

Microconchus cravenensis n. sp.: a giant among microconchid tubeworms

Authors: Zatoń, Michał, and Mundy, David J.C.

Source: Journal of Paleontology, 94(6) : 1051-1058

Published By: The Paleontological Society

URL: <https://doi.org/10.1017/jpa.2020.45>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Microconchus cravenensis n. sp.: a giant among microconchid tubeworms

Michał Zatoń¹  and David J.C. Mundy²

¹University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Earth Sciences, Będzińska Street 60, PL-41-200 Sosnowiec, Poland <mzaton@wnoz.us.edu.pl>

²111 Woodside Circle SW, Calgary, Alberta, Canada T2W 3K1 <mundyd@shaw.ca>

Abstract.—A new species of microconchid tubeworm, *Microconchus cravenensis* is described from the Mississippian Cracoean reefs of North Yorkshire, United Kingdom. Despite the fact that some other microconchid species could have attained large tube length, the new species possesses the largest recorded diameter (to 7.7 mm) of the planispirally-coiled (attachment) tube and the largest recorded aperture diameter (8.3 mm) in the helically uncoiled portion. Thus, with respect to these features, *Microconchus cravenensis* n. sp. is the largest and most robust microconchid species recognized so far. At present, it is only known from the Craven Reef Belt of North Yorkshire, where it attached to corals and possibly bivalve shells, and was preyed upon by small durophagous animals, as indicated by repaired injuries preserved on one of the tubes.

UUID: <http://zoobank.org/2ba8f87b-ec1c-4bb3-8615-115e7a527376>

Introduction

Microconchids were small encrusting tubeworms that originated during the Late Ordovician and went extinct at the end of the Middle Jurassic (late Bathonian) (e.g., Taylor and Vinn, 2006; Zatoń and Vinn, 2011). Until Weedon (1990, 1991) affiliated the microconchids with tentaculitoids, these spirorbiform or serpuliform tubeworms were generally treated as sedentary polychaetes or vermetid gastropods (e.g., Peryt, 1974; Burchette and Ridding, 1977; Beus, 1980; Bełka and Skompski, 1982). During their long evolutionary history, microconchids were very successful in colonizing various paleoenvironments, ranging from normal marine, through brackish to more freshwater settings (e.g., Dreesen and Jux, 1995; Caruso and Tomescu, 2012; Zatoń et al., 2012a; Zatoń and Peck, 2013). Their wide paleoenvironmental tolerance seemed to be a key factor in surviving mass extinctions and biotic crises, in the aftermaths of which they became the dominant opportunistic epibionts (Fraiser, 2011; Zatoń and Krawczyński, 2011a; He et al., 2012; Yang et al., 2015; Zatoń et al., 2017).

Although the majority of microconchids were characterized by *Spirorbis*-like, planispirally coiled tubes, several genera produced unique morphologies. For example, some Carboniferous (Mississippian) species formed long, helically uncoiled tubes (e.g., Burchette and Riding, 1977), whereas the Lower Triassic *Spathioconchus* Zatoń et al., 2016b formed straight, trumpet-like tubes (Zatoń et al., 2016b) and the Permian *Helicoconchus* Wilson, Vinn, and Yancey, 2011 had long, helically uncoiled tubes that showed budding (Wilson et al., 2011).

Irrespective of tube morphology, all microconchids recognized so far possessed diminutive, millimeter-sized attachment portions and small tube diameters. Some species possessed uncoiled portions of significant size, e.g., the Permian bioherm-building *Helicoconchus* (Wilson et al., 2011), and the Carboniferous biostrome-forming ‘*Serpula*’ cf. *S. advena* Salter, 1863 (Burchette and Ridding, 1977). However, the majority of microconchid species were rather tiny, inconspicuous encrusters.

Here, we describe a new microconchid species from the Mississippian Cracoean reefs of the United Kingdom that possessed a robust tube. Its large, planispirally coiled attachment portion, as well as its large tube diameter, make it a giant among Paleozoic and Mesozoic microconchids recognized so far.

Geological setting

Geology and stratigraphy.—Mississippian Cracoean reefs of the UK formed marginal facies to rimmed shelves developed on stable basement blocks (Mundy, 1994, 2007; Aitkenhead et al., 2002). In North Yorkshire, the Cracoean reef tract (‘Craven Reef Belt’ of Hudson, 1930) defined the southern limit of the Asbian shelf limestones of the Askriigg Block and bridged the transition into the Craven Basin (Fig. 1). Exposures occur in three separate outcrops along a 23 km west-to-east tract (Fig. 1), with the intervening areas covered by Serpukhovian siliciclastics of the Bowland Shale and Pendleton formations. This once-continuous reef belt was broken into fault slices during movements on the Craven Faults (Arthurton et al., 1988) and was substantially eroded

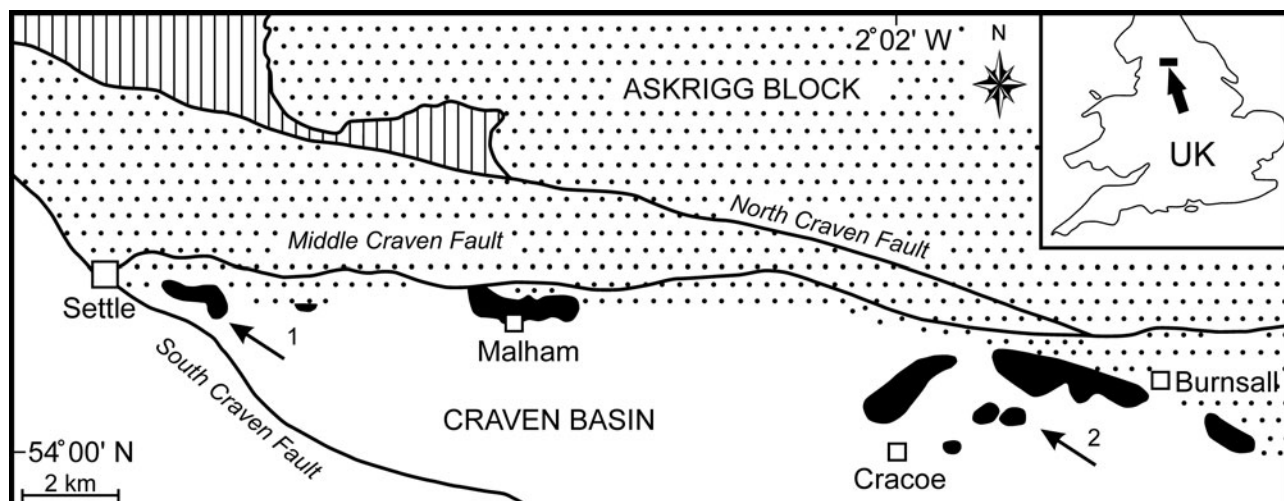


Figure 1. Simplified geological map of the Late Viséan Craven Reef Belt of North Yorkshire, UK (location marked by arrow in the inset), showing the main reef outcrops (black), the southern limit of shelf facies on the Askrigg Block (stippled), the basin facies (white), the Lower Paleozoic inlier (vertically ruled), and the Craven Faults. The outcrop of Serpukhovian (early Namurian) siliciclastics has been omitted for clarity (after Brunton and Mundy, 1988). Localities yielding *Microconchus cravenensis* n. sp. are marked by arrows: (1) Scaleber; (2) Stebden Hill.

prior to burial by Bowland Shale mudrocks (Hudson, 1930, 1932, 1944). Remnants of a shelf-contiguous ‘apron reef,’ together with isolated reef mounds, are represented.

