Sensory structures on the siphons of wood-boring bivalves (Pholadidae: Xylophagainae: *Xylophaga*)

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ABSTRACT

Deep-sea bivalves of Xylophagainae spend their entire post-metamorphic lives boring into wood that has fallen to the seafloor. Although their boreholes seemingly provide a protected, imperturbable habitat, scanning electron microscopy reveals that the siphons of three species of *Xylophaga* examined carry elaborate structures that are interpreted as chemoreceptors or mechanoreceptors. Sensory structures occur on the siphonal surface of *Xylophaga oregona* Voight, 2007, and *X. multichela* Voight, 2008. The large complex papillae of *X. multichela* are scattered on the distal incurrent siphon and arrayed in two longitudinal rows along its dorsal surface. The distal incurrent siphon of *X. oregona* carries minute structures, barely projecting above the surface, that are crowned by tufts of cilia. Both siphonal openings of *X. microchira* Voight, 2007, carry cirri. At the excurrent opening, cirri have long cilia emerging from terminal pits. At the incurrent opening, cirri form two rings. The inner cirri appear to be unique in that cilia emerge from between scales that cover their inner surfaces. The structures observed may be useful in species taxonomy and systematics, but we suspect that their elaboration is linked to predation pressure, which might relate to depth distribution.

Additional keywords: Goblet organs, scanning electron microscopy, depth distribution, predation, deep-sea

INTRODUCTION

Deep-sea bivalves of the Xylophagainae spend their post-metamorphic lives using toothed ridges on their shells to bore into wood that has fallen to the seafloor. Only the siphons emerge from the resulting dead-end boreholes. Although most bivalves suspension-feed by extracting food from water moving across the gills, the small ctenidia and the labial palps of representatives of Xylophagainae lack significant sorting mechanisms (Purchon, 1941). Purchon (1941) proposed that these animals ingest wood scrapings, which are digested with the help of endosymbiotic bacteria (Distel and Roberts, 1997).

This paper reports scanning electron microscope (SEM) investigations of the siphons of three species of *Xylophaga* Turton, 1822, the most diverse genus of wood-boring bivalves, with more than 50 named species (Voight, 2008). Sensory structures, known from the siphons of a few shallow-water bivalves representing a wide taxonomic range (e.g., Hodgson and Fielden, 1984; Pekkarinen, 1986; Fishelson, 2000), are here documented in three congeneric species. Differences among the structures in these species are largely consistent with inferred ecological differences.

MATERIALS AND METHODS

Although most Xylophagainae species are known only from their type localities, recovery of experimental wood deployments from the deep Northeast Pacific (Voight, 2007) provided abundant specimens of the Xylophagainae and allowed for SEM study of the siphons of *Xylophaga oregona* Voight, 2007 (Field Museum of Natural History, Chicago, FMNH 308705) and of *X. microchira* Voight, 2007 (FMNH 309602), from 2211 m depth. Specimens were recovered inside a lidded box on a subsea vehicle in 2003 and 2004, respectively, fixed in 8% buffered formalin in seawater, and transferred within 48 hours to 70% ethanol. No attempt was made to relax the specimens prior to fixation. A single lot of *X. multichela* Voight, 2008 (Scripps Institution of Oceanography Benthic Invertebrate Collections, SIO-BIC M11567) was collected by trawl in 1973 from between 106 and 113 m depth, fixed in formalin and later moved to 80% ethanol. All specimens were dehydrated in ethanol and then critical point-dried with CO_2.

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Each sample was sputter-coated with gold palladium in a Hummer sputter-coater and examined using a Zeiss Leo Evo 60 Scanning Electron Microscope (SEM). Ecological data reported here are from species descriptions (Voight, 2007, 2008).

