



FOSSILIZED DIGESTIVE SYSTEMS IN 23 MILLION-YEAR-OLD WOOD-BORING BIVALVES

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ABSTRACT

Fossilized remnants of parts of the digestive system of wood-boring pholadoidean bivalves are reported from late Oligocene–early Miocene deep-water sediments in western Washington State, USA. They are reconstructed using serial grinding tomography and computer-based 3D visualizations. Two types are distinguished: (1) a U-shaped structure with a groove on its inner side, interpreted as the caecum of xylophagines; (2) an elongate structure with a central groove and thin tubes running parallel to it on its dorsal and ventral side, interpreted as the caecum and the intestine, respectively, of teredinids. Petrological thin-section observations show that these structures are filled by a mass of fine woody material, suggesting that being filled with woody material facilitated their fossilization. Screening the fossil record for similar structures in Mesozoic pholadoidean fossils can potentially help to clarify feeding strategies, phylogenetic relationships and the evolution of feeding strategies among early pholadoidean bivalves.

INTRODUCTION

Wood-boring bivalves are the main decomposers of wood in marine environments (Turner & Johnson, 1971). They live in symbiosis with cellulolytic and nitrogen-fixing bacteria that presumably aid in digesting the wood (Rosenberg & Breiter, 1969; Popham & Dickson, 1973; Distel & Roberts, 1997; Lechene *et al.*, 2007). Teredinids, also known as shipworms due to their elongate bodies, are the dominant wood-borers in shallow water and have a rich fossil record, especially because they produce calcitic linings of their boreholes, which have a high fossilization potential (Kelly, 1988a; Haga & Kase, 2011). Besides their shells and borehole linings, their protective accessory structures called pallets have also been found preserved in the fossil record (e.g. Huggett, Gale & Evans, 2000). Their deep-water counterparts, the xylophagines, not only decompose wood, but by doing so play an important role in driving the ecosystems around wood on the deep-sea floor (Turner, 1973, 1978). This is because the large amount of faecal pellets produced by the xylophagines creates anoxia in the sediment underneath and the resulting hydrogen sulphide attracts chemosymbiotic bivalves with sulphur-oxidizing symbionts (Kiel & Goedert, 2006b; Kaim, 2011). Furthermore, the boreholes and their faecal linings provide habitat and shelter a variety of small invertebrates (Turner, 1978; Wolff, 1979; Marshall, 1988; Schander *et al.*, 2010). Fossil shells as old as Early Cretaceous may belong to the xylophagines (Kelly, 1988b). Fossil remains

of their activities, such as faecal linings of their boreholes and faecal pellets surrounding the wood, however, are rare with only a few reports from the Late Cretaceous and the Eocene–Oligocene, respectively (Kiel, 2008; Kiel *et al.*, 2009). Here we report fossilized remains of the digestive system of late Oligocene–early Miocene teredinids and xylophagines from deep-water sediments in western Washington State, USA, using grinding tomography and computer-based 3D reconstructions.

MATERIAL AND METHODS

A calcareous concretion about 5 × 2 × 2 cm with permineralized wood was found loose on a beach terrace at a locality locally known as Merrick's Bay, on the shore of the Strait of Juan de Fuca in Clallam County, western Washington State, USA (Fig. 1), where mudstones from near the top of the Pysht Formation are exposed; this is USGS loc. 26897. These sediments are of latest Oligocene to earliest Miocene age, were deposited in bathyal depth and contain abundant pieces of bored wood (Addicott, 1976; Snively, Niem & Pearl, 1977; Kiel, 2008). Mollusc fossils associated with the piece of wood used in this study include chemosymbiotic bivalves such as *Conchocele bisecta* and *Idas? olympicus*, predatory and bacteria-grazing gastropods, and faecal tubes of xylophagines (Kiel & Goedert, 2006a, 2007; Kiel, 2008).

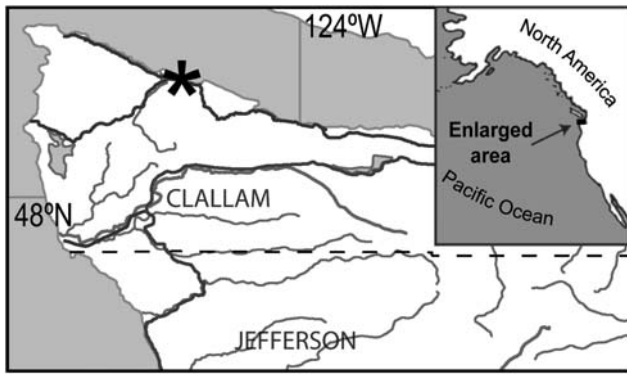


Figure 1. Locality of the fossil specimen.

