Annales Societatis Geologorum Poloniae (2013), vol. 83: 37–50.

MORPHOLOGY AND PALAEOECOLOGY OF NEW, NON-MARINE MICROCONCHID TUBEWORM FROM LOWER CARBONIFEROUS (UPPER MISSISSIPPIAN) OF WEST VIRGINIA, USA

Michał ZATOŃ[1] & Robert L. PECK[2]

[1] *University of Silesia, Faculty of Earth Sciences, Będzińska 60, PL-41-200 Sosnowiec, Poland; e-mail: mzaton@wnoz.us.edu.pl*
[2] *Concord University, Division of Natural Sciences, Athens, West Virginia 24712, USA; e-mail: fossilpecker@netscape.net*

Zatoń, M. & 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*, 83: 37–50.

Abstract: A new species of a non-marine microconchid (Tentaculita) tubeworm, *Microconchus hintonensis*, from the Lower Carboniferous (Upper Mississippian, Chesterian) of West Virginia, USA, is described. Non-marine microconchids occur abundantly in the deposits of the Bluefield, lower Hinton, Princeton and Bluestone Formations of the Mauch Chunk Group, where they are either associated with land plant remains and bivalve shells, or are preserved loose in the host sediment. The specimens attached to plant remains and bivalve shells, are poorly preserved, but those occurring loose in the deposits are well-preserved in three dimensions. The interpretation presented here, is that the loose specimens of *Microconchus hintonensis* sp. nov. also originally encrusted plants (land plants, algae) and bivalve shells, but became detached after substrate degradation and dissolution. The association of land plant remains, charophyte gyrogonites, bivalves, ostracodes, conchostracans, and fish teeth and scales, and the concomitant lack of strictly marine fossils indicate that the microconchid-bearing deposits of the lower Hinton, Princeton and Bluestone Formations were deposited in fresh-water environments. *Microconchus hintonensis* sp. nov. is regarded as a highly fecund, opportunistic species that in large numbers colonized every available substrate in its habitat. Its abundance in the deposits investigated indicates that the species was well-adapted to the environments it occupied, even during episodes of higher sedimentation rates and/or competition with other soft-bodied encrusters. During such episodes, microconchids were able to grow vertically by uncoiling and elevating their tubes, in order to escape potential burial and/or overgrowth by other encrusters.

Key words: Microconchids, Mississippian, Carboniferous, encrusters, palaeoecology, fresh-waters.

Manuscript received 29 April 2013, accepted 18 June 2013

INTRODUCTION

Microconchids (Order Microconchida Weedon, 1991) are extinct, sedentary, tentaculitoid tubeworms. Having calcitic skeletons, they are characterised by an excellent fossil record, ranging from the Late Ordovician to the Middle Jurassic (Taylor and Vinn, 2006; Vinn and Mutvei, 2009; Zatoń and Vinn, 2011). Originating in marine environments at least since the Early Devonian, microconchids started to invade fresh-water habitats as well (Taylor and Vinn, 2006; Caruso and Tomescu, 2012). Their occurrence in a wide suite of environmental settings, from normal marine through brackish- to fresh-water habitats (Zatoń *et al.*, 2012a), and their clear domination on hard substrates and microbialites during times following mass extinctions (Fraiser, 2011; Zatoń and Krawczyński, 2011a; He *et al.*, 2012; Zatoń *et al.*, 2013), make them a group of opportunistic organisms. Although included in the Class Tentaculita by Weedon (1991), the morphological and microstructural features of the tube indicate their lophophorate affinity (Vinn and Mutvei, 2009; Taylor *et al.*, 2010; Wilson *et al.*, 2011; Zatoń *et al.*, 2012b), being even related to such suspension-feeders as phoronids (Taylor *et al.*, 2010). However, their true biological affinity is still uncertain and specimens with exceptionally preserved soft tissues would be highly desirable for deciphering their position on the animal phylogenetic tree.

Carboniferous microconchids, like others from different systems, used to be treated and described under the polychaete generic names *Spirorbis* or *Serpula* in the older (e.g., McCoy, 1844; Etheridge, 1880; Whitfield, 1882; Branson, 1937; Elias, 1957; Howell, 1964; Leeder, 1973; Sando, 1984; Kietzke, 1990) and some recent literature (e.g., Lescinsky, 1997; Aitkenhead *et al.*, 2002; Cassle *et al.*, 2003; Falcon-Lang, 2005; Williams *et al.*, 2005), even though many of them have been observed in strictly non-marine settings. On the basis of their cemented mode of life and lamellar tube micro-

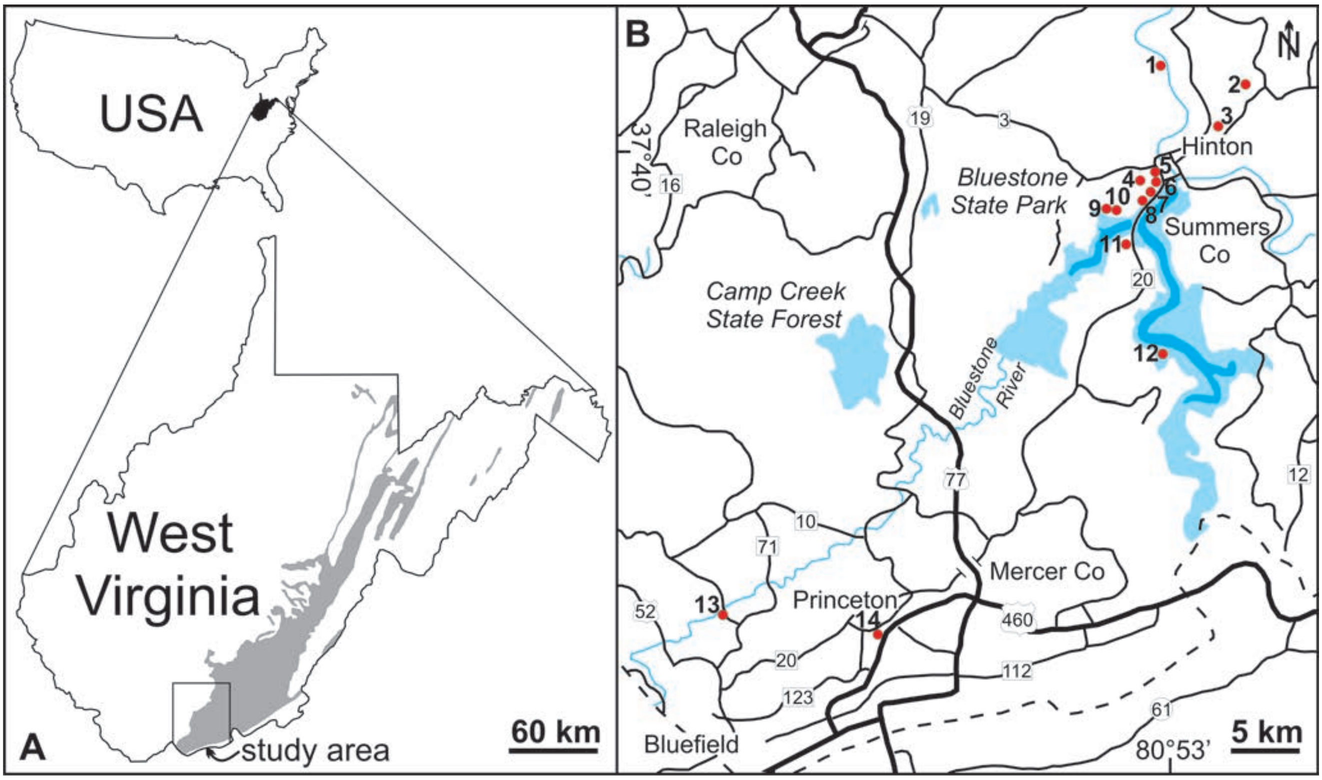

Fig. 1. Location of study area. **A.** Sketch map of West Virginia State, showing Mississippian deposits (shaded) and study area. **B.** Study area between Hinton and Bluefield. Circles indicate locations of sampled sections (see Table 1 for details)

structure, some Lower Carboniferous 'spirorbids' were re-interpreted as vermetid gastropods by Burchette and Riding (1977), who later were supported by Wright and Wright (1981), Bełka and Skompski (1982) and Paszkowski and Szydłak (1986). It is noteworthy that Bełka and Skompski (1982) were the first to investigate the tube external morphology, with the aid of the scanning electron microscope (SEM), an indispensable tool in modern studies of this group of fossils. Except for the studies of Weedon (1990, 1991), who classified the Carboniferous 'vermiform' gastropods and 'spirorbids' of earlier authors in the Order Microconchida, there is a lack of modern studies deciphering the taxonomy of Carboniferous microconchid tubeworms, which definitely would assist recognition of the diversity of these enigmatic fossils during that period. Although the majority of modern studies were focused on marine forms (e.g., Vinn, 2006; Vinn and Taylor, 2007; Zatoń and Krawczyński, 2011b), there is a significant gap in taxonomic studies, concerning fresh- and brackish-water species. Recognition of the diversity of such species would provide the answers to many questions, such as: 1) are there any morphological and microstructural similarities/differences between fresh-and brackish-water and marine forms?, 2) could the same species have lived in both fresh- and brackish-water or even marine environments?, or 3) in what environments and at what times did they attain the greatest diversity? To answer these interesting questions, some weight should now be put on fresh- and brackish-water settings.

In the present paper we turn the emphasis toward the understanding of some of the problems of the fresh- and brackish-water microconchids. As an example, we present a detailed study of the Lower Carboniferous (Upper Mississippian, Chesterian) microconchids from the Mauch Chunk Group of southern West Virginia, USA. On the basis of a rich collection of specimens, thorough morphological and microstructural observations enabled recognition of a new microconchid species. Apart from taxonomy, its palaeoecology is also discussed on the basis of taphonomic observations of many specimens preserved in the host sediments. This is thus the first detailed, taxonomic and palaeoecological study of fresh- and brackish-water microconchids in general.

