Tube microstructure of Recent and Jurassic serpulid polychaetes and the question of the Palaeozoic 'spirorbids'

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Weedon, M.J. 1994. Tube microstructure of Recent and Jurassic serpulid polychaetes and the question of the Palaeozoic 'spirorbids'. Acta Palaeontologica Polonica $\mathbf{39}$, 1, 1–15.

'Ordered' and 'unordered chevron structures' in serpulid tubes comprise minute calcite lath-like crystals. In ordered chevron structure (*Pomatoceros triqueter*) the crystals parallel each other within each chevron layer, whilst between layers the alignment direction alternates. The laths have no alignment in unordered chevron structure (*Spirorbis* and locally in *Pomatoceros triqueter*). In 'homogeneous chevron structure' (found in Jurassic pomatocerids) the layers comprise a granular or homogeneous fabric. This structure possibly represents a diagenetic replacement of lath-like crystals. Serpulid chevron structures are quite dissimilar from any shell microstructures described in molluscs or lophophorates. The secretion of microstructures comprising lath-like crystals may have allowed rapid tube growth. Spherulitic prismatic structure is identified in *Spirorbis*; the structure occurs locally in the outer part of the tube. The microstructure of Recent spirorbids is quite dissimilar to that of Palaeozoic fossils (microconchids) previously assigned to the genus *Spirorbis*.

Key words: serpulids, microstructure, biomineralization, ordered chevron structure, unordered chevron structure, homogeneous chevron structure, spherulitic prismatic structure.

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Introduction

In contrast to the vast proliferation of papers concerning the microstructure of molluscs and some other invertebrate groups, serpulid worm tube microstructure and biomineralization has been all but ignored until very recently. This may be due to the lack of a calcareous tube in the majority of polychaete taxa and hence the lack of taxonomic interest in this feature

for neontologists. The surfeit of soft part characters of Recent polychaetes has meant that there has been little perceived need to study tubes. Additionally the nature of the tube as a housing place for the worm rather than as an integral part of the organism (molluscs and brachiopods) may have contributed to the dearth of research in this field. A general belief (based on studies carried out before SEM was available) that serpulids showed very little variation in microstructure has persisted. Frustratingly, new information on serpulid microstructure is often recorded merely as a footnote to studies by neontologists, physiologists and biochemists (e.g. Bubel *et al.* 1983; Gaill & Hunt 1988). Studies of Recent serpulid tubes have also been undertaken as a minor part of comparative studies with non-serpulid fossils, e.g. Pomatoceros triqueter Linné 1758, compared to 'vermiform gastropods' (microconchids of Weedon 1991a) by Burchette & Riding (1977) and Ditrupa compared to Hyolithes kingi Richter & Richter 1941 by Bandel (1986). Simplistic models of secretion and skeletal growth have been based around experiments concerning a restricted range of taxa and on very limited microstructural and ultrastructural knowledge. More detailed studies of note include those of Neff [1969: Hydroides brachyacantha Rioja and Eupomatus dianthus (Verrill); 1971: Pomatoceros caeruleus (Schmarda)], Nott & Parkes [1975: Spirorbis spirorbis (Linné 1758)], Lommerzheim (1979), Clark (1976: aspects of secretion and calcification), Bubel et al. [1983: Pomatoceros lamarckii (Quatrefages 1865)], ten Hove & Zibrowius [1986: Laminatubus alvini ten Hove & Zibrowius 1986, Protis hydrothermica ten Hove & Zibrowius 1986, Placostegus tridentatus (Fabricius 1779)], Zibrowius & ten Hove [1987: Neovermilia falcigera (Roule 1898), Neovermilia sphaeropomata (Benham 1927), Ditrupa arietina (Müller 1776), Ditrupa strangulata (Deshayes 1825)] and ten Hove & Smith (1990: Ditrupa gracillima Grube 1878). SEM studies of some of these fossil and Recent serpulid taxa have revealed a much greater diversity of microstructural types than was previously recorded. New microstructures quite unlike the familiar molluscan structures have been discovered that demand fresh attention (e.g. Bubel et al. 1983; Bandel 1986; ten Hove & Zibrowius 1986: Zibrowius & ten Hove 1987: ten Hove & Smith 1990). Importantly these workers record differences in microstructures between some supraspecific taxa. The wide range of structures cannot wholly be explained by current knowledge of secretion based on a limited spread of species. It is no longer tenable to dismiss serpulid structures as '...invariably simple ... derived from a granular secretion that is compacted and moulded into a sleeve encasing the body' (Simkiss & Wilbur 1989: p. 190). An extensive and comprehensive survey of biomineralization and microstructure in Recent and fossil serpulids, using modern techniques, is long overdue.

