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Deep-sea wood-boring bivalves of *Xylophaga* (Myoida: Pholadidae) on the Continental Shelf: a new species described

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Deep-sea organisms are generally considered to be restricted to the great ocean depths, unable to enter shallower habitats except perhaps at the isothermic polar latitudes, due to physiological constraints, or more intense biotic interactions. Wood-boring bivalves of Xylophaga, *however, are here shown to be exceptional. A clade, formally recognized by Turner in 2002, united by the derived characters of a complex mesoplax and a truncated excurrent siphon, papillose incurrent siphon with a longitudinal dorsal trough bordered by lappets, and often carrying white or glass-like granules, occurs at significantly shallower and warmer depths than do other species of the genus. Here, description of the new species* X. multichela *from 106 m depth off the Pacific coast of Guatemala illustrates the characters that unite the clade. Because wood-boring bivalves face intense competition and high levels of predation at depths of 2200 to 3250 m, they may not perceive biotic interactions at shallower depths to be dramatically more intense. In addition, members of this group are hypothesized to tolerate reduced oxygen availability, a requisite if animals are to occur in warm waters.*

Keywords: Xylophagainae, on-shore migration, predation, competition, hypoxia

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INTRODUCTION

Species of *Xylophaga* are known to range from between 10 and 5050 m depth from the equator to near the Arctic Circle (Knudsen, 1961; Schiøtte, 2005). As do shallow-water teredinids, species of *Xylophaga* use their ridged shells to bore into vegetation, most often wood, that has fallen to the sea floor. The bivalves ingest wood fragments and, with the help of endosymbiotic bacteria hosted on their gills (Distel & Roberts, 1997), digest it. Despite the apparent rarity of seafloor wood, the species of the Xylophagainae appear to be unusually diverse, with four to six co-occurring in comparatively small oceanic areas (Turner, 2002). With over a third of the 55 known species of *Xylophaga* having been described since 1996 (Table 1), patterns of distribution of the group are becoming apparent.

Although species of deep-sea groups such as *Xylophaga* typically occur deeper than the photic zone or the 'thermocline' (Knudsen, 1961), some species occur at shallow depths. Most frequently, deep-sea species make shallow water incursions at high latitudes, where the water column is isothermic. A description of two *Xylophaga* species from 10 m depth in Norway (Santhakumaran, 1980) indicates that the group shows this pattern, but the description here of a new species of the genus from near 100 m depth on the Pacific coast of Guatemala documents that additional mechanisms are at work. The derived character states of a truncated excurrent siphon that continues as lappets on the dorsal incurrent siphon, and ear-shaped mesoplax plates place this species in Turner's (2002) species Group 6. All species in this group, in addition to sharing those morphological features, occur above 350 m depth, and most occur in the upper 150 m.

This paper describes a new species, *Xylophaga multichela*. The depth distributions of this and related species, are hypothesized to form a clade because they share what are argued to be highly derived characters. The occurrence of this clade on the continental shelf may relate to the high biotic interactions typical of the wood fall habitat and the hypothesized tolerance of this group for reduced oxygen availability.

MATERIALS AND METHODS

The 32 specimens examined were from the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC). They were removed from the vegetation (reeds) in which they had been collected and formalin-fixed and were transferred to 80% ethanol by the author. The duration of storage in formalin and its strength were unknown. All specimens were examined under light microscopy; all illustrations were made using a camera lucida to ensure their accuracy. Shell measurements of the holotype, including length, height and breadth (across both intact valves) were made with electronic callipers. Characters used in species descriptions are those of the shell, mesoplax and siphons, as is traditional within this genus (Knudsen, 1961; Turner, 2002). Two specimens of *Xylophaga multichela* sp. nov. were placed in a series of increasing ethanol solutions, critical-point dried and sputter-coated with gold; structures on the incurrent siphon were then examined by scanning electron microscopy.

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Table 1. Species of *Xylophaga* arranged by Turner's (2002) groups (with species not readily assigned to a group listed at the end), with depth range in m, absolute value of average latitude, geographical area and estimated maximum ambient temperature at depth (where available). An asterisk after the species name indicates that the species is considered to brood its young. Depth ranges of species occurring in the upper 500 m are in bold type.

