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Identification of fossil worm tubes from Phanerozoic hydrothermal vents and cold seeps

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One of the main limitations to understanding the evolutionary history of hydrothermal vent and cold seep communities is the identification of tube fossils from ancient deposits. Tube-dwelling annelids are some of the most conspicuous inhabitants of modern vent and seep ecosystems, and ancient vent and seep tubular fossils are usually considered to have been made by annelids. However, the taxonomic affinities of many tube fossils from vents and seeps are contentious, or have remained largely undetermined due to difficulties in identification. In this study, we make a detailed chemical (Fourier-transform infrared spectroscopy and pyrolysis gas-chromatography mass-spectrometry) and morphological assessment of modern annelid tubes from six families, and fossil tubes (seven tube types from the Cenozoic, 12 Mesozoic and four Palaeozoic) from hydrothermal vent and cold seep environments. Characters identified from these investigations were used to explore for the first time the systematics of ancient vent and seep tubes within a cladistic framework. Results reveal details of the compositions and ultrastructures of modern tubes, and also suggest that two types of tubes from ancient vent localities were made by the annelid family Siboglinidae, which often dominates modern vents and seeps. Our results also highlight that several vent and seep tube fossils formerly thought to have been made by annelids cannot be assigned an annelid affiliation with any certainty. The findings overall improve the level of quality control with regard to interpretations of fossil tubes, and, most importantly, suggest that siboglinids likely occupied Mesozoic vents and seeps, greatly increasing the minimum age of the clade relative to earlier molecular estimates.

Keywords: Annelida; polychaete; chemosynthesis; evolutionary history; cladistics; deep-sea

Introduction

Hydrothermal vents and cold seeps are remarkable sites in the deep sea, characterized by the ejection of chemically reduced fluids from the seafloor that fuel abundant life through the process of chemosynthesis (Van Dover 2000). Annelids are some of the most conspicuous dwellers of modern hydrothermal vent and cold seep ecosystems, occurring as large habitat-forming tubeworm bushes, on the walls of vent chimneys, and showing remarkable adaptations that enable them to thrive in these environments. Tube-building annelids such as siboglinids, serpulids and chaetopterids often occur at vents and seeps, and siboglinids are especially well adapted to these environments by possessing chemosynthetic endosymbionts. Not long after the discovery of vent and seep ecosystems in the late 1970s and early 1980s (Lonsdale 1977; Corliss *et al.* 1979; Paull *et al.* 1984), multiple fossil analogues of

these communities were also described. These have shown the occupation of vents and seeps by animal life to be ancient, dating back to the Silurian period, approximately 443–419 Ma (Little *et al.* 1997; Barbieri *et al.* 2004). Phanerozoic vent and seep deposits contain brachiopod, gastropod and bivalve fossils, and commonly tubular fossils often considered to have been made by annelids. While the taxonomy of non-tube fossil groups is generally uncontroversial, that of the tube fossils has remained elusive. Many tubular fossils are referred to simply as ‘worm tubes’, rather than being assigned to specific modern or fossil lineages, or have received controversial assignments (Campbell 2006; Vrijenhoek 2013). This has hindered our ability to understand the evolutionary history of chemosynthetic communities.

The majority of annelids are entirely soft-bodied and in general this phylum has a very poor fossil record (Parry *et al.* 2014). However, the dwelling tubes that many

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annelids create are often more robust structures that have a greater likelihood of becoming preserved as fossils (Ippolitov *et al.* 2014; Georgieva *et al.* 2015a), and especially so within vents and seeps where rapid mineral precipitation often favours fossilization.

Some annelids can produce only thin, temporary mucus tubes, but many construct dwelling tubes with greater durability (Gaill & Hunt 1988; Merz 2015). Non-mucus or robust annelid tubes can be divided into three broad categories: calcium carbonate tubes, agglutinated tubes comprised of inner organic layers and outer exogenous material (e.g. sediment grains), and tubes comprised purely of an organic secretion. Calcareous tubes are almost exclusively confined to the family Serpulidae, but single extant sabellid and cirratulid genera also produce calcareous tubes (Ippolitov *et al.* 2014). Calcareous tubes can be formed of either calcite or aragonite, or of both minerals, and may also exhibit distinct crystal microstructures (Vinn *et al.* 2008). Agglutinated tubes occur in families such as Sabellidae and Terebellidae, or only in a subset of members of a family, e.g. the genus *Mesochaetopterus* (Chaetopteridae). Purely organic tubes (referred to as 'organic' tubes hereafter) often have a high protein content which co-occurs with a carbohydrate (Merz 2015). For example, chaetopterid tubes are considered to be formed of a highly ordered fibrous protein embedded within a carbohydrate matrix (Gaill & Hunt 1988), and also to contain furfural (Berkeley 1922). The tubes of *Alvinella* spp. (Alvinellidae) are primarily comprised of protein (Vovelle & Gaill 1986). Other organic tubes may be formed of a β -chitin and protein complex. The latter composition most notably occurs in the tubes of siboglinids (Brunet & Carlisle 1958; Shillito *et al.* 1995), which constitute the most prominent tubicolous annelid family occupying modern vents and seeps. Chitin content can vary throughout the length of siboglinid tubes (Julian *et al.* 1999), and has also recently been detected in the tubes of spionids and oweniids (Guggolz *et al.* 2015). Annelid builders of calcareous, agglutinated and organic tubes all occur at modern hydrothermal vents and cold seeps (Olu *et al.* 1996; Desbruyères *et al.* 2006; Levin & Mendoza 2007; Kupriyanova *et al.* 2010).

Many of the tubular fossils at ancient vent and seep sites are considered to have originally been organic in composition (e.g. Little *et al.* 1999a, b; Goedert *et al.* 2000; Himmler *et al.* 2008), but identification based on their morphologies has proved difficult. This is because: (1) many fossil tubes lack diagnostic characters; (2) often only short fragments of fossil tubes are found, making it difficult to assess the morphology of the whole tube; (3) the same type of tube can exhibit a range of preservations; and (4) tube surfaces with diagnostic characters may be obscured by mineralization. Existing taxonomic designations of fossil tubes to the annelids are made based on their resemblance at various morphological scales to

tubicolous annelid lineages as well as on environmental considerations in some instances. Potential annelid affinities of originally calcareous fossil tubes may also be evaluated on their ultrastructure if this is well preserved (e.g. Taylor & Vinn 2006), and Palaeozoic fossil tubes are also assessed for their resemblance to non-annelid tube-builders from this period such as cornulitids, microconchids and tentaculitids (e.g. Vinn *et al.* 2016).

Identification of fossil vent and seep tubes is further complicated by poor understanding of the taphonomy and fossilization of different tube types within these settings. The few existing studies show that vestimentiferan and alvinellid tubes at hydrothermal vents are preserved primarily by iron sulphides, with details of outer tube ornament and fibrous textures sometimes very intricately replicated (Cook & Stakes 1995; Georgieva *et al.* 2015a). At seeps, aragonite can preserve the original finely multi-layered structure of the tube walls of the vestimentiferan *Escarpia southwardae*, also retaining details of fraying of the fibrous tube wall and the delamination (layer separation) of tube walls (Haas *et al.* 2009). At seeps, the original wall structure of an annelid tube may be preserved, allowing the determination of whether the tube was originally calcareous or organic; however, at vents this is more difficult as carbonate is rapidly dissolved and replaced. While it is known that organic compounds (biomarkers) specific to methane- and sulphur-cycling micro-organisms may be preserved at vents and seeps (Peckmann *et al.* 2004; Blumenberg *et al.* 2012), the preservation of annelid tube biomarkers during fossilization within these environments has not been investigated. If preserved, biomarkers can potentially provide additional information to aid in the identification of problematic vent and seep tube fossils due to the different compositions of organic annelid tubes (Gaill & Hunt 1988).

Based on tube morphology and occurrence within an ancient vent environment, many fossil vent and seep tubes have been assigned to the vestimentiferans (a subgroup of siboglinids comprising its larger members) (Little *et al.* 1999c, 2004; Shpanskaya *et al.* 1999). However, these identifications have been challenged as the morphological characters used to make the diagnoses are not unique to the vestimentiferans, being also present in other annelid families as well as non-annelid fossil taxa (Kiel & Dando 2009). Such characters include longitudinal wavy ridges, tube collars (or flanges) and multi-layered tube walls, as well as the size and mass occurrence of tubes. However, no comprehensive comparison of modern organic and fossil annelid tubes has yet been attempted to determine whether there are clear morphological features that can distinguish tubicolous annelid lineages in the fossil record.

Interpretations of Palaeozoic and Mesozoic vent and seep tubes as vestimentiferans are also at odds with the age of the siboglinids as determined through molecular

clock methods. The oldest putative vent siboglinid, *Yamankasia rifeia*, is ~440 million years old, which vastly exceeds the range of molecular age estimates for the family Siboglinidae Caullery, 1914, of 50–126 million years (Little & Vrijenhoek 2003; Vrijenhoek 2013). Recently discovered borings of the bone-eating siboglinid worm *Osedax* in Late Cretaceous (~100 million year old) plesiosaur and turtle bones (Danise & Higgs 2015), however, suggest that the older molecular age estimates for this family may be more accurate. The above study also highlights that better morphological assessment of fossils is needed to clarify the evolutionary ages of vent and seep fauna.

To advance the understanding of the evolutionary history of deep-sea hydrothermal vents and cold seep communities, this study aims to improve the taxonomy of the abundant but problematic fossil annelid tubes from Phanerozoic vents and seeps. Firstly, by investigating both modern annelid and fossil tubes from vents and seeps, we aim to define a range of morphological criteria by which tubes from different lineages may be distinguished. We also aim to clarify whether modern organic annelid tubes exhibit significantly different chemical compositions, and whether these can be detected in the fossil record. Secondly, we analyse these data within a more objective, modern cladistic framework.

Materials and methods

Modern and fossil tube selection

Fossil tubes for identification were selected based on the availability of material, and are therefore a non-random subsample of all the reported tubes from fossil vent and seep localities (Supplemental File 1, Table S1). An effort was made to include tubes from a range of geological time periods and exhibiting a range of morphologies (summarized in Supplementary File 1, Table S2).

Tubes from modern annelid families for detailed study and comparison with fossil material (Supplementary File 1, Table S3) were chosen on the basis of two main criteria: (1) those that occur within modern vents and seep environments, and (2) those for which difficulties in discrimination in the fossil record of vents and seeps have been noted. As potential confusion between siboglinid and chaetopterid tubes in the fossil record has been highlighted (Kiel & Dando 2009), analyses of modern material were focused on tubes from these two families, with an effort made to cover the range of tube morphologies exhibited by each family (Supplementary File 1, Table S3).

In addition to vestimentiferans, the family Siboglinidae includes another two monophyletic lineages that construct durable organic tubes: the frenulates and the moniliferans. Both of these lineages build small-diameter (mostly less than 1 mm) tubes that are often long compared to their

diameter, with frenulate tubes generally exhibiting greater morphological diversity. The tubes of vestimentiferans, *Sclerolinum* (moniliferan) and frenulates were all included in tube comparisons. Siboglinid tubes are known to exhibit variation from their anterior to posterior sections (Southward *et al.* 2005). Vestimentiferan tubes can produce extensive posterior tube regions buried in substrate that lack ornamentation and are sometimes termed ‘roots’ (Dattagupta *et al.* 2006). For such tubes, the morphology of the anterior, middle and posterior regions were noted. Chaetopterid tubes can also show morphological variation along their length, although this is more rarely observed than in siboglinid tubes.

Serpulid tubes that may resemble siboglinid tubes were also included in tube comparisons, as were the tubes of the genera *Alvinella* (Alvinellidae) and *Glyphanostomum* (Ampharetidae) because they construct organic tubes and occur at vents (and also seeps for the latter genus) (Reuscher *et al.* 2009, 2012). Agglutinated tubes from several families (Sabellidae, Chaetopteridae, Oweniidae) were included for comparison with non-agglutinated tubes. Palaeozoic fossil tubes were also compared to the tubes of Palaeozoic non-annelids, using existing literature describing the latter.

Morphological analysis

Fossil tubes were photographed and measured in hand specimen, and a selection of these were also imaged uncoated using a FEI Quanta 650 FEG-ESEM scanning electron microscope at the Natural History Museum, UK (NHMUK). Fossil tubes from each locality were also prepared as polished thin sections, and visualized using light microscopy. Selected modern tubes were initially photographed, after which lengths of approximately 10 mm were cut from a subset of these for further analyses. For tubes that showed differentiation along their length, 10 mm sections were cut from each different region (e.g. the anterior, middle and posterior portions of frenulate tubes). For tubes preserved in ethanol, sections were initially critical-point dried, and all tube sections were subsequently visualized using scanning electron microscopy (SEM). Following this, tube sections were embedded in resin, prepared as polished thin sections and visualized using light microscopy.

Aspects of the overall morphology, ultrastructure and composition (see below) exhibited by modern tubes were used to identify characters that can be used to distinguish annelid tubes, with an attempt made to include all of the features that a tube may exhibit. This was important because tubes, especially when fossilized, generally possess relatively few characters compared to annelid soft tissues. The 48 characters (see Supplementary File 2, Fig. S4) are all binary-coded to maximize the amount of information obtainable.

Principal coordinate and phylogenetic analyses

Selected tube characters were used to create a character matrix (Supplementary File 1, Table S4) in which morphological and compositional aspects of modern and fossil tubes were scored using findings from this study as well as the existing literature. During creation of the character matrix, the differing anterior and posterior sections of four vestimentiferan tubes were scored individually to test for any effects of this on subsequent analyses. Fossil tubes from two localities (Bear River, Wilbur Springs) were also removed from the character matrix prior to any subsequent analyses. These tubes were only available in thin section; therefore, broader tube morphology could not be assessed.

The resulting character matrix was firstly used to conduct a principal coordinate analysis (PCA), to assess the similarity of tubes based on the 48 identified characters within a low-dimensional space. PCA was performed using PAST (Hammer *et al.* 2001), which has the ability to handle an incomplete matrix. Similarity was computed with the Gower Similarity index.

The tube character matrix was also used to conduct phylogenetic analyses to determine whether compositional and morphological criteria can reconstruct currently accepted relationships of modern annelid lineages as inferred from soft tissues and DNA (Rouse & Fauchald 1997; Weigert & Bleidorn 2016), and where fossils fit in relation to these. These were performed using the parsimony program TNT v. 1.1 (Goloboff *et al.* 2008), for the following two data sets: (1) modern taxa, tube data only (43 taxa, 48 characters); and (2) modern and fossil taxa, tube data only (64 taxa, 48 characters). To explore congruence between DNA-based phylogenies and tube morphology, an additional three data sets were created that included molecular data for modern annelids (Supplementary File 1, Table S5). These data sets were analysed using the Bayesian program MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) (see Supplementary File 1: Methods Supplement 1). Outgroup choice for all analyses was based on the findings of Weigert *et al.* (2014).

For analyses performed using TNT, all characters were treated as non-additive (unordered) and were weighted using implied character weighting, which is deemed more appropriate for data sets in which homoplasy is likely to occur (Goloboff 1993; Legg *et al.* 2013). The degree to which homoplastic characters are down-weighted during the analysis is determined by the concavity constant k , which is set to 3 by default in TNT. Greater values of k down-weight homoplastic characters to a lesser extent, and our data sets were analysed with both $k = 3$ and $k = 4$ due to the suggested high potential for homoplasy when dealing with tubicolous annelids (Merz & Woodin 2006; Kiel & Dando 2009). Tree searching was conducted using the new technology search option, as this is regarded as the

most suitable search tool for finding the shortest trees when handling data sets that contain 50 or more taxa (Goloboff 1999). Tree search parameters were as follows: 200 random stepwise addition sequences, 3000 iterations each of drifting and ratcheting, and 100 rounds of tree fusing. Symmetric resampling of 1000 replicates was used to measure nodal support as this technique is unaffected by character weighting (Goloboff *et al.* 2003; Legg *et al.* 2013).

Tube compositional analysis

Several modern organic tubes covering a range of annelid families were initially analysed using Fourier transform infrared spectroscopy (FTIR). This technique is used to identify the types of bonds or functional groups present within an organic sample (Williams & Fleming 1980), and was employed to provide an overview of similarity in organic composition between tubes from various taxonomic lineages. FTIR analyses were performed using a Nicolet Nexus FTIR bench unit (Thermo Scientific, Waltham, MA, USA) at Imperial College, London (ICL) in attenuated total reflectance mode. Spectra were collected at a resolution of four data points per reciprocal centimetre, and converted to absorbance using Nicolet OMNIC software (Thermo Scientific).

A subset of the modern organic tubes that showed different FTIR spectra were then analysed in more detail using pyrolysis gas-chromatography mass-spectrometry (py-GC-MS; also performed at ICL) to identify the structural components of the tubes. Py-GC-MS is widely employed for analysis of organics preserved in fossils, as it allows rapid detection of complex polymers and requires very little material (Gupta & Cody 2011). For this analysis, small pieces of modern dry annelid tube were placed inside quartz pyrolysis tubes plugged with quartz wool at each end. Further details of the py-GC-MS methods used can be found in Supplementary File 1, Methods Supplement 2.

To determine whether fossil tubes contained any preserved organic matter (and would hence make good targets for py-GC-MS), thin sections of fossil tubes were initially viewed using confocal laser scanning microscopy (CLSM) with a Nikon A1-Si confocal microscope at the NHMUK, operated in auto-fluorescence mode. Fossil tubes were selected for py-GC-MS if they showed pronounced fluorescence relative to surrounding minerals with CLSM and were therefore suspected to contain preserved organic matter. For py-GC-MS, the walls of fossil tubes were carefully separated from the host rock, ground to a fine powder, placed inside pyrolysis tubes, and analysed using the same instrument parameters as modern tubes. Fossil tubes from two localities (Humptulips, Wai-iro) were assessed only for organics content (with

py-GC-MS; Supplementary File 1, Table S2) and were therefore not included in the character matrix.

Organization of results

The results section follows a systematic review of ancient vent and seep tube fossils organized by geological age (youngest to oldest). Results of principal coordinate, phylogenetic and tube compositional analyses are subsequently presented.

Sample identification codes for fossil tube material in the systematics section (e.g. RK-5) are locality codes and/or codes assigned by collectors/donors of material.

Repository abbreviations. **NHMUK**, Natural History Museum, London, UK; **UL**, University of Leeds, Leeds, UK; **LACMIP**, Natural History Museum of Los Angeles County, Invertebrate Paleontology section, USA; **PMO**, Palaeontological Museum, Oslo, Norway; **NRC**, Natural Resources Canada.

Systematic palaeontology

Phylum **Annelida** Lamarck, 1809

Family *incertae sedis*

'Rocky Knob tubes'

(Fig. 1)

2008 worm tubes Campbell, Francis, Collins, Gregory, Nelson, Greinert, & Aharon: 90, fig. 4b, c.

2010 worm tubes Saether, Little, & Campbell: 510, fig. 3c.

2011 ?Siboglinidae Saether: 73, fig. 5.1e–i.

Material. RK-5, block of many large-diameter tubes, mostly in the same orientation. RK-15B-6, block of small-diameter tubes mostly in the same orientation. RNT1, many similar-sized tubes, mostly in the same orientation. RNT2, dense aggregation of small-diameter tubes in a range of orientations. 12-RK, small and larger diameter tubes, mostly in the same orientation. Donated by K. A. Campbell and collected by C. T. S. Little.

Occurrence. Rocky Knob, northern Hawke's Bay area, east coast of North Island, New Zealand (~38°19'S, 177°56'E). Seep carbonates occurring as isolated lenses in mudstone, Bexhaven Limestone Formation, Tolaga Group, Middle Miocene (Campbell *et al.* 2008; Saether *et al.* 2010; Saether 2011).

Description. Carbonate tubes mostly straight and exhibiting a wide range of diameters, from 1.0 to 7.9 mm, preserved in clusters mostly of similar-sized tubes (Fig. 1A, B). In some clusters, tubes are preserved in the same orientation (Fig. 1B). The tubes are non-branching, large-diameter fragments taper somewhat (Fig. 1A), and some

tube walls appear to be touching others (Fig. 1B, F). Tube walls are mostly smooth (Fig. 1C); however, one tube exhibits small round textures on its surface (Fig. 1D) while another small-diameter tube bears fine, long, continuous longitudinal wrinkles (Fig. 1B). Tube walls appear to have been originally fibrous as in places torn fibres are preserved (Fig. 1E), and some of the tubes also seem to have been originally flexible due to the occurrence of irregular tube cross-sections (Fig. 1F). The tubes show pronounced organic content (Fig. 1G; Supplementary File 1, Table S9). The tubes also appear originally to have been multi-layered (Fig. 1E, G, H), with delamination occurring between some layers (Fig. 1H). Some tube sections show well-consolidated lamination that is many layers thick (Fig. 1G, H).

Remarks. Tubes from Rocky Knob have previously been tentatively ascribed to siboglinids (Saether 2011). However, cluster and cladistic analyses (Figs 22, 24) failed to place these tubes among the siboglinids or any other annelid families included in the analyses. Noting their similarity to vestimentiferan tubes, we therefore assign these tubes to the annelids only, as more information would be required to assign them to siboglinids. The abundance of these tubes at this ancient seep, large diameter range, generally smooth organic tube walls, and the thick, neatly multi-layered tube wall appearance in some of the specimens do suggest a vestimentiferan affinity. The round structures (Fig. 1D) present on the surface of a large-diameter tube may constitute the circular bases of aragonite botryoids (Fig. 1F).

Phylum *incertae sedis*

'Upper Waiiau River tubes'

(Fig. 2)

Material. UWT3-4, clumps of tubes preserved mostly in the same orientation, one large-diameter tube has a very grainy tube wall. Donated by K. A. Campbell.

Occurrence. Upper Waiiau River, northern Hawke's Bay area, east coast of North Island, New Zealand (~38°13'S, 178°5'E). Seep carbonates occurring as isolated lenses in mudstone, Bexhaven Limestone Formation, Tolaga Group, ?late early Miocene–middle Miocene (Campbell *et al.* 2008; Saether 2011).

