

SYSTEMATIC PALEONTOLOGY

Class TENTACULITA Bouček, 1964

Order MICROCONCHIDA Weedon, 1991

Genus MICROCONCHUS Murchison, 1839

Type species.—*Microconchus carbonarius* Murchison, 1839.

Diagnosis.—Tube planispirally coiled with a tendency for helical uncoiling in later ontogeny. Exterior ornamented by variously developed growth lines, perpendicular ridges and longitudinal striae. Microstructure lamellar with minute punctae.

Remarks.—The genus *Microconchus* differs from *Palaeoconchus* (Vinn, 2006; Zatoń and Krawczyński, 2011b) in possessing tiny pores (punctae) penetrating the tube. From *Punctaconchus* (Vinn and Taylor, 2007) it differs in having much smaller punctae and a tube with a tendency to uncoil. *Helicoconchus* (Wilson et al., 2011) differs in lacking punctae and in budding new tubes from existing ones.

MICROCONCHUS UTAHENSIS new species

Figures 2.1–2.6, 3.1

Diagnosis.—Tube planispirally coiled, dextral. Exterior ornamented with widely spaced transverse ridges and fine growth lines. Microstructure lamellar with tiny punctae deflecting wall laminae outwards.

Description.—Tube small, dextral, planispirally coiled throughout ontogeny, attached by its entire length, circular or semi-circular in outline (Fig. 2.1–2.5). Umbilicus narrow, with rounded margin. Tube is most convex at the umbilical margin, then gently sloping toward the base that may be smooth in outline along the entire tube length or slightly undulating. Tube base not widened, cross-section semielliptical. Average aperture diameter ~520 μ m. Tube exterior ornamented with low, widely spaced transverse ridges and fine growth lines, starting at the umbilical margin and running down to the base (Fig. 2.1, 2.3, 2.4). Longitudinal striae are lacking. Tube ultrastructure microlamellar, the microlaminae being deflected towards the exterior by distinct punctae, with cement-filled cores, about 7 μ m wide and spaced up to 10 μ m apart (Fig. 2.6). Punctae may be visible on the exfoliated tube exterior as closely spaced pits (Fig. 3.1). During growth, the punctae seem to be less discernible, but deflection of the wall laminae is still well visible.

Etymology.—From the state name where it was found, Utah.

Types.—Holotype: USNM 546207/2 (Fig. 2.4), Lower Triassic (Spathian), Moenkopi Group, Virgin Formation, Beaver Dam Mountains, Utah, USA. Paratypes: USNM 546207/1 (Fig. 2.3), USNM 546207/3–4 (Figs. 2.5, 3.1), USNM 546208 (Fig. 2.6), Lower Triassic (Spathian), Moenkopi Group, Virgin Formation, Beaver Dam Mountains, Utah, USA; USNM 546205–546206 (Fig. 2.1, 2.2), Lower Triassic (Spathian), Moenkopi Group, Virgin Formation, Hurricane Cliffs, Utah, USA.

