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Authors: Kiel, Steffen, and Dando, Paul R.

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Chaetopterid tubes from vent and seep sites: Implications for fossil record and evolutionary history of vent and seep annelids

STEFFEN KIEL and PAUL R. DANDO



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Vestimentiferan tube worms living at deep-sea hydrothermal vents and cold seeps have been considered as a clade with a long and continuing evolutionary history in these ecosystems. Whereas the fossil record appears to support this view, molecular age estimates do not. The two main features that are used to identify vestimentiferan tubes in the fossil record are longitudinal ridges on the tube's surface and a tube wall constructed of multiple layers. It is shown here that chaetopterid tubes from modern vents and seeps—as well as a number of fossil tubes from shallow-water environments—also show these two features. This calls for a more cautious interpretation of tubular fossils from ancient vent and seep deposits. We suggest that: current estimates for a relatively young evolutionary age based on molecular clock methods may be more reliable than the inferences of ancient “vestimentiferans” based on putative fossils of these worms; not all of these putative fossils actually belong to this group; and that tubes from fossil seeps should be investigated for chitinous remains to substantiate claims of their potential siboglinid affinities.

Key words: Vestimentifera, Pogonophora, Siboglinidae, Chaetopteridae, tube worms, chemosynthetic ecosystems, hot vents, cold seeps.

Steffen Kiel [steffen.kiel@gmx.de], Institut für Geowissenschaften, Christian-Albrechts-Universität, Ludewig-Meyn-Str. 10, 24118 Kiel, Germany;

Paul R. Dando [pdando@mba.ac.uk], Marine Biological Association of the UK, Citadel Hill, Plymouth PL1 2PB, UK.

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Introduction

The evolutionary origin of the fauna at hydrothermal vents and cold seeps is a major question in deep-sea biology (Van Dover et al. 2002; Kiel and Little 2006). These ecosystems are inhabited by a suite of animals that rely on chemosynthetic bacterial symbionts for nutrition (Van Dover 2000). Due to their exceptional level of endemism at high taxonomic rank, it was suggested that these faunas have a long and continuing evolutionary history that ranges back into Palaeozoic times. One example of such a presumably ancient group are vestimentiferan tube worms (Newman 1985; Little 2002; Peckmann et al. 2005). However, morphological and molecular data show that Vestimentifera are not a vent and seep-obligate phylum but are annelids within the family Siboglinidae (McHugh 1997; Rousset et al. 2004), and molecular clock studies indicate that they have a quite recent origin (Black et al. 1997; Halanych et al. 1998).

The fossil record can potentially test these hypotheses because it provides direct evidence for the minimum geologic age of the animals in question. Although vents and seeps have an extensive fossil record (Campbell 2006), palaeontological and molecular data seem to provide contradicting results. Little and Vrijenhoek (2003) emphasised that molecu-

lar clocks indicate a Cainozoic origin for many vent and seep animals, whereas the fossil record suggests a Mesozoic or even Palaeozoic origin. In two out of their three examples (bathymodiolin mussels and vesicomid clams), however, the putative Mesozoic occurrences subsequently proved to be misidentifications (e.g., Amano and Kiel 2007; Amano et al. 2008; Kiel and Peckmann 2008). The confirmed oldest occurrences of these two bivalve groups are from the mid-Eocene and thus in relatively good agreement with the molecular age estimates (Kiel 2006; Amano and Kiel 2007). This calls for an evaluation of the criteria on which vestimentiferans have been identified in the fossil record.

The interpretation of tubes from fossil vent and seep deposits as vestimentiferans is generally based on two assumptions. First, longitudinal ridges on the surface of the tubes have been considered unique to vestimentiferans (Little et al. 2004). This argument has mainly been used for vent fossils because they often preserve delicate features of the tube's surface (Little et al. 1999, 2004). Second, the de-lamination of tube layers due to mineral deposition is regarded as specific to vestimentiferans (Peckmann et al. 2005), implying that layered tube walls are unique to this group. At cold seeps this layered structure facilitates growth of aragonite needles between the layers, resulting in a delaminated, calcified tube

that can also be recognised in petrographic thin sections of fossil specimens (Goedert et al. 2000; Peckmann et al. 2005; Haas et al. 2009). Early mineral precipitation within the layered tube facilitates its fossilisation also at vents (Maginn et al. 2002). Bacteria are likely to contribute to the mineralisation and de-lamination of the tube walls (Lechaire et al. 2002). The validity of these two assumptions is assessed here in the light of the tube structure of chaetopterid annelids from vents and seeps. In addition, the use of tube size and tube mass occurrences to infer vestimentiferan affinities of ancient tubes is evaluated.