Description. Relatively straight carbonate tubes, 2.3–6.6 mm in diameter (Fig. 2A). Tube walls smooth (Fig. 2A) or with a grainy appearance (Fig. 2B, C) created by what seems to be aragonite growth around many small spheres. In section, tube walls appear to have a high organic content (Fig. 24; Supplementary File 1, Table S9), and comprise multiple brown layers of varying thickness. Preserved tears (Fig. 2D) also suggest that the original tube wall had an organic component. The brown



Figure 1. ‘Rocky Knob tubes’, Middle Miocene, New Zealand. **A**, RK-5, larger tube fragments in hand specimen. **B**, RNT-1, smaller, parallel-aligned tubes, with one tube exhibiting fine longitudinal wrinkles on its surface (white arrow). **C**, 12-RK, detail of smooth tube wall. **D**, RNT-1, tube exhibiting round concretions on its surface. **E**, RK-15B-6B, tube in transverse section showing preserved torn fibres. **F**, RK-15B-6B, tube with irregular cross section suggesting it may originally have been flexible. **G**, RK-15B-6A, detail of joint between three tubes with thick, multi-layered walls in transverse section; imaged using confocal laser scanning microscopy (see online for colour version). **H**, detail of tube transverse section showing delamination of its thick, multi-layered tube wall. Scale bars: A = 20 mm; B = 5 mm; C = 2 mm; D, F = 1 mm; E = 100 μm ; G, H = 200 μm .

layers sometimes have a thick carbonate band occurring along their outer edge (Fig. 2D, E). The small spheres that likely give the tube its grainy appearance are located on the outside of this layer (Fig. 2D).

Remarks. These tubes were resolved among siboglinids only within the cladistic analysis that allowed more homoplasy (Fig. 23B). However, the amount of missing data for the tubes (Supplementary File 1, Table S4) makes this

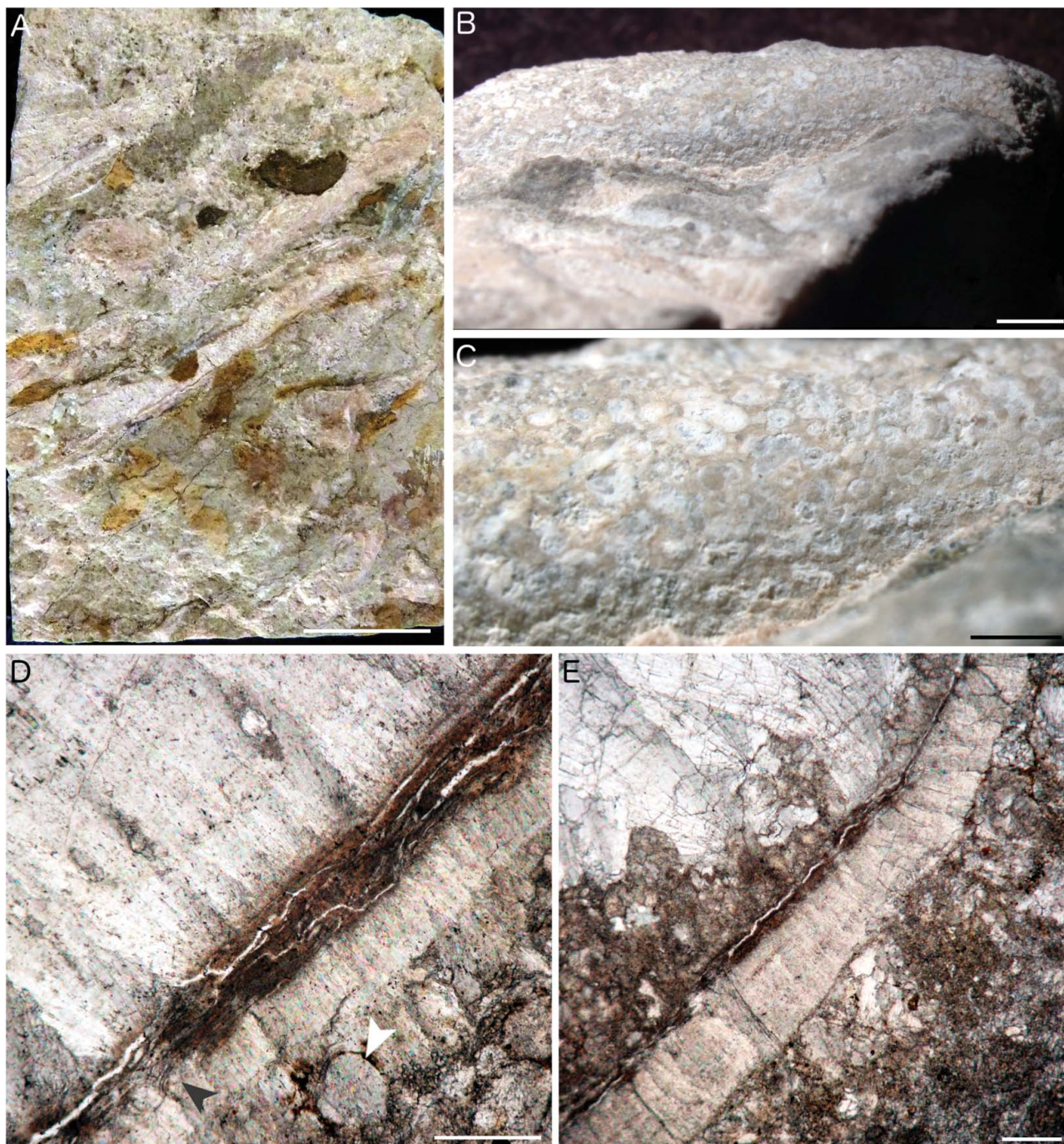


Figure 2. ‘Upper Waiau River tubes’, UWT3-4, ?late Early Miocene–Middle Miocene, New Zealand. **A**, tubes in hand specimen. **B**, tube with grainy wall in hand specimen. **C**, detail of tube wall in **B**. **D**, detail of tube wall in near transverse section showing brown bands that make up the multi-layered tube wall, where a tear in the wall is also preserved (grey arrow); a small sphere is preserved towards the outside of the tube (white arrow). **E**, detail of tube wall in transverse section showing a thick calcareous band occurring on the outside of the brown tube wall layers. Scale bars: A = 20 mm; B = 2 mm; C = 1 mm; D, E = 200 μm .

result uncertain. In addition, the small spheres present on the surface of these tubes make them difficult to place. These spheres are not located on top of the organic fibrous layers as would be expected in an agglutinated tube. Instead, the spheres are located on top of another layer of

mineralization, suggesting that they formed on the tube during or after mineralization. Similarly preserved tubes have been observed in the Devonian Hollard Mound deposit (Peckmann *et al.* 2005). The tube assemblage at Upper Waiau River warrants further investigation and

therefore these tubes are not presently assigned to a modern annelid or non-annelid lineage.

Phylum **Annelida** Lamarck, 1809
 Family **Serpulidae** Rafinesque, 1815
 ‘**Bexhaven tubes**’
 (Fig. 3)

Material. BXG, many small-diameter tubes occurring clustered together (Fig. 3A). Collected by C. T. S. Little.

Occurrence. Bexhaven locality, northern Hawke’s Bay area, east coast of North Island, New Zealand ($\sim 38^{\circ}3'S$, $178^{\circ}5'E$). Seep carbonates occurring as isolated lenses in mudstone, Bexhaven Limestone Formation, Tolaga Group, Middle Miocene (Campbell *et al.* 2008; Saether 2011).

Description. Carbonate tubes 0.5–1.9 mm in diameter, non-branching, somewhat sinuous (wavy) (Fig. 3A), and appearing to have been originally rigid as they demonstrate clean fractures (Fig. 3E). Tubes do not taper in the fragments observed. Tube wall surfaces exhibit numerous fine, parallel transverse wrinkles (Fig. 3B). Tubes are clearly attached to each other (Fig. 3C, D), and show chevron-like multi-layered tube wall structure (Fig. 3E), while in some cases the tube walls have been replaced (Fig. 3D). Tube walls do not appear to contain preserved organic matter (Fig. 25).

Remarks. The attachment exhibited by the tubes and the chevron-like structure of their walls clearly point to the tubes having been made by Serpulidae Rafinesque, 1815, and they are identified as such by both cluster and cladistic analyses (Figs 22, 24). The tube wall ornamentation of fine closely spaced transverse wrinkles is also seen in

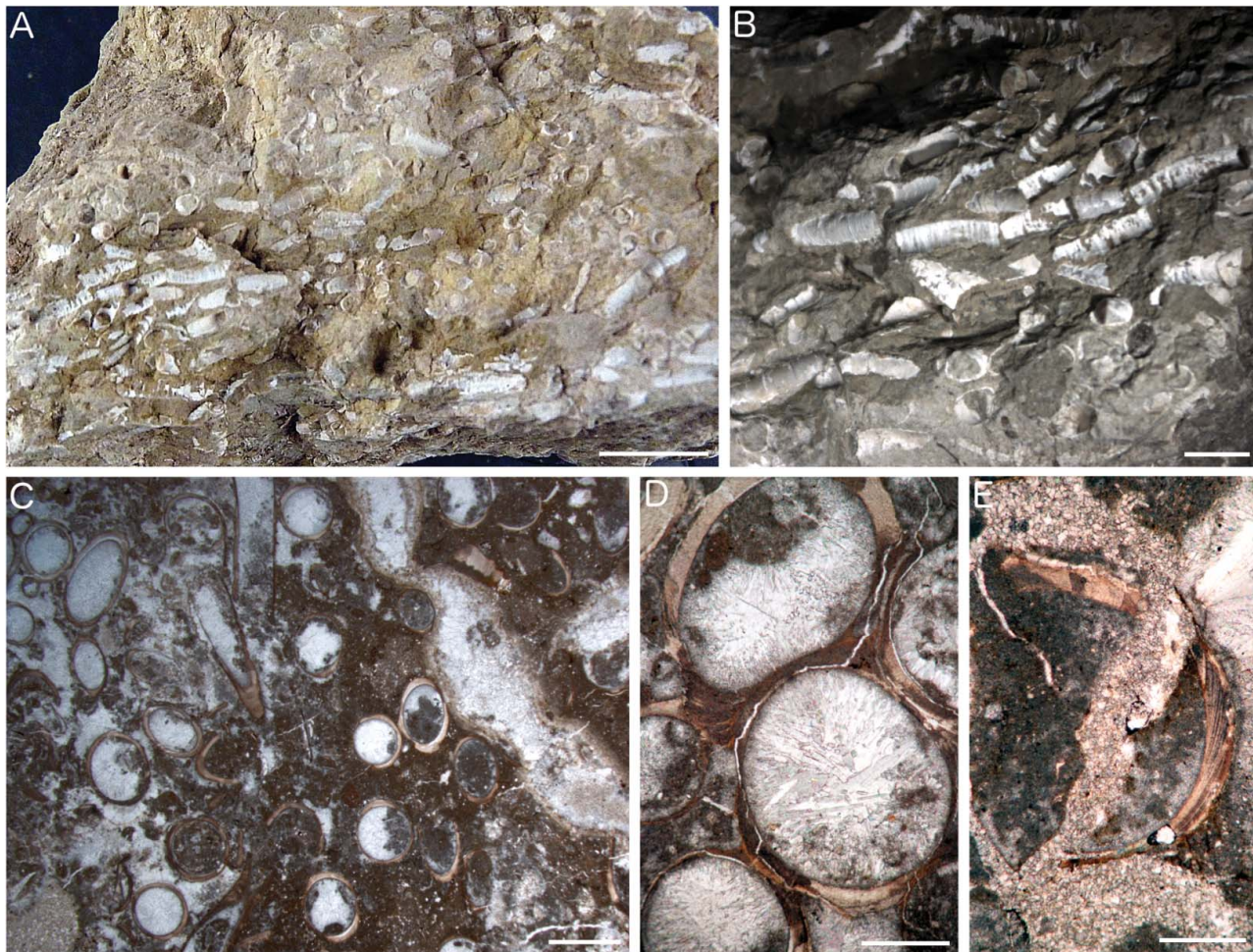


Figure 3. Serpulidae sp., ‘Bexhaven’, BXG, Middle Miocene, New Zealand. **A**, tubes in hand specimen. **B**, detail of tubes in hand specimen showing fine parallel transverse wrinkles on tube surfaces. **C**, tubes in section. **D**, cluster of five attached tubes in transverse section. **E**, detail of partial transverse section of tube wall showing its chevron-like appearance. Scale bars: A = 20 mm; B = 3 mm; C = 2 mm; D, E = 500 μm .

many members of this family (e.g. *Serpula* spp.). Serpulids have also tentatively been suggested to occur at the Haunui and Ugly Hill localities (Saether 2011).

?Family **Siboglinidae** Caullery, 1914
'West Fork Satsop River tubes'
 (Fig. 4)

Material. JLG459C, WFSR-3B, several wavy tubes. WFSR-3A-1, several tubes observed in thin section. Donated by J. L. Goedert.

Occurrence. West Fork Satsop River, Grays Harbor County, Washington State, USA (~47°16'N, 123°33'W). Float seep limestone blocks. Lincoln Creek Formation,

Oligocene (Campbell & Bottjer 1993; Kiel & Amano 2013).

Description. Carbonate tubes up to 2.4 mm in diameter, somewhat sinuous, non-branching, and not appearing to have been agglutinated or to taper in the observed fragments (Fig. 4A, B). Tubes appear inflexible and unattached, and the tube walls are free of ornamentation. In thin section, the tube walls are brown, of variable thickness but finely multi-layered (Fig. 4C, D). An originally organic composition of the tube walls is also supported by confocal microscopy (Fig. 25), and breaks in the tube wall can be observed showing potential frayed fibre endings (Fig. 4D).

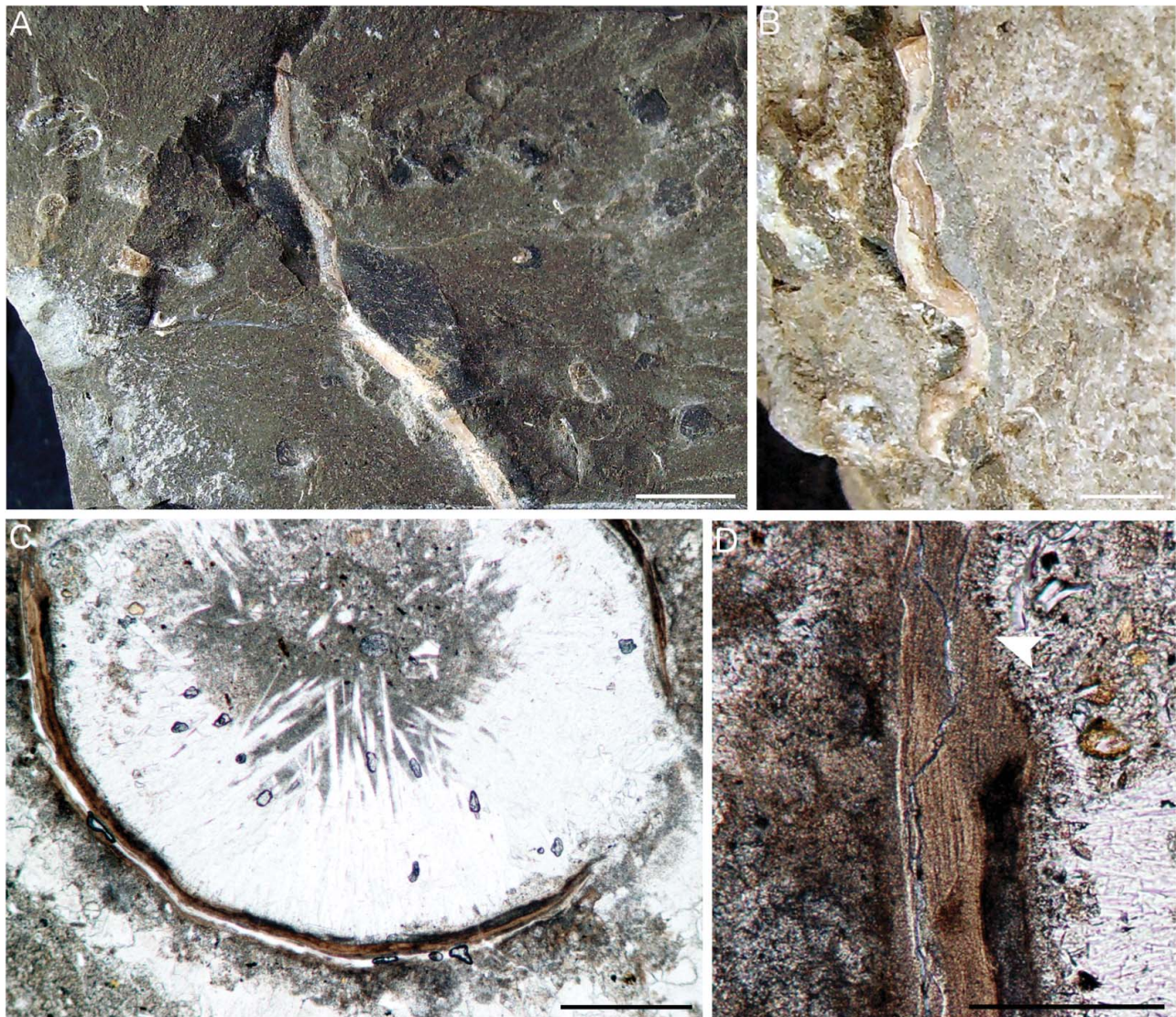


Figure 4. 'West Fork Satsop River tubes', Oligocene, Washington State, USA. **A, B**, WFSR-3B and WFSR JLG 459C, respectively, tubes in hand specimen showing wavy nature and smooth tube walls. **C, D**, WFSR 3A-1; **C**, transverse section of tube showing multi-layered brown walls of varying thickness; **D**, detail of tube wall where a potential preserved fibrous tear occurs, revealing frayed fibre endings (white arrow). Scale bars: A = 10 mm; B = 5 mm; C = 300 μ m; D = 100 μ m.

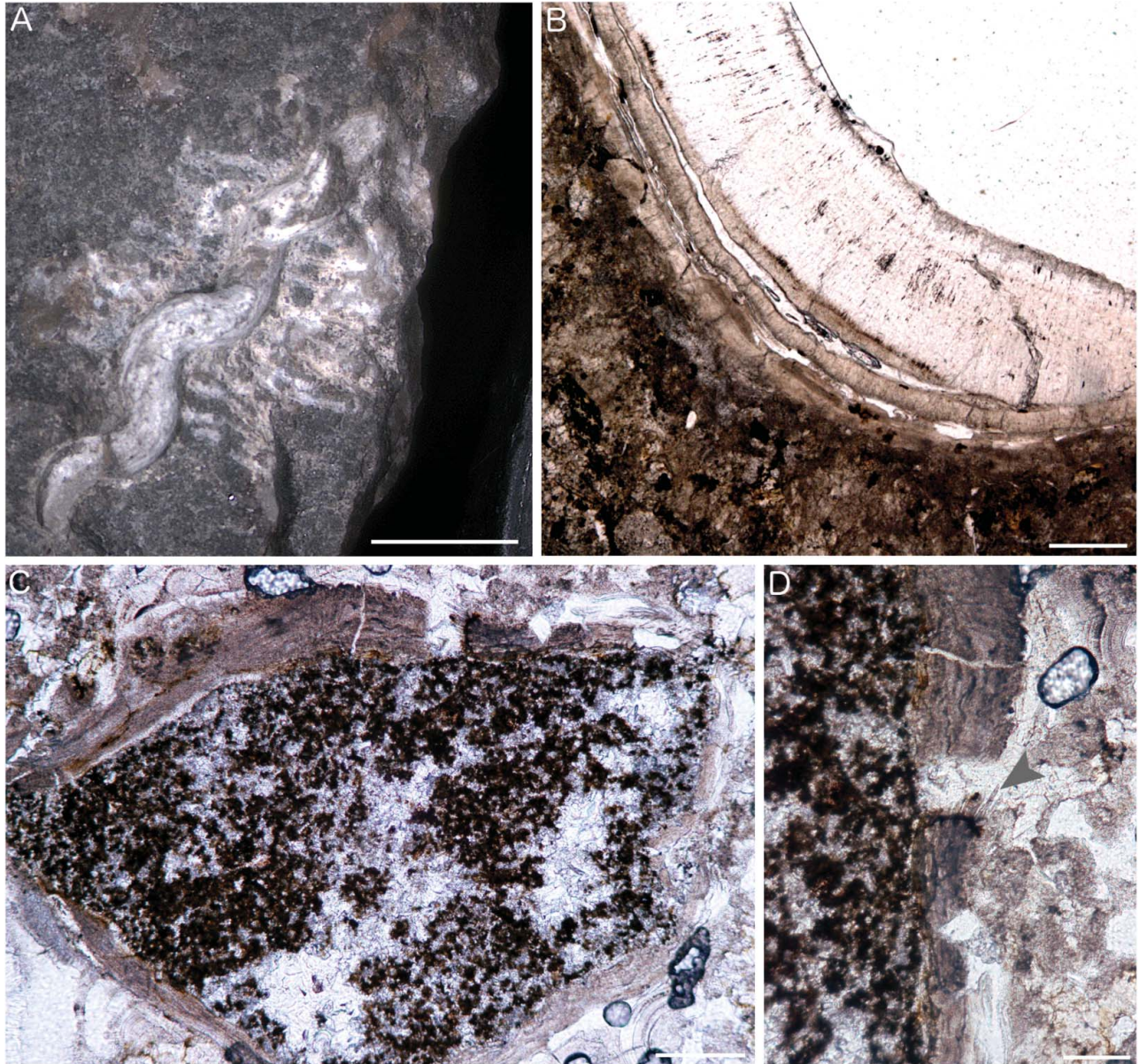


Figure 5. ‘Murdock Creek tubes’, WA-MC LACMIP loc. 6295, Early Oligocene, Washington State, USA. **A**, a single tube in hand specimen possibly bearing longitudinal wrinkles. **B**, detail of tube wall in transverse section with thick, multi-layered and delaminated tube wall. **C**, transverse section of tube which appears to have originally been flexible. **D**, detail of tube wall where a preserved tear occurs, revealing fibre endings (grey arrow). Scale bars: A = 5 mm; B = 150 μm ; C = 100 μm ; D = 50 μm .