Lithostratigraphically, these reefs were traditionally assigned as a facies of the contiguous shelf succession, thus the Malham Formation on the Askrigg Block (Arthurton et al., 1988). However, the name Cracoe Limestone Formation has been introduced for the Cracoean reefs and adjacent limestones (not all reefal) in the Cracoe-Burnsall area (Dean et al., 2011, p.106; Waters et al., 2017). Chronostratigraphically, reefal deposition occurred mostly during the Asbian stage but extended into early Brigantian with representatives of the ammonoid biozones ?B₁ to P_{1b} (Bisat, 1924, 1934; Mundy, 1980, 2000; Riley, 1990; Waters et al., 2017). Localities yielding the new microconchid range in age from Asbian B_{2a} to early P_{1a}.

Facies development.—The term ‘Cracoean’ (Hudson and Philcox, 1965) was introduced as a facies designation to apply to certain late Viséan ‘shallow-water’ reefs in a way similar to the usage of ‘Waulsortian.’ Cracoean reefs are hybrid buildups, an amalgam of ‘mudmound,’ substantial frameworks (both

microbialite and lithostrotionid) and shelly bioaccumulations, which reflected a long period of growth, punctuated by frequent emergent episodes. Facies subdivision of the reefs (Fig. 2) was proposed by Mundy (1994, 2007). Shallow ramp bioclastic packstones with colonies of lithostrotionid corals, locally interbedded with crinoidal floatstones, formed the foundation of the reefs. These pass upward into prograding lenticular pack-wackestones containing a typical ‘reefal’ fauna and then into massive bedded-bank facies. The latter are bioclastic wackestones and floatstones (often with a clotted micritic matrix) that produced lenticular and tabular geometries and contain a shallow-water biota with a conspicuous component of in situ *Gigantoproductus* Prentice, 1950. Passage from ramp packstones to the bank facies was postulated to be microbially mediated (Mundy, 1994, 2007).

At intervals during the growth of the buildups, microbialite frameworks developed, attaining thicknesses to 40 m, and often initiated during flooding recolonization following emergence. The frameworks were constructed by microbialite and an encrusting consortium of bryozoans, tabulate corals, and lithistid sponges (Mundy, 1994; Rigby and Mundy, 2000) that locally bound in situ groves of small solitary rugosans. A unique shelly fauna is present, consisting of attached productoids and cemented pseudomonotid bivalves (Mundy and Brunton, 1985; Brunton and Mundy, 1988). Thickets of *Siphonodendron* McCoy, 1849 developed on the leeside of some frameworks.

Basin-facing foreslopes of the reefs consist of bedded flank facies that attained depositional dips of 35° and could span a paleobathymetry of 100–170 m. Lithologies are bioclastic wackestones and floatstones that locally grade to cementstones where radial fibrous calcite is significant. These yield a distinctive and diverse fauna for which the reefs are renowned. Brachiopods, quasi-infaunal productoids, and pediculate taxa (spriferoids and rhynchonelloids) dominate the fauna at most bathymetric levels, but there are pronounced changes in community from upper to lower (shallow to deeper water) flank.

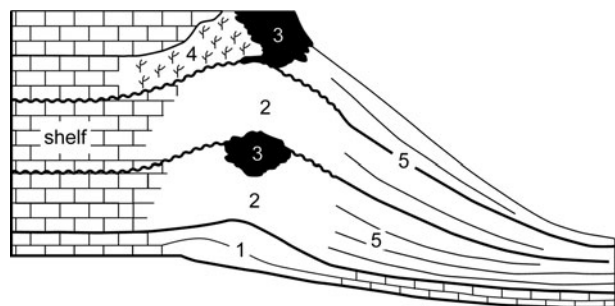


Figure 2. Component subfacies of the Cracoean reefs (after Mundy, 2007): (1) foundation; (2) bank; (3) microbialite framework; (4) *Siphonodendron* (coral) thicket; (5) flank.

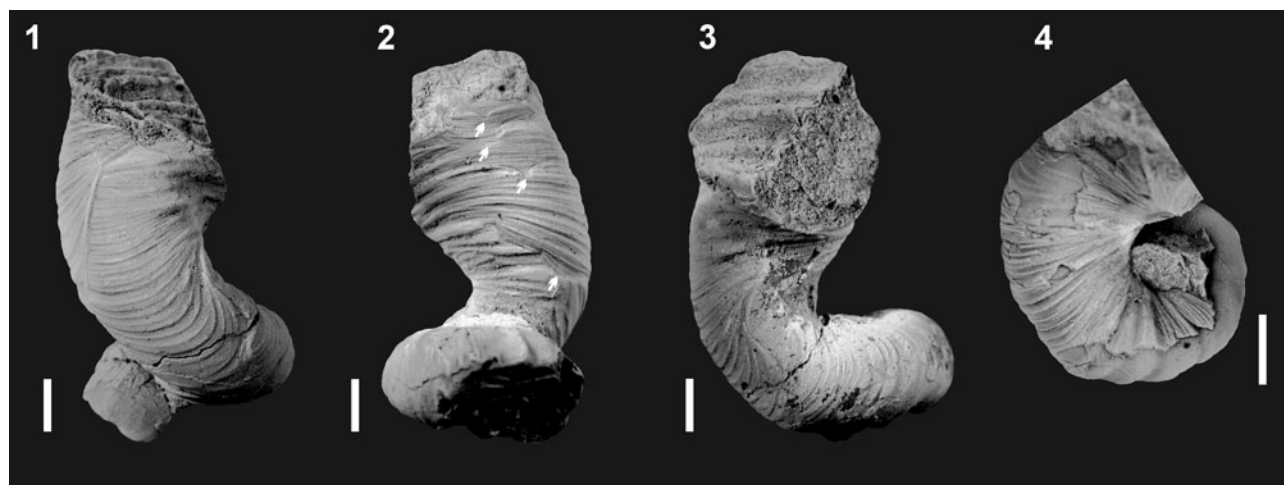


Figure 3. *Microconchus cravenensis* n. sp. from the Mississippian Cracoean reefs: (1–3) holotype, NHM PG 10009, Scaleber, east of Settle, North Yorkshire, UK, three views (arrows indicate repaired injuries); (4) paratype, NHM PG 10007, Stebden Hill, near Cracoe, North Yorkshire, UK. Both specimens show the planispirally coiled tube followed by the uncoiled stage. Scale bars = 2 mm.