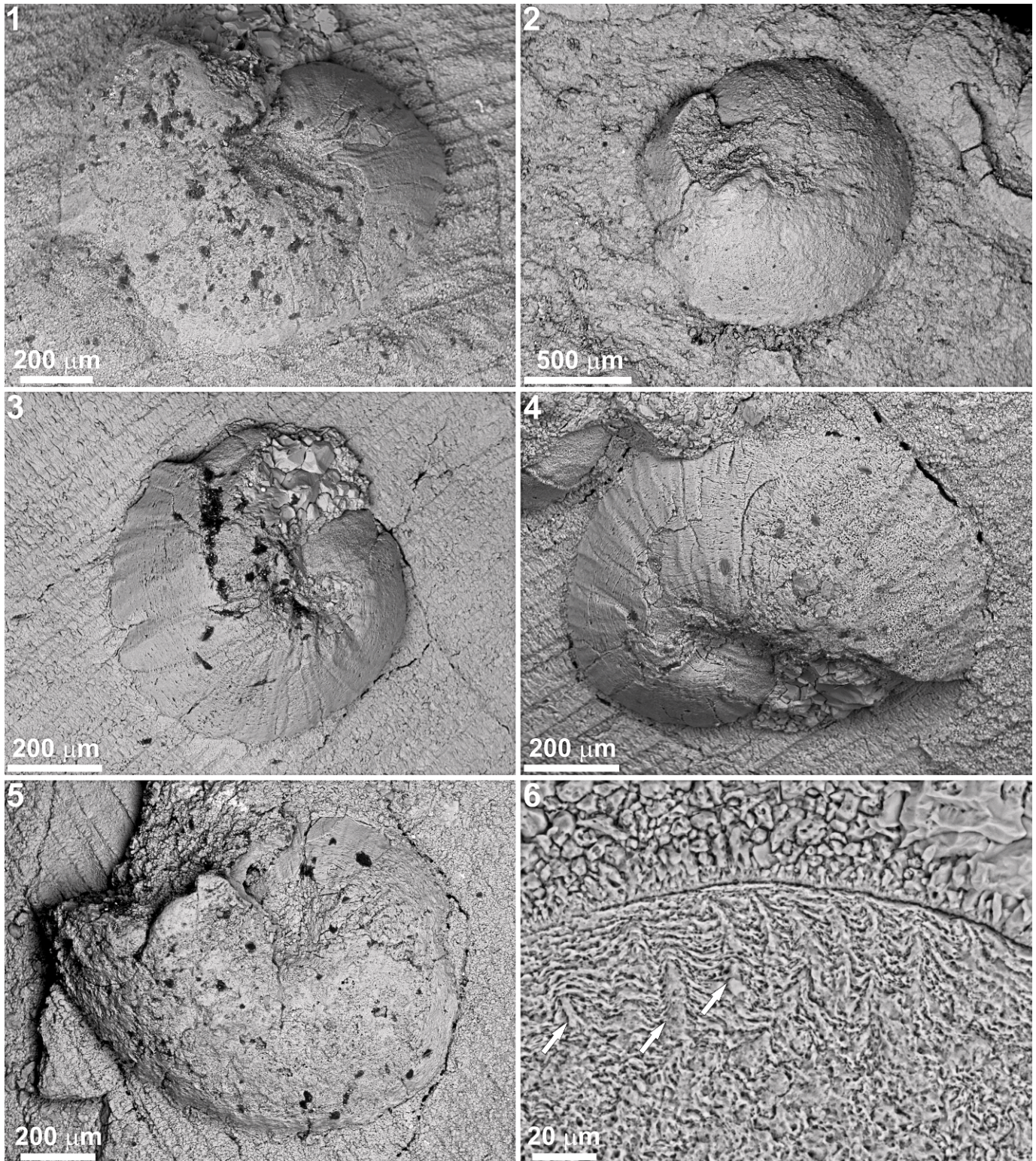


FIGURE 2—Microconchid *Microconchus utahensis* n. sp. from the Lower Triassic (Spathian) Virgin Limestone of Utah. 1, 2, Hurricane Cliffs specimens: 1, USNM 546205; 2, USNM 546206; 3–6, Beaver Dam Mountains specimens: 3, USNM 546207/1; 4, USNM 546207/2, holotype; 5, USNM 546207/3; 6, USNM 546208, structural details of a tube (inner whorl), showing distinct microlamellar fabric interrupted by cone-like punctae the cores of which are filled with cement (arrows).

Material.—Hundreds of variously preserved specimens encrusting shelly substrates.

Occurrence.—Lower Triassic (early Spathian, Olenekian), Moenkopi Group, Virgin Formation of Utah, U.S.A.

Remarks.—The Lower Triassic microconchids from Hurricane Cliffs and the Beaver Dam Mountains are very similar with respect to size, coiling, external ornamentation and microstructural details, and are therefore regarded as the same species. The