U-shaped structures were seen in a thin section of this wood-bearing concretion (Fig. 2B, C). In order to visualize these structures in 3D and to investigate their abundance and position within the wood, the sample was processed at the Grinding Tomography Laboratory at the Institute for Earth Sciences at the University of Heidelberg. First, the sample was embedded within blue resin and carbonate gravel in a 5 × 5 cm metallic mould. The outer surfaces of the hardened block were polished with a precision surface grinding machine G&N MPS 2-R300 to reach a micron-precise orthogonality of the block. For serial grinding the G&N grinder was set to automatic mode with a repetitive abrasion of 50 µm. After each step the polished surface of the sample was scanned by a custom-built flatbed scanner (based on an Epson Perfection V750 Pro) in a water bath. The scanning resolution was 2400 dpi and the tomograms were saved as 16-bit colour TIFF files (for detailed information on methodology, see Pascual-Cebrian, Hennhöfer & Götz, 2012). A total thickness of 13.95 mm was removed from the sample, resulting in a stack of 280 tomograms; a video sequence of these tomograms is provided in the Supplementary Data. Areas of interest were extracted from the complete set of images using the ‘image stacks’ functions implemented in the software packages ImageJ v. 1.45s (Abramoff, Magalhaes & Ram, 2004) and Photoshop CS v. 5.1.

Digital reconstructions were produced from these subsamples using OsiriX biomedical image software (Rosset, Spadola & Ratib, 2004), Meshlab v. 1.3.0a and Voreen v. 2.6.1. OsiriX is compatible with JPG and TIFF image files from scanning. The OsiriX reconstructions are based on isosurfaces and volume rendering (Ratib & Rosset, 2006) and were smoothed by applying the Laplacian smooth filter in Meshlab. Renderings produced with Voreen used the ‘single volume ray-caster’ function with linear texture filtering and the ‘clamp to edge’ texture clamp.

The remnants of the specimen and the full set of digital images are stored at the Geoscience Museum of the University of Göttingen, repository number GZG.IF.08854.

RESULTS

Fossilized features of the wood-boring bivalves

The investigated piece of wood is riddled with boreholes and is partially crushed (Fig. 2A). The boreholes are filled with a variety of carbonates, including clotted micrite and sparry calcite, as well as pyrite framboids (see Kiel, 2008 for details). There are two types of boreholes. The first type has calcitic linings, reaches 4.5 mm in diameter and is typically parallel to the grain of the wood. Only a few small (up to 5 mm long) borings of this type, just beneath the surface of the wood, are

perpendicular to the grain. The diameter of the individual boreholes of this type does not notably change throughout the investigated length of the piece of wood (*c.* 14 mm). Teredinid pallets have been seen in one such borehole in a thin section (Kiel, 2008: fig. 9A) but not in the 3D renderings presented here. In a few of these boreholes we found structures interpreted here as parts of the digestive system of teredinids. These structures are elongate, oval in cross section and a central groove runs along most of the length of the ventral side (Fig. 3A). In addition, there are thin tubes running along their dorsal and ventral sides (Figs 3, 4). In an individual with preserved shell fragments, the anterior side of this structure starts at about half the shell’s length; a part of the thin tube appears to extend past the anterodorsal end of the main structure, where it curves upward in a U-shaped fashion (Fig. 3).

The second type of borehole occurs more or less perpendicular to the grain of the wood and is short compared with the first type, shows a rapid increase in diameter to a maximum of about 6.5 mm and lacks calcitic lining. Instead, its posterior part (toward the wood’s surface) has a lining of a light brown substance; this lining is often fragmented and, when preserved, horn- or funnel-shaped, reflecting the shape of the borehole (Figs 5B, 6). Virtually all intact boreholes of this type contain a U-shaped structure, here interpreted as the caecum of xylophagaine bivalves. These structures are up to 3 mm wide, slightly wider than high, oval in cross section, and have a groove in the inner side of the U (Fig. 5G, H). One tip of the U is often slightly pointed, while the other is evenly rounded (Fig. 5F–H). Shell remains are seen in some boreholes of this type, but not in others; when they occur they are frequently fragmented or distorted (Fig. 5C–E). The U-shaped structure is typically found adjacent to the inner margin of the borehole or of the shell and, when intact, is mostly orientated with the tips of the U-shaped caecum pointing to the anterior side of the borehole (Figs 5A, B, 6). These structures seem to retain their (assumed) original shape, including individuals in crushed boreholes. Other individuals in crushed boreholes show various degrees of plastic deformation, ranging from individuals with one arm of the U bent either toward or away from the other arm to individuals who are flattened in various directions (Fig. 5C–E). However, we have not seen fragmented individuals with the fragments scattered throughout the boreholes.