GEOLOGICAL SETTING

The geological setting of the Upper Mississippian of southeastern West Virginia (Fig. 1A) has been fairly well studied due to the interest in the Mississippian – Pennsylvanian boundary that is exposed in the study area. The rocks of the Upper Mississippian Mauch Chunk Group show a transition from shallow, open marine limestones of the Greenbrier Series, into the mixed, terrestrial deposits with thin, marine incursions of the Mauch Chunk Group (Fig. 2), and then into the coal-bearing, Pennsylvanian siliciclastic deposits (Ettensohn, 2009). This influx of clastics reflects a major change in sedimentation that was at least partly conditioned by the movement of the Appalachian Basin northwards into a more humid, tropical climate belt (Cecil *et al.*, 2004). The change in lithology from limestones to siliciclastics was primarily a result of tectonic plate movements. This could well reflect the change from the tectonically passive conditions of the Greenbrier to the more active tectonism of the Mauch Chunk and Pennsylvanian along the Alleghanian orogen. This could be a product of the early Alleghanian Orogeny and increasing, tectonic activity (Chesnut and Greb, 2009) or a relaxational response to previous convergence at the SE margin of Laurussia in the final phases of the Acadian Orogeny (Ettensohn, 2009).

The Lower Carboniferous (Mississippian) System of the Appalachian Basin comprises a third-order sequence, defined by an unconformity or abrupt transition at the base of the Sunbury Shale and by an early Pennsylvanian unconformity at the top (Ettensohn, 2009). The Upper Mississippian Mauch Chunk Group in southeastern West Virginia is subdivided into the Bluefield, Hinton, Princeton, and Bluestone Formations, with a maximum aggregate thickness of approximately 1051 m, of which approximately 650 m are exposed in the map area (Matchen *et al.*, 2011).

The basal Upper Mississippian Bluefield Formation (Fig. 2), comprising gray, calcareous shales and blocky, reddish mudstones, begins the upward trend toward siliciclastic deposits with the Glenray and Reynolds Limestones, the products of two spasms of marine incursion near the bottom of the Formation. Subsequently, siliciclastic deposits were the rule. The Coney Shale of Reger (1926) near the top of the formation contains marine fossils, including brachiopods. The thin Coney Limestone, which only has microconchids, fish teeth and scales, and ostracodes (Stencil, 2012), gives way to the Hinton Formation and the Stony Gap Sandstone Member (Maynard *et al.*, 2006).

The Stony Gap Sandstone, the basal member of the Hinton Formation (Fig. 2), mainly comprises a white, fine- to medium-grained quartz arenite, although it changes locally to a light gray, fine-grained, lithic arenite. The unit is typically cross-bedded, with both trough and planar crossbeds present. It has a fluvial-estuarine origin, associated with palaeovalley incision and a basinward shift of fluvial environments during a time of lowered, relative sea level (Miller and Eriksson, 2000). Alternatively, Englund (1979) suggested that the Stony Gap Sandstone was a series of marine bars. Above the Stony Gap Sandstone and a fossiliferous shale (mostly non-marine bivalves) overlying it, the rocks become terrigenous deposits, consisting mainly of red mudstones and thin, interbedded, lenticular or channel-fill sandstones. Occasional intervals of black mudstones and tan to yellowish or gray-green, limey mudstones (Fig. 3A) contain microfossils (microconchids, ostracodes, and fish teeth and scales). Charophyte oogonia and conchostracan *Hemicycloleaia* specimens have been found in separate horizons, reflecting a rather fresh-water palaeoenvironments (R. L. Peck, field observations). However, most of the mudstones are red and often exhibit characteristics of palaeosols. They probably originated as overbank flood deposits. The mudstones and sandstones reflect deposition in terrestrial and coastal environments (Miller and Eriksson, 2000). Horizons of plant fossils are found from the Stony Gap Sandstone through the entire Formation into the Princeton Sandstone, supporting the interpretation that subaerial exposure occurred fairly frequently.

Near the middle of the Hinton Formation, a marine limestone, the Little Stone Gap Member (formerly the Avis Limestone, see Beuthin and Blake, 2004) occurs. It is predominately micritic and argillaceous and contains a typical Chesterian fauna of brachiopods, bryozoans, corals, bivalves, gastropods, ostracodes, trilobites, pelmatozoans, and cephalopods (Reger, 1926; Gordon and Henry, 1981; Beuthin and Blake, 2004; Matchen *et al.*, 2011). The Little Stone Gap Member provides a brief change from the red mudstones of the lower Hinton Formation that lack the regionally identifiable, marine units (Beuthin and Blake, 2004). A variable succession of mudstone, sandstone, and limestone, with limited occurrences of coal, occurs above the marine Little Stone Gap Member. In this part of the formation (upper Hinton Formation), thin, fairly widespread, marine zones are found in the Fivemile and Eads Mill members (see Fig. 2; Beuthin and Blake, 2004; Vance, 2007; Matchen *et al.*, 2011), containing

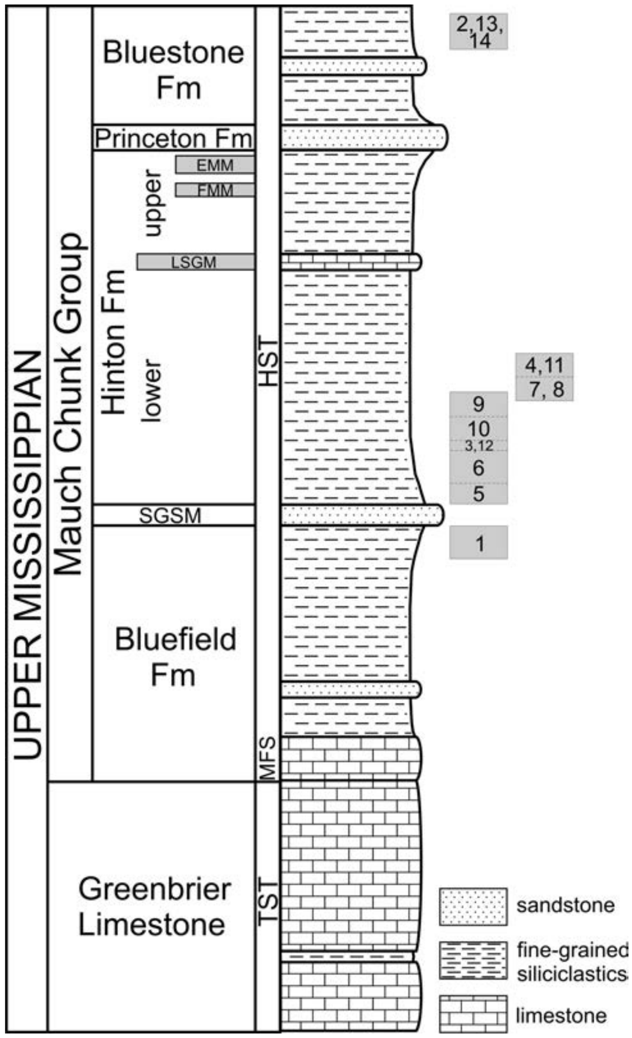

Fig. 2. Stratigraphy of Upper Mississippian Mauch Chunk Group with general section, showing mainly siliciclastic deposits (simplified after Stencil, 2012) in stratigraphic framework as second-order sequence (after Maynard *et al.*, 2006). Shaded, horizontal bars in upper Hinton Formation refer to marine members (after Beuthin & Blake, 2004). Shaded vertical bars refer to general stratigraphic range of sampled sections at particular localities (for numbers, see Fig. 1B and Table 1). SGSM – Stony Gap Sandstone Member, LSGM – Little Stone Gap Member, FMM – Five Mile Member, EMM – Eads Mill Member, TST – transgressive system tract, MFS – maximum flooding surface, HST – highstand systems tract

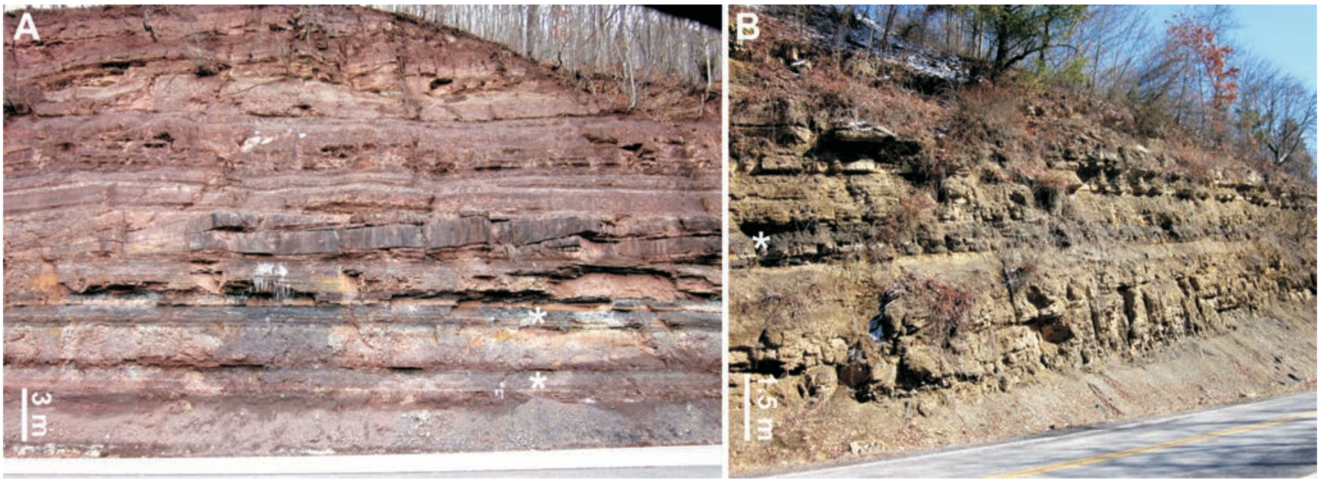

Fig. 3. Examples of sampled sections. **A.** Section with deposits of lower Hinton Formation at State Route 20, Bluestone Lake, Summers County (locality no. 8). Beds, indicated by asterisks, refer to fossiliferous mudstones with myalinid bivalves, *Hemicycloleaia* branchiopods, ostracodes, fish teeth and scales, as well as abundant microconchids. **B.** Section with deposits of Bluestone Formation at County Road 11, Crane Creek Road, Montcalm, Mercer County (locality no. 13). Sampled gray to black, shaly mudstone is indicated by asterisk

a typical Chesterian fauna of brachiopods, bryozoans, corals, bivalves, gastropods, ostracodes, trilobites, pelmatozoans and cephalopods (Reger, 1926; Cooper, 1948, 1961; Henry and Gordon, 1979, 1992).