Institutional abbreviation.—SMF, Senckenberg Museum, Frankfurt, Germany.

Material and methods

The chaetopterid from the Blake Ridge seep site was collected during *Alvin* dive 3712 (32°29.623' N, 76°11.467' W; 2155 m depth; cf., Van Dover et al. 2003). The tubes have length of at least 50 mm and have a maximum diameter of 2 mm. Chaetopterids from the Gulf of California were collected from a mud volcano during the *El Puma* WAG-01 cruise at 31°3.771' N, 114°5.189' W; 103 m depth. The tubes had a maximum length of at least 400 mm and diameters from 0.7–2.8 mm. Chaetopterids from the Mid-Atlantic Ridge vent site Ashadze were collected by the ROV *Victor 6000* during the SERPENTINE cruise on dive 311-2 (12°58.3530' N, 44°51.7835' W; 4085 m depth; cf. Fouquet et al. 2008). The tubes have a length of at least 200 mm and have a maximum diameter of 6 mm. Specimens of *Ridgeia* spp. from *Alvin* dive 3236 to vent sites at the Endeavour Ridge were available for comparison.

Specimens for SEM observations were cleaned in alcohol and in an ultrasound bath of distilled water. One specimen was embedded in resin to produce a polished longitudinal cross section of the tube. This specimen was carbon sputtered prior to examination on a LEO 1455VP scanning electron microscope with attached EDS detector, at the Geologisch-Paläontologisches Institut, Universität Hamburg. Cleaned and air dried specimens were mounted on stubs and gold sputtered for SEM work. The mineralogy of the brownish-red crust on the surface of tubes from the Ashadze vent site was analysed using powdered samples on a Siemens D5000 Bragg-Brentano diffractometer, at the Institut für Geowissenschaften, Universität Kiel.

Results and discussion

Chaetopterid tubes.—Chaetopterids secrete complex polysaccharide tubes (Berkeley 1922). Most chaetopterids live partly buried in the sediment in a, more or less, vertical tube that does not conspicuously taper, although some have a restricted anterior opening (Barnes 1965). A few species have U-, L-shaped or branched tubes, while the tubes of some spe-

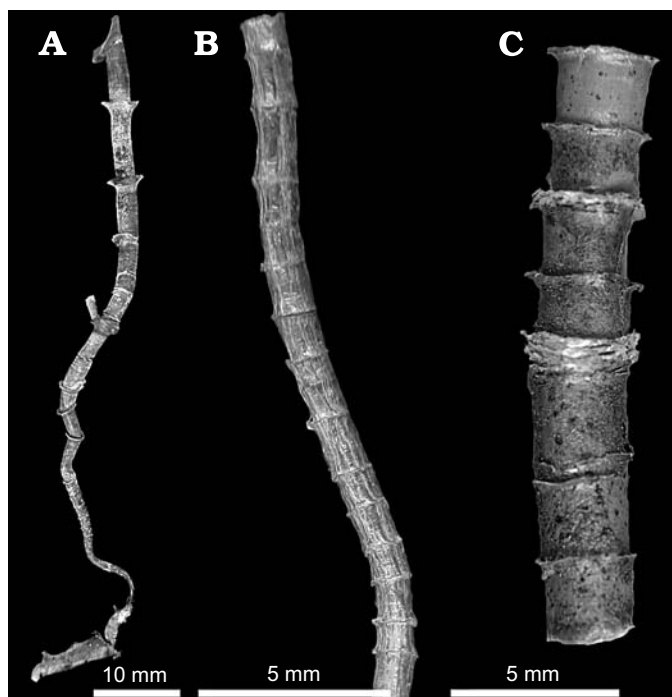


Fig. 1. Vestimentiferan and chaetopterid tubes from modern vents and seeps. A. *Ridgeia* sp. from a vent site on the Endeavour Ridge (SMF 18862). B. Chaetopterid tube from the Gulf of California (SMF 18863). C. Chaetopterid tube from the Ashadze vent site (SMF 18864).

cies lie mainly horizontally on the substratum (Barnes 1965; Sendall et al. 1995). The tubes have thickened annulae between secreted tube sections (Barnes 1965) that are flanged in some species (Fig. 1).

