At the bottom of the deep blue sea: a new wood-boring bivalve (Mollusca, Pholadidae, *Xylophaga*) from the Cape Verde Abyssal Plain (subtropical Atlantic)

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ABSTRACT
Bivalves of *Xylophaga* Turton, 1822 require access to wood or other vegetation on the seafloor, into which they bore. They ingest the wood and, with the aid of bacteria, digest it to survive. Their complete dependence on vegetation for survival suggests that the group would be rare on the abyssal plains, as the availability of terrestrial vegetation declines with distance from land masses. Deployment of a small block of wood on a mooring at 4626 m depth in the Cape Verde Abyssal Plain, over 1600 km west of Africa tested that suggestion. When recovered seven months after deployment, the wood carried an estimated 170 boreholes/cm^2 evidence of extremely and surprisingly rapid colonization by a previously unknown species, here described as *Xylophaga alexisi* n. sp. The species is unique in having an incomplete siphon, a posterior adductor scar made of linear elements and in lacking cirri at both siphonal openings. Atlantic species described by Harvey (1996) are compared to this and other species. The bivalves are estimated to have grown 0.011 mm per day, comparable to growth estimates of *X. ricei* Harvey, 1996 at 5000 m depth. The high density of this species at this site, the great distance of the site from the continent which is so arid to be Saharan in character and the minimal input the site receives from surface and bottom currents argue strongly that wood-boring species thrive in the largest benthic habitat on Earth, the abyssal plain.

KEY WORDS
Sunken wood,
Xylophagainae,
deep-sea species,
recruitment rate,
growth rate.

RÉSUMÉ

Dans les profondeurs de la mer bleue : un nouveau bivalve des bois coulés (Mollusca, Pholadidae, Xylophaga*) de la plaine abyssale du cap Vert (Atlantique subtropical).*
Les bivalves *Xylophaga* Turton, 1822 sont des foreurs de bois ou d'autres végétaux coulés au fond des océans. Ils ingèrent le bois et le digèrent grâce à des bactéries. Leur dépendance étant complète à l'égard des restes végétaux et la disponibilité des végétaux terrestres décroissant avec la distance des terres émergées, on peut imaginer que le groupe est rare dans les plaines abyssales, comme la disponibilité des végétaux terrestres décroît avec la distance des continents. Le déploiement d'un petit bloc de bois immergé sur un mouillage à 4626 m de profondeur dans la plaine abyssale du cap Vert, à plus de 1600 km à l'ouest de l'Afrique, a permis de tester cette hypothèse. Récupéré sept mois après le déploiement, le bois présentait environ 170 perforations/cm^2, résultat d'une colonisation étonnament très rapide par une espèce précédemment inconnue, ici décrite comme *Xylophaga alexisi* n. sp. L'espèce est remarquable par son siphon incomplet, une empreinte du muscle adducteur postérieur faite d'éléments linéaires, et par l'absence de papilles sur les ouvertures siphonales. L'espèce nouvelle est comparée entre autres aux espèces atlantiques décrites par Harvey (1996). La croissance des bivalves est estimée à 0.011 mm par jour, ce qui est comparable aux évaluations de croissance de *X. ricei* Harvey, 1996, à 5000 m de profondeur. La densité élevée de *X. alexisi* n. sp. sur un site éloigné du continent saharien, où les courants de surface et de fond sont faibles, suggère fortement que les espèces de bois coulés sont en fait très répandues dans les plaines abyssales, qui constituent le plus vaste habitat benthique de la planète.

MOTS CLÉS
Bois coulés,
Xylophagainae,
espèces marines profondes,
taux de recrutement,
taux de croissance.

INTRODUCTION

The abyssal plains of the world's oceans are the largest benthic habitat on Earth and are among the least explored. Their great distance from continental land masses, the source of nutrients that sustain biological productivity, limit the abundance of animal life on the plains. Dedicated study of one such site on the Cape Verde Abyssal Plain, Oligotroph, was outlined by Auffret *et al.* (1992). Vertical nephelometry profiles performed at Oligotroph found very low suspended load near the bottom (Vangriesheim *et al.* 1993). Sediment trapping experiments show minimal near-bottom material supply; in addition, the extremely slow currents (mean of 3.3 cm/sec) measured at depth at Oligotroph (Khripounoff *et al.* 1998) limit lateral advection of particles. No major surface currents overlie the area, positioned just north of the North Equatorial Current. Understandably, as the scarcity of resources and the limited mixing generated by feeble currents predict, animals at Oligotroph are few and small (Galéron *et al.* 2000).