The Hinton Formation is overlain by the Princeton Formation (Fig. 2), comprising medium- to coarse-grained, quartzose sandstone to quartz arenite, and containing quartz pebbles and conglomerate beds. Thin beds of mudstone, sandstone, coal, and palaeosols are also locally observed above the sandstone (Matchen *et al.*, 2011). The sandstone is another incised valley fill (Miller and Eriksson, 2000).

Above the Princeton Formation, the Bluestone Formation (Fig. 2) occurs, in the form of mudstones, shales, siltstones, and sandstones (Fig. 3B), with discontinuous beds of coalesced, authigenic limestone and siderite nodules (Matchen *et al.*, 2011). A few thin, discontinuous, impure coal beds are present, as well (Matchen *et al.*, 2011). Bluestone marine zones (Bramwell Member) contain a typical Upper Mississippian (Chesterian) fauna of brachiopods, bryozoans, corals, bivalves, gastropods, ostracodes, trilobites, pelmatozoans, and cephalopods (Reger, 1926; Henry and Gordon, 1979, 1992; Hoare, 1993).

Correlation of biostratigraphic data with European successions indicates that the Bluefield Formation corresponds to the Upper Viséan, and the Hinton to Bluestone Formations correspond to the lower part of the Namurian (see Beuthin and Blake, 2004; Maynard *et al.*, 2006; Ettensohn, 2009).

MATERIAL AND METHODS

All the material investigated here, comes from the Lower Carboniferous (Upper Mississippian) Mauch Chunk Group of West Virginia, USA (Figs 1, 2). The deposits of all formations of the Mauch Chunk Group were inspected with respect to microconchids. The bulk of specimens were found in the Hinton and Bluestone formations, while a few specimens of microconchids were retrieved from the Bluefield Formation. In general, however, microconchids were noticed in both fresh-, brackish and marine deposits of the Mauch Chunk Group in the area studied, but not all deserved special attention, owing to their state of preservation. For example, the marine deposit of the Eads Mill Member of the upper Hinton Formation contained *Composita* brachiopods with some encrusting microconchids, but their state of preservation was insufficient for detailed study. The same might be said of the microconchids encrusting bivalve shells and plant fragments, preserved in the siliciclastics of the Bluefield, lower Hinton, Princeton and Bluestone Formations. Although they may be numerous where attached to these substrates, their poor state of preservation obscured the details of their tubes. Additionally, many specimens were preserved as traces of their tubes on the shelly and plant substrates. Such specimens, of course, are not suitable for morphological and microstructural investigation. However, they do provide interesting material for taphonomic and palaeoecological observations. Many samples with such microconchid-encrusted bivalve shells and plant fragments (shoots and leaves) were collected for these purposes. A number of siliciclastic rock samples from the lower Hinton Formation were rich in microconchid tubes, scattered in the host sediment along with ostracode carapaces. On the bedding planes, the tubes appeared to be well-preserved. Therefore, it was decided to retrieve the fossils by boiling the rock samples with Quaternary-O. To do so, the rock samples (0.5 to ca 3 kg) were put in a pot, covered with water, and about a tablespoon of Quaternary-O was added. This prepared mix was then slowly boiled for several hours. Next, the samples were gently washed with hot water to flush out the floating particles and the Quaternary-O. After drying the samples, they were sieved through a mesh of 1.4 mm (No. 14), 0.5 (No. 35) and 0.212 mm (No. 70) and the resulting residues were examined for fossils. Microconchids, along with other microfossils, occurred to be in the residues of the 1.4 and 0.5 mm sieves. These residues were

Table 1

Details on provenance of samples used for extraction of microconchids from Upper Mississippian Mauch Chunk Group of West Virginia, USA

Locality		Sample	Stratigraphy	Lithology
1	River Road, County Road 26, Raleigh County	182	Coney Limestone, Bluefield Formation	Yellow tan to olive gray, mottled, poorly lithified, calcareous mudstone
2	Tug Creek Mountain Road, County Road 44/6, Summers County	130	Gray member, Bluestone Formation	Black, coaly, poorly lithified mudstone
3	Elk Knob Road, County Road 9, Hinton, Summers County	107	Bellepoint Limestone?, lower Hinton Formation	Yellow tan to gray black, calcareous, shaly mudstone
4	Leatherwood Road, County Road 44/7, Hinton, Summers County	153-154	Lower Hinton Formation	Gray to black, whitish when weathered, thinly laminated, shaly mudstone
5	State Route 20, below Bluestone Dam, Hinton, Summers County	070, 157	Lower Bellepoint Shale?, lower Hinton Formation	Black silty mudstone, thin to thick laminations, with ostracodes and Carbonicola bivalves
6	State Route 20, below Bluestone Dam, Hinton, Summers County	111-113, 115	Lower Bellepoint Shale?, lower Hinton Formation	Beds of tan and gray to black shaly, silty mudstones sandwiched between sandstones and siltstones
7	State Route 20, S of Leatherwood Road, County Road 44/7, Hinton, Summers County	195, 197	Lower Hinton Formation	Blackish mudstone to claystone with ostracodes
8	State Route 20, Bluestone Lake, Summers County	007, 020, 045-046, 088, 094, 121, 147, 171-172, 175, 198, 199-201	Lower Hinton Formation	Shaly, laminated mudstones, gray at the bottom with myalinid bivalves and Hemicycloleaia branchiopods to black, coaly, poorly indurated mudstone at top
9	County Route 20/2, Bluestone State Park, Summers County	097, 099-100	Lower Bellepoint Shale?, lower Hinton Formation	Black, highly carbonaceous to almost coaly, shaly mudstone
10	County Route 20/2, Bluestone State Park, Summers County	086, 090-081, 122, 166, 178, 184	Lower Bellepoint Shale?, lower Hinton Formation	Yellow tan mudstone to claystone with Carbonicola bivalves, charophyte gyrogonites, and ostracodes
11	State Route 20, S of Bluestone Bridge, True, Summers County	093	Lower Bellepoint Shale?, lower Hinton Formation	Gray to black mudstone
12	County Road 44/11, Road to Bull Falls, Bluestone Lake, Summers County	170	Bellepoint Limestone?, lower Hinton Formation	Orange tan to gray, calcareous mudstone
13	County Road 11, Crane Creek Road, Montcalm, Mercer County	162	Gray Member, Bluestone Formation	Gray to black shaly mudstone
14	US Route 460, Princeton, Mercer County	048, 168	Gray Member, Bluestone Formation	Black, thinly laminated, shaly mudstone with bivalves and ostracodes

Locality numbers correspond to those in Figure 1B. Each sample number is preceded by acronym, GIUS 5

rinsed 3 to 6 times in hot water, dried and then picked for microfossils. We used this method for 42 samples from different horizons of the Mauch Chunk Group (Fig. 2) in Raleigh, Summers and Mercer Counties, near Hinton and Princeton (Fig. 1B; for details, see Table 1): the Bluefield Formation (one sample), the lower Hinton Formation (37 samples) and the Bluestone Formation (4 samples). Surprisingly, this method provided a number of microconchid specimens, the majority of which come from the lower Hinton Formation.

The preservation of specimens varies, from tubes being completely obliterated, owing to ferrous oxides, to those with calcareous tubes. The latter comprise specimens with both flattened tubes due to compaction and those with three-dimensionally well-preserved tubes. The number of specimens per treated sample differs widely, from as few as 4 specimens to as many as dozens to hundreds of specimens for a given sample. After initial inspection of all specimens under the binocular microscope, those from two samples of the lower Hinton Formation and two samples from the Bluestone Formation were discarded, owing to their poor state of preservation. From the remaining 38 samples, the best-preserved specimens were selected for further, detailed observations. In total, 175 microconchids were mounted on steel tables using carbon tape, and examined in an uncoated state using a Philips XL 30 low-vacuum environmental scanning electron microscope (ESEM), housed at the Faculty of Earth Sciences in Sosnowiec, Poland. Images were generated using backscattered electrons (BSE detector). Additionally, 8 specimens were embedded in epoxy resin and polished for microstructural observation of the tubes. Measurements of the microconchids were performed directly on the ESEM photomicrographs.

The specimens are housed at the Faculty of Earth Sciences, University of Silesia in Sosnowiec, Poland, designated GIUS 5-3620.

SYSTEMATIC PALAEONTOLOGY

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 surfaces ornamented with variously developed growth lines, perpendicular ridges, longitudinal striae and tubercles or nodes. Minute punctae penetrate lamellar tube microstructure.

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

Microconchus hintonensis new species
Figs 4, 6–8

Diagnosis: Tube planispirally coiled at the first stages of tube growth, followed by helical uncoiling of it. Tube exterior ornamented with variously spaced, thicker, transverse rib-like ridges crossed by thinner, longitudinal striae. The crossing ridges and striae form distinct, but variously developed tubercles and nodes. Tube origin (protoconch) bulbous, ornamented with widely-spaced, sharp, perpendicular ridges.

Etymology: From the name of the Hinton Formation.

