EXPERIMENTAL DEEP-SEA DEPLOYMENTS REVEAL DIVERSE NORTHEAST PACIFIC WOOD-BORING BIVALVES OF XYLOPHAGAINAE (MYOIDA: PHOLADIDAE)

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ABSTRACT

Only a single species of deep-sea wood boring bivalve has been known off the forested northwest coast of North America, although the Xylophagainae are so diverse in other areas that up to five species occur in a given length of wood. To determine whether additional species were present in the Northeast Pacific and if so, how they coexist, lengths of wood were experimentally deployed on heavily sedimented sites on the Cascadia Basin and Escanaba Trough, non-hydrothermally active basalt on Gorda Ridge and Axial Volcano, and an isolated sediment pond within the axis of Juan de Fuca Ridge, at depths of between 1,530 and 3,232 m. All locations were between 41°and 48°N, at least 240 km off the North American coast. Six previously unknown species, *Xylophaga corona* n. sp., *X. zierenbergi* n. sp., *X. heterosiphon* n. sp., *X. oregona* n. sp., *X. microchira* n. sp. and *Xylopholas crooki* n. sp., were collected and are described here. Dominant species differed in recoveries made after 10 and 24 months at Juan de Fuca Ridge and Cascadia Basin localities. *Xylophaga microchira* n. sp. dominated four of five deployments recovered within 12 months, but its abundance declined by 24 months, being largely replaced on Juan de Fuca Ridge by *X. oregona* n. sp., a species known only from this Ridge and from an incidental collection on the Nootka Fracture Zone. At Cascadia Basin sites, the abundances of *X. heterosiphon* n. sp. and of what are likely to be predatory polyclad flatworms increased as that of *X. microchira* n. sp. declined. *Xylophaga microchira* n. sp. is hypothesized to be specialized for early colonization, but to be competitively inferior to *X. oregona* n. sp., and more vulnerable to predators than *X. heterosiphon* n. sp. The dominance of competitively superior and more predator-resistant species in older deployments argues that biotic interactions contribute to coexistence of multiple species of wood-borers despite direct competition among them.

INTRODUCTION

The 49 known species of wood-boring bivalves of the Xylophagainae occur from 10 to 5,050 m depth, from the equator to near 75°N (Knudsen, 1961, 1967; Okutani, 1975; Santhakumaran, 1980; Harvey, 1996; Turner, 2002; Schiøtte, 2005); arguably they form the deep-sea and high-latitude ecological replacements of teredinids or ship-worms. These bivalves bore into wood sunken to the seafloor using toothed ridges on their anterior shells and ingest wood fragments (Purchon, 1941); gill-associated symbiotic bacteria aid in the digestion of wood (Distel & Roberts, 1997). The Xylophagainae, being restricted not only to the deep-sea, but also to what appear to be rare and often ephemeral pieces of wood on the seafloor, remain little known. Species descriptions are often the primary source of information on the group.

As inferred from type localities of species (Knudsen, 1961; Santhakumaran, 1980; Harvey, 1996; Turner, 2002), as many as six species of Xylophagainae have been collected together, with up to five species known from a single piece of wood (Hoagland & Turner, 1981). Only one species, *Xylophaga washingtona* Bartsch, 1921, however, is known from the eastern Pacific north of California (Coan, Scott & Bernard, 2000), despite the presence of lush temperate rainforests on coastal northwest North America. This species occurs from at least Vancouver Island, British Columbia to Santa Barbara Islands, California from 18 to 2,066 m depth; only at the southern end of its distribution, south of 34°N, are two other species of Xylophagainae known to occur (Turner, 2002).

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To investigate species that associate with wood falls in the Northeast Pacific, wood was experimentally deployed at depths of from 1,550 to 3,232 m and recovered after one and two years using subsea vehicles. This paper reports six new species of wood-boring bivalves recovered with those deployments, and documents species distributions over time. Despite limited replicate sampling, consistent patterns of species replacement are suggested. Discovery of these species furthers our knowledge of the diversity of wood-boring molluscs in the North Pacific; apparent patterns of species replacement suggest that biotic interactions mediate direct competition among them, allowing survival of multiple sympatric species.

Taxonomic history of North Pacific species and discussion of characters

Turner (1955) synonymized Bartsch's (1921) *Xylophaga californica* and *X. washingtona*, retaining the species name *washingtona*, despite the precedence of *californica*, because the type specimen of the latter species (a dry valve) was in poor condition. Based on specimens collected near 100 fm (183 m) depth in Tosa Bay, Shikoku, Japan, Taki & Habe (1950) named *X. japonica*, retaining it in the type genus and erected the genus *Neoxylophaga* to accommodate the type species *rikuzenica* Taki & Habe, 1945 and their new species, *N. teramachii*. The rather small white triangular mesoplax (=protoplax) covered by a thick brown periostracum were cited as characters defining the genus. In the same paper, these authors erected the genus *Metaxylophaga* with a small, triangular, vertically oriented mesoplax for the single new species *supplicata*. After study of the type specimens

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Table 1. Synopsis of species groups in *Xylophaga* (Turner, 2002).

Group # Member species	Group 1 *X. erecta* Knudsen, 1961	Group 2 *X. grevei* Knudsen, 1961	Group 3 *X. supplicata* Taki & Habe, 1950	Group 4 *X. abyssorum* Dall, 1886	Group 5 *X. washingtona* Bartsch, 1921	Group 6 *X. dorsalis* Turton, 1822
Mesoplax	Simple, flat or slightly curved; erect; Posterior to anterior adductor	Shape varies. Set at acute angle over dorsal anterior adductor No ventral portion	Nearly flat, with tubes or folds. At acute angle forming inverted V; No ventral portion	Dorsal portion smooth, folded or lobed. Ventral portion variable	Triangular. Ventral portion width variable	Ear-shaped
Siphon	Equal or subequal	Equal or subequal	Equal	Equal or subequal	Excurrent truncated, near shell or $\frac{1}{2}$ to $\frac{3}{4}$ of incurrent length	Excurrent truncated near shell, fringed lateral lobes on dorsal incurrent siphon
Cirri	Present or absent	Excurrent Large on sides; Incurrent Small	Small	At one or both	Present, if excurrent long; if short, dorsal folds on incurrent siphon	

of the above genera and of *Protoxylophaga* Taki & Habe, 1945, Turner (1955) placed them all in synonymy with *Xylophaga* with minimal comment. Knudsen (1961), after describing 17 new species, considered a classification based solely on siphon and mesoplax morphology to be untenable. Okutani (1975) cited *Neoxylophaga* as a subgenus for his new species *X. knudseni* from 30°46.5′ N 141°24.4′ E at 3,100 m depth. In 1977, Habe erected the genus *Mesoxylophaga* for *X. teramachii*.

Only one North Pacific representative was among four species named in the two new genera, *Xyloredo* Turner, 1972a and the monotypic *Xylopholas* Turner, 1972b. *Xyloredo naceli* was recorded from off southern California's Channel Islands.

Turner (2002) described seven additional species of *Xylophaga*, including *X. muraokai* from off southern California, and diagnosed six species groups using the characters in Table 1; the groups encompass all but the two species of *Xylophaga* known only from empty valves, *X. teramachii* and *X. tomlinii* Prashad, 1932. Characters that contribute to species descriptions are schematically depicted in Figure 1. The number of toothed ridges on the anterior beak is routinely reported in species descriptions, although Turner (2002) found the number varies with substrate density in *X. washingtona*.

MATERIAL AND METHODS

Individual deployments consisted of a mesh diver's bag containing one 45.7-cm long piece of machine-cut, bark-free, green 10.1-cm square Douglas fir (*Pseudotsuga* sp.) and an identical piece of oak (*Quercus* sp.) and secured by cable ties. Use of wood of different densities assured that if boring were so heavy that the softer fir disintegrated, the harder oak would remain. Deployments were made in three habitats: sediment, basalt and basalt talus at the edge of a hydrothermal vent. Figure 2 and Table 2 provide deployment localities and dates. The

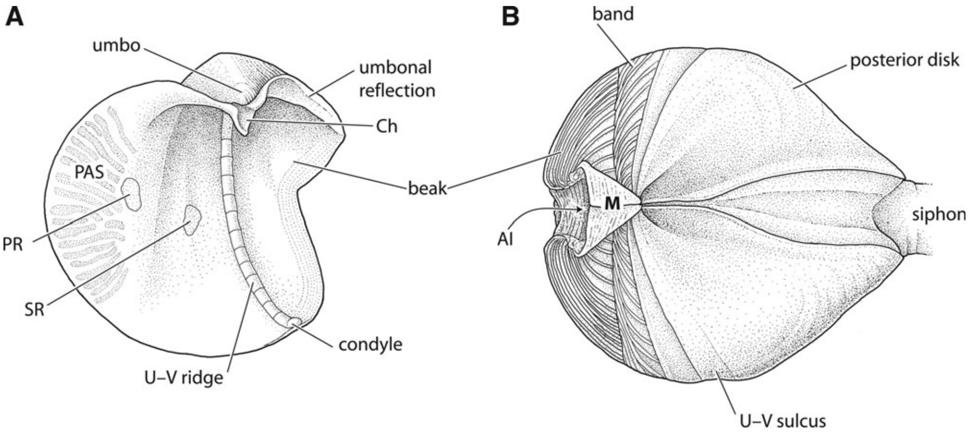

Figure 1. Schematic of shells of *Xylophaga*. **A.** View of inner left valve, indicated are PAS, posterior adductor scar; PR, Pedal Retractor scar; SR, Siphonal Retractor Scar; U-V Ridge, Umbonal-Ventral Ridge; Ch, Chondrophore. **B.** View of dorsal surface of intact individual, M, mesoplax; U-V Sulcus, Umbonal-Ventral Sulcus; AI, Anterior Incision; Band, vertical band of toothed ridges just posterior to beak.

Table 2. Localities and dates of deployments and recoveries.

