Microscopic evidence of serpulid affinities of the problematic fossil tube ‘Serpula’ etalensis from the Lower Jurassic of Germany

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‘Serpula’ etalensis (Piette, 1856) is a carbonatic tubicolous fossil of probable serpulid affinities, found in the Lower Jurassic of France, Germany and England (M. Jäger, personal observation). It differs from typical serpulid tubes in terms of its regularly spaced peristomes and free unattached tube (Fig. 1A), which may have been attached to a substrate during the juvenile stage. These well-developed, closely spaced regular peristomes were probably an adaptation to the life on the surface of soft sediment, acting as anchors (Jäger 1996).

The unattached tube of ‘Serpula’ etalensis somewhat resembles scaphopods and, more closely, heteromorphic ammonites (Piette 1856). Quenstedt (1856) described a similar although somewhat different species as a tentaculitid-like problematic fossil from the Jurassic of Germany. There are presumably several closely related species described under the name of ‘Serpula’ etalensis in the Lower Jurassic and the whole group needs a systematic revision (M. Jäger, personal observation).

In the Triassic Period, majority of worm tubes revealed to belong to the microconchids (Taylor & Vinn 2006; O. Vinn personal observation). The Jurassic Period was a time of first major diversification of serpulid polychaetes (Parsch 1956) and one could expect a large variety of serpulid tube morphologies from that period. However, the morphologically convergent microconchids did not become extinct until the end of Middle Jurassic (Taylor & Vinn 2006; Vinn & Taylor 2007). Thus, serpulid affinities of Lower Jurassic worm tubes need a support from the data of tube structure and ultrastructure.

The aim of this paper is to verify the probable serpulid affinities of ‘Serpula’ etalensis through scanning electron microscope (SEM) observations of tube structure and ultrastructure. This paper also deals with mineralogy of the tube, focusing on the effects of diagenetic changes on the tube ultrastructure and original mineralogy.

Material and methods

The current research comprises the following fossil material: (1) ten tube fragments from the Upper Pliensbachian of eastern Germany, from borehole ‘Barth 5/64’ near the town of Stralsund, depth is 444.4–446.2 m, box no. 165, sample no. 51 (Fig. 1A, B, D, E); (2) ten tube fragments from the Upper Sinemurian of southwestern Germany, from a small pit situated at the lowest point of the ‘B27’ motorway between the towns of Hechingen and Bisingen, ca. 60 kilometres southwest of Stuttgart (Fig. 1C, F, G).

Examined tube fragments were ground in longitudinal and transverse direction in epoxy resin, polished and treated with a 1:1 mixture of 25% glutaraldehyde and 1% acetic acid, to which Alcian blue was added (Mutvei’s solution) for 20 min before SEM study.
Fig. 1. □A–F. 'Serpula' etalensis (Piette 1856). □A. Untreated fragment of the tube, Upper Pliensbachian, eastern Germany; TUG-1284-1. □B. Longitudinal section, showing growth lamellae (grl), Upper Pliensbachian, eastern Germany, TUG-1284-2. □C. Longitudinal section of the tube wall with evident growth lamellae (grl), Upper Sinemurian, southwestern Germany, TUG-1284-3. □D. Longitudinal section, irregularly oriented prismatic structure, Upper Pliensbachian, eastern Germany, TUG-1284-2. □E. Detailed view of (D), arrow points at the oriented substructure of long rod-like crystallites of the irregularly oriented prismatic structure. □F. Transverse section, homogeneous angular crystalline structure, Upper Sinemurian, southwestern Germany, TUG-1284-3. □G. Detailed view of (F), homogeneous angular crystalline structure. Institutional abbreviation: TUG, University of Tartu, Natural History Museum.
Serpulid affinities of the problematic fossil ‘Serpula’ etalensis (Schöne et al. 2005). To make comparisons, tubes of Recent serpulids Apomatus globifer and Ditrupa arietina were also compared under SEM with those of ‘Serpula’ etalensis (Figs 1G, 2A, B, C). They were previously ground in longitudinal direction in epoxy resin, polished and treated with 1% acetic acid for 2 min, then covered with gold. The serpulid species were selected and their tube ultrastructures were compared with those of ‘Serpula’ etalensis from 50 studied species (O. Vinn, unpublished database of serpulid tube ultrastructures).