Types: Holotype: GIUS 5-3620/121/01 (Fig. 4J), *Hemicycloleaia* bed, lower Hinton Formation, Mauch Chunk Group, Upper Mississippian, State Route 20, Bluestone Lake, Summers County, West Virginia, USA. Paratypes: GIUS 5-3620/020/02, GIUS 5-3620/046/03, GIUS 5-3620/086/01, GIUS 5-3620/086/06, GIUS 5-3620/097/02, GIUS 5-3620/097/05, GIUS 5-3620/097/07, GIUS 5-3620/097/12, GIUS 5-3620/097/15, GIUS 5-3620/099/02, GIUS 5-3620/121/01, lower Hinton Formation, Mauch Chunk Group, Upper Mississippian, West Virginia, USA; GIUS 5-3620/130/05, Bluestone Formation, Mauch Chunk Group, Upper Mississippian, West Virginia, USA.

Material: Hundreds of variously preserved specimens, of which 183 specimens (including 8 sectioned ones) have been studied in detail using ESEM.

Description: Tube small, planispirally (dextrally) coiled (e.g., Fig. 4A, C–E, G–I) up to ca 2170 μm in diameter, being later helically uncoiled (Fig. 4B, F). Umbilicus open, differing in width in different specimens (129–568 μm, mean = 322 μm, n = 79), with rounded margin and gently inclined slope. Aperture rounded to semi-rounded, up to 978 μm in diameter. The increase in tube width proceeds as the tube diameter increases. The umbilical width, on the other hand, is not so well correlated with tube diameter growth (Fig. 5), suggesting a greater developmental plasticity in the latter feature.

Tube exterior ornamented by fine growth lines and more or less thicker, transverse rib-like ridges, running straight or sinuous to tube base or around the tube in uncoiled specimens (Fig. 4). The ridges and growth lines are irregularly crossed by longitudinally running (in the tube growth direction) thinner striae. The striae may be developed on a whole tube surface, or may be confined only to its lateral side. They also may run continuously along the tube growth direction, or, more commonly, be interrupted, giving a wrinkle-like appearance (e.g., Fig. 4B, D, G, L). In many specimens, the juxtaposition of perpendicular ridges and longitudinal striae results in the formation of thickened elevations, tubercles or even node-like structures (Fig. 4A, C, K). The intensity of the latter structures varies widely in different specimens. However, intermediate stages of their development are evident. In specimens, in which the outermost tube layer is worn away, perpendicular ridges are the only ornamental features.

Tube origin bulbous, elliptical in outline, ca 243 μm in width and 260 μm in length, separated from the rest of the tube by distinct constriction. Its exterior is ornamented by straight, perpendicular ridges, ca 63 μm apart (Fig. 6).

Tube consists of lamellar layer with microlaminae, penetrated by tiny punctae (Fig. 7A–C). The punctae are circular in outline and ca 2.2 μm in diameter (Fig. 7B, C).

Discussion – variability: The species *Microconchus hintonensis* sp. nov. shows a clear, intraspecific variability with respect to coiling pattern and tube ornamentation (Fig. 4). The coiling pattern may vary widely among different individuals. Some tubes show evidence of regular coiling during the animal growth, leaving the umbilicus open throughout (e.g., Fig. 4B, F, H), while others are tightly coiled in the last whorl, resulting in a narrow or even closed umbilicus (Fig. 4C, E). Many specimens were attached throughout their growth, which may be reflected in the flat tube base along its growth direction. However, others have the terminal part of their tube oriented vertically upwards. This may be a tendency for tube uncoiling and vertical growth at some point in their development, as many specimens in different samples have even the greater part of their tubes uncoiled, and with a vertical orientation (Fig. 4F). This problem is discussed in detail in the palaeoecological section.

The ornamentation of the tube exterior shows considerable variation. This should not be surprising, since in other microconchids such variability of ornamentation also was noted (e.g., Zatoń and Krawczyński, 2011a). The variability not only affects the transverse ridges, which may be straight or sinuous, and thin or thicker, but also the longitudinal, thin striae, crossing the ridges perpendicularly. The striae may be fine along the tube. However, more commonly they have an irregular thickness, resulting in a wrinkle-like or wavy appearance in places, where they are thicker (see Fig. 4). Moreover, in some individuals they develop into forms of tubercles or nodes, where they cross the ridges. Their appearance is also irregular on the tube exterior. Such tuberculation may appear very early in microconchid ontogeny, occurring just after the protoconch. In many specimens, such tuberculation is absent. In such specimens, the longitudinal striae are also lacking and only transverse ridges are present. However, in many cases such specimens are characterised by a worn tube exterior. That the wrinkle and tuberculate ornamentation may depend on the state of preservation is well exemplified by partially crushed tubes: in depressions, where such ornamentation is well-preserved, and on the top, where it is lacking (Fig. 8A). Therefore, it is believed that on the one hand, the presence of tubercles/nodes may depend on the state of preservation of the specimens, being developed on tubes having a well-preserved outer surface. On the other hand, the presence of tuberculation also may depend on well-developed striae, crossing the transverse ridges. The presence of tubes with more or less well-developed tuberculation in the specimens studied indicates the presence of a morphologically variable species that lived during sedimentation of both the lower Hinton and Bluestone Formations. The characteristically ornamented protoconches, in the form of transverse, widely spaced ridges, occurring in both tuberculated tubes and in those, where the exteriors are devoid of well-developed longitudinal striae, also may indicate the presence of a single, albeit morphologically variable species. This may also be supported by the presence of similar sizes of punctae, a feature that may vary between different species of the same genus (e.g., *Punctaconchus*, see Vinn and Taylor, 2007).

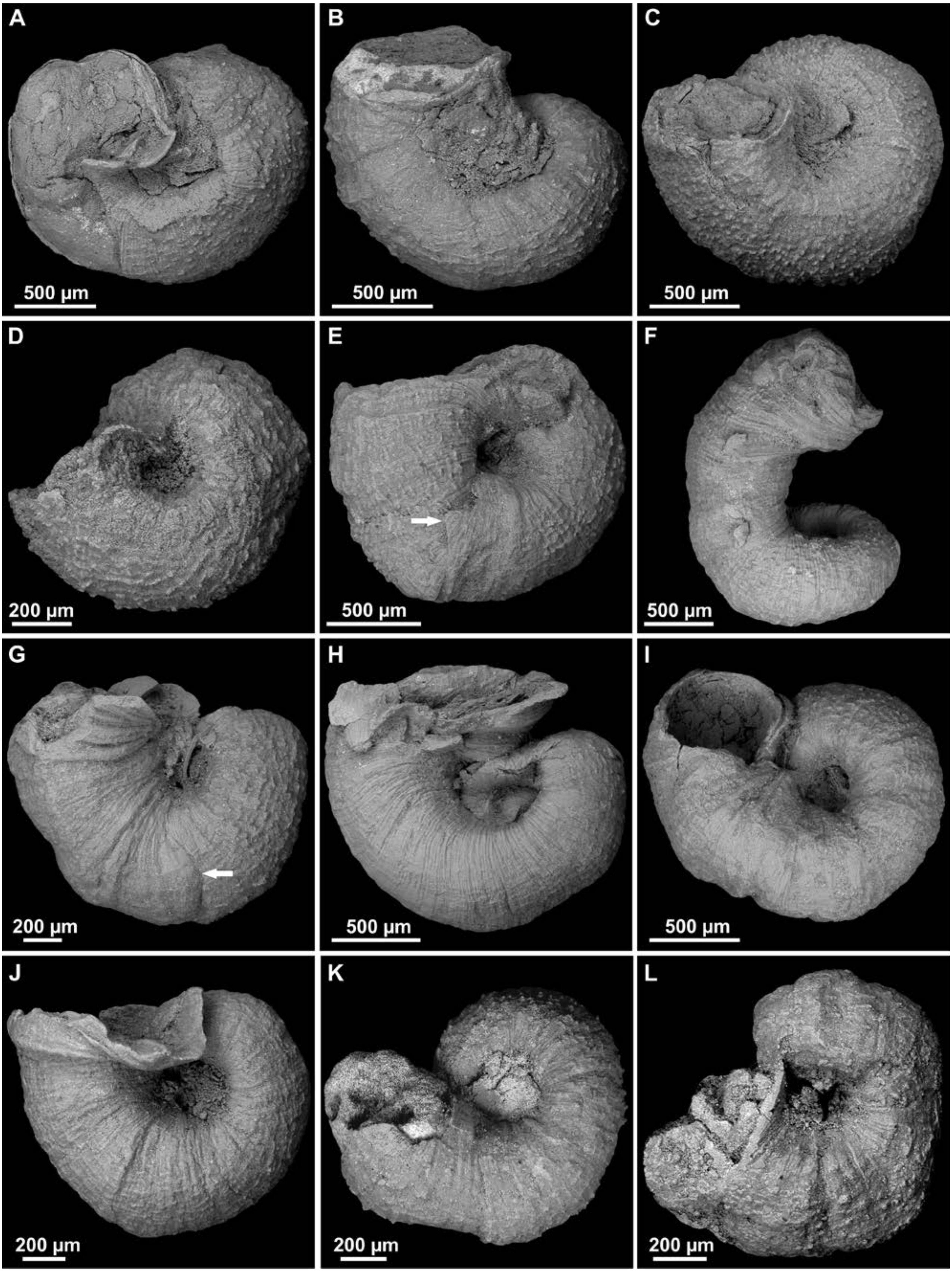

Fig. 4. Microconchids *Microconchus hintonensis* sp. nov. from Upper Mississippian Mauch Chunk Group of West Virginia, USA. **A.** GIUS 5-3620/020/02, **B.** GIUS 5-3620/046/03, **C.** GIUS 5-3620/086/01, **D.** GIUS 5-3620/086/06, **E.** GIUS 5-3620/097/15, **F.** GIUS 5-3620/097/05, **G.** GIUS 5-3620/097/02, **H.** GIUS 5-3620/097/12, **I.** GIUS 5-3620/097/07, **J.** GIUS 5-3620/121/01 (holotype), **K.** GIUS 5-3620/099/02, **L.** GIUS 5-3620/130/05. Arrows indicate healed injuries. A–K – lower Hinton Formation, L – Bluestone Formation. BSE ESEM images of uncoated specimens