RESULTS

Images of these specimens are clear, despite the absence of specific preparation for SEM studies. The lack of appropriate fixation is not likely to have resulted in the different morphologies and distributions of structures seen, although it may have induced some artifacts in the fine details of the siphon surfaces. Therefore we focus on the morphology of the large structures. The species, which all have an incomplete siphon (the excurrent is distinctly shorter than the incurrent siphon), are discussed below.

Xylophaga oregona (Figures 1–4), competitive dominant, depth 1550–2211 m

For a view of the whole siphon of *Xylophaga oregona*, see Voight (2007, Figure 8A). The excurrent opening lies under an apparently featureless C-shaped hood of tissue near the posterior valve (Figure 1). The incurrent siphonal opening of *X. oregona* lacks cirri (Figure 2). The incurrent siphon distal to the excurrent opening is slightly dorsally flattened; low marginal walls border the dorsal surface (Figure 1). The surface of the incurrent siphon carries concentric ridges (Figures 1, 2). Distally, very small (12–18 μm diameter) structures (Figures 3, 4) emerge apparently at random from the surface ridges. Each structure has a terminal pit from which numerous cilia emerge (Figure 4).

Xylophaga multichela (Figures 5–8), ecology unknown, depth 106–119 m

For a full view of the siphon of *Xylophaga multichela*, see Voight (2008, Figure 1A). In *X. multichela*, the excurrent siphon opens near the posterior valve to form a U-shaped base of a longitudinal groove (Figure 5). Papillae border the groove and are scattered on the lateral and ventral distal incurrent siphon (Figure 6). The opening of the incurrent siphon lacks cirri; however, its tip is morphologically distinct with concentric ridges, rather than a smooth or papillate surface (Figure 7). The papillae bordering the groove (Figure 6) carry terminal cilia (Figure 8) and form fringed lappets. The papillae on the distal siphon also have terminal cilia and appear morphologically similar to, but smaller than, those lateral to the groove. Concentric folds (annulations) on the papillae (Figure 6) and differences in the visibility of the papillae among specimens in light microscopy (unpublished data) suggest that the cilia-topped papillae of the lappets and on the distal siphon are retractable.