This paper reports the findings of the initial part of a broader microstructural examination of the tubes of fossil and Recent serpulid taxa. It is hoped that the results will broaden the knowledge of microstructural patterns and help elucidate processes of biomineralization in serpulids.



Fig. 1. \Box A–C, E–F. SEM photomicrographs of the microstructure of Recent *Pomatoceros triqueter* Linné 1758; BRSUG 24201a. A. Longitudinal section through tube, showing chevron lamellae of the ordered chevron structure (anterior to bottom right); × 195. B. Detail of chevron lamellae of A; × 325. C. Detail of lamellae in A and B, showing alternating orientation of imbricated, parallel-aligned crystals; × 1600. E. Detail of lath-like crystals in C; × 3375. F. High magnification of parallel-aligned crystals; × 8500. \Box D. Crossed lamellar structure in gastropod *Vermetus* sp., demonstrating similarity with ordered chevron structure. BRSUG 24173. Note alternating direction of growth of crystals between alternate lamellae; × 1300. All specimens are polished and etched (technique 2).

The paper presents the results of SEM and XRD examination of the tubes of the following taxa: Recent *Pomatoceros triqueter* Linné 1758, Jurassic pomatocerids, *Spirorbis* cf. *rupestris* Gee & Knight-Jones 1962, and *Spiror*- *bis* sp. (both Recent). The taxa are representative of the families Serpulidae Burmeister 1837 and Spirorbidae Pillai 1970 with the familiar chevron tube structure of which the most satisfactory models of secretion have been applied.

Material and methods

Material was obtained from field localities and museum collections. All material is currently housed in the Department of Geology, University of Bristol. Locality information is given under the sections dealing with each genus. Specimens were prepared for SEM in two ways: (1) fractured surfaces, prepared by simple breakage before mounting on stubs, (2) specimens were embedded in epoxy resin, which was allowed to set very hard before cutting, grinding and polishing to 1 μ m carborundum powder. The polished tubes were then etched using 2% EDTA solution for 4–5 minutes, or in 1.5% HCl for 5 seconds.

The fractured surfaces show the microstructure unaltered by etching, but owing to irregularities in the fracture, lamellae and original orientations of crystals may be obscured or altered. Etching polished surfaces enhances detail such as lamellae, but some fine microstructural detail may also be obscured by the process. For each taxon, material was assessed to determine which preparation method produced the most informative results. Preparation details for each sample are specified in the sections dealing with each taxon. All specimens were sputter-coated with gold-palladium and viewed using a Cambridge 250 Mk 3 Scanning Electron Microscope. X-ray diffraction was carried out on representative examples of each species in order to determine the mineral content of the tubes. SEM stubs containing multiple specimens illustrated are listed under each section. Additional material of all taxa studied is also stored in the Museum of the Department of Geology, University of Bristol.

Tube microstructure of Recent Pomatoceros triqueter

lllustrated material: BRSUG 24201–24204 [SEM stubs]. Specimens of *P. triqueter* tubes were collected from coastal rocks near Weymouth, southern England. SEM studies were made using both fractured surfaces and etched polished surfaces (HCl and EDTA; i.e. techniques 1 and 2). The latter technique yielded the most useful information.

This species is typical of the family Serpulidae (e.g. ten Hove 1979). The tubes appear as non-shiny, white, tapering, attached tubes, roughly triangular in transverse section, and with a pronounced dorsal keel.

P. triqueter has a principal layer of 'ordered chevron structure' (= 'Parabelschichten' structure of Schmidt 1955, and see description below), with subsidiary 'unordered chevron structure' (see *Spirorbis* below) toward the outer margin of the tube.



Fig. 2. Microstructure of *Pomatoceros triqueter* Linné 1758. $\Box A$. Block diagram of tube microstructure: upper surface is parallel to wall outer surface, left hand surface is a transverse section and right hand surface is a longitudinal section through ordered chevron structure; × 100. $\Box B$. Detail of ordered chevron structure representing area of box in A; × 2500. $\Box C$. Alternating crystal directions in alternate lamellae; × 5000.

