Zootaxa 5493 (3): 275–290
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5493.3.4
http://zoobank.org/urn:lsid:zoobank.org:pub:B43B0839-8A0A-4028-B5EF-72489CBB235F

Three new species of wood-boring bivalves (Mollusca: Xylophagaidae) from the deep Northwest Atlantic Ocean

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Abstract

Ruth Turner's studies of xylophagaids, wood-boring bivalves, documented the very existence of wood-borers in the deep sea and made the northwestern Atlantic fauna among the best known. However, her work focused on specimens from less than 2000 m depth. Here study of specimens from depths over 2000 m deposited in the Smithsonian collections extends our knowledge of this fauna. Despite the lack of molecular data, three species, *Xylophaga microdactylus* n. sp., *Xylophaga platyplax* n. sp. and *Xylophaga lambula* n. sp. are described; only *X. lambula* n. sp. pertains to *Xylophaga* s.s. Turton. Additional records of the known species, *Xyloredo nooi* Turner, *Xylonora atlantica* (Richards), *Abditoconus* cf. *anselli* (Harvey), *Xylophaga clenchi* Turner & Culliney, *Feaya dostwous* (Voight), and *Xylopholas* cf. *altenai* Turner are provided, with some supplemental information on morphological characters. The presence of *Xylophaga microdactylus* n. sp., which is remarkably similar to *X. microchira* Voight, suggests a close relationship between the xylophagaids of the deep northwestern Atlantic and northeastern Pacific. The depth distributions of northwest Atlantic species are detailed with supplemental data from the literature to explore potential patterns of distribution.

Key words: Bivalvia, Pholadoidea, wood-borers, deep sea, marine diversity

Introduction

The Northwest Atlantic Ocean is generally considered to be comparatively well-sampled for many taxa, including the deep-sea xylophagaids, bivalves that bore into, ingest and digest wood that has sunk to the seafloor. Symbiotic bacteria power the xylophagaids (Distel and Roberts 1997); they are necessary for the digestion of the wood and to fix and provision nitrogen to the animals. Ruth Turner, whose career was instrumental in demonstrating the very existence of wood-borers at depth (Turner 1973), worked extensively in the northwest Atlantic; the nine Atlantic species she named (Table 1) are nearly all from the continental shelf to 2000 m deep. Other than *Feaya dostwous* (Voight, 2016) collected by Turner from over 3500 m depth, few species have been described from the great depths of the northwest Atlantic Ocean.

This study considers Northwest Atlantic specimens from depths below 2000 m to improve our understanding of the wood-boring fauna. Voight (2009) hypothesized that nearshore xylophagaid species are largely distinct from those off-shore, due to predictable differences in resource availability (Voight 2015). That hypothesis was tested using data from the Pacific's narrow continental shelf, the much broader shelf of the Atlantic offers a second test of the generality of the hypothesis.

Materials and methods

The xylophagaid specimens treated here were collected from north of 20° N in the West Atlantic Ocean and are housed in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. Comparisons were made to material in the collections of the Museum of Comparative Zoology (MCZ), which holds Turner's

Accepted by N. Malchus: 15 Jul. 2024; published: 12 Aug. 2024

material, those of the Field Museum of Natural History (FMNH) and pertinent types at the Natural History Museum, London (BMNH).

Shell measurements were made with digital calipers and are reported in mm. Illustrations were made using a camera lucida. Anatomical terms and orientation follow those illustrated by Turner (2002) and Voight (2007; 2016).

The depth ranges were compared among species to test if the available data, although limited, support the hypothesis that the relatively shallow or nearshore species are distinct from those of deeper or off-shore waters. Species depth records were taken from the literature, notably Turner (2002), and pooled with those discovered here. When a range of depths was reported for a given specimen, the average was calculated and used. To test if a reported species depth range of greater than 1000 m was associated with the species having been collected more often, a Mann-Whitney *U* test was applied to the number of collections of species known from more than a single record.

TABLE 1. West Atlantic xylophagaid species, north of 20° N, ordered by their West Atlantic depth records, with collection area and references. Depth records within 300 m indicated by a dash; records of gaps over 300 m separated by semicolons. An asterisk identifies species of the *X. dorsalis* clade, defined by Voight *et al.* (2019), which have a significantly shallower distribution than do other members of the family (Voight 2008).

Taxon name	Depth (m)	Reported Collections	References; number of collections here reported parenthetically
Species generally shallow (<2100 m)			
**Xylophaga depalmai* Turner, 2002	45–174; 500	FL to Mass; Bahamas	Turner 2002; Tyler *et al.* 2007
**Xylophaga bayeri* Turner, 2002	152–365	FL; PR	Turner 2002
**Xylophaga tipperi* Turner, 2002	152	FL	Turner 2002
**Xylophaga whoi* Turner, 2002	338–914	FL, Cuba	Turner 2002
Xylophaga abyssorum Dall, 1886	338–420; 1722	FL, Bahamas	Turner 2002
Xylophaga gerda Turner, 2002	283–374; 2072 (Panama)	FL to Bahamas; Panama	Turner 2002
Xylopholas altenai Turner, 1972	311–366; 660; 1745	FL; VA	Turner 2002; this study (2)
Species with wide depth range			
Xylonora atlantica (Richards, 1942)	0–3173; 4879	Newfoundland to VA	Turner 1955, 2002; this study (1)
Xylophaga clenchi Turner & Culliney, 1971	35–830; 1363–2178; 2935–3085; 4879	Iceland to Bahamas	Turner 2002; this study (7)
Xylophaga platyplax n. sp.	660; 1362–1745; 2178–2260; 2935	E or NE of Norfolk, VA	This study (7)
Species from >1700 m			
Xylophaga profunda Turner, 2002	1722; 2066	Bahamas	Turner 2002
Xyloredo nooi Turner, 1972	1737–1830; 2175–2631; 3085	Bahamas; NE of Norfolk; DE	Turner 1972; this study (5)
Abditoconus cf. *anselli* (Harvey, 1996)	2178; 2935–3085	56–57°N 09–10°E; NE of Norfolk, VA	this study (3)
Xylophaga microdactylus n. sp.	2625–2640	38.5°N 72.5°W	This study (3)
Feaya dostwous (Voight, 2016)	2935; 3506	38° 18.4′ N 69° 35.6′W; 36° 57.9 N, 73° 21.5 W	Voight 2016; this study (1)
Xylophaga lambula n. sp.	4879	E of Norfolk, VA	This study (1)

Systematics

Superfamily PHOLADOIDEA Lamarck, 1809

Family Xylophagaidae Purchon, 1941

Xylophaga microdactylus n. sp.

(Fig. 1, 2, 3)

Type material: Holotype USNM 756989. SE Cape Henlopen, DE; 30 July 1975; 38° 29.8'N 72° 32.9'W; 2625–2640 m; R/V EASTWARD; 30 July 1975; C. Lamb! Shell Length: 2.6; height 2.7; width 2.3.

Paratypes: USNM 1607142 n = 6 wet, collected with the holotype.

USNM 1607138 NE Norfolk VA; 38° 29.8 N, 72° 32.9 W to 38° 28.5 N 72° 35.0W 2625–2640 m; R/V EASTWARD; 30 July 1975; C. Lamb! n = 32 wet n = 6 dry valves.

Material examined USNM 1607127 (wet & dry) SE Cape Henlopen, DE; 30 July 1975; 38° 29.8'N 72° 32.9'W; 2625–2640 m; R/V EASTWARD; 30 July 1975; C. Lamb!

USNM 1607139 (wet & dry) NE Norfolk VA; 38° 29.8 N, 72° 32.9 W to 38° 28.5 N 72° 35.0W 2625–2640 m; R/V EASTWARD; 30 July 1975; C. Lamb!

USNM 1607144 NE of Norfolk, VA 2245–2275 m depth. C. Lamb! n = 1

USNM 757341 NE Norfolk, VA 3080–3090 m; R/V GILLISS; 15 Sept 1975 C. Lamb! Dry.

Etymology: micro- (G) Little; -dactyl (G), fingers; that is, the cirri. The name also reflects the species' similarity to *X. microchira* Voight, 2007 small hand.

Diagnosis: Shell: small, thin, translucent. Mesoplax plates: weakly calcified, erect or flat, medially depressed, roughly triangular with ventral extensions, may appear eye-brow shaped. Siphons long, most often subequal. Excurrent opening with 3-4 cirri; incurrent siphon without conspicuous cirri. Large umbonal reflection.

Description: Shell thin, translucent, smooth, white. Umbonal-ventral sulcus weakly impressed, valve slightly inflated posteriorly. In lateral view, posterior dorsal shell nearly as tall as umbo. Anterior slope projects slightly (Fig. 1).

Anterior adductor cover: translucent, calcified mesoplax plates with ventral extension; lateral corners erect, medial portion depressed, anteriorly directed; usually erect in smaller individuals, in larger ones, plates form horizontal triangles over the proximal anterior adductors (Fig. 2).