Xylophaga microchira (Figures 9–15), early colonist, depth 1550–2656 m

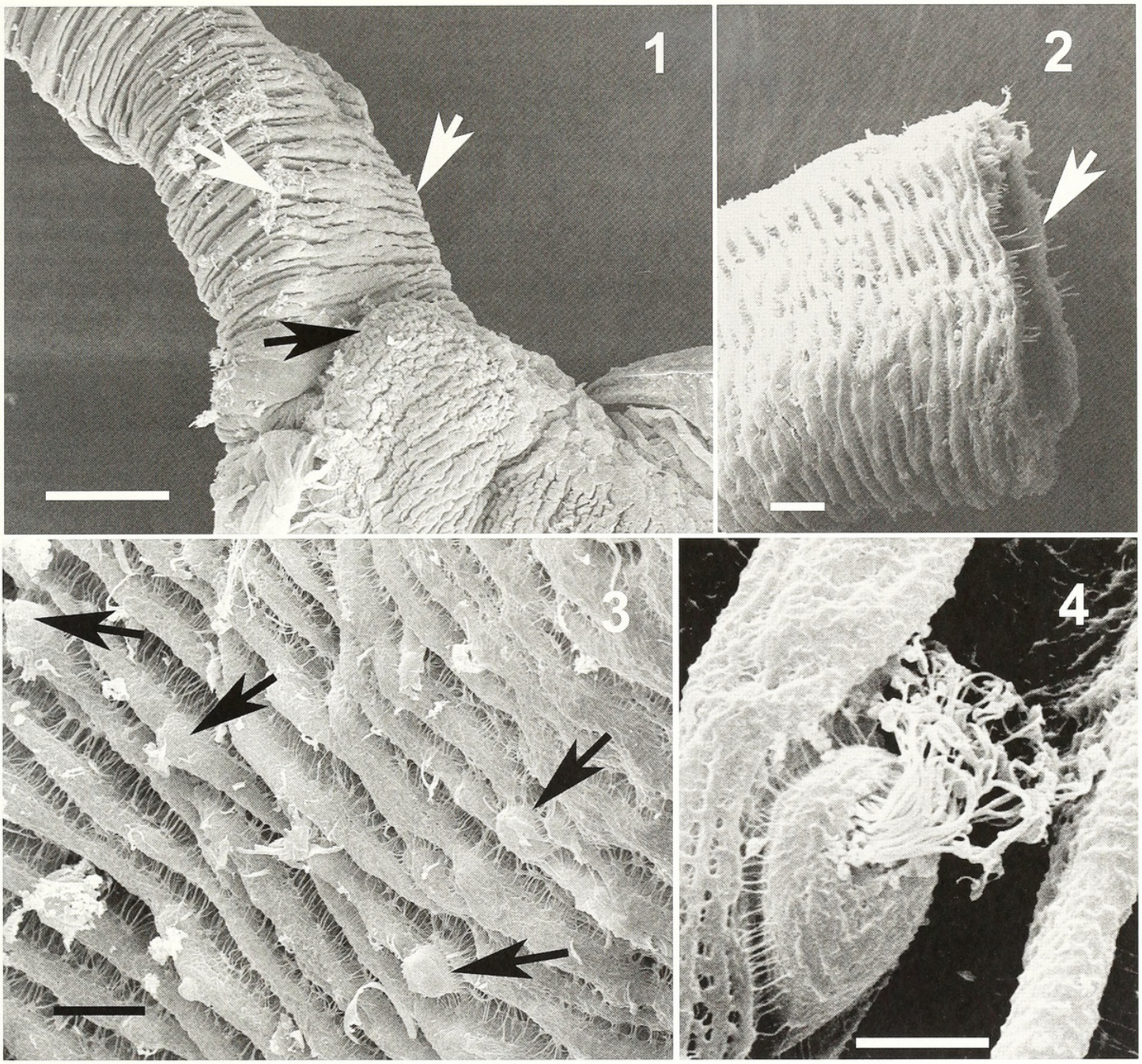
The siphon of *Xylophaga microchira* is circular in cross section and both siphonal openings carry cirri (Figure 9). The opening of the excurrent siphon is near the middle of the siphon and is flanked by very long cirri (up to 420 μm; Figure 10). Cilia emerge from pits at the tips of the cirri (Figure 11). Although the surface of the siphon is ridged, which may be due to contraction, structures such as those seen in *Xylophaga oregona* (Figure 3) appear to be absent.

The incurrent opening has two concentric rings of cirri (Figure 12). The outer cirri are smooth whereas the inner cirri, especially their inner surfaces, appear scaly (Figures 13, 14). Cilia emerge from between the scales (Figures 13, 14) and are densest at the periphery of each cirrus (Figures 14, 15).

DISCUSSION

All structures documented here, whether on the siphonal surface or at the tip of a cirrus (= tentacle sensu Fishelson, 2000), share a terminal opening with an emergent tuft of equal-length cilia. The absence of a long central flagellum leads us to interpret these structures as sensory organs, reportedly common in bivalves (Fishelson, 2000). Distinguishing between mechanoreceptor and chemoreceptor cells is difficult (Hodgson and Fielden 1984), even if neuronal connections are traced (Fishelson, 2000). Earlier comparison of transmission electron microscopy (TEM)-documented ultrastructure of sensory cells to that of known chemoreceptors or mechanoreceptors was said to identify modality of the cells (e.g. Jouin et al., 1985; Chia and Koss, 1989). However, variability in the fine structure of sensory cells led Schaefer (2000: 208) to question this method. Behavioral and physiological data are integral to assign function to sensory cells (Schaefer, 2000; Zhadan et al., 2004). Given that these representatives of *Xylophaga* live inside wood on the ocean floor, at depths of over 2 km, and no material was suitably fixed for TEM study, the modality of the sensory structures documented here cannot be assigned. In general, chemoreceptors have been considered to be the most abundant sensory structure on bivalve siphons (Fishelson, 2000), however, the goblet organs of *Macoma balthica* (Linnaeus, 1758) may be mechanoreceptors (Pekkarinen, 1984).