Species authority	Depth	Latitude	Area	Temperature
Group 1 N = 3				
X. erecta Knudsen, 1961	5050	8	Indonesia	10.6
*X . concava** Knudsen, 1961	3270–3670	6	Gulf of Panama	2–5
X. gerda Turner, 2002	**283–2072**	18	Caribbean	
Group 2 N = 8				
*X. grevei** Knudsen, 1961	545–7290	2	Mindanao Sea/Banda Tren	4–7
*X. wolffi** Knudsen, 1961	5050	8	Sulu Sea	10.6
X. hadalis Knudsen, 1961	6660–6770	36	South Pacific	2
*X. galatheae** Knudsen, 1961	4530	31	New Zealand	1
*X. murrayi** Knudsen, 1967	**347–384**	5	Zanzibar	13
*X. africana** Knudsen, 1961	2550	1	East Atlantic	3
*X. panamensis** Knudsen, 1961	915–975	7	Gulf of Panama	5
*X. clenchi** Turner & Culliney, 1971	**35–4862**	25	Iceland to Venezuela	
Group 3 N = 9				
X. supplicata (Taki & Habe, 1950)	**183**	33	Tosa Bay, Japan	11–12
*X. lobata** Knudsen, 1961	5050	8	Indonesia	10.6
*X. tubulata** Knudsen, 1961	2000	4	Makassar Strait	3.6
*X. bruuni** Knudsen, 1961	1500	9	Mindanao Sea	10
*X. obtusata** Knudsen, 1961	915	7	Gulf of Panama	5
*X. whoi** Turner, 2002	**336–910**	18	Southern Florida to Colombia	
*X. profunda** Turner, 2002	1722–2066	25	Bahamas	
X. n. sp*	1792–1875	27	Guaymas Basin	
X. n. sp. C* Voight, in review	1225–3950	31	Southern California	
Group 4 N = 5				
*X. abyssorum** Dall, 1886	**342–1722**	20	Florida to Lower Antilles	4–15
X. duplicata Knudsen, 1961	**109–915**	7	Tropical east Pacific	5
X. muraokai Turner, 2002	1615	33	Southern California	
X. foliata Knudsen, 1961	2000	4	Indian Ocean	3.6
X. atlantica Richards, 1942	**15–1242**	43	West Atlantic	23
Group 5 N = 9				
X. washingtona Bartsch, 1921	**20–2000**	33	North-east Pacific	10–15
X. rikuzenica Taki & Habe, 1945	**183–1270**	35	Honshu, Japan	6
X. aurita Knudsen, 1961	915	7	Gulf of Panama	5
X. turnerae Knudsen, 1961	915	7	Gulf of Panama	5
X. praestans Smith, 1903	**30–82**	50	North-east Atlantic	4–18
X. nidarosiensis Santhakumaran, 1980	**10**	63	Norway	
X. oregona Voight, 2007	2200	43	North-east Pacific	2
X. sp. S* Voight in review	1100–2750	21	North-east Pacific	
X. sp. m Voight, in ms	4626	21	East Atlantic	
Group 6 N = 10				
X. dorsalis Turton, 1822	**0–2500**	40	East Atlantic	10–13
X. depalmai Turner, 2002	**30–520**	26	Massachusetts to Florida, US; Bahamas	7–9.5
X. guineensis Knudsen, 1961	**46–2250**	2	Gulf of Guinea	3
X. mexicana Dall, 1908	**35**	16	East Pacific	5
X. tipperi Turner, 2002	**153**	26	North-west Atlantic	
X. bayeri Turner, 2002	**150–365**	18	Caribbean, Florida	
X. globosa Sowerby, 1835	**0–245**	0	North-east Atlantic	19
X. japonica Taki & Habe, 1950	**183–384**	8	Japan/Burma/Java	11–12
X. indica E. A. Smith, 1904	**339**	13	Andamans	12
X. multichela n. sp.*	**106-113**	13	Guatemala	15
***Incertae sedis* N = 12**				
X. anselli Harvey, 1996	1370–2195	56	Hebridean Slope	
X. corona Voight, 2007	2701	41	North-east Pacific	2
*X. gagei** Harvey, 1996	1370–2195	57	Hebridean Slope	
X. heterosiphon Voight, 2007	2600	42	North Pacific	2
X. knudseni Okutani, 1975	3100	30	West Pacific	
X. microchira Voight, 2007	1550–2658	47	North-east Pacific	2
X. noradi Santhakumaran, 1980	**10**	63	Norway	
X. ricei Harvey, 1996	5000	31	Madiera Abyssal Plain	2
X. teramachii (Taki & Habe, 1950)	**33**	34	Shikoku, Japan	
X. tomlini Prashad, 1932	1301	1	Indo-Malayan waters	4
X. zierenbergi Voight, 2007	3232	42	North-east Pacific	2
X. sp. D* Voight, in review	1235–2500	36	North-east Pacific	

