DIVERSITY AND REPRODUCTION OF NEAR-SHORE *VS* OFFSHORE WOOD-BORING BIVALVES (PHOLADIDAE: XYLOPHAGAINAE) OF THE DEEP EASTERN PACIFIC OCEAN, WITH THREE NEW SPECIES

JANET R. VOIGHT

Department of Zoology, Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605 USA

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ABSTRACT

The ability of obligate wood-boring bivalves of the Xylophagainae to colonize wood seemingly wherever it lays on the seafloor remains enigmatic. The continuous, if patchy, deposition of vegetation in near-shore deep-water areas is hypothesized to allow woodborers to develop opportunistic species that exploit offshore wood falls and to produce larvae that colonize isolated wood-falls on the distant seafloor. Examination of specimens and literature accounts from near-shore (within 1.5° longitude of the continent) and offshore (more than 2.3° longitude from the continent) areas tests the hypothesis that the same species occur in both areas. The hypothesized role of near-shore populations as sources of offshore colonists is refuted; the 18 species of Xylophagainae documented in the Northeast Pacific Ocean appear to form two nearly distinct groups based on their proximity to the continent. Of 11 near-shore species of Xylophagainae recorded off western North America, including three (*Xylophaga siebenalleri* n. sp.; *X. pacifica* n. sp., *Xylopholas scrippsorum* n. sp.) described here, only one is also known from offshore sites. Four near-shore species are documented to range from the San Diego Trough to Oregon, including three that apparently brood young. Brooded young are considered to restrict the offshore dispersal of species, but not to limit their movement along the continental margin.

INTRODUCTION

Bivalves of the Xylophagainae appear to be obligate wood-borers and occur in all oceans to depths of 7,250 m (Knudsen, 1961). The bivalves bore wood that has fallen to the seafloor, using toothed ridges on the anterior beak of their shells. The ingested fragments are digested with the help of symbiotic bacteria in the bivalves' gills, which also contribute to nitrogen fixation (Distel & Roberts, 1997). Although the availability of wood in the deep ocean would appear to limit strongly the diversity of woodborers, the subfamily contains 55 named species, many of which occur in microsympatry (Turner, 2002; Voight, 2007). Their nearly inaccessible deep-water habitat and the patchy distribution of wood on the seafloor limit information available on the biology of the group.

In deep-water areas off the mouths of rivers or off swampy or wooded coasts where vegetation is common (Bruun, 1959), wood-dependent bivalves may be expected to sustain consistent populations. From these continuing, if shifting, habitats, opportunistic species capable of exploiting isolated wood falls far out to sea have been predicted to evolve, and flourishing near-shore populations have been predicted to produce larvae able to colonize isolated offshore wood falls (Turner, 1973; Hoagland & Turner, 1981).

To test whether near-shore deep-water species of the Xylophagainae provide larvae that colonize isolated wood falls far out to sea, species from the continental margin of western North America are contrasted with those from comparable latitudes and depths at least 240 km off the continent. Three new species are described among the near-shore species. Limited specimen availability results in emphasis on collections from the Oregon Margin and southern California, especially the San Diego Trough and Santa Catalina Basin.

Correspondence: J.R. Voight; e-mail: jvoight@fieldmuseum.org

MATERIAL AND METHODS

Two collections have provided the bulk of the wood-boring bivalve specimens from which the near-shore deep-water western North American species have been inventoried. The Scripps Institution of Oceanography Benthic Invertebrates Collection (SIO-BIC) houses a significant collection of vegetation trawled from off southern California, generally from Santa Catalina Basin and San Diego Trough (32°10′N 117°15′W to 33°10′N 117°30′W) at about 1,225 m depth. The Field Museum of Natural History (FMNH) houses specimens collected from the Oregon Margin between 44° and 45°N at 1,350–2,850 m depth. Examination of additional specimens in the United States National Museum (USNM) has greatly enhanced this work. Three previously unknown species encountered among this material are described here, but some undescribed species are not represented by specimens sufficiently intact to serve as the basis for species definitions. Here, species represented only by specimens in which the shell had dissolved are distinguished from others, but not named, in the hope that additional material will become available to allow their future description. Inclusion of literature accounts ensured maximal coverage of the fauna.

Specimens from SIO-BIC were removed from formalin-fixed vegetation by the author and placed in 80% ethanol; the duration of storage in formalin solution and its concentration are unknown. Specimens from FMNH were preserved *in situ* at sea in 8% buffered formalin in sea water; most specimens were removed from the vegetation and transferred to 70% ethanol within 2 weeks of collection. The vegetation was also transferred to ethanol and a few additional specimens removed at later dates. Empty shells encountered were dried to allow their examination and to ensure their physical stability. Characters used to distinguish species were those employed by Knudsen (1961), Turner (2002) and Voight (2007), emphasizing shell