Site	Latitude Longitude	Depth	Deployments	Recovery
Cascadia Basin				
Wuzza Bare	47°47.087′ N 127°41.479′ W	2,656 m	1 and 4 September 2002	3 September 2004
Baby Bare	47°42.637′ N 127°47.625′ W	2,639 m	5 September 2002	8 July 2003
ODP 1026b	47°45.755′ N 127°45.441′ W	2,658 m	12 September 2002	11 July 2003
Ridge systems				
Escanaba Trough	41°00.016′ N 127°29.685′ W	3,232 m	23 and 25 July 2002	30 August 2004
Sea Cliff – Gorda	42°45.258′ N 126°42.572′ W	2,701 m	28 July 2002	31 August 2004
Axial – Juan de Fuca	45°56.021′ N 129°58.962′ W	1,520 m	14 September 2002	3 September 2003
Endeavour – Juan de Fuca	47°56.781′ N 129°5.822′ W	2,211 m	16 September 2002	15 July 2003, 2 September 2004
Cleft – Juan de Fuca	44°39.8′ N 130°21.3′ W	2,100 m	summer 1999	July 2000
Nootka Fracture Zone				
Nootka F. Z.	49°17.71′ N 127°40.71′ W	2,100 m	September 2004	September 2005

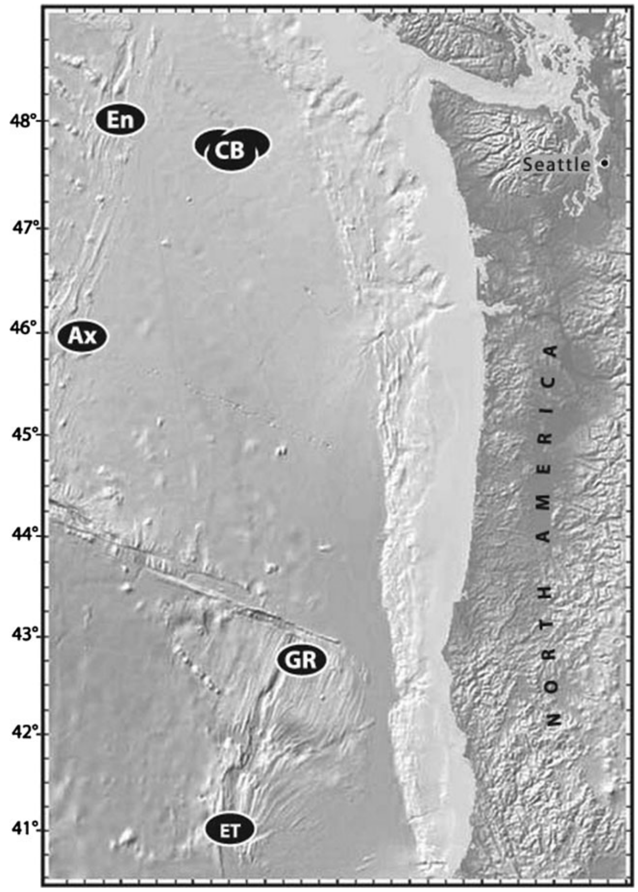

Figure 2. Deployment localities: ET, Escanaba Trough; GR, Gorda Ridge or Seacliff; Ax, Axial Volcano; En, Endeavour Segment; CB, three deployments on Cascadia Basin (map modified from Carbotte *et al.*, 2004).

sediment-hosted deployments were two bags on a heavy layer of terrigenous sediment in Escanaba Trough and four near each of three sites on Cascadia Basin: small Baby Bare and Wuzza Bare Seamounts and the Ocean Drilling Program (ODP) Drill Hole 1026B (drilled in summer of 1996). The seamounts and ODP hole provided only navigational landmarks and place names for the deployments. The basalt-hosted deployments were composed of seven bags in the axial valley of Juan de Fuca Ridge: four on an isolated sediment pond on Endeavour Segment and three in the caldera of Axial Volcano. None of the mid-ocean ridge deployments were made within 30 m of hydrothermal activity and no temperature anomalies were detected at any of the deployment sites. The basalt talus deployment was composed of one bag near the off-axis Sea Cliff (GR-14) Hydrothermal Field, Gorda Ridge, at the margin of a small group of tubeworms of *Ridgeia piscesae* Jones, 1985, with a thin morphology indicative of low sulphide availability (Southward, Tunnicliffe & Black, 1995; Urcuyo *et al.*, 2003). In addition to specimens recovered from these deployments, specimens from Cleft Segment on Juan de Fuca Ridge and from Nootka Fracture Zone were recovered from wood that had been deployed incidentally with geophysical instruments.

All 22 deployments descended from the surface tied on a Remotely Operated Vehicle (ROV), which made navigational fixes at the deployment sites; the ROV *Tiburon* made the Escanaba Trough and Gorda Ridge deployments and the ROV *Jason* made those on the Juan de Fuca Ridge and in Cascadia Basin. During descent, the wood became negatively buoyant due to increasing hydrostatic pressure. In 2003, the ROV's *Jason 2* and *ROPOS* recovered eight deployments that had spent roughly 10 months on the bottom; 14 months later the DSV *Alvin* made nine additional recoveries. Use of subsea vehicles avoided the insurmountable problem of finding wild wood-falls and allowed the deployments to be exact duplicates of known ages. In addition, recovery of the deployments inside a lidded box on a submersible protected against loss of associated species during ascent (Turner, 1978), allowing species interactions to be considered.

Once aboard the ship, the wood was placed in 4°C seawater. Boring bivalves were removed from the wood by either chopping or using an electrical saw to expose them or by pulling the wood apart by hand. Specimens were either preserved and are stored in 85%–95% ethanol, or were fixed in 8% buffered formalin in seawater and are now stored in 70% ethanol. Where possible, sections of wood were split between formalin fixation and ethanol preservation, with additional bivalves removed from the wood after preservation. Specimens included in this report are catalogued in the collections of the Field Museum of Natural History (FMNH) Chicago, IL, USA, and the Scripps Institution of Oceanography Benthic Invertebrates Collection (SIO-BIC), LaJolla, CA, USA. The total number of specimens extracted from each deployment was tallied (Supplementary Data, Appendix 1) and the abundance of each species calculated.

Shell height (dorso-ventral) and length (antero-posterior) of the holotype specimens, measured with electronic callipers, are reported in millimetres in the text, as are shell height and

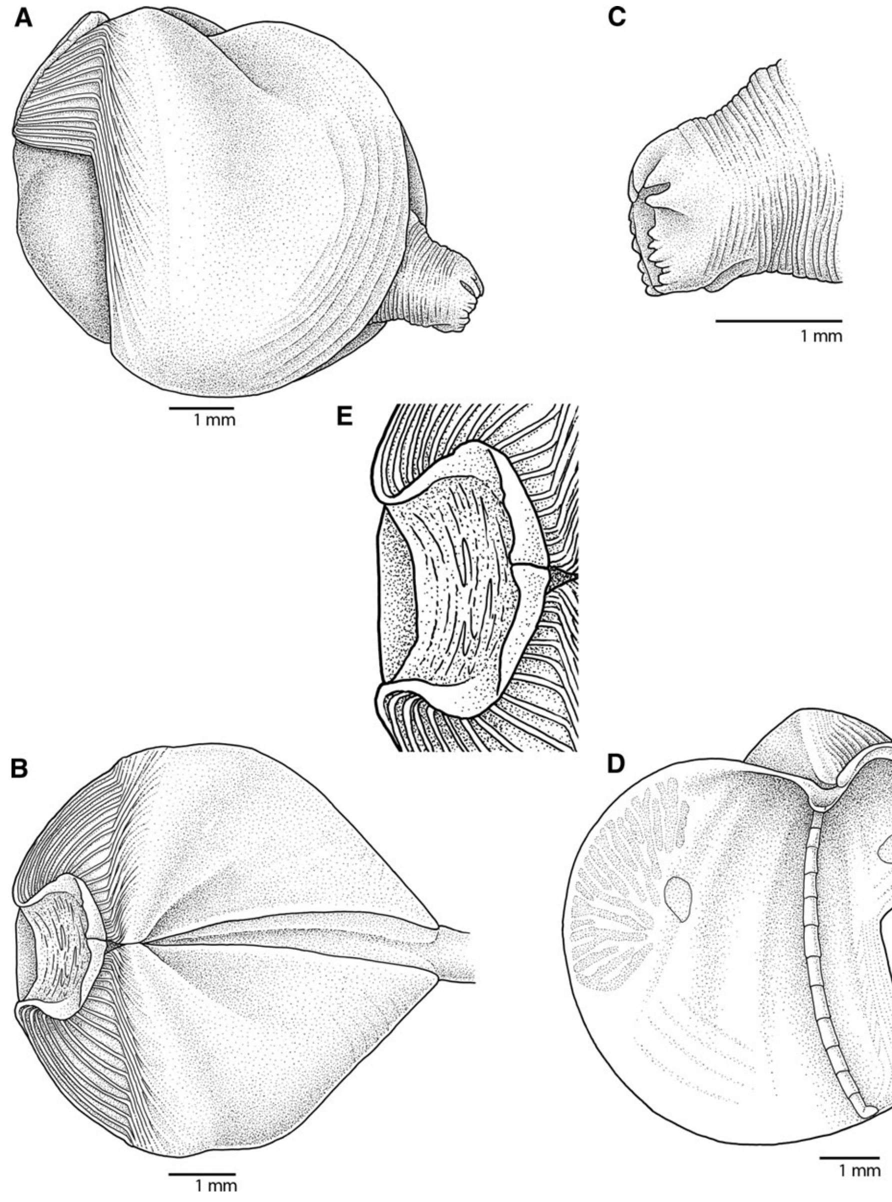

Figure 3. *Xylophaga corona* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell with soft parts. **C.** Lateral view of siphon tips. **D.** Inner shell. **E.** Enlarged view of the mesoplax *in situ*. Scale bars = 1.0 mm.

length ranges of paratypes of *X. zierenbergi* n. sp., *X. corona* n. sp., *X. microchira* n. sp. and *X. oregona* n. sp. A more complete set of measurements for these four species, including shell height, length and width (measured across intact specimens) and either complete siphon length (e.g. *X. zierenbergi* n. sp.), or incurrent and excurrent siphon lengths (e.g. *X. corona* n. sp., *X. microchira* n. sp. and *X. oregona* n. sp.) are reported in Supplementary Data, Appendix 2. Specimens of *X. heterosiphon* n. sp. and *Xylopholas crooki* n. sp. were very fragile and often damaged, allowing only minimal measurements to be made for these taxa. Additional material examined is reported in Supplementary Data, Appendix 3. After transformation to natural logarithms, incurrent and excurrent siphon lengths of *X. microchira* n. sp. and *X. oregona* n. sp. were plotted to determine siphon growth rates. Earlier work on soft-bodied molluscs (Voight, 1991) showed that muscles respond equally to preservation, virtually eliminating artefact if tissues of the same structure are compared. Because the siphon lengths show very tight correlations, despite being only weakly correlated with shell measurements (unpublished data), they are assumed to have responded to preservation uniformly.