The structures interpreted here as remnants of the digestive systems of teredinid and xylophagaine bivalves are filled with a fine, brown substance (Fig. 2B, C) that, in some cases, is recrystallized to white, sparry calcite. In the ground surfaces, these fillings appear dark (Fig. 2A).

Interpretation

The structures described above are here interpreted as the wood-storing caecum and parts of the intestine of teredinids and xylophagaines, because: (1) they are very similar in shape to these features in extant species (see below); (2) they are filled with a fine, brown substance that appears to be small, most likely ingested, wood fragments; and (3) because the xylophagaine caeca were found in boreholes perpendicular to the grain of the wood, while teredinid caeca were found mostly in boreholes parallel to the grain, which is consistent with the boring behaviour of living teredinids and xylophagaines (Knudsen, 1961; Voight, 2008).

A schematic drawing of the soft anatomy of a teredinid by Turner & Johnson (1971: fig. 4D) is here reproduced (Fig. 7A) to illustrate the similarity of the shape and the position of its digestive tract to the structures documented here from elongate boreholes with calcitic lining. Moll (1914: fig. 6) provided a similar reconstruction. The wood-storing caecum of these teredinids is an elongate sac with a centro-ventral typhlosome and the intestine runs adjacent to the typhlosome along the entire length of the

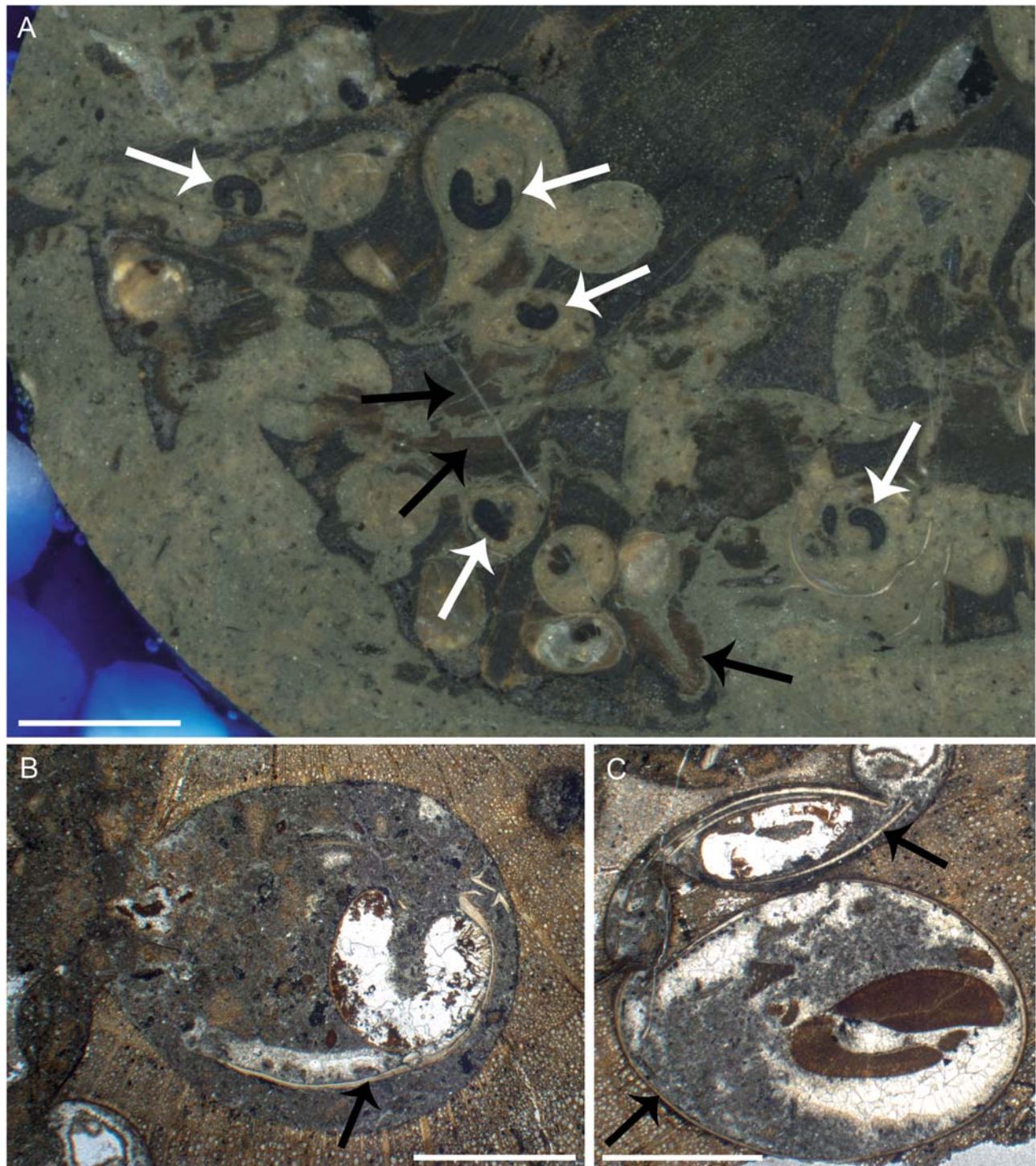


Figure 2. Fossil wood with remains of xylophagous bivalves. **A.** Scanned section showing several caeca (white arrows) and faecal tubes (black arrows). **B.** Thin section image of a borehole with a U-shaped xylophagaine caecum resting against the shell (black arrow); remnants of woody material visible inside the caecum, but most of it is recrystallized to white, sparry calcite. **C.** Thin section image of two teredinid borings with thin calcitic lining (black arrows) and with cross sections of the caeca; the upper borehole and the containing caecum are crushed, the content of the caecum largely recrystallized to white, sparry calcite; the caecum in the lower borehole is filled with woody material; the smaller woody fragments adjacent to the caecum may be cross sections of the intestine. Scale bars: A = 2.0 mm; B and C = 3.0 mm.