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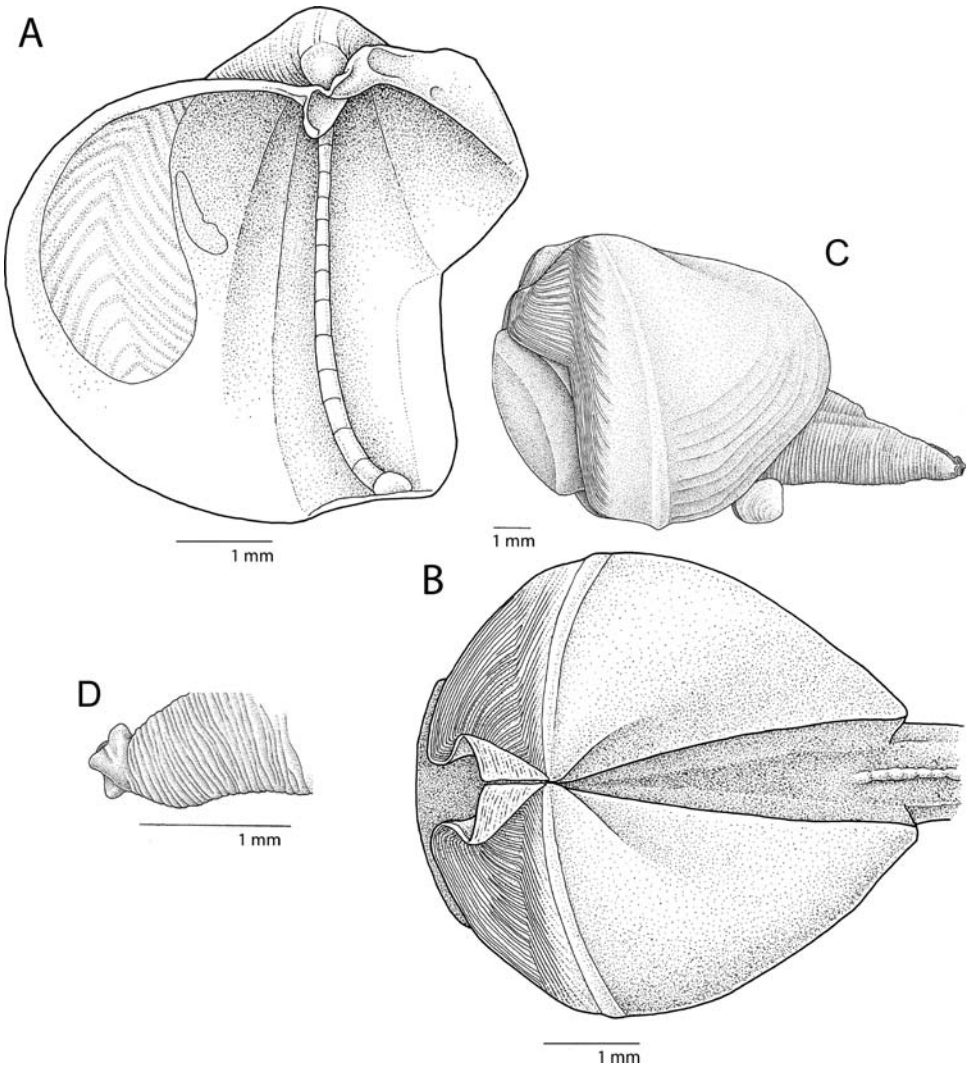

Figure 1. *Xylophaga siebenalleri* n. sp. **A.** Inner shell of holotype. **B.** Dorsal view of intact specimen. **C.** Lateral view of intact specimen. **D.** Tip of incurrent siphon.

and mesoplax shape, siphon length, cirri at siphon openings, and the presence or absence of small individuals attached to larger specimens, considered to be brooded young.

Measurements of shell length, height and breadth of holotype specimens were taken with electronic callipers. Specimen counts are exclusive of brooded young. Illustrations were made using a camera lucida. Collection data are summarized for type specimens of each species in the text; the Appendix reports full data by geographic area.

Collection localities within 1.5° longitude of land were termed near-shore; those more than 2.3° longitude from land were termed offshore. In addition to comparing the species present in near-shore and offshore collections, the presence of brooded young was compared between near-shore and offshore species using a contingency table and a hand-calculated G-test.

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 shell. Mesoplax divided; shape and size variable. Siphons united for part or all of their length; otherwise variable; excurrent siphon may be truncated.

Xylophaga siebenalleri new species

(Fig. 1)

Type Material: Holotype: FMNH 312300 x-SIO-BIC M 11568; Catalina Basin, trawl stn 4, 32°55.7′N 118°22.7′W to 32°59.2′N 118°27.4′W, 1,099–1,104 m, 16′ otter trawl, 4 Sept. 1974, *R/V Oconostota*; coll. J. Siebenaller; shell height 5.8 mm; length 5.7 mm; breadth 6.0 mm; 18 paratypes: SIO-BIC M 11568, $n = 2$ wet specs, also dry valves, collected with holotype; SIO-BIC M 994, $n = 11$, Catalina Basin, Allozyme A-28; FMNH 312302 x-SIO-BIC M 2467, $n = 4$, San Diego Trough, 70-I-12; FMNH 312301 x-FMNH 278337, $n = 1$, Oregon Margin, Stn 12.

Etymology: Named in honour of Joe Siebenaller, collector of many of the type specimens and Chief Scientist of the *R/V Wecoma* cruise that provided most of the other material, in thanks for his many courtesies.

Diagnosis: Excurrent siphon truncated; two longitudinal ridges on dorsal incurrent siphon. Umbonal-ventral sulcus markedly wider ventrally; posterior bounding ridge rounded, very pronounced. Posterior adductor scar very large, with herringbone pattern. Shell elongate, no conspicuous posterior extension. Up to four (usually one or two) brooded young.

Description: Beak slightly protruding in large specimens; over 20 fine, toothed rows parallel to ventral margin, ridges veer dorsally near anterior incision; over 20 fine, toothed rows in very wide vertical band at junction of beak and anterior disk (Fig. 1B).

Mesoplax triangular, small relative to shell, surface smooth or with growth lines, edge occasionally curved; begins between or posterior to very large prodissoconchs (Fig. 1B), slight to fairly large ventral extension.