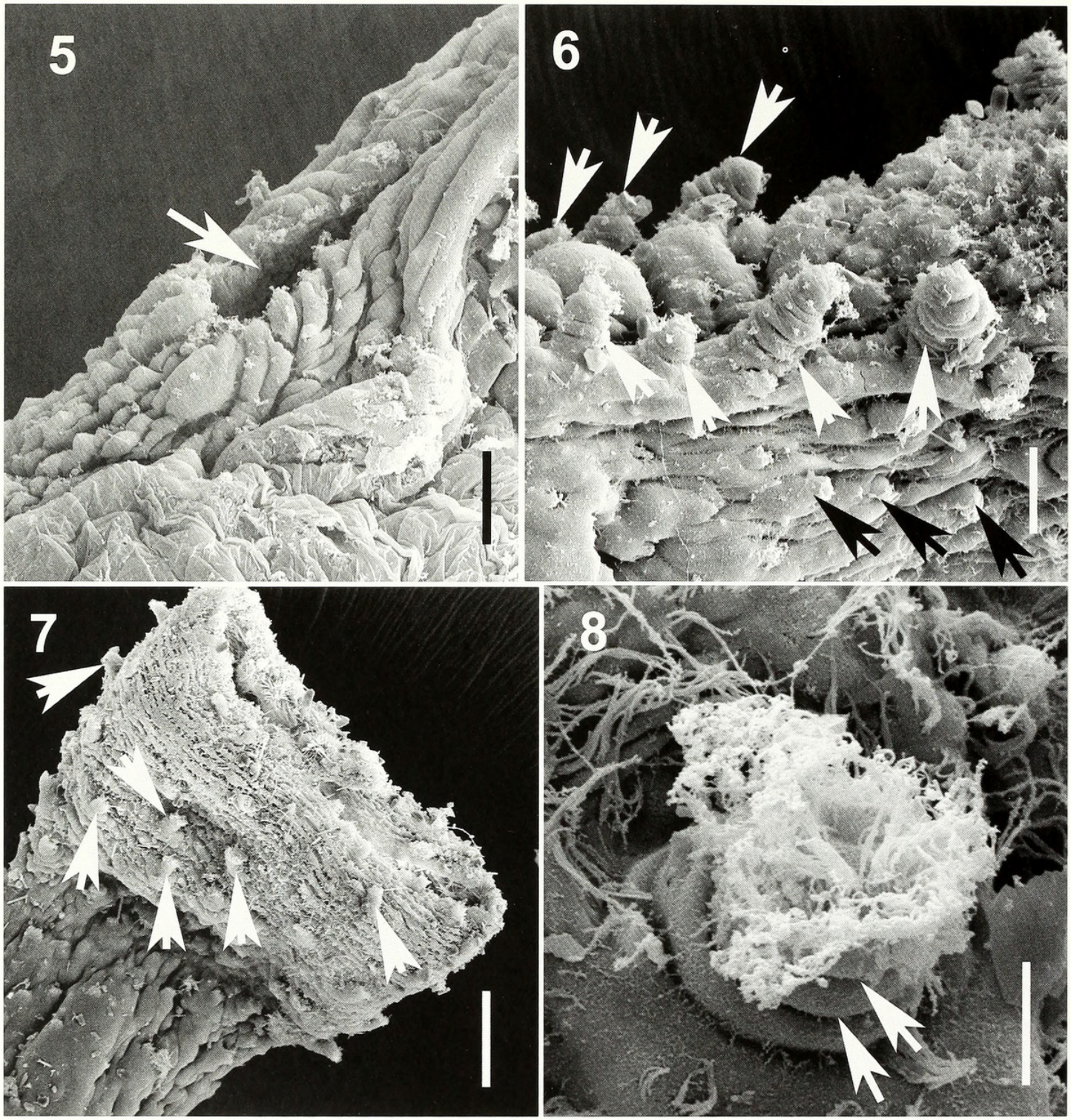
These SEM images reveal that the distribution, shape and size of the sensory structures (Figures 1–15) differ distinctly among these wood-boring bivalves. *Xylophaga oregona* (Figures 1–4) and *X. multichela* (Figures 5–8) share an excurrent siphon that is truncated near the shell (Voight, 2007, 2008); their sensory structures lie on the siphonal integument, in contrast with those on cirri at siphonal openings in *X. microchira*, a species with the excurrent opening near the middle of the siphon (Figures 9–15). These data are consistent with the hypothesis (Voight, 2007), based on differences in siphonal