Characteristically, the upper (shallow) flank limestones contain large productoids (*Gigantoproductus* and *Linoprotonia* Ferguson, 1971) and rostroconchs, yield proportionally more gastropods, and locally have abundant green algae. Lower (deeper) flank communities are notably crinoidal, contain large fenestellid bryozoan colonies, have abundant ammonoids and nautiloids, and are associated with the solitary rugosan *Amplexus* Sowerby, 1814.

The microconchid specimens occurred mostly in shallow-flank facies, with a single specimen located in a microbialite framework and the holotype from bank- or possibly shallow-flank facies.

Materials and methods

Materials.—The microconchid specimens were collected by one of us (DM) during fieldwork along the Craven Reef Belt between 1971 and 1981. These specimens were obtained from two localities in the Craven Reef Belt: Scaleber, east of Settle, and Stebden Hill, near Cracoe (Fig. 1). The material consists of one well-preserved, albeit still incomplete, specimen, and three fragmentary specimens, together with a specimen observed in thin section. Ornamentation patterns and microstructure of the tubes are well preserved in the specimens.

Methods.—Microstructure was observed on uncoiled specimens using a Philips XL 30 environmental scanning electron microscope (ESEM) in back-scattered mode; comparative observations were made from a thin section. The specimens were too large to be photographed using the ESEM, thus they were coated with ammonium chloride and photographed using a Canon digital camera.

Repositories and institutional abbreviations.—NHM PG = Department of Earth Sciences, The Natural History Museum, London, UK; TS = thin section collection, D.J.C. Mundy, Calgary, Alberta, Canada.

Systematic paleontology

Class Tentaculita Bouček, 1964

Order Microconchida Weedon, 1991

Family Microconchidae Zatoń and Olempska, 2017

Genus *Microconchus* Murchison, 1839

Type species.—*Microconchus carbonarius* Murchison, 1839

Microconchus cravenensis new species

Figures 3–5, 6.3

Type specimens.—Holotype, NHM PG 10009, Scaleber, east of Settle, North Yorkshire, UK, west bank of Stockdale Beck, Mundy Locality 136 (National Grid Reference SD 8416 6319), Mississippian (Asbian Stage, B_{2a} ammonoid biozone), Cracoean Facies, Malham Formation. Paratypes from Stebden Hill, Cracoe, North Yorkshire, UK, NHM PG 10006, Mundy Locality St 25A (NGR SE 0030 6076); NHM PG 10007 and 10008, Mundy Locality St 116 (NGR SE 0017 6083), both localities Mississippian (Asbian Stage, B_{2b} ammonoid biozone), Cracoean Facies, Cracoe Limestone Formation.

Diagnosis.—Large microconchid with helically uncoiled tube, ornamented by thin, transverse riblets.

Occurrence.—Mississippian (upper Viséan) of Scaleber near Settle, and Stebden Hill near Cracoe, North Yorkshire, UK.

Description.—The attachment portion of the tube is planispiral, dextrally (clockwise) coiled, 5.4–7.7 mm in diameter. Later, the tube helically uncoils to the preserved height of 16 mm in the holotype. The aperture is round and the tube diameter increases rapidly. In the attachment portion, the aperture can be ~4 mm (PG 10007) to 5 mm in diameter (holotype), whereas in the terminal, helically uncoiled part, it increases to 8.3 mm in diameter (holotype, Fig. 3.1–3.3). However, this is a minimum size because the tube is incomplete. The

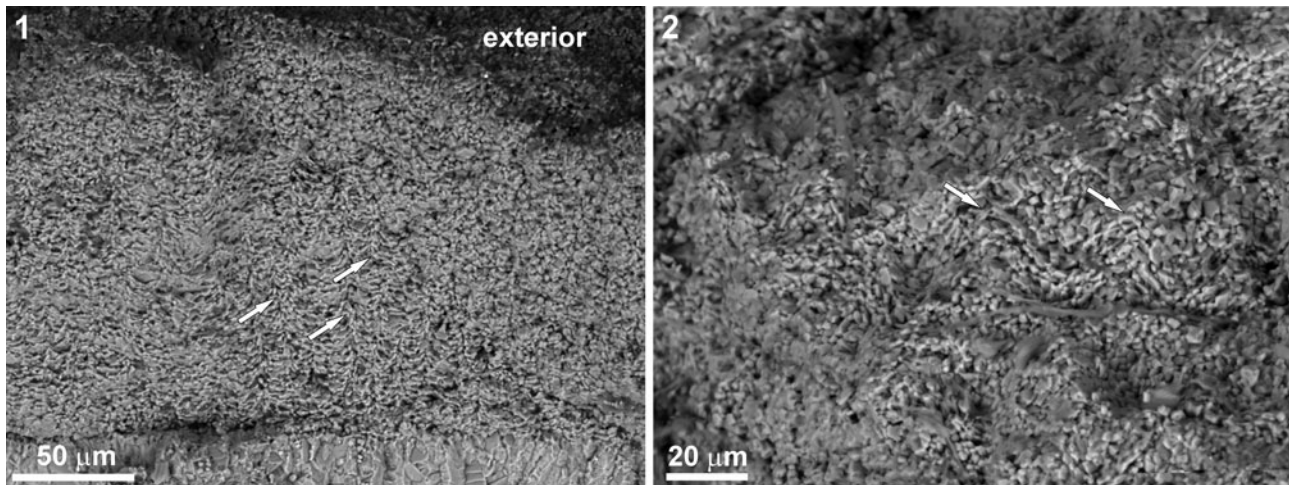


Figure 4. Tube microstructure of *Microconchus cravenensis* n. sp. from the Mississippian Cracoean reef of Stebden Hill near Cracoe, North Yorkshire, UK, ESEM photomicrographs showing microlamellar fabric interrupted by cone-like punctae (arrows): (1) NHM PG 10007, with exterior indicated; (2) NHM PG 10008, tube interior.

umbilicus is open, ~2 mm in diameter, with a gently dipping, rounded umbilical slope. The exterior of the tube is ornamented with fine, closely spaced transverse riblets of varying width that can be thickened at the flank of the planispirally coiled tube, and form well-spaced rib-like structures (Fig. 3). The riblets run sinuously across the tube from the umbilical slope to the attachment base and around the helically uncoiled portion of the tube. In the uncoiled part of the holotype, signs of tube regeneration occur, manifested by a distinct interruption of ornament pattern (Fig. 3.2). No longitudinal striae have been observed.

Tube microstructure is lamellar and punctate (Figs. 4–5.3), with the punctae clearly deflecting the laminae throughout the tube thickness (Fig. 4). The presence of septa is not excluded (Fig. 5.2).

Etymology.—For the Craven Reef Belt (North Yorkshire, UK) where the species was found.

Materials.—Type specimens, plus thin section TS 25, Stebden Hill, Mundy Locality St 55 (NGR SE 0026 6083), age and formation as above.