Taxonomic history of wood-boring bivalves from the eastern tropical Pacific, other than Knudsen's (1961) description of six species collected from three sites in the Gulf of Panama, is lacking. Voight (2007, in press) reports the Xylophagainae from the eastern Pacific Ocean north of the US–Mexico border.

Turner (2002) defined six species groups in the genus *Xylophaga* based on unpolarized characters. Groups 5 and 6 share a truncated excurrent siphon that otherwise appears to be unique among the Pholadidae, and very rare among bivalves in general, and a longitudinal trough on the dorsal incurrent siphon defined laterally by lobes or folds, also referred to as low walls (in Group 5), or fringed lappets (in Group 6). In addition, species of Group 6 share roughly ear-shaped mesoplax plates, the truncation of the excurrent siphon being near the valves, and continuing as fringed lateral lobes along the dorsal incurrent siphon. Because recognition of Group 6 could make Group 5 paraphyletic, both groups are considered here, with Group 6 being the focal group for this study.

Latitudinal and depth records for each species of *Xylophaga* were compiled from the taxonomic literature (Harvey, 1996; Knudsen, 1961, 1967; Okutani, 1975; Santhakumaran, 1980; Turner, 2002; Voight, 2007, in press), as most species are known only from their type localities. Sea temperature at the collecting site was taken from available reports (notably Knudsen, 1961) and web-based references (e.g. http://faculty.washington.edu/kessler/pacs/inverse/epac.html). Differences between Groups 5 and 6 and between those species and others in the genus (Groups 1 to 4) in depth and geographical range, and in ambient temperature were analysed using Kolmogorov–Smirnov tests, nonparametric tests of differences in two samples. Knudsen (1961) reported two species of Group 6, *X. guineensis* Knudsen, 1961 and *X. dorsalis* Turton, 1822, from depths over 2000 m. Turner (2002) however, argued that Knudsen's examination of the former species relied on dead shells that were transported post-mortem. Schiøtte (2005) stated that *X. dorsalis* has a shallow rather than the wide depth range Knudsen (1961: Table 3) cited based on Dautzenberg (1927). This latter comment echoes Knudsen's (1961) text caution that Dautzenberg's (1927) report should be re-evaluated. The greater maximum depth records are retained in this dataset, despite these caveats, as they will act only to bias the test toward accepting the null hypothesis that no significant differences exist in depth distribution between the focal group and the other species of *Xylophaga*.

SYSTEMATICS

Order MYOIDEA Stoliczka, 1870
Family PHOLADIDAE Lamarck, 1809
Genus *Xylophaga* Turton, 1822
Xylophaga multichela sp. nov.
(Figures 1–2)

TYPE MATERIAL

Holotype: (FMNH 312307 x-SIO-BIC M 11567), MV 73-I-47; Champerico, Guatemala; 13° 50.0′N 92° 01.7′W to 13° 52.5′N 92° 02.3′W; 113–106 m; 40′ otter trawl; 13 April 1973; RV 'Agassiz'; Coll. Hubbs & Luke. Measurements of holotype: shell length 2.6; height 2.4; breadth 2.7; incurrent siphon length 2.3.