Ordered chevron structure

Description. — This structure consists of convex forward lamellae or chevrons. These lamellae are laid down successively from the anterior (apertural end) of the tube, being sub-parallel to the surface of the tube only near the inner and outer surfaces, and curving round as a convexforward layer, wrapping the aperture of the tube (Figs 1A–B, 2).

The chevrons are not simple laminar layers, but rather comprise a fabric of discrete lath-like crystals. These crystals are very small, long, euhedral prisms of calcite (confirmed by XRD), aligned parallel to each other and imbricated obliquely to the direction of the edge of the principal layer (Figs 1C, E–F, 2B–C). Crystals are uniform in size at about 0.25 μ m width and 2 μ m long. The banded effect of consecutive lamellae is the result of the alternation of the growth directions of the lath-like crystals. The angle between parallel long axes of crystals in alternate chevron lamellae is up to 90° (Fig. 1C, E–F). The combination of aligned lath-like crystals and lamellae make up the ordered chevron structural layer.

Discussion. — At high magnifications, the alternating bands of parallelaligned crystals of calcite are very reminiscent of crossed lamellar structures, common in molluscs (Fig. 1D). Crossed lamellar microstructures consist of very similar long thin prismatic crystals, differing from the serpulid structure in the pattern of banding of the lamellae. This similarity between microstructural types reflects the relatively simple process involved in the manufacture of a layer comprising many small, easily secreted microcrystals. TEM studies of sectioned secretory organs have shown the development and increasing calcification (replacing organic matrix) of secretory granules of roughly rhombic section, within the calcium-secreting gland of the congeneric *Pomatoceros caeruleus* (Neff 1971). These granules correspond well in size and shape with the lath-like crystals of the *P. triqueter* tube.

The nature of the calcareous annelid tube is distinct from the molluscan shell in the 'separation' of the worm from its tube. The tube provides a protective dwelling-place for the animal rather than an integral skeletal part of the animal itself. The skeletons of molluscs, brachiopods and bryozoans are epithelial secretions with a mineralized component locally succeeding the formation of an organic cuticle or periostracum. Detailed processes of tube secretion in serpulids are not well known: the tubes of Pomatoceros trigueter and P. caeruleus are secreted beneath the anterior collar by calcium-secreting glands and the epithelium of the ventral shield (e.g. Neff 1971). The tube forming material is secreted as a viscous white fluid or paste of acid mucopolysaccharide bearing microcrystals of calcite in suspension. This slurry is then shaped by the collar as it solidifies (e.g. Hedley 1958; Neff 1971). This type of secretion, where the calcareous paste is in effect plastered onto the tube, may explain the shape of the chevron layers which are laid down by the worm over previous layers at the tube aperture. The banding is perhaps the result of moulding of the calcitesaturated mucus in forward and backward applications (see Hedley 1958). The alternation in the direction of the crystal long axes provides strength to the tube, like successive plywood layers of alternating grain direction. With the relative ease of production of small simple lath-like crystals, the tube is secreted quickly and efficiently to produce a robust microstructural laver.

Chevron lamellae have been recorded in serpulids (e.g. Wrigley 1950; Hedley 1958, Schmidt 1951; Burchette & Riding 1977), but the fine crystalline microstructural component of the layers has hitherto been all but ignored. Ordered chevron structure, despite its superficial resemblance to crossed lamellar structure, is unique to serpulids. Bubel *et al.* (1983) described the tube of *Pomatoceros lamarckii* as comprising small (c. 0.4m wide) prismatic crystals of calcite in an orderly arrangement parallel

Fig. 3. SEM photomicrographs of the unordered chevron and spherulitic prismatic microstructures of *Spirorbis* cf. *rupestris* Gee & Knight-Jones 1962. BRSUG 24216c. Material prepared by combination of techniques 1 and 2. \Box A. Axial section through tube, attached to vermetid shell; × 28. \Box B. Longitudinal section through tube showing chevron lamellae; × 400. \Box C. Detail of lamellae showing unordered crystals; × 1475. \Box D. Detail of outer part of tube showing unordered crystals; × 1600. \Box E. Spherulitic prismatic structure in outer part of tube (arrowed) × 800. \Box F. Detail of unordered crystals in D; × 4000. \Box G. Detail of spherulitic prismatic structure (arrow points to same place as arrow in E); × 3000. \Box H. Detail of spherulitic prismatic structure, showing fine acicular crystals; × 7500.



to one another and to the tube surfaces. This is in contrast to the chevron layering in *P. triqueter* described here. However, it is probable that Bubel *et al.* (1983) in using small tube fragments, only observed the very outer and inner portions of the tube where chevron layers tend to parallel the tube walls.