With abundant (over 1,100) specimens of *X. microchira* n. sp. and *X. oregona* n. sp., siphons of these species were examined after critical-point drying and sputter-coating with gold using a LEO Zeiss Scanning Electron Microscope.

SYSTEMATIC DESCRIPTIONS

Genus *Xylophaga* Turton, 1822

Type species: *Teredo dorsalis* Turton, 1819 by original designation.

Diagnosis: Teredo-like shells lacking apophyses, but with chondrophore and internal ligament. Animal entirely contained within the shell. Mesoplax divided; shape and size variable.

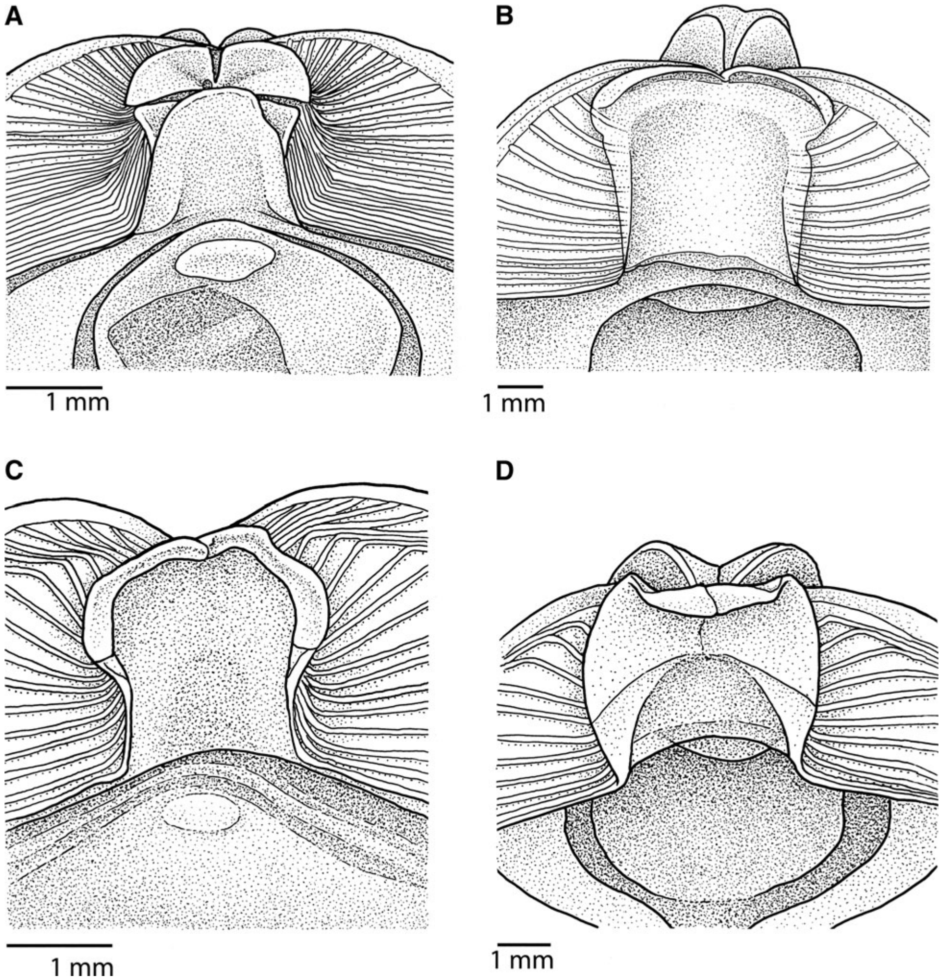

Figure 4. Frontal view of the anterior beak and foot of **A.** *Xylophaga* sp. **B.** *Xylophaga zierenbergi* n. sp. **C.** *Xylophaga corona* n. sp. **D.** *Xylophaga muraokai* Turner, 2002.

Siphons united for part or all of their length, otherwise variable, excurrent siphon may be truncated.

Xylophaga corona new species

(Figs 3, 4C)

Type material: Holotype FMNH 308165 (shell 5.8 height × 5.9 length); 33 paratype specimens FMNH 308676, FMNH 308695, FMNH 308697, FMNH 309615 (shell range 6.2 height × 5.2 length to 8.5 height × 8.3 length) from margin of Sea Cliff (GR-14) Hydrothermal Field, Gorda Ridge (42°45.258′ N 126°42.572′ W, 2,701 m).

Etymology: From *corona*, Latin for crown, for the crown-shaped mesoplax.

Diagnosis: Mesoplax: shallow triangle with long lateral limbs, medial dorsad curve. Excurrent opening: subterminal, 5–7+ long cirri; incurrent opening: double ring of short cirri. Inner shell: no strong ridges or folds.

Description: Beak: 15–22 fairly widely spaced toothed ridges parallel ventral edge (Fig. 3A); 7–11 toothed ridges in relatively narrow vertical band at junction of beak and anterior disk; generally only one ridge at ventral tip of valve; non-protruding. Shell spherical. Anterior incision: narrow relative to shell breadth, possibly due to retracted siphons. Umbonal-ventral sulcus: wide, shallow, perceptible due to defining ridges, posterior ridge a broadly inflated rise (Fig. 3B).

Mesoplax: thin, nearly translucent, medial joint moveable and smooth. In dorsal view: shallow, laterally elongate triangle (Fig. 3E), with medial dorsad curve; forms a crown over dorsal third of anterior incision (Fig. 4C), ventrally extensive.

Siphons: contracted to less than half shell length. Excurrent opening: 5–7+ long, equal cirri dorsally (Fig. 3C), in one specimen, cirri restricted to contacts with incurrent siphon. Incurrent opening: outer ring of 12–24 simple cirri, inner ring of more complex folded cirri that appear to occlude aperture. Faecal chimneys small, poorly organized. Foot musculature weak, cecum visible through foot.

Posterior adductor scar: individual elements comparatively short, broad, linear with few branches (Fig. 3D), entire scar short dorso-ventrally, ventrally bounded by rounded, roughly continuous line. Umbonal-ventral ridge: delicate with a weak condyle. Pedal retractor muscle scar: shiny oval, somewhat variable in shape. Faint muscle scar near ventral edge of inner beak. Other muscle scars poorly defined. Chondrophore short. Inner shell: smooth, no well-defined ridges. Posterior disk with concentric growth lines.

Distribution: Known only from near the Sea Cliff hydrothermal vent field on Gorda Ridge.

Remarks: The smooth, shallow mesoplax, the round shell, non-protruding beak, subtle umbonal-ventral sulcus and subequal siphons readily distinguish this species from all others. This species is most similar to *X. muraokai* Turner. The mesoplax of

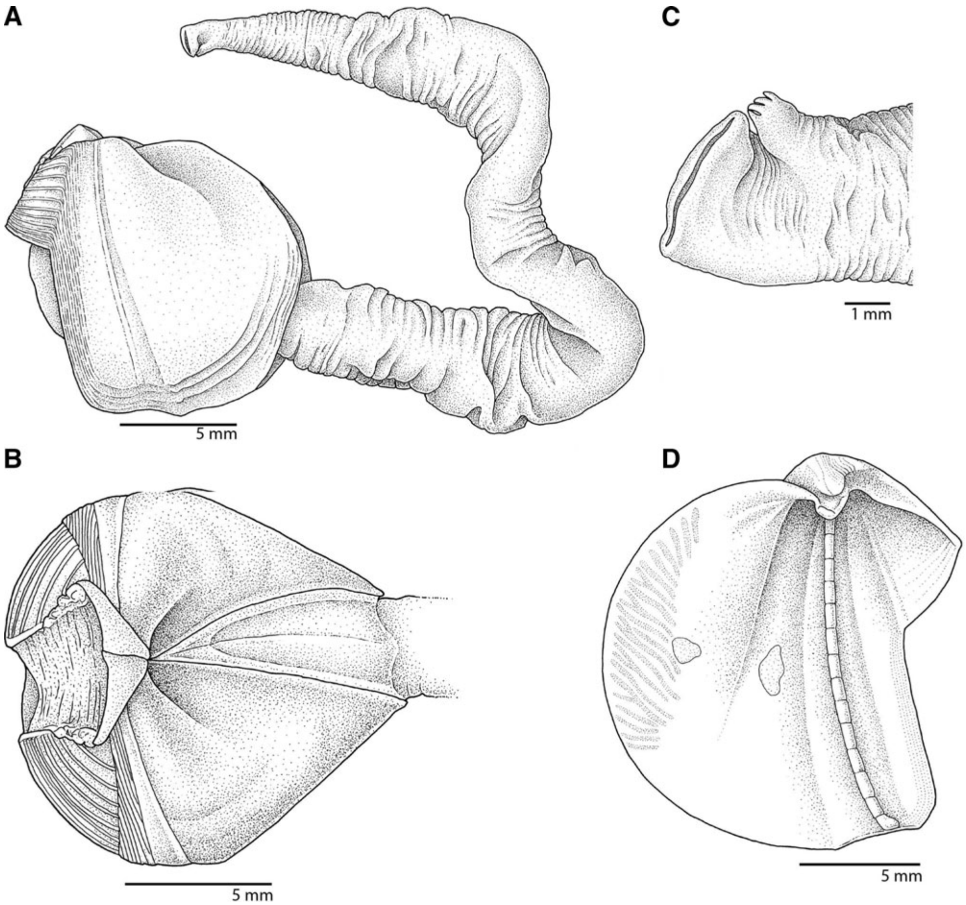

Figure 5. *Xylophaga zierenbergi* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell with soft parts. **C.** Lateral view of siphon tips. **D.** Inner shell. Scale bars **A**, **B**, **D** = 5.0 mm; **C** = 1.0 mm.

22 paratype specimens of *X. muraokai* (Fig. 4D), however, is consistently more angular than is that of the present species (Fig. 4C), easily distinguishing them.

Xylophaga zierenbergi new species

(Figs 4B, 5)

Type material: Holotype FMNH 308166 (shell 13.7 height × 12.2 length); 10 paratypes FMNH 308675, FMNH 308716 (shell size range 13.0 height × 11.9 length to 15.7 height × 14.7 length); from deployment on thick sediment 30 m north of Central Hill, Northern Escanaba Trough (41°0.016′ N 127°29.685′ W; 3,232 m) and one paratype (FMNH 308651) from Endeavour Segment, Juan de Fuca Ridge (47°56.781′ N 129°5.822′ W; 2,211 m).