This resource-limited site, with minimal input from the distant, Saharan African land mass would seemingly be inhospitable for bivalves of the Xylophagainae that require vegetation, such as wood or large algae, to survive. The bivalves bore holes into vegetation on the seafloor using toothed ridges on their anterior shells; their lives are spent inside their boreholes where they rely on symbiotic microbes to exploit the energy in their substrate. The 57 named species in the genus *Xylophaga* Turton, 1822, the most diverse genus in the xylophagains, have primarily been found near land masses, as is vegetation, their obligate habitat. 12 species of *Xylophaga* are known from hadal depths (Knudsen 1961), most of these were collected from trenches where ocean floor is subducted under a continental land mass or in the immediate proximity to continents. Just as dissolved nutrients decrease in abundance with distance from the continent, so too does the availability of the particulate vegetation that xylophagains require. The rarity of collections from abyssal plains, however, may pose a greater limit to our knowledge of the fauna than had been suspected.

In this paper, we describe *Xylophaga alexisi* n. sp. from specimens removed from a wood block deployed with a biological trapping experiment at site Oligotroph on the Cape Verde Abyssal Plain at 4626 m depth and recovered 216 days later. Colonization and growth rates of this species inferred from this deployment are compared to those that have been reported for other species.

MATERIAL AND METHODS

A single block of wood (likely *Pinus* sp.) measuring 6 by 7 cm, 1.5 cm thick was fixed by one of us (MS) to the structure of an autonomous colonization module (MAC) which was designed to rest on the bottom after deployment. The module was deployed on 17th Feb. 1991 during EUMELI 2 cruise at 21°03.81'N, 31°12.21'W at 4626 m depth (Fig. 1) and recovered on 21st Sept. 1991, during the cruise EUMELI 3, N/O *L'Atalante* (Kripounoff *et al.* 1998). The site, named Oligotroph, is over 1600 km west of Africa.

The wood and associated fauna recovered were preserved in 10% formalin at sea, and later transferred to 70% ethanol. To estimate the number of boreholes present on the surface of the wood, two squares 1 cm in linear dimension were marked on the most densely settled surface and the number of boreholes inside the squares counted and averaged. Specimens were removed from the preserved wood by hand. 16 specimens from 0.5 to 2.3 mm in shell length were measured to the nearest 0.1 mm with electronic callipers. Measurements were transformed to natural logarithms and the growth coefficients of the siphons calculated. Some specimens were taken through increasing concentrations of alcohol, and critical point dried to allow examination by SEM. Illustrations were made using a camera lucida.

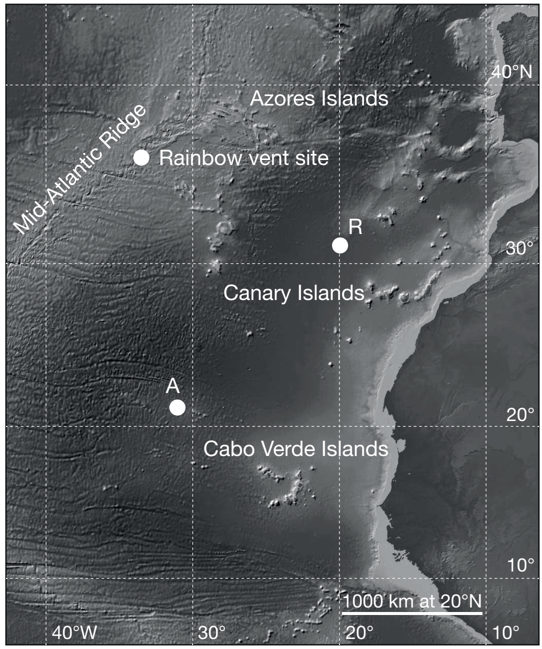

Fig. 1. — **A**, collection locality of *Xylophaga alexisi* n. sp. at 21°N, 30°W; **R**, collection locality of *Xylophaga ricei* Harvey, 1996 at 31°N, 20°W. (From Ryan et al. 2009, modified by Y. Lagabrielle.)

Abbreviations

FMNH	Field Museum of Natural History, Chicago;
MNHN	Muséum national d'Histoire naturelle, Paris;
USNM	National Museum of Natural History, Washington;
MAC	autonomous colonization module (module autonome de colonisation);
SEM	scanning electron microscope.