Siphons: long, never retracted. Relative lengths variable: subequal most often, but excurrent siphon may be equal, slightly or much shorter than incurrent. Excurrent opening with 3–4 large but fairly inconspicuous cirri, cirri nearly absent (just nubs) from incurrent opening.

Inner shell: muscle scars: glossy, poorly defined. Umbonal-ventral ridge more defined in ventral part of shell; condyle: smooth, rounded. Immediately posterior to chondrophore, posterior edge of shell extends dorsally, nearly equaling or exceeding height of umbo. Umbonal reflection large, shiny extends roughly halfway up the largely undifferentiated prodissoconch.

No dwarf males seen.

Remarks: The present species is very similar to *Xylophaga microchira*, but lacks the conspicuous cirri at the excurrent and incurrent siphonal openings characteristic of that species; this character likely most easily distinguishes them. Additional characters include the more projecting anterior slope in the present species, its considerably higher posterior dorsal shell edge, commencing just posterior to the chondrophore, its ventral shell with a smaller ventral extension near the condyle; in the present species the inner shell has a larger, more uniform umbonal reflection, a smaller ridge between the umbonal-ventral ridge and the posterior adductor scar, and a smaller umbonal-ventral ridge than does the Pacific species. This species' siphons are most often subequal with few, relatively inconspicuous cirri at the siphonal openings; the siphons of *X. microchira* are variable, but usually incomplete, with the excurrent siphon growing isometrically with the incurrent (Voight 2007). The variation in the relative length of the siphons in that species was attributed to predation (Voight 2007), perhaps it is innate. Elongate cirri with apparent sensory structures (Reft & Voight 2009) occur at the excurrent opening of *X. microchira*. Differences between these species in siphonal cirri might relate to the minimal preservation-linked siphonal contraction in this species, which contrasts to the more strongly contracted siphons with elongate cirri in specimens of *X. microchira*. If they do, the subtle differences in the shells noted here should serve to separate the species, but when suitably preserved specimens become available, molecular methods should be used to compare them.

The lots USNM 1607127 and 1607139 have the same collection details. Based on the better condition of the specimens in the former lot, they were likely collected and preserved first. The second lot has many fewer intact specimens.

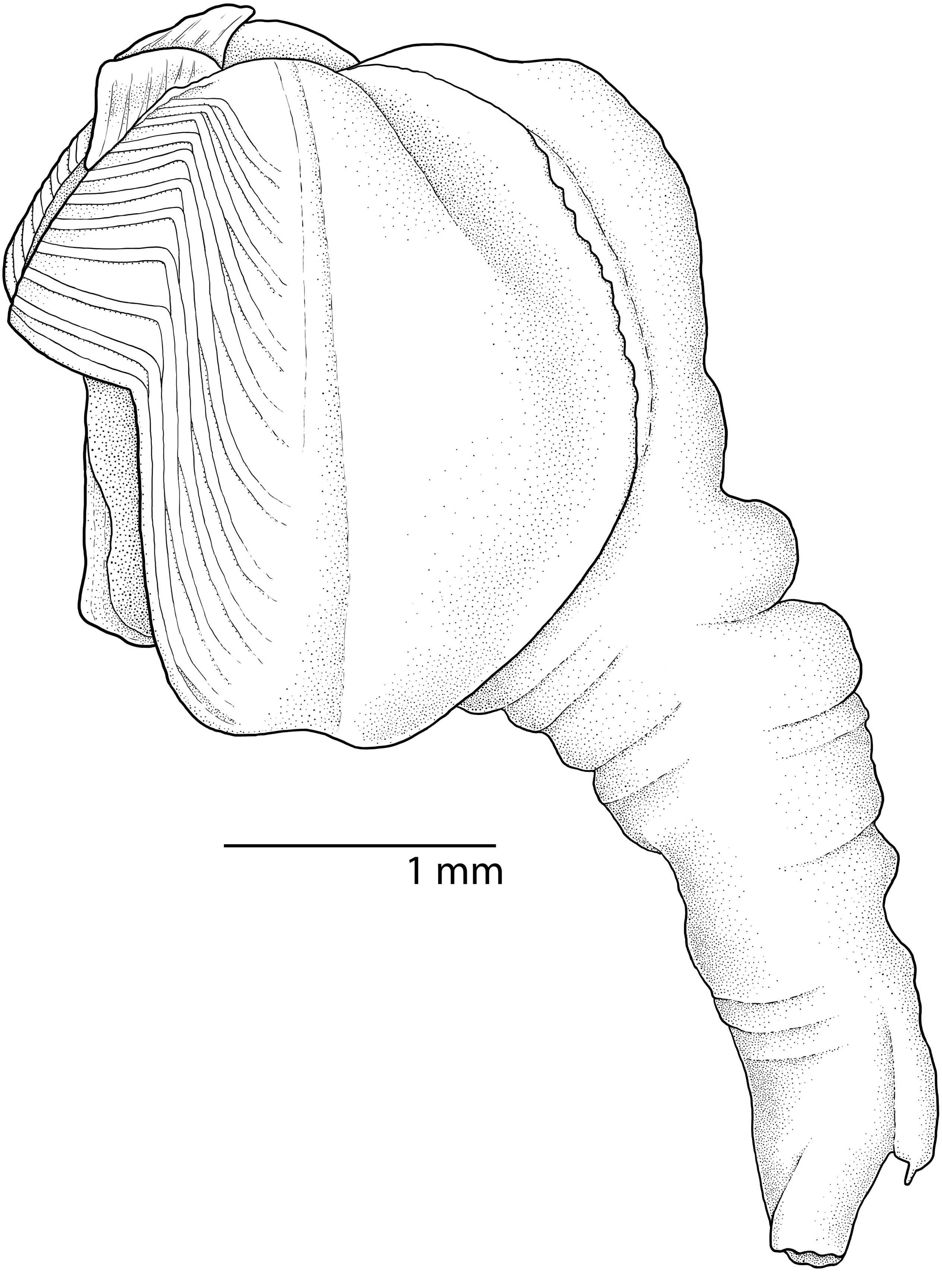

FIGURE 1. *Xylophaga microdactylus* n. sp. Holotype USNM 756989 lateral view; note the subequal siphons with few cirri.

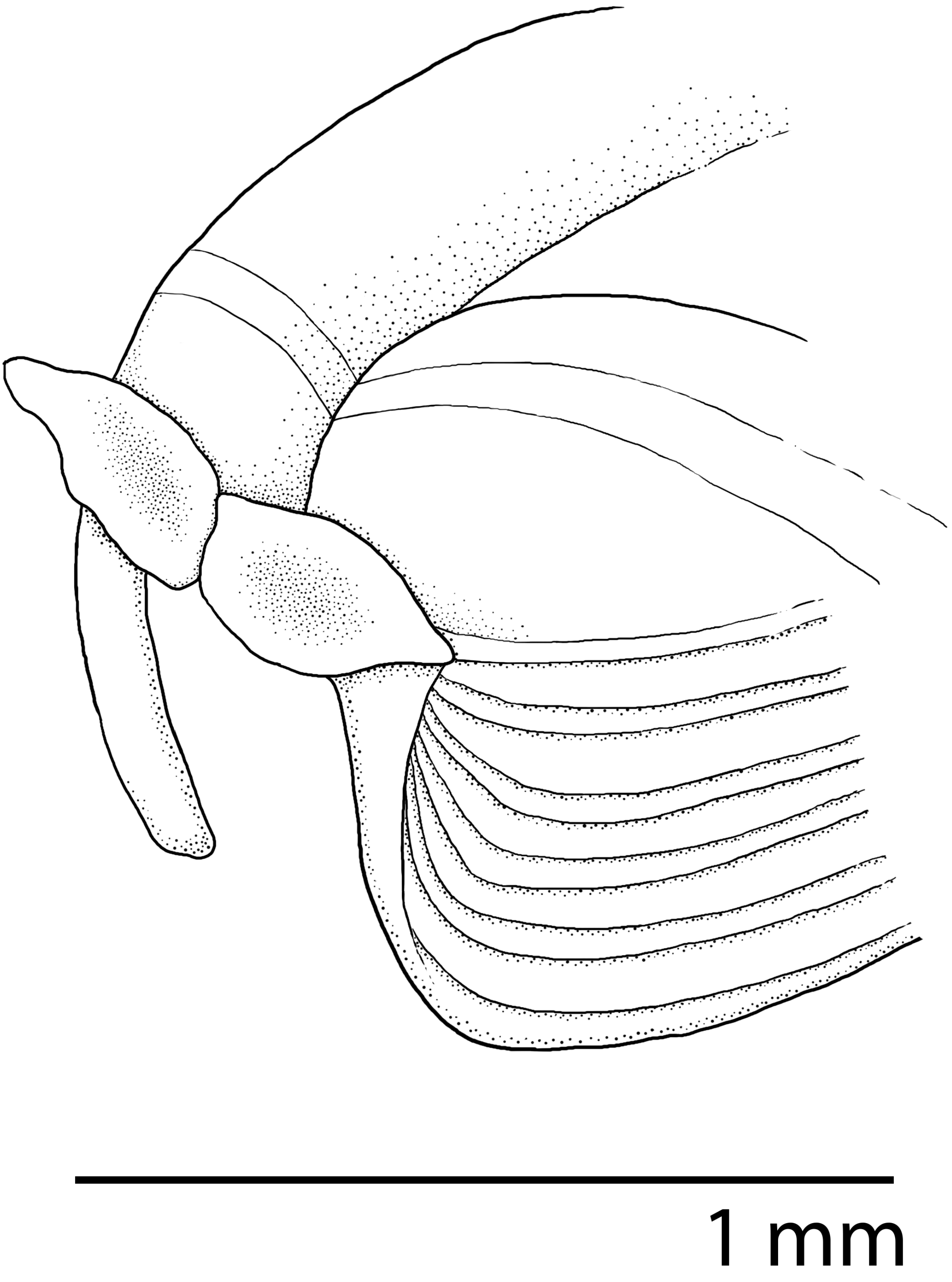

FIGURE 2. *Xylophaga microdactylus* n. sp. Holotype USNM 756989. Close up of the diagnostic mesoplax.