Tube microstructure of Spirorbis cf. rupestris and Spirorbis sp.

Illustrated material: BRSUG 24210–24216 [SEM stubs]. Specimens of Recent *Spirorbis* cf. *rupestris* were collected from shoreline rocks of the foreshore at Dunbar, Scotland. Specimens of a *Spirorbis* sp. attached to a vermetid from Victoria, Australia were donated by the BM(NH). SEM studies were made using both fractured surfaces and etched polished surfaces (HCI and EDTA; i.e. techniques 1 and 2).

These serpulids are coiled anticlockwise (viewed from above), white, flat-lying spiral tubes with transverse ribbing ornament, and are typical members of the Spirorbidae.

The tube of *Spirorbis* (Figs 3–4) contains two calcitic microstructural units: 'unordered chevron structure' and 'spherulitic prismatic structure'. These microstructures have not previously been recorded. The tube is calcitic as confirmed by XRD.

Unordered chevron structure

Description. — The bulk of chevron layers in the tube of *Spirorbis* comprise a structure which is here termed 'unordered chevron structure' (Figs 3–4). Unordered chevron structure has chevron shaped lamellae very similar to those of ordered chevron structure. However, the banding is less well defined, and marked by breaks in secretion, rather than by contrasting crystalline long axes directions. The structure also differs from ordered chevron structure in that the individual lamellae comprise seemingly randomly-arranged lath-like crystals. Locally the banding between chevrons is indistinguishable and the microstructure becomes a mass of randomly-oriented lath-like crystals. These crystals differ from those of ordered chevron structure only in their orientation.

Discussion. — Unordered chevron structure is the dominant component of *Spirorbis* microstructure. This structure also occurs locally in the outer part of the shell of *Pomatoceros triqueter* (see above). Structures comprising similar prismatic crystals, arranged with little or no directional fabric, have been recorded in other Recent serpulid taxa. Such structures include the inner layers of *Laminatubus alvini*, *Protis hydrothermica* (ten Hove & Zibrowius 1986), and *Ditrupa arietina* (Bandel 1986; Zibrowius & ten Hove 1987) and *D. gracillima* (ten Hove & Smith 1990). In the latter two taxa the prismatic crystals are sub-parallel to the outer surface of the tube (Zibrowius & ten Hove 1987; ten Hove & Smith 1990), although none of these structures are associated with chevron structure.



Fig. 4. Microstructure of Recent *Spirorbis* cf. *rupestris* Gee & Knight-Jones 1962. $\Box A$. Block diagram of tube microstructure: upper surface is parallel to wall outer surface (with spherulitic prismatic structure), left hand surface is a transverse section and right hand surface is a longitudinal section through unordered chevron structure; × 100. $\Box B$. Detail of unordered chevron structure representing area of box in A; × 250. $\Box C$. Unordered crystal directions in unordered chevron structure; × 5000.

Spherulitic prismatic structure

Description. — This microstructure is locally distributed in the *Spirorbis* tube (Fig. 3E). It consists of spherulitic prisms with more or less straight boundaries, comprising fine acicular crystals radiating from the outer edge of the structure which are truncated by prism boundaries (Fig. 3E, G–H). The crystals are about 0.2µm in thickness and >10µm long, and form in parallel clusters which diverge as spherulites. A continuous accretionary lamination passes through the prism boundaries; individual laminae are <10 µm thick (Fig. 3E, G–H).

Discussion. — The constituent fibrous crystallites are considerably finer and longer than the corresponding crystals of the chevron structures. They are also more complex in construction, and have a less uniform appearance. Each crystallite is made of many parallel, constituent needlelike fibres (Fig. 3H). The local difference in microstructure may be a response to differing environmental conditions or may reflect a different method or source of secretion by the worm. The microstructure appears mainly as an infilling 'cement' between the main bulk of the tube and the attachment substrate, or between successive whorls of the tube. It always occurs on the outer margins of the tube. This material is secreted on the outside of the tube after the main tube has been created by the chevron pasting secretion. The specific cementing or peripheral shell-strengthening function (or response to damage) presumably requires a different, perhaps more flexible, adhesive, rapidly secreted microstructure.