Dense aggregations of chaetopterid tubes have been found at vent sites on the Mid-Atlantic Ridge (Desbruyères et al. 2001, 2006; Fouquet et al. 2008) and the Lau Basin (Nishi and Rouse 2007), and around mud volcanoes in the Gulf of California, the Barbados Accretionary Prism (Olu et al. 1996), on the Blake Ridge Diapir (Van Dover et al. 2003), at cold seep sites in Sagami Bay, Japan (Nishi et al. 1999), and around whale-falls in Monterey Bay, California (Braby et al. 2007). They are also more common at cold seeps on the Californian margin than at equivalent non-seep sites (Levin et al. 2000). Chaetopterids probably thrive at vent and seep sites, given suitable substrate, because of the high bacterial biomass that they can collect for food by filtering water through the mucosal sacs they form in their tubes (Barnes 1965; Sendall et al. 1995). In addition, the flux of seawater through their tubes into the sediment would prevent their exposure to high sulphide concentrations. They are also able to reverse the water flow, thus preventing toxic fluids from entering the tube (Barnes 1965).

Longitudinal ridges on tubes from vents and seeps.—Chaetopterid tubes of two species from the Gulf of California have distinct longitudinal ridges on their surface. SEM images show that these ridges are the longitudinal edges of the individual sheets comprising the tube wall (Fig. 2A). They