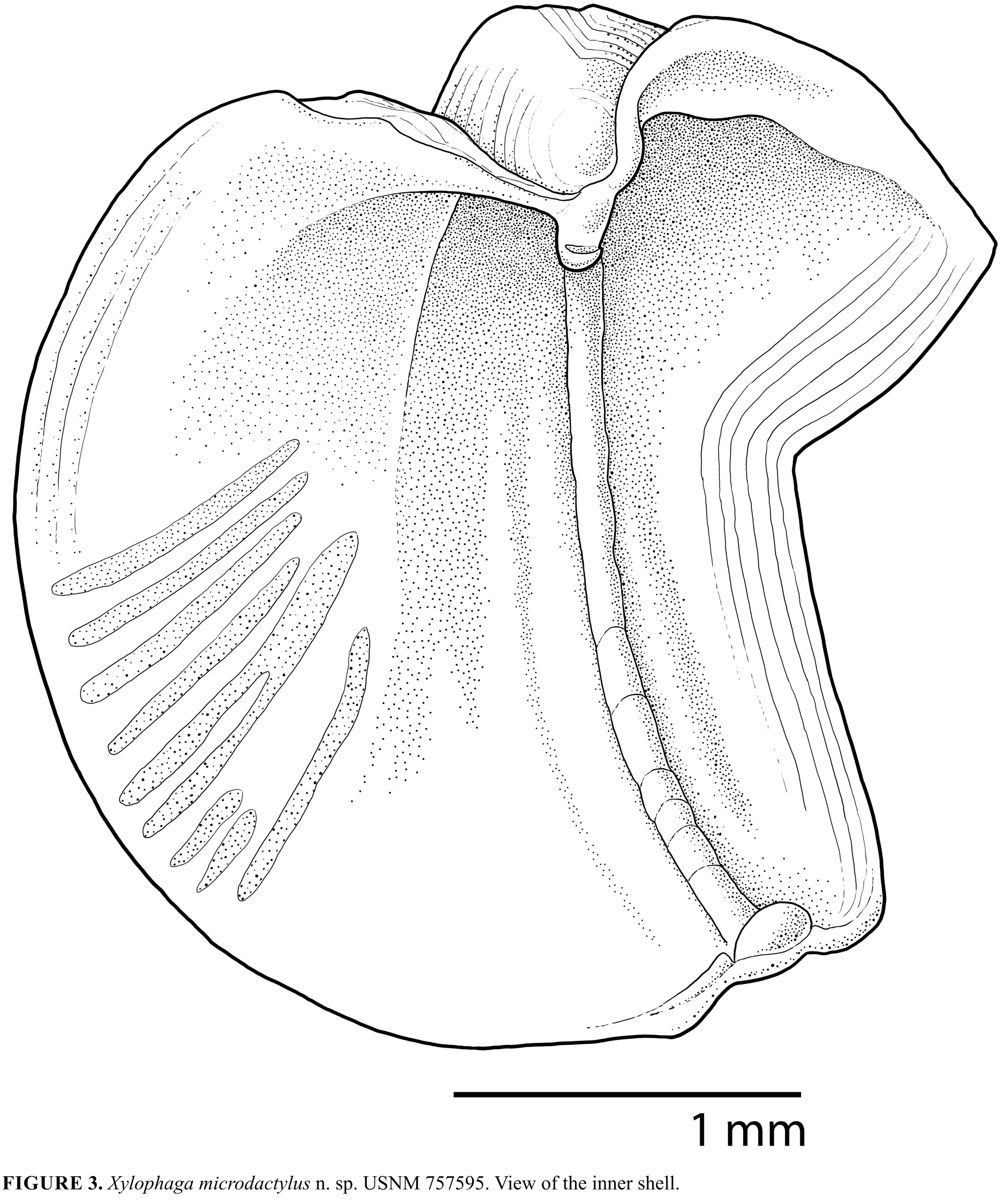

FIGURE 3. *Xylophaga microdactylus* n. sp. USNM 757595. View of the inner shell.

Xylophaga platyplax n. sp.

(Fig. 4, 5, 6)

Type material: **Holotype:** USNM 757298. NE of Norfolk, VA 37° 01.7 N, 73° 59.1 W to 37° 00.5 N, 73° 57.0 W; 2245–2275 m; R/V GILLISS; 13 Sept 1975. C. Lamb! Shell length 12.2; height 13.3; width 13.5.

Paratypes: USNM 1607126 (soft parts removed, stored separately) E of Norfolk, VA 36° 39'N 74° 21.8'W; 1625–1670 m; R/V EASTWARD; 23 July 1975 C. Lamb! stored dry, two with mesoplax plates; soft parts stored in ethanol, heavily damaged.

USNM 1607152 E of Norfolk, VA 36° 43.5 N, 74° 34.5 W to 36° 42.6 N, 74° 37.0 W; 570–750 m; R/V GILLISS; 18 Sept 1975; C. Lamb! n = 1 wet specimen.

USNM 1607149 NE of Norfolk 36° 57.9 N, 73° 21.5 W to 36° 58.0 N, 73° 19.4 W; 2915–2955 m; R/V GILLISS; 14 Sept 1975; C. Lamb! n = 10 wet specimens.