The secretion mechanism for production of spherulitic prismatic structure in Spirorbis is unknown, and requires further investigation, but is beyond the scope of this study. The spherulitic prismatic microstructure reported here in Spirorbis has not previously been recorded in annelid tubes. Regular and irregular spherulitic prismatic microstructure has, however, been recorded in molluscs and bryozoans (Erben et al. 1968; Taylor et al. 1969; Sandberg 1977, 1983; Carter 1990). Regular spherulitic prismatic microstructure occurs in the monoplacophoran Neopilina galathea Lemche 1957 (Erben et al. 1968). Irregular spherulitic prismatic microstructure, with less well-defined prism boundaries and interdigitating conical prisms, occurs in aragonite in the outer layer of Nautilus and in the outer layer of many lucinacean bivalves (Carter & Clark 1985; Carter 1990), and locally as calcite in the outer layer of Mytilus (the 'flabellate' structure of Oberling 1964). Spherulitic structure occurs as an effectively inorganic cementing structure in oysters, apparently by the leaking of extrapallial fluids through the periostracum (Harper 1991). A similar structure with flattened conical prisms occurs in certain bryozoans, where the structure has been termed 'planar spherulitic structure' (Sandberg 1977, 1983). It also occurs in certain aragonitic and calcitic corals (Carter & Clark 1985).

Tube microstructure of Jurassic pomatocerids

Illustrated material: BRSUG 24221–24223 [SEM stubs]. Specimens of a pomatocerid species from the Jurassic of Villers-sur-mers, France were made available from the collections of the British Museum (Natural History) [BM(NH)]. SEM studies were made using etched polished surfaces (HCl and EDTA; i.e. preparation technique 2).

The fossils closely resemble a large Recent *Pomatoceros* cf. *triqueter* and are found attached to fossil oysters. The tubes comprise a single microstructural type, here termed 'homogeneous chevron structure'. The fossils were selected for study owing to their similarity to Recent *Pomatoceros*, in order to assess possible diagenetic alteration in the Jurassic specimens.

Homogeneous chevron structure

Description. — The tubes of the Jurassic pomatocerids studied have a chevron structure which at low magnifications is apparently identical to that of *Pomatoceros triqueter* (compare Fig. 1A and Fig. 5A). However, higher magnifications reveal the absence of the prismatic crystals of ordered or unordered chevron structures. Instead, the fabric comprises homogeneous or granular (*sensu* Carter 1980) calcite crystals (Fig. 5B).



Fig. 5. SEM photomicrographs of the homogeneous chevron structures of Jurassic pomatocerids. BRSUG 24222b. Material prepared by technique 2. $\Box A$. Longitudinal section through tube showing chevron lamellae; × 60. $\Box B$. Detail of lamellae showing homogeneous structure; × 1500.

Subtle size differences or packing of the calcite 'grains' emphasise the banding of the chevrons.

Discussion. — The homogeneous or granular structure may be derived from the neomorphic diagenetic alteration of an original lath-like crystalline fabric akin to that in ordered and unordered chevron structures. Zibrowius & ten Hove (1987) in their description of the tube microstructure of Recent Ditrupa arietina and Eocene D. strangulata found a granular inner layer for both taxa (Zibrowius & ten Hove 1987). However their illustrations of this layer in the respective taxa show crude alignment of lath-like prismatic crystals in the Recent Ditrupa arietina (Zibrowius & ten Hove 1987, fig. 3B) and a granular or homogeneous fabric in the fossil D. strangulata (Zibrowius & ten Hove 1987, Fig. 3E). This suggests a possible diagenetic alteration in the fossil Ditrupa from lath-like prisms to the granular fabric. A similar change has presumably occurred in the fossil pomatocerids. The presence of a homogeneous microstructure as a neomorphic fabric has implications for the interpretation of a number of serpulids and indeed molluscs which apparently have homogeneous or granular microstructures.

Discussion and conclusions

Four distinct microstructural types have been recognised in the taxa examined during this brief study:

- (1) Chevron structures:
 - (a) ordered chevron structure,
 - (b) unordered chevron structure,
 - (c) homogeneous chevron structure.
- (2) Spherulitic prismatic structure.

Previous workers have described chevron structures in serpulids, but have not described the detailed compositional fabric which is here used to distinguish the varieties of this microstructure. Spherulitic prismatic structure (*Spirorbis*) is here described for the first time in serpulids. The validity of homogeneous or granular structure as a genuine microstructural type rather than a diagenetic artefact is debatable. Comparison with the homogeneous structure with an overprint of chevron structure occurring in Jurassic pomatocerids most probably represents a neomorphic replacement of ordered or unordered chevron structure.