Remarks. These tubes were resolved only within the cladistic analysis that allowed for more homoplasy (Fig. 23B), in which they fall among siboglinids. The fibrous organic composition and concentrically multi-layered walls are, however, also consistent with the tubes of chaetopterids, although the smooth walls and sinuosity of these tubes suggest that they are possibly more likely to have been made by siboglinids. We therefore tentatively suggest a siboglinid affinity.

?Family **Siboglinidae** Caullery, 1914
 ‘Murdock Creek tubes’
 (Fig. 5)

Material. WA-MC LACMIP loc. 6295, one spiralling tube (Fig. 5A), another tube with a $\sim 90^\circ$ bend, and a smaller tube observed in thin section only. Donated by J. L. Goedert.

Occurrence. Murdock Creek, Clallam County, Washington State, USA ($\sim 48^\circ 9' \text{N}$, $123^\circ 52' \text{W}$). Loose seep carbonate blocks. Pysht Formation, late Early Oligocene (Goedert & Squires 1993; Kiel & Amano 2013; Vinn *et al.* 2013).

Description. Carbonate tubes 0.7–3.0 mm in diameter, appearing non-branched, non-agglutinated and non-tapering in the tube fragments observed. The spiralling

tube (Fig. 5A) appears to have coarse longitudinal wrinkles on its surface, but whether these are original is uncertain. In thin section, tube walls are thick and concentrically multi-layered (Fig. 5B–D), and occasionally delaminated (Fig. 5B). Some of the tubes appear to have originally been flexible (Fig. 5C) and to have had fibrous walls due to visible preserved wall tears in thin section (Fig. 5D).

Remarks. These tubes appear to have been organic originally due to preserved tube wall tears that reveal a fibrous nature. The size of the tubes, their thick, multi-layered walls and the spiralling that they exhibit suggest that the tubes may have been made by vestimentiferans, as the combination of these features are not commonly encountered in other organic tube-building annelids that occur at vents and seeps. Due to a limited amount of material available for study, and as these tubes were only resolved among those of siboglinids when homoplastic characters are downweighted less within cladistic analyses (Fig. 23B), the tubes are only tentatively assigned to the siboglinids.

?Family **Siboglinidae** Caullery, 1914

(?vestimentiferan)

‘Canyon River tubes’

(Fig. 6)

2000 vestimentiferan worm tubes Goedert, Peckmann, & Reitner: 995, fig. 3.

Material. WA-CR LACMIP 16957, several large, straight tubes preserved in the same orientation. JLG 473, tubes embedded in carbonate matrix, thin sections of tubes only. Donated by J. L. Goedert.

Occurrence. Canyon River, south-west Washington State, USA (47°18.18'N, 123°30.52'W). Seep carbonate within siltstone, Lincoln Creek Formation, lower Oligocene (Goedert *et al.* 2000; Peckmann *et al.* 2002).

Description. Carbonate tubes from this locality were originally described by Goedert *et al.* (2000). They measure 1.1–7.0 mm in diameter, and are non-branching, non-agglutinated and not attached to other tubes (Fig. 6A–C). Tubes taper slightly, and the walls of the majority of the tubes are smooth and lack ornamentation (Fig. 6A, B), while longitudinal wrinkles are present in one small-diameter tube (Fig. 6C). Tube walls are thick and multi-layered, and at times delaminated (Fig. 6D), suggesting an originally organic composition. The tubes appear to have originally been rigid as walls are generally not compressed, both in hand specimen (Fig. 6A–C) and thin section (Fig. 6E), and fluorescence during CLSM analysis of the tube walls further suggests that the tubes were originally organic (Fig. 6F).

Remarks. These tubes were suggested to have been made by vestimentiferans by Goedert *et al.* (2000), resembling tubes made by the genus *Escarpia*. Despite the tubes being largely unresolved in the cladistic and cluster analyses (Figs 22, 24), they closely resemble those of vestimentiferans owing to their smooth walls and columnar morphology. The diameter range of the tubes, as well as the hard, organic, mostly thick and multi-layered nature of the tube walls, are typical of most vestimentiferans. We therefore suggest that vestimentiferans are the most likely builders of these tubes, but this assignment is tentative due to the poor resolution of these tubes in the cladistic analysis.

Phylum *incertae sedis*

‘Bear River tubes’

(Fig. 7)

Material. LACMIP 5802 BRB-1, several small tubes preserved in close proximity and embedded within the carbonate matrix. Donated by J. L. Goedert.

Occurrence. Bear River, Pacific County, Washington State, USA (46°19.94'N, 123°55.96'W). Large seep deposit, siltstone of Cliff Point, late Eocene (Vinn *et al.* 2013).

Description. Tubes are 0.4–2.3 mm in diameter, and appear non-agglutinated and not attached to other tubes (Fig. 7A). As the tubes are fairly round in thin section, it is inferred that they were originally rigid (Fig. 7A). Whether or not the tubes taper is unknown, and details of wall ornamentation could not be assessed. In thin section, the tube walls are thick (Fig. 7B, C) and in places remnants of tube wall appear multi-layered (Fig. 7C). The brown, filmy nature of the tube walls (Fig. 7B, C) suggests that they were likely originally organic in composition.

Remarks. The thick, multi-layered organic tube walls suggest that these tubes could potentially have been made by annelids, perhaps siboglinids. However, due to the inability to assess outer tube wall characters and availability of only a limited number of sections, these tubes have not been assigned to a modern annelid lineage.

Phylum **Annelida** Lamarck, 1809

?Family **Siboglinidae** Caullery, 1914

(?vestimentiferan)

‘Omagari tubes’

(Fig. 8)

2003 possible vestimentiferan worm tubes Hikida, Suzuki, Togo, & Ijiri: 336, figs 3.1, 4.1, 4.4, 4.5, 5, 8.

Material. Many small, similar-diameter tubes preserved together. OMG03-4a, pinkish calcite with many



Figure 6. ‘Canyon River tubes’, Oligocene, Washington State, USA. **A–C**, WA-CR LACMIP 16957; **A**, large-diameter tubes in hand specimen; **B**, smooth small-diameter tubes; **C**, small-diameter tube with longitudinal wrinkles. **D–F**, JLG 473; **D**, delaminated tube wall with a fragment of preserved multi-layered tube wall (white arrow); **E**, uncompressed transverse section of a small diameter tube; **F**, detail of tube wall showing fluorescent bands that likely indicate the presence of preserved organic matter from the tube wall, imaged using confocal laser scanning microscopy (see online for colour version). Scale bars: A = 20 mm; B = 5 mm; C = 3 mm; D = 150 μm ; E = 300 μm ; F = 30 μm .

worm tubes with brown walls (Fig. 8A, B). OMG03-4b, brown-walled tubes observed in thin section. OMG03-1, many tubes in muddy, crumbly matrix (Fig. 8C, D). OMG03-2, OMG03-3a, OMG03-3b, many tubes with light-coloured walls preserved in hard cement. Donated by Y. Hikida.

Occurrence. Omagari, Nakagawa-cho region, north-western Hokkaido, northern Japan ($44^{\circ}39.58'N$, $142^{\circ}2.22'E$). Approximately 10 m wide seep carbonate deposit, Omagari Formation, Yezo Supergroup, Campanian, Cretaceous (Hikida *et al.* 2003; Majima *et al.* 2005; Kiel *et al.* 2008a).

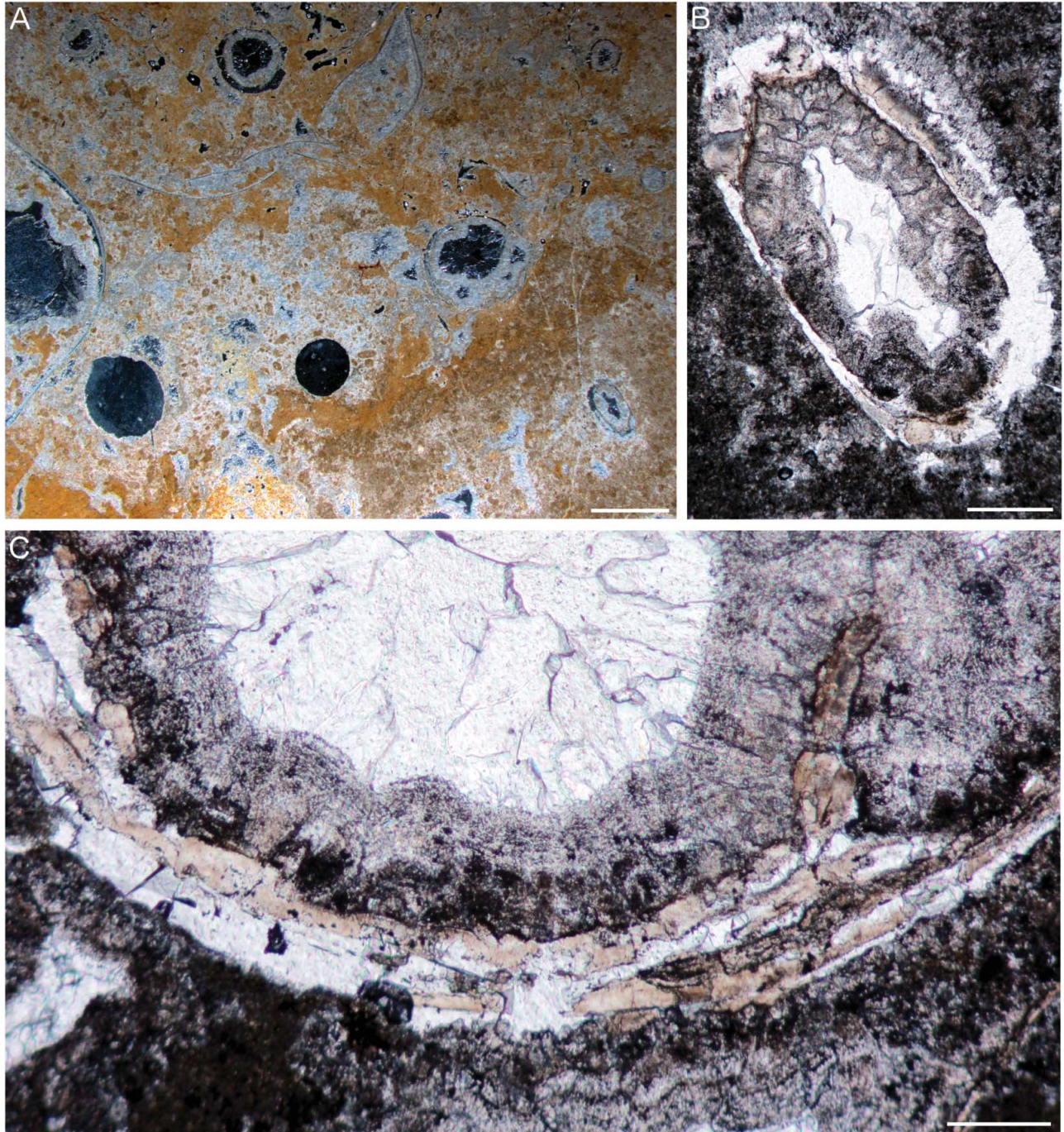


Figure 7. ‘Bear River tubes’, LACMIP 5802 BRB-1, late Eocene, Washington State, USA. **A**, multiple tubes in transverse section with neat round profiles. **B**, small-diameter tube with thick wall. **C**, large-diameter tube with thick wall and showing evidence of multi-layering. Scale bars: A = 2 mm; B = 300 μm ; C = 200 μm .

Description. Non-agglutinated tubes, many of which are partially or fully replaced by silica or siderite, resulting in a dark brown-black or reddish colour, respectively. The tubes do not appear to be branching (Fig. 8A–D), and have walls that, where visible, appear smooth (Fig. 8B, D). Tube diameters range from 0.8 to

2.7 mm, and tubes do not appear to taper distinctly along their lengths. Tube walls are uncompressed, suggesting that they may have originally been rigid, and are multi-layered (Fig. 8E, F). Tube walls are generally not very thick, apart from in a subset of tubes in which the walls are thick and exhibit many layers



Figure 8. A–H, ‘Omagari tubes’, Campanian, Hokkaido, Japan; **A**, OMG03-4a, hand specimen with many, similar-diameter tubes with brown walls encased in carbonate; **B**, OMG03-3b, detail of tube with brown wall, outer wall appears smooth; **C**, **D**, OMG03-1, cluster of tubes (**C**) with mineralized walls but not encased in carbonate, and detail of individual tubes (**D**); **E**, OMG03-2, tubes with brown walls in section; **F**, OMG03-4b, large-diameter tube in transverse section with wall comprised of many layers; **G**, OMG03-1, preserved tear in the wall of a tube suggesting an originally fibrous nature; **H**, clump of Omagari tubes (reproduced from Hikida *et al.* 2003). **I**, clump of the roots of the seep vestimentiferan *Lamellibrachia luymsesi* (donated by C. Fisher). Scale bars: A = 10 mm; B = 1 mm; C = 5 mm; D, E = 2 mm; F = 500 μ m; G = 50 μ m; H, I = 20 mm.

(Fig. 8F). Preserved tears of the tube wall reveal an originally fibrous nature (Fig. 8G).

Remarks. These tubes were interpreted as those of vestimentiferans by earlier work (Hikida *et al.* 2003), but are difficult to identify owing to their lack of ornamentation. They fall among siboglinids when more homoplasy is permitted in the cladistic analysis (Fig. 23B). The tubes were clearly organic, due to preserved wall tears that reveal a fibrous nature. Transverse ornamentation typical of some frenulates or chaetopterids is absent, and the size and clumped nature of the tubes, combined with walls that are sometimes thick and neatly multi-layered, suggests that the Omagari tubes are most likely the roots/posterior portions of vestimentiferan tubes. The morphology of Omagari tube clumps very closely resembles a clump of the roots of the seep vestimentiferan *Lamellibrachia luyesi* (Fig. 8H, I). We therefore tentatively suggest that the Omagari tubes may be vestimentiferan tube roots.

Family *incertae sedis*
 ‘Okukinenbetsu yellow tubes’
 (Fig. 9A–D)

Material. OKb4, OKb4-2, OKb4-4, yellowish-walled tubes observed in thin section. OKb4-5, similar-sized tubes with yellowish walls preserved in a range of orientations. Donated by F. Gill.

Occurrence. Okukinenbetsu River (Kanajirisawa Creek) seep carbonate, Obira-machi, north-western Hokkaido, northern Japan. Mudstone of Middle Ezo Group, Cenomanian, Cretaceous (Majima *et al.* 2005; Kaim *et al.* 2008; Kiel *et al.* 2008a).

Description. Small carbonate tubes, 1.1–2.4 mm in diameter, fairly straight, non-branching and non-agglutinated (Fig. 9A). Tubes are not attached to each other and do not seem to taper much, and the tube walls appear to have originally been somewhat flexible (Fig. 9A). The only ornamentation visible on the tubes is fine, continuous longitudinal wrinkles which occasionally bifurcate (Fig. 9A, B). In thin section, the tube walls are preserved as brown-yellow rims showing evidence of multi-layering and mineral growth between tube layers (delamination) (Fig. 9C, D). Some of the tube sections also show signs of compression and/or shrinkage.

Remarks. Fine longitudinal wrinkles such as those found on these tubes are most often associated with vestimentiferan tubes, and they very closely resemble the small-diameter tubes with longitudinal wrinkles from Canyon River. However, these tubes could not be resolved by the cladistic analysis (Fig. 23) likely due to the poor state of preservation of their wall structure, and are therefore presently only ascribed to the annelids.

?Family *Siboglinidae* Caullery, 1914
 ‘Okukinenbetsu brown tubes’
 (Fig. 9E–I)

Material. OKb4-3, larger tubes with brown walls largely obscured by rock matrix. Donated by F. Gill.

Occurrence. Okukinenbetsu River (Kanajirisawa Creek) seep carbonate, Obira-machi, north-western Hokkaido, northern Japan. Mudstone of Middle Ezo Group, Cenomanian, Cretaceous (Majima *et al.* 2005; Kaim *et al.* 2008; Kiel *et al.* 2008a).

Description. Large brown silicified tubes 3.7–4.3 mm in diameter, uncompressed in section (Fig. 9E) and with clear multi-layering (Fig. 9F–I) that is very thick and well consolidated in some of the tubes (Fig. 9I). Highly frayed edges can be seen, suggesting that tubes were originally organic and fibrous (Fig. 9F).

Remarks. The clear round transverse sections of the larger brown tubes suggests that the tubes were originally rigid. Their size may indicate that the inhabitants were not frenulates, while the structure of the tube wall indicates that they are more likely to have been made by siboglinids than chaetopterids due to the thick, well-consolidated multi-layering. These tubes fall among siboglinids when more homoplasy is permitted in the cladistic analyses (Fig. 23B); therefore, this affinity is only tentatively suggested.

?Family *Siboglinidae* Caullery, 1914
 (?vestimentiferan)
 ‘Troodos collared tubes’
 (Fig. 10A–C)

1999a vestimentiferan worm tubes Little, Cann, Herrington, & Morisseau: 1028, fig. 2b, c.

Material. Kambia 401b, 4061, 4062; Kapedhes 2031, 2051, 2081; Memi 212b2, 2021; Sha 3011, Small worm tubes with collars, generally occurring with other similar tubes. Collected by C. T. S. Little.

Occurrence. Massive sulphide deposits. Troodos Ophiolite, Cyprus. Turonian, Late Cretaceous (Oudin & Constantinou 1984; Little *et al.* 1999a).

Description. Pyritic worm tubes 0.6–1.9 mm in diameter, which appear to have been hard, sinuous, non-branching and not attached to other tubes (Fig. 10A, B). It is not discernible whether or not the tubes taper. The tubes possess short collars which are sometimes slightly flaring and at times are positioned at an oblique angle relative to the tube (Fig. 10C). The tube surface between adjacent collars appears smooth and unornamented (Fig. 10B).

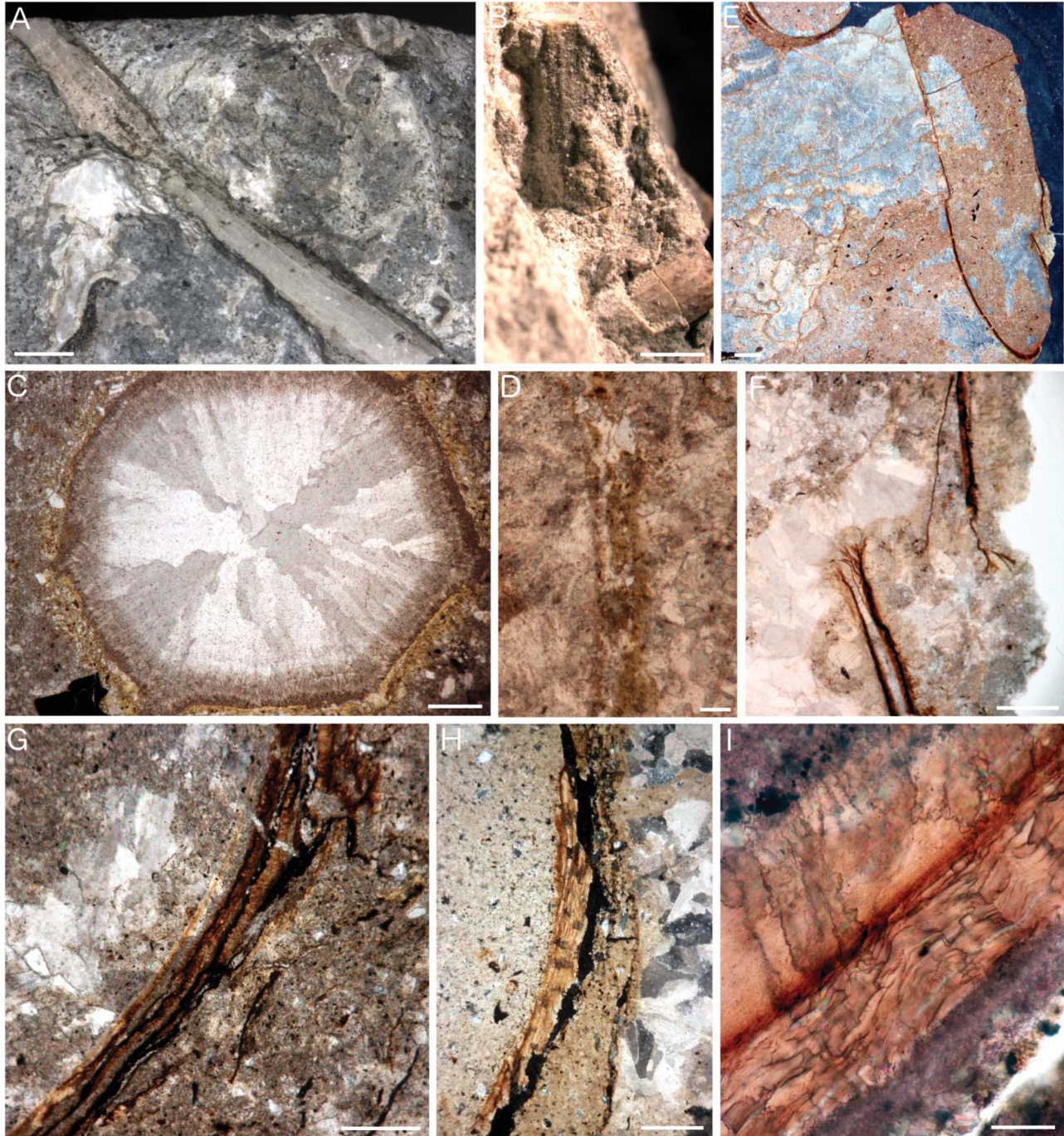


Figure 9. Cenomanian tubes from Okukinenbetsu River, Japan. **A–D**, ‘Okukinenbetsu yellow tubes’; **A**, OKb4-5, long fragment of a tube exhibiting fine longitudinal wrinkles; **B**, OKb4-5, short tube fragments also exhibiting fine longitudinal wrinkles; **C**, OKb4-4, transverse section of tube with yellowish walls; **D**, OKb4-2, detail of a yellow tube wall, showing some evidence of multi-layering. **E–I**, ‘Okukinenbetsu brown tubes’; **E**, OKb4, partial longitudinal and transverse sections of a tube with brown walls; **F**, OKb4, detail of brown-walled tube revealing a multi-layered, fibrous nature; **G–I**, detail of thick, multi-layered brown-walled tubes in OKb4-3 (**G**), OKb4-2 (**H**) and OKb4 (**I**). Scale bars: A, B = 2 mm; C, F = 300 μm ; D, I = 50 μm ; E = 1 mm; G = 150 μm ; H = 200 μm .