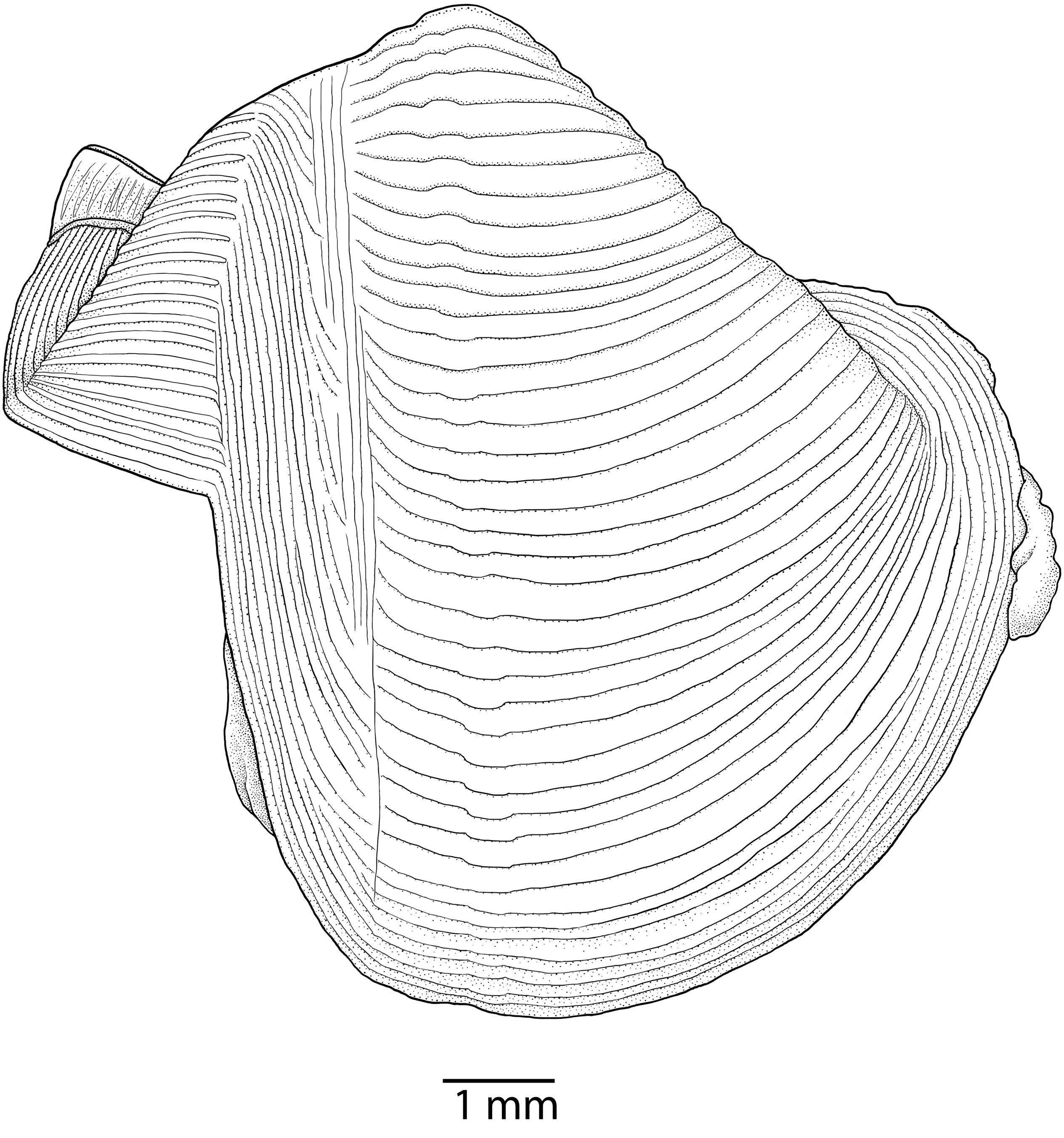

FIGURE 4. *Xylophaga platyplax* n. sp. Holotype USNM 757298. Lateral view.

Material examined:

USNM 1607130 (Wet & dry) NE of Norfolk 36° 57.9 N, 73° 21.5 W to 36° 58.0 N, 73° 19.4 W; 2915–2955 m; R/V GILLISS; 14 Sept 1975; C. Lamb! one with 3 dwarf males n = > 25

USNM 756946 (dry) E of Cape Henlopen, DE; 38° 51'N 72° 44.1'W; 1275–1450 m; R/V EASTWARD; 28 July 1975 C. Lamb!

USNM 1607126 E of Norfolk, VA 36° 39'N 74° 21.8'W; 1625–1670 m; R/V EASTWARD; 23 July 1975 C. Lamb! soft parts stored in ethanol separate from valves.

USNM 1607158 E Norfolk, VA 38° 38.7 N, 74° 23.0 W to 38° 39.8 N, 74° 22.0 W; 1730–1760 m; R/V GILLISS; 19 Sept. 1975; C. Lamb! n = 9

USNM 1607156 NE Norfolk. VA 37° 02.4 N, 74° 08.5 W to 37° 02.0 N, 74° 07.0 W 2130–2225 m R/V GILLISS 13 Sept 1975 C. Lamb! n = 10

Etymology: platy- (G) flat; plax referring to mesoplax.

Diagnosis: Posterior adductor scar: dorsally many individual dots, ventral-anterior edge, beginning of herringbone pattern. Calcified mesoplax plates flat, elongate triangles expanding anteriorly; anterior edge straight, bordered laterally by thick periostracum; plate base inserts into shell. Anterior slope protruding, anterior adductor scar well-marked. Shell wide, umbo inflated.

Description: Shells large chalky, heavily pitted at umbos, white with conspicuous brown periostracum; medial beak strongly projects dorsally to support the mesoplax. Shell slightly wider than long, low posterior slope; umbo inflated. Umbonal-ventral sulcus modest, no bordering ridges (Fig. 4).

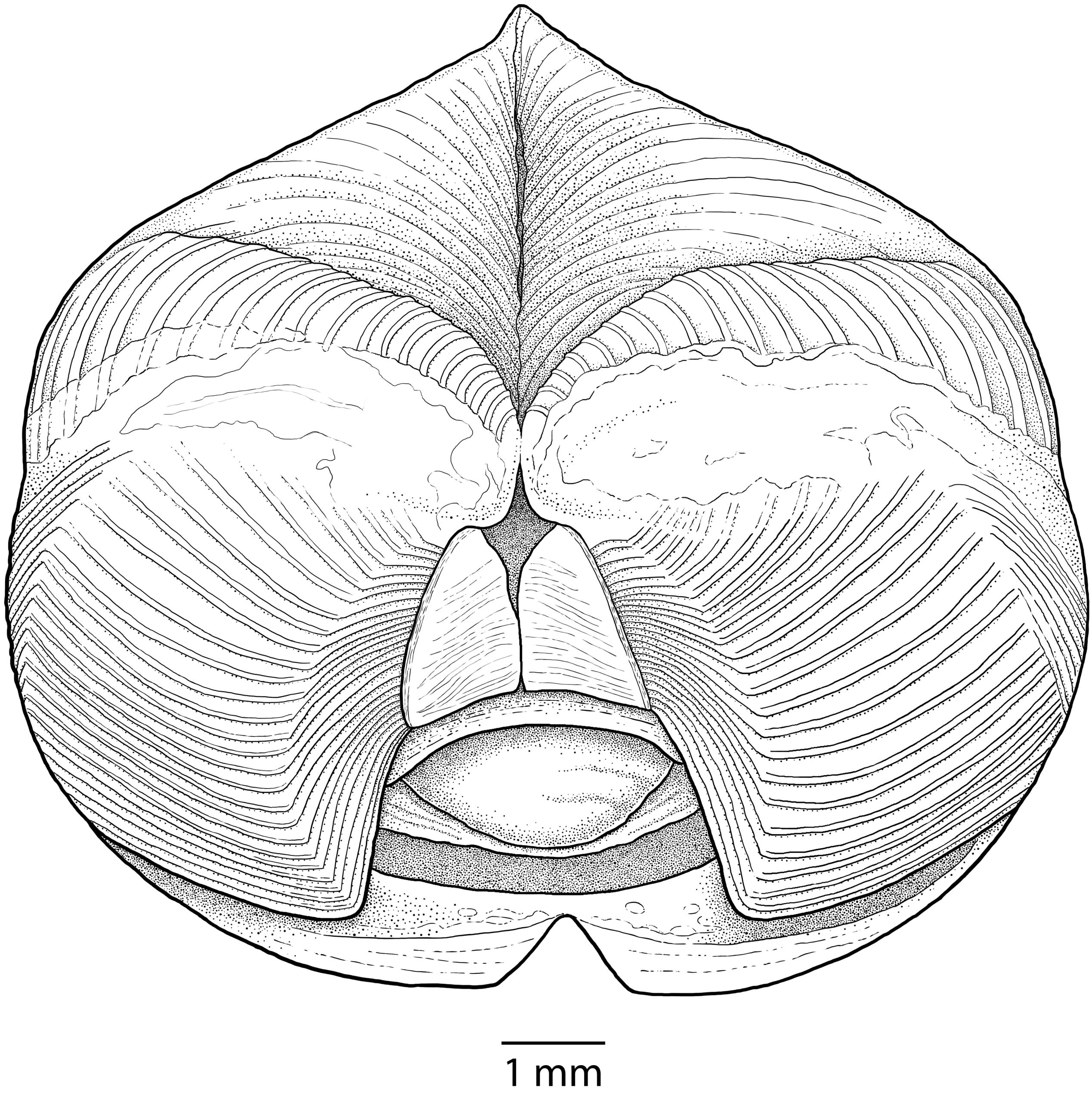

FIGURE 5. *Xylophaga platyplax* n. sp. Holotype USNM 757298. Dorsal/frontal view.

Anterior adductor cover: calcified, paired mesoplax plates. Flat, elongate triangles that expand anteriorly; anterior edge straight, regular growth lines, flat or subtly curved, no ventral extension , conspicuous brown periostracal lateral and medial borders (Fig. 5). Proximal base of mesoplax plate nestles into niche anterior to chondrophore, plates often retained in empty shells (Fig. 6).