caecum, turns around at the end to run back along the upper side of the caecum; past the caecum the intestine turns upward to open into the anal canal (Beuk, 1899; Moll, 1914; Turner, 1966; Turner & Johnson, 1971; Lopes *et al.*, 2000). The specimen reconstructed in Figure 3 shows all these features and is thus interpreted

as preserving a large part of the shipworm's digestive system. In several of the fossil individuals, the caecum is divided into two elongate tubes with a bean-shaped cross section (Fig. 4), a feature we consider as an artefact of preservation, resulting from a split along the typhlosole (compare Figs 4, 7B).

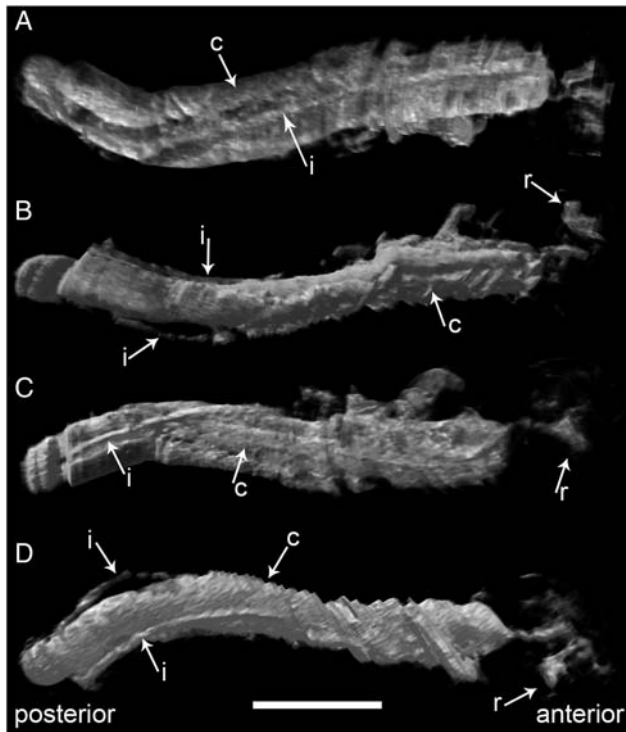


Figure 3. Rendered digestive tract of teredinid. Abbreviations: c, caecum; i, intestine; r, rectum. Scale bar = 1 mm.

An illustration of the alimentary canal of *Xylophaga dorsalis* by Purchon (1941: fig. 7) is here reproduced (Fig. 7C); a similar illustration of *X. atlantica* with more anatomical details was provided by Turner & Johnson (1971: fig. 3B). The caecum of *Xylophaga* is essentially a thick U that is about as wide as high, with the tips of the U pointing dorsally and the intestine wraps around it in several loops. Thus the shape of the caecum is identical to the U-shaped structures observed in the short boreholes with rapidly expanding diameter. Occasionally we found associated with the caeca thin, elongate structures with a similar brownish colour as the caeca, but they were never continuous or associated with the caeca in a uniform or recurrent manner. Thus it is uncertain whether these thin structures are remnants of the intestine.

DISCUSSION

Occurrence and preservation

The co-occurrence of teredinid and xylophagaine borings in a single piece of wood does not necessarily imply that both taxa colonized the wood simultaneously. It is also possible (and more likely) that the teredinids colonized the wood while it was floating in surface waters and that the xylophagains colonized it only when it had sunk to the sea floor.