Remarks.—The lamellar tube microstructure and the presence of tiny punctae suggest that the microconchids can be classified in the family Microconchidae. Although the punctae on the cross section of the tubes observed under ESEM look like deflections of the laminae (Fig. 4), these seem better discernible in the thin section (Fig. 5.3). The manifestation of punctae on the tube exterior of other representatives of the family Microconchidae is simply due to exfoliation of the tube exterior (e.g., Zatoń and Peck, 2013; Zatoń et al., 2014b; Zatoń and Olempska, 2017), which was not observed on the specimens studied here. Thus, classification of the new species in the family Microconchidae seems justified. The punctae present in much younger (Jurassic) representatives of the family Punctaonchidae occur in the form of large pores (Vinn and Taylor, 2007; Zatoń and Olempska, 2017) and thus differ markedly from those present in Microconchidae.

The ornament pattern and large size, especially of the planispiral portion of the tube and its robust uncoiled part with a wide aperture, make these specimens distinct from all other microconchid species described so far. Ornamentation of the Mississippian species still known by the informal name ‘*Serpula*’ cf. *S. advena* (see Burchette and Riding, 1977) appears

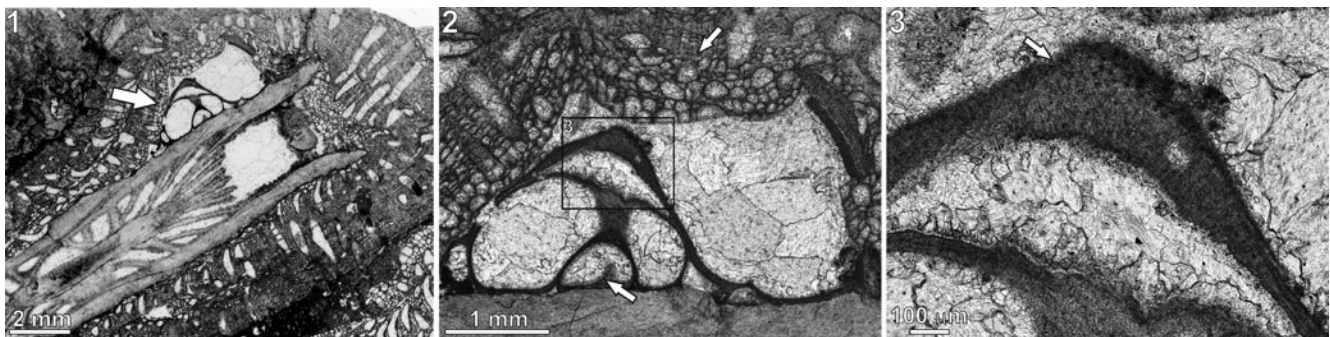


Figure 5. *Microconchus cravenensis* n. sp., TS 25, Stebden Hill, near Cracoe, North Yorkshire, UK, in thin section: (1) specimen (arrow) encrusting the coral *Cyathaxonia cornu*; (2) same specimen as (1) under higher magnification, showing the bryozoan *Fistulipora incrustans* that encrusted the tube after death of the microconchid (upper arrow) and putative septum inside the tube (lower arrow); (3) enlarged portion of the tube, indicated by rectangle in (2), showing visible punctation (arrow).

Table 1. Tube size of selected Paleozoic and Mesozoic microconchid species.

Species	Age	Tube diameter in planispiral stage (mm)	Aperture diameter in planispiral stage (mm)	Tube height in uncoiled stage (mm)	Aperture diameter in uncoiled stage (mm)	References
<i>Palaeoconchus minor</i> Vinn, 2006	Late Ordovician	0.3–1.2	0.10–0.4	-	-	Vinn (2006)
<i>Annuliconchus siluricus</i> Vinn, 2006	Late Silurian	~1.9	~0.6	-	-	Vinn (2006)
<i>Tuberoconchus wilsoni</i> (Zatoń et al., 2016c)	Late Silurian	to 2.7	to 0.6	-	-	Zatoń et al. (2016c); Zatoń and Olempska (2017)
<i>Palaeoconchus sanctacrucensis</i> Zatoń and Krawczyński, 2011b	Early Devonian	0.9–3.1	0.3–0.8	-	-	Zatoń and Krawczyński (2011b)
<i>Spinuliconchus angulatus</i> (Hall, 1861)	Middle Devonian	to 4.03	to 1.4	-	-	Zatoń et al. (2012b); Zatoń and Olempska (2017)
<i>Polonoconchus skalensis</i> Zatoń and Krawczyński, 2011b	Middle Devonian	1.9–2.45	0.48–0.66	-	-	Zatoń and Krawczyński (2011b)
<i>Microconchus vinni</i> Zatoń and Krawczyński, 2011b	Middle Devonian	1.48–1.88	0.3–0.67	1.44–2.16	0.5–0.79	Zatoń and Krawczyński (2011b)
<i>Palaeoconchus variabilis</i> Zatoń and Krawczyński, 2011a	Late Devonian	1.6–4.1	0.5–1.3	-	-	Zatoń and Krawczyński (2011a)
<i>'Serpula' helicalis</i> Beus, 1980	Late Devonian	-	-	10.0	0.5–1.0	Beus (1980)
<i>'Serpula' cf. S. advena</i> Salter, 1863	Early Carboniferous	to 3.0	?	to 70.0	3.0	Burchette and Riding (1977)
<i>Microconchus hintonensis</i> Zatoń and Peck, 2013	Early Carboniferous	to 2.2	to 0.98	~2.1	~0.80	Zatoń and Peck (2013)
<i>Microconchus cravenensis</i> n. sp.	Early Carboniferous	5.4–7.7	4.0	16.0	to 8.3	This paper
<i>Helicoconchus elongatus</i> Wilson, Vinn, and Yancey, 2011	Early Permian	0.8–1.9	0.6	50.0 or longer	0.9–1.5	Wilson et al. (2011)
<i>Spathioconchus weedoni</i> Zatoń et al., 2016b	Early Triassic	to 0.3	0.27	~1.75	0.5	Zatoń et al. (2016b)
<i>Microconchus utahensis</i> Zatoń, Taylor, and Vinn, 2013	Early Triassic	to 1.6	~0.52	-	-	Zatoń et al. (2013)
<i>Microconchus aberrans</i> (Hohenstein, 1913)	Middle Triassic	?	1.5	~16.0	to 1.7	Vinn (2010b)
<i>Microconchus valvatus</i> (Münster in Goldfuss, 1831)	Middle Triassic	to 2.3	~1.0	-	-	Zatoń et al. (2014b)
<i>Punctaconchus ampliaporus</i> Vinn and Taylor, 2007	Middle Jurassic	1.08–2.2	0.5–0.76	-	-	Vinn and Taylor (2007); Zatoń and Taylor (2009)