Etymology: Named for R. A. Zierenberg in recognition of his long-term and fruitful research at Escanaba Trough and in thanks for his invaluable help making the deployments that resulted in collection of this species.

Diagnosis: Mesoplax: laterally extensive, moderately deep triangle covering umbos. Siphons subequal, long, moderately robust. Excurrent opening: 6–8 cirri; incurrent opening: no cirri.

Description: Beak: 16–20 toothed ridges parallel ventral edge; about 9–11 toothed ridges in crowded vertical band where beak joins anterior disk (Fig. 5A). Shell: large, spherical, moderately fragile. Transparent membrane closely follows inner shell. Umbonal reflection: thin transparent layer extending as a half-moon dorsally over, and adherent to, anterior disk near centre of anterior incision. Posterior shell: weakly concave from some angles; with concentric growth lines. Chimney poorly developed.

Mesoplax: simple triangle, at most only a gentle dorsad curve on anterior edge, with basal flanges (Fig. 4B); positioned between, or even posterior to, umbos (Fig. 5B); covers only most posterior anterior adductor. Umbonal-ventral sulcus: shallow with moderate posterior ridge.

Siphon: two and three times shell length, despite potential longitudinal contraction. Excurrent opening: terminal, or slightly subterminal, with 4–8 small cirri (Fig. 5C). Incurrent opening: flaccid, 2 mm across, without cirri. Siphon orientation relative to shell variable.

Posterior adductor scar: as seen through shell of intact specimen, linear with limited branching (Fig. 5D). Umbonal-ventral ridge: slender, weak segmentation, poorly defined condyle. Inner shell: strong ventral-dorsal fold anterior to oval pedal retractor scar, not externally visible. Periostracum thin, transparent, restricted to inner shell.

Distribution: Known only from Escanaba Trough (3,232 m depth) and Endeavour Segment, Juan de Fuca Ridge (2,211 m depth).

Remarks: The smooth, low, broad triangular mesoplax (Figs. 4B, 5B) and the absence of cirri on the incurrent siphon combine to make this species unique. Most similar to *X. muraokai*, this species is readily distinguished by its smooth mesoplax (Fig. 4B vs D) and a rounder shell lacking a posterior extension. Four other species of *Xylophaga*, *X. whoi* Turner, 2002, *X. abyssorum* Dall, 1886, *X. africana* Knudsen, 1961 and *X. aurita* Knudsen, 1961,

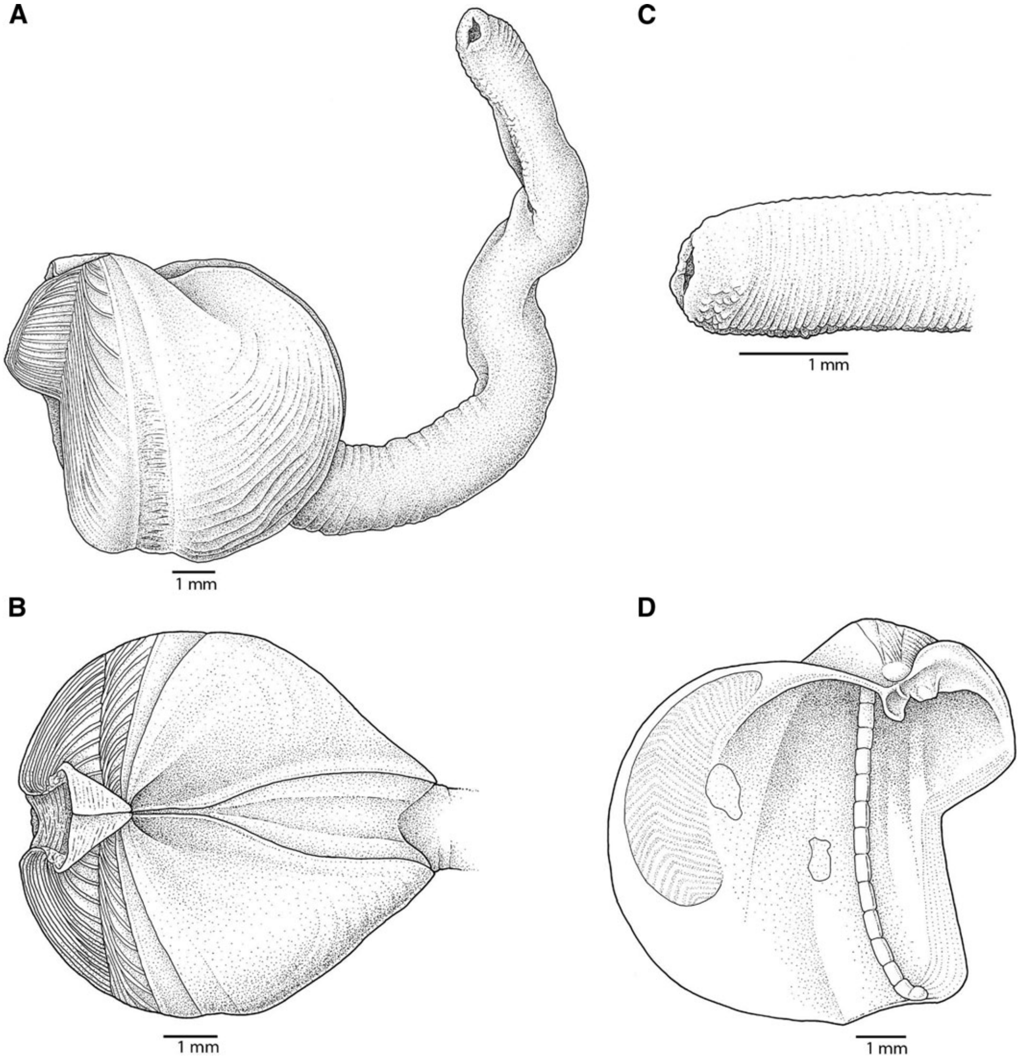

Figure 6. *Xylophaga oregona* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell with soft parts. **C.** Lateral view of incurrent siphon opening. **D.** Inner shell. Scale bars = 1.0 mm.

lack cirri on the incurrent siphon. The tubes and folds of the mesoplax on *X. whoi* and *X. abyssorum* readily distinguish them; the formation of a pointed arch by the mesoplax in *X. africana* distinguishes it. The incomplete siphon of *X. aurita* makes it distinct.

Xylophaga oregona **new species**

(Figs 6,8A)

Type material: Holotype FMNH 308167 (shell 8.1 height × 8.1 length); 32 paratypes FMNH 308168, FMNH 308169, FMNH 308170, FMNH 308171 (shell size range 3 height × 3 length to 8.2 height × 7.8 length) from deployment on isolated sediment pond on Endeavour Segment, Juan de Fuca Ridge (47°56.781′ N 129°5.822′ W; 2,211 m).

Etymology: Named for the state of Oregon, the proximity of which to the state of Washington reflects the outward similarity of this species to *X. washingtona*.

Diagnosis: Shell: spherical. Beak non-protruding. Umbo-ventral sulcus: no ventral expansion. Posterior adductor scar: herringbone pattern. Mesoplax: irregular triangle originating over, or between, umbos. Common siphon: loose membranous cover, with irregular, faint brown fuzz. Excurrent siphon: truncated, no cirri. Incurrent siphon: two low, longitudinal ridges distal to excurrent; no cirri.

Description: Beak: non-protruding (Fig. 6A); 10–24 toothed ridges parallel ventral edge. Rarely 6, generally 9–14, toothed ridges in vertical band at intersection of beak and anterior disk. Shell: valves spherical, no posterior extension; umbonal-ventral sulcus: broad, uniform, no ventral widening or deepening (Fig. 6A).

Mesoplax: irregular triangle, often narrow posteriorly; partly covers anterior incision (Fig. 6B); surface with irregular growth lines; thin, clear periostracal covering. Lateral extensions follow the anterior disk, not united ventrally.

Siphon: incomplete. Excurrent siphon: one-third to over half incurrent siphon length; no cirri. Incurrent siphon up to three times shell length, may contract to roughly equal shell length; immediately distal to excurrent opening, low rounded ridges lateral the flattened dorsal surface (Fig. 8A), becoming indistinct distally, much more pronounced in ethanol-preserved specimens; no cirri (Fig. 6C). Faintly brown, loose periostracal membrane on common siphon, most conspicuous laterally. Faecal chimney very well developed.