SYSTEMATICS

Family Pholadidae Lamarck, 1809
Genus *Xylophaga* Turton, 1822

Xylophaga alexisi n. sp.
(Figs 1-5; 6A)

"*X.* sp. m Voight, in ms." – Voight 2008: table 1.

Type material. — Holotype (MNHN 24465). — Paratypes: 5 ex. (MNHN 24466); 5 ex. (USNM 1132964); 18 ex. (FMNH 318671).

TABLE 1. — *Xylophaga alexisi* n. sp. compared in key characters to overtly similar species. Abbreviation: PAS, posterior adductor scar.

Species	Siphon	Incurrent cirri	Excurrent cirri	PAS pattern
Xylophaga alexisi n. sp.	incomplete	no	no	linear
X. ricei Harvey, 1996	subterminal	yes	yes	linear
X. anselli Harvey, 1996	subterminal	yes	no	lobed
X. heterosiphon Voight, 2007	complete	yes	no	linear
X. microchira Voight, 2007	incomplete	yes	yes	linear
X. washingtona Bartsch, 1921	incomplete	yes	yes	herringbone

OTHER MATERIAL EXAMINED. — *Xylophaga alexisi* n. sp. (FMNH 312486). — *Xylophaga ricei* Harvey, 1996, type locality, 6 ex. (FMNH 312285). — *Xylophaga microchira* Voight, 2007, type locality, 14 ex. (FMNH 308173 and 308174). — *Xylophaga anselli* Harvey, 1996, type locality, 2 ex. (FMNH 312286).

TYPE LOCALITY. — Cape Verde Abyssal Plain, 21°03.81'N, 31°12.21'W, 4626 m (Fig. 1).

DISTRIBUTION. — Only known from the type locality. Wood block fixed to the benthic MAC 4, at least 50 cm above the bottom; deployed 17/02/1991, recovered 21/09/1991.

ETYMOLOGY. — The species is named in honour of Alexis Khripounoff for his accomplishments in the study of particulate flux and organism supply in numerous deep-sea fields.

DIAGNOSIS. — Shell small (< 2.5 mm), delicate; posterior adductor scar composed of linear elements. Siphon incomplete; no cirri on either siphonal opening. Incurrent siphon 1.1 to 3.5 times shell length. Mesoplax shape changes from an erect sheet to an anteriorly directed shallow triangle without strong vertical extensions with growth.

DESCRIPTION

Shells exceedingly fragile, either due to long storage in formalin or to the great depth at which they were collected; almost always crumple when dried. Posterior adductor scar, as seen through intact shell, made of short, linear elements that appear to extend from near ventral shell edge to posterior-dorsal edge. Slight posterior extension (Fig. 2A). Prodissoconch II 412 µm across, with regular growth lines (Fig. 3). Pronounced fold between posterior adductor scar and umbonal-ventral sulcus. Umbonal-ventral sulcus weak, shell slightly flattened at condyle. Posterior ridge broadly inflated, shell narrows dramatically just posterior to the inflation (Fig. 2A). Umbonal reflection well developed, in larger individuals, supports the mesoplax. Gape between the right and left beaks notably broad. Beak with comparatively few toothed ridges parallel ventral margin. Ridges form narrow band at junction of beak and shell.

Mesoplax in small specimens, erect, comparatively thin, translucent, nearly invisible in dorsal view (Fig. 2C), becoming more anteriorly directed and calcified with growth; in larger specimens, forms a fairly broad triangle (Fig. 2B); with only minimal rounded vertical extensions.

Siphons, incomplete; excurrent siphon truncated (Fig. 2A). Excurrent opening a very small flap without detectable cirri, even in larger individuals (Fig. 4). Very faint impressions of longitudinal walls detectable immediately distal to excurrent opening visible in limited number of specimens (Fig. 4B). Incurrent siphon long, 2.5 to 3.5 times shell length (Fig. 2A), opening lacks cirri (Figs 2A; 5). Growth of excurrent and incurrent siphons isometric relative to each other.

No small individuals found attached to larger ones.

Measurements of holotype

Shell length 2.3 mm; width 2.5 mm; height 2.5 mm. Incurrent siphon length 6.3 mm; excurrent siphon length 2.5 mm.