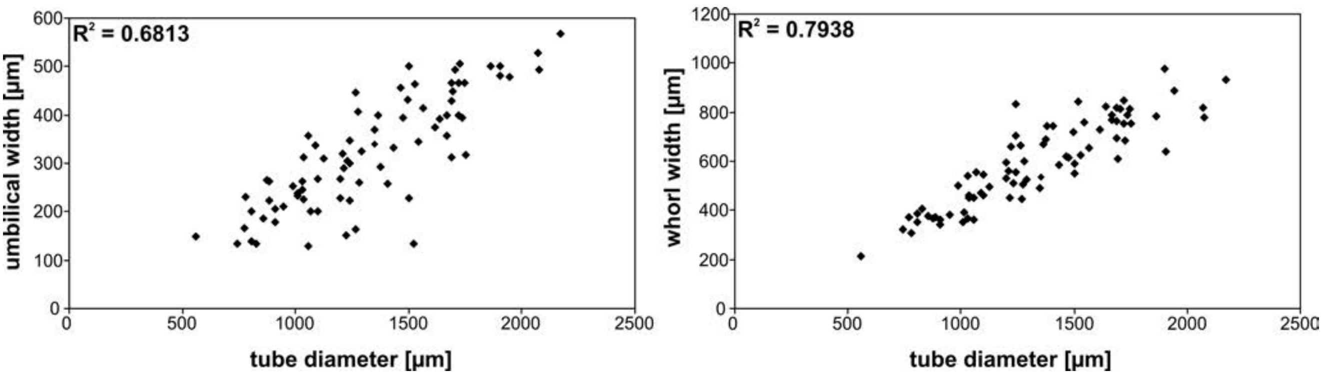

Fig. 5. Plots of umbilical width and whorl width against tube diameter for *Microconchus hintonensis* sp. nov.

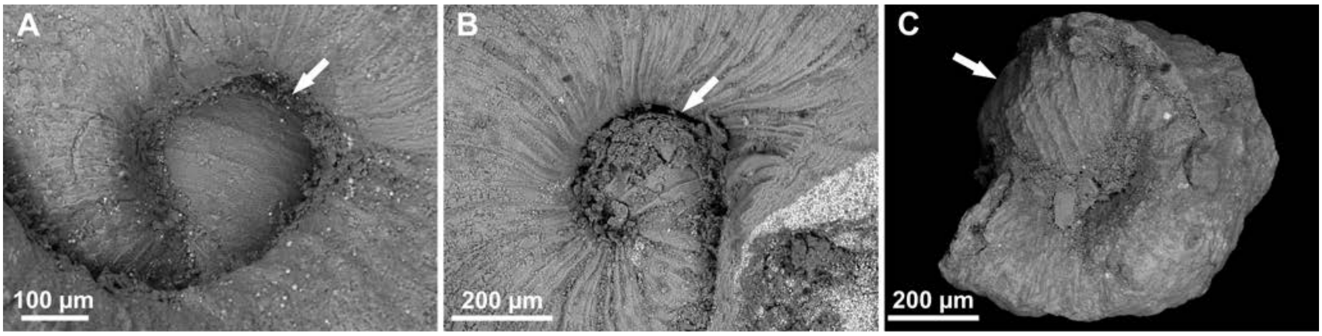

Fig. 6. Morphology of tube origin (arrowed) in *Microconchus hintonensis* sp. nov. from lower Hinton (A, B) and Bluefield (C) Formations. **A.** GIUS 5-3620/097/01, **B.** GIUS 5-3620/168/03, **C.** GIUS 5-3620/182/03. BSE ESEM images of uncoated specimens

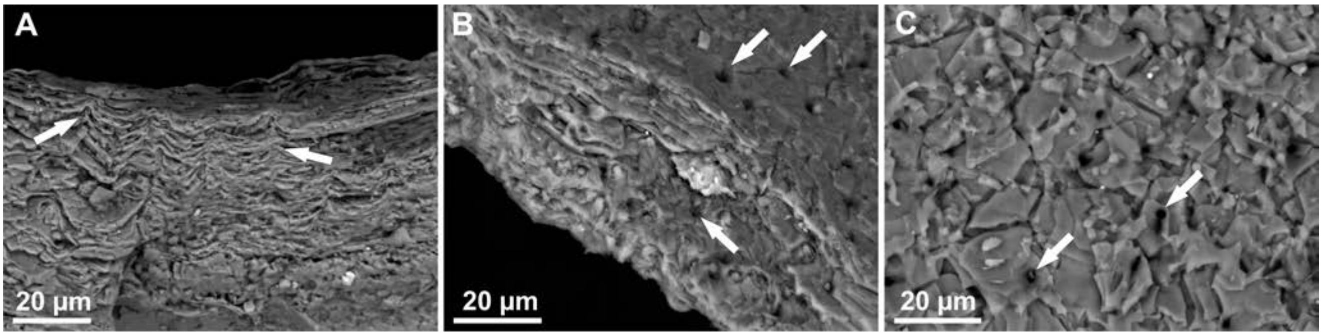

Fig. 7. Tube microstructure of *Microconchus hintonensis* sp. nov., showing wavy microlaminae (A, B), punctured by tiny punctae (A–C, arrowed). **A.** GIUS 5-3620/099/06, **B.** GIUS 5-3620/097/04, **C.** GIUS 5-3620/020/06. BSE ESEM images of uncoated specimens

A handful of specimens, derived from the Bluefield Formation (Coney Limestone), seem to be devoid of individuals with the wrinkle-like and tuberculate ornamentation, characteristic for the specimens from the lower Hinton and Bluestone Formations. However, the majority of specimens are small (presumably juveniles) and those larger (presumably adults) have the tube exterior too poorly preserved for the original ornamentation to be deciphered. But, as in the tubes from the lower Hinton and Bluestone Formations (Fig. 6A, B), the Coney Limestone specimens have similarly ornamented protoconchs (Fig. 6C). Thus, it is plausible that they might represent the same species.

Discussion – comparisons: The comparison of the species described here, is rather limited as the great majority of previously described and illustrated Carboniferous microconchids (usually under the name *Spirorbis*) were investigated using classic methods that employed a binocular microscope. Therefore, any detailed documentation, comprising SEM photomicrographs of the tube surface and tube microstructure, are simply lacking. Moreover, descriptions of each microconchid species in the 19th Century literature are supplemented only with hand-drawings, showing a rather general tube appearance. The only work, including detailed SEM photomicrographs of Carboniferous microconchids, is that of Bełka and Skompski (1982). The specimens came from the Polish Lower Carboniferous (Viséan), and then were considered to be archaeogastropods by the authors. They are characterised by helically uncoiled tubes, with strong, thick and more or less regularly spaced, transverse ridges, dissimilar to the ornamentation patterns of *Microconchus hintonensis* sp. nov. As Bełka and Skompski (1982) stated, the tubes are close to those described under the name *Spirorbis caperatus* by McCoy (1844). *Microconchus pusi-*

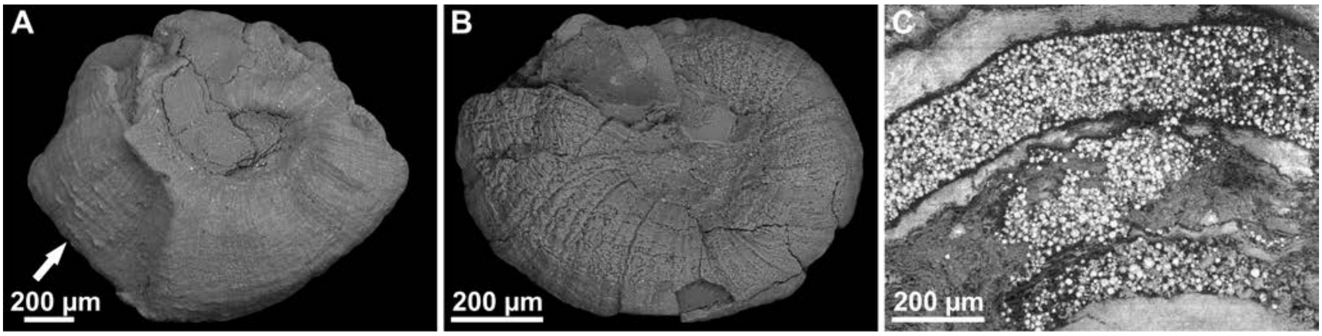

Fig. 8. Different states of preservation of *Microconchus hintonensis* sp. nov. tubes. **A.** Wrinkle ornamentation, preserved in depressed (concave) portion of tube (arrowed), while top of three-dimensionally (convex) preserved part is nearly devoid of it. **B.** Mould of tube, showing only remnants of transverse ridges, while perpendicular wrinkle ornamentation is lacking. **C.** Cross-section of tube, showing infilling of it by carbonate and pyrite mineral phases. BSE ESEM images of uncoated specimens

llus (Martin) from Westphalian of Yorkshire is also dissimilar, having closely-spaced fine transverse ridges and a completely smooth tube origin. However, it has similar, tiny tube punctation (see Taylor and Vinn, 2006, fig. 1K, L). Several species of Carboniferous '*Spirorbis*' were described and illustrated from Great Britain by Etheridge (1880). Of them, only one species, '*Spirorbis*' *spinosa* (de Koninck) may be somewhat similar in having "small, sharp prickles, or abortive spines, arranged in quincunx" (Etheridge, 1880, p. 262) on the tube surface. However, *Microconchus hintonensis* sp. nov. clearly differs from this species, as it has no spines, possesses additional transverse ridges and longitudinal striae, and its tube base is not crenulated.

Another form that is noteworthy is a species described as '*Spirorbis*' *nodulosus* ((Hall) (see Whitfield, 1882, pl. 9, fig. 31), from the Lower Carboniferous of Indiana, USA. Its tube, however, possesses large nodes, regularly arranged in three rows; sharp, short ridges near the umbilical margin and a dorsal crest, running half of the way to the last whorl. So, although they have nodes, these are completely different from irregularly scattered, small tubercles in *Microconchus hintonensis* sp. nov. '*Spirorbis*' *moreyi*, a marine Mississippian species from Wyoming, described by Branson (1937, pl. 89, figs. 1, 2), possesses slightly sinuous, transverse ridges and probably also fine, longitudinal striae, as may be deduced from the description. However, it lacks the characteristics for *Microconchus hintonensis* sp. nov., including the irregular, wrinkled pattern, formed by the crossing, transverse ridges and longitudinal striae, as well as tuberculation.