All preparations were observed with a Hitachi S-4300 SEM at the Swedish Museum of Natural History, Stockholm. The beam was operated at 5–10 kV and 1 nA.

The mineral composition of ‘Serpula’ etalensis was studied by means of X-ray diffraction in powdered sample on a Dron-3 M diffractometer to distinguish the calcite or aragonite composition of tubes at the Institute of Geology, University of Tartu, Estonia.

Results

Tube structure

The tube is single layered (Fig. 1B, C). The growth lamellae are straight with outwards declined distal ends, as mostly evident at the peristomes, having a chevron-shaped habit, in the longitudinal section (Fig. 1B, C). In the internal part of the tube wall, growth lamellae are tilted outwards about 30 degrees from the tube’s internal wall. The distal ends of the growth lamellae are situated at about 90 degrees from tube’s internal wall.

Tube ultrastructure

The Upper Pliensbachiian specimens have an irregularly oriented prismatic structure (Fig. 1D, E). The irregularly oriented prismatic crystals forming the tube wall are 3–6 µm in length and 0.5–1.0 µm in diameter. They have an oriented substructure of long rod-like crystallites, which are 0.1–0.3 µm in diameter and 1.5–3.0 µm in length (Fig. 1E). The boundaries between first order crystals are sharp. The Upper Sinemurian specimens have a homogeneous angular crystalline structure. The diameter of individual crystals is about 100 µm, which is two orders of magnitude larger than in irregularly oriented prismatic structure of Upper Pliensbachiian specimens (Fig. 1F, G).

Tube mineralogy

X-ray diffraction analyses show pure calcitic composition for Upper Sinemurian specimens from
southwestern Germany, and pure aragonitic composition for younger specimens (Upper Pliensbachian specimens from eastern Germany).

Discussion

Preservation and mineralogy

The tube ultrastructure of Upper Pliensbachian specimens is supposed to represent the original tube mineralogy and ultrastructure of the species, because of the presence of growth lamellae, tube ultrastructure and mineralogy which are common in Recent serpulids (Vinn et al. in press). In Jurassic calcite seas, aragonitic invertebrate skeletons would have tended to dissolve (Palmer et al. 1988). However, preservation of skeletal aragonite is not uncommon in clay facies of Jurassic age, especially in the Lower Jurassic which was perhaps before the complete onset of calcite seas (Hall & Kennedy 1967). Aragonite is also commonly replaced by calcite in diagenesis, supporting the diagenetic origin of the tube’s mineralogy and ultrastructure in the Upper Sinemurian specimens (Fig. 1F, G).

‘Serpula’ etalensis represent the earliest record of aragonitic mineralogy for serpulids. The mineral composition of serpulid tubes has been reported to be either calcitic, aragonitic or a combination of both (Lowenstam 1954; Bornhold & Milliman 1973; Simkiss & Wilbur 1989; Vovelle et al. 1991). However, all Recent purely calcitic and dominantly calcitic serpulid species (Bornhold & Milliman 1973; Vinn et al. in press) form the terminal branch of the phylogenetic tree (Kupriyanova et al. 2006). On the contrary, dominantly aragonitic species are spread all over the phylogenetic tree. Moreover, the lack of calcitic or dominantly calcitic species in the basal part of the phylogenetic tree of serpulids indicates that aragonite is presumably the primitive biominaler for serpulids. There is no evidence of unequivocal serpulids from the Palaeozoic (ten Hove & van den Hurk 1993; Vinn & Mutvei 2005; Vinn 2006a, b; Taylor & Vinn 2006). Thus, the earliest serpulids presumably began to calcify in the aragonitic seas of the Triassic Period.