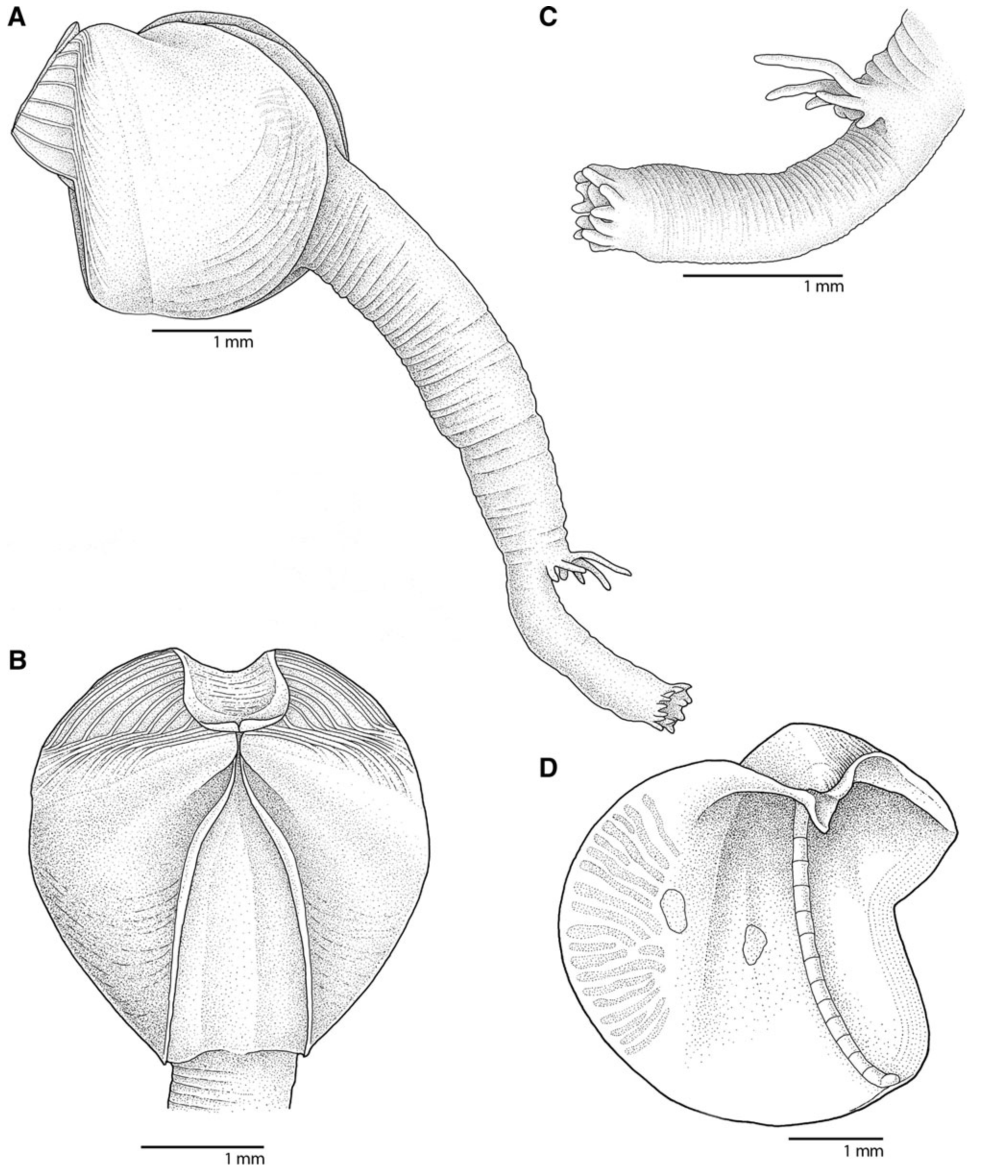

Figure 7. *Xylophaga microchira* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell with soft parts. **C.** Lateral view of siphon tips. **D.** Inner shell. Scale bars = 1.0 mm.

Umbonal reflection: pronounced thickening forms dorsal shoulder of anterior incision, extends beyond prodissoconch as a thin C, exceptionally reaches the height of the umbo. Posterior adductor scar: herringbone pattern, central line more posterior dorsally (Fig. 6D). Pedal retractor scar: single oval, just anterior to middle of posterior adductor scar. Other muscle scars usually faint. Umbonal-ventral ridge: prominent, especially dorsal half; condyle not enlarged. Umbonal-ventral sulcus apparently expressed inside the shell as a fold just posterior to umbonal-ventral ridge.

Distribution: Collected from deployments on Juan de Fuca Ridge (Endeavour, Cleft Segments, Axial Volcano) and on Nootka Fracture Zone, 1,550–2,211 m depth.

Remarks: The strong fold on the inner shell apparently associated with the umbonal–ventral sulcus of this species may create the spherical shell shape that readily distinguishes this species from *X. washingtona* of Turner's Group 5 (2002) to which it is most similar. Collection of this species from the axial valley of Juan de Fuca Ridge (physically isolated from the normal seafloor by the basalt walls that form the ridge), and its apparent absence from identical deployments on Cascadia Basin, between the ridge and the known range of *X. washingtona*, provide further evidence that this species is distinct.

The present species can be distinguished from the Japanese species *X. rikuzenica* Taki & Habe, 1945 by its non-protruding beak, thin periostracum over the mesoplax, narrow umbo-ventral sulcus and less inflated, more linear mesoplax with minimal ventral projections that do not meet ventrally. It is distinguished from *X. turnerae* Knudsen, 1961 by the more massive shell, and cirri on the incurrent opening of that species. It is distinguished from *X. aurita* Knudsen, 1961 by the vertical mesoplax of that species, its lack of a periostracal covering on the common siphon and its posterior shell extension. The prominent ridge posterior to the umbonal-ventral sulcus and the smaller posterior adductor scar of *X. praestans* Smith, 1903 distinguish that species from the present one. This species has a non-protruding beak, separating it from *X. nidarosiensis*

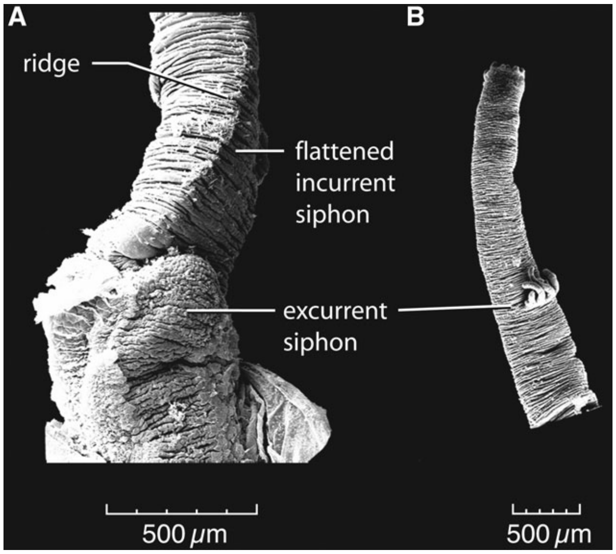

Figure 8. SEM of *Xylophaga* siphons **A.** *X. oregona* n. sp. Ridge lateral to dorsally flattened incurrent siphon and excurrent siphon opening indicated. **B.** *X. microchira* n. sp. Note incurrent siphon is round distal to excurrent siphon opening and incurrent siphon is longer than in Figure 4A. Scale bars = 500 μm.

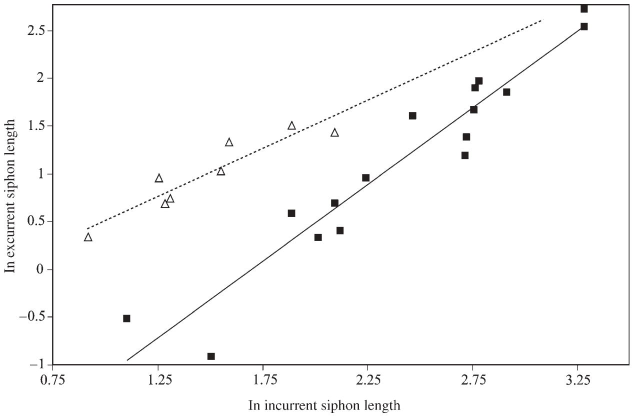

Figure 9. Bivariate plot of natural log (ln) excurrent siphon length and ln incurrent siphon length in *X. oregona* n. sp. (solid squares) and *X micro-chira* n. sp. (open triangles). Equation of the line for *X. microchira* n. sp.: $y = 1.0\,x - 0.49$; for *X. oregona* n. sp.: $y = 1.6x - 2.72$.

Santhakumaran, 1980. This species is unique among those assigned to Group 5 by Turner (2002) due to its spherical shell, the more dorsal extension of its umbonal reflection, the more posterior origin of its mesoplax, the umbo–ventral sulcus paralleling the disk edge and the absence of cirri from both siphons.

The plot of incurrent versus excurrent siphon lengths for *X. oregona* n. sp. shows that the excurrent siphon is positively allometric relative to the incurrent siphon (Fig. 9). As the bivalve grows, the siphon openings thus become closer together, creating the variable length of the excurrent siphon relative to the incurrent siphon, as reported in *X. washingtona* (Turner, 2002). The positive allometry of the excurrent siphon may relate to construction of the conspicuous faecal chimney characteristic of both species.

This species dominated deployments recovered from Axial Volcano after 10 months and Endeavour after 24 months (Fig. 12). Both deployments were so heavily bored that the wood could be crushed by hand (Fig. 13). On some specimens from these deployments, the toothed ridges on the beak were heavily eroded and more numerous and the ridge posterior to the umbo-ventral sulcus appeared more prominent. These characters are attributed to shell wear and crowding, following Turner's (1959) attribution of comparable characters in teredinids to crowding.

***Xylophaga microchira* new species**

(Figs 7,8B)

Type material: Holotype FMNH 308172 (shell 3.2 height × 3.4 length); 28 paratype specimens FMNH 308173, FMNH 308174, FMNH 308184, FMNH 308185 (shell size range 1.7 height × 1.6 length to 3.5 height × 3.4 length) from deployment on sediment 150 m SE of Baby Bare Seamount (47°42.637′ N 127°47.625′ W 2,639 m). Three paratype specimens (FMNH 308175), nine paratype valves (FMNH 309617) from Endeavour Segment, Juan de Fuca Ridge (47°56.781′ N 129°5.822′ W; 2,211 m).

Etymology: From *micro* small and *chir*, hand (Greek), named for the curved cirri at excurrent opening resembling a small hand.

Diagnosis: Siphon: incomplete, robust, wrinkled. Incurrent siphon round in cross-section, no longitudinal papillae or ridges. Excurrent opening: 5–8 long, prominent, curved cirri. Incurrent opening: variable double ring of cirri.

Description: Beak: 10–18 toothed ridges parallel ventral edge, typically only 4–6 toothed ridges in a vertical band of average width at beak-disk junction (Fig. 7A). Shell: translucent, small, fragile (Fig. 7D). Ventral shell margin protrudes immediately adjacent to condyle, valves askew and overlapped in preserved specimens. Posterior valves: weakly concave; mantle protrudes (Fig. 7B).

Mesoplax: in smallest specimens, translucent eyebrow-shaped, oriented vertically; in larger sizes, dorso-medial portion folds anteriorly; with further growth, a tiny horizontal shelf covers part of anterior incision (Fig. 7B); growth lines present in largest specimens.

Siphon: incomplete, never retracted into the shell; between 1.5 and 2 times shell length; common siphon robust, especially at base, with concentric wrinkles. Incurrent siphon: round, no longitudinal ridges or thickenings (Fig. 8B); can be notably thin and unusually short, as in holotype (Fig. 7A), or longer (Fig. 8B). Excurrent opening: 5–8 finger-shaped curved cirri, longest dorsally, (Figs 7A, C; 8B). Incurrent opening: two rings of 7–10 short cirri, best seen in exceptionally well-preserved specimens, more often, about 12 cirri in single ring.

Umbonal reflection: prominent thickening of medial anterior incision, extends as narrow C-shaped shoulder on beak, returns to anterior incision at anterior edge of umbo.