similar, but no photographs of its external details have been presented. However, this species has a planispiral attached tube of smaller diameter and significantly smaller (nearly three times) aperture diameter, even in the helically uncoiled tube (Table 1). Moreover, aperture diameter of the new species increases more rapidly. Other Mississippian microconchids having uncoiled tubes, e.g., *Microconchus hintonensis* Zatoń and Peck, 2013, from nonmarine deposits of the USA (Zatoń and Peck, 2013) and an unnamed, marine microconchid (described as a vermiform gastropod) from Poland (Belka and Skompski, 1982), differ in their tiny sizes and ornamentation patterns, which includes additional longitudinal striae and widely spaced ridges, respectively. A helically uncoiled Mississippian ?tubeworm fragment illustrated by McCoy (1844) and described under the name *Serpula scalaris* McCoy, 1844, shows distinct, widely spaced transverse ridges, unlike the closely spaced, thin riblets present in the new species. Moreover, the tube diameter of *Serpula scalaris* is ~4.2 mm ('two lines' of McCoy, 1844), two times smaller than in *Microconchus cravenensis* n. sp. Similarly, the Middle Devonian species *Microconchus vinni* Zatoń and Krawczyński, 2011b from the Holy Cross Mountains, Poland, is also several times smaller at each developmental stage (Table 1), and differs in having widely spaced, sharp transverse ridges (Zatoń and

Krawczyński, 2011b). The differences between the new specimens and others, especially Carboniferous microconchids, justify the naming of this new species.

Discussion

The great majority of microconchids are small, inconspicuous tubeworms dwelling on various firm and hard substrata (e.g., Taylor and Vinn, 2006; Zatoń et al., 2012a). In most cases, these are characterized by a dominant planispiral stage of tube development, with only a short uncoiled part to 2 mm in height (see e.g., Zatoń and Krawczyński, 2011b; Zatoń and Peck, 2013). However, helical uncoiling, resulting in long, vertically oriented tubes, occurs in a few species, some of which are still undescribed. These species include (Table 1) the 1 cm long '*Serpula' helicalis* Beus, 1980, *Microconchus aberrans* (Hohenstein, 1913) with a 1.6 cm long tube, '*Serpula' cf. S. advena* with tubes to 7 cm in height, and *Helicoconchus elongatus* Wilson, Vinn, and Yancey, 2011, which has an uncoiled tube 5 cm or more in length (Wilson et al., 2011). Although the preserved uncoiled tube of *Microconchus cravenensis* n. sp. is 1.6 cm in height, it could certainly have been larger when complete. However, there is a feature of the new species that surpasses all other

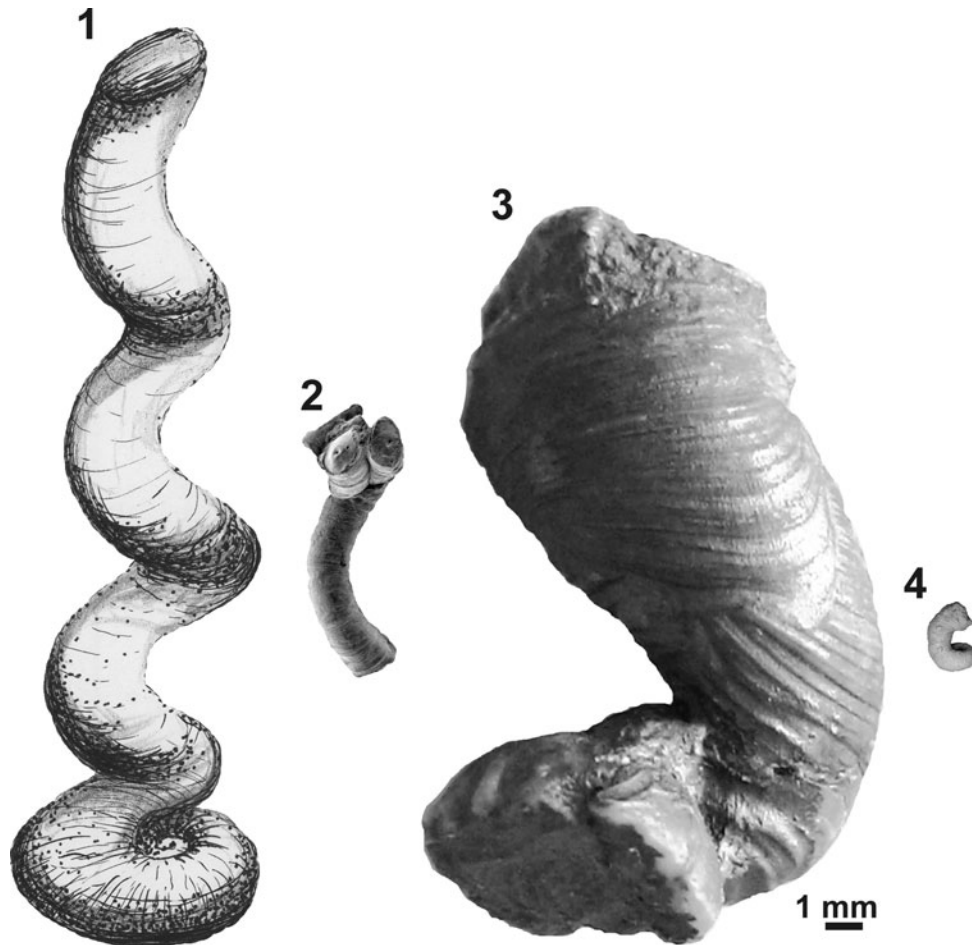


Figure 6. Comparative apertural size of selected microconchids showing the giant nature of the new species: (1) ‘*Serpula*’ cf. *S. advena*, Mississippian, UK (redrawn from Burchette and Riding, 1977); (2) *Helicoconchus elongatus* Wilson, Vinn, and Yancey, 2011, Lower Permian, USA (courtesy of Mark A. Wilson via Wikimedia Commons); (3) *Microconchus cravenensis* n. sp., Mississippian, UK (NHM PG 10009, holotype, this paper); (4) *Microconchus hintonensis*, Mississippian, USA (from Zatoń and Peck, 2013). All specimens presented to scale with reference to apertural diameters.

microconchid species, even those having the largest tubes. This is the large aperture diameter, which gives this new species such a robust appearance. Its aperture in the uncoiled stage is not only five times larger than that in the similarly high *Microconchus aberrans* from the Middle Triassic (Vinn, 2010b), but nearly three times larger than the aperture in the highest tube of ‘*Serpula*’ cf. *S. advena*, and five and a half times larger than the aperture in the similarly long tube of *Helicoconchus elongatus* (Table 1; Fig. 6). If the aperture size reflects the size of the animal dwelling within the tube, then *Microconchus cravenensis* n. sp. is the largest among all known microconchids.