REMARKS

Based on the specimens examined, all over 1.2 mm in length, the present species is unique in having an incomplete siphon with no cirri on either siphonal opening and having a linear rather than herringbone pattern to the posterior adductor scar. Table 1 compares this species to those previously named that are overtly similar. *Xylophaga alexisi* n. sp. is separable from *X. ricei*

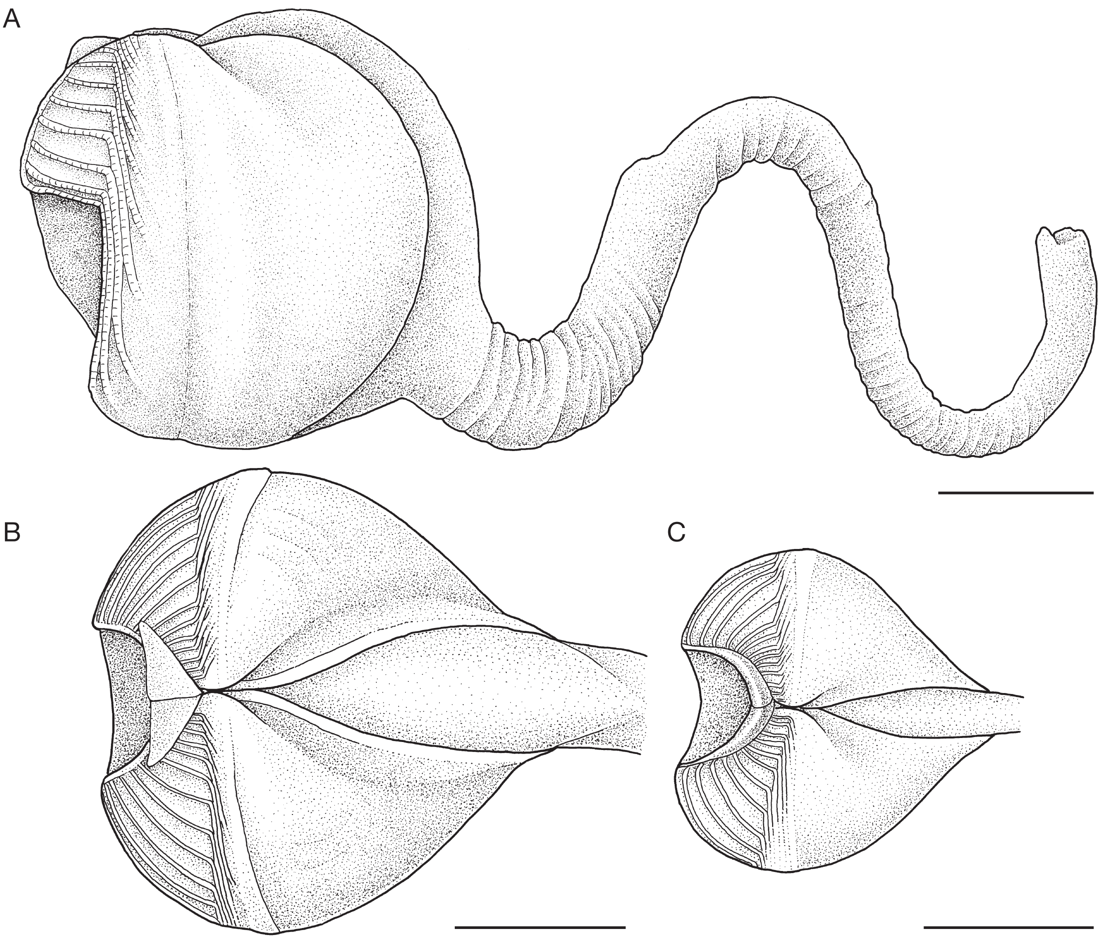

Fig. 2. — **A**, lateral view of an intact specimen of *Xylophaga alexisi* n. sp.; **B**, dorsal view of intact, larger specimen of *X. alexisi* n. sp. (note anteriorly directed mesoplax); **C**, dorsal view of smaller specimen of *X. alexisi* n. sp., mesoplax in erect stage, not readily seen from dorsal view. Scale bars: 1 mm.

from 31°N, 20°W, *c*. 5000 m depth (Fig. 1) by the subterminal excurrent siphon in that species and the incomplete siphon in the present species. *Xylophaga ricei* is similar to *X. pacifica* Voight, 2009, but lacks brooded young. The incomplete siphon of *X. alexisi* n. sp. separates it from *X. anselli* Harvey, 1996 with a complete siphon (Figure 6 illustrates the difference between these character states); the latter species appears similar to *X. heterosiphon* Voight, 2007. Its incomplete siphon also distinguishes it from *X. atlantica* Richards, 1942; this species, reported on the Mid-Atlantic Ridge (Gaudron *et al*. 2010), has an excurrent siphon only slightly shorter than the incurrent. The linear elements in the posterior adductor scar distinguish this species from *X. oregona* Voight, 2007, *X. washingtona* Bartsch, 1921 and other species in Turner's (2002) group 5.