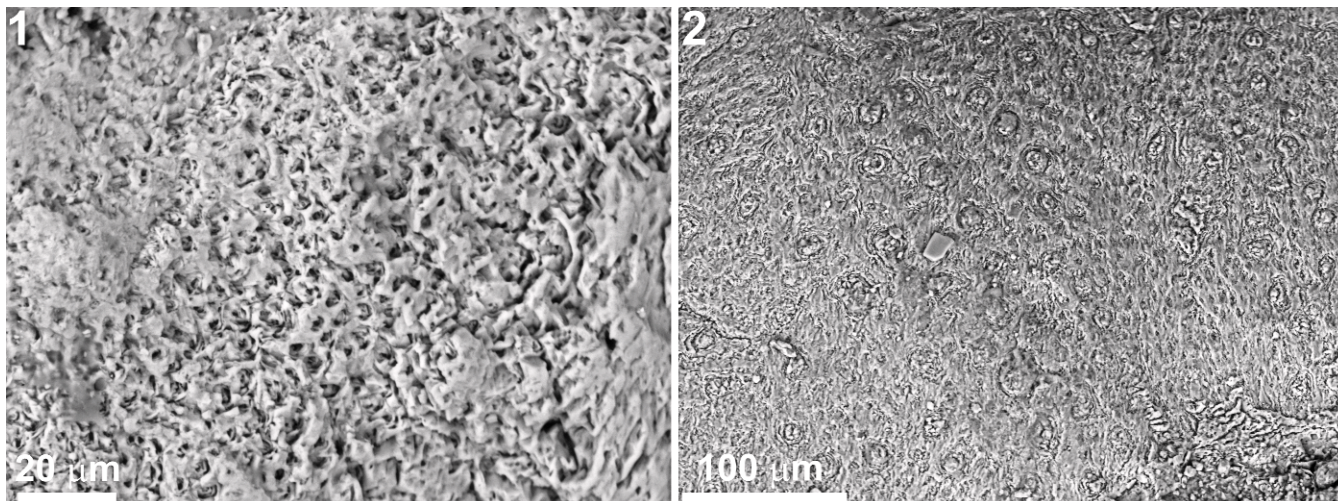


FIGURE 3—Comparison of microconchid punctae visible when the tube is exfoliated. 1, small-sized punctae of the Lower Triassic (Spathian) *Microconchus utahensis* n. sp. from the Virgin Limestone of the Beaver Dam Mountains, Utah (USNM 546207/4); 2, much larger punctae in the Middle Triassic (Upper Muschelkalk) *Microconchus valvatus* (Goldfuss) from Ummenhofen, Germany (2080/2).

presence of punctae with cores filled with cement (Fig. 2.6), disturbing the microlamellar fabric of the tube, indicate that the microconchids belong to the genus *Microconchus*.

The stratigraphically closest species, from the Smithian Sinbad Formation, referred to as ‘*Spirorbis*’ cf. *valvata* (Nützel and Schulbert, 2005), differs from the new species in having a smooth exterior in coiled portions of the tube and faint but dense annulations in the erect, helical portion. The lowest Triassic (Griesbachian) microconchids from the western U.S.A. recently reported by Fraiser (2011) cannot be determined due to the poor preservation of the material illustrated. Microconchids (‘*Spirorbis*’ sp.) from the Triassic of New Mexico, illustrated by Kietzke (1989), possess distinct and dense ‘ribs’ or striae and differ considerably in the more evolute coiling of their tubes. They also come from a fresh- or brackish water paleoenvironment, contrasting with the fully marine conditions inhabited by *Microconchus utahensis* n. sp.

A microconchid originally described as *Spirorbis phlyctaena* Brönnimann and Zaninetti, 1972 from the Lower Triassic of northern Italy, Iran and possibly the Middle Triassic of France, was established on the basis of thin sectioned specimens and is difficult to compare directly with *M. utahensis* n. sp. The microlamellar tube structure and the possible presence of punctae (minute pits in Brönnimann and Zaninetti, 1972), suggests that *S. phlyctaena* may belong to *Microconchus*. The more evolute coiling and the presence of both dextral (clockwise) and sinistral (counterclockwise) coiling in *S. phlyctaena* is unusual and raises the possibility that more than one species may be represented by this taxon.

Another European species, *Microconchus valvatus* (Goldfuss, 1831) from the Middle Triassic (Anisian) of Germany, is more evolute, possesses a more rounded tube cross-section and is ornamented with fine, closely spaced growth lines and thickened riblets. It also has much larger punctae (Fig. 3.2) than the Lower Triassic specimens from Utah described here. The Anisian microconchid *Microconchus aberrans* (Hohenstein, 1913), on the other hand, differs in its distinct external perpendicular striations and the presence of poorly developed pseudopunctae, as well the fact that tubes become helically coiled and erect in late ontogeny (Vinn, 2010). Pseudopunctation is particularly characteristic of Paleozoic microconchids (Vinn, 2006; Zatoń and

Krawczyński, 2011b), and thus the affiliation of *M. aberrans* with the genus *Microconchus* is questionable.

The freshwater, spirally coiled tubes of ‘*Spirorbis*’ *inexpectatus* from the Upper Triassic of Pennsylvania (Wanner, 1921) differ in having thick transverse ‘ribs’ bent slightly backward to the tube coiling direction.