The fact that we have seen only plastic deformation but not fragmentation among the xylophagaine caeca suggests that the deformations took place either while the caecum was still enclosed in soft tissue, or that the wood fragments were held together perhaps by bacterial mucus. The position of the caeca on the inner side of either the shell or the borehole suggests that they slowly sank into this position during the progressive decay of the soft tissue around them. The intuitively paradoxical situation that the 'soft' caecum is preserved also in boreholes where the 'hard' shell is not preserved, as seen in some

cases, may be explained by the development of an acidic microenvironment due to the decay of the clam's soft tissue, which dissolved the calcareous shell but did not affect the wood-filled caecum. The lithification of the entire association was probably a rapid, microbially mediated process; the boreholes show abundant clotted micrite, a carbonate fabric that is typically formed *in situ* due to microbial oxidation of organic matter (Burne & Moore, 1987). The presence of pyrite (iron sulphide) suggests that this process took place under anoxic conditions and involved sulphate-reducing bacteria (Suess, 1978).

The simplest explanation for the preservation of these caeca and intestines is their infill with wood fragments. Microbiological studies have shown that the bacteria aiding the digestion of the wood break down cellulose and similar substances, but not lignin (Rosenberg & Breiter, 1969; Dean, 1978). Thus the resistance of lignin to bacterial decay may have facilitated the fossilization of those parts of the digestive tract that were filled with lignin-rich wood remains. Why the intestine is preserved in some teredinid specimens, but not in any of the many xylophagaine specimens, remains unclear. Possible explanations include that the xylophagaine intestine was not filled with (enough) wood, was only discontinuously filled with wood resulting in fragmentation during the decay of the soft tissue, or that the wood in the intestines of teredinids and xylophagains is altered in chemically different ways, resulting in a different fossilization potential.

Preserved digestive tracts are extremely rare in the fossil record of molluscs and are quite disparate regarding the type of preservation. A platyceratid gastropod with preserved intestines was documented using grinding tomography from the Silurian of Herefordshire, England, where the soft tissue is preserved as calcite infills in nodules in a volcanoclastic ash (Sutton *et al.*, 2006). From the Jurassic of Gloucestershire, England, nuculid bivalves with moulds of coiled intestines have been reported (Gavey, 1853; Cox, 1959). A trochoid gastropod with phosphatized intestines was documented by Casey (1960) from the Early Cretaceous of Kent, England, and Roger (1944) reported a coleoid cephalopod from the Late Cretaceous of Syria with preserved intestines and other organs. Thus the digestive tracts reported here from the late Oligocene–early Miocene of Washington State, USA, appear to be the first Cenozoic record of such an exceptional preservation.

Implications for pholadoidean evolution

The teredinids and xylophagains are the only wood-boring and wood-feeding bivalves, so that their phylogeny and the evolution of their wood-feeding habit have long been of interest. There are two contrary taxonomic and evolutionary hypotheses. One classifies teredinids and xylophagains in different families among the Pholadoidea and suggests that the wood-feeding habit (xylotrophy) evolved independently in each (Turner, 1966, 1967, 1969). Other authors propose a sister-group relationship of xylophagains and teredinids and that xylotrophy evolved only once among the Bivalvia (Purchon, 1941; Monari, 2009; Distel *et al.*, 2011). Based on a molecular phylogeny, Distel *et al.* (2011) proposed several characters for the last common ancestor of Teredinidae and Xylophaginae, including some for which fossil evidence may be found: they burrowed into and fed on wood, had a caecum for wood storage and digestion, and may have possessed apophyses and formed lined burrows that were sealed by paired pallets.

The fossil record provides insights into the order of events in the evolution of pholadooids and can be used to test hypotheses of character evolution derived from molecular (and other)