The incomplete siphon of the present species (Fig. 6) could be argued to ally it with species in Turner's groups 5 or 6; Turner understood this character to be unique to these two groups. The present species, however, appears to be more closely allied with the enigmatic *X. microchira* Voight, 2007, a

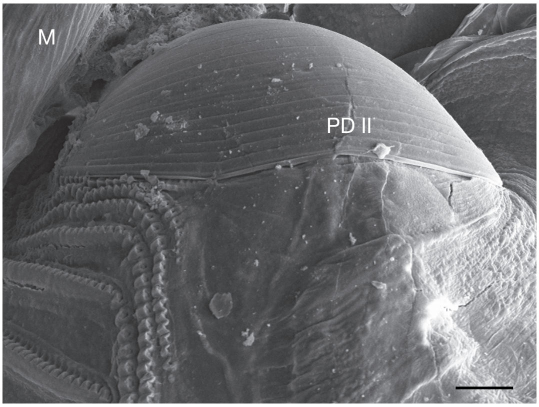

Fig. 3. — SEM image of the umbo region of a specimen of *Xylophaga alexisi* n. sp.: **M**, mesoplax; **PD II**, prodissoconch II. Inferior to the edge of the prodissoconch, note the shell records the growth series during which it developed the characteristic wood-boring shape. Also note the ventral elaboration and ventral reflection of the toothed ridges on the dorsal beak. Scale bar: 50 µm.

member of the off-shore northeast Pacific fauna (Voight 2009). Both species share an incomplete siphon, a mesoplax that develops an anterior fold with growth and an excurrent siphon that grows isometrically relative to the incurrent siphon; the relationship between the siphon lengths in the present species is y = 1.0 x-0.99; $r^2 = 0.92$, essentially parallel to that of *X. microchira*, reported by Voight (2007). The presence of conspicuous cirri at the excurrent opening in *X. microchira*, shown by Reft & Voight (2009), and the smaller cirri at the incurrent siphon readily separate the species. The present species is distinct from *X. galatheae* Knudsen, 1961 by its shell shape, less pronounced umbonal-ventral sulcus and lack of a pronounced posterior extension. Although specimens of *X. alexisi* n. sp. were examined by SEM, no apparent sensory structures such as those reported by Reft & Voight (2009) were found.

Habitat notes

As noted in the Introduction, the type locality is on a nutrient-limited abyssal plain with a fauna depauperate in both diversity and density. No major surface currents overlie the site. The bottom temperature is 2.4°C and its current speed is 3.3 cm/sec. Details of the site are reported by Auffret *et al.* (1992), Vangriesheim *et al.* (1993), Khripounoff *et al.* (1998) and Galéron *et al.* (2000).

Settlement and Growth

The wood, after 216 days at 4626 m depth, carries an estimated 170 boreholes/cm^2. Borers reached such high densities that the wood is transparent between adjacent, non-overlapping boreholes. Young bivalves appear to still have been recruiting to the block of wood, as very small, nearly circular individuals were seen on the block's surface.

Shell lengths of *X. alexisi* n. sp. are up to 2.4 mm; siphons lengths are up to 8.3 mm. The growth rate of the largest specimen extracted would have been 0.011 mm per day, or 0.33 mm per month, assuming it settled on the first day the wood was available at depth.