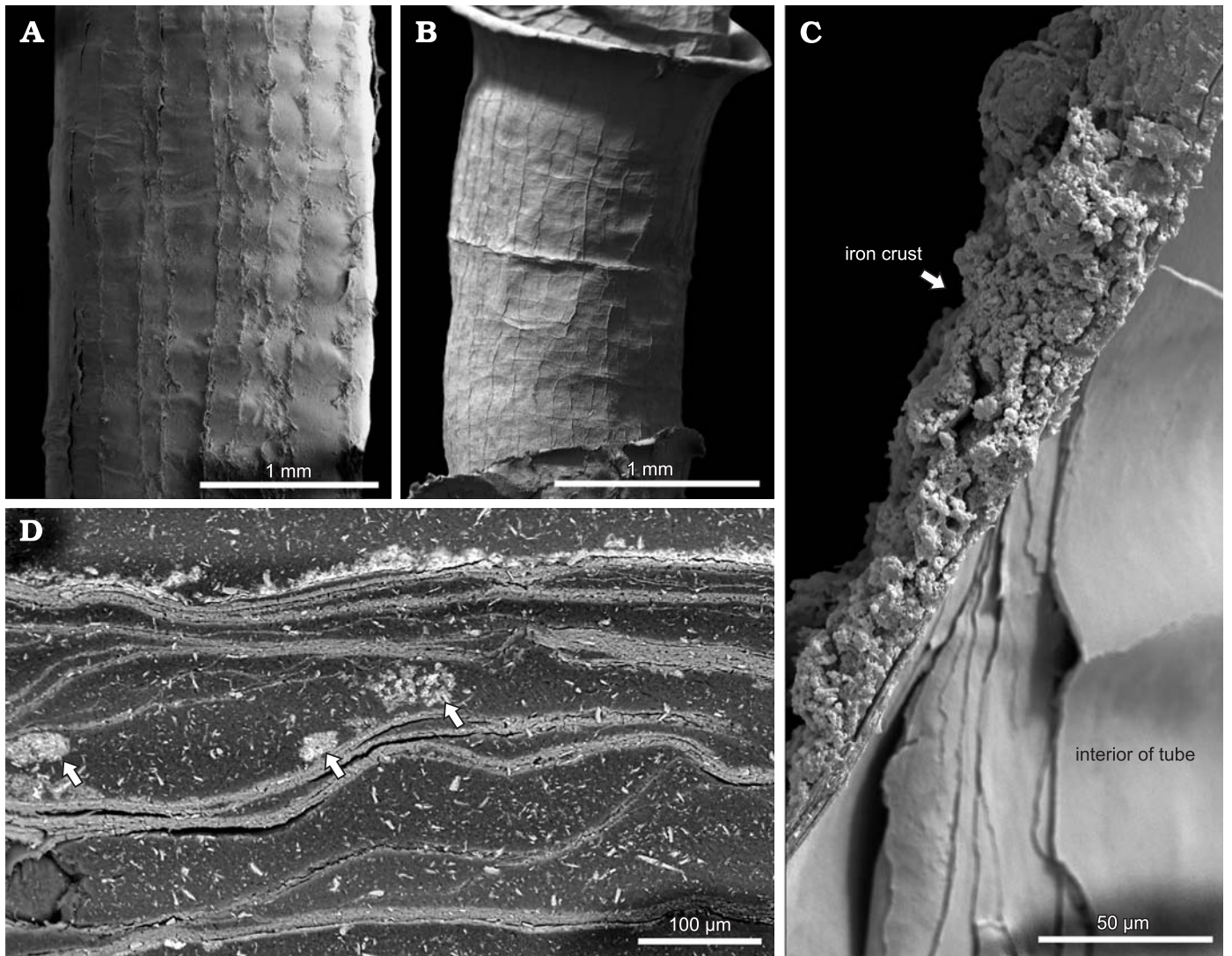


Fig. 2. Chaetopterid and vestimentiferan tubes from modern vents and seeps. **A.** Chaetopterid tube from the Gulf of California showing longitudinal ridges (SMF 18865). **B.** Tube of *Ridgeia* sp. for comparison (SMF 18866). **C.** Longitudinal fracture through the tube wall of a chaetopterid from the Ashadze vent site showing the iron crust on the surface and the layered structure of the tube wall (SMF 18867). **D.** SEM backscatter image of a longitudinal section of the tube wall showing iron-silica precipitates between the individual sheets of the tube wall; same specimen as in C.

are thus structurally identical with the longitudinal ridges on tubes of *Ridgeia* spp. and other Vestimentifera (Fig. 2B), although the edges appear to be smoother in vestimentiferan tubes, perhaps due to a difference in material. However, the edges have the widths of a few micrometers and it remains to be shown that this difference is discernable in vent fossils. This character is therefore insufficient to identify Vestimentifera in the fossil record. In addition, longitudinal ridges are absent or only confined to the anterior few centimetres of the tubes of many Vestimentifera, such as species of *Lamelli-brachia* (Webb 1969; Dando et al. 1992; Hughes and Crawford 2006) and in *Arcovestia ivanovi* (Southward and Galkin 1997). They are also absent from the tubes of most frenulate and moniliferan pogonophores in the Siboglinidae (Webb 1964; Flügel 1990), although some can have wrinkles on inner layers (Smirnov 2000). Similarly the tubes of many species of chaetopterids lack these ridges (Bhaud et al. 1994;

Bhaud and Petti 2001) while others have an outer tube layer of cemented sand grains (Barnes 1965). However, most of the chaetopterid species examined from vent and seep sites exhibit wavy longitudinal ridges on the outside of the tubes.

The preservation of delicate external features on tubes at fossil vents requires the early formation of a cast of the tube's surface. Maginn et al. (2002) emphasised the importance of the early mineralisation of the tube wall for its fossilisation. But the fact that also external features of the organic periostracum of molluscs are preserved in vent fossils (cf., Little et al. 1999) clearly shows that a cast of the surface is more important for preserving its external morphology than the mode of mineralisation of the surface itself. Chaetopterid tubes from the Ashadze vent site show the formation of such an early cast. They are covered by a thin, brownish-red crust that appears as a bright layer in SEM backscatter images (Fig. 2C, D). EDS analyses indicate that this crust is mainly

composed of iron and minor amounts of manganese, magnesium, and silica; XRD shows that the crust is amorphous rather than crystalline. Surface features of chaetopterid tubes have thus a high potential to become fossilised.

Tube wall structure.—All investigated chaetopterid tubes from the Mid-Atlantic ridge vents at Ashadze and from the Gulf of California mud volcano and the Blake Ridge seep are constructed of multiple sheets of cornified organic material. This is evident from SEM observations on dry, fractured tubes and on resin-embedded longitudinal sections of tubes (Fig. 2C, D). No carbonate precipitates have been observed between the individual sheets of the chaetopterid tubes from the Blake Ridge seep site. However, only few specimens were available for study.

Chaetopterids pump water through their tubes. Those with vertically-orientated tubes release the water into the sediment through the posterior end of the tube (Barnes 1965; Sendall et al. 1995), thus injecting sulphate into the sediment, like cold-seep vestimentiferans (Dattagupta et al. 2006). In methane seep situations chaetopterids should also stimulate anaerobic methane oxidation, carbonate precipitation and the de-lamination of the tube as described for vestimentiferan tubes from the Congo fan (Haas et al. 2009). Chaetopterid tubes from the Ashadze vent site show iron-silica precipitates between the individual sheets of the tube wall (Fig. 2D), providing further support for this suggestion. In methane-seep settings, mineralisation of chaetopterid tubes is more likely to occur than those of seep vestimentiferans, since the latter excrete protons into the sediment (Dattagupta et al. 2006) and this would inhibit precipitation of carbonates and other minerals.

Tube size and mode of occurrence.—Similarities in tube size, as well as the mass occurrence of such tubes, have been used to link tubes from fossil vents and seeps to modern Vestimentifera (Little et al. 1999; Peckmann et al. 2005). Chaetopterid tubes can have tube diameters up to several centimetres (Enders 1909) and some species, such as *Mesochaetopterus rickettsi*, can extend vertically for more than 2 m (MacGinitie and MacGinitie 1949). Thus vestimentiferan and chaetopterid tubes have very similar size ranges. The proposed Devonian seep vestimentiferan fossils (Peckmann et al. 2005) are also odd in that the tubes are described as not tapering, whereas all seep Vestimentifera have tapering tubes that narrow towards the posterior end (cf., Webb 1969) and need to do so because of their mode of nutrition (Dattagupta et al. 2006).