Inner shell: white and glossy. Posterior adductor scar: linear, little branching (Fig. 7D). Pedal retractor scar: linear, at inner posterior adductor scar, roughly parallels individual elements in the scar. Umbonal–ventral ridge: low, weakly segmented; weakly inflated elongate condyle. Strong dorso-ventral groove inside shell between umbonal-ventral ridge and posterior adductor scar, shell thickens slightly just posterior to groove. Muscles insert on shell via very well-developed ligaments.

No faecal chimneys, although faecal accumulations seen in borings of exceptionally small bivalves in wood from Baby Bare site.

Distribution: Collected at depths of 1,520–2,658 m at all deployments in Cascadia Basin, Juan de Fuca Ridge and Nootka Fracture Zone recovered within 12 months (Fig. 12). After 24 months, relatively very few specimens of this species at Endeavour Segment; two specimens taken at Wuzza Bare after 24 months.

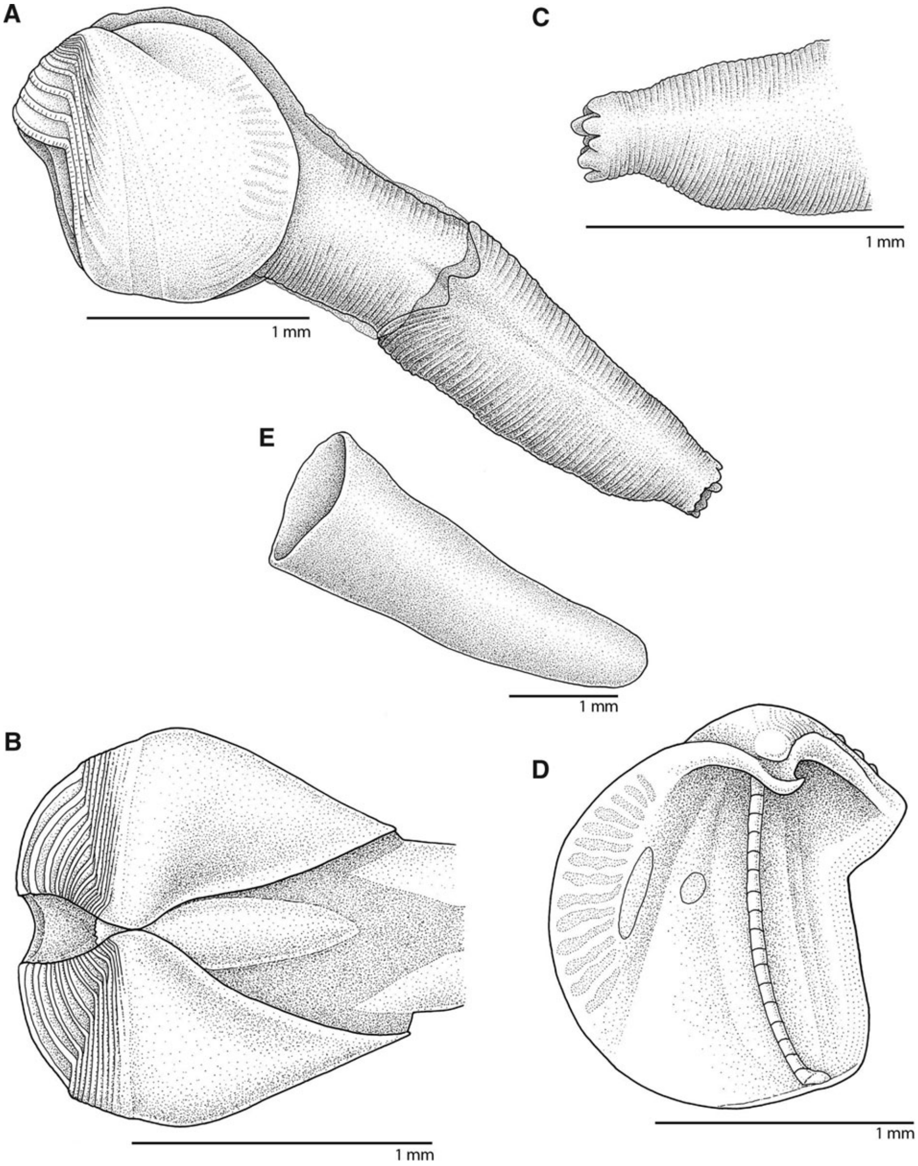

Figure 10. *Xylophaga heterosiphon* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell with soft parts. **C.** Lateral view of siphon tips. **D.** Reconstructed view of inner shell (FMNH 309618). **E.** Periostracal cone (FMNH 309614). Scale bars = 1.0 mm.

Remarks: The incomplete siphon in this species, in which the incurrent siphon is round in cross-section (Fig. 8B) contrasts sharply with the dorsally flattened incurrent siphon of the other species in the genus with an incomplete siphon (e.g. Fig. 8A), making this species unique. Although Turner, 2002 cited a truncated excurrent siphon as diagnostic of her species Groups 5 and 6 (Table 1), any hypothesized homology is refuted not only by the difference mentioned above, but by the difference in excurrent siphon allometries (Fig. 9). The excurrent siphon grows at the same rate as does the incurrent siphon in *X. microchira* n. sp. but it grows more rapidly in *X. oregona* n. sp. (Fig. 9), and likely in other Group 5 species based on Turner's (2002) statement that in *X. washingtona* the excurrent siphon length varies relative to incurrent length. Its distinctive incomplete siphon, and the long cirri at the excurrent siphon opening distinguish this species from all others.

If only shells were available for comparison, this species would appear to be most similar to the following species, assigned by Turner to her Group 2. This species can be distinguished from *X. galatheae* Knudsen, 1961, by the more dorsal posterior adductor scar in that species, a character that also separates the present species from *X. grevei* Knudsen, 1961, *X.*, *wolffi* Knudsen, 1961, *X. hadalis* Knudsen, 1961 and *X. panamensis* Knudsen, 1961. It is separable from *X. murrayi* Knudsen, 1967 and *X. africana* Knudsen, 1961 by the triangular mesoplax of those species, and from *X. clenchi* Turner & Culliney, 1971 by that species' strongly projecting beak. The size-related changes in the mesoplax that result in the eyebrow-shape developing an increasingly anterior bend with growth readily distinguish this species from any other.

A group of specimens collected from heavily bored 24 month-old deployments from Endeavour Segment (Fig. 13) and attributed to this species, but not included among the types, deserves mention. These specimens have more numerous toothed ridges (12–16) at beak/anterior disk junction and on the beak than do others. The ridges on the beak are so heavily eroded as to be uncountable. Ridges peripheral to the umbo-ventral sulcus also show heavy erosion and the cirri at the excurrent siphon occasionally number over 10. These features are consistent with heavy shell wear discussed

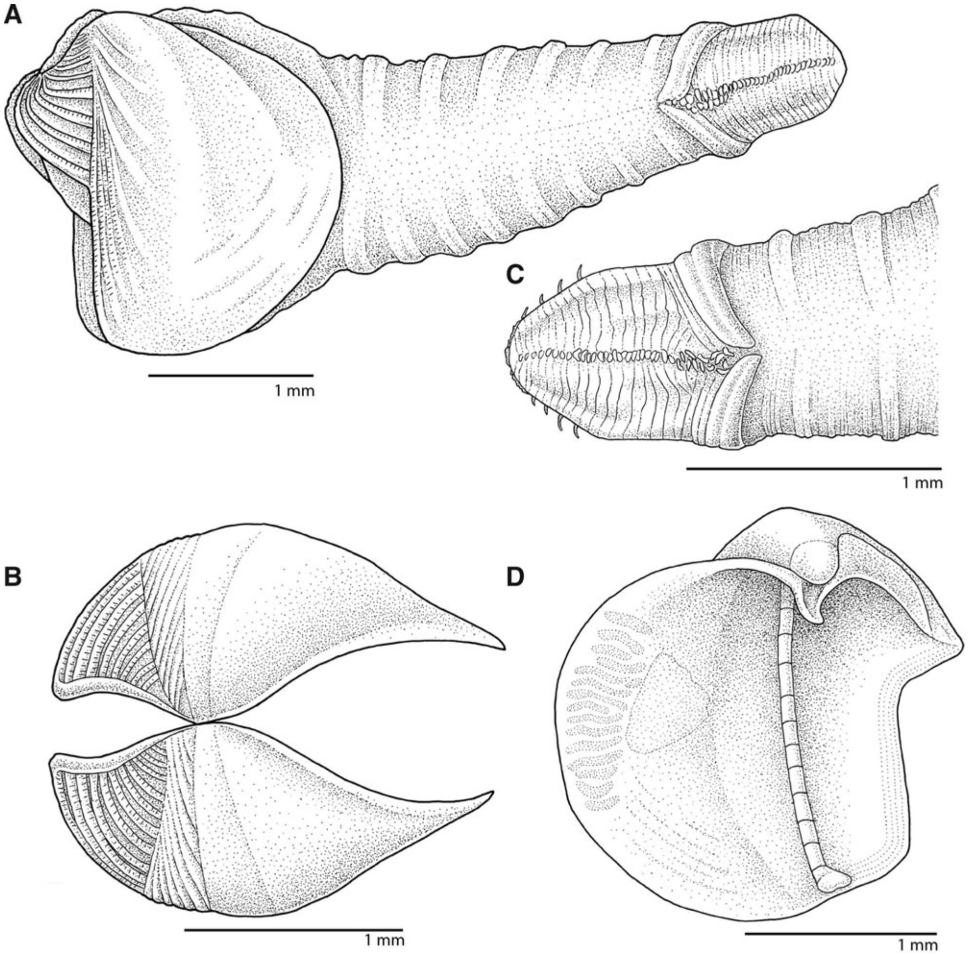

Figure 11. *Xylopholas crooki* n. sp. holotype. **A.** Lateral view. **B.** Dorsal view of shell, soft parts removed. **C.** Lateral view of siphonal plate. **D.** Inner shell (FMNH 308693). Scale bars = 1.0 mm.

above for *X. oregona* n. sp. The siphons of these specimens are notable; not only can they be nearly equal, they can also appear to be nearly transparent. The translucence and near-equal length siphons are suggested to be due to physiological effects of crowding, or to energy- or oxygen limitation. *Xylophaga noradi* Santhakumaran, 1980 was based on a single specimen that had comparatively large, translucent, nearly equal siphons but was reported to be otherwise consistent with *X. dorsalis* Turton. Habitat information for the holotype is not available. If molecular studies support the attribution of these unusual specimens to *X. microchira* n. sp., *X. noradi* might merit reassessment.