Shell elongate antero-posteriorly (Fig. 1C); umbonal-ventral sulcus widens ventrally; bounding ridges, especially posterior, prominent (Fig. 1C). Umbonal reflection large, projects anteriorly then folds dorsally toward umbo (Fig. 1A). Inner shell with interior ridge posterior to umbonal-ventral ridge. Posterior adductor scar with herringbone pattern, huge (Fig. 1A), extends nearly from inner ridge to posterior shell edge, stops at dorsal posterior shell; central line medial relative to scar edges throughout. Pedal retractor scar large, often deep, with slight hint of individual elements. Umbonal-ventral ridge unremarkable, condyle with small terminal inflation.

Siphons short relative to shell size, possibly retracted (Fig. 1C). Excurrent siphon truncated near or rarely within valves, no cirri apparent. Incurrent siphon with low longitudinal ridges dorsally. Incurrent opening with inner ring of cirri of variable conspicuousness; end often collapsed (Fig. 1D). Half of specimens with up to four, typically one or two, young on ventral mantle or siphon (Fig. 1C); if siphon retracted, young sometimes within valves. Smallest individual with attached young 1.15 mm long.

Distribution: Known from Catalina Basin, San Diego Trough and the Oregon Margin; 732–2,750 m depth.

Remarks: The truncated excurrent siphon, longitudinal ridges on the dorsal incurrent siphon, posterior adductor scar with a herringbone pattern and the triangular mesoplax clearly ally this species with *X. washingtona* Bartsch, 1921 and the group containing *X. rikuzenka* Taki & Habe, 1945, *X. aurita* Knudsen, 1961, *X. turnerae* Knudsen, 1961, *X. praestans* Smith, 1903 and *X. oregona* Voight, 2007. The thick brown periostracum of *X. rikuzenka* makes that species distinct. The erect mesoplax plates of *X. aurita* are unique within this group, as is its projecting anterior incision. The round posterior adductor scar without sculpture in *X. turnerae* and the distinctly striated posterior adductor scar that is restricted to the dorsal half of the shell of *X. praestans* distinguish those species from *X. siebenalleri* n. sp. The present species is unique within this group in brooding young. Knudsen (1961), however, included *X. aurita*, assigned by Turner (2002) to this group, in his table of species with attached juveniles without comment, possibly because of its large prodissoconch. The present species is distinct in having an abnormally large posterior adductor scar that originates towards the centre of the shell, does not approach the umbo, and in which the medial limb remains centred rather than trending dorsally, as it does in *X. oregona*. Turner (2002) described morphological variation in shells of *X. washingtona* from wood of different densities; in shells with an enlarged adductor scar, the posterior shell extension and the umbonal-ventral sulcus, which broadened ventrally, were also prominent. These three features do not co-occur in this species. The present species can be separated from *X. oregona* by the well-defined umbonal-ventral sulcus, rounder umbonal reflection, and more dorsal projection of the posterior shell of that species. One specimen (FMNH 306555) is referred to this species despite having seven attached young, including one on the dorsal siphon, and a more complex ridge posterior to the umbonal-ventral sulcus than is seen on the type specimens.

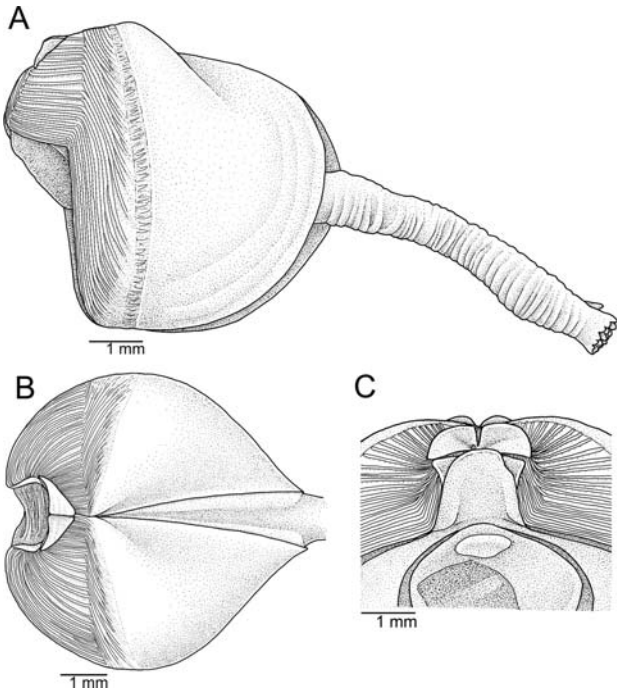

Figure 2. *Xylophaga pacifica* n. sp. **A.** Lateral view of intact specimen. **B.** Dorsal view of intact specimen. **C.** Anterior view of mesoplax and anterior incision.

The presence of brooded young in only 50% of the specimens is consistent with the species having separate sexes, as Tyler *et al.* (2007) documented in *X. depalmai* Turner, 2002, rather than protandry as Purchon (1941) suggested occurs in *X. dorsalis*.

***Xylophaga pacifica* new species**

(Fig. 2)

Xylophaga sp. Voight, 2007: fig. 4a.

Type material: Holotype: FMNH 306572, Oregon Margin, Stn 8, 44°45′53″N 125°31′33″W to 44°37′37″N 125°34′32″W, 2,750–2,800 m, 18–19 April 1997, 40′ otter trawl, *R/V Wecoma*; coll. J. Voight; shell height 5.9 mm; shell length 6.2 mm; shell breadth 6.3 mm; 7 paratypes: FMNH 278335, $n = 4$, Oregon Margin, Stn 1; SIO-BIC M 11925 x-FMNH 278336, $n = 2$, Oregon Margin, Stn 1; FMNH 278337, $n = 1$, Oregon Margin, Stn 12.