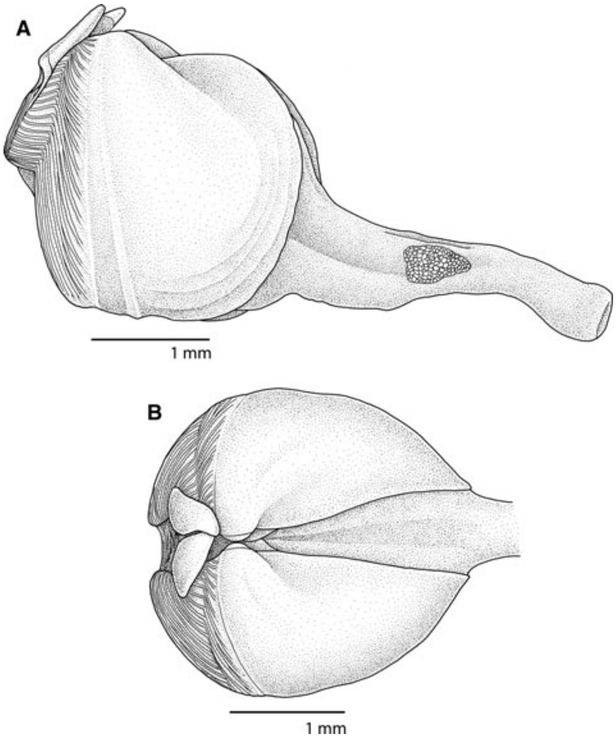

Fig. 1. *Xylophaga multichela* sp. nov. (A) Line drawing of lateral intact holotype, triangular cluster of hooks positioned near halfway point of siphon; (B) line drawing of dorsal view of intact holotype. Scale bars: 1 mm.

Paratypes: 31 adults (SIO-BIC M11567) collected with the holotype.

DIAGNOSIS

Large, ear-shaped mesoplax. Incomplete siphon: excurrent siphon truncate near valves; incurrent siphon with deep, dorsal channel, papillate edges. Triangle of white granules with recurved tips on lateral siphon distal to excurrent opening. Papillae variably present on distal incurrent siphon. Young brooded on common siphon.

ETYMOLOGY

Named after the triangle of hooks just distal and lateral to excurrent siphon opening (Latin: *multi-*; Greek *-chela* claw).

DESCRIPTION

Beak (Figure 1A): non-protruding, 20 toothed rows parallel to ventral edge, forming broad vertical band of 16–20 toothed rows at junction of beak and disk. Umbonal reflection: simple outward fold near dorso-lateral edge of anterior incision.

Mesoplax (Figure 1B): large, conspicuous, ear-shaped, with posterior coiling; plates always meet at midline, general form somewhat variable; posterior extensions reaching between umbos variably present.

Shell (Figure 1A): small, very white, glossy, delicate, often broken. Umbonal-ventral sulcus: narrow, very weak, sharply prominent ridge posterior to sulcus. Inner shell: dry shells iridescent when lit from some angles. Posterior adductor muscle scar: poorly defined shiny rectangle oriented diagonal to dorso-ventral axis of shell, without individual elements. Pedal retractor scar: anterior, slightly dorsal to posterior adductor scar.