The Mississippian species, known as '*Spirorbis*' *kentuckiensis*, described by Howell (1964), possesses only thick, transverse ridges. Interestingly, it is represented by tubes of both dextral (clockwise) and sinistral (anticlockwise) coiling and thus may be allied to Middle Devonian species, such as '*Spirorbis*' *arkonensis* (Nicholson, 1874).

The most similar species, with a tube ornamented with similar, transverse ridges and longitudinal striae, giving a wrinkle-like pattern, is a microconchid described as '*Spirorbis*' sp. A, from the marine Pennsylvanian deposits of New Mexico, USA (Kietzke, 1990). Whether it is a separate new species, or maybe a form conspecific with *Microconchus hintonensis* sp. nov., is uncertain. First, a detailed study of a large number of the New Mexico specimens using SEM, should be conducted and, second, the preferences of *Microconchus hintonensis* sp. nov. for marine environments must be confirmed, on the basis of a large number of well-preserved specimens.

Occurrence: Upper Mississippian (Mauch Chunk Group, certainly in the lower Hinton and Bluestone Formations, possibly in the Bluefield Formations, as well) from the environs of Hinton and Bluefield, West Virginia, USA.

TAPHONOMY AND PALAEOECOLOGY

Microconchids from the Mississippian Mauch Chunk Group of the area studied are differently preserved in particular formations. The specimens, retrieved from bulk samples from deposits of the Bluefield, lower Hinton and Bluestone Formations, differ from the totally or partially flattened (Fig. 8A) to three-dimensionally preserved tubes. Microconchids, attached to plant shoots and leaves (Bluefield and Princeton Formations), as well as to bivalve shells (lower Hinton Formation), are usually flattened, and the external surfaces of their tubes are badly preserved (Fig. 9A–C). Commonly, the microconchids, preserved on plants or shells, are also preserved in the form of traces of their tube bases (Fig. 9C); the specimens themselves most probably had fallen out. Microconchid tubes, attached to plants or shells in fresh-water deposits, usually are poorly preserved, with tubes diagenetically altered by dolomite (Zatoń and Mazurek, 2011; Caruso and Tomescu, 2012). Such a state of preservation hampers the direct comparison of these microconchids to those well-preserved specimens, retrieved from the host sediment. However, it is believed that well-preserved microconchids, occurring as both loose specimens, scattered in the host sediment (Fig. 9D) and attached to organic substrate in the Bluefield and lower Hinton Formations, belong to the same species, *Microconchus hintonensis* sp. nov. The flattening of the tubes presumably resulted from later sediment load on the specimens. However, those uncompacted and three-dimensionally preserved tubes were affected by early diagenetic precipitates, especially carbonates and pyrite, filling the empty spaces within them (Fig. 8C). Although many specimens from the host sediments have the tubes worn, part of them still retains the calcareous tube mineralogy with a well-preserved lamellar microstructure (Fig. 7). The differences in the occurrences of such tube preservation may depend on changing microenvironments within the sediment. It is plausible that episodically the tubes were buried in sediment, rich in plant detritus, the degradation of which may have lowered the alkalinity of the pore waters, thus resulting in tube etching and dissolution (Fig. 8B).

The presence of land plant remains, bivalves (myalinids, *Modiolus*, *Carbonicola*, *Anthraconaia*), ostracodes, branchiopods, fish teeth and scales, as well as charophyte

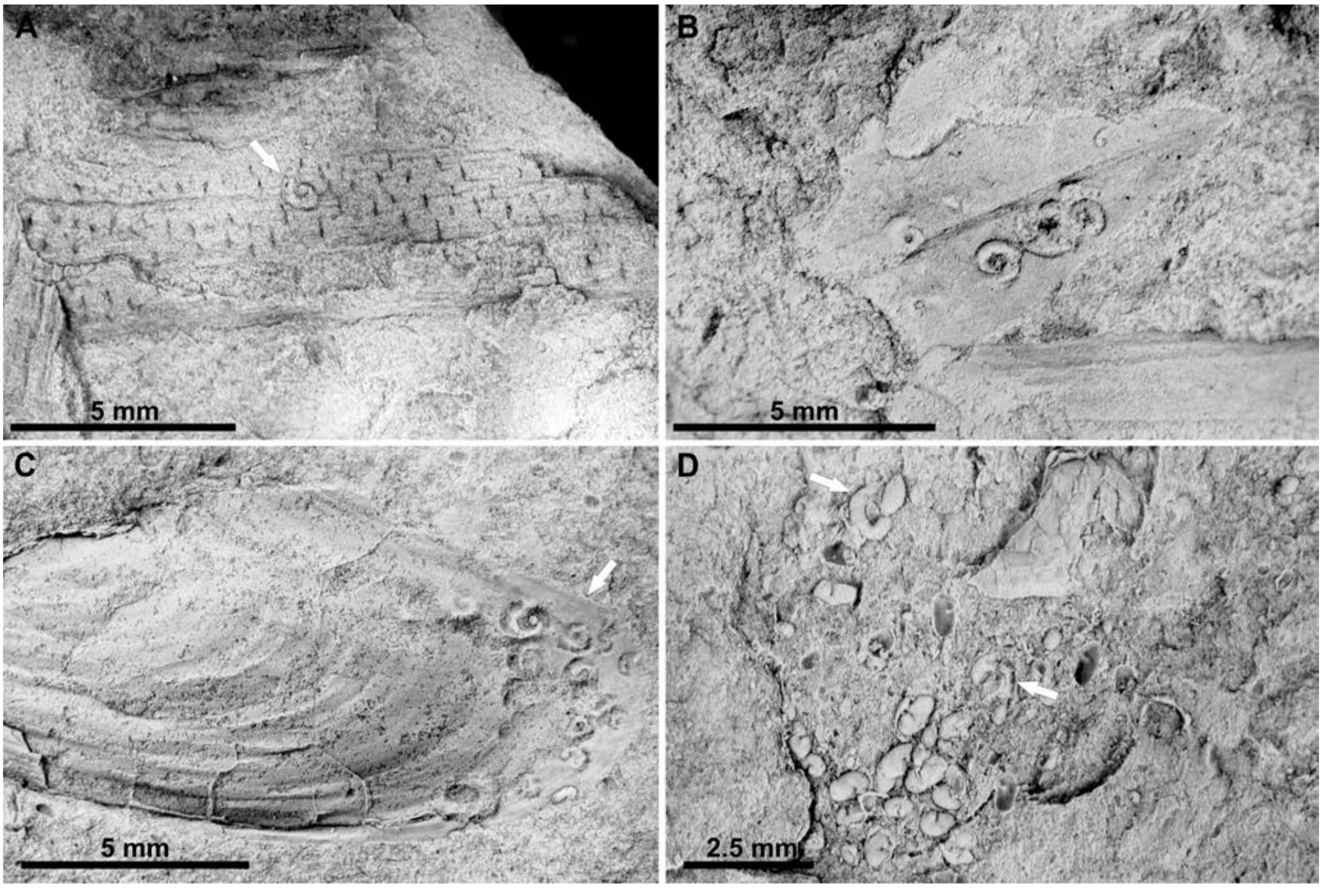

Fig. 9. Microconchids and their substrates. **A.** microconchid (arrowed), encrusting the land plant's shoot, Bluefield Formation. **B.** Microconchids, encrusting leaflet of land plant, Princeton Formation. **C.** Several microconchids encrusting posterior part (arrowed) of shell of *Modiolus* bivalve, lower Hinton Formation. **D.** Microconchids (arrowed), detached from their substrate and preserved loose in sediment together with abundant ostracode carapaces, lower Hinton Formation. Images of specimens, coated with ammonium chloride

gyrogonites in some horizons, and the lack of a strictly marine fauna indicate that the siliciclastic deposits of the lower Hinton, Princeton and Bluestone Formations were deposited in fresh-water environments. It is very likely that the palaeoenvironment took the form of terrestrial flood plains, where overbank flood deposits left swamps and ephemeral lakes. The tan *Carbonicola* bed (locality 10), including ostracodes and charophyte gyrogonites, may represent such a lacustrine environment. Similarly the laminated mudstones with *Hemicycloleaia* branchiopods and bivalves (locality 8) may represent overbank flood deposits.

The Coney Limestone of the Bluefield Formation, containing microconchids, as well as fish teeth and scales, ostracodes and a sporadic marine fauna (Reger, 1926; Stencil, 2012), presumably was deposited in brackish waters. The presence of the abundant ostracode, *Whipplella*, in the Coney Limestone indicates a transitional shoreline-nearshore environment with partial carbonate-forming conditions (Tibert and Dewey, 2006), yet the appearance of paraparchitaceans and kloedenellaceans suggests this may have been a shoreline transitional environment (Stencil, 2012). Therefore, it is evident that the species *Microconchus hintonensis* sp. nov. was able to thrive prolifically in fresh-water, and possibly also in brackish-water (Coney Limestone) conditions during sedimentation of the Upper Mississippian Mauch Chunk Group. The presence of *Microconchus hintonensis* sp. nov. in other formations, such as the Princeton Formation or within the marine units of the upper Hinton Formation (Eads Mill Member), cannot be confirmed, owing to the poor state of preservation of the specimens.