Remarks. The similarity of these tubes to those made by vestimentiferans was highlighted by Little *et al.* (1999a), in particular to the spiralling tubes of *Alaysia spiralis*. Siboglinid, chaetopterid and serpulid tubes may all possess collars and occur at vents, while siboglinid and

serpulid tubes may both be highly spiralling. Although the cladistic analysis grouped these tubes with siboglinids when more homoplasy was allowed (Fig. 23B), they cluster near serpulids within the PCA plot (Fig. 21). Although small, the collars of the tubes are at times flaring and



Figure 10. Tubes from the Turonian of Cyprus. **A–C**, ‘Troodos collared tubes’: **A, B**, Kambia 4061 and Memi 212b2, respectively, sinuous worm tubes with collars; **C**, Kambia 401b, worm tube with collar attached at an oblique angle. **D, E**, ‘Troodos wrinkled tubes’, Kapedhes 2101 and 204b, respectively, worm tubes bearing longitudinal and transverse wrinkles. **F, G**, ‘Troodos attached tubes’, Memi 2021 and Kinoussa 2023, respectively, sinuous tubes that appear attached to a surface, tubes in **F** bearing fine parallel transverse wrinkles. Scale bars: **A–D, F, G** = 1 mm; **E** = 0.5 mm.

attached at an oblique angle with respect to the tube, which are features more readily observable on siboglinid tubes (those of vestimentiferans and frenulates). These tubes are therefore tentatively suggested to have been made by vestimentiferans rather than serpulids.

Family **Siboglinidae** Caullery, 1914

(vestimentiferan)

‘**Troodos wrinkled tubes**’

(Fig. 10D, E)

1999a vestimentiferan worm tubes Little, Cann, Herrington, & Morisseau: 1028, fig. 2e.

Material. Kambia 4051, 4061, 6061, t3; Kapedhes 204b, 2101, worm tubes with walls ornamented by transverse and longitudinal wrinkles. Collected by C. T. S. Little.

Occurrence. Massive sulphide deposits. Troodos Ophiolite, Cyprus. Turonian, Late Cretaceous (Oudin & Constantinou 1984; Little *et al.* 1999a).

Description. Generally straight or slightly curving pyritic tubes 1.2–4.5 mm in diameter, which do not show signs of having been flexible and are not attached to other tubes (Fig. 10D, E). Whether tubes taper cannot be assessed with certainty due to the short length of preserved fragments. Tubes do not have collars, and instead possess fine transverse and longitudinal wrinkles on their surfaces, with the transverse wrinkles often being more pronounced and fairly regular (Fig. 10D). Longitudinal wrinkles are fine and occasionally bifurcating (Fig. 10E). One tube specimen has a smaller tube preserved within it.

Remarks. These tubes are resolved among siboglinids by both cladistic and cluster analyses (Figs 22–24), as a result of the fine, bifurcating longitudinal wrinkles as well as the fine transverse wrinkles which they possess. The features above are not observed on serpulid tubes, which sometimes possess coarse longitudinal wrinkles. The longitudinal wrinkles of chaetopterid tubes are often coarser (Kiel & Dando 2009), and have not been observed to be cross-cut by fine transverse wrinkles. We therefore suggest that the most likely builders of these tubes are vestimentiferans, which do exhibit such ornamentation patterns (cf. *Ridgeia piscesae* tubes, Fig. 15G).

Family *incertae sedis*
‘Troodos attached tubes’
 (Fig. 10F, G)

1999a vestimentiferan worm tubes Little, Cann, Herrington, & Morisseau: 1028, fig. 2a.

Material. Kinousa 2023, Memi 2021, sinuous worm tubes that appear attached to a surface, several tubes often occurring together. Collected by C. T. S. Little.

Occurrence. Massive sulphide deposits. Troodos Ophiolite, Cyprus. Turonian, Late Cretaceous (Oudin & Constantinou 1984; Little *et al.* 1999a).

Description. Pyritic tubes 0.2–0.5 mm in diameter, very sinuous (Fig. 10F, G). The tubes have the appearance of being attached to a surface as they are mostly sinuous in two dimensions. Some of the tubes have smooth walls (Fig. 10G) whereas others possess regular fine transverse wrinkles (Fig. 10F). The wrinkled tubes are also somewhat tapering, whereas the smooth tubes do not appear to taper in the fragments observed.

Remarks. These tubes are resolved near siboglinids in cladistic analyses when more homoplasy is permitted (Fig. 23B), and cluster near to serpulids within the PCA plot (Fig. 21). Their attachment suggests an annelid affinity to a lineage such as Serpulidae, Alvinellidae or vestimentiferans (posterior tube sections), in which this characteristic is often observed. For the tubes that exhibit closely spaced transverse wrinkles and taper, Serpulidae

are the most likely tube-builders as these characters are not observed in the tubes of Alvinellidae or in the posterior sections of vestimentiferan tubes. However, this is less clear for the smooth tubes, and it is difficult to tell whether the smooth and transversely wrinkled tubes were made by the same or different taxa. Therefore, these tubes are presently only assigned to the annelids.

?Family **Siboglinidae** Caullery, 1914
 (?vestimentiferan)
‘Ellef Ringnes tubes’
 (Fig. 11A, B, D, E)

1989 serpulid worm tubes Beauchamp, Harrison, Nassichuk, Krouse, & Eliuk: 54, fig. 2.

1992 serpulid worm tubes Beauchamp & Savard: 438, figs 2b, 5b.

2013 tubeworms Willisicroft: 20, fig. 5c, d.

2017 vestimentiferan worm tubes Willisicroft, Grasby, Beauchamp, Little, Dewing, Birgel, Poulton, & Hryniewicz: 797, fig. 8l, m.

Material. NRC C-581891 QQA 10-22, clustered broken fragments of large tubes, mostly in various orientations however some tubes are aligned parallel to each other. NRC C-541891 CPPL, tubes observed in thin section. Provided by S. E. Grasby.

Occurrence. Ellef Ringnes Island seep carbonates, Arctic, Canada. Christopher Formation, Lower Albian, Cretaceous (Beauchamp *et al.* 1989; Beauchamp & Savard 1992; Willisicroft 2013).

Description. Carbonate tubes are non-branching, do not appear attached to other tubes, and are not agglutinated (Fig. 11A, B). They are 2.0–10.0 mm in diameter, more or less straight, and have smooth walls. In thin section, the tubes show very thick, concentrically multi-layered walls (Fig. 11D, E) that are very likely organic due to the presence of breaks in the tube wall that reveal potential torn misaligned layers that have curved slightly away from each other (Fig. 11D, E). The round cross sections suggest that the tubes are likely to originally have been rigid and inflexible.

Remarks. These tubes were previously considered to have been made by serpulids (Beauchamp & Savard 1992; Willisicroft 2013), but have more recently been interpreted as vestimentiferan worm tubes (Willisicroft *et al.* 2017). Evidence of an originally calcareous tube wall such as chevron-like layering is absent, while torn fibres point to the tubes having been originally organic in composition. The thick tube walls and neat, well-consolidated multi-layering are very characteristic of vestimentiferan tubes, and the size of these tubes and their hardness support this interpretation. However, these tubes

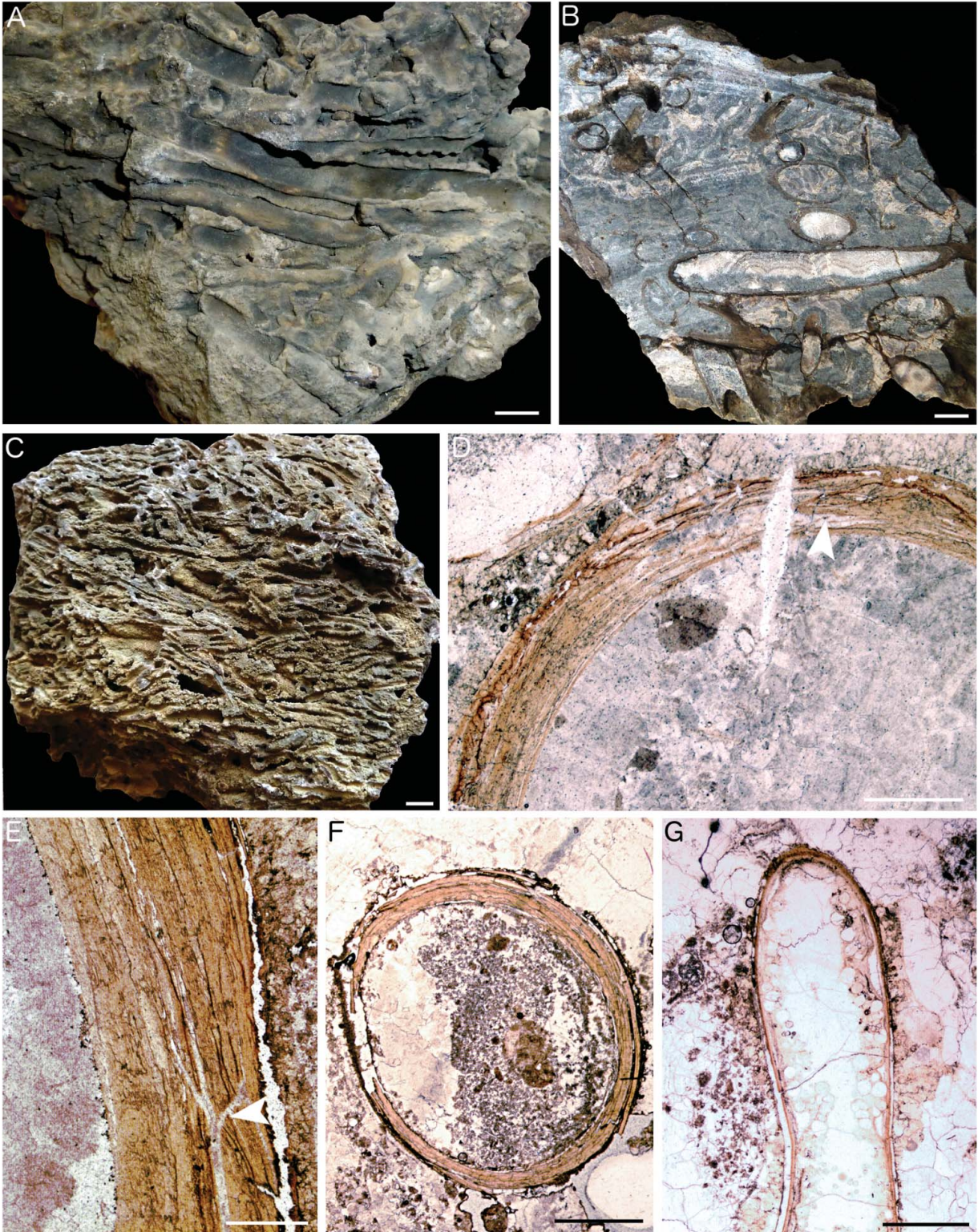


Figure 11. Tubes from the Albian Christopher Formation, Canada. **A, B, D, E**, ‘Ellef Ringnes tubes’: **A**, NRC C-581891 QQA-10-22, tubes in hand specimen; **B**, NRC C-581891 QQA-10-22, sections of tubes; **D**, NRC C-541891CPPL, detail of a transverse section of a tube showing thick, multi-layered tube walls, with some possible misaligned torn fibres (white arrow); **E**, NRC C-541891CPPL, detail of a transverse section of a tube showing a break in the tube wall where it appears broken fibres have curved slightly and misaligned (white arrow). **C, F, G**, ‘Prince Patrick tubes’: **C**, NRC C-453952 1–4, tubes in hand specimen; **F**, NRC C-453961PPL, transverse section of a tube exhibiting thick, multi-layered tube walls; **G**, NRC C-453989PPL, longitudinal section of a tube with thinner walls containing round pellets. Scale bars: A–C = 10 mm; D, F, G = 1 mm; E = 500 μ m.

only group among modern siboglinid tubes when more homoplasy is permitted within the cladistic analysis (Fig. 23B). For the above reasons, we tentatively suggest that the large tubes from Ellef Ringnes Island are likely the anterior sections of vestimentiferan tubes.

?Family **Siboglinidae** Caullery, 1914
(?vestimentiferan)
'Prince Patrick tubes'
(Fig. 11C, F, G)

1992 serpulid worm tubes Beauchamp & Savard: 438, figs 2a, 5a, 8c, d.

Material. NRC C-453952 1-4, Prince Patrick Island, many small tubes cemented together in a large bundle. NRC C-453961 PPL, C-453989 PPL, tubes observed in thin section. Provided by S. E. Grasby.

Occurrence. Prince Patrick Island seep carbonates, Arctic, Canada. Christopher Formation, Lower Albian, Cretaceous (Beauchamp *et al.* 1989; Beauchamp & Savard 1992).

Description. Carbonate tubes mostly 1.0 mm in diameter, but tubes of up to 5 mm also occur in these clumps (Fig. 11C). Tubes are unattached, non-branching and non-agglutinated. Ornamentation of the tube walls is largely obscured due to surface mineralization. In thin section, the tube walls are very similar to those of the large tubes from the same deposit: they are mostly thick and comprise many superimposed layers (Fig. 11F), but some are thin-walled (Fig. 11G). Tube cross-sections are distinctly round (Fig. 11F) suggesting that tubes were originally rigid. Some of the smaller tubes contain small transparent spheres within their interior (Fig. 11G).

Remarks. Tubes from Prince Patrick Island have also been interpreted as having been made by serpulids (Beauchamp & Savard 1992). However, these tubes were probably not originally calcareous in composition due to the absence of chevron-like layering, their neatly laminated tube walls and the separation of wall layers in places, which is unlikely to occur in cemented mineral tubes. Although outer tube wall ornamentation could not be assessed, the at times thick walls that these tubes possess, in combination with the morphology of the tube cluster, suggest that they may represent the fossilized root portions of vestimentiferan tubes (cf. Fig. 8I). These tubes are resolved near siboglinid tubes in the PCA plot (Fig. 21) and near vestimentiferans in the less conservative cladistic analysis (Fig. 24B), and are therefore also tentatively assigned to the vestimentiferans.

Family *incertae sedis*
'Cold Fork Cottonwood Creek tubes'
(Fig. 12)

1995 possibly Pogonophoran worm tubes Campbell: 46, fig. 22.

2002 worm tubes Campbell, *et al.* 71, fig. 9.

Material. CFCC-2A, 2B, CC-F8, CFC-G, CFCC-10-02, yellowish-walled tubes, many occurring together in a range of orientations. Donated by K. A. Campbell.

Occurrence. Cold Fork Cottonwood Creek, northern California, USA. Seep carbonate lenses and nodules with complex cement sequence, Great Valley Group, Aptian–Albian, Cretaceous (Campbell 1995; Campbell *et al.* 2002).

Description. Calcite tubes 0.2–5.4 mm in diameter, non-branching, wavy, non-agglutinated and not appearing to taper along their length (Fig. 12A). Tube walls are smooth in several samples (Fig. 12B) but are generally obscured by the host rock. Tube walls appear poorly preserved (Fig. 12C) and are likely recrystallized (Campbell *et al.* 2002), but seem to have been originally organic due to the presence of folds in the tube layers visible in thin section (Fig. 12D). In places the tubes also appear multi-layered (Fig. 12E). Internal septa have been observed in some of the tubes (Campbell *et al.* 2002), but not during the present study.

Remarks. These tubes have been likened to those of vestimentiferans due to their diameter range (Campbell *et al.* 2002) but with the exception of *Riftia pachyptila* (Gaill *et al.* 1997), internal septa are not reported in the tubes of vestimentiferans. Septa are more commonly observed in chaetopterid and occasionally serpulid tubes, and for this reason these tubes group among chaetopterids in the cladistic analyses. However, the tubes are on the whole difficult to interpret due to the inability to assess tube ornamentation and the poor state of preservation of the tube walls. Therefore, they have not been assigned to a modern annelid group.

Phylum *incertae sedis*
'Wilbur Springs tubes'
(Fig. 13)

Material. WS45A, single tapering tube with a smooth wall, more tubes revealed in thin section. Donated by K. A. Campbell.

Occurrence. Wilbur Springs, northern California, USA. Seep carbonate lenses in serpentinites and siltstone

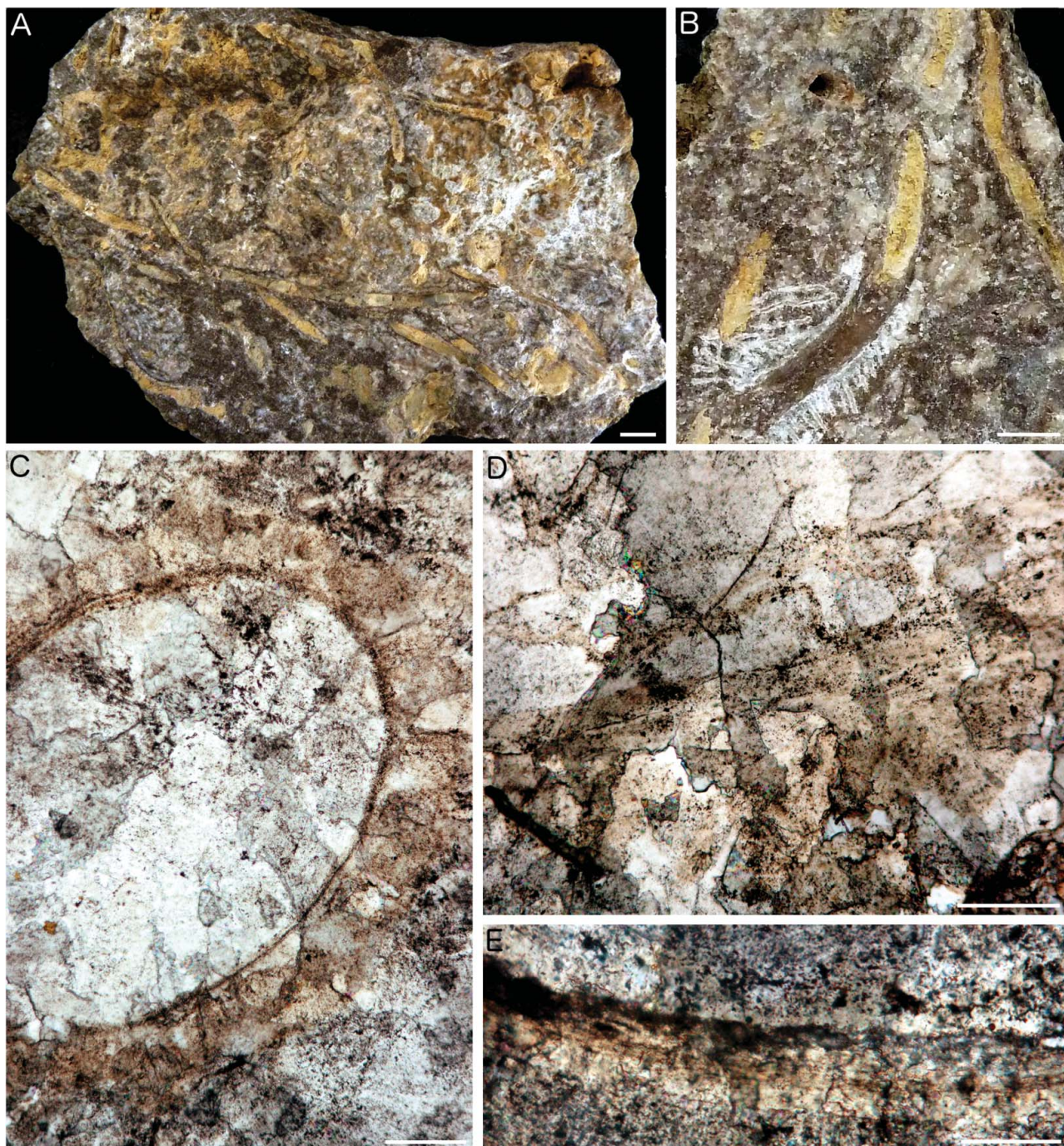


Figure 12. ‘Cold Fork Cottonwood Creek tubes’, Hauterivian, California, USA. **A**, CFC-G, tubes in hand specimen, walls largely obscured by rock matrix. **B**, CFCC-10-02, tube with some visible wall which appears smooth. **C**, CC-F8, transverse section of a tube showing the hazy nature of the walls. **D**, CFCC-2A, detail of tube wall in transverse section showing delaminated, curving tube layers. **E**, CC-F8, detail of tube wall in transverse section showing multi-layered nature. Scale bars: A = 10 mm; B = 5 mm; C, D = 100 μm ; E = 50 μm .

turbidites, Great Valley Group, Hauterivian, Cretaceous (Campbell 1995; Campbell *et al.* 2002).