DISCUSSION

Rapid and dense colonization by *Xylophaga alexisi* n. sp. of a single small piece of wood in an oligotrophic area, well away from any source of terrestrial vegetation, demonstrates that wood-dependent species thrive on the abyssal plain. The 57 named species of *Xylophaga* (those listed by Voight 2008 plus *X. rhyabtshikovi* Kudinova-Pasternak, 1975) are known almost exclusively from near continents or other land masses. Of the 12 species known from greater than 3000 m depth (Voight 2008), six were collected from trenches, where the ocean floor is subducted under a continental landmass, and four were collected from near land masses. One (*X. zierenbergi* Voight, 2007) is known only from an experimental deployment, as is the other species from an abyssal plain, *X. ricei* Harvey, 1996. *Xylophaga ricei* is known from fairly near the Canary Islands (Fig. 1), in the area impacted by the Canary Current. Specimens identified as the species *X. atlantica* have been reported at low densities from an experimental deployment on the Rainbow vent field (Fig. 1) on the Mid-Atlantic Rise (Gaudron *et al.* 2010). Wood-boring bivalve density was just over 50% that reported in a substrate deployed for two weeks in the eastern Mediterranean. Focused on animals endemic to deep-sea reducing habitats, the study made no special comment on the presence of wood-boring bivalves in the middle of the ocean.

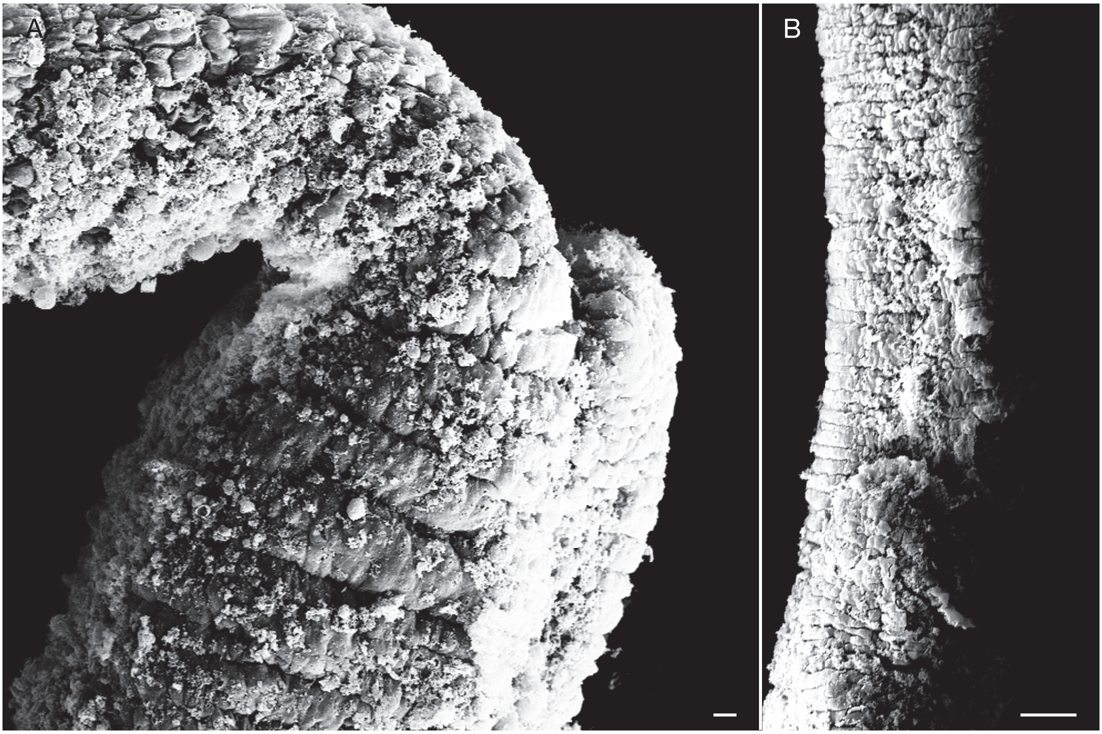

Fig. 4. — Excurrent siphonal opening of *Xylophaga alexisi* n. sp., SEM: **A**, lateral view; **B**, dorsal view. Scale bars: A, 10 µm; B, 100 µm.

It is very unlikely that sunken wood occurs at the Oligotroph locality naturally. The site is isolated by over 1600 km from the continent of Africa (Fig. 1); as the closest African land mass is Saharan, it yields only minimal terrestrial vegetation. No established surface currents overlie the site, therefore delivery of vegetation is considered to be rare. Bottom current speeds at this site are 3.3 cm/sec with little variation (Khripounoff *et al.* 1998). Although one cannot refute the hypothesis that the 18 box corers, two multiple corers and four beam trawls conducted in the immediate area between January 1991 and June 1992 (Galéron *et al.* 2000) failed to locate an existing source population of *X. alexisi* n. sp., we hypothesize that the planktonic young of the species can disperse over long distances, and perhaps survive long periods in the plankton. Species in the diverse genus *Xylophaga* are shown here to range beyond the seafloor impacted by the continent to encompass the largest benthic habitat on Earth, the abyssal plain.