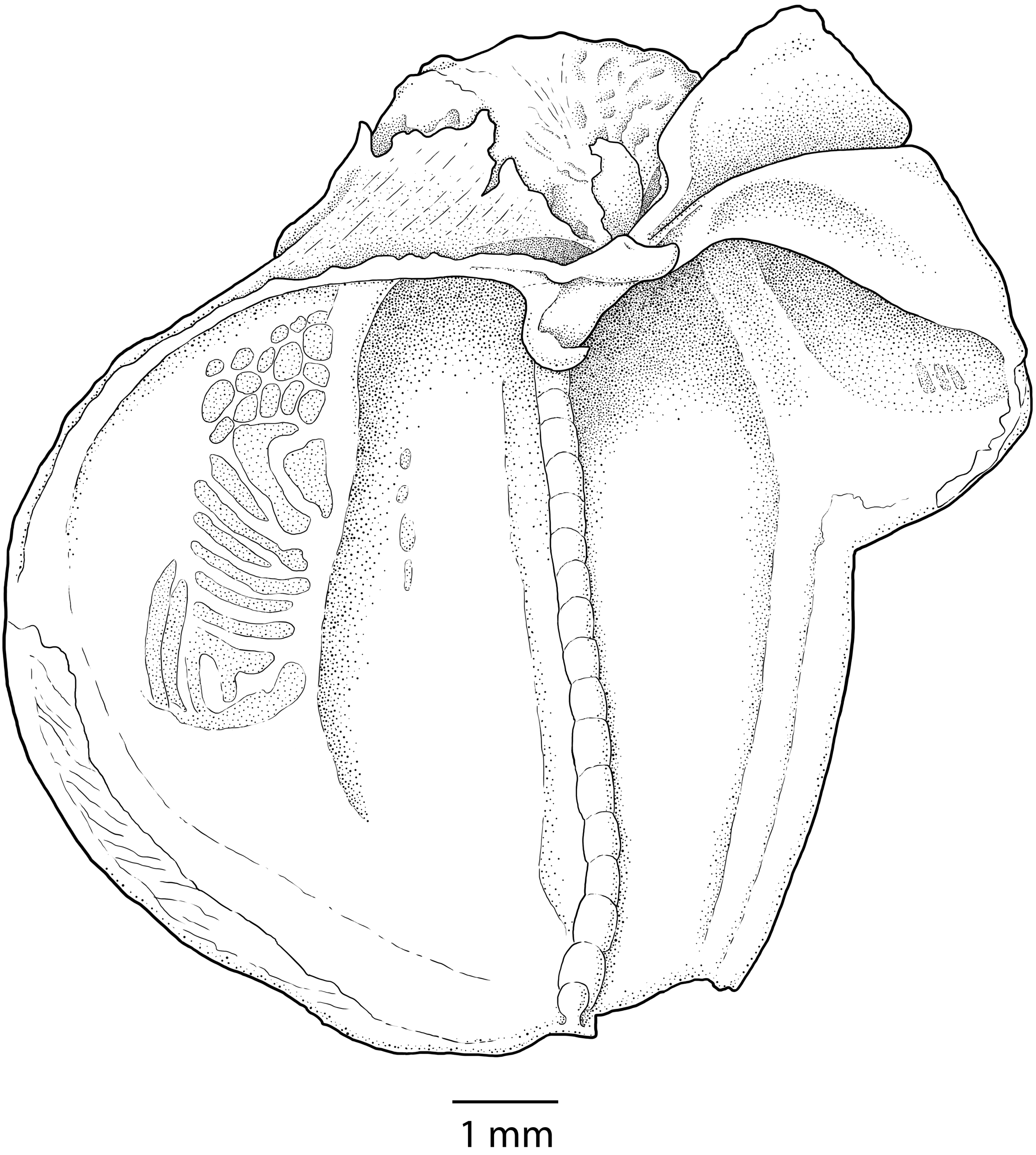

FIGURE 6. *Xylophaga platyplax* n. sp. USNM 756876. View of inner shell.

Siphons: usually fully retracted. Tips of holotype's siphons caught between valves appear subequal, both openings with cirri.

Inner shell: posterior adductor scar poorly marked at small sizes when inner shell glossy, becomes clearer with growth. Two-parted posterior adductor scar with partial herringbone pattern better defined in ventral-anterior area, and speckles or dots dorsally (Fig. 6). Umbonal-ventral ridge with poorly defined, uneven segments dorsally, becoming more prominent ventrally. Condyle not enlarged. Shell inflated anterior to posterior adductor scar. Chondrophore exceptionally large, projecting, e.g. compare fig 6 to fig. 3. Anterior adductor scar prominent (Fig. 6).

Dwarf males: one dry specimen with three presumed males attached to dorsum posterior to umbo.

Remarks: To my knowledge, the basal insertion of the mesoplax plate into the shell is unique in the family. Whether the plates' size and relative security affect their boring is unknown. Potentially, the large periostracal borders of the plates store elastic energy, increasing boring efficiency.

Xylophagaids with a regular herringbone posterior adductor scar which Turner (2002) linked to an incomplete siphon had been unknown in the Western Atlantic. *Xylophaga praestans* Smith, 1903 a rare species in the North (Smith 1903; Tebble 1966) and Mediterranean Seas (Tebble 1966; Janssen & Krylova 2014), with a depth range from 500 m (GBIF 2022) to 2173 m (Janssen & Krylova 2014), has this type of scar and siphon (Santhakumaran & Sneli 1984). Knudsen (1961) made minimal mention of the posterior adductor scar's pattern in *X. praestans*, but Turner (2002) noted its similarity to that of *X. washingtona* Bartsch, 1921. My examination of the type at the BMNH supported Turner's (2002) description. These species also share the unusually projecting anterior beak. The squat triangular, medially depressed mesoplax plates of *X. praestans* readily separate it from the elongate triangular mesoplax plates of the present species as does its vague, partially herringbone posterior adductor scar. The presence of dwarf males on the dorsum of a specimen appears inconsistent with its placement in *Xylophaga* s.s. a group in which they are typically on the ventrum (Voight, Marshall, Judge *et al.* 2019).

The mesoplax of *X. platyplax* n. sp. might appear superficially similar to that of Morphotype C of *Xylonora atlantica* illustrated by Romano, Voight, Pérez-Portela & Martin (2014 Fig. 7A, D). However, the plates of the present species are more uniform, the anterior edge is straight and their bases insert into the shell anterior to the umbonal reflection. In *X. atlantica*, the plates are usually shorter, when elongate the anterior edge is rounded (Romano *et al.* 2014, fig. 7A, D). The posterior adductor scar of *X. atlantica* has linear elements with a common orientation rather than a herringbone pattern with dots dorsally. In *X. atlantica*, a low, rounded ridge lies posterior to the umbonal-ventral sulcus, and the beak does not project.

When small, members of this species have smooth, translucent white shells in strong contrast to the pitted, dense chalky shells of animals that may be full sized. Regardless, the mesoplax plates are prominent, even at small sizes.

Turner (1955) noted with surprise that *X. atlantica* had gone unnoticed until its 1942 description. *Xylophaga platyplax* n. sp. similarly seems to have awaited discovery for an inordinate amount of time given it can be locally abundant and occurs at depths as shallow as 570 to 750 m.

***Xylophaga lambula* n. sp.**

(Fig. 7)

Type material: Holotype: USNM 1607163 E of Norfolk 36° 54' 30" N 68° 04' 30"W 4879 m; R/V COLUMBUS ISELIN 28 Feb. 1978; J. A. Musick! Shell length = 4.5 mm; height 3.8; width 3.4.

Etymology: named with thanks for Cathy Lamb, who as a museum technician collected all but four of the 33 lots of specimens reported here, although not this one. Only her previously unsung efforts made these discoveries possible. The diminutive suffix "ula" (L); Little refers to the size of the specimen, not the size of the thanks due.

Diagnosis: Siphons incomplete, incurrent opening with short cirri. Well-defined ridge posterior to umbonal-ventral sulcus. Calcified mesoplax plates triangular; roughly equal, flat dorsal and ventral layers separated by ventral extension.

Description: Thick, white shell with brown, thin periostracal cover. Projecting anterior slope. Well-defined ridge posterior to umbonal-ventral sulcus. Umbonal reflection, primarily over anterior slope, reduced near inflated umbo.

Anterior adductor cover: calcified mesoplax plate (only one present due to damage) with roughly equal, flat dorsal and ventral layers, separated by a vertical section. Periostracum over anterior adductors and plate.

Siphons: incomplete, excurrent opening mid-siphon, separated by short furrow with tissue walls on dorsal incurrent siphon. Incurrent siphonal opening with at least one ring of short cirri, likely two.

Inner shell: not exposed for fear of additional damage. Umbonal-ventral ridge seen to enlarge ventrally at terminal 3 segments, no distinct condyle.