Diagnosis: Siphons subequal, excurrent opening with 5–8 long cirri dorsally; incurrent opening with two rings of cirri, about 20 in outer ring, inner typically within siphon. Mesoplax squat, with long ventral projections. Umbonal-ventral sulcus very wide ventrally. Young attach to ventral mantle.

Description: Beak not remarkable (Fig. 2A); toothed ridges on beak gently reflect dorsally near anterior incision. Mesoplax triangular, wider from right to left than from anterior to posterior (Fig. 2B); flat dorsally; large, angular ventral extensions rest on reflected edge of anterior incision; transition from horizontal to ventral abrupt.

Shell with posterior slope slightly concave in dorsal view (Fig. 2B). Umbonal-ventral sulcus a fairly narrow groove near umbo, poorly demarcated, dramatically widens ventrally, so ventral shell feels dented (Fig. 2A). Inner shell with linear elements of posterior adductor scar generally restricted to dorsal half of posterior shell.

Siphons subequal, often fully retracted into shell; excurrent siphon consistently slightly shorter than incurrent (Fig. 2A). Excurrent opening with 5–8 long dorsal cirri. Incurrent opening with outer ring of about 20 small, rounded cirri; inner ring of cirri nearly fully contained inside siphon, more complex, likely branching. Mantle exposed between valves, unusually thick, spongy, velvety. Two young at ventral lateral edge of mantle, ventral to siphon. Caecum frequently visible through foot.

Distribution: San Diego Trough (SIO-BIC M 11581) and Oregon Margin (type series). Depths 1,235–2,700 m.

Remarks: This species shares siphon and shell characters with three others in the North Pacific, *X. muraokai* Turner, 2002, *X. corona* Voight, 2007 and *X. zierenbergi* Voight, 2007, which were illustrated in frontal view by Voight (2007: fig. 4). The more erect mesoplax, the dorsad reflection of the toothed ridges near the anterior incision and brooded young distinguish this species from all others.

Xylophaga cf. *abyssorum* Dall, 1886

Material: SIO-BIC M 2448, $n = 1$ and partial dry valve, M 70-III-8, W of Patton Escarpment, 31°35′N 120°18.3′W, 3,916–3,950 m, 23 March 1970, 25′ otter trawl, *R/V Melville*, coll. Luke.

Remarks: Collected a full three degrees longitude from the continent, and 700 m deeper than any known eastern Pacific Xylophagainae, this offshore species is represented by one alcohol specimen with only one mesoplax plate intact and its siphon entirely withdrawn. The ridge immediately posterior to the umbonal-ventral sulcus is very strong and the mesoplax lobed and folded. The one partial dry valve available shows one condyle at the base of a weak umbonal-ventral ridge, the valve posterior to the ridge largely missing, although two young attach to the periostracum posterior to the umbo. These characters unite this specimen with the Atlantic species known from Florida, the Bahamas and Lesser Antilles at depths of 342–1,722 m (Turner, 2002).

Xylophaga sp. C

Material: SIO-BIC M 11583, x-SIO-BIC M 11565, $n = 2$, San Diego Trough, M-7 Stn 1. SIO-BIC M 11580, $n = 1$, San Diego Trough, MV 71-I-62.

Description: Mesoplax carries two lobes on anterior face, which in one specimen fuse to form prominent tubes. Concentric lines appear to extend from beak and mesoplax onto the posterior disk; these are strongly pronounced in largest specimen, especially on the ridge posterior to umbonal-ventral sulcus. Foot is relatively small. Many small rows of toothed ridges crowd the beak and anterior disk and form a very wide vertical band. Umbonal-ventral ridge is nearly flush with inner shell, but condyle suddenly enlarges. Siphons are completely retracted; excurrent siphon is shorter than incurrent and both openings have cirri. Two to four young attach to the dorsal shell, posterior to the umbo, on large specimens.

Remarks: Information on this species is limited. The shells, which show considerable breakage, also have translucent patches that indicate dissolution. The siphons are extremely contracted. The tubes on the mesoplax are similar to those of *X. lobata* Knudsen, 1961 from the Sulu Sea of the western Pacific Ocean.

Xylophaga heterosiphon Voight, 2007

Material: FMNH 308176; FMNH 308619; FMNH 308067.

Remarks: Described from Cascadia Basin, 47°45.755′ N, 127°45.441′W, 2,658 m; also known from the Oregon Margin at 44°45′57″N 125°31′46″W to 44°38′48″N 125°38′50″W; 2,750 m; and Gorda Ridge 42°45.258′N 126°42.572′W; 2,701 m (Voight, 2007).

Xylophaga mexicana Dall, 1908

Remarks: The type locality, off Acapulco, Guerrero, Mexico at 257.9 m depth (USNM 122947), and Santa Monica Bay, CA, 35 m depth are the species' only known occurrences (Turner, 2002).

Xylophaga muraokai Turner, 2002

Material: Museum of Comparative Zoology, Harvard University 316747, $n = 22$.

Remarks: Known only from the type locality: 33°44′N 120°45′W, 1615 m, near Port Hueneme, CA.

Xylophaga cf. *obtusata* Knudsen, 1961

Remarks: SIO-BIC M 11577 x-SIO-BIC M 11565, $n = 4$, San Diego Trough, M-7 Stn 1.