Description. The single tapering carbonate tube section (27 mm long) measures 2.4–3.6 mm in diameter. Tube

wall is smooth and shiny (Fig. 13A). In thin section, carbonates from Wilbur Springs reveal two types of tubes: thick-walled tubes ~ 2.3 mm in diameter which appear to have been replaced by large calcite crystals (Fig. 13B), and similar-sized tubes that exhibit tube walls with a hazy

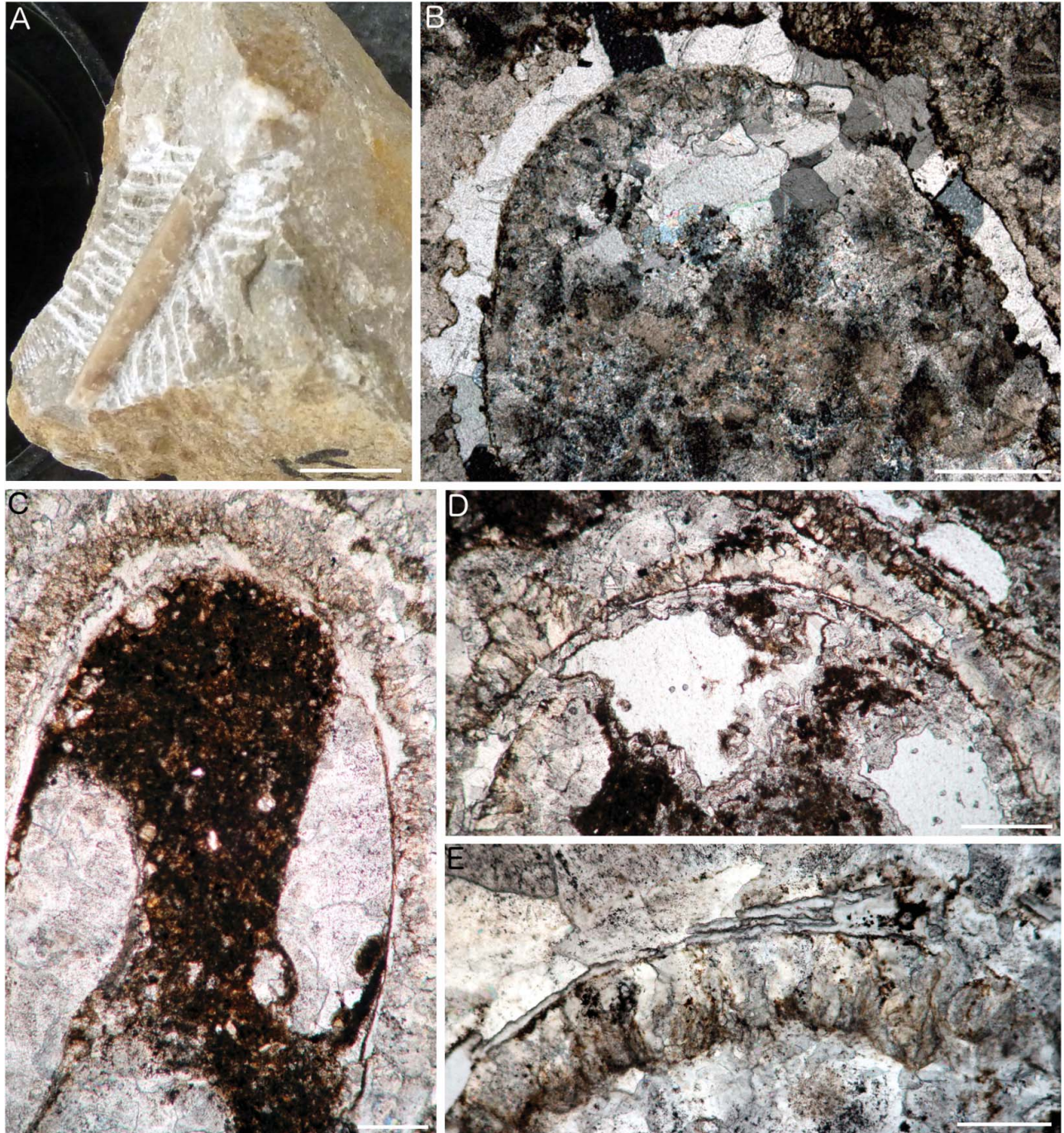


Figure 13. ‘Wilbur Springs tubes’, WS-45, Hauterivian, California, USA. **A**, smooth-walled, tapering tube in hand specimen. **B**, transverse section of tube with replaced wall that may have been originally calcareous in composition. **C–E**, tube walls in near-transverse section with poorly preserved walls that may have originally been organic in composition. Scale bars: A = 10 mm; B = 500 μm ; C, E = 200 μm ; D = 400 μm .

brown rim (Fig. 13C–E). However, due to the poor state of preservation, very few characters can be discerned from either type of tube.

Remarks. These tubes are not preserved well enough to be assigned to a particular animal group, and were not included in cladistic and cluster analyses as so few characters could be coded. However, it is worth noting

that the degree of tapering and smooth wall of the single tube in hand specimen resemble the shells made by scaphopods.

Phylum **Annelida** Lamarck, 1809
 Family *incertae sedis*
 ‘Sassenfjorden area tubes’

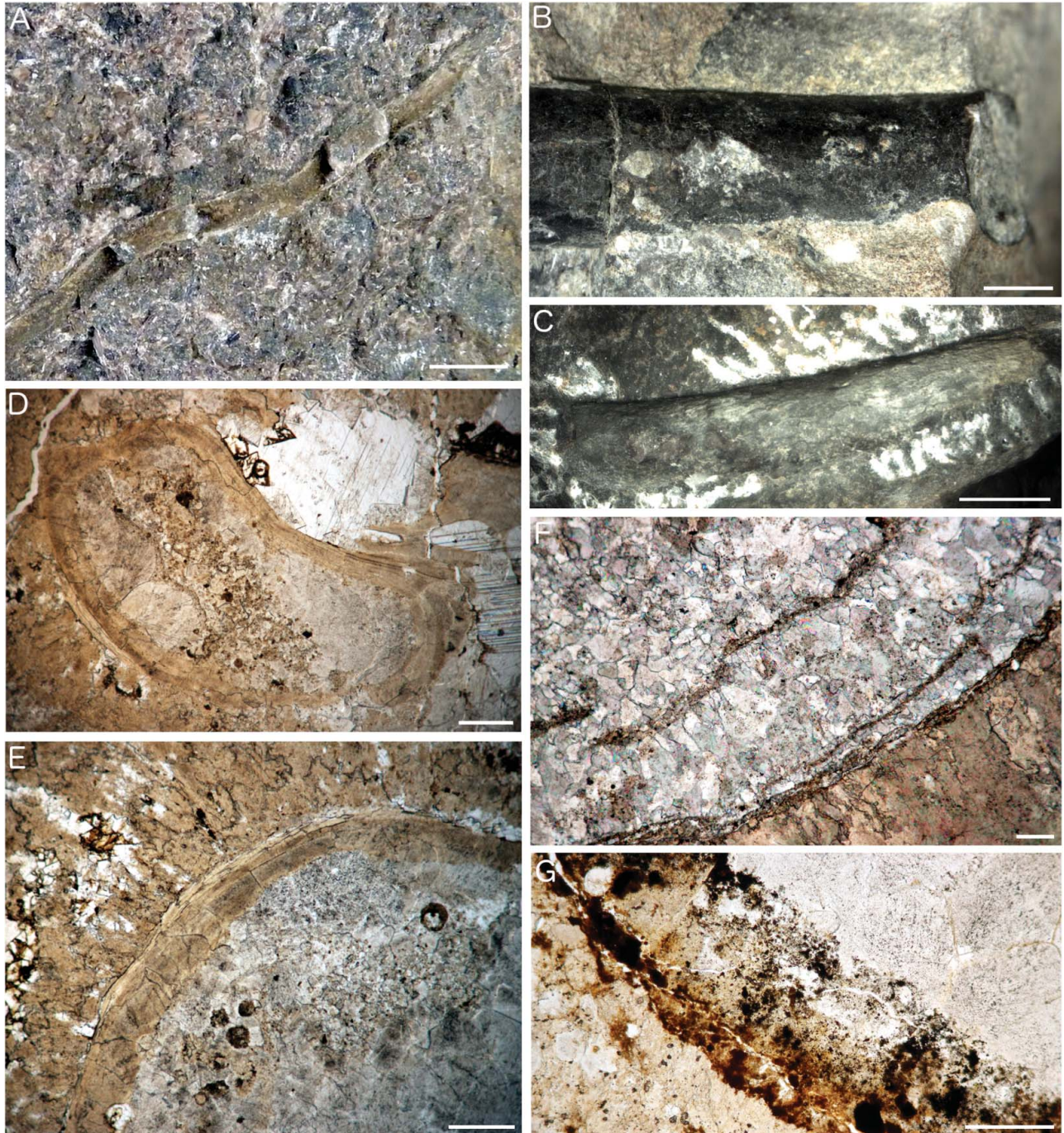


Figure 14. ‘Sassenfjorden area tubes’, Volgian–Ryazanian, Svalbard. **A–C**, hand specimens of tubes; **A**, Svalbard 2007-03, long tube with poorly preserved walls; **B**, PMO 2009-01, smooth-walled tube possibly with a small collar; **C**, PMO 2009-03, tube with possible longitudinal wrinkles. **D, E**, 171.002D, near-transverse sections of tubes with thick, neatly-multi-layered walls. **F**, 170.996, detail from transverse section of a tube where the tube exhibits curving layers that have separated. **G**, 171.027, tube with poorly preserved walls. Scale bars: A = 10 mm; B = 2 mm; C = 5 mm; D, E = 300 μm ; F = 100 μm ; G = 200 μm .

(Fig. 14)

2011 ‘vestmentiferan’ worm tubes Hammer *et al.* 21, fig. 5d.

2012 worm tubes Hryniewicz, Hammer *et al.* 118, fig. 5a.

Material. Svalbard 2007-03, long tube with yellowish wall. PMO 2009-01, single tube with dark black wall. PMO 2009-03: single tube with longitudinal wrinkles. 171.002D, 170.996, 171.027, selection of thin sections of different tubes. Donated by K. Hryniewicz.

Occurrence. Sassenfjorden area, Svalbard. Seep carbonates in shale and shale and siltstone, Slottsmøya Member, upper Agardhfjellet Formation, Volgian–Ryazanian (latest Jurassic–earliest Cretaceous) (Hammer *et al.* 2011; Hryniewicz *et al.* 2012, 2015; Vinn *et al.* 2014).

Description. Carbonate tube sections measuring 2.9–5.7 mm in diameter, all fairly straight, and not attached to other tubes. The long tube appears unornamented (Fig. 14A) and the tube with a black wall is smooth and shows no ornamentation apart from a possible small collar (Fig. 14B), while the remaining tube fragment bears what may be faint longitudinal wrinkles (Fig. 14C). In thin section, some of the tubes exhibit thick, neatly multi-layered walls (Fig. 14D, E). Curving delaminated layers can also be observed in some of the tube sections (Fig. 14F), suggesting that they were originally organic in composition. A subset of tubes exhibit diffuse (poorly preserved?) tube walls (Fig. 14G).

Remarks. Non-serpulid, originally organic-walled tubes from the Sassenfjorden area were suggested to have been made by siboglinids (Hammer *et al.* 2011; Hryniewicz *et al.* 2015). However, the tubes examined do not clearly group with the tubes of modern annelid families included in cladistic and cluster analyses (Figs 22, 24). The tube sections with thick, neatly multi-layered walls that were observed within this study were possibly made by vestimentiferans, in which this tube structure is widely observed. However, the broad morphology of this tube is presently unknown, and tubes from this deposit in general warrant further investigation as several different tube types are present. Hence, these tubes are broadly ascribed to the annelids.

Family **Siboglinidae** Caullery, 1914
(vestmentiferan)
‘Figueroa tubes’
(Fig. 15 A–F, H, I)

1999b Vestimentiferan tube worm Little *et al.*: 168, fig. 2b–d.

2004 Vestimentiferan tube indeterminate Little *et al.*: 545, figs 7.3, 8.1–8.7, 11.5

Material. FF-10, FFC-00, FFC-12, FFC-18, FFC-19, FFC-37, blocks of vent sulphides containing fossilized tube fragments, tubes often occurring singly. Collected by C. T. S. Little.

Occurrence. Figueroa massive sulphide deposit, San Rafael Mountains, southern California, USA. Franciscan Complex, Pliensbachian, Lower Jurassic (Little *et al.* 1999a, 2004).

Description. Pyritic tubes are 0.3–6.9 mm in diameter, appear to have been originally rigid as they do not exhibit folds or depressions in their walls, and are fairly straight (Fig. 15A). One long tube fragment appears to taper along its length (Fig. 15A). Tubes possess collars (Fig. 15B–D) which are large and flaring in some cases (Fig. 15B, D), some tubes showing several collars in short succession (Fig. 15B), the collars sometimes oriented obliquely (Fig. 15C). The tube walls are ornamented with fine, bifurcating longitudinal and irregular transverse wrinkles (Fig. 15A–C, E, F). In section, tube walls are preserved by colloform and framboidal pyrite, and it is unclear whether tubes were originally multi-layered (Fig. 15H, I).

Remarks. These tubes group with siboglinids in both PCA and cladistic analyses (Figs 22, 24). The presence of large, flaring collars suggests that they are unlikely to have been made by chaetopterids. Serpulids and vestimentiferans both produce collars which are large and flaring; however, the pattern of fine longitudinal and irregular transverse wrinkles on tube surfaces suggests that the tubes are more likely to have been made by vestimentiferans, as fine longitudinal wrinkles are not commonly observed in serpulid tubes. The ornamentation of the Figueroa tubes also greatly resembles that of *Ridgeia piscesae* tubes (Fig. 15G). Therefore, we infer that the most likely constructors of the Figueroa tubes were vestimentiferans.

Family *incertae sedis*

Tevidestus serriformis Shpanskaya, Maslennikov & Little, 1999
(Fig. 16A–C)

1999c *Tevidestus serriformis* Little *et al.*: 1062, fig. 4.

Material. NHMUK VF71, single tube fragment. Collected by C. T. S. Little.

Occurrence. Sibay massive sulphide deposit, southern Ural Mountains, Russia (52°41.66'N, 58°38.15'E). Lower–Middle Devonian (Little *et al.* 1999c; Shpanskaya *et al.* 1999).

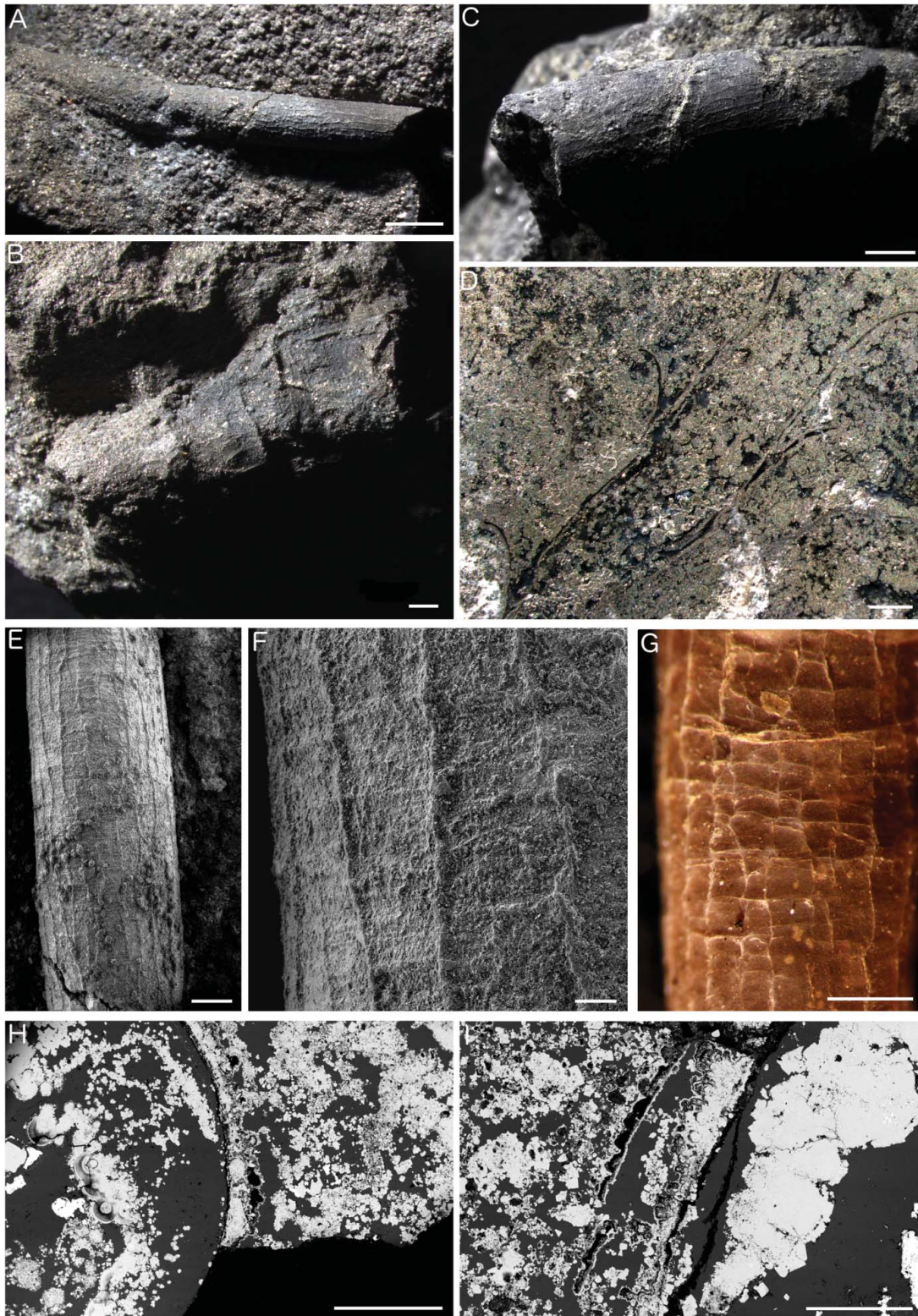


Figure 15. A–F, H, I, ‘Figueroa tubes’, Pliensbachian, California, USA; A–C, tubes in hand specimen; A, FFC-12, straight, tapering tube with fine longitudinal wrinkles; B, FFC-00-21, tube fragment bearing longitudinal wrinkles and collars; C, FFC-18B, tube with longitudinal wrinkles and a fine, obliquely positioned collar; D, FFC-18, longitudinal section of tube exhibiting long, flaring collars; E, FFC-12, scanning electron microscopy (SEM) image showing details of tube wall ornamentation; F, FFC-12, greater detail of same tube; H, FFC-19, detail of tube transverse section showing preservation of tube walls; I, FFC-19, detail of tube wall in transverse section. G, *Ridgeia piscesae* (Siboglinidae) tube, JdF317, showing detail of the ornamentation. Scale bars: A, C = 2 mm; B, D, G, H = 1 mm; E = 500 μ m; F = 100 μ m; I = 300 μ m.

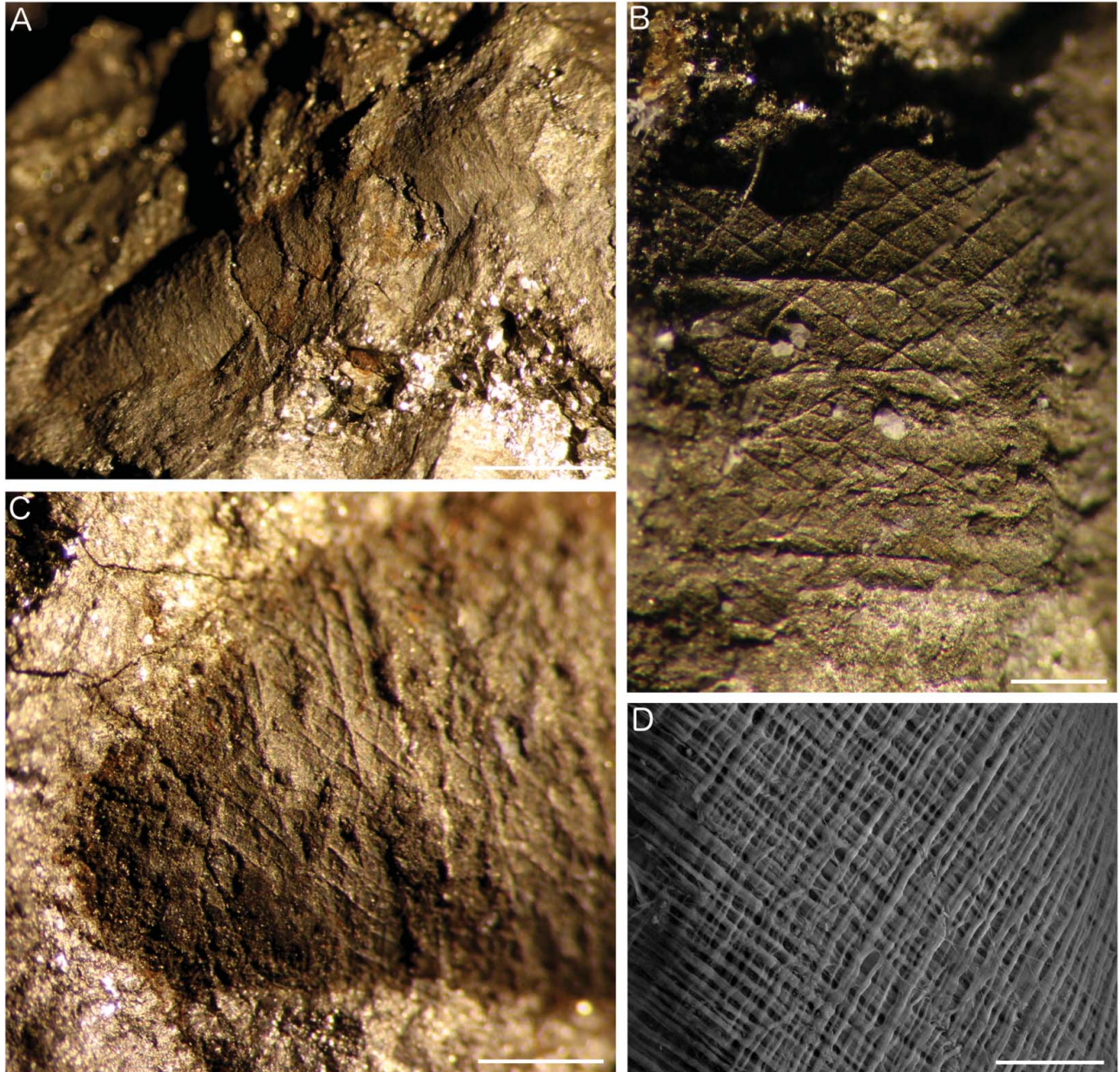


Figure 16. A–C, *Tevidestus serriformis* tubes, Devonian, Sibay, Russia, NHMUK VF71; A, tube fragment exhibiting numerous short collars; B, C, detail of tube wall showing small collars and meshwork of fibres. D, *Phyllochaetopterus prolifica* outer tube wall detail for comparison, NHMUK 1915.5.1.4-6. Scale bars: A = 4 mm; B, C = 1 mm; D = 10 μ m.