Our estimated growth and colonization rates for *X. alexisi* n. sp. appear to be comparable to those documented in a handful of other species. *Xylophaga ricei* offers the best comparison. Harvey (1996) reported over 400 specimens of the species had colonized two strips of wood (35 by 12 mm and 40 by 15 mm) that had been attached to a camera frame deployed to near 5000 m depth for 627 days. As we do, Harvey (1996) assumed that the largest specimen of *X. ricei*, 6.3 mm, settled on the first day the wood was available at the bottom and grew 0.315 mm per month (0.0105 mm per day), comparing well with our estimated growth rate of *X. alexisi* n. sp. of 0.33 mm per month (0.011 mm per day) at 4626 m depth. *Xylophaga ricei* was collected at the margin of the Canary Current which could carry and deposit terrestrial vegetation.

Three other studies estimated growth in xylophagains from shallower depths. Turner (1973) described a wood panel (36 × 16 × 2 cm) that carried

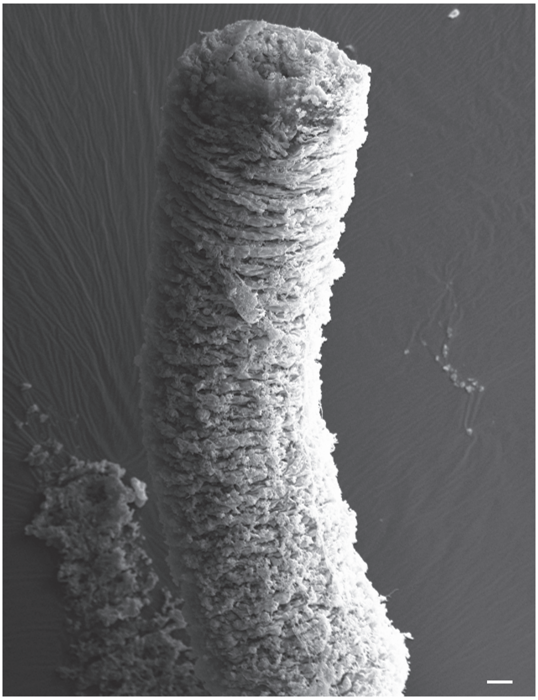

Fig. 5. — Incurrent siphonal opening of *Xylophaga alexisi* n. sp., SEM. Note absence of cirri. Scale bar: 30 µm.

a mean of 150 boreholes/cm^2 made by two Xylophagainae species after 104 days at 1830 m depth at 39°46'N, 70°41'W, a locality impacted by the Gulf Stream. The present wood panel carries about 170 boreholes/ cm^2 after 216 days at 4626 m depth. A shell dimension of 2 mm can be estimated from a photo in Turner (1973), suggesting a maximum shell length increase of 0.019 mm per day, comparable with Romey *et al.*'s (1994) estimate of 0.012 mm/day over six months in *Xylophaga atlantica* in 100 m depth in temperatures of 5 to 14°C. In contrast to these growth rates, Tyler *et al.* (2007) estimated a comparatively rapid six month growth rate of 0.060 mm/day in *X. depalmai* Turner, 2002 at about 500 m depth. We suggest that these different growth rates may be due to crowding. In each of the studies that report growth rates of about 0.01 mm/day (Turner 1973; Romey *et al.* 1994; Harvey 1996 and the present study), xylophagains occupy the wood so completely that the wood is crumbling. Romey *et al.* (1994) were the first to note that crowding clearly "stunted" individuals of *Xylophaga*, slowing growth and resulting small maximum sizes. Each of the species in these studies may have much higher potential growth than has been observed.

Voight (2009) reported that in the northeast Pacific, wood-boring bivalves formed two nearly discrete sets. Eleven species of wood-boring bivalves known from within 1.5° longitude of North America constituted the inshore set, and had almost no overlap with the seven off-shore species known from comparable depths at least 2.3° longitude from the continent. If eastern Atlantic xylophagains partition the seafloor in the same way, *X. alexisi* n. sp. and *X. ricei* form part of the off-shore wood-boring fauna. These animals would be specialized to locate vegetation that sank after a long journal from the continent; once located, the species would exploit the resources the vegetation contains completely. Off-shore and inshore habitats must differ dramatically in the predictability of wood falls. This difference may result in resident xylophagains relying on distinct life history strategies, a selective pressure that could speed speciation. Additional collections from the eastern Atlantic and other areas are required to test this hypothesis.