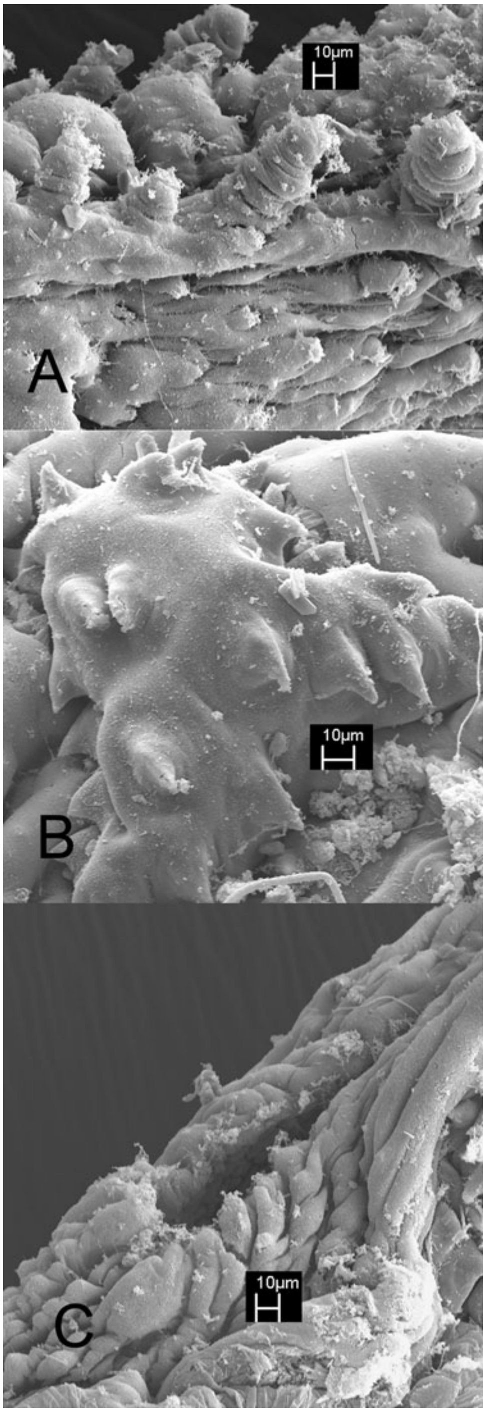

Fig. 2. *Xylophaga multichela* sp. nov. (A) Scanning electron microscope (SEM) image of papillae that border the longitudinal trough on dorsal incurrent siphon; (B) SEM view of triangle of hooks just distal and lateral to excurrent opening; (C) SEM view of opening of excurrent siphon. Scale bar in each 10 µm.

Siphon (Figure 1A): length variable, generally about equal to shell length, muscle transparency suggests some artefact likely; common siphon covered by thin periostracal membrane from shell to excurrent siphon opening. Excurrent siphon: truncated, margin of opening (Figure 2C) forms deep U, continuous with longitudinal channel on dorsal incurrent siphon; opening lacks cirri. Incurrent siphon: often papillate, especially at mid-siphon, opening without cirri, dorsal trough bordered by intermittent papillae (Figure 2A), trough lacks papillae. Triangle of hooks curved toward shell, distal to excurrent opening on lateral siphon (Figures 1A & 2B), position slightly varies due to variable contraction, hook tips clear, shiny, bases white.

Muscles: foot small relative to shell, vertical line on face. Mantle often transparent; longitudinal muscles in common siphon and ventral shell adductors visible.

Reproduction: 7 of 36 individuals carry 1–2 juveniles on common siphon. Additional juvenile-sized bivalves found unattached.

DISTRIBUTION

Only known from the type locality. Estimated ambient temperature 15°C.

REMARKS

The ear-shaped mesoplax, truncated excurrent siphon, laterally papillate incurrent siphon with a dorsal longitudinal trough definitively place this species in Turner's Group 6. The triangular cluster of opaque white hooks on the lateral incurrent siphon and the presence of brooded young separate this species from all others. Of species in this group, neither *X. globosa* nor *X. bayeri* has granules on the siphon according to Turner (1955) and (2002), respectively. Turner (2002) described fine, irregular opaque or glass-like white granules in a linear array on incurrent siphons of *X. tipperi*, *X. depalmai*, *X. guineensis*, *X. japonica* and *X. mexicana*. The clustered granules in the present species distinguish it. The present species is distinguished from *X. dorsalis* by that species' projecting beak, more massive mesoplax plates and cirri on the incurrent opening; it is distinguished from *X. indica* by the two distinct ridges defining the umbonal-ventral sulcus and the simpler mesoplax of that little-known species. The type localities of both *X. multichela* sp. nov. and *X. mexicana* lie between the US–Mexico border and the Gulf of Panama and both species share a prominent, but narrow ridge posterior to the umbonal-ventral sulcus. The distribution of granules on the siphon and the strongly projecting beak of *X. mexicana* versus the non-projecting beak of *X. multichela* sp. nov. readily distinguish them. Turner (2002) illustrated barb-shaped granules on *X. tipperi* and Knudsen (1961) noted that some calcareous bodies on the siphon of *X. praestans*, assigned by Turner to her species Group 5, had curved spines. The granules of the present species are therefore not unique.

Brooding by only seven individuals of the 32 individuals of *X. multichela* sp. nov. available for study may indicate a flexible reproductive strategy, as Tyler *et al.* (2007) document in *X. depalmai*.

DISTRIBUTIONAL PATTERNS AMONG *XYLOPHAGA* SPECIES

The latitudinal distributions of species in Turner's species Groups 5 and 6 (Table 1) are statistically identical to those of other species in the genus ($D = 0.1562$; $P = 0.899$), as are the latitudinal distributions of Group 5 and of Group 6 ($D = 0.4000$; $P = 0.313$). Species of Groups 5 and 6 occur at significantly more shallow depths (Table 1) than do the other species in the genus ($D = 0.4753$; $P = 0.006$ for maximum depths; $D = 0.5592$; $P = 0.001$ for minimal depths). Group 6 species occur at significantly shallower maximum depths than do those of Group 5 ($D = 0.6000$; $P = 0.031$), but their minimal depths of occurrence are not significantly different ($D = 0.5000$; $P = 0.111$). The available temperature data for collection sites for other species in the genus do not differ from those of Groups 5 and 6 ($D = 0.400$; $P = 0.086$), although Group 6 species occur in significantly warmer waters than do those of Group 5 ($D = 0.600$; $P = 0.031$).