Description. Pyritic tubes 10–20 mm in diameter possessing closely spaced collars that can have curved edges (Fig. 16A) (Shpanskaya *et al.* 1999). Collars may be short (Fig. 16B) or slightly flaring. The outer tube wall exhibits a fine mesh of what appear to be pyritized fibres (Fig. 16B, C), which cross each other at near right angles and suggest that these tubes were originally organic in composition.

Remarks. When compared with modern annelid tubes, the fibrous and collared appearance of *Tevidestus*

serriformis tubes suggests they are most likely to have been made by an annelid such as a siboglinid or chaetopterid. These tubes group near chaetopterids and ampharetids in the PCA (Fig. 21), but group with chaetopterids in the more conservative cladistic analysis (Fig. 23A) and are unresolved when more homoplasy is permitted (Fig. 23B). The chaetopterid genera *Phyllochaetopterus* and *Spiochaetopterus* produce tubes with a distinct fibre alignment whereby the sheets of parallel fibres overlap with adjacent sheets at near right angles (Fig. 16D) (Bhaud 1998). However, the fibres that comprise

chaetopterid tubes are much finer than those observed on the tube of *T. serriformis*. The presence of both small and large flaring collars on *T. serriformis* tubes would be more indicative of vestimentiferan tubes; however, as such large fibres are not observed in vestimentiferan tube walls either, it is not possible to assign *T. serriformis* tubes to a particular modern annelid group. *Tevidestus serriformis* tubes also do not resemble Palaeozoic non-vent/seep tubes. *Tevidestus serriformis* tubes are not rapidly tapering like cornulitids (Vinn & Mutvei 2005) and *Hyolithellus* (Skovsted 2006). *Gaojishania cyclus* tubes bear small annulations resembling collars (Cai *et al.* 2013); however, these tubes are more irregular along their length, while *Conotubus* fossils do not possess the mesh-fibre pattern preserved on *T. serriformis* tubes. *Tevidestus serriformis* tubes are therefore presently assigned to the annelids.

?Phylum **Annelida** Lamarck, 1809

Family *incertae sedis*

‘Sibay tubes’

(Fig. 17)

1999c Indeterminate annelid? tube Little, Maslennikov, Morris, & Gubanov: 1061, figs 4, 5.

Material. NHMUK VF71, cluster of tubes. Collected by C. T. S. Little.

Occurrence. Sibay massive sulphide deposit, southern Ural Mountains, Russia (52°41.66'N, 58°38.15'E). Middle-Lower Devonian (Little *et al.* 1999c; Shpanskaya *et al.* 1999).

Description. Pyritic tubes 0.3–7.0 mm in diameter, non-tapering, sometimes gently curved and with smooth walls (Fig. 17A, B) (Little *et al.* 1999c). The tube walls were

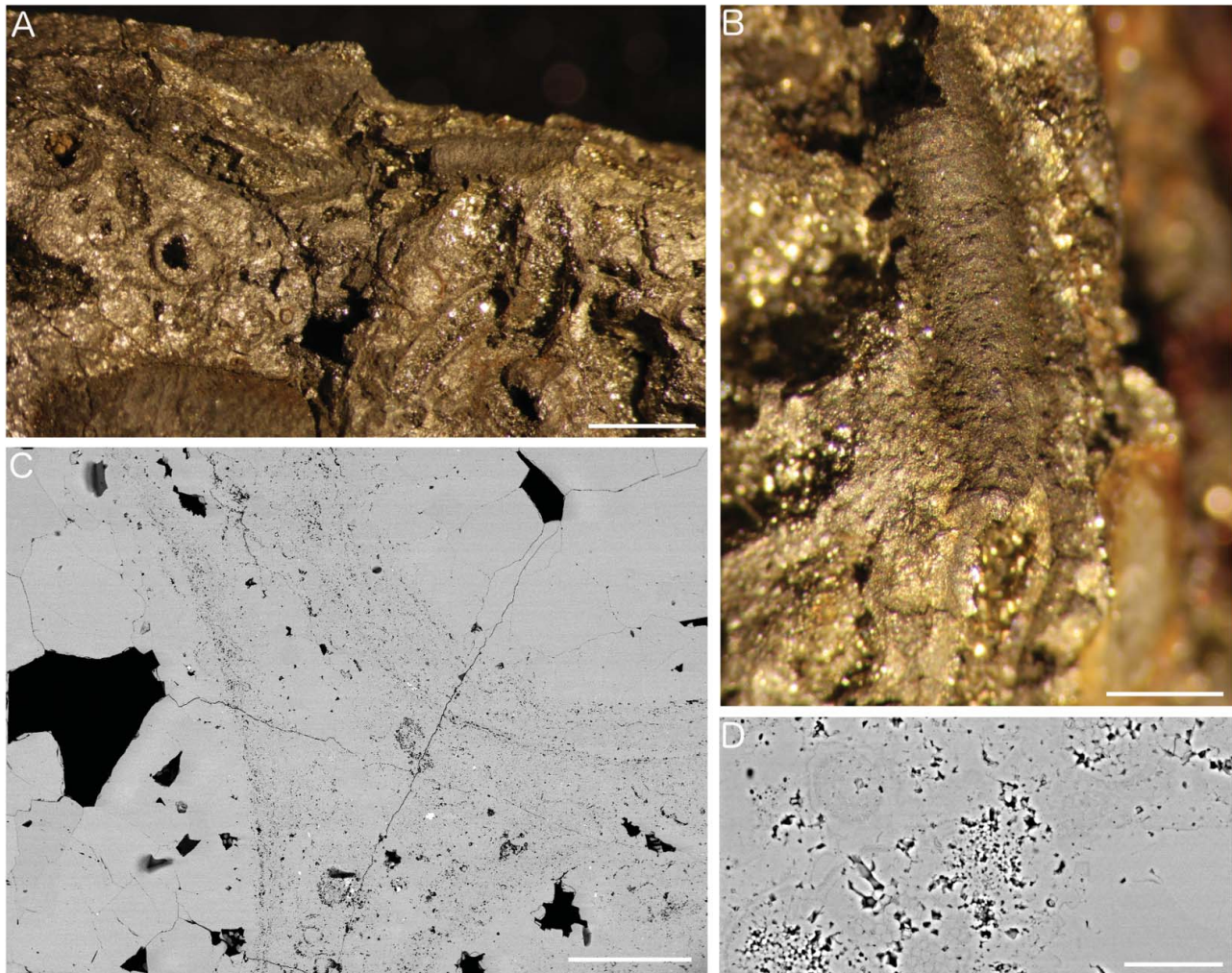


Figure 17. ‘Sibay tubes’, NHMUK VF71, Devonian, Sibay, Russia. **A**, hand specimen showing cluster of tubes in various orientations. **B**, detail of tube wall showing smooth appearance. **C**, detail of the walls of three adjacent tubes in transverse section; walls appear thick and multi-layered. **D**, detail of framboidal pyrite preserving tube walls. Scale bars: A = 3 mm; B = 1 mm; C = 500 μm ; D = 10 μm .

originally described to be formed of fine-grained pyrite which is occasionally colloform (Little *et al.* 1999c). In thin sections examined during the present study, the tube walls appear thick and may be multi-layered (Fig. 17C), and some also appear to be comprised of framboidal pyrite (Fig. 17D).

Remarks. These tubes exhibit few distinguishing characteristics, which led to their previous diagnosis as indeterminate ?annelid tubes (Little *et al.* 1999c). As we were unable to find further characters, the tubes were largely unresolved within cluster and cladistic analyses (Figs 22, 24). The indeterminate status of the tubes is therefore maintained. They are tentatively suggested to be annelid tubes due to their smooth, thick and possibly multi-layered walls, and as they do not closely resemble the tubes of other Palaeozoic tubicolous animals.

Phylum *incertae sedis*

Eoalvinellodes annulatus Little, Maslennikov,
Morris, & Gubanov, 1999c
(Fig. 18)

1999c *Eoalvinellodes annulatus* Little, Maslennikov,
Morris, & Gubanov: 1060, fig. 5.

2006 *Eoalvinellodes annulatus* Buschmann & Maslennikov:
146, figs 5, 6, 8.

Material. NHMUK VF50-55, 57, 60-61, 102, NHMUK OR 1388a, tubes occurring either singly or in small clumps. UL YKB-1, thick-walled tubes observed in thin section. Collected by C. T. S. Little.

Occurrence. Yaman Kasy massive sulphide deposit, southern Ural Mountains, Russia (51°24.43'N, 57°41.63'E). Late Ordovician or earliest Silurian (Little *et al.* 1999c; Shpanskaya *et al.* 1999; Buschmann & Maslennikov 2006).

Description. Small pyrite-walled tubes 0.1–3.5 mm in diameter, non-branching and slightly tapering (Fig. 18A, B) (Little *et al.* 1999c; Buschmann & Maslennikov 2006). Tubes are straight to wavy, and do not show evidence of having been flexible before fossilization (Fig. 18A–C). The tubes show ornamentation of pronounced transverse wrinkles, which occasionally bifurcate, on what is considered to be their inner surface, and are smooth externally (Little *et al.* 1999c). In section, tube walls comprise a single thick layer of framboidal pyrite (Little *et al.* 1999c), or can be preserved with thick walls of finely layered colloform pyrite (Fig. 18D–F).

Remarks. These tubes were originally suggested to have been made by an alvinellid-like polychaete due to their proximity to hydrothermal vent chimneys (Little *et al.* 1999c). However, alvinellid tubes do not exhibit the neat,

bifurcating transverse wrinkles seen in *Eoalvinellodes annulatus* tubes; alvinellid tubes are often much more disorganized. Similar transverse folded fabric-like textures occur in the tubes of chaetopterids, some frenulates and the Palaeozoic fossils *Sabellidites cambriensis* (Moczyłowska *et al.* 2014) and *Sinotubulites* (Cai *et al.* 2015). This texture is, however, much finer on frenulate and *S. cambriensis* tubes than *E. annulatus* tubes. *Eoalvinellodes annulatus* tubes group with those of chaetopterids when more homoplasy is permitted within the cladistic analysis (Fig. 23B) due to the coarse transverse wrinkles which they both exhibit. The wrinkles on *E. annulatus* tubes have a somewhat neater appearance, and also resemble *Glyphanostomum* tubes (Fig. 20N). As several types of annelid and non-annelid tubes are found to possess this type of tube wall ornamentation, it is not possible to infer the taxonomic affinity of the tube maker.

Phylum *incertae sedis*

Yamankasia rifeia Shpanskaya, Maslennikov &
Little, 1999
(Fig. 19)

1999 *Yamankasia rifeia* Shpanskaya, Maslennikov &
Little: 225, plate 3, figs 1–6.

1999c *Yamankasia rifeia* Little, Maslennikov, Morris, &
Gubanov: 1064, figs 6, 7.

2006 *Yamankasia rifeia* Little *et al.*; Buschmann &
Maslennikov: 147, figs 7, 8.

Material. NHMUK VF78, 80, 84, 89, 97, NHMUK OR 6468a, 6468b, very large tubes mostly preserved singly. UL 61633, partial tube in polished block. Collected by C. T. S. Little.

Occurrence. Yaman Kasy massive sulphide deposit. Ural Mountains, Russia (51°24.43'N, 57°41.63'E). Late Ordovician or earliest Silurian (Little *et al.* 1999c; Shpanskaya *et al.* 1999; Buschmann & Maslennikov 2006).

Description. These are the largest of the fossil vent and seep tubes, 3.0–39.0 mm in diameter, with pyritic walls (Fig. 19A). They are not branching and are thought to taper at their base (Little *et al.* 1999c; Buschmann & Maslennikov 2006). The tubes appear to have been originally flexible as they often show folding and creases (Fig. 19B), suggesting an originally fibrous and organic nature, and one tube also exhibits possible fossilized fibres on its surface (Fig. 19C). The tubes are fairly straight, and some well-preserved tubes show very fine parallel and closely spaced longitudinal wrinkles on their outer tube surfaces (Fig. 19D). The tubes may also be transversely wrinkled (Buschmann & Maslennikov 2006). In thin section, the tubes

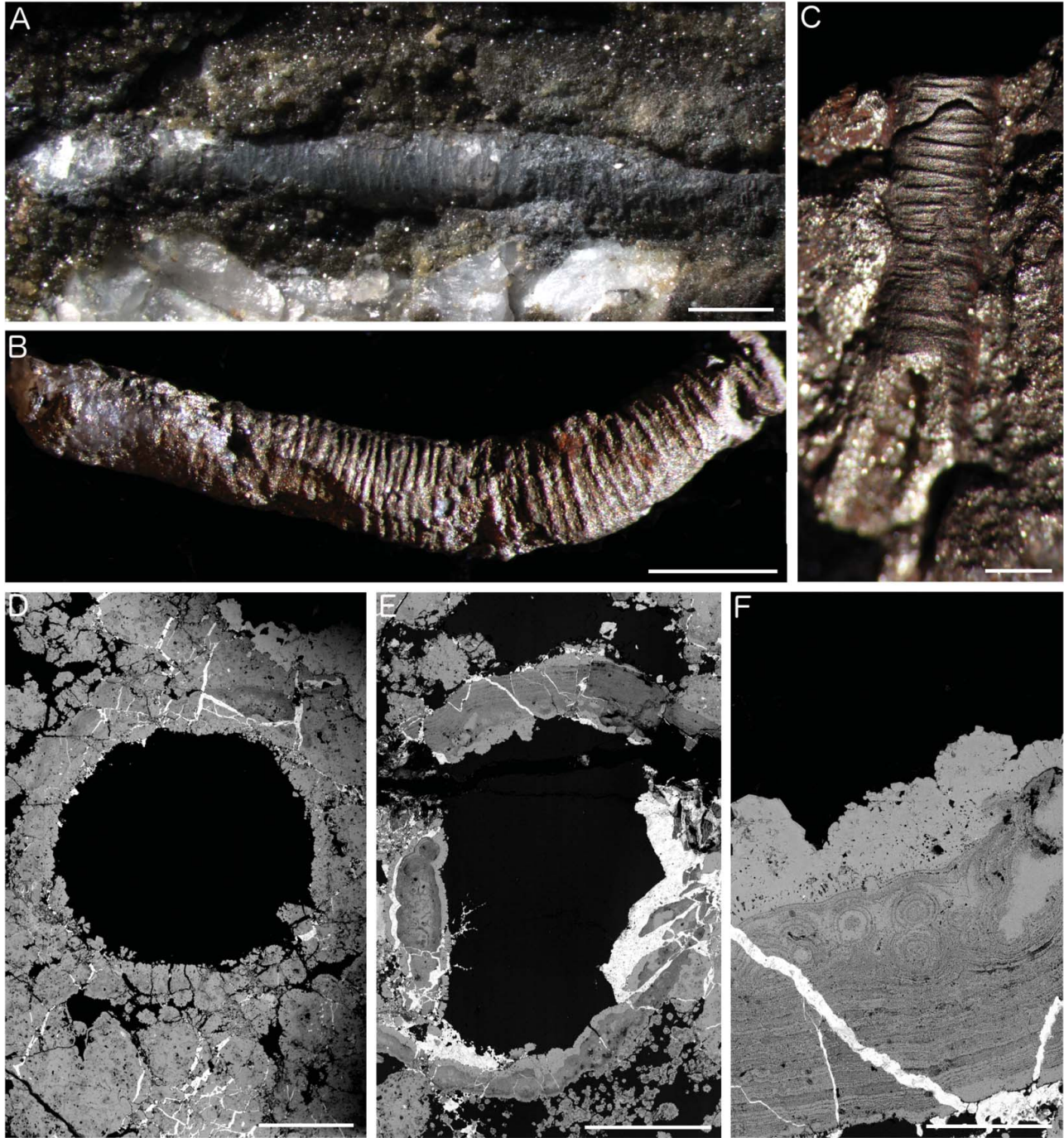


Figure 18. *Eoalvinellodes annulatus*, Silurian, Yaman Kasy, Russia. **A–C**, NHMUK OR1388a, NHMUK VF52 and NHMUK VF53, respectively, hand specimens of gently curving tubes with folded fabric-like tube wall texture. **D, E**, UL YKB1, transverse sections of tubes showing thick walls with thick, possibly multi-layered walls. **F**, UL YKB1, detail of tube wall in transverse section showing preservation by colloform pyrite many layers thick. Scale bars: A, B = 2 mm; C = 1 mm; D, E = 500 μm ; F = 100 μm .

comprise several concentric layers of framboidal pyrite (Fig. 19E, F), while in some specimens colloform pyrite is interpreted to have grown on the outside of the tubes (Fig. 19G) (Little *et al.* 1999c).

Remarks. These tubes are unique amongst hydrothermal vent and cold seep fossils because of their size, and also their distinct fine and parallel longitudinal wrinkles. Very large tubes at modern hydrothermal vents are constructed

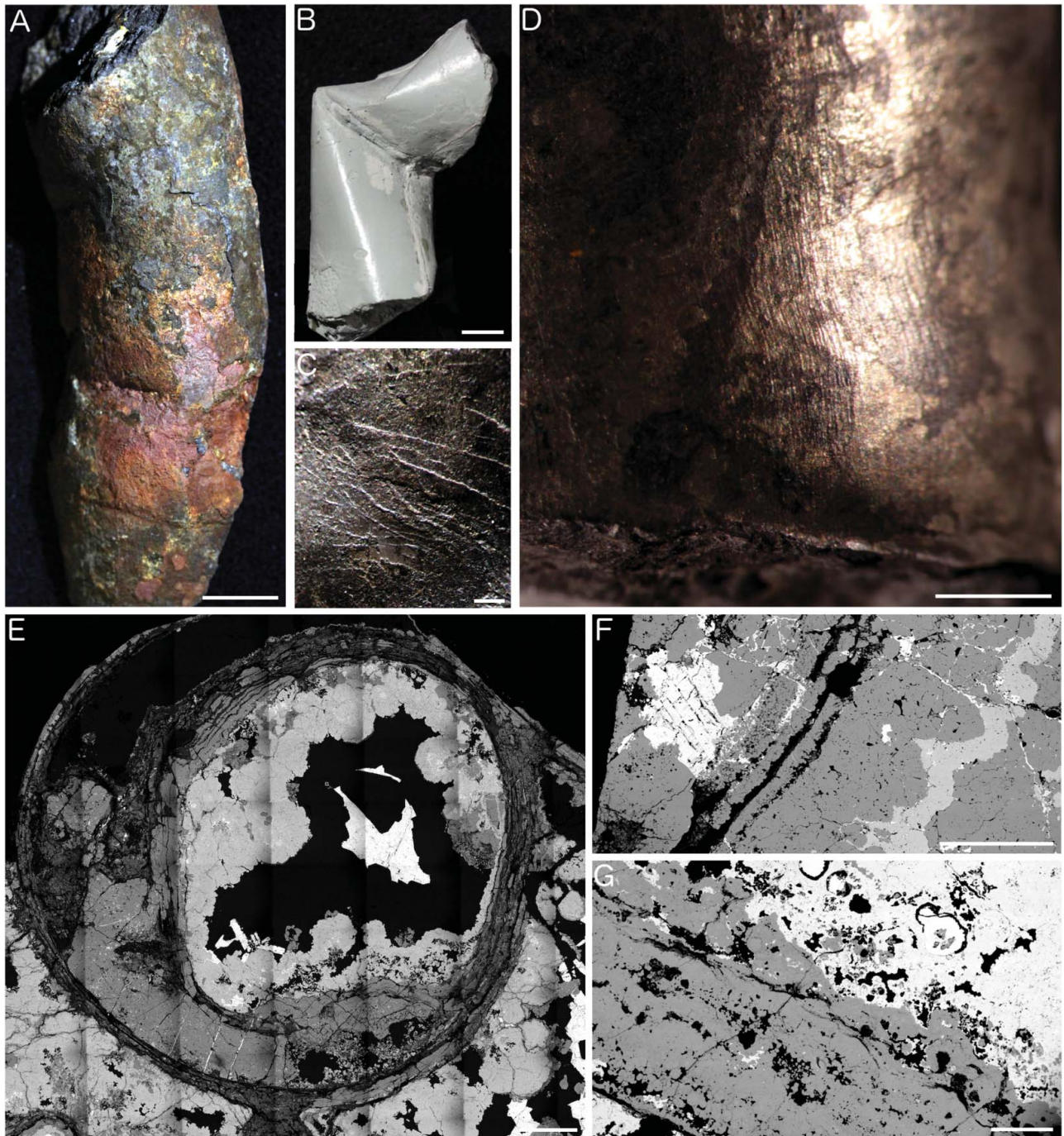


Figure 19. *Yamankasia rifeia*, Silurian, Yaman Kasy, Russia. **A**, NHMUK VF84, large tube in hand specimen. **B**, NHMUK VF97, cast of tube exhibiting fold. **C**, NHMUK VF78, pyritized fibres or filamentous micro-organisms preserved on the outside of a tube. **D**, NHMUK VF78, fine longitudinal wrinkles preserved on outer tube surface. **E**, NHMUK OR6468a, tube in transverse section with thick, multi-layered wall. **F**, NHMUK OR6468b, tube wall in transverse section preserved as several layers. **G**, UL 61633, detail of tube transverse section showing colloform pyrite interpreted as having grown on the outside of the tube. Scale bars: A = 10 mm; B = 5 mm; C = 500 μm ; D = 3 mm; E = 1.5 mm; F, G = 500 μm .

by *Riftia pachyptila* but these do not show the same ornamentation. The root tubes of some vestimentiferans show similar ornamentation of parallel closely spaced longitudinal wrinkles, but it is unlikely that the tubes of

Yamankasia rifeia are root portions because of their size. The large size also means that they are unlikely to be frenulate tubes, despite grouping with frenulates in the cladistic and PCA analyses (Figs 22, 24). The above



Figure 20. Morphology of tubes made by annelid lineages occurring at modern hydrothermal vents and cold seeps (see Supplementary Table S3 for details). **A**, disorganized tubes of *Alvinella* spp. (Alvinellidae). **B**, agglutinated tube of *Mesochaetopterus taylori* (Chaetopteridae). **C**, agglutinated Sabellidae tube. **D**, branched tube of *Phyllochaetopterus claparedii* (Chaetopteridae). **E**, segmented tubes of *Spiochaetopterus costarum* (Chaetopteridae). **F**, *Phyllochaetopterus polus* (Chaetopteridae) tubes bearing short collars and wrinkled-fabric ornamentation. **G**, collared Serpulidae tubes (likely *Serpula narconensis*). **H**, collared tubes of *Serpula vermicularis* (Serpulidae). **I**, large tube of the vestimentiferan *Riftia pachyptila* (Siboglinidae). **J**, collared, ornamented tube of the vestimentiferan *Ridgeia piscesae* (Siboglinidae). **K**, smooth tube of the vestimentiferan *Escarpia southwardae* (Siboglinidae). **L**, collared tubes of the frenulate *Polybrachia canadensis* (Siboglinidae). **M**, hard tubes of the frenulate *Siphonobrachia lauensis* (Siboglinidae). **N**, *Glyphanostomum* tube. **O**, detail of the wall of an *Alvinella* spp. tube in transverse section. **P**, detail of the wall of an *M. taylori* tube in transverse section. **Q**, detail of the wall of a *Megalomma vesiculosum* (Sabellidae) tube in transverse section. **R**, detail of the wall of a Serpulidae tube in transverse section. **S**, **T**, detail of the wall of a *Spiochaetopterus typicus* (Chaetopteridae) tube; **S**, transverse section; **T**, same tube in longitudinal section. **U**, **V**, detail of the wall of a *P. polus* tube; **U**, transverse section; **V**, same tube in longitudinal section. **W**, **X**, *E. southwardae* tube; **W**, detail of the anterior tube wall in transverse section; **X**, transverse section of the posterior tube wall. **Y**, **Z**, **A'**, frenulate *Unibrachium colombianum* (Siboglinidae) tube; **Y**, transverse section of the very anterior portion of the tube; **Z**, longitudinal section of the ringed middle region of the same tube; **A'**, transverse section of the middle tube region. Scale bars: A, B, D, E, F, H, I, J, M = 10 mm; G = 3 mm; C, L = 5 mm; K = 20 mm; N = 1 mm; O = 200 μm ; P, S, U, V = 500 μm ; Q, Y = 300 μm ; R = 50 μm ; T, W, Z, A' = 200 μm ; X = 125 μm .

characteristics are also not consistent with the tubes of other Palaeozoic tubicolous animals and therefore *Y. rifeia* tubes are not likened to any particular modern annelid group.