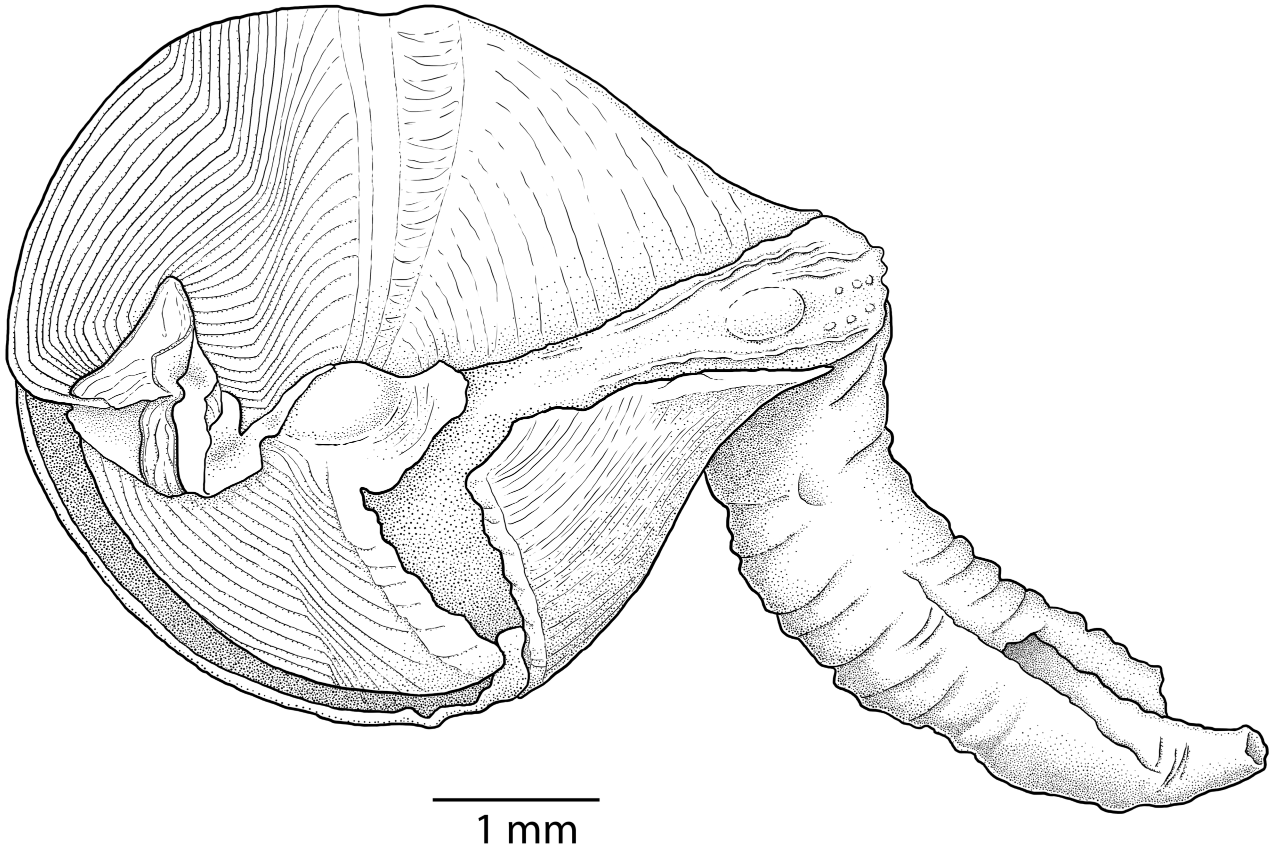

FIGURE 7. *Xylophaga lambula* n. sp. Holotype and only known specimen USNM 1607163. Dorsal view; note the incomplete siphon, and the (misaligned) flat, triangular mesoplax plate on the specimen's right side.

Remarks: Turner (2002), writing in reference to *X. rikuzenica* Taki & Habe, 1945, stated that truncated excurrent siphons with tissue ridges on the dorsal incurrent siphon were always linked to a regular herringbone pattern of the posterior adductor scar, with the word "regular" excluding species such as *Xylophaga platyplax* n. sp. In this specimen, I chose not to expose the posterior adductor scar lest additional damage ensue (the shell is partially broken over left anterior slope) but I use her generality to suggest a relationship with species such as *X. washingtona*.

This species is most similar to *Xylophaga siebenalleri* Voight, 2009; they share an incomplete siphon, cirri at the incurrent siphon, a projecting anterior slope and a ridge posterior to the umbonal-ventral sulcus. That species is distinguished by its low posterior slope, simple mesoplax with only limited ventral extensions and relatively small siphon for the size of the shells. The cirri at the incurrent siphon opening separate this species from *X. praestans*, *X. aurita* Knudsen, 1961, *X. whoi* Turner, 2002, *X. oregona* Voight, 2007 and *X. alexisi* Voight & Segonzac, 2012. The ridge posterior to the umbonal-ventral sulcus separates it from *X. washingtona* and *X. rikuzenica.* From *X. turnerae* Knudsen, 1961, it is separated by the large ventral portion of its mesoplax plate; this also separates it from *X. abyssorum* Dall, 1886, *Xylophaga platyplax* n. sp. and from species in which the mesoplax is ear-shaped, or carries tubes or folds. This species is somewhat similar to *X. abyssorum*, but the ridge posterior to the umbonal-ventral sulcus is less pronounced here, the mesoplax is nearly equally split into dorsal and ventral, and the shell has a higher posterior slope. Although size could contribute to some of these differences, Turner (2002, plate 14) illustrated a specimen of *X. abyssorum* just slightly larger than this specimen in which the mesoplax also had two levels, but the edges were rounded and uneven rather than square and flat.

Xylophaga cf. *turnerae* Knudsen, 1961

Material: USNM 1607143 NE of Norfolk, VA C. Lamb! 2245–2275 m depth. N = 1 Shell length 2.0 mm.

Description: Shell mostly dissolved; periostracum present. Incomplete siphon, excurrent terminates near shell; ridges extend on dorsal incurrent siphon halfway to its opening. Incurrent opening with two rings of cirri. Mesoplax plates periostracal, triangular with modest ventral extension. Posterior adductor muscle in herringbone pattern.

Remarks: This specimen is not definitively assigned to a species; although similar to *X. lambula* n. sp., it is sufficiently different that it could very well represent a different taxon. It shares with *X. turnerae* and with *X. aurita* conspicuous ridges on the proximal incurrent siphon. A better preserved specimen is necessary prior to full determination.

Abditoconus cf. *anselli* (Harvey, 1996)

USNM 1607155 NE Norfolk. VA 37° 02.4 N, 74° 08.5 W to 37° 02.0 N, 74° 07.0 W 2130–2225 m R/V GILLISS 13 Sept 1975 C. Lamb! n = 3, only 1 with shell.

USNM 1607146 NE Norfolk 36° 59.0 N, 72° 58.0 W 36° 58.9 N, 72° 56.0 W 3080–3090 m; R/V GILLISS; 15 Sept. 1975. C. Lamb! n = 5.

USNM 757359 NE of Norfolk 36° 57.9 N, 73° 21.5 W to 36° 58.0 N, 73° 19.4 W 2915–2955 m; R/V GILLISS; 14 Sept 1975; C. Lamb n = 3 dry valves.

Remarks: Distinguishing species in this genus is complicated; the siphonal cover may affect how the siphons are fixed. Additional complications affecting these species include: the siphons of specimens of *A. heterosiphon* (Voight, 2007) appear to have been stained by the wood they bored, the topotypes of *A.* cf. *anselli* (FMNH 312286) have shell lengths of less than 1 mm, and the much larger paratypes of *A. brava* (FMNH 328599; 328600) are stenomorphic. Romano *et al.*'s (2014) reliance on molecular data was not due to chance. The 15 USNM specimens are heavily damaged, have shell lengths <1.5 mm and, if cones were present, they were not preserved. These factors preclude their description.

Characters that may contribute to distinguishing these specimens from all other species in the genus include fewer cirri (8) at the siphonal openings than in *A. heterosiphon* (35), *A. brava* (Romano, Pérez-Portela & D. Martin, 2014) (16–22) and *A. anselli* (12–15); however, the number of cirri at siphonal openings may increase with size (Romano *et al.* 2014). The present species has an umbonal-ventral ridge that appears to expand ventrally to form a condyle, potentially separating it from *A. brava* which is illustrated with a full ridge; confirming this would require dissection of a paratype. It appears to have a larger umbonal reflection than does *A. anselli*. The proximal siphon of *A. investigatoris* MacIntosh and Voight, 2021, has unique texture that distinguishes it from all other species in the genus.

Appropriately preserved material is needed to allow molecular comparison of western and eastern Atlantic specimens. There appear to be no barriers to larval transport across the North Atlantic, potentially allowing long distance dispersal as Romano *et al*. (2014) showed in *Xylonora atlantica*.

Xyloredo nooi Turner, 1972

USNM 756971 with dry. Cape Henlopen DE; 38° 34'N 72° 41.5'W; 2375–2500 m; R/V EASTWARD; 30 July 1975; C. Lamb! n = 10.

USNM 1607165 NE Norfolk, VA; 3080–3090 m; R/V GILLISS; 15 Sept 1975; C. Lamb! n = 1.

USNM 757342 dry NE Norfolk 36° 59.0 N, 72° 58.0 W to 36° 58.9 N, 72° 56.0 W 3080–3090 m; R/V GILLISS 15 Sept 1975; C. Lamb! n =10.

USNM 1607153 NE Norfolk, VA 36° 54.6 N, 74° 27.5 W; 1446–1565 m; R/V COLUMBUS ISELIN; 14 June 1974; J. Musick *et al.*! n = 2.

USNM 1607132 with dry NE Norfolk. VA 37° 02.4 N, 74° 08.5 W to 37° 02.0 N, 74° 07.0 W 2130–2225 m R/V GILLISS 13 Sept 1975 C. Lamb! n =10

USNM 757593 with dry NE of Norfolk, VA 38° 34.0 N, 72° 41.5 W to 38° 33.8 N 72° 43.5 W 2375–2600 m; R/V EASTWARD; 30 July 1975 C. Lamb! n = 10

USNM 1607162 NE Norfolk VA; 38° 29.8 N, 72° 32.9 W to 38° 28.5 N 72° 35.0W; 2625–2640 m; R/V EASTWARD; 30 July 1975; C. Lamb! n = 1.