DISCUSSION

A derived clade within the deep-sea or 'sub-thermocline' (Knudsen, 1961) genus *Xylophaga* is argued here to have colonized continental shelf depths, typically shallower than 300 m (Table 1). Deep-sea taxa have been suggested to be restricted to great, cold depths by the reduced oxygen availability associated with warmer temperatures (Jacobs & Lindberg, 1998) and by increased biotic interactions in shallow water (Vermeij, 1987), perhaps driven by onshore origination of evolutionary novelties that only later extend to greater depths (Jablonski *et al.*, 1983). Vermeij (1987) argued that low temperatures and limited productivity slow biological processes in the deep sea, making it an ideal safe place for 'adaptively anachronistic' taxa. Turner (1973), however, demonstrated that species of the Xylophagainae can bore wood extremely rapidly at 1830 m depths.

Wood-borers may perceive differences between shallow and deep water differently than do most taxa. To species of *Xylophaga*, the shallow continental shelf may appear to be comparatively free of competition. At depth, multiple species of *Xylophaga* can occur in microsympatry (reviewed by Voight, 2007); up to five species of *Xylophaga* have been recorded from one piece of wood (Hoagland & Turner, 1981). Although shipworms of the Teredinidae can be abundant in shallow water, and are known from great depths (Knudsen, 1961; Turner, 1966) they tend to bore with the grain of the wood; in contrast, bivalves of *Xylophaga* bore at right angles to the grain (Knudsen, 1961; personal observation). Physical partitioning of the wood fall habitat may reduce competition between species of *Xylophaga* and teredinids and increase it among members of each group.

Species of the Xylophagainae have also been suggested to face high predation pressure at depth (Voight, 2007). Experimental wood deployments recovered inside lidded boxes from as deep as 3232 m supported high densities of polyclad flatworms of the Euryleptidae and of the echinoderm *Xyloplax janetae*, likely predators of newly settled bivalves (Quiroga *et al.*, 2006; Voight, 2005, 2007). Despite trawl-collection, euryleptid flatworms were also recovered with these specimens of *X. multichela* sp. nov., although the poor preservation of the flatworms prevent further identification (M. Litvaitis, personal communication). In shallow-water habitats a greater diversity of predators may be encountered. The morphological features that unite this species group, and define this hypothesized clade, may also increase their physical defences against predation. The elaborate three-dimensional mesoplax can extend over the umbo and potentially could block predators. The siphon's hook-shaped granules may maintain the bivalve's position in its borehole, a role also attributed to the faecal chimney (Purchon, 1941), precluding attempts to extract the animal. The incurrent siphon's fringed papillae (Figure 2A) could be sensory in nature to increase the animal's ability to detect potential threats.

Oxygen is less soluble in warmer water, therefore less available in shallow water at temperate and tropical latitudes. In addition, each 5° increase in temperature can double oxygen uptake by the sediment, due to increased bacterial metabolic rates, and every 10° increase in temperature can double the metabolic oxygen requirement of benthic animals (Jacobs & Lindberg, 1998). Turner (2002) documented that *X. washingtona*, a shallow-water species in Group 5 that may enter the Oxygen Minimum Zone of the Eastern Pacific, tolerates low oxygen tensions. Closely similar is *X. oregonae*, a species that generates dense accumulations of faecal chimneys (Voight, 2007; Figure 13). Voight (2007) suggested that the chimneys lowered oxygen availability, and thus were evidence that this species like *X. washingtona* tolerates lower oxygen concentrations. Although the existence of such a physiological tolerance of low oxygen is documented in only one species, this physiological character could be a key innovation to allow invasion of shallow water.

Discovery of a second lot of *Xylophaga multichela* n. sp. (UMML 30.15163: RV 'Gilliss' Station 9, 6°36′N, 77°27′W, 119 m, 16 January 1972, 10-ft. otter trawl) extends the species range to Golfo de Cupica, Chocó, Colombia. The mesoplax of the 27 specimens shows considerable variation in morphology.

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