Observations of plant remains (shoots and leaves) and bivalves within the formations investigated indicate that microconchids preferred both kinds of substrates for attachment and later growth. It is not surprising, as the presence of Carboniferous microconchids on such types of substrate is well known in the literature (e.g., Trueman, 1942; Mastalerz, 1996; Aitkenhead *et al.*, 2002; Falcon-Lang, 2005; Zatoń and Mazurek, 2011; Florjan *et al.*, 2012). A great number of specimens also occur as detached tubes, free of substrate (Fig. 9D). Those tubes, occurring near bivalves, may indicate that the microconchids occupied shells, but were later detached, owing to, e.g., dissolution of the aragonitic shell. The presence of characteristic depressions from microconchid tubes on the bivalve molds (Fig. 9C) supports this scenario. Microconchid tubes also may have detached, following the degradation of the land plant remains, to which they were originally attached during life. The preservation of plant fragments on the tube bases of some of the specimens may support this statement. However, the large numbers of microconchid tubes, dispersed in the deposits of the Bluefield, lower Hinton and Bluestone Formation, away from any land plant remains, is interesting. In this case, it is interpreted that the tubes either fell off dissolved bivalve shells and/or, alternatively, became detached from algal fronds, on which they may have originally been encrusted. It is generally assumed that the presence of microconchid tubes, detached from substrates, is an indication that they originally encrusted hard, but aragonitic substrates that dissolved, or organic substrates (soft-bodied taxa) that degraded, leaving no trace (e.g., Vinn and Taylor, 2007; Zatoń and Krawczyński, 2011b). The hypothesis of microconchids settling on algae is very possible, as the preservation of microconchid-encrusted algal thalli is also known from the Upper Devonian of Germany (Jux, 1964). The presence of gyrogonites in some horizons may indicate that at least some of the algae, serving as a substrate for microconchids, were represented by charophytes.

The statement of Trueman (1942) about possible commensalism between Carboniferous microconchids and some non-marine bivalves is difficult to support and the authors do not subscribe to this hypothesis. Instead, it is believed that microconchids, as opportunistic organisms, colonized any suitable, firm and hard substrate in a given environment. Currently, there are no data supporting the idea that certain microconchid species preferred a special kind of substrate. Recently published data from the marine Upper Devonian (Zatoń and Krawczyński, 2011a; Zatoń and Borszcz, 2013) indicated that microconchids colonized brachiopod shells, since they served as an unlimited source of hard substrate in the environment. Moreover, no preferences of microconchid settlement concerning particular sites on the brachiopod shells, have been detected. Therefore, in the case of the Upper Mississippian microconchids studied, it is suggested that *Microconchus hintonensis* sp. nov. settled on a variety of suitable substrates, present in the soft-bottom environments, ranging from algae, transported land plants and bivalve shells. Thus, competition for space among these organisms must have been minimal or non-existent. This may be supported by the fact that very few microconchids are present, with respect to a given inspected plant fragment or bivalve shell (Table 2).

The microconchids investigated are represented by three morphological types, adapted to certain, ecological and environmental conditions (Vinn, 2010): 1) planispiral completely substrate-cemented tubes; 2) planispiral tubes with elevated apertures, and 3) loosely coiled, solitary tubes. Unlike morphological type 1, types 2 and 3 include specimens, growing on a hard substrate in the environment and experiencing at least periodic disturbances. In the case of type 2, the elevation of the tube aperture was an escaping response to overgrowing by neighbouring encrusters. Type 3 is characteristic of environments, where faster sedimentation rates forced the microconchids to grow upwards, resulting in helical uncoiling of their tubes (see also Burchette and Riding, 1977). It must be noted, however, that morphological type 3 may have also resulted from competition with other soft-bodied encrusters (animals or algal cover) which were not fossilised. The presence of these three tube morphologies in the microconchids studied indicates that generally calm environmental conditions were interrupted by disturbances, in the form of either higher sediment input or competition with other encrusting organisms. However, as the higher sediment input may be supported indirectly by the presence of land plant fragments, the competition hypothesis is difficult to prove, because of the lack of evidence.

Table 2

Number of microconchids
encrusting particular bivalve shells

Bivalves	Microconchid #
Modiolus sp.	1
Modiolus sp.	2
Modiolus sp.	1
Modiolus sp.	8
Carbonicola sp.	3
Carbonicola sp.	1
Carbonicola sp.	4
Carbonicola sp.	2
Carbonicola sp.	3
Carbonicola sp.	3
myalinid	2
myalinid	1

On the basis of distinct signs of tube regeneration (Fig. 4E, G), it may be concluded that some microconchids in a given population may have suffered from attempted predation by other animals, probably some kind of small arthropods or fish. Probably while trying to catch the tentacles, a potential predator must have injured the tube along with the tube-secreting epithelium, causing a deviation in its growth. Similar deviations in tube growth, related to failed predation, were noted in cornulitids (Vinn, 2009), which were close relatives of the microconchids. Therefore, predation on similarly small-sized, tube-dwelling organisms, such as microconchids, must have occurred as well and, importantly, was not lethal to all individuals in a given population. This problem, however, awaits further investigation.

CONCLUSIONS

The investigated deposits of the Bluefield, lower Hinton and Bluestone Formations of the Upper Mississippian Mauch Chunk Group of the southern part of the West Virginia, USA revealed the presence of abundant microconchids, assigned to a new species *Microconchus hintonensis*. The new species shows considerable variability in tube coiling and ornamentation pattern, a feature known also in other described, microconchid species. *Microconchus hintonensis* sp. nov., as an opportunistic, highly fecund species, inhabited in large numbers fresh-water (lower Hinton and Bluestone Formations), and possibly also brackish-water (Coney Limestone, Bluefield Formation) habitats, as evidenced by fossil associations, comprising land plant remains, charophyte gyrogonites, freshwater bivalves, conchostracans, ostracodes, as well as fish teeth and scales. There, microconchids have been found, encrusting bivalve shells and land plant remains, although a large number of specimens were also found loose in the host sediments. The latter specimens may have originally encrusted bivalve shells and plants (including algal thalli, as well), but fell off the substrates, after dissolution of the aragonitic shells and degradation of the plant remains. The occurrence of many specimens with helically uncoiled tubes may indicate that they responded with vertical tube growth to episodic, high rates of sedimentation and/or more intense competition with other, soft-bodied encrusting organisms. The healed injuries, marked in the tube by deviation in its growth, clearly indicate that these microconchids also witnessed some predation pressure from other animals in the environment.

Although microconchids are also present in other formations, including the marine intervals of the upper Hinton Formation (Eads Mill Member) and Bluefield Formation, their assignment to the species *Microconchus hintonensis* sp. nov. is uncertain, owing to the poor preservation of specimens, which are attached to brachiopod shells.

Finally, this study shows that bulk sample maceration and sieving is a very promising method for microconchid extraction from deposits, where any firm or hard substrate, in the form of plant remains and animal shells respectively, has been degraded and dissolved.

Acknowledgements

We would like to thank Mark Wilson (Ohio, USA) and Olev Vinn (Tartu, Estonia), the journal referees, for their constructive reviews and the journal editors for their careful checking of the final version of the manuscript.

REFERENCES

Aitkenhead, N., Barclay, W. J., Brandon, A., Chadwick, R. A., Chisholm, J. I., Cooper, A. H. & Johnson, E. W., 2002. *The Pennines and Adjacent Areas* (4th edition). British Regional Geology Series. British Geological Survey, Keyworth, 206 pp.

Bełka, Z. & Skompski, S., 1982. A new open-coiled gastropod from the Viséan of Poland. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 7: 389–398.

Beuthin, J. D. & Blake, B. M., 2004. Revised stratigraphy and nomenclature for the Upper Hinton Formation (Upper Mississippian) based on recognition of regional marine zones, southern West Virginia. *Southeastern Geology*, 42: 165–178.

Branson, C. C., 1937. Stratigraphy and fauna of the Sacajawea Formation, Mississippian, of Wyoming. *Journal of Paleontology*, 11: 650–660.

Burchette, T. P. & Riding, R., 1977. Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes. *Lethaia*, 10: 17–28.

Caruso, J. A. & Tomescu A. M. F., 2012. Microconchid encrusters colonizing land plants: the earliest North American record from the Early Devonian of Wyoming, USA. *Lethaia*, 45: 490–494.

Cassle, C. F., Gierlowski-Kordesch, E. H. & Martino, R. L., 2003. Late Pennsylvanian carbonates of the northern Appalachian Basin; criteria to distinguish brackish and freshwater conditions. *Geological Society of America, Abstracts with Programs*, 35: 600.

Cecil, C. B., Brezinski, D. & DuLong, F., 2004. The Paleozoic record of changes in global climate and sea level: Central Appalachian Basin. In: Southworth, S. & Burton, W. (eds), *Geology of the National Capital Region – Field Trip Guidebook*. U.S. Geological Survey Circular 1264: 77–135.

Chesnut, D. R., Jr. & Greb, S. F., 2009. Introduction. In: Greb, S. F. & Chesnut, D. R., Jr. (eds), *Carboniferous of the Appalachian and Black Warrior Basins*. Kentucky Geological Survey, Special Publication 10, Series XII: 3–9.

Cooper, B. N., 1948. Status of Mississippian stratigraphy in the central and northern Appalachian region. *The Journal of Geology*, 56: 255–263.

Cooper, B. N., 1961. *Grand Appalachian Excursion*. Virginia Polytechnic Institute Engineering Extension Series, Geological Guidebook I, Blacksburg, 187 pp.

Elias, M. K., 1957. Late Mississippian fauna from the Redoak Hollow Formation of southern Oklahoma, Part I. *Journal of Paleontology*, 31: 370–427.

Englund, K. J., 1979. Mississippian System and lower series of the Pennsylvanian System in the proposed Pennsylvanian System stratotype area. In: Englund, K. J., Arndt, H. H. & Henry, T. W. (eds), *Proposed Pennsylvanian System Stratotype, Virginia and West Virginia*. American Geological Institute, Selected Guidebook Series No. 1, Guidebook for Ninth International Congress of Carboniferous Stratigraphy and Geology Field Trip No. 1: 69–72.

Ettensohn, F. R., 2009. The Mississippian of the Appalachian Basin. In: Greb, S. F. & Chesnut, D. R., Jr. (eds), *Carboniferous of the Appalachian and Black Warrior Basins*. Kentucky Geological Survey, Special Publication 10, Series XII: 22–31.