It is important to note that the chevron microstructures described here are fundamentally distinct from any known structures of molluscs and lophophorates. All shell microstructures which occur in brachiopods and bryozoans have been recorded in molluscs. Aragonitic nacres are the only structures unique to molluscs (Carter 1979, 1990; Carter & Clark 1985). The similarity and identity of molluscan and lophophorate microstructures is controlled by the nature of shell secretion and the physical constraints of aragonite/calcite crystal growth within a certain organic framework. The fundamental difference between tube secretion in serpulids and epithelial shell secretion in molluscs and lophophorates may account for the fundamental dissimilarity of most of the microstructural types. The development of distinct tube microstructures in serpulids may be controlled by the different functional and biomechanical requirements of the taxa. Many of the microstructures described are composed of very small, lath-like, prismatic crystals. This crystal form appears as the basic 'building block' of a variety of serpulid structures (e.g. see Bandel 1986; ten Hove & Zibrowius 1986; Zibrowius & ten Hove 1987; ten Hove & Smith 1990; Weedon 1991b). Secretion of small crystals in a mucus paste is a rapid and simple way of producing a calcareous tube, allowing the growth of up to 1cm/week recorded in some serpulids (e.g. ten Hove 1979). Such a system is presumably employed in the chevron-dominated tubes of Pomatoceros and Spirorbis. Both genera have tubes which are attached to the substrate for almost their entire length. Serpulids have a specialised organs of secretion through which mucus-bound calcite/aragonite crystals can be pasted to the growing tube (Neff 1971; Dixon 1980). The presence of such organs has led to the formulation of secretion models for chevron structures (e.g. Hedley 1958). Clearly the pasting models are not wholly satisfactory in explaining the production of the full range of serpulid microstructures, and completely new models are required to explain the secretion of structures such as the prismatic structures of Ditrupa (ten Hove & Smith 1990) and the spherulitic prismatic microstructure of Spirorbis. However formulation of new secretory models is beyond the scope of this project.

Comparison with Palaeozoic 'spirorbids'

The chevron microstructure of Recent *Spirorbis* described here is completely dissimilar in fabric from the microstructure of Palaeozoic 'spiror-

bids' which are seemingly identical in external appearance (Burchette & Riding 1977; Weedon 1990, 1991b). The confusion was compounded by very early attempts to determine the microstructure using optical microscopy (Dawson 1868). These 'spirorbiform' fossils, which have recently been assigned to the order Microconchida Weedon 1991 of the class Tentaculita Bouček 1964 (Weedon 1991a), have been demonstrated to possess a punctate micro-lamellar calcitic structure identical to the irregular crossed bladed structure which occurs in thick walled tentaculitids, brachiopods and bryozoans and perhaps certain bivalves (Burchette & Riding 1977; Towe 1978; Carter 1979; Larsson 1979; Sandberg 1983; Weedon 1990, 1991a, b). Certain microconchid taxa possess an outer blocky prismatic layer, though when present this structure is not locally distributed as is the spherulitic prismatic structure of Recent Spirorbis (Burchette & Riding 1977; Weedon 1990, 1991b). Spherulitic prismatic structures also occur locally in the outer part of the shell of the coiled Devonian tentaculitoid Trypanopora (order Trypanoporida Weedon 1991). although this may be a diagenetic fabric (Weedon 1991a).

Acknowledgements

I am very grateful to D.E.G. Briggs, V.P. Wright and P.D. Taylor for discussion and critical comments. The work was funded by a University of Bristol Tratman Scholarship.

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Streszczenie

Mikrostruktura kalcytowych rurek wieloszczetów z rodziny Serpulidae jest zupełnie odmienna od mikrostruktur występujących w muszlach mięczaków i ramienionogów, czy też w zooeciach mszywiołów. Nie jest również podobna do struktury ścianek paleozoicznych skamieniałości tradycyjnie uważanych za rurki wieloszczetów *Spirorbis*. W poprzednich pracach autora zostało wykazane, że paleozoiczne spirorbidy miały mikrostrukturę identyczną jak grubościenne tentakulity, ramienionogi i mszywioły. Na tej podstawie reaktywowana została nazwa rodzajowa *Microcornus*, użyta niegdyś do tych skamieniałości, i utworzony został rząd Microconchida, wraz z pokrewnym Trypanoporida włączony do gromady Tentaculita.