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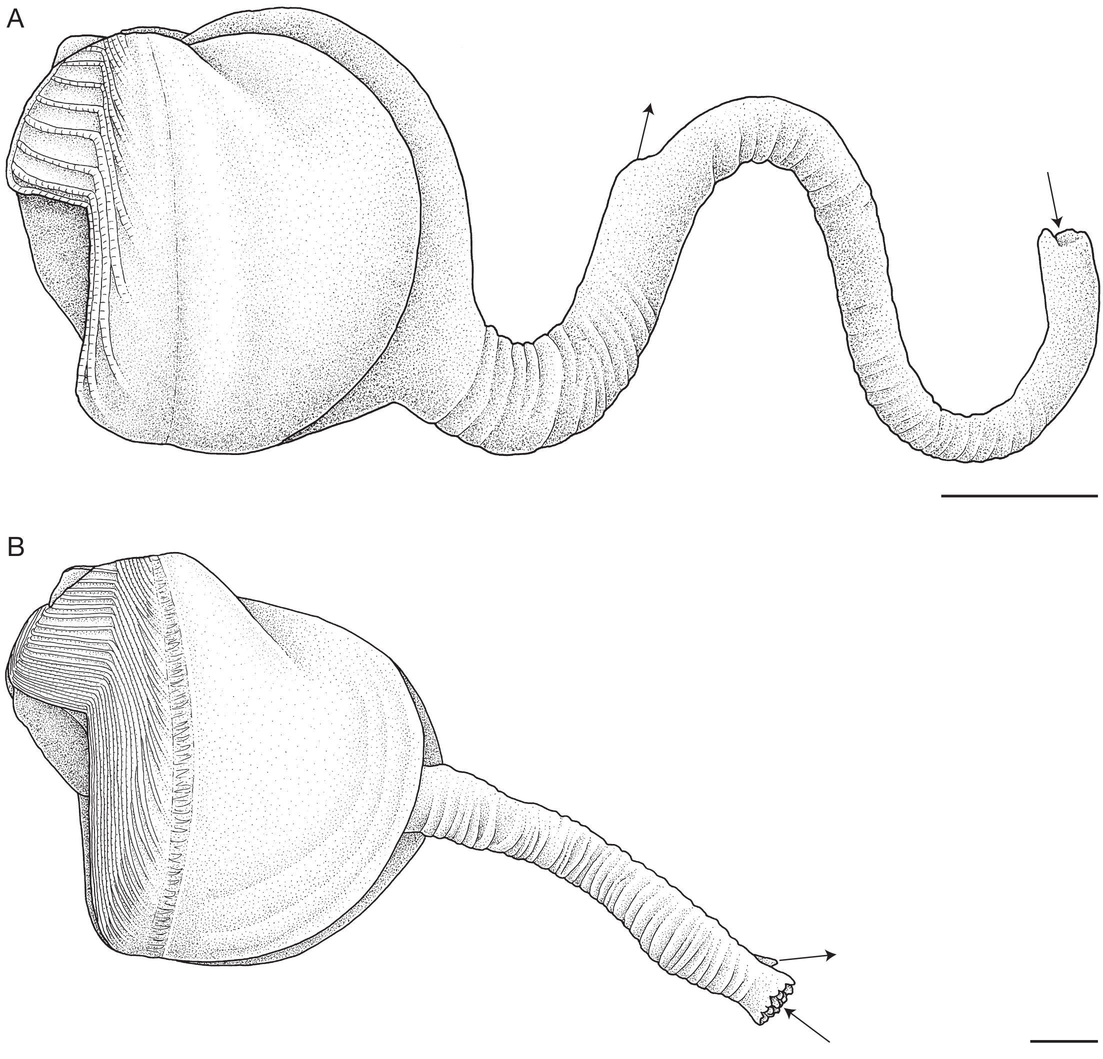

Fig. 6. — **A**, *Xylophaga alexisi* n. sp., lateral view to define "incomplete siphon" in which the excurrent siphon is considerably shorter than the incurrent siphon; **B**, *Xylophaga pacifica* Voight, 2009, lateral view to define "complete siphon", in which both siphonal openings are roughly equal in length. Scale bars: 1 mm.

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