DISCUSSION AND CONCLUSIONS

Population structure and recovery after the end-Permian mass extinction.—In common with other microconchid assemblages (e.g., Vinn and Taylor, 2007; Zatoń and Krawczyński, 2011a, 2011b), *Microconchus utahensis* n. sp. from both the Beaver Dam Mountains and Hurricane Cliffs localities is represented by individuals of variable size, ranging from tiny post-embryonic stages to likely mature individuals with well-coiled planispiral tubes. The sample from the Beaver Dam Mountains is characterized by larger individuals than that from Hurricane Cliffs, the highest frequency of individuals having a tube diameter of 1.0 to 1.4 mm in the Beaver Dam Mountains compared with 0.6 to 1.3 mm at Hurricane Cliffs (Fig. 4). A *t*-test shows that the size difference is statistically significant at $p < 0.01$. A statistically significant size difference between these two populations was also obtained by McGowan et al. (2009). As the sampled Beaver Dam Mountains sediments were deposited in deeper, more offshore settings than those from Hurricane Cliffs (McGowan et al., 2009; Hautmann et al., 2011), the observed size differences between these two populations may be related to depth. Microconchids inhabiting deeper environments are hypothesized to have suffered less disturbance from physical agents, especially storms, than populations living in shallower water environments where frequent, storm-related disturbances could have repeatedly overturned shelly substrates, inhibiting microconchid growth. Alternatively, or additionally, the size difference between the two populations may reflect food resources or/and competition for food with the other suspension feeders, with stunting at the Hurricane Cliffs locality produced by reduced planktonic food resources. Marine conditions more favorable with respect to the physical and/or biological factors mentioned above in the area of the Beaver Dam Mountains is also suggested by the greater abundance of microconchids on each shelly substrate. The density of the richest samples averages about 60 individuals/cm² in the Beaver Dam Mountains compared to about 21 individuals/cm² at Hurricane Cliffs.

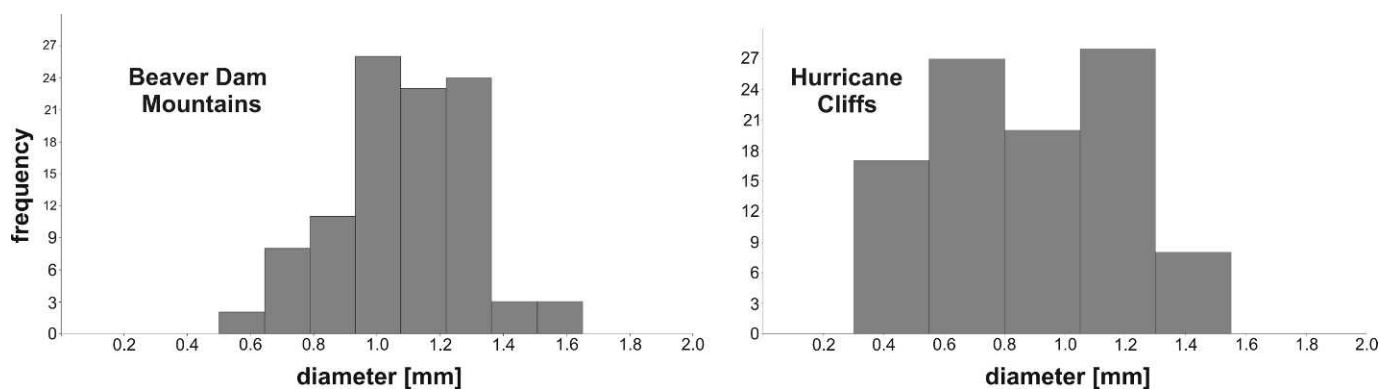


FIGURE 4—Tube diameter distribution in *Microconchus utahensis* n. sp. populations from the Beaver Dam Mountains and Hurricane Cliffs.

The depth-correlated size differences observed in microconchids here and by McGowan et al. (2009) should be taken into account when the small sizes of fossils—the so-called Lilliput Effect (e.g., Fraiser and Bottjer, 2004; Twitchett, 2007; Harries and Knorr, 2009; but see also Brayard et al., 2010)—following mass extinctions are interpreted in the context of post-extinction environmental stress.

Importantly, microconchids are the dominant component of otherwise impoverished Virgin Formation encrusting assemblages. Only rare bivalves and probable foraminifera are also present (Fraiser, 2011). Such a pattern of epibiont diversity is in stark contrast to other Paleozoic and Mesozoic encrusting assemblages where, apart from microconchids, a variety of other encrusters are typically present (e.g., Liddell and Brett, 1982; Alvarez and Taylor, 1987; Bordeaux and Brett, 1990; Lescinsky, 1997; Zatoń et al., 2012). Fraiser (2011) has shown recently that in the immediate aftermath of the end-Permian mass extinction, Early Triassic (Griesbachian) hard substrate assemblages were dominated by encrusting microconchids and that not before the Spathian did other sclerobionts (especially endobionts) appear in significant numbers, although endobionts consisting of various borings of annelids, phoronids, cirripedes and sponges have been recorded from the Spathian (Fraiser, 2011).