Figures 1–4. *Xylophaga oregona*. **1.** Excurrent siphon. Black arrow indicates hood of tissue over the opening of the excurrent siphon. White arrows indicate marginal ridges that border a longitudinal flat area of the dorsal siphon. Scale bar = 200 µm. **2.** Tip of incurrent siphon. Arrow indicates the edge of the siphon; note the lack of cirri. Scale bar = 40 µm. **3.** Surface of distal incurrent siphon. Note the ridged appearance and the round projections indicated by arrows. Scale bar = 20 µm. **4.** Finer detail of a round structure indicated in Figure 3. Scale bar = 6 µm.

allometry and overall appearance, that the truncated excurrent siphons are not uniquely derived.

The round structures of *Xylophaga oregona* (Figures 3, 4) strongly resemble the goblet organs detailed by Pekkarinen (1984 Figures 8 and 11, 1986 Figure 5) in the veneroid bivalve *Macoma balthica*, which is only distantly related to the myoid *Xylophaga* species considered here. In both species, the small (10–20 µm) structures are associated with ridges on the distal incurrent siphonal surface, and have long cilia that emerge from a central opening (Figure 4) (Pekkarinen, 1984, 1986). The subtle shape differences could relate to differences in fixation. The goblet organs of *M. balthica* form six longitudinal rows that correspond to the course of the main longitudinal nerves (Pekkarinen, 1984, 1986); sensory structures in *X. oregona* appear to be randomly arranged. Apparent goblet organs, termed type III sensory organs by Hodgson and Fielden (1984) and Ansell et al. (1999), have also been observed on incurrent siphons of the veneroid *Donax trunculus* Linnaeus, 1758 (Fishelson, 2000, Figure 5H).



Figures 5–8. *Xylophaga multichela*. **5.** Opening of the excurrent siphon. Arrow indicates longitudinal groove originating at the opening. Scale bar = 40 µm. **6.** Two rows of papillae (white arrows) form fringed lappets lateral to groove that extends distally from the opening of the excurrent siphon. Black arrows indicate a row of papillae inferior to the lappets. Scale bar = 40 µm. **7.** Tip of incurrent siphon. Note the ridged surface at the siphonal tip and randomly scattered cirri (arrows). Scale bar = 80 µm. **8.** Finer detail of a lappet from the distal incurrent siphon. Note the tuft of equal-length cilia emerging from the center. Arrows indicate folds on a cirrus. Scale bar = 8 µm.

Bivalves living in high-energy habitats with heavy sedimentation tend to have elaborate, branched cirri on the incurrent siphon (Fishelson, 2000). Turner (1971) suggested that the elaborate cirri of shipworms (teredinids) form a sieve across the incurrent opening to protect the animal from debris. However, Lopes and Narchi (1998) found that the tentacles did little themselves to block the entrance to the incurrent siphon in the teredinid *Nausitora fusticula* (Jeffreys, 1860), rather contraction of the siphon base served to block the opening. The incurrent siphon of *Xylophaga microchira* carries structures highly compatible with a sieving function. In this species, the

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