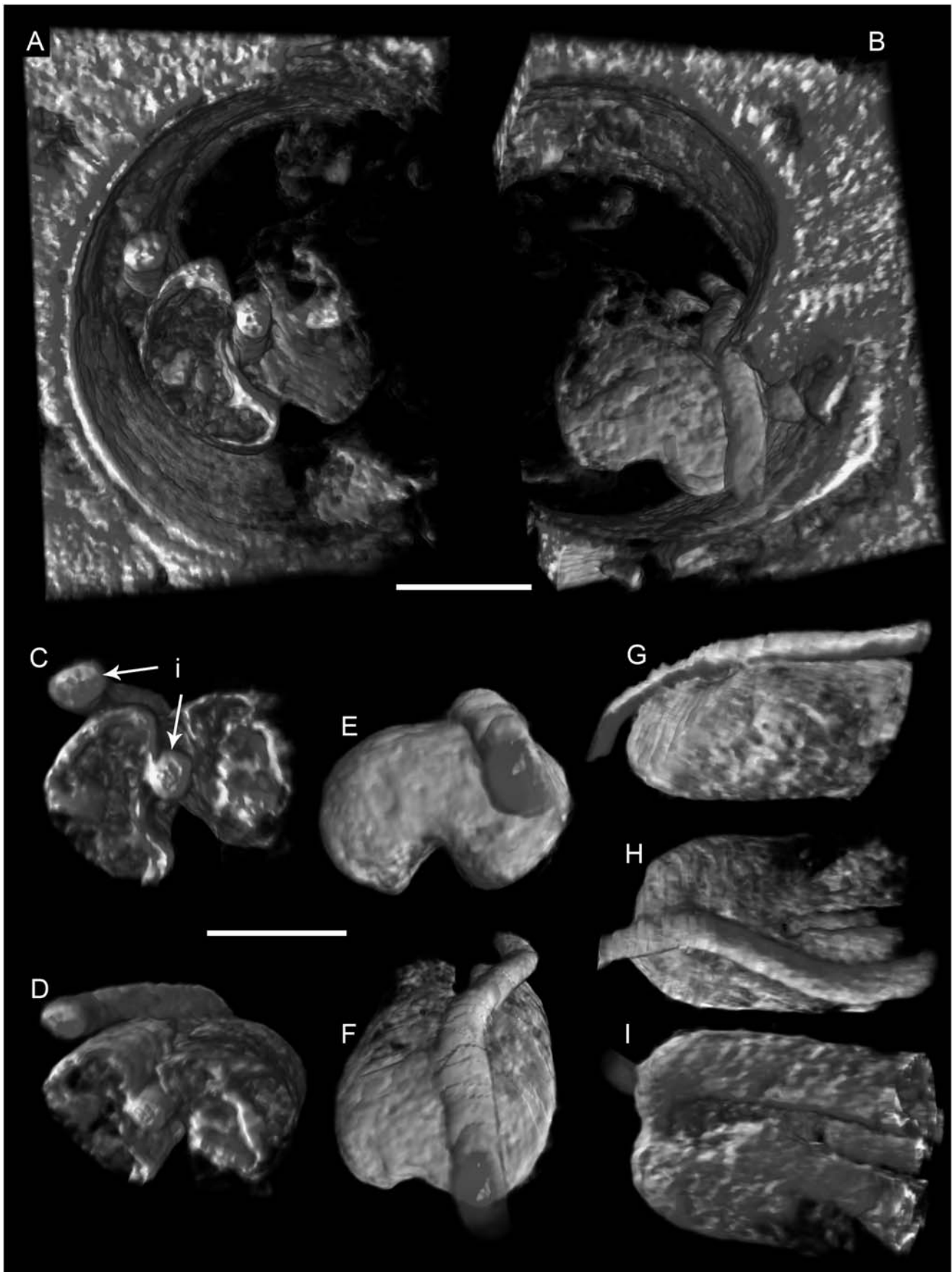


Figure 4. Rendered anterior part of caecum and intestine of a tereidid. **A.** Borehole partially visible; view from the posterior side, showing a cross section of the caecum. **B.** Borehole partially visible; view from the posterior side, showing a cross section of the caecum. **C–I.** The specimen seen from different angles; from posterior (**C, D**), from anterior (**E, F**), side view, dorsal and ventral views (**G–I**) with anterior side to the left. Abbreviation: i, intestine. Scale bars = 1 mm.