Molluscs

Aragonitic irregularly oriented prismatic ultrastructure occurs in molluscs too (Carter et al. 1990), but it is usually not forming the entire shell wall. Molluscs are lacking chevron-shaped growth lamellae characteristic to ‘Serpula’ etalensis. Ammonites have internal shell layer composed of mother of pearl. Such internal layer is absent in ‘Serpula’ etalensis (Mutvei 1972).

Thus, in aspect of tube structure, ‘Serpula’ etalensis could not be affiliated with molluscs.

Tentaculitoids

Tentaculitoids sensu lato comprise a number of phyletogenically related worm-like fossils from the Palaeozoic and early Mesozoic, which share characters of the tube structure and ultrastructure. Tentaculitoids include thick-walled tentaculitids (Larsson 1979), cornulitids (Vinn & Mutvei 2005), microconchids (Weedon 1991), trypanoporids (Weedon 1991), Tymbachoos (Vinn 2006b) and Anticypraea (Vinn & Isakar 2007). Their exact zoological affinities are unknown, but they most likely belong to the lophophorates (Taylor & Vinn 2006; Vinn & Isakar 2007). Free-living tentaculitoids are known from the Ordovician to Carboniferous (Niko 2000); substrate cemented microconchids have a range from the Ordovician to Middle Jurassic (Weedon 1991; Taylor & Vinn 2006; Vinn 2006a; Vinn & Taylor 2007). The external annulation of free-living tentaculitids (Larsson 1979) resembles peristomes of ‘Serpula’ etalensis. Tentaculitids can lack internal annulation and have a smooth tube lumen similar to ‘Serpula’ etalensis. However, free-living tentaculitids are not known from Mesozoic and substrate cemented tentaculitids have a laminar ultrastructure (Larsson 1979), different from that of ‘Serpula’ etalensis. Microconchids usually possess a smooth tube interior and their external annulaion can resemble peristomes in ‘Serpula’ etalensis. However, they differ in having a laminar shell structure with the punctae and spirally coiled tube (Weedon 1990; Taylor & Vinn 2006) (Fig. 2C). The irregularly oriented prismatic structure and aragonitic tube composition are not known in tentaculitoids (O. Vinn, personal observation). Thus, in aspect of tube structure and mineralogy, ‘Serpula’ etalensis could not belong to tentaculitoids.

Serpulids

The growth lamellae of recent serpulids are mostly chevron-shaped (Weedon 1994; O. Vinn, personal observation) similar to those of ‘Serpula’ etalensis. The irregularly oriented prismatic structure is most common Recent serpulid tube ultrastructure (Fig. 2A, D) and occurs in 60% of serpulid species (Vinn et al. in press). This structure is also common in fossil serpulids (Vinn 2007). Pure aragonitic tubes with irregularly oriented prismatic structure occur in Recent serpulids (Vinn et al. in press). Serpulids, with the exception of Spiraserpula (Pillai & ten Hove 1994), have a smooth tube’s lumen similar to that of ‘Serpula’ etalensis. Among Recent serpulids, unattached
tubes occur in Ditrupa (ten Hove & Smith 1990) and Serpula israelitica (Sanfilippo 2003). The tube of Ditrupa arietina is composed of two layers: outer oriented prismatic layer (Fig. 2A, B) and inner irregularly oriented prismatic layer (Fig. 2A). The ultrastructure of inner tube layer of Ditrupa arietina (Fig. 2A) resembles that of entire tube wall of Serpula etalensis. Single-layered tubes of Apomatus globifer (Fig. 2D) have similar ultrastructure to Serpula etalensis. Only regularity of peristomes in Serpula etalensis is not common in serpulids (Jaeger 1996). However, tube’s structure and ultrastructure of Serpula etalensis unequivocally support the serpulid affinities of that fossil.

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