Interestingly, all microconchids having helically uncoiled tubes were associated with organic buildups and some even formed their own bioconstructions—biostromes and bioherms (Leeder, 1973; Peryt, 1974; Burchette and Riding, 1977; Toomey and Cys, 1977; Beus, 1980; Suttner and Lukeneder, 2004; Wilson et al., 2011; Zatoń et al., 2018). Such a niche could have been advantageous (see Vinn, 2010a), providing protection against overgrowth and sediment covering, and lessening competition for suspended food in a higher tier. The microconchids in this setting had the ability to keep pace with the growth of encrusting algae and microbialite with which they were typically associated (e.g., Peryt, 1974; Burchette and

Riding, 1977; Dreesen and Jux, 1995; Zatoń et al., 2016b). Only such a growth mode allowed microconchids to develop primary frameworks (Vinn, 2010a). The microconchid described here did not form bioconstructions but was a minor component of the prolifically fossiliferous Cracoean reefs, which have yielded 568 known macrofaunal species (Mundy, 2000). This fauna is dominated by brachiopods and mollusks with a modest diversity of bryozoans, corals, arthropods, and echinoderms, together with rare sponges. The biota also includes microbialite, ‘skeletal’ microbes, and algae.

At present, *Microconchus cravenensis* n. sp. is only known from the Craven Reef Belt, where it is extremely rare. Just 10 specimens were recorded from six localities despite extensive collecting (from 378 exposures) along the reef tract (Mundy, 1980). One specimen (the holotype) came from an exposure at Scaleber, east of Settle, and nine specimens were recorded from five exposures on the Stebden Hill reef mound, Cracoe, of which four specimens are extant. In limestones of B₂₆ zone age on Stebden Hill, a single specimen of *Microconchus cravenensis* n. sp. was located in a microbialite framework where it was attached to the epitheca of the small solitary rugosan *Cyathaxonia cornu* Michelin, 1847, and is sited just short of the calice (Fig. 5.1). The coral and the attached microconchid

were postmortally encrusted by the cystoporate bryozoan *Fistulipora incrustans* (Phillips, 1836) (Fig. 5.1, 5.2). Seven specimens were recovered from a coeval 'shoal' deposit in the upper flank facies that abuts the framework and its contiguous *Siphonodendron* thicket. There, the microconchids occur in a floatstone-grainstone that contains a typical upper flank (shallow-water) fauna, albeit with a high percentage of disarticulated shells. Conspicuous microbial (oncolitic) coatings by the microorganisms *Aphralysia* Garwood, 1914 and *Girvanella* Nicholson and Etheridge, 1878 are present on many of the shell fragments. The attachment substratum for these microconchids is unknown but is inferred to be shells or shell fragments. A further specimen was located in younger lower flank limestones (P_{1a} zone age) in a stressed community that was deposited immediately prior to an emergent episode. Here again, the substratum is unknown, but it is interesting that within this community and the overlying 'lowstand' brachiopod-dominant coquinas, attachment scars of small *Microconchus* spp. were evident, mostly attached to bivalve shells. Depositional setting at the Scaleber locality is unclear because the exposure occurs in a slab of the reef front displaced from the main reef trend and likely a late Mississippian slope failure. The occurrence of *Gigantoproductus* in this exposure suggests a bank- or shallow-flank facies setting.

The holotype of *Microconchus cravenensis* n. sp. bears distinct signs of repair and regeneration of the uncoiled tube. These occurred after a puncture or breakage and were characterized by deviation of the ornament pattern in the subsequently secreted tube material. Such regeneration occurred five times during the tube development. The first occurred at the beginning of the uncoiled part and was followed by the second one, which is the most severe tube breakage (Fig. 3.2). There, the epithelium, along with a large portion of the tube, must have been damaged. However, the individual survived and regenerated the tube. Subsequently, there was damage at three further locations, again with regeneration (Fig. 3.2). Such sublethal injuries are known in other Carboniferous microconchids and the percentage of damaged tubes varies widely from < 1–34% (Zatón et al., 2014a; Zatón et al., 2016a). The sublethal injuries were likely caused by external biological agents, namely failed attempts at predation (Vinn, 2009; Zatón et al., 2014a, 2016a). In the Cracoean reefs, repaired predation injuries on brachiopods were documented by Mundy (1982), who suggested that fish, crustaceans, and cephalopods were potential predators. These could also have been the perpetrators of damage in the robust *Microconchus cravenensis* n. sp., which could have provided a good food source for small durophagous animals. It cannot be entirely excluded that the paucity of *Microconchus cravenensis* n. sp. in the Craven Reef Belt could be the result of successful predation.

Acknowledgments

We gratefully acknowledge C. Sendino and Z. Hughes, curators at The Natural History Museum, London, for facilitating the loan of the specimens. P. Taylor (UK), an anonymous referee, and the journal Associate Editor J. Botting provided many constructive comments, useful remarks, and corrections, which is greatly appreciated.