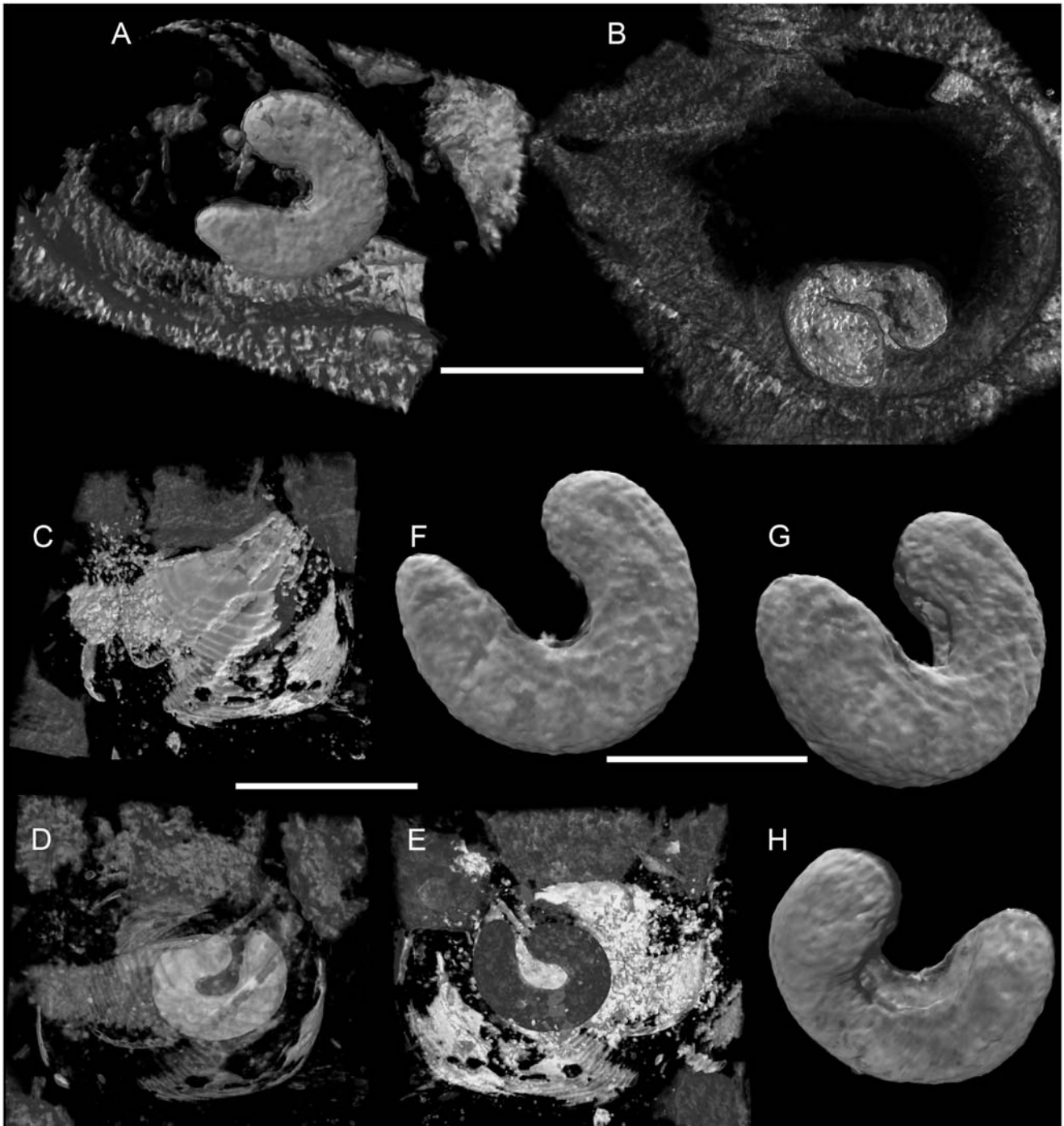


Figure 5. Renderings of xylophagaine: occurrence, caeca and shells. **A.** Specimen *in situ*, placed against poorly preserved shell fragments. **B.** Another specimen *in situ*, lying on the bottom of the borehole. **C–E.** Deformed specimen with preserved shell fragments in partially collapsed borehole; view with shell in the foreground (**C**); similar view as in **C** but with semi-transparent shell (**D**); view with shell in the background (**E**). **F–H.** Three views of the caecum from **A**, showing the internal groove. Scale bars: A–E = 2.0 mm; F–H = 1.0 mm.

phylogenies. The appearance of pholadoidean characters in the fossil record is largely congruent with the hypotheses of Distel *et al.* (2011). The oldest borings in wood resembling those of modern pholadoids are of early Jurassic (late Pliensbachian) age; the oldest pholadiform shells associated with such borings are from the middle Jurassic (Bajocian) (Kelly, 1988a). Late Jurassic (Kimmeridgian–Tithonian) pholadoid shells assigned to the genus *Opertochasma* bear apophyses (Kelly, 1988a; Haga & Kase, 2011). The first recognized

borings in wood with calcareous linings and associated shells (*Turnus kotickensis*) appear in the early Cretaceous (Albian) (Kelly, 1988a). Possibly also of Albian age are the oldest pallets: Woodward (1880: 507) mentioned a teredinid with elongated and penniform pallets in the Greensand of Blackdown, but did not indicate where this fossil is deposited (if at all), thus this record remains doubtful; the oldest pallets actually figured are from the Late Cretaceous (Santonian) of New Zealand and are of the segmented, nested-cups-type