In another variant of this species, some specimens from the Cascadia Basin sites of ODP and Baby Bare in 2003 and Wuzza Bare in 2004 had what appeared to be truncated incurrent siphons, to the point in some that the siphons were nearly equal length. This condition is likely due to injury and subsequent regeneration; it may explain why the incurrent siphon in some specimens, including the holotype, can be considerably narrower than the common siphon and shorter than normal (compare Figs 7A, 8A). The holotype (Fig. 7A) was selected because of its undamaged shell.

Xylophaga heterosiphon new species

(Fig. 10)

Type material: Holotype FMNH 308176 (shell 1.3 height × 1.2 length); 26 paratype specimens FMNH 308177, FMNH 308179, FMNH 308180, FMNH 308181, FMNH 309618 from deployment on heavy sediment 155 m E of ODP Hole 1026b (47°45.755′ N, 127°45.441′ W 2,658 m). Two paratypes (FMNH 308067) from deployment on margin of Sea Cliff Hydrothermal Field, Gorda Ridge.

Etymology: From *Hetero* different (Greek), siphon, named for the different appearances of the proximal and distal parts of the common siphon.

Diagnosis: Siphon complete; distal, proximal sections distinct in colour, texture. Proximal siphon: loose transparent cover; distal siphon naked with uniform concentric wrinkles. Openings, terminal, surrounded by a flower-like double ring of cirri. Periostracal cone over siphon, rarely seen intact. Mesoplax: small, poorly calcified hood over most posterior anterior incision.

Description: Beak: 8 – 11 well spaced toothed ridges parallel ventral edge (Fig. 10A); 5 – 6 toothed ridges form narrow vertical band at beak-disk junction. Shells: white, delicate, very often broken. Umbonal-ventral sulcus: weak, shallow. Posterior shell: a bit concave, often gapes (Fig. 10B), membrane over protruding mantle and proximal siphon.

Mesoplax: small, clear, very lightly calcified at most, covers posterior-most anterior incision.

Siphons: Complete, proximal and distal parts distinct, separated by scalloped margin: mid-dorsal, mid-ventral and mid-lateral points most proximal; relative lengths appear inconsistent; longitudinal septum present (Fig. 10A). Openings terminal, inside double ring of cirri; outer ring with about 35 cirri, inner ring hard to see with about 20 shorter cirri (Fig. 10C); small tube extends from excurrent in some specimens (Fig. 10C). Distal siphon: dark-coloured, regular striations, like edges of pages in a book. Proximal siphon: light-coloured, dark mid-dorsal colour originates as tapering V from mantle (Fig. 10B); mid-ventral longitudinal stripe comparable but narrower; loose, glossy smooth membrane from mantle to siphon's dorsal midline covers proximal siphon. Periostracal cone (Fig. 10E) more often recovered in substrate than on specimen.

Posterior adductor scar, as seen through the shell of a large intact specimen (Fig. 10D), linear, unbranched. Caecum visible through muscles in foot.

Distribution: Most abundant as small individuals from the Cascadia Basin sites ODP and Wuzza Bare (Fig. 12), but two large (up to 24-month old) individuals were recovered from the Sea Cliff deployment. Also known from the Oregon Margin (FMNH 306555 $n = 2$. North Pacific Ocean; Oregon Margin; 44°45′57″ N 125°31′ 46″W to 44°38′ 48″ N 125°38′ 50″ W; 2,750 m; R/V WECOMA Sta. 5; 17 April 1997).

Remarks: The present species can be readily distinguished from all others by the distinct appearance of proximal and distal siphon, its nearly uncalcified mesoplax, a single ring of cirri around both siphon openings, smooth periostracal cone, small umbonal reflection and few toothed ridges on the beak. This species, distinct from any known to Turner (2002) appears to be most similar to *X. gerda* Turner, 2002 with which it shares a thin shell, periostracal siphonal cover, faint posterior adductor scar, and thin muscle of the foot through which the caecum is visible. The species are readily distinguished by the shell shape, oval in *X. heterosiphon* n. sp. versus round in *X. gerda*; in addition, the smooth beak of *X. heterosiphon* n. sp. contrasts with the protruding beak of *X. gerda*. The smooth periostracal cone in *X. heterosiphon* n. sp. is distinct from the leaflet-carrying cone of *X. gerda*. Although the unified siphon tips surrounded by a single ring of cirri in *X. heterosiphon* n. sp. would appear to readily separate this species from *X. gerda*, in which the siphons have separate rings of cirri, Turner (2002) noted that in contracted specimens of *X. gerda*, the two rings of cirri appear to be one. However only 19 specimens, all under 4 mm long, were available to Turner, while 184 specimens of the present species were examined. None of these specimens had a double ring of cirri, including the large specimens from Sea Cliff.

Some characters of *X. heterosiphon* n. sp., notably the siphons with proximal and distal parts, periostracal cone, a poorly calcified mesoplax and shell shape are reminiscent of *Xyloredo naceli* Turner, 1972a. The present species can, however, be distinguished by its lack of a calcareous tube lining, which in part defines the genus *Xyloredo*, its united siphons that open within one ring of cirri, segmented umbonal-ventral ridge and smooth siphonal cone.

Genus *Xylopholas* Turner, 1972b

Type species: *Xylopholas altenai* Turner, 1972b by original designation.

Diagnosis: Valves and mesoplax typical for *Xylophaga*, animal long, incapable of retraction into valves; periostracal siphonal sheath posterior to valves and paired lateral chitonlike siphonal plates at posterior end.

Xylopholas crooki new species

(Fig. 11)

Type Material: Holotype FMNH 308182 (shell 1.5 height × 1.5 length); two paratype specimens FMNH 308679, FMNH 308183 from deployment on heavy sediment 150 m W of Wuzza Bare Seamount (47°47.087′ N 127°41.479′ W, 2,656 m).

Etymology: Named in honour of Tom Crook, at-sea JASON Navigator of Woods Hole Oceanographic Institution (WHOI) in recognition to his years of service to science, specifically his superlative efforts during the 2002 cruise, the last before his retirement from WHOI, which allowed the deployments to be relocated and these species to be discovered.

Diagnosis: Shell and siphons typical for genus; siphonal plate with minute, clear, recurved hooks on posterior edge, midline with simple hooks.

Description: Beak: projecting, otherwise unexceptional (Fig. 11A); 10–12 toothed ridges parallel ventral edge; fairly wide vertical band of 4–6 ridges at beak – anterior disk junction (Fig. 11B). Shell: small (length 1.5), fragile, nearly translucent. Mantle protrudes between posterior valves, loose transparent membrane cover, no young seen. Ventral shell tip: no vertical ridges. Umbo-ventral sulcus: not evident.

Mesoplax: very poorly calcified, nearly transparent; extends in vague horseshoe shape over dorsal and lateral edges of anterior incision.

Siphons: bulky, 3.1 mm long, comparatively thick, tightly covered by distinctly banded pale yellow transparent sheath (Fig. 11A). Siphonal plate broad, rounded pentagon in shape (Fig. 11C) minute, clear, recurved hooks on posterior edge; at midline, a row of simple hooks that appear to connect to faint dorso-ventral lines. Siphonal collar: small, fairly narrow.

Dry shell: unusually translucent, muscle scars poorly defined (Fig. 11D). Pedal retractor, broad area of shiny inner shell. Posterior adductor scar, as seen through shell of an intact specimen, linear elements (Fig. 11D) obscured by overlying concentric growth lines of posterior disk.

Distribution: Known only from Wuzza Bare, Cascadia Basin.

Remarks: The armature on the siphonal plate clearly distinguishes this, the second recognized species in the genus *Xylopholas*, from *X. altenai* with rounded smooth plates. In addition, the protruding beak, the more linear chondrophore, simple siphonal collar, the bands on the siphonal sheath, the lack of attached young, the smaller posterior adductor scar with smaller individual elements, the larger and vaguely defined pedal retractor scar all separate this species from *X. altenai*.

RESULTS

None of the 2,700 specimens collected and examined in this study represent *Xylophaga washingtona*. Of the six new species found, three were collected from a single deployment.

Species composition differed among sites and over time (Fig. 12). At the southern sites of Escanaba Trough and Sea Cliff on Gorda Ridge, *X. zierenbergi* n. sp. and *X. corona* n. sp., respectively, dominated. In this study, only one other specimen of either species, that of *X. zierenbergi* n. sp., was recovered. *Xylophaga microchira* n. sp. had the widest areal distribution (Fig. 12), being absent only from Gorda Ridge and Escanaba Trough. Bivalves of *X. oregona* n. sp. were collected from the Juan de Fuca Ridge and Nootka Fracture Zone localities, but were absent from the southern sites and from Cascadia Basin to the east; bivalves of *X. heterosiphon* n. sp. were collected from deployments from Cascadia Basin and Gorda Ridge, but were unknown from Escanaba Trough or the Juan de Fuca Ridge. Specimens of *Xylopholas crooki* n. sp. were recovered only at Wuzza Bare.