Etheridge, R., 1880. A contribution to the study of the British Carboniferous tubicolar Annelida. *Geological Magazine*, 7: 258–266.

Falcon-Lang, H. J., 2005. Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. *Journal of the Geological Society, London*, 162: 485–500.

Florjan, S., Pacyna, G. & Borzęcki, R., 2012. First find of microconchids (Tentaculita) on Upper Carboniferous seed fern *Karinopteris daviesii* from Nowa Ruda (Lower Silesia, Poland). *Przegląd Geologiczny*, 60: 273–275. [In Polish, English summary].

Fraiser, M. L., 2011. Paleoecology of secondary tierers from Western Pangean tropical marine environments during the aftermath of the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 308: 181–189.

Gordon, M. & Henry T. W., 1981. Late Mississippian and Early Pennsylvanian invertebrate faunas, east-central Appalachians – a preliminary report. In: Roberts, T. G. (ed.), *GSA Cincinnati '81 Field Trip Guidebooks, Vol. 1: Stratigraphy, Sedimentology*. *Geological Society of America*: 165–171.

He, L., Wang, Y., Woods, A., Li, G., Yang, H. & Liao, W., 2012. Calcareous tubeworms as disaster forms after the end-Permian mass extinction in south China. *Palaios*, 27: 878–886.

Henry, T. W. & Gordon, M., 1979. Late Devonian through Early Permian (?) invertebrate faunas in proposed Pennsylvanian System stratotype area. In: Englund, K. J., Arndt, H. H. & Henry, T. W. (eds), *Proposed Pennsylvanian System Stratotype, Virginia and West Virginia*. American Geological Institute, Selected Guidebook Series No. 1, Guidebook for Ninth International Congress of Carboniferous Stratigraphy and Geology Field Trip No. 1: 97–103.

Henry, T. W. & Gordon, M., 1992. Middle and upper Chesterian brachiopod biostratigraphy, eastern Appalachians, Virginia and West Virginia. In: Sutherland, P. K. & Manger, W. L. (eds), *Recent Advances in Middle Carboniferous Biostratigraphy – a Symposium*. Oklahoma Geological Survey Circular 94: 1–21.

Hoare, R. D., 1993. Mississippian (Chesterian) bivalves from the Pennsylvanian stratotype area in West Virginia and Virginia. *Journal of Paleontology*, 67: 374–396.

Howell, B.F., 1964. A new serpulid worm, *Spirorbis kentuckiensis*, from the Chester group of Kentucky. *Journal of Paleontology*, 38: 170–171.

Jux, U., 1964. *Chaetocladus strunensis* n. sp., eine von *Spirorbis* besiedelte Pflanze aus dem Oberen Plattenkalk von Bergisch Gladbach (Devon, Rheinisches Schiefergebirge). *Palaeontographica, Abt. B*, 114: 118–134.

Kietzke, K. K., 1990. Microfossils from the Flechado Formation (Pennsylvanian, Desmoinesian) near Talpa, New Mexico. *New Mexico Geological Society Guidebook, 41st Field Conference, Southern Sangre de Cristo Mountains, New Mexico, 1990*: 259–276.

Leeder, R. M., 1973. Lower Carboniferous serpulid patch reefs, bioherms and biostromes. *Nature*, 242: 41–42.

Lescinsky, H. L., 1997. Epibiont communities: Recruitment and competition on North American Carboniferous brachiopods. *Journal of Paleontology*, 71: 34–53.

Mastalerz, K., 1996. "*Spirorbis*" from lacustrine deposits of the coal-bearing Carboniferous of the Intra Sudetic Depression (SW Poland). *Przegląd Geologiczny*, 44: 164–167. [In Polish, English summary].

Matchen, D. L., Allen J. L., Peck R. L., Mercier, D., Gooding, S. E., & Hunt, P. J., 2011. *Bedrock Geologic Map of the Bluestone National Scenic River, Flat Top and Pipestem 7.5' Quadrangles, West Virginia*. West Virginia Geological and Economic Survey PUB OF-1101.

Maynard, J. P., Eriksson, K. A. & Law, R. D., 2006. The upper Mississippian Bluefield Formation in the Central Appalachian basin: A hierarchical sequence-stratigraphic record of a greenhouse to icehouse transition. *Sedimentary Geology*, 192: 99–122.

McCoy, F. 1844. A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland. Dublin, 169 pp.

Miller, D. J. & Eriksson, K. A., 2000. Sequence stratigraphy of Upper Mississippian strata in the central Appalachians: A record of glacioeustasy and tectonoeustasy in a foreland basin setting. *American Association of Petroleum Geologists Bulletin*, 84: 210–233.

Nicholson, H.A., 1874. Descriptions of new fossils from the Devonian formation of Canada. *Geological Magazine*, 1: 197–201.

Paszkowski, M. & Szydłak, T., 1986. Evidence of hypersaline sedimentary environment in Dinantian carbonate deposits in area of Krzeszowice near Kraków. *Annales Societatis Geologorum Poloniae*, 56: 385–397.

Reger, D. B., 1926. *Mercer, Monroe, and Summers Counties*. West Virginia Geological Survey County Report, 963 pp.

Sando, W. J., 1984. Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah. *Journal of Paleontology*, 58: 185–196.

Stencil, B., 2012. *Biofacies analysis of late Mississippian ostracodes and their use as paleoenvironmental indicators in the Bluefield Formation, Mercer County, West Virginia*. Unpublished MSc. Thesis, Faculty of Mississippi State University, Mississippi, 155 pp.

Taylor, P. D. & Vinn, O., 2006. Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications. *Journal of the Geological Society, London*, 163: 225–228.

Taylor, P. D., Vinn, O. & Wilson, M. A., 2010. Evolution of biomineralisation in 'lophophorates'. *Special Papers in Palaeontology*, 84: 317–333.

Tibert, N. E. & Dewey, C. P., 2006. *Velatomorpha*, a new healdioidean ostracode genus from the Early Pennsylvanian Joggins Formation, Nova Scotia, Canada. *Micropaleontology*, 52: 51–66.

Trueman, A. E., 1942. Supposed commensalism of Carboniferous spirorbids and certain non-marine lamellibranchs. *Geological Magazine*, 79: 312–320.

Vance, T., 2007. *Marine paleoecology of the Eads Mill Member, Hinton Formation, Upper Mississippian, West Virginia and Virginia*. Unpublished MSc. Thesis, West Virginia University, Morgantown, 80 pp.

Vinn, O., 2006. Two new microconchid (Tentaculita Boucek 1964) genera from the Early Palaeozoic of Baltoscandia and England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2: 89–100.

Vinn, O., 2009. Attempted predation on Early Paleozoic cornulitids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273: 87–91.

Vinn, O., 2010. Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292: 211–221.

Vinn, O. & Mutvei, H., 2009. Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences*, 58: 286–296.

Vinn, O. & Taylor, P. D., 2007. Microconchid tubeworms from the Jurassic of England and France. *Acta Palaeontologica Polonica*, 52: 391–399.

Weedon, M. J., 1990. Shell structure and affinity of vermiform 'gastropods'. *Lethaia*, 23: 297–309.

Weedon, M. J., 1991. Microstructure and affinity of the enigmatic Devonian tubular fossils *Trypanopora*. *Lethaia*, 24: 223–227.

Whitfield, R. P., 1882. On the fauna of the Lower Carboniferous limestones of Spergen Hill, Ind., with a revision of the descriptions of its fossils hitherto published, and illustrations of the species from the original type series. *Bulletin of the American Museum of Natural History*, 1: 1–97.

Williams, M., Stephenson, M., Wilkinson, I. P., Leng, M. J. & Miller, C. G., 2005. Early Carboniferous (Late Tournaisian – Early Viséan) ostracods from the Ballagan Formation, central Scotland, UK. *Journal of Micropalaeontology*, 24: 77–94.

Wilson, M. A., Vinn O. & Yancey, T. E., 2011. A new microconchid tubeworm from the Lower Permian (Artinskian) of central Texas, U.S.A. *Acta Palaeontologica Polonica*, 56: 785–791.

Wright V. P. & Wright, E. V. G., 1981. The palaeoecology of some algal-gastropod bioherms in the Lower Carboniferous of South Wales. *Neues Jahrbuch für Geologie und Paläontologie, Monatschefte*, 9: 546–558.

Zatoń, M. & Borszcz, T., 2013. Encrustation patterns on post-extinction early Famennian (Late Devonian) brachiopods from Russia. *Historical Biology*, 25: 1–12.

Zatoń, M. & Krawczyński, W., 2011a. Microconchid tubeworms across the upper Frasnian – lower Famennian interval in the Central Devonian Field, Russia. *Palaeontology*, 54: 1455–1473.

Zatoń, M. & Krawczyński, W., 2011b. New Devonian microconchids (Tentaculita) from the Holy Cross Mountains, Poland. *Journal of Paleontology*, 85: 757–769.

Zatoń, M. & Mazurek, D., 2011. Microconchids–a little known group of fossil organisms and their occurrence in the Upper Carboniferous of the Upper Silesia. *Przegląd Geologiczny*, 59: 157–162. [In Polish, English summary].

Zatoń, M., Taylor, P. D. & Vinn, O., 2013. Early Triassic (Spathian) post-extinction microconchids from western Pangea. *Journal of Paleontology*, 87: 159–165.

Zatoń, M. & Vinn, O., 2011. Microconchids and the rise of modern encrusting communities. *Lethaia*, 44: 5–7.

Zatoń, M., Vinn, O. & Tomescu, A. M. F., 2012a. Invasion of freshwater and variable marginal marine habitats by microconchid tubeworms – an evolutionary perspective. *Geobios*, 45: 603–610.

Zatoń, M., Wilson, M. A. & Vinn, O., 2012b. Redescription and neotype designation of the Middle Devonian microconchid (Tentaculita) species '*Spirorbis*' *angulatus* Hall, 1861. *Journal of Paleontology*, 86: 417–424.