Ecological analogues suggest that the mass occurrence of tubes at ancient vents and seeps, resembling those of Vestimentifera at modern sites, are not conclusive evidence for the presence of Vestimentifera at the ancient vents. Various tube-dwelling annelids are known to form dense clusters, given that enough food is available, including chaetopterids, serpulids, and sabellariids (Barnes 1965; Bosence 1973; Kirtley 1994). Likewise, one would expect extinct annelids adapted to vents and seeps to occur at these sites in large clusters, as several modern forms do at such sites today (Van Dover 2000; Levin 2005; Desbruyères et al. 2006).

At a Devonian hydrothermal vent deposit tube fossils of a presumed pogonophoran annelid were found parallel to the bedding of the sulphides (Little et al. 1999), which the authors interpreted as its epifaunal life position. Recently Fouquet et al. (2008: fig. 6b) showed that the chaetopterids at the Ashadze vent site are entirely epifaunal and live in dense clusters on the bare seafloor. This mode of life is thus not restricted to siboglinid tube worms.

Flanges.—Annulae or trumpet-like flanges are seen in many vestimentiferan tubes in irregular intervals (Fig. 1A) and have also been reported from alleged fossil vestimentiferans (e.g., Little et al. 2004). This feature is not unique to vestimentiferans, but can for example also be seen in chaetopterid tubes from the Ashadze vent site (Fig. 1C) and were observed on chaetopterid tubes from the Blake Ridge seep. Similar flanges are known from the calcareous tubes of serpulids, including the deep-water species *Vermiliopsis infundibulum* (Bailey-Brock 1972) and have been reported from tubes of the enigmatic Ediacaran *Cloudina* (Bengtson and Zhao 1992).

Other tubes.—Layered tube walls are not unique to Vestimentifera but also exist in chaetopterids and in the chitin-containing tubes of phoronids (Hyman 1958; Emig 1982). However, phoronid tubes can be distinguished from the anterior ends of vestimentiferan tubes by their lack of segmentation and because they have an outer tube wall that is coated with sand grains and debris from the sediment (Adegoke 1967; Emig 1982). Morphological and molecular data indicate that Vestimentifera and chaetopterids are not closely related (cf., Rouse and Pleijel 2001; Rousset et al. 2004; Struck et al. 2007), suggesting that layered tubes may potentially occur in other annelids as well, or may have existed in extinct annelid clades in the geologic past. In addition, layered organic tubes may not be restricted to annelids and phoronids. Chen et al. (2008) documented that the tube wall of the enigmatic Ediacaran fossil *Sinotubulites* is composed of thin, presumably organic sheets. Longitudinal ridges can be seen on the elongate-conical tubes of Palaeozoic cornulitids; these are ornamental features that may have served to stabilise the tube (Vinn and Mutvei 2005). In other aspects cornulitid tubes are very unlike those of Vestimentifera (they are calcareous and have septae) but they demonstrate—along with the examples provided above—that longitudinal ridges of different structure are present on a wide range of annelid and non-annelid tubes.

Since all annelids can form chitin, they have chitinous chaetae (Purschke 2002), it is probable that extinct annelid groups could also have formed tubes of this material. For example, tubes of the Cambrian *Hyolithellus* have been interpreted as belonging to the pogonophorans because they are chitinous (Carlisle 1964). More recent authors seem to prefer not to assign this fossil to any class or phylum, cf., Skovsted (2006). More fossils with well-preserved tube remains are needed so that evidence for chitin in putative vestimentiferans can be obtained.

Conclusions

To summarise, the features currently used to identify Vestimentifera in the fossil record are not unique to this group. This calls for a more cautious interpretation of tubular fossils at ancient vents and seeps. Comparison to the geologic ranges and molecular age estimates of other taxa inhabiting these ecosystems, particular molluscs, suggests that not all "vestimentiferan" fossils actually belong to this group. Instead, extinct clades of annelids are just as likely to have flourished at vents and seeps in the geologic past. It is suggested that (i) molecular clocks provide a more reliable estimate for the evolutionary age of vestimentiferan tube worms than the geologic record of tubular fossils, and (ii) tubular fossils from ancient seep deposits should be investigated for chitinous tube remains to provide evidence for possible siboglinid affinities.

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