References

- Aitkenhead, N., Barclay, W.J., Brandon, A., Chadwick, R.A., Chisholm, J.L., Cooper, A.H., and Johnson, E.W., 2002, British Regional Geology: The Pennines and Adjacent Areas (fourth edition): Nottingham, British Geological Survey, 206 p.
- Arthurton, R.S., Johnson, E.W., and Mundy, D.J.C., 1988, Geology of the country around Settle: Memoirs of the British Geological Survey, Sheet 60 (England & Wales), 147 p.
- Belka, Z., and Skompski, S., 1982, A new open-coiled gastropod from the Viséan of Poland: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 7, p. 389–398.
- Beus, S.S., 1980, Devonian serpulid bioherms in Arizona: Journal of Paleontology, v. 54, p. 1125–1128.
- Bisat, W.S., 1924, The Carboniferous goniatites of the north of England and their zones: Proceedings of the Yorkshire Geological Society, v. 20, p. 40–124.
- Bisat, W.S., 1934, The goniatites of the *Beyrichoceras* zone in the north of England: Proceedings of the Yorkshire Geological Society, v. 22, p. 280–309.
- Bouček, B., 1964, The *Tentaculites* of Bohemia: Prague, Czechoslovakian Academy of Sciences, 125 p.
- Brunton, C.H.C., and Mundy, D.J.C., 1988, Strophalosiacean and aulostegacean productoids (Brachiopoda) from the Craven Reef Belt (late Viséan) of North Yorkshire: Proceedings of the Yorkshire Geological Society, v. 47, p. 55–88.
- Burchette, T.P., and Riding, R., 1977, Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes: Lethaia, v. 10, p. 17–28.
- Caruso, J.A., and Tomescu, A.M.F., 2012, Microconchid encrusters colonizing land plants: The earliest North American record from the Early Devonian of Wyoming, USA: Lethaia, v. 45, p. 490–494, doi:10.1111/j.1502-3931.2012.00305.x.
- Dean, M.T., Browne, M.A.E., Waters, C.N., and Powell, J.H., 2011, A lithostratigraphical framework for the Carboniferous succession of northern Great Britain (onshore): British Geological Survey Research Report, RR/10/07, 165 p.
- Dreesen, R., and Jux, U., 1995, Microconchid buildups from the late Famennian peritidal-lagoonal settings (Evieux Formation, Ourthe Valley, Belgium): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 198, p. 107–121.
- Ferguson, J., 1971, *Linoprotonia*, a new genus of lower Carboniferous productoid: Proceedings of the Yorkshire Geological Society, v. 38, p. 549–564.
- Fraiser, M.L., 2011, Paleocology of secondary tierers from western Pangean tropical marine environments during the aftermath of the end-Permian mass extinction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 308, p. 181–189, doi:10.1016/j.palaeo.2010.12.002.
- Garwood, E.J., 1914, Some new rock building organisms from the lower Carboniferous beds of Westmorland: Geological Magazine, v. 1, p. 265–271.
- Goldfuss, A., 1831, Petrefacta Germaniae tam ea Quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhemiae Rhennae servantur Quam alia Quaecunque in Museis Hoeninghusiano Muensteriano Aliisque extant: Iconibus et descriptionibus illustrata, Erster Theil, Lieferung 3: Düsseldorf, Arnz & Comp., p. 165–240.
- Hall, J., 1861, Contribution to Palaeontology: Continuation of Appendix C, Descriptions of New Species of Fossils from the Upper Helderberg, Hamilton and Chemung Groups, Continued from Page 109 of the Fourteenth Annual Report of the Regents of the University upon the State Cabinet: Albany, Charles Van Benthuysen, Printer, 109 p.
- He, L., Wang, Y., Woods, A., Li, G., Yang, H., and Liao, W., 2012, Calcareous tubeworms as disaster forms after the end-Permian mass extinction in South China: Palaios, v. 27, p. 878–886, doi:10.2307/23362144.
- Hohenstein, V., 1913, Beiträge zur Kenntnis des Mittleren Muschelkalks und des unteren Trochitenkalks am östlichen Schwarzwaldrand: Geologisch-paläontologische Abhandlungen, Neue Folge, v. 12, p. 173–272.
- Hudson, R.G.S., 1930, The Carboniferous of the Craven reef belt, the Namurian unconformity at Scaleber, near Settle: Proceedings of the Geologist's Association, v. 41, p. 290–322.
- Hudson, R.G.S., 1932, The pre-Namurian knoll topography of Derbyshire and Yorkshire: Transactions of Leeds Geological Association, v. 5, p. 49–64.
- Hudson, R.G.S., 1944, A pre-Namurian fault-scarp at Malham: Proceedings of the Leeds Philosophical and Literary Society (Scientific Section), v. 4, p. 226–232.
- Hudson, R.G.S., and Philcox, M.E., 1965, The lower Carboniferous stratigraphy of the Buttevant area, Co. Cork: Proceedings of the Royal Irish Academy, v. 64, p. 5–79.
- Leeder, R.M., 1973, Lower Carboniferous serpulid patch reefs, bioherms and biostromes: Nature, v. 242, p. 41–42.
- McCoy, F., 1844, A synopsis of the characters of the Carboniferous Limestone fossils of Ireland: Dublin, Ireland, University Press (M.H. Gill), 207 p.