Description: Posterior-dorsal surface of each mesoplax plate carries a small tube that nearly contacts umbo. Toothed rows that normally disappear at posterior edge of vertical band, continue onto ridge immediately anterior to umbonal-ventral sulcus, often conspicuous. Foot with superficial vertical line that extends dorsally about 50% of foot diameter. Retracted siphons subequal; excurrent siphon slightly shorter. Excurrent opening with six to eight cirri that cluster at contact with incurrent siphon. Incurrent opening with double row of shorter cirri. Three specimens carry two to four young dorsally, posterior to umbo.

Remarks: The above characters unite these specimens with *X. obtusata* known only from two type specimens from the Gulf of Panama in 915 m depth. Given the size variation Knudsen (1961) noted in the mesoplax lobes in *X. obtusata*, and the rather delicate nature of these specimens, their identification remains tentative.

Xylophaga washingtona Bartsch, 1921

Material: SIO-BIC M 4537, Oceanside, CA, 107 m, anchor box, 12 Sept.–4 Jan. 1956. Holotype: USNM 334478.

Remarks: Bartsch (1921) described *Xylophaga californica* and *X. washingtona*; Turner (1955) synonymized these species, retaining the name *washingtona* due to the better condition of its type specimen. The range of this species is at least from 59°37′37″N 142°41′11″W, 561 m (USNM 894148) to as far south as the present record. Depth distribution: 33°44′N 120°45′W, 1,615–2,066 m, the type locality of *X. muraokai*, to Hermosa Reef, CA in 18.3 m (Turner, 2002). Of 18 records listed by Turner (1955, 2002), only three are deeper than 800 m.

Genus *Xylopholas* Turner, 1972

Type species: *Xylopholas altenai* Turner, 1972a, by monotypy.

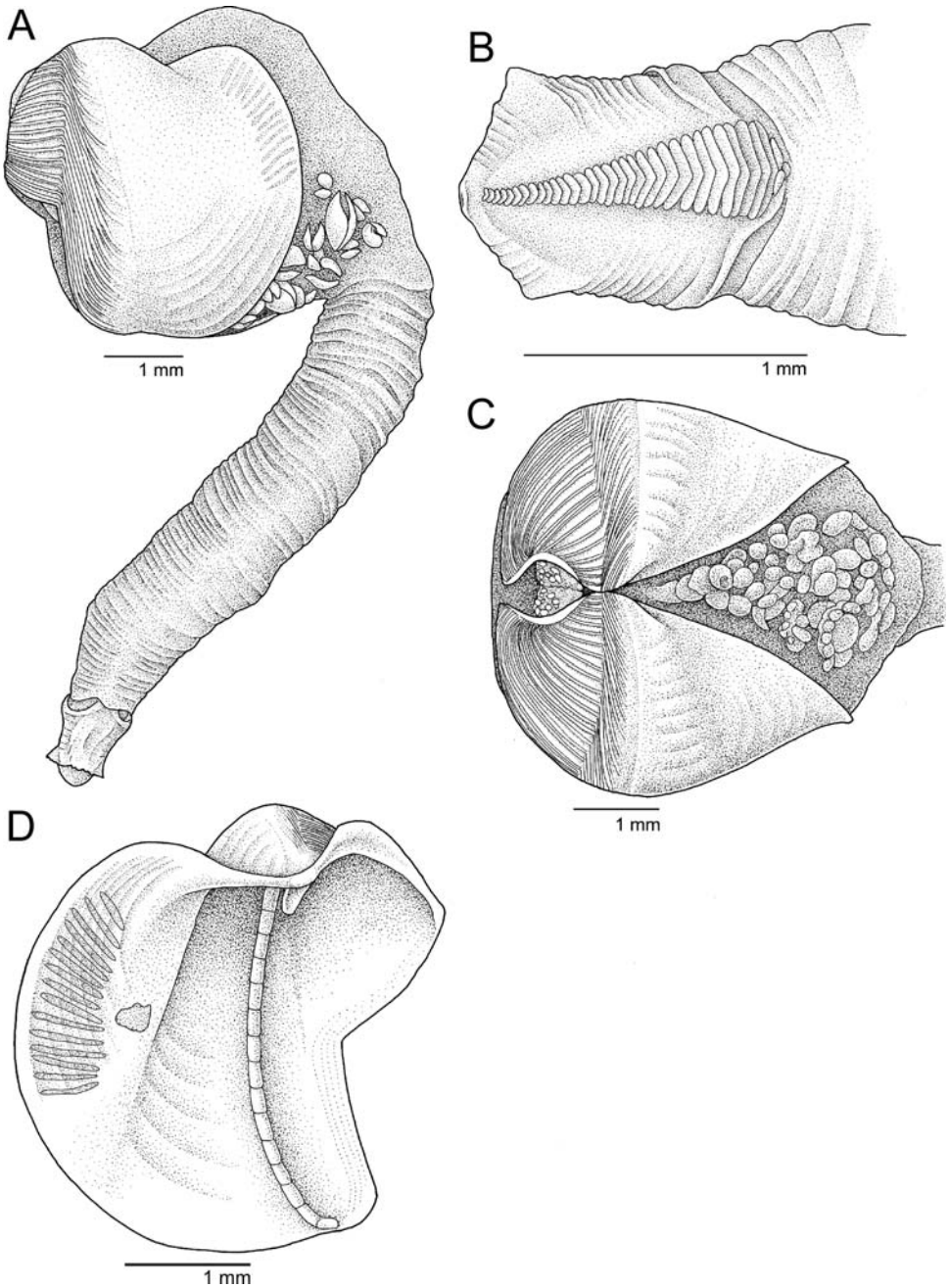

Figure 3. *Xylopholas scrippsorum* n. sp. **A.** Lateral view of intact specimen. **B.** Close-up of lateral siphonal plate **C.** Dorsal view of intact specimen. **D.** Inner shell view (reconstructed from fragments of intact shell).