Although the other benthic fauna present in the early Spathian Virgin Formation is quite diverse (McGowan et al., 2009; Hautmann et al., 2011; Hofmann et al., 2012) and thus may indicate that faunal recovery after the end-Permian mass extinction was well under way during the Spathian (Hautmann et al., 2011; Hofmann et al., 2012), this appears not to have been the case for hard substrate biotas. Spathian hard substrate assemblages are impoverished, especially with respect to encrusters (Taylor and Wilson, 2003). In fact, diverse, typically mid-Mesozoic sclerobiont assemblages dominated by cyclostome bryozoans and serpulid polychaetes did not appear until the Rhaetian (Taylor and Michalik, 1991). The delayed recovery of sclerobiont communities may point to some kind of post-extinction environmental stress (cf. Schubert and Bottjer, 1995; Boyer et al., 2004; Pruss and Bottjer, 2004; Mata and Bottjer, 2011), impacting the hard substrate biotas. While this may have resulted in a genuine scarcity of Early-Middle Triassic sclerobionts, it is possible that communities were dominated by soft-bodied encrusting taxa. For example, phylogenetic analysis of bryozoans (Waeschenbach et al., 2012) implies the survival of several clades of soft-bodied ctenostome bryozoans through the end-Permian extinction event, whereas it is well-known that calcified stenolaemate bryozoans were hit hard at this time (Powers and Bottjer, 2009). The possibility of Early Triassic sclerobiont communities being dominated by soft-bodied encrus-

ters such as sponges, ctenostome bryozoans and ascidians may be testable by seeking evidence of bioimmuration.

Microconchid-dominated sclerobiont assemblages of low diversity but high abundances characterized Early Triassic post-extinction communities (Fraiser, 2011). A similar opportunistic behavior of microconchids following a biotic crisis is also known for the Frasnian-Famennian event (Zatoń and Krawczyński, 2011b), and thus may be characteristic for other stress-related biotic turnovers.

Evolution of microconchid tube punctation.—Tube punctation developed progressively during microconchid evolution, from pseudopunctae to small punctae to large punctae. In early Paleozoic (Ordovician–Devonian) microconchids, true punctae (i.e., pores) were apparently lacking, although deflections of wall laminae produced pseudopunctae in *Palaeoconchus* (Vinn, 2006; Zatoń and Krawczyński, 2011b). However, tubes of the Carboniferous species *Microconchus pusillus* (Martin) (Taylor and Vinn, 2006, fig. 1L) contain minute punctae. Some Permian microconchids, including *Helicoconchus*, lacked either punctae or pseudopunctation (Wilson et al., 2011). Small punctae continued to be present in other microconchids at least until the Early Triassic, as exemplified by the new species described here. Larger punctae are apparent in the Middle Triassic *Microconchus valvatus* (Fig. 3.2). Nevertheless, some Middle Triassic species, such as *M. aberrans* (Vinn, 2010), were pseudopunctate.

The occurrence of punctae similar to late Paleozoic microconchids in the Early Triassic *M. utahensis* n. sp. indicates that events at the close of the Paleozoic (Late Permian ecosystem reconstruction and end-Permian mass extinction) did not cause rapid changes in the evolution of microconchid shell structure. Middle Jurassic microconchids of the genus *Punctaconchus* (Vinn and Taylor, 2007; Zatoń and Taylor, 2009a), representing the last survivors of this group have particularly large punctae.

As the outermost part of Paleozoic and Triassic microconchid tubes very often consists of a thin calcitic layer, most probably diagenetic in origin, it is uncertain whether the punctae originally penetrated through to the tube exterior. In Middle Jurassic *Punctaconchus* it is clear that punctae did penetrate as pores through to the outermost calcified part of the tube (Vinn and Taylor, 2007; Zatoń and Taylor, 2009a).

The function of punctation in microconchids is uncertain. The hypothesized wall-strengthening role of pseudopunctae has recently been cast in doubt by Vinn (2010) on the basis of helically coiled *M. aberrans*. Similarities are evident between microconchid pseudopunctae and brachiopod punctae and bryozoan acanthostyles, and of punctae to the pseudopores of cyclostome bryozoans (Zatoń and Taylor, 2009b; Taylor et al., 2010), suggesting comparable biomineralization patterns (Taylor et al., 2010). Microconchid punctae may have helped to maintain

and directly link the outer organic layer (cuticle or periostracum) covering the mineralized tube with soft tissues inside the tube (Vinn and Taylor, 2007; Taylor et al., 2010). As suggested by Vinn and Taylor (2007) for *Punctaconchus*, punctae may have made the worm tube easier to repair when damaged. Finally, it is worth noting that the punctae of brachiopods have been suggested to include sensory, storage and respiratory functions (Pérez-Huerta et al., 2009).

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