- McCoy, F., 1849, On some new genera and species of Palaeozoic corals and Foraminifera: The Annals and Magazine of Natural History, v. 2, no. 3, p. 1–20, 119–136.
- Michelin, H., 1840–1847, Iconographie Zoophytologique: Description par Localités et Terrains des Polypiers Fossiles de France et Pays Environnants: Paris, P. Bertrand, 348 p.
- Mundy, D.J.C., 1980, Aspects of the palaeoecology of the Craven Reef Belt (Dinantian) of North Yorkshire [Ph.D. dissertation]: Manchester, University of Manchester, 540 pp.
- Mundy, D.J.C., 1982, A note on the predation of brachiopods from the Dinantian reef limestones of Cracoe, North Yorkshire: Transactions Leeds Geological Association, v. 9, p. 73–83.
- Mundy, D.J.C., 1994, Microbialite-sponge-bryozoan-coral framestones in the lower Carboniferous (late Viséan) buildups of northern England (U.K.), in Beauchamp, B., Embry, A.F., and Glass, D.J., eds., Pangea: Global Environments and Resources: Canadian Society of Petroleum Geologists Memoir, v. 17, p. 713–729.
- Mundy, D.J.C., 2000, Yorkshire Geological Society Field Meeting to the Craven Reef Belt: Settle & Cracoe, Sunday 23 July 2000, Guidebook: Calgary, Talisman Energy Inc., 83 pp.
- Mundy, D.J.C., 2007, Upper Viséan Cracoean reefs, Great Britain and Ireland, in Vennin, E., Aretz, M., Boulvain, F., and Munnecke, A., eds., Facies from Palaeozoic Reefs and Bioaccumulations: Mémoires du Muséum d'Histoire Naturelle, v. 195, p. 247–248.
- Mundy, D.J.C., and Brunton, C.H.C., 1985, Morphological similarities in some British Dinantian and Permian Texas reef brachiopods: Compte Rendu du Congrès International de Stratigraphie et de Géologie de Carbonifère, 9th, Urbana, Illinois, 1979, v. 5, p. 225–232.
- Murchison, R.I., 1839, The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coal-fields and overlying formations: London, John Murray, 768 p.
- Nicholson, H.A., and Etheridge, R., Jr., 1878, A Monograph of the Silurian Fossils of the Girvan District in Ayrshire with Special Reference to Those Contained in the 'Gray Collection,' Volume 1, Fasciculus 1, Rhizopoda, Actinozoa, Trilobita: Edinburgh, W. Blackwood and Sons, 135 p.
- Peryt, T.M., 1974, Spirorbis-algal stromatolites: Nature, v. 249, p. 239–240.
- Phillips, J., 1836, Illustrations of the Geology of Yorkshire, Part 2, The Mountain Limestone District: London, John Murray, 253 p.
- Prentice, J.E., 1950, The genus *Gigantella* Sarytcheva: Geological Magazine, v. 87, p. 436–438.
- Rigby, J.K., and Mundy, D.J.C., 2000, Lower Carboniferous sponges from the Craven Reef Belt of North Yorkshire: Proceedings of the Yorkshire Geological Society, v. 53, p. 119–128, doi:10.1144/pygs.53.2.119.
- Riley, N.J., 1990, Revision of the *Beyrichoceras* Ammonoid-Biozone (Dinantian), N W Europe: Newsletters on Stratigraphy, v. 21, p. 149–156.
- Salter, J.W., 1863, On the Upper Old Red Sandstone and Upper Devonian Rocks: Quarterly Journal of the Geological Society, v. 19, p. 474–496.
- Sowerby, J., 1814, The Mineral Conchology of Great Britain, Part 1 (13): London, B. Meredith, p. 153–168.
- Sutner, T.J., and Lukeneder, A., 2004, Accumulations of late Silurian serpulid tubes and their palaeoecological implications (Blumau-Formation; Burgenland; Austria): Annalen des Naturhistorischen Museums in Wien, ser. A, v. 105, p. 175–187.
- Taylor, P.D., and Vinn, O., 2006, Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications: Journal of the Geological Society, London, v. 163, p. 225–228, doi:10.1144/0016-764905-145.
- Toomey, D.F., and Cys, J.M., 1977, Spirorbis/algal stromatolites, a probable marginal marine occurrence from the lower Permian of New Mexico, U.S.A.: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1977/6, p. 331–342.
- Vinn, O., 2006, Two new microconchid (Tentaculita Bouček 1964) genera from the early Palaeozoic of Baltoscandia and England: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 2006/2, p. 89–100, doi:10.1127/njgpm/2006/2006/89.
- Vinn, O., 2009, Attempted predation on early Paleozoic cornulitids: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 273, p. 87–91, doi:10.1016/j.palaeo.2008.12/004.
- Vinn, O., 2010a, Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms, Palaeogeography, Palaeoclimatology, Palaeoecology, v. 292, p. 211–221, doi:10.1016/j.palaeo.2010.03.046.
- Vinn, O., 2010b, Shell structure of helically coiled microconchids from the Middle Triassic (Anisian) of Germany: Paläontologische Zeitschrift, v. 84, p. 495–499, doi:10.1007/s12542-010-0064-y.
- Vinn, O., and Taylor, P.D., 2007, Microconchid tubeworms from the Jurassic of England and France: Acta Palaeontologica Polonica, v. 52, p. 391–399.
- Waters, C.N., Haslam, R.B., Cózar, P., Somerville, I.D., Millward, D., and Woods, M., 2017, Mississippian reef development in the Cracoe Limestone Formation of the southern Askrigg Block, North Yorkshire, UK: Proceedings of the Yorkshire Geological Society, v. 61, p. 179–196, doi:10.1144/pygs2016-374.
- Weedon, M.J., 1990, Shell structure and affinity of vermiform 'gastropods': Lethaia, v. 23, p. 297–309.
- Weedon, M.J., 1991, Microstructure and affinity of the enigmatic Devonian tubular fossils *Trypanopora*: Lethaia, v. 24, p. 223–227.
- Wilson, M.A., Vinn, O., and Yancey, T.E., 2011, A new microconchid tubeworm from the lower Permian (Artinskian) of central Texas, U.S.A.: Acta Palaeontologica Polonica, v. 56, p. 785–791, doi:10.4202/app.2010.0086.
- Yang, H., Chen, Z.-Q., Wang, Y., Ou, W., Liao, W., and Mei, X., 2015, Palaeoecology of microconchids from microbialites near the Permian-Triassic boundary in South China: Lethaia, v. 48, p. 497–508, doi:10.1111/et.12122.
- Zatoń, M., and Krawczyński, W., 2011a, Microconchid tubeworms across the upper Frasnian–lower Famennian interval in the Central Devonian Field, Russia: Palaeontology, v. 54, p. 1455–1473, doi:10.1111/j.1475-4983.2011.01110.x.
- Zatoń, M., and Krawczyński, W., 2011b, New Devonian microconchids (Tentaculita) from the Holy Cross Mountains, Poland: Journal of Paleontology, v. 85, p. 757–769, doi:10.1666/11-005.1.
- Zatoń, M., and Olempska, E., 2017, A family-level classification of the order Microconchida (class Tentaculita) and the description of two new microconchid genera: Historical Biology, v. 29, p. 885–894, doi:10.1080/08912963.2016.1261858.
- Zatoń, M., and Peck, R.L., 2013, Morphology and palaeoecology of new, non-marine microconchid tubeworm from lower Carboniferous (Upper Mississippian) of West Virginia, USA: Annales Societatis Geologorum Poloniae, v. 83, p. 37–50.
- Zatoń, M., and Taylor, P.D., 2009, Microconchids (Tentaculita) from the Middle Jurassic of Poland: Bulletin of Geosciences, v. 84, p. 653–660, doi:10.3140/bull.geosci.1167.
- Zatoń, M., and Vinn, O., 2011, Microconchids and the rise of modern encrusting communities: Lethaia, v. 44, p. 5–7, doi:10.1111/j.1502-3931.2010.00258.x.
- Zatoń, M., Vinn, O., and Tomescu, A.M.F., 2012a, Invasion of freshwater and variable marginal marine habitats by microconchid tubeworms—an evolutionary perspective: Geobios, v. 45, p. 603–610, doi:10.1016/j.geobios.2011.12.003.
- Zatoń, M., Wilson, M.A., and Vinn, O., 2012b, Redescription and neotype designation of the Middle Devonian microconchid (Tentaculita) species '*Spirorbis*' *angulatus* Hall, 1861: Journal of Paleontology, v. 86, p. 417–424, doi:10.1666/11-115.1.
- Zatoń, M., Taylor, P.D., and Vinn, O., 2013, Early Triassic (Spathian) post-extinction microconchids from western Pangea: Journal of Paleontology, v. 87, p. 159–165, doi:10.2307/23353815.
- Zatoń, M., Grey, M., and Vinn, O., 2014a, Microconchid tubeworms (class Tentaculita) from the Joggins Formation (Pennsylvanian), Nova Scotia, Canada: Canadian Journal of Earth Sciences, v. 51, p. 669–676, doi:10.1139/cjes-2014-0061.
- Zatoń, M., Hagdon, H., and Borszcz, T., 2014b, Microconchids of the species *Microconchus valvatus* (Münster in Goldfuss, 1831) from the upper Muschelkalk (Middle Triassic) of Germany: Palaeobiodiversity & Palaeoenvironments, v. 94, p. 453–461, doi:10.1007/s12549-013-0128-6.
- Zatoń, M., Dębowiec, A., and Peck, R.L., 2016a, Sublethal injuries in non-marine microconchid tubeworms from the lower Carboniferous of West Virginia, USA: Historical Biology, v. 28, p. 1125–1132, doi:10.1080/08912963.2015.1111886.
- Zatoń, M., Niedzwiedzki, G., Blom, H., and Kear, B., 2016b, Boreal earliest Triassic biotas elucidate globally depauperate hard substrate communities after the end-Permian mass extinction: Scientific Reports, v. 6, p. e36345, doi:10.1038/srep36345.
- Zatoń, M., Vinn, O., and Toom, U., 2016c, A new microconchid species from the Silurian of Baltica: Estonian Journal of Earth Sciences, v. 65, p. 115–123, doi:10.3176/earth.2016.09.
- Zatoń, M., Borszcz, T., and Rakociński, M., 2017, Temporal dynamics of encrusting communities during the Late Devonian: A case study from the Central Devonian Field, Russia: Paleobiology, v. 43, p. 550–568, doi:10.1017/pab.2017.8.
- Zatoń, M., Niedzwiedzki, G., Rakociński, M., Blom, H., and Kear, B.P., 2018, Earliest Triassic metazoan bioconstructions from East Greenland reveal a pioneering benthic community in the immediate aftermath of the end-Permian mass extinction: Global and Planetary Change, v. 167, p. 87–98, doi:10.1016/j.gloplacha.2018.05.009.

Accepted: 7 June 2020