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

***Xylopholas scrippsorum* new species**

(Fig. 3)

Type material: Holotype: FMNH 312303 x-SIO-BIC M 11564, San Diego Trough, M-7 Stn 1, 32°26′N 117°29′W to 32°31′N 117°32′W, 670–680 fm (1,225–1,244 m); shell height 4.0 mm; shell length 3.7 mm; shell breadth 4.4 mm; 16 paratypes: SIO-BIC M 11564, $n = 5$, collected with holotype; SIO-BIC M 11578 x-SIO-BIC M 11570, $n = 5$; FMNH 312304 x-SIO-BIC M 11578 x-SIO-BIC M 11570, $n = 5$, both from San Diego Trough, MV 71-I-62; FMNH 306660, $n = 1$, Oregon Margin, Stn 21.

Etymology: Named for the Scripps Institution of Oceanography, in recognition of its foresight in maintaining the collections that allowed discovery of these species.

Diagnosis: Siphonal plates with broad median row of chevrons tapering distally; dorsal and ventral corners project. Young attached to ventral lateral siphon.

Description: Beak with 8–16 toothed rows parallel to ventral edge; nearly 20 in vertical band between beak and anterior disk (Fig. 3A); density and number vary. Mesoplax translucent to transparent, spans anterior incision, generally amorphous

(Fig. 3C). Anterior incision bowed, due to slight outward turn of edges (Fig. 3C).

Shell small, white; concentric growth lines (best seen on posterior disk) extend to anterior disk, apparently continuous with toothed ridges from beak (Fig. 3A). Umbonal-ventral sulcus weak, very poorly defined. Umbonal reflection can appear triangular, dorsally limited to the dorso-lateral edge of anterior incision. Posterior adductor scar overlain by concentric growth lines that give the impression of a herringbone appearance; many linear non-branching elements (Fig. 3D). Chondrophore short. Pedal retractor scar a small shiny oval just proximal to posterior adductor scar. Umbonal-ventral ridge thin, more pronounced ventrally; condyle not inflated. Well-defined ridge on inner shell between umbonal-ventral ridge and posterior adductor scar (Fig. 3D). At posterior shell gape, long, convoluted caecum clearly visible through transparent membrane.

Siphon thick, cannot be withdrawn into shell; typically ventrally oriented; perisotracal covering with few regularly spaced smooth areas, attached to midline, junction of the siphons (Fig. 3A). Foot small relative to anterior opening.

Siphonal plates roughly hexagonal; lateral face with broad median row of raised, broadly open chevrons suggestive of tyre tread, narrowing distally; small ridges on plates from chevron to tips give impression of broad U; corners project (Fig. 3B).

All individuals over 1.3 mm in maximum shell dimension carry up to 24 small individuals on ventral mantle (Fig. 3A); when abundant, young extend onto proximal third of lateral siphon.

Distribution: Known from San Diego Trough and Oregon Margin from 1,225 to 2,400 m depth.

Remarks: The present species is distinguished from *Xylopholas altenai* by the more complex siphonal plate with a medial band tapering rather than expanding distally, the non-protruding beak, and the lack of a distinct siphonal collar. It is distinguished from *X. crooki* Voight, 2007 by the broad medial ornamentation of the siphonal plates, angularity and unarmed tips of the siphonal plates and lack of the siphonal collar. The bowed appearance of the anterior incision is reminiscent of *Xyloredo ingolfia* Turner, 1972b.

Of the 66 individuals in non-type lot SIO-BIC M 11924, all 34 larger than 1.0 mm in maximum shell dimension are brooding young. The ventral mantle and proximal siphons of some larger individuals carry brown spots, possibly where the small individuals had attached.

Genus *Xyloredo* Turner, 1972

Type species: Xyloredo nooi Turner, 1972b, by original designation.

Diagnosis: Valves indistinguishable from those of *Xylophaga*. Mesoplax small, poorly calcified. Burrow 5 to 30 times length of specimen, posterior two-thirds with distinctly ringed calcareous lining, in very small specimens, all periostracal or only lightly calcified. Covered by thin outer periostracum. Periostracal covering of valves extends to the posterior as a sheath continuous with heavy periostracal band at anterior of tube. Combined siphons extend the length of tube, attach to calcareous lining at anterior end of siphons. Siphons short, separate, few cirri at openings.

Xyloredo sp.

Material: SIO-BIC M 11563, $n = 2$, San Diego Trough, M-7 Stn 1. SIO-BIC M 11579, $n = 1$, San Diego Trough, MV 71-I-62.

Table 1. Offshore and near-shore species, with depth range.

Offshore, $n = 7$	Depth range (m)	
Xylophaga zierenbergi	2,211–3,232	
X. corona	2,701	
X. heterosiphon	2,656–2,750	
X. microchira	1,550–2,656	
X. oregona	1,550–2,211	
X. cf. *abyssorum**	3,916–3,950	
Xylopholas crooki	2,656	
Near-shore, $n = 11$	Depth range (m)	Area
Xylophaga siebenalleri n. sp.*	732–2,750	C–O
X. pacifica n. sp.*	1,235–2,700	C–O
X. heterosiphon	2,656–2,750	O
X. washingtona	18.3–2,066	C–BC
X. muraokai	1,615.4	C
Xylopholas scrippsorum n. sp.*	1,225–2,400	C–O
Xyloredo naceli	2,072	C
Xylophaga mexicana[s]	35–257.9	C–Guer
X. sp. C*[s]	1,225–1,244	C
*X. cf. obtusata**[s]	1,225–1,244	C
Xyloredo sp.*[s]	1,225–1,244	C

Offshore species from 41° to almost 48°N (Voight, 2007) and 31°35′N (SIO-BIC M 2448). Collection area of near-shore species indicated by C = California; O = Oregon; BC = British Columbia; Guer = Acapulco, Guerrero. Brooders indicated with an asterisk. Among near-shore species are four (indicated with an [s]) with such shallow distributions that they cannot be considered here.