Tube similarities and phylogenetic relationships

The PCA analysis showed distinct clustering of modern annelid tubes according to family (Fig. 21). Fossil tubes were largely positioned between modern tube groupings, although some fossil taxa plotted in closer proximity to siboglinid tubes. Scores for the first two coordinate axes

account for approximately 30% of the variation in the data (Supplementary File 1, Table S6).

The cladistic analysis of modern tubes only (Fig. 22) was able to group most of the taxa according to established annelid taxonomic lineages based on the 48 defined tube morphological characters. The majority of chaetopterids grouped with other chaetopterid species, and all serpulids grouped together, despite also grouping with chaetopterids. Siboglinid and sabellid tubes also mostly grouped with members of the same family. However, the defined characters did not resolve relationships between annelid families according to established annelid phylogenies (e.g. Weigert *et al.* 2014).

When fossils are included in the cladistic analyses, many taxa, including the majority of fossils, are left

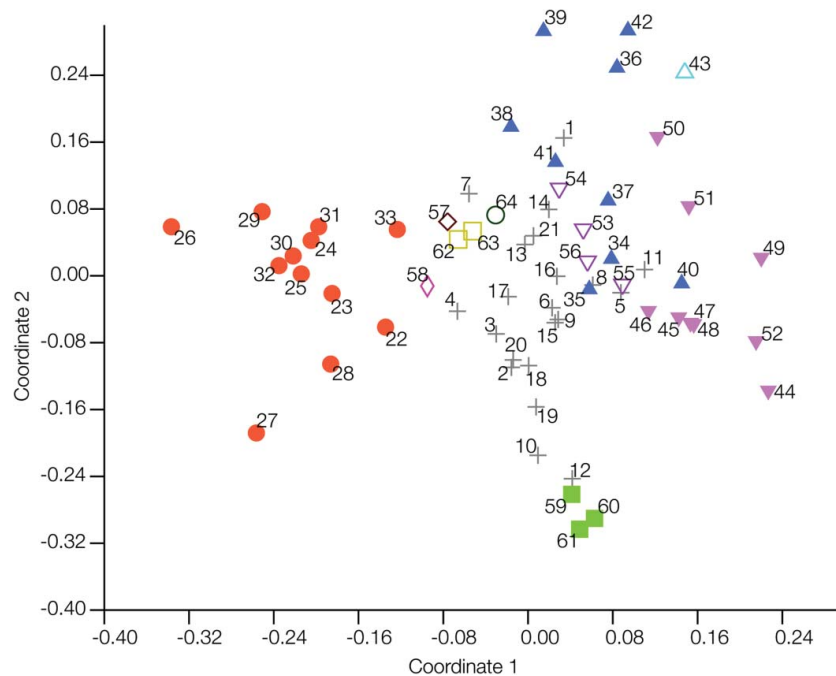


Figure 21. Principal coordinate analysis plot of modern and fossil annelid tubes, based on the 48 characters scored for this study. Fossils (grey crosses): 1. *Yamankasia rifeia*; 2. *Eoalvinellodes annulatus*; 3. ‘Sibay tubes’; 4. *Tevidestus serriformis*; 5. ‘Figuroa tubes’; 6. ‘Sassenfjorden area tubes’; 7. ‘Cold Fork Cottonwood Creek tubes’; 8. ‘Prince Patrick tubes’; 9. ‘Ellef Ringnes tubes’; 10. ‘Troodos attached tubes’; 11. ‘Troodos wrinkled tubes’; 12. ‘Troodos collared tubes’; 13. ‘Okukinenbetsu yellow tubes’; 14. ‘Okukinenbetsu brown tubes’; 15. ‘Omagari tubes’; 16. ‘Canyon River tubes’; 17. ‘Murdock Creek tubes’; 18. ‘West Fork Satsop River tubes’; 19. Serpulidae sp., ‘Bexhaven’; 20. ‘Upper Waiiau River tubes’; 21. ‘Rocky Knob tubes’. Modern tubes: Chaetopteridae (orange dots): 22, *Chaetopterus cf. variopedatus*; 23, Chaetopteridae id83; 24, *Phyllochaetopterus polus*; 25, *P. gigas*; 26, *P. claparedii*; 27, *P. prolifica*; 28, *P. socialis*; 29, *Spirochaetopterus izuensis*; 30, *S. sagamiensis*; 31, *S. costarum*; 32, *S. typicus*; 33, *Mesochaetopterus taylori*. Siboglinidae, frenulata (dark blue filled triangles): 34, *Galathealinum arcticum*; 35, *Lamellisabella denticulata*; 36, *Oligobrachia gracilis*; 37, *Polybrachia canadensis*; 38, *Siboglinum ekmani*; 39, *S. lacteum*; 40, *Siphonobrachia lauensis*; 41, *Unibrachium colombianum*; 42, *Zenkevitchiana longissima*; 43. Siboglinidae, *Sclerolinum* (light blue outline triangle): *S. contortum*; Siboglinidae, vestimentiferans (light purple filled inverted triangles): 44, *Alaysia spiralis*; 45, *Arcovestia ivanovi*; 46, *Escarpia southwardae*; 47, *Lamellibrachia anaximandri*; 48, *Paraescarpia echinospica*; 49, *Ridgeia piscesae*; 50, *Riftia pachyptila*; 51, *Tevnia jerichonana*; 52, *Seepiophila jonesi*; Siboglinidae, vestimentiferan roots (dark purple outline inverted triangles): 53, *E. southwardae* root; 54, *L. anaximandri* root; 55, *S. jonesi* root; 56, *P. echinospica* root; Alvinellidae (maroon outline diamond): 57, *Alvinella* sp.; Ampharetidae (fuchsia outline rhombus): 58, *Glyphanostomum* sp.; Serpulidae (lime filled squares): 59, Serpulidae sp. JCR; 60, *Serpula vermicularis*; 61, *Vermiliopsis infundibulum*; Sabellidae (yellow outline squares): 62, *Sabella pavonina*; 63, *Megalomma vesiculosum*; Oweniidae (dark green outline dot): 64. *Owenia fusiformis*.

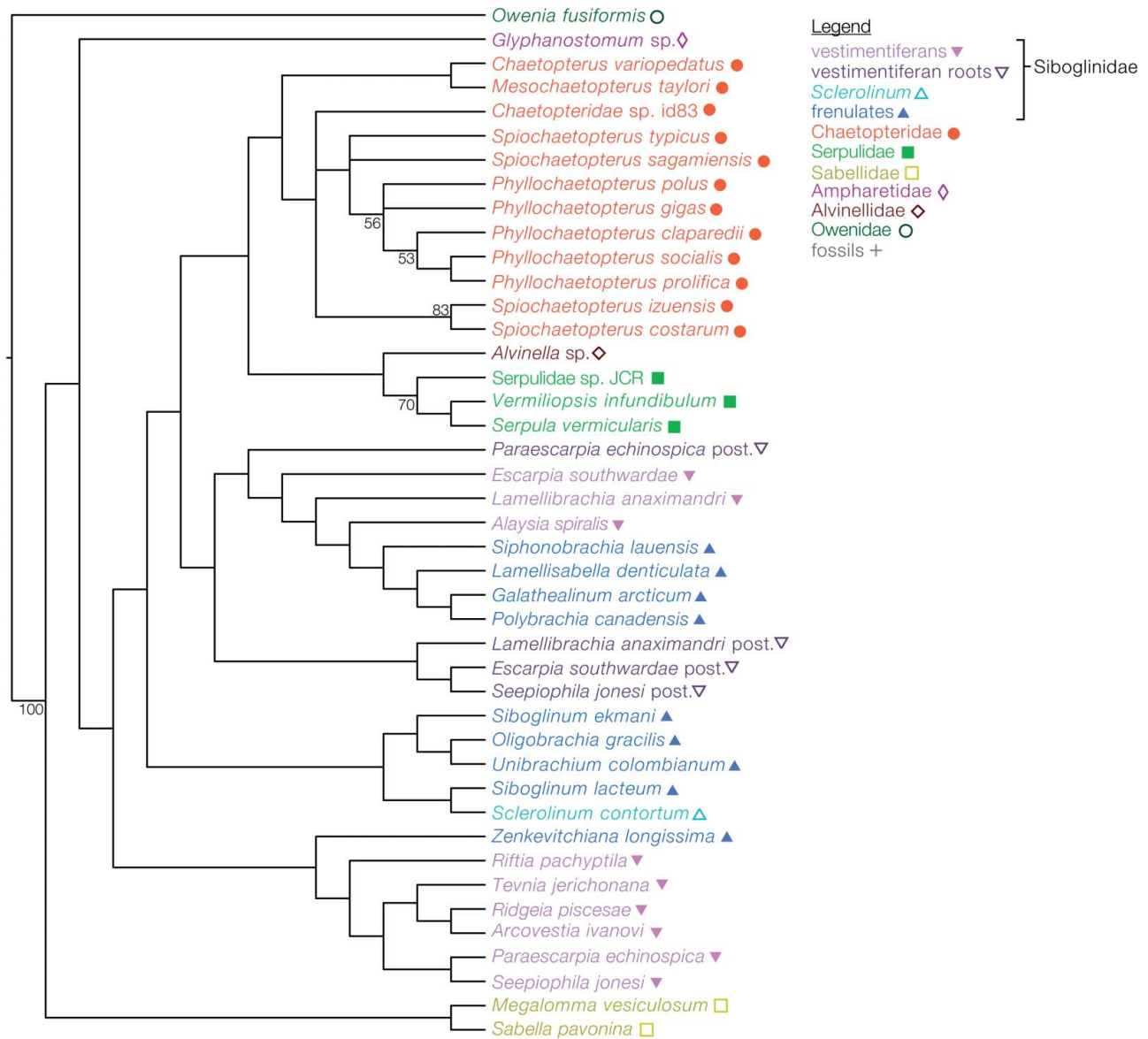


Figure 22. Strict consensus cladogram of the three most parsimonious trees of tubes built by a total of 43 modern annelid taxa (best score = 14.344, consistency index = 0.308, retention index = 0.629). The analysis was based on the 48 mostly morphological tube characters and was performed using implied character weighting ($k = 3$). Numbers on nodes represent groups present/contradicted support values. Symbols/colours indicate taxonomic affinities.

unresolved when homoplastic characters are down-weighted to a greater extent ($k = 3$; Fig. 23A). When homoplastic characters are down-weighted less ($k = 4$; Fig. 23B), a greater proportion of fossil taxa are resolved. With both of these analyses, however, modern siboglinid and chaetopterid tubes are divided. Consistency and retention indices for the cladistic analysis reflect a high degree of homoplasy, and that characters mostly retain potential synapomorphies in the modern taxa only (Fig. 22) and the $k = 4$ fossils-included analyses (Fig. 23B), but not within the $k = 3$ analysis including fossils (Fig. 23A). The inclusion of molecular data for the modern tubicolous annelids improved the resolution of

evolutionary relationships between annelid families (Supplementary File 1, Figs S1, S2). However, this did not improve the resolution of trees containing fossil taxa (Supplementary File 1, Fig. S3).

Organic constituents of modern tubes and their preservation

Screening of organic tubes for potential differences in composition using FTIR showed that tubes from the annelid families Siboglinidae and Alvinellidae had distinctly

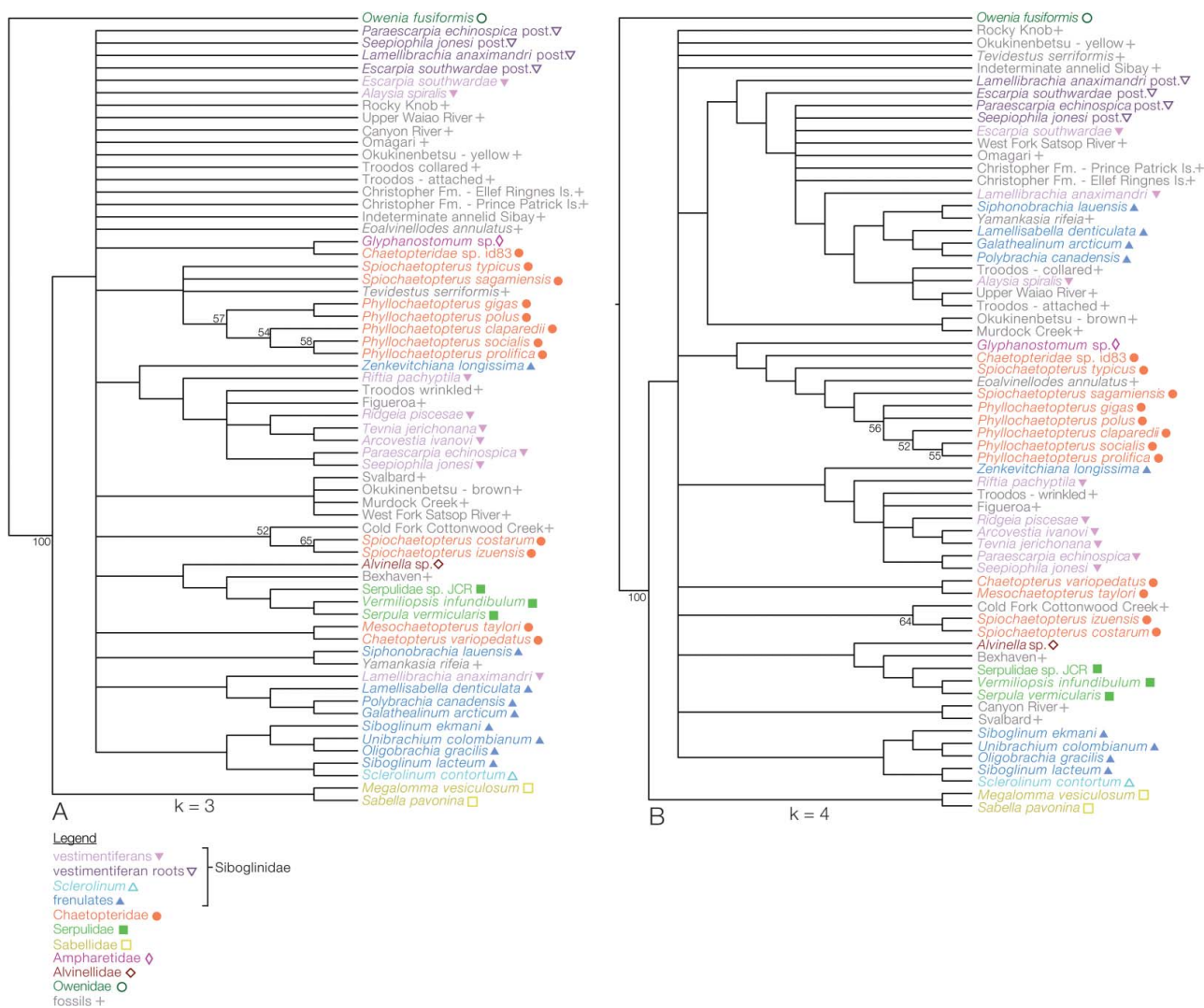


Figure 23. Strict consensus cladograms constructed using a total of 64 modern and fossil annelid taxa and 48 mostly morphological tube characters. Analyses were performed using implied character weighting, with the concavity constant set as default ($k = 3$; A), and also set to downweight homoplastic characters less ($k = 4$; B). Numbers on nodes represent groups present/contradicted support values. Modern taxa are coloured according to taxonomic groups; fossil taxa are in grey. **A**, consensus of 271 most parsimonious trees (best score = 15.387, consistency index = 0.195, retention index = 0.264); **B**, consensus of 60 most parsimonious trees (best score = 13.568, consistency index = 0.232, retention index = 0.569). Symbols/colours indicate taxonomic affinities.

different FTIR spectra to Chaetopteridae tubes (Fig. 24). Chaetopterid tube spectra lacked -NH peaks and showed only weak -CH peaks. The *Alvinella* tube spectrum generally resembled those of several siboglinids, such as *Scierolinum contortum* which only showed one -NH peak, whereas vestimentiferan and frenulate tubes exhibited two -NH peaks.

More in-depth analyses of the compositions of these modern tubes using py-GC-MS (Supplementary File 1, Table S7) revealed divergent compositions between siboglinid, chaetopterid and alvinellid tubes, with siboglinid tubes (both anterior and posterior tube regions) being rich in the compounds 3-acetamido-5-methylfuran and acetamido-pyrones, and often also acetamide and 3-

acetamidofuran. A single alvinellid and five chaetopterid tubes largely lacked these compounds, which are considered among the most important pyrolysis products indicative of chitin (Gupta & Cody 2011). Tubes from all three families were, however, rich in compounds considered to be pyrolysis products of proteins, and several of the analysed chaetopterid tubes also contained furfural.

Assessment of fossil tubes for preserved organic matter was performed using confocal microscopy. The walls of vestimentiferan tubes replaced by aragonite from modern cold seeps emitted a distinct fluorescence signal compared to surrounding carbonate minerals (Fig. 25A), suggesting that tube wall organics had been preserved during the mineralization process. A similar fluorescence pattern

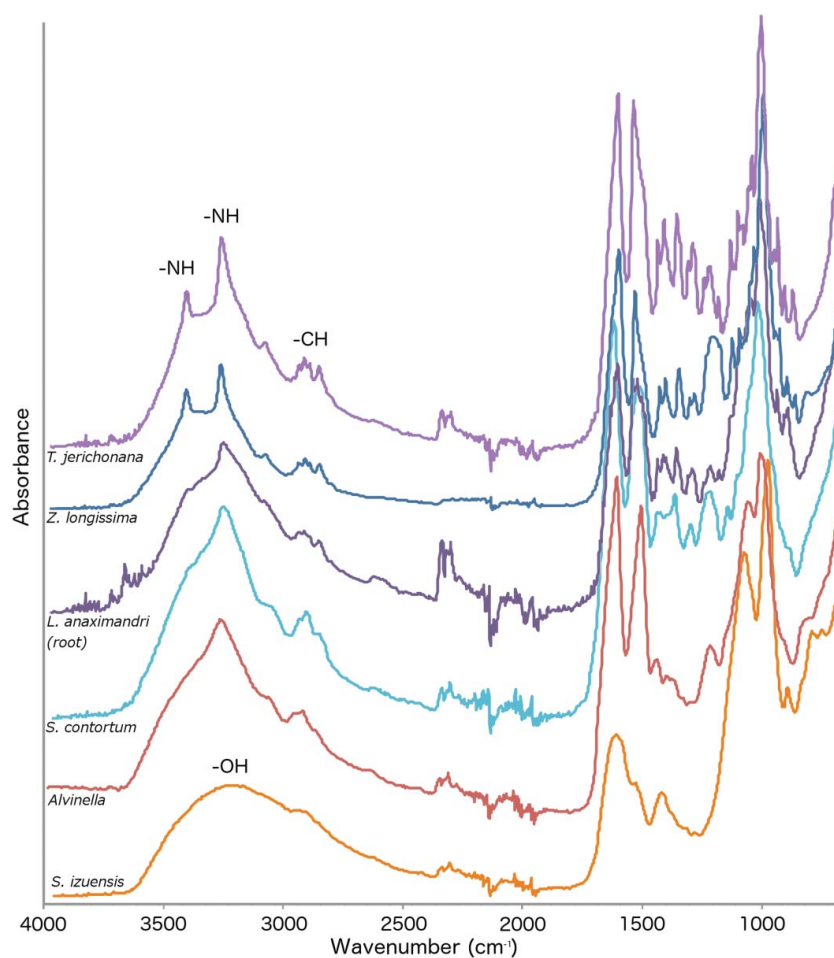


Figure 24. Fourier transform infrared (FTIR) spectroscopy spectra of the organic tubes of vent and seep annelids. Spectra are offset on the absorbance axis, and key spectral absorbance peaks are labelled with the types of chemical bonds they represent: -NH, nitrogen-hydrogen; -CH, carbon-hydrogen; -OH, oxygen-hydrogen. The regions of the tube analysed are as follows: *Tevnia jerichonana* (anterior, inner tube wall); *Zenkevitchiana longissima* (middle, outer tube wall); *Lamellibrachia anaximandri* (posterior, outer tube wall); *Sclerolium contortum* (anterior, outer tube wall); *Alvinella* sp. (middle); *Spiochaetopterus izuensis* (middle, outer tube wall).

was also obtained for a number of ancient tubes from seep deposits (Fig. 25B, C). Fossil serpulid tube walls from ancient seeps showed no fluorescence (Fig. 25D), suggesting that the observed fluorescence is unique to tubes considered to have been originally organic. When organic components preserved in recently mineralized and ancient fossil tubes from seeps were analysed in more detail through py-GC-MS, aragonite-replaced roots of *Escarpiia southwardae* and *Lamellibrachia luymesii* tubes did not contain the characteristic chitin pyrolysis products recorded in unmineralized tubes. Sixteen ancient fossil tube samples from seeps also showed that although organics were present in the tube walls, these were mostly protein constituents and none could be associated with a particular modern annelid group (Supplementary File 1, Table S9).