If the duration of a deployment predicted species occurrence, equal-aged deployments would be expected to have the same species in nearly the same abundances. However, species composition differed between equal-aged deployments in the same

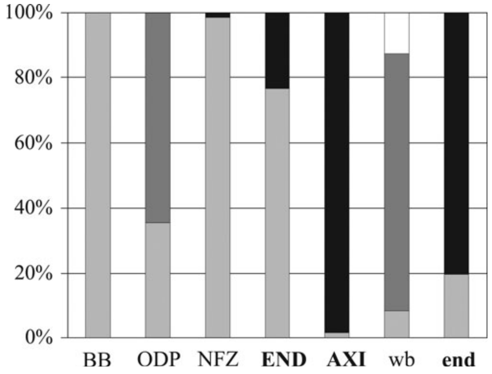

Figure 12. Species abundances at northern sites. Site abbreviations (*x*-axis), BB, Baby Bare, Cascadia Basin; ODP, Ocean Drilling Program platform, Cascadia Basin; NFZ, Nootka Fracture Zone; **END**, Endeavour Segment, Juan de Fuca Ridge; **AXI**, Axial Volcano, Juan de Fuca Ridge; wb, Wuzza Bare, Cascadia Basin; **end**, Endeavour Segment, Juan de Fuca Ridge. Upper case indicates recoveries made within 12 months of deployment; lower case = 24 month deployment. Bold indicates on-axis deployment. Species colour-coded: light grey = *X. microchira* n. sp.; dark grey = *X. heterosiphon* n. sp.; black = *X. oregona* n. sp.; white = other comparatively rare species. Not included here are the southern sites (Escanaba Trough = 100% *X. zierenbergi* n. sp.; Sea Cliff = 96% *X. corona* n. sp.; 4% *X. heterosiphon* n. sp.).

areas. Recoveries made from Cascadia Basin after 10 months were dominated by *X. microchira* n. sp. at Baby Bare, while roughly 7 km away at ODP, *X. heterosiphon* n. sp. dominated (Fig. 12). After 24 months, bivalves of *X. heterosiphon* n. sp. dominated at Wuzza Bare, the only recovery made on Cascadia Basin that year. The 10-month recoveries from Juan de Fuca Ridge also differed. At Axial Volcano, *X. oregona* n. sp. not only dominated, it had colonized the wood so heavily that after only 10 months on the seafloor it could be crushed by hand; 10-month old deployments at Endeavour Segment and Nootka Fracture Zone were dominated by *X. microchira* n. sp. By 24 months *X. oregona* n. sp. had also become dominant at Endeavour (Fig. 12), and the wood was crushable by hand (Fig. 13).

DISCUSSION

As in other areas of the world's oceans where they have received study, deep-sea wood-boring bivalves of the Xylophagainae in the Northeast Pacific are represented by multiple species that occur in, and apparently compete for, the same piece of wood; at least two species cooccurred in six of eight sites considered (Fig. 12). How species of Xylophagainae coexist despite being in direct competition for what appears to be the highly limiting resource of sunken wood in the deep sea is unknown.

Competition within a given piece of wood can be significant (Fig. 13), but Hoagland & Turner, 1981 concluded that due to the irregular availability of wood, its temporal instability and staggered settlement by different species that use different modes of larval dispersal, competition was unlikely to be a major factor in the evolution and ecology of wood-borers. Support for this conclusion stemmed from the observation that different species colonized wood unpredictably, as is seen here.

Although in this study, deployments in the same areas generally had the same species of *Xylophaga*, deployments of the same age both on the Juan de Fuca Ridge and Cascadia Basin differed in which species was most abundant (Fig. 12). Given what can only be viewed as the unpredictable delivery of wood to the seafloor 240 km off the continent, this supports Hoagland & Turner's (1981) view, however, the subsequent recoveries suggest a pattern. On Juan de Fuca Ridge after 24 months, *X. oregona* n. sp., the dominant species at Axial at 10 months, had also come to dominate at Endeavour. On Cascadia Basin after 24 months, *X. heterosiphon* n. sp, the dominant species at one 10-month old deployment, had also come to dominate at Wuzza Bare, the only recovery made in the area.

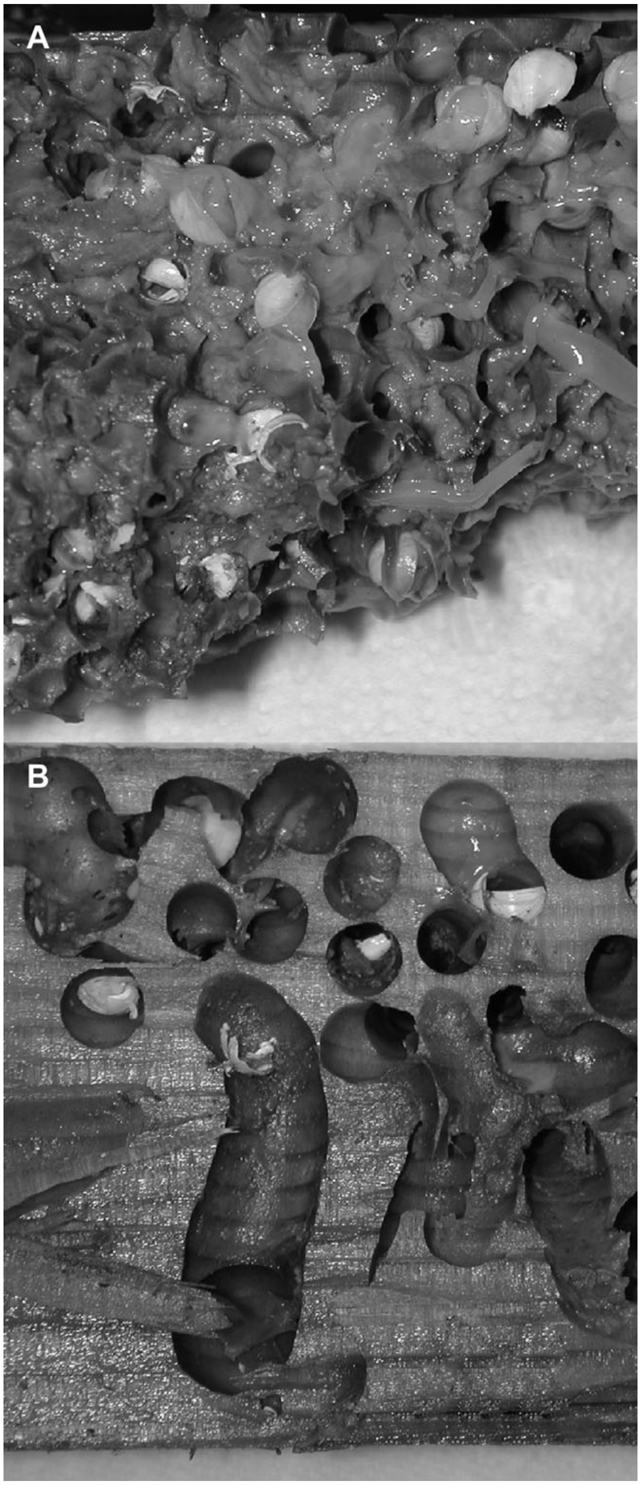

Figure 13. Photographs of contrasting 24-month old fir deployments. **A.** From Endeavour Segment, Juan de Fuca Ridge; so heavily bored by *X. oregona* n. sp. that it can be crushed by hand. **B.** From Gorda Ridge; bored by *X. corona* n. sp. but largely intact.

Changes in species dominance appear to be nonrandom. *Xylophaga microchira* n. sp. is hypothesized to be specialized for rapid colonization of new substrate, as evidenced by its wide geographic range, high abundance in most 10 month recoveries, and low abundances at 24 months. The cost of this specialization may be a reduced competitive ability. The dominance of *X. oregona* n. sp. at Axial at 10 months, and at Endeavour after 24 months and the clear evidence of stress, in terms of exaggerated shell wear and translucent siphons in specimens of *X. microchira* n. sp. collected with high densities of this species, argue that *X. oregona* n. sp. is competitively dominant.

The mechanism by which this species dominates may relate to the faecal chimney that every individual builds within its borehole. The function of these chimneys is unknown, but one would surmise that they contain a fairly large amount of bacteria that consume oxygen, especially when present in high densities (Fig. 13). Turner (2002) reported that the overtly similar *X. washingtona* had an exceptionally high tolerance of low oxygen availability. If that physiological trait is shared with *X. oregona* n. sp., as is the siphon allometry, high densities of this species likely could eliminate competing species in microsympatry. Chemicals associated with the chimneys may also provide a settlement cue for conspecifics.

At Cascadia Basin, predation rather than competition may moderate interactions between wood-boring species. Although Turner (1978) inferred that capitellid, crysoptellid and polynoid polychaetes, gastropods, galatheid crabs and probably fish likely preyed on wood-boring clams, recovery of Cascadia Basin deployments inside a lidded box revealed extraordinarily high densities of acotylean polyclad flatworms of *Anocellidus profundus* Quiroga, Bolaños & Litvaitis, 2006. Acotylean polyclads are known to be major bivalve predators in shallow water (Galleni *et al*., 1980 and references therein), with high bivalve mortality resulting from heavy flatworm infestations of up to 90 per m^2 (Newman, Cannon & Govan, 1993). Although turbellarian flatworms had been considered to be absent from the deep sea (Herring, 2002), 10-month-old deployments at Cascadia Basin supported 51.6 (Baby Bare) and 73.4 (ODP) flatworms per m^2; after 24 months, flatworm density at Wuzza Bare reached 386.7 per m^2.

The truncated incurrent siphons frequently seen in specimens of *X. microchira* n. sp. may result from nonlethal predation by flatworms. Possible replacement of this species by *X. heterosiphon* n. sp., a species with a periostracal cone over the siphons (Fig. 10), and the appearance of *Xylopholas crooki* n. sp., with siphonal sheaths and plates (Fig. 11), suggest that these structures confer predator resistance. The costs of deep-sea research unfortunately preclude additional replicates and longer time series that are required to more fully establish patterns of species coexistence.

With only single recoveries from Escanaba Trough and Gorda Ridge, temporal examinations of species abundance are impossible. However, high (232 per m^2) densities at Escanaba Trough of the flatworms *A. profundus* and *Oligocladus voightae* Quiroga, Bolaños & Litvaitis, 2006 and at Gorda Ridge of the echinoderm *Xyloplax janetae* Mah, 2006 (321 per m^2), also a possible bivalve predator (Voight, 2005), suggest that predation also acts here.

One variable in species dispersal was not accounted for here. None of these species had young attached to the adult shells, indicating that all produce planktonic young. Roughly a third of *Xylophaga* species however, are described as having young attached to the adult shell (Knudsen, 1961; 1967; Santhakumaran, 1980; Harvey, 1996; Turner, 2002). Because this study placed substrates randomly on the seafloor far from the continent, species likely had to disperse considerable distances to colonize them. Species that rely on brooded young may be more closely associated with the continental margin (unpub. data) where suitable substrate is much more likely to be available (Bruun, 1959). How using the reproductive mode of brooded young impacts species colonization potential merits study, as restricted dispersal would seem an unlikely strategy in animals that must exploit a temporally and spatially unpredictable resource.

The newly discovered diversity of species of wood-boring bivalves in the Northeast Pacific documented here increases our knowledge of the deep-sea radiation of the group. Multiple instances of microsympatry among these species and what is hypothesized to be a predictable ecological succession from a specialized early colonist species to competitively superior and more predator-resistant species suggest that competition among wood-borers and biotic interactions in general have significantly influenced the diversification of this group.

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SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Molluscan Studies online.

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