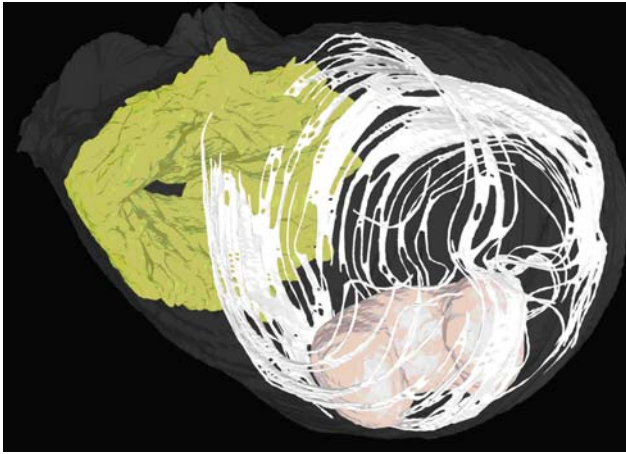


Figure 6. Rendered false colour image of an entire xylophagaine borehole (grey). Colours: white, shell remains; pink, caecum; green, faecal tube.

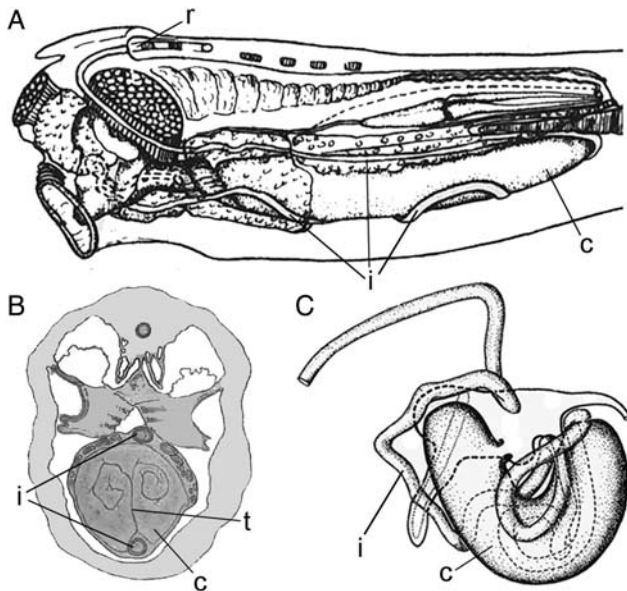


Figure 7. Reconstructions of the anatomical features of pholadoidean bivalves discussed herein. **A.** Anterior part of *Teredo poculifer*, from Turner & Johnson (1971). **B.** Cross section of a *Teredo* from the Mediterranean ('Triester Form'), from Beuk (1899). **C.** Alimentary canal of *Xylophaga dorsalis*, from Purchon (1941). Abbreviations: c, caecum; i, intestine; r, rectum; t, typhlosole.

(McKoy, 1978), a morphology considered characteristic for Teredininae (i.e. *Bankia* and more derived taxa, cf. Distel *et al.*, 2011). Only slightly younger (Campanian) are the oldest boreholes with faecal tubes, in wood from deep-water sediments (Kiel *et al.*, 2009), indicating that xylophagines had adapted to life in the deep sea by this time. Thus while all fossil pholadoids until the mid-Cretaceous (Albian) show characters attributed by Distel *et al.* (2011) to the last common ancestor of teredinines and xylophagines, these two groups had clearly separated by Late Cretaceous time.

Pinning down the origin of the xylotrophic lifestyle (as opposed to only wood boring) is more difficult using fossil evidence and has previously been based on inferences drawn from the length of the boreholes. It is believed that boreholes that

are extraordinarily long compared to the length of the shell are today only built by xylotrophic taxa (i.e. teredinids and xylophagines), while boreholes that are short compared to shell length are built by filter-feeders (Kelly, 1988a). Therefore, long and winding boreholes have been used as evidence for a xylotrophic lifestyle and the origin of this trait has been placed in the Middle Jurassic (Skwarko, 1974; Kelly, 1988a; Haga & Kase, 2011). However, boreholes of xylophagines are often quite short, despite their xylotrophic lifestyle. More direct evidence for xylotrophy are provided by the distinctive woody faecal pellets found in a Late Cretaceous faecal tube by Kiel *et al.* (2009). Also the preserved parts of the digestive tracts documented here provide clear evidence for xylotrophy, but are geologically too young to test hypotheses of character-state evolution by reference to the last common ancestor of teredinines and xylophagines. However, they demonstrate that caeca and intestines, when filled with wooden particles, have the potential to fossilize. Mesozoic wood with well-preserved pholadoideans and associated boreholes might thus also preserve such features and are likely to provide valuable insights into the origin of xylophagy in pholadoidean bivalves.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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