Remarks: Specimens characterized by fairly smooth periostracal sheath (in one individual sheath has dark dots), by (on SIO-BIC 11579) two pronounced pores on the mantle just anterior to the ventral siphon and by equal length siphons with cirri at the openings. The mantle pores may be comparable to those reported by Knudsen (1961) for *Xylophaga wolffi*. Shell with posterior extension. Posterior adductor scar composed of linear elements (as seen through translucent shell). Beak with 25 toothed rows; vertical band between the beak and anterior disk formed by 11 toothed rows. Caecum strictly vertical in the gap between the posterior valves. The specimens were removed from reeds rather than woody vegetation, although none were found in tubes, pieces of tubes were present in the vegetation.

Xyloredo naceli Turner, 1972

Remarks: Definitively known only from eight specimens from type locality (33°46′N 120°45′W, 2,072.6 m) (Turner, 1972b).

RESULTS AND DISCUSSION

Eleven species of the Xylophagainae have been recorded from near-shore areas off southern California and Oregon (Table 1). Only one species, *Xylophaga heterosiphon*, occurs in both near-shore and offshore areas (Table 1). Of seven offshore species, one, *X. cf. abyssorum*, was found with young attached; six near-shore species were brooding young (Table 1). This difference in the incidence of brooding approaches statistical significance ($G = 3.08$, $df = 1$, $P < 0.10$). Species that brood would seemingly have only limited dispersal potential, however three (*X. siebenalleri* n. sp., *X. pacifica* n. sp. and *Xylopholas scrippsorum* n. sp.) range from at least the San Diego Trough to the Oregon Margin.

Discovery of these near-shore deep-water species increases the number of Xylophagainae known in the eastern North

Pacific to 18 (Table 1), easily the most diverse wood-boring fauna in the world. Moreover, additional species likely remain undiscovered, because only two of these 18 species are known from the upper 500 m. Despite the reputation of the Xylophagainae as a generally deep-water taxon, eight of the nine species of *Xylophaga* that Turner (2002) reported from the northwestern Atlantic occur at depths as shallow as 350 m or above. The broader continental margin of the northwestern Atlantic may increase species diversity at these comparatively shallow depths or, more likely, historic use of wooden lobster pots in this area provided an effective means to sample the group.

Near-shore species of Xylophagainae, although hypothesized to provide larvae that colonize isolated wood falls far out to sea (Turner, 1973; Hoagland & Turner, 1981), evidently do not. Offshore species differ almost entirely from near-shore species in the northeastern Pacific Ocean (Table 1). The existence of two nearly fully distinct faunas isolated by distance from the continent is a striking demonstration of how little we know of the biogeography of these deep-sea animals and their patterns of species diversity.

Near-shore and offshore Xylophagainae faunas not only show minimal overlap in species composition, their reproductive modes are largely distinct (Table 1). Six of eleven near-shore species of Xylophagainae brood young; only one of seven offshore species broods. The high incidence of brooding is exceptional. Other than the species considered here, only 16 species of *Xylophaga* are known to brood (data from Knudsen, 1961, 1967; Santhakumaran, 1980; Harvey, 1996; Turner, 2002; Voight, 2007); of those, 14 were assigned by Turner (2002) to her Groups 2 and 3. Turner erected these Species Groups based on mesoplax and siphonal characters, without reference to character polarity. The character of the young brooded on the dorsal shell rather than on the ventral mantle and siphon as seen here, appears to be unique to these Groups and could offer another character unifying the clades. In the case of the present species, the highly incised continental margin and the narrow continental shelf of western North America may result in terrigenous vegetation being predictably deposited to form, as Turner (1973) stated, a continuous habitat for woodborers. By brooding, these near-shore species may more completely exploit this continuous and predictable habitat.

Although brooded young would appear to reduce the dispersal ability of near-shore species, and may in fact prevent them from colonizing isolated wood falls far out to sea, brooding species do disperse. All near-shore deep-water species that brood range at least from southern California to Oregon (Table 1). In addition, assuming that Turner's Groups 2 and 3 constitute clades, the presence of the brooding species that compose these groups in all major oceans and at depths of from 183 to 7,290 m (Knudsen, 1961), supports the hypothesis that brooding is not necessarily an evolutionary liability to wood-boring bivalves.

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APPENDIX I

Collection localities of the near-shore species treated here with each specimen lot listed by area.

San Diego Trough

70-I-12; 32°37.0′N 117°32.6′W to 32°33.2′N 117°33.1′W; 1,171–1,217 m; 25′ otter trawl; 29 Oct. 1970; R/V *Agassiz*; Coll. Rokop. *Xylophaga siebenalleri* n. sp.: Paratype FMNH 312302 x-SIO-BIC M 2467, $n = 4$.