Description: Xylophagaid bivalves, distal boreholes with ridged calcareous lining. Strong valves: round when small, posterior dorsal margin becomes laterally reflected with growth, inner disk with fold, posterior adductor scar two-parted when larger. Umbonal-ventral ridge flattened. Anterior adductor cover: broad periostracal membrane with two small elongate calcified mesoplax strips.

Siphons: complete, long, usually well-defined straight seam splits proximal from distal sections; openings simple, separate (following Voight 2022).

Xylopholas cf. *altenai* Turner, 1972

USNM 1607150 E of Norfolk, VA. 36° 43.5 N, 74° 34.5 W to 36° 42.6 N, 74° 37.0 W; 570–750 m; R/V GILLISS 18 Sept. 1975; C. Lamb! n = 1 Shell length = 1 mm.

USNM 1607159 E Norfolk, VA 38° 38.7 N, 74° 23.0 W to 38° 39.8 N, 74° 22.0 W; 1730–1760 m; R/V GILLISS; 19 Sept. 1975; C. Lamb! n = 1, but 1 valve (shell length = 1.3), 1 soft parts without valve.

Remarks: These specimens are from greater depths than are previously reported western Atlantic specimens (Turner 2002, 311–366 m depth), perhaps this contributes to their small size.

Feaya dostwous (Voight, 2016)

USNM 1607147 NE of Norfolk, VA 36° 57.9 N, 73° 21.5 W to 36° 58.0 N, 73° 19.4 W; 2915–2955 m; R/V GILLISS; 14 Sept 1975; C Lamb. n = 1 Shell length 3 mm.

Remarks: This, the second known collection of this monotypic genus, is fairly close to the type locality of 38° 18.4′ N 69° 35.6′ W; 3506 m depth collected 29 July 1980 (from Voight 2016). The uneven margin of the ventral valve and periostracum at the siphon tip readily identify it. Although Voight (2016) reported apparent dwarf males attached to the siphons of autonomous borers superficially by only their shell margin. One dwarf male here attached to the ventral siphon of an autonomous borer with its valves splayed open against the autonomous borer's siphon.

Xylonora atlantica (Richards, 1942)

USNM 832948 E of Norfolk 36° 54' 30" N 68° 04' 30"W 4879 m; R/V COLUMBUS ISELIN 28 Feb. 1978; J. A. Musick! N = 7.

Remarks: This widely distributed species remains poorly known. Turner (2002) said the ventral portion of its mesoplax was narrow, she did not illustrate it. Neither does the holotype, a dry valve show the mesoplax. Here the presence of a ventral portion of the mesoplax is used to identify this species, distinguishing it from *Xylophaga clenchi* Turner and Culliney, 1971. Additional characters such as the ridge posterior to the umbonal-ventral sulcus, posterior adductor scar placement and shape were not considered as they vary in these specimens. Distinctions between *Xylonora atlantica* and *Xylophaga clenchi* should be addressed with molecular methods.

Xylophaga clenchi Turner and Culliney, 1971

USNM 1607164 E of Cape Henlopen, DE 38° 51'N 72° 44.1'W 1275–1450 m; R/V EASTWARD; 28 July 1975; C. Lamb! n = 2.

USNM 1607128 NE Norfolk 36° 59.0 N, 72° 58.0 W to 36° 58.9 N, 72° 56.0 W 3080–3090 m; R/V GILLISS 15 Sept 1975 C. Lamb! n = 6.

USNM 1607129 wet & dry NE of Norfolk 36° 57.9 N, 73° 21.5 W to 36° 58.0 N, 73° 19.4 W; 2915–2955 m; R/V GILLISS; 14 Sept 1975; C. Lamb! n > 25.

USNM 757427 E of Norfolk, VA. 36° 43.5 N, 74° 34.5 W to 36° 42.6 N, 74° 37.0 W; 570–750 m; R/V GILLISS 18 Sept. 1975; C. Lamb! n = 1.

USNM 1607154 NE Norfolk. VA 37° 02.4 N, 74° 08.5 W to 37° 02.0 N, 74° 07.0 W 2130–2225 m R/V GILLISS 13 Sept 1975 C. Lamb! n = 9.

USNM 757583 E Norfolk, VA 38° 38.7 N, 74° 23.0 W to 38° 39.8 N, 74° 22.0 W; 1730–1760 m; R/V GILLISS; 19 Sept. 1975; C. Lamb! n = 6.
USNM 832947 E Norfolk, VA 36° 54’ 30” N 68° 04’ 30” W 4879 m Feb 1978. M. Vecchione! n = 4.

Remarks: Turner (2002) reported this widely distributed species to lack any ventral portion of the mesoplax plates as seen in a photograph of specimens from 61° 30’N; 22° 30’W (Ockelmann & Dinesen 2011, Fig. 5) that Haga & Kase (2013) identified as *X. clenchi*. I used that character, the inflated umbo, attached dwarf males and concentric rings on the posterior disk to identify this species. In these specimens, the shell is tall with ridges on both sides of the umbonal-ventral sulcus. The posterior disk has what can be conspicuous concentric lines continuous with toothed ridges of beak. The anterior slope of beak noticeably protrudes dorsally, supporting the mesoplax. The inner shell is most often glossy without clearly defined scars. The siphons were withdrawn in all specimens. Dwarf males could be seen attached to the posterior dorsal mantle edge of some specimens.

Turner (2002) distinguished *X. clenchi* from *Xylonora atlantica* by the mesoplax lacking a ventral part (in *X. atlantica* the ventral part is narrow, forming only a small posterior cavity for the posterior end of anterior adductor), in the shape and type of marking on the posterior adductor scar which, comparing the photo of the holotype (ASNP 2022) to the illustration of *Xylophaga clenchi* in Turner 2002, has fewer marks, in having a broad rounded ridge posterior to umbonal ventral sulcus and arrangement of the siphonal cirri. The inner shell of *X. clenchi* as illustrated by Turner (2002) also shows the mesoplax support is essentially horizontal, rather than angled as in *Xylonora atlantica*. The latter character could be size-biased, but the shells appear comparable. Turner (2002) unfortunately did not illustrate *X. atlantica*, except for the lateral shell and a close-up of siphons on Plate 20. Regrettably, *X. atlantica* has yet to receive a proper description. Although Romano *et al.* (2014) illustrated morphological variation in specimens that their molecular data found to be conspecific, the mesoplax of each lacked ventral extensions, they did not examine the voucher specimen of the GenBank sequences (if one exists) nor did they access the type, which lacks a mesoplax. Turner (2002) emphasized that *Xylophaga clenchi* had what she termed brooded young and *Xylonora atlantica* did not. Currently, this character is viewed as plastic, potentially linked to crowded conditions (Voight 2015). As Romano *et al.* (2014) suggested, the species may not be distinct but to fully demonstrate this, given that a dry valve is the holotype of *X. atlantica*, would require ingenuity.

Depth distributions

The 16 West Atlantic xylophagaid species show diverse depth distributions (Table 1); as predicted (Voight 2008), the four members of the *X. dorsalis* clade (Voight *et al.* 2019) are most shallow, being restricted to depths above 1000 m. Three xylophagaids, *X. abyssorum*, *X. gerda* and *Xylopholas altenai* primarily occur above 1000 m but have been recorded once at >1700 m depth. Three additional species *Xylonora atlantica*, *Xylophaga clenchi*, and *X. platyplax* n. sp. appear to range from > 1000 m to great depths. Two, *Xylophaga profunda* Turner, 2002, and *Xyloredo nooi*, occur near 1700 m and at greater depths. The remaining four species are known only from >2000 m depth.

A wide depth distribution does not appear to be an artifact of sampling. Species with depth ranges of over 1000 m were not statistically more likely to have been sampled more frequently than were those with narrower depth ranges ($U = 10$, $n_1 = 6$; $n_2 = 7$ $p>0.05$).

Discussion

The literature treating Atlantic xylophagaids tends to be biased toward shallow-water species, due to the relative inaccessibility of deep-sea specimens. Relatively shallow-water species are more often encountered, especially given the historic use of wooden lobster pots (e.g. Romey *et al.* 1994). Adding these deeper-water species may dramatically improve our understanding of the xylophagaid fauna. Molecular studies would be a welcome aid in further distinguishing morphologically similar but distinct (or perhaps morphologically divergent but conspecific) taxa. Unfortunately the current lack of suitably preserved specimens makes that impossible.

Discovery of *Xylophaga microdactylus* n. sp. in the northwest Atlantic which is very similar to the deep-water Pacific species *X. microchira* in siphon morphology and shell characters suggests the two are sister taxa and the xylophagaid faunae shared a history between the areas. Similarity, however, is not proof of sister taxon status.