For *Alvinella* and *Ridgeia piscesae* tubes replaced by sulphide minerals from modern hydrothermal vents

(Supplementary File 1, Table S8), py-GC-MS analyses detected sulphurous compounds but none of the characteristic pyrolysis products of chitin and proteins recorded in unmineralized tube specimens.

Discussion

Can tube organics help to identify fossil vent and seep tubes?

This study constitutes the first major comparative evaluation of the organic compositions of modern annelid tubes, which were initially screened using FTIR and then analysed in greater detail through py-GC-MS. Assessment of the organic constituents of alvinellid, chaetopterid and siboglinid tubes confirms the different compositions of the tubes built by these families, thereby suggesting that tube

organics can be taxonomically informative. While there has been some confusion as to whether chaetopterid tubes contain chitin (Barnes 1964; Ippolitov *et al.* 2014; Parry *et al.* 2014), our FTIR (Fig. 24) and py-GC-MS (Supplementary File 1, Table S7) results from four chaetopterid genera suggest that they do not, as three major chitin marker pyrolysis products that were commonly observed in siboglinid tubes

were absent from the tubes of chaetopterids. Py-GC-MS showed that the majority of chaetopterid tubes analysed contained furfural, as previously reported (Berkeley 1922). The absence of key chitin markers, as well as furfural, distinguished *Alvinella* tubes from those of the siboglinids and chaetopterids, respectively. The above analyses also confirmed the presence of chitin in *Sclerolinum*, as well as the

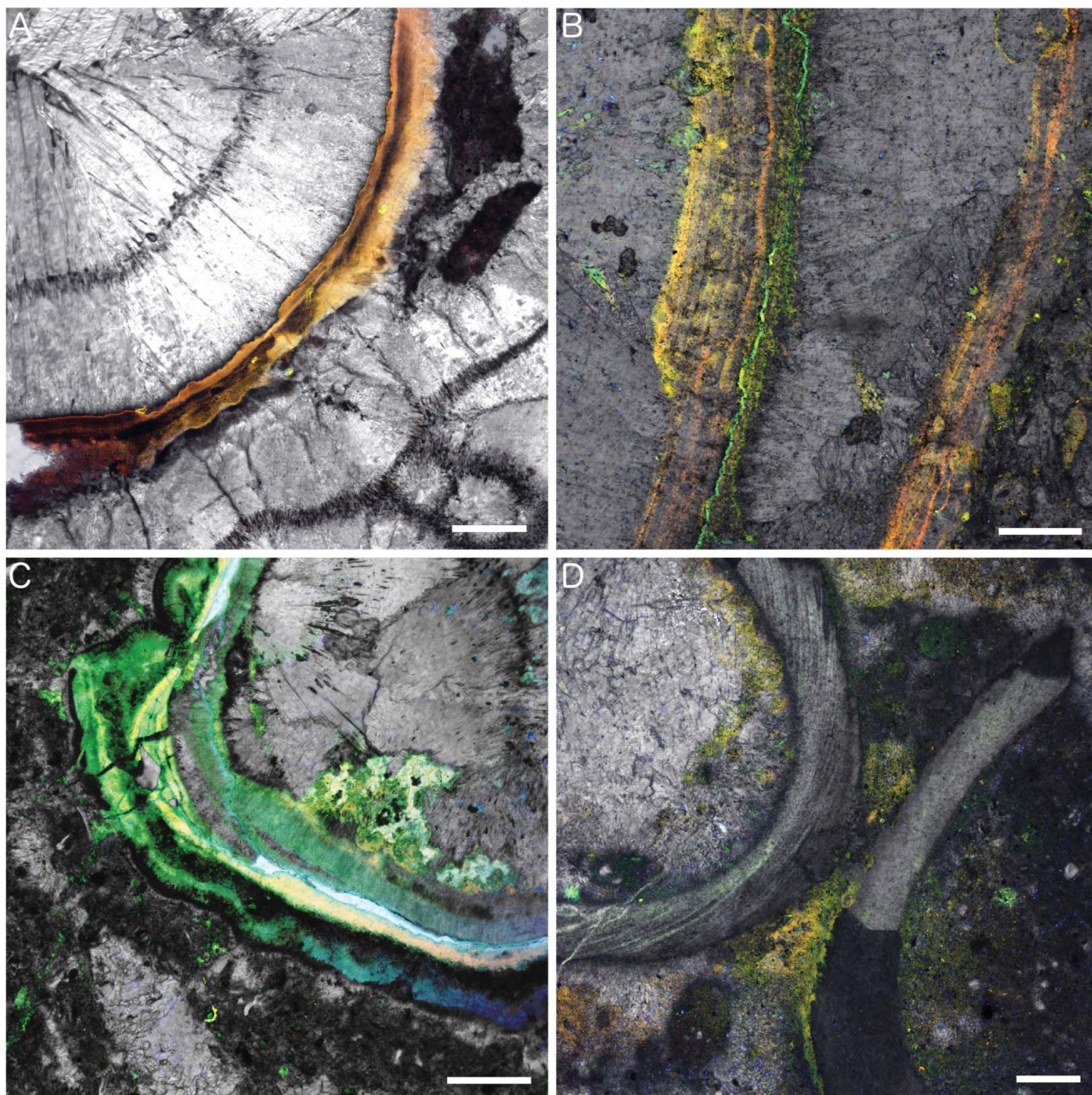


Figure 25. Results of confocal laser-scanning microscopy (CLSM) of recently mineralized and ancient fossil annelid tubes (see online edition for colour version). Tubes are imaged in auto-fluorescence mode, where areas of fluorescence likely reflect the presence of organic matter. **A**, detail of mineralized *Escarpia southwardae* (Siboglinidae) tube transverse section. **B**, fossil tube from Upper Waiiau River, New Zealand (UWT3-4), detail of transverse section. **C**, fossil tube from West Fork Satsop River, Washington State, USA (WFSR 1A), detail of transverse section. **D**, fossil tubes from Bexhaven, New Zealand (BXG), detail of two near-transverse sections. Scale bars: A = 100 μm ; B–D = 200 μm .

Table 1. Summary of systematic designations of tubes from ancient hydrothermal vent and cold seep environments.

Fossil vent/seep tubes	Previous assignment	Current assignment	Notes
Rocky Knob	?Siboglinidae (Saether 2011)	Annelida <i>incertae sedis</i>	Not resolved by PCA or cladistics, broadly resemble vestimentiferan tubes.
Upper Waiau River	-	Animalia <i>incertae sedis</i>	Not resolved by more conservative cladistic analysis (Fig. 23A); missing data and surface concretions make them difficult to place.
Bexhaven	-	Serpulidae	Well preserved calcareous walls, resolved near serpulids by all analyses.
West Fork Satsop River	-	?Siboglinidae	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity.
Murdock Creek	-	?Siboglinidae	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity.
Canyon River	Siboglinidae vestimentiferan (Goedert <i>et al.</i> 2000)	?Siboglinidae ?vestimentiferan	Not resolved by cladistic analyses; however, closely resemble vestimentiferan tubes.
Bear River	-	Animalia <i>incertae sedis</i>	Outer morphology of these tubes could not be assessed.
Omagari	Siboglinidae vestimentiferan (Hikida <i>et al.</i> 2003)	?Siboglinidae ?vestimentiferan	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity; resembles vestimentiferan roots.
Okukinenbetsu yellow tubes	-	Annelida <i>incertae sedis</i>	Not resolved by cladistic analyses; outer morphology suggests likely annelid affinity.
Okukinenbetsu brown tubes	-	?Siboglinidae	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity.
Troodos collared tubes	Siboglinidae vestimentiferan (Little <i>et al.</i> 1999b)	?Siboglinidae ?vestimentiferan	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity. Also resemble serpulid tubes, but resemble siboglinid tubes more closely.
Troodos wrinkled tubes	Siboglinidae vestimentiferan (Little <i>et al.</i> 1999b)	Siboglinidae vestimentiferan	Resolved near vestimentiferans by all analyses.
Troodos attached tubes	Siboglinidae vestimentiferan (Little <i>et al.</i> 1999b)	Annelida <i>incertae sedis</i>	Less conservative cladistic analysis (Fig. 23B) suggests possible siboglinid affinity, but cluster near serpulids in PCA plot. Characters consistent with both annelid families.
Christopher Fm. – Ellef Ringnes Island	Serpulidae (Beauchamp & Savard 1992), vestimentiferan (Williscroft <i>et al.</i> 2017)	?Siboglinidae ?vestimentifera	Less conservative cladistic analysis (Fig. 23B) suggests possible vestimentiferan affinity.
Christopher Fm. – Prince Patrick Island	Serpulidae (Beauchamp & Savard 1992)	?Siboglinidae ?vestimentifera	Less conservative cladistic analysis (Fig. 23B) suggests possible vestimentiferan affinity.
Cold Fork Cottonwood Creek	?Siboglinidae ?vestimentifera (Campbell <i>et al.</i> 2002)	Annelida <i>incertae sedis</i>	Cladistic analyses suggest possible chaetopterid affinity but outer tube morphology could not be assessed.
Wilbur Springs	-	Animalia <i>incertae sedis</i>	Poorly preserved walls; single tube for which outer morphology could be assessed resembles scaphopod.
Svalbard	?Siboglinidae ?vestimentiferan (Hammer <i>et al.</i> 2011; Hryniewicz <i>et al.</i> 2015)	Annelida <i>incertae sedis</i>	Do not clearly group within a modern annelid family in cladistic analyses, although one tube resembles those of siboglinids in section.

(continued)

Table 1. (Continued)

Fossil vent/seep tubes	Previous assignment	Current assignment	Notes
Figueroa	Siboglinidae vestimentiferan (Little <i>et al.</i> 2004)	Siboglinidae vestimentifera	Resolved among vestimentiferans by all analyses.
<i>Tevidestus serriformis</i>	Siboglinidae vestimentiferan (Little <i>et al.</i> 1999c; Shpanskaya <i>et al.</i> 1999)	Annelida <i>incertae sedis</i>	Group near chaetopterid tubes in more conservative cladistic analysis (Fig. 23A); unresolved by less conservative cladistic analysis. Also resemble siboglinid tubes in some respects.
Indeterminate annelid Sibay	?Annelida <i>incertae sedis</i> (Little <i>et al.</i> 1999c)	?Annelida <i>incertae sedis</i>	Unresolved by cladistic analyses; tubes possibly resemble those of annelids more than those of other tubicolous animals.
<i>Eoalvinelodes annulatus</i>	Annelida <i>incertae sedis</i> (Little <i>et al.</i> 1999c)	Animalia <i>incertae sedis</i>	Less conservative cladistic analysis (Fig. 23B), suggests possible chaetopterid affinity, but morphology consistent with several annelid and potentially non-annelid lineages.
<i>Yamankasia rifeia</i>	Siboglinidae vestimentiferan (Little <i>et al.</i> 1999c; Shpanskaya <i>et al.</i> 1999)	Animalia <i>incertae sedis</i>	Group with frenulates in cladistic analyses, but the combination of large size and fine parallel wrinkles does not closely resemble any of the modern annelid tubes investigated.

PCA: principal coordinate analysis.

root portions of two vestimentiferan tubes (Supplementary File 1, Table S7), and the inclusion of tube organic constituents within the tube character matrix also helped to resolve modern annelid families within cladistic analyses (Fig. 22).

The utility of organic composition for tube identification does, however, appear to diminish during fossilization at vents and seeps. While confocal microscopy (Fig. 25) and py-GC-MS revealed that organic matter had been preserved in the walls of recently mineralized vestimentiferan tubes from seeps, only one sample showed the presence of chitin markers upon pyrolysis (Supplementary File 1, Table S8). This suggests that chitin does not generally fossilize within seep environments. A selection of ancient tube fossils from seeps also showed preserved organics but no traces of chitin or furfural derivatives (Supplementary File 1, Table S9). We were therefore unable to determine whether ancient seep tubes could potentially have been built by siboglinids or chaetopterids based on the above analyses. At vents, recently mineralized tubes of *Alvinella* spp. and *Ridgeia piscesae* showed very little organic content at all (Supplementary File 1, Table S8). While chitin has been detected in fossils through py-GC-MS (e.g. Stankiewicz *et al.* 1997), it is generally considered to have a low preservation potential within normal sedimentary settings (Sephton *et al.* 2009), and it appears that this is also the case in hydrothermal vent and cold seep environments. Although our analyses of organics in fossil tubes proved inconclusive, tube wall organics may still aid in the identification of fossil seep material through the development of additional biomarkers for organic annelid tubes that are less affected by fossilization, or in cases where tube walls are exceptionally well preserved.

Tube morphology

As annelid dwelling tubes are not joined to the annelid body and the adaptive evolution of tubes is considered independent to that of soft tissues (Ippolito *et al.* 2014), tubes have generally been considered to have limited utility in taxonomy. However, there are recognized characters of fossil tubes, such as tube wall structure in fossil serpulid tubes from seeps (Vinn *et al.* 2012), that can enable taxonomic designation. In this study, tube characters that are important for taxonomic determination have been expanded, as well as clarified. While aspects of tube morphology such as longitudinal ridges, tube wall structure, tube size, mode of occurrence and collars have been highlighted as being problematic in fossil tube identification as they are shared by several modern lineages (Kiel & Dando 2009), we were able to show that many of these features can still be taxonomically useful. This is due to additional details observed within this study, such as the orientation of collars with respect to the tube, the collar size, and the type of longitudinal wrinkles and how they

combine with other tube morphological characters. Features such as rings of frenalate tubes (Fig. 20Z) appeared unique to this group, and are therefore a key identifying character for this lineage, whereas segments or wrinkled fabric-type textures that were observed in frenalate tubes can also occur in the tubes made by other families. Fossil tubes exhibiting the latter features would therefore be difficult to place, and for these reasons, we suggest that the Neoproterozoic fossil *Sabellidites cambriensis* may not have been made by a siboglinid, as suggested by Moczyłowska *et al.* (2014).

It is also important to note that for tube morphology, absence of evidence is not evidence of absence, and therefore the identification of a fossil tube is only possible if some diagnostic features of the tube have been retained following fossilization. The tube-builders of poorly preserved tubes such as the Cold Fork Cottonwood Creek specimens are therefore unlikely to be identified using morphology. With such fossils it is difficult to determine whether there was an original absence of characters or whether these were not preserved (Sansom 2015), which may be more of a problem for tubes fossilized at seeps as vent tubes occasionally retain very fine ornamental details (Little *et al.* 1998).

Cladistic analyses

Through the application of cladistics, the taxonomic identification of fossil tube material from ancient vents and seeps has been placed within a modern comparative context, allowing affinities of vent and seep tubes to be assessed more objectively. In summary, this analysis revealed that out of eight fossil tube types that were previously interpreted as having been made by vestimentiferans, siboglinid affinities could be upheld for only two of these, three were changed to possibly siboglinid, two were ascribed to the annelids only, and one tube type was ascribed to Animalia only (Table 1). Among the tube types that were not previously ascribed to siboglinids, an additional five are here suggested to have possibly been made by siboglinids. Notably, this includes mid-Cretaceous tubes from the Christopher Formation in the Canadian Arctic, which were previously considered to have been made by serpulids (Beauchamp & Savard 1992), and, more recently, vestimentiferans (Williscroft *et al.* 2017).

The ability of the cladistic analysis of only modern tubes (Fig. 22) to resolve taxa among families confirms that tubes do possess enough information for taxonomic assignment. The analysis also demonstrates that coding tube characters and analysing them within a cladistic framework does allow determination of the probable identity of a tube, and thus could do so for a fossil tube if sufficiently well preserved. However, the lack of correspondence of deeper annelid branches within our analyses to existing annelid molecular phylogenies (e.g. Weigert *et al.* 2014), even

when molecular data were included (Supplementary File 1, Figs S1, S2), likely reflects the more limited sampling of annelid taxa within our analyses.

The generally poorer resolution of cladograms which included fossil tubes (Fig. 23) further highlights that alteration during fossilization is often significant, and the small number of characters that can be gleaned subsequently from fossil tubes makes their identification difficult, even at broad taxonomic levels. This is also demonstrated by the PCA plot (Fig. 21), in which the majority of fossil vent and seep tubes cluster with each other rather than with the tubes of modern annelid lineages, and is reflected in the overall increased uncertainty of fossil tube taxonomic interpretations (Table 1). The inclusion of molecular data worsened fossil taxon resolution (Supplementary File 1, Fig. S3), likely as a result of conflicts arising from homoplasies in the morphological data. The cladistic analyses including fossils (Fig. 23) especially appeared to encounter problems in placing smooth-walled tube fossils, which is how many of the fossil seep and several vent tubes are preserved. Even tubes from Canyon River, which are generally accepted as having been made by vestimentiferans, are not well resolved in the cladistics analysis. Tubes with more detailed outer wall ornamentation, for which there was greater information to base these identifications upon, resolved more definitively among modern annelid groups. These tubes comprised Cretaceous tubes from the Troodos Ophiolite, and Jurassic tubes from the Figueroa deposit, which were both resolved among modern vestimentiferan tubes (Fig. 23).

While helping to resolve the identities of only a small proportion of the fossil tubes investigated, this study has nevertheless improved the level of quality control within palaeontological interpretations of fossil vent and seep tubes, which was greatly needed (Kiel & Dando 2009; Vrijenhoek 2013). Gaining an understanding of evolutionary history also requires authors to be cautious, as over-identifications of fossils can lead to false conclusions of taxon evolutionary ages (Bell *et al.* 2010; Parham *et al.* 2012). Cladistic comparative methods are widely used for fossil identifications because they increase transparency in the fossil identification process and clearly demonstrate which characters are attributed to each fossil, thereby adding objectivity to fossil identifications that may be inherently difficult (Crepet *et al.* 2004). Overall, the use of cladistics has greatly improved knowledge of the types of characters that can be gleaned from both fossil and modern tubes, which of these are homoplastic, and also which characters can result in more definitive identifications.

The above methods, however, need to be applied with greater caution for very ancient tube fossils (such as those from the Palaeozoic), as the identity of these fossils will largely be evaluated with respect to modern tubes from which they are very distant in time. The Palaeozoic fossils

are also the most likely to belong to now-extinct taxa that do not have modern morphological analogues.

Implications for vent and seep evolutionary history

The evolutionary history of the annelid family Siboglinidae is controversial, owing to conflicting theories of its origins from fossil and molecular age estimates (Vrijenhoek 2013). Our study suggests that Late Cretaceous tubes from the Troodos Ophiolite and Early Jurassic tubes from the Figueroa deposit were made by vestimentiferans, which greatly extends the age of this lineage beyond that suggested by molecular clock analyses. This finding is supported by a further piece of independent evidence: the discovery of mid Cretaceous *Osedax* fossils (Danise & Higgs 2015) suggesting that the more derived siboglinid lineages have a Mesozoic origin. However, we were unable to find definitive evidence that Devonian and Silurian vent fossils were made by siboglinids, thereby reinforcing doubts that this family could extend back into the Palaeozoic (Vrijenhoek 2013) and certainly not back to the Neoproterozoic (Moczyłowska *et al.* 2014). Four types of tubes that are tentatively assigned to the vestimentiferans by this study are from Cretaceous deposits (Table 1), and while their designation remains uncertain, if vestimentiferans originated during the Jurassic or earlier, they are likely to have been abundant within Cretaceous vents and seeps.

The faunal compositions of hydrothermal vents and cold seeps have undergone dynamic shifts over evolutionary time. Although it has been difficult to attribute many of these transitions to large-scale environmental upheaval events (Kiel & Little 2006), a proportion of the dominant modern vent and seep fauna is considered to have originated during the Cenozoic (Vrijenhoek 2013). The occurrence of Mesozoic siboglinid fossils constitutes a diversion from this pattern, correlating better with the Jurassic origins ascribed to vent and seep molluscs such as provannids (Kiel *et al.* 2008b; Kaim & Kelly 2009). The confirmed and suspected presence of siboglinids in many ancient vent and seep deposits is perhaps due to their possession of weedy characteristics such as wide habitat preferences and distant dispersal abilities (Georgieva *et al.* 2015b), which may have enabled them to make use of vent and seep environments repeatedly and over long periods of time. The surprising fossil discoveries of Danise & Higgs (2015) and the reinterpretations presented here emphasize that the evolutionary history of this remarkable family warrants further investigation, and we therefore urge that an earlier origin for the main tube-building vent and seep annelid lineage, the vestimentiferans, be considered and incorporated into a much-needed new molecular age estimation for Siboglinidae.

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Supplemental data

Supplementary material for this article can be accessed at: <https://doi.org/10.1080/14772019.2017.1412362>

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