MV 71-I-62; 32°21.8′N 117°24′W to 32°30.7′N 117°32.8′W; 1,235 m; 25′ otter trawl; 1–2 June 1971; R/V *Agassiz* coll. Hubbs, Wisner, Luke. *Xylophaga siebenalleri* n. sp.: SIO-BIC M 11570, $n = 6$. *X. pacifica* n. sp.: SIO-BIC M 11581, $n = 6$. *X.* sp. C: SIO-BIC M 11580, $n = 1$. *Xylopholas scrippsorum* n. sp.: Paratype FMNH 312304 x-SIO-BIC M 11578, $n = 5$; Paratype SIO-BIC M 11578, $n = 5$. SIO-BIC M 11924 x-SIO-BIC M 11578 $n = 66$. *Xyloredo* sp.: SIO-BIC M 11579, $n = 1$.

M-6 Sta. 2; 32°56′N 117°30′W to 32°51.2′N 117°31.4′W; 400–470 fm (732–860 m); 25′ otter trawl; 13 Aug. 1971; R/V *Agassiz*; Coll. Matsui. *Xylophaga siebenalleri* n. sp.: SIO-BIC M 2340, $n = 5$.

M-7 Sta. 1; 32°26′N 117°29′W to 32°31′N 117°32′W; 670–680 fm (1,225–1,244 m); 40′ Otter Trawl; 14 Sept. 1971; R/V *Agassiz*; Coll. Matsui. *Xylophaga* cf. *obtusata*: SIO-BIC M 11577, $n = 4$. *X.* sp. C: SIO-BIC M 11583, $n = 2$. *Xylopholas scrippsorum* n. sp.: Holotype FMNH 312303 x-SIO-BIC M 11564; Paratype SIO-BIC M 11564, $n = 5$; SIO-BIC M 11565, $n = 3$. *Xyloredo* sp.: SIO-BIC M 11563, $n = 2$.

Catalina Basin

Sta. 19; 32°59.3′N 118°26.2′W to 32°57.4′N 118°23.3′W 1,116 m; 16′ otter trawl; 11 Dec. 1972; R/V *Agassiz*; Coll. P. Jumars. *Xylophaga siebenalleri* n. sp.: SIO-BIC M 11569, $n = 2$.

Trawl station 4; 32°55.7′N 118°22.7′W to 32°59.2′N 118°27.4′W; 1,099–1,104 m; 16′ otter trawl; 4 Sept. 1974; R/V *Oconostota*; coll. J. Siebenaller. *Xylophaga siebenalleri* n. sp.: Holotype FMNH 312300 X- SIO-BIC M 11568; Paratype SIO-BIC M 11568, n wet = 2; also dry valves. SIO-BIC M 11920 x-SIO-BIC M 11568, n wet = 3.

Allozyme A-28; 32°56′N 118°24′W; 1,143 m; 25′ Otter trawl; 6 Aug. 1975; R/V *Agassiz*; Coll. J. Siebenaller. *Xylophaga siebenalleri* n. sp.: Paratype SIO-BIC M 994, $n = 11$; SIO-BIC M 11922 x-SIO-BIC M 994 wet $n = 3$; SIO-BIC 11923, dry valves x-SIO-BIC M 994, $n = 11$.

Oceanside, California

Oceanside Ca., 107 m Anchor Box 12 Sept. 1955–4 Jan. 1956. *Xylophaga washingtona*: SIO-BIC M 4537, abundant specimens.

Oregon Margin

Sta. 1; 44°45′29″N 125°32′10″W to 44°36′49″N 125°36′15″W 2,850 m; 16 April 1997; 40′ otter trawl; R/V *Wecoma*; coll. J. Voight. *Xylophaga pacifica* n. sp.: Paratype FMNH 278335, $n = 4$; Paratype SIO-BIC M 11925 x-FMNH 278336, $n = 2$.

Sta. 5; 44°45′57″N 125°31′46″W to 44°38′48″N 125°38′50″W 2,750 m; 17–18 April 1997; 40′ otter trawl, R/V *Wecoma*; coll. J. Voight. *Xylophaga siebenalleri* n. sp.: FMNH 306555, $n = 1$. *X. pacifica* n. sp.: FMNH 307910, $n = 9$; FMNH 312305 x-FMNH 306555, $n = 11$.

Sta. 7; 44°45′52″N 125°31′08″W to 44°37′14″N 125°36′52″W 2,700 m; 18 April 1997; 40′ otter trawl, R/V *Wecoma*; coll. J. Voight. *Xylophaga pacifica* n. sp.: FMNH 306558, $n = 3$; FMNH 306560, $n = 57$.

Sta. 8; 44°45′53″N 125°31′33″W to 44°37′37″N 125°34′32″W; 2,750–2,800 m; 18 –19 April 1997. 40′ otter trawl, R/V *Wecoma*; coll. J. Voight. *Xylophaga pacifica* n. sp.: Holotype FMNH 306572.

Sta. 12; 44°45′48″N 125°31′28″W to 44°38′39″N 125°34′39″W 2,700–2,750 m. 40′ otter trawl; 20 April 1997; R/V *Wecoma*; coll. J. Voight. *Xylophaga siebenalleri* n. sp.: Paratype FMNH 312301 x-FMNH 278337, $n = 1$. *Xylophaga pacifica* n. sp.: Paratype FMNH 278337, $n = 1$.

Sta. 21; 44°28′41″N 125°12′16″W to 44°27′26″N 125°17′43″W 1,350–2,400 m; 22 April 1997; 40' otter trawl, R/V *Wecoma*; coll. J. Voight. *Xylopholas scrippsorum* n. sp.: Paratype FMNH 306660, $n = 1$; FMNH 306659, $n = 4$.