Large pieces of wood are predicted to float longer; smaller pieces are predicted to sink sooner, that is in comparatively shallow water close to land (Häggblom 1982). Wood-dependent species living well off-shore should then be specialized to locate and use large, rare wood resources. Nearshore species should be specialized to locate and exploit small but relatively abundant wood resources (Voight 2015). These differences would force xylophagaid species composition to change with depth. Despite the comparatively few records, the northwest Atlantic species appear to show such a pattern (Table 1), although some species range over considerable depths, possibly indicative of their necessarily opportunistic nature. Accurate species determinations, additional collections may allow examination of the protoconchs to test whether their size supports the hypothesized pattern. Regardless, additional collections are essential to determine whether for instance the wide but spotty depth distribution of *Xylophaga gerda* reflects its regular distribution, or if the extreme limits are flukes, unlikely to ever be repeated.

Acknowledgements

L. Kanellos executed the illustrations. David Reid at the BMNH allowed access to *Xylophaga praestans* type specimen; Ellen Strong and Paul Greenhall permitted the loan of these specimens; Abigail Reft and Kathryn Ahlfeld extended many courtesies and issued new catalogue numbers. Simon Cragg, Nikolaus Malchus and an anonymous reviewer provided helpful comments that improved the manuscript. My thanks to them all and to Cathy Lamb.

References

ASNP (2022) Available from: http://clade.ansp.org/malacology/collections/details.php?mode=details&catalognumber=178741 (accessed 14 July 2022)

Dall, W.H. (1886) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake", Lieut.-Commander C.D. Sigsbee, U.S.N. and Commander J.R. Bartlett, U.S.N. commanding. XXIX. Report on the Mollusca. Part 1, Brachiopoda and Pelecypoda. *Bulletin of the Museum of Comparative Zoology at Harvard College,* 12 (6), 171–318, pls. 1–9.

GBIF (2022) Available from: https://www.gbif.org/occurrence/search?basis_of_record=PRESERVED_SPECIMEN&taxon_key=2288781 (accessed 25 April 2022)

Haga, T. & Kase, T. (2013) Progenetic dwarf males in the deep-sea wood-boring genus *Xylophaga* (Bivalvia: Pholadoidea). *Journal of Molluscan Studies*, 79, 90–94.
https://doi.org/10.1093/mollus/eys037

Häggblom, A. (1982) Driftwood in Svalbard as an indicator of sea ice conditions. *Geografiska Annaler*, Series A, 64, 81–94.
https://doi.org/10.1080/04353676.1982.11880057

Harvey, R. (1996) Deep water Xylophagaidae (Pelecypoda: Pholadacea) from the North Atlantic with descriptions of three new species. *Journal of Conchology*, 35, 473–481.

Janssen, R. & Krylova, E.M. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Bivalvia. *Invertebrate Zoology*, 11 (1), 43–82.
https://doi.org/10.15298/invertzool.11.1.06

Knudsen, J. (1961) The bathyal and abyssal *Xylophaga*. *Galathea Reports*, 5, 163–209.

Lamarck, J.-B.M. (1809) *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux*. F. Savy, Paris, 412 pp.

MacIntosh, H. & Voight, J.R. (2021) Deep-sea wood-boring bivalves (Xylophagaidae) from southeast Australia, with a new species described. *Molluscan Research*, 41, 16–25.
https://doi.org/10.1080/13235818.2020.1861681

Ockelman, K.W. & Dinesen, G.E. (2011) Life on wood—the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). *Marine Biology Research*, 7, 71–84.
https://doi.org/10.1080/17451001003714504

Purchon, R.D. (1941) On the biology and relationships of the lamellibranch *Xylophaga dorsalis*. *Journal of the Marine Biology Association of the United Kingdom*, 25, 1–39.
https://doi.org/10.1017/S0025315400014259

Reft, A.J. & Voight, J.R. (2009) Sensory structures on the siphons of wood-boring bivalves (Pholadidae: Xylophagainae: *Xylophaga*). *Nautilus*, 123, 43–48.

Richards, H.G. (1942) *Xylophaga atlantica***,** new species. *Nautilus*, 56, 68.

Romano, C., Voight, J.R., Pérez-Portela, R. & Martin, D. (2014) Morphological and genetic diversity of the wood- boring *Xylophaga* (Mollusca, Bivalvia): new species and records from deep-sea Iberian canyons. *PLoS ONE*, 9 (7), e102887.
https://doi.org/10.1371/journal.pone.0102887

Romey W.L., Bullock, R.C. & DeAlteris, J.T. (1994) Rapid growth of a deep-sea wood-boring bivalve. *Continental Shelf Research*, 14, 1349–1359.
https://doi.org/10.1016/0278-4343(94)90052-3

Santhakumaran, L.N. & Sneli A.-J. (1984) Studies on the marine fouling and wood-boring organisms of the Trondheimsfjord (Western Norway). *Gunneria*, 48, 1–36.

Smith, E.A. (1903) On *Xylophaga praestans* on the English coast. *Proceedings of the Malacological Society, London*, 5, 328–330.

Taki, I. & Habe, T. (1945) Classification of Japanese Pholadacea. *Japanese Journal of Malacology*, 14, 108–123.

Tebble, N. (1966) *British bivalve seashells. A handbook for identification*. British Museum (Natural History), Departement of Zoology. London, 212 pp.

Turner, R.D. (1955) The family Pholadidae in the western Atlantic and the eastern Pacific. Part II—Martesiinae, Jouannetiinae and Xylophaginae. *Johnsonia*, 3, 65–160.

Turner, R.D. (1972) *Xyloredo*, a new teredinid-like abyssal wood-borer (Mollusca, Pholadidae, Xylophagainae). *Breviora*, 397, 1–13.

Turner, R.D. (1972) A new genus and species of deep water wood-boring bivalve (Mollusca, Pholadidae, Xylophagainae). *Basteria*, 36, 97–104.

Turner, R.D. (1973) Wood-boring bivalves, Opportunistic species in the deep sea. *Science*, 180, 1377–1379.
https://doi.org/10.1126/science.180.4093.1377

Turner, R.D. (2002) On the subfamily Xylophagainae (Family Pholadidae, Bivalvia, Mollusca). *Bulletin of the Museum of Comparative Zoology*, 157, 223–307.

Turner, R.D. & Culliney, J. (1971) Some anatomical and life history studies of wood boring bivalve systematics. *Annual Report of the American Malacological Union for 1970*, 1971, 65–66.

Turton, W. (1819) *A Conchological Dictionary of the British Islands*. J. Booth, London, xxvii + 272 pp., 28 pls.

Turton, W. (1822) *Conchylia Insularum Britanicarum*. *The shells of the British Islands, systematically arranged*. M.A. Nattali, London, 344 pp.
https://doi.org/10.5962/bhl.title.10443

Tyler, P.A., Young, C.M. & Dove, F. (2007) Settlement, growth and reproduction in the deep-sea wood-boring bivalve mollusc *Xylophaga depalmai*. *Marine Ecology Progress Series*, 343, 151–159.
https://doi.org/10.3354/meps06832

Voight, J.R. (2007) Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). *Journal of Molluscan Studies*, 73, 377–391.
https://doi.org/10.1093/mollus/eym034

Voight, J.R. (2008) Deep-sea wood-boring bivalves of *Xylophaga* (Myoida: Pholadidae) on the Continental Shelf. *Journal of the Marine Biological Association of the United Kingdom*, 88, 1467–1472.
https://doi.org/10.1017/S0025315408002117

Voight, J.R. (2009) Diversity and reproduction of near-shore vs. offshore wood-boring bivalves (Pholadidae: Xylophagainae) of the deep eastern Pacific Ocean, with three new species. *Journal of Molluscan Studies*, 75, 167–174.
https://doi.org/10.1093/mollus/eyp012

Voight, J.R. (2015) Xylotrophic bivalves: aspects of their biology and the impacts of humans. *Journal of Molluscan Studies*, 81, 175–186.
https://doi.org/10.1093/mollus/eyv008

Voight, J.R. (2016) New insights on *Xylopholas* (Mollusca: Xylophagaidae): Diversity, growth and reproduction. *American Malacological Bulletin*, 34 (2), 138–146.
https://doi.org/10.4003/006.034.0210

Voight, J.R. (2022) Species synonymies in the deep-sea wood-boring bivalve genus *Xyloredo* (Mollusca: Xylophagaidae). *Malacologia*, 64 (2), 163–168.
https://doi.org/10.4002/040.064.0201

Voight, J.R., Marshall, B.A., Judge, J., Halanych, K.M., Li, Y., Bernardino, A.F., Grewe, F. & Maddox, J.D. (2019) Life in wood: Molecular phylogeny of deep-sea wood-boring bivalves (Mollusca: Xylophagaidae). *Journal of Molluscan Studies*, 85 (2), 232–243.
https://doi.org/10.1093/mollus/eyz003