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Life in wood: preliminary phylogeny of deep-sea wood-boring bivalves (Xylophagaidae), with descriptions of three new genera and one new species

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ABSTRACT

Xylophagaid bivalves link terrestrial and deep-sea ecosystems by making energy and nutrients from sunken wood available to other animals. They bore into what can be sulphide-rich wood with their valves and digest it using bacterial enzymes. The evolutionary history of the roughly 60 named xylophagaid species remains largely unknown. We sequenced 18S and 28S rDNA genes of 59 specimens from the northeastern Pacific, southwestern Pacific off New Zealand and the Atlantic Ocean. We analysed these together with data from GenBank (thus increasing the species represented by sequences from 7 to 22) using maximum likelihood and Bayesian inference to reconstruct the group's phylogeny. Newly discovered taxa are: *Spiniapex gilsonorum* n. gen., n. sp.; *Feaya* n. gen. (for *Xylopholas dostwous*) and *Abditoconus* n. gen. (for *X. heterosiphon*, *X. anselli* and *X. brava* that share a two-parted siphon and a periostracal cone). Specimens of *Xyloredo* from New Zealand, Brazil, the Gulf of Mexico and California USA are a single species. The genus *Xylopholas* is not unequivocally monophyletic; the presence/absence of a faecal mass in the distal intestine is the most conspicuous difference between the species included. The mesoplax (paired calcified plates over the anterior adductor) evolved convergently in two distinct clades assigned to the genus *Xylophaga*, which is not monophyletic. All clades represented by at least four taxa occur in every geographic area included. Rather than evolving to exploit sulphide associated with wood falls, xylophagaids may have evolved protection from it. This is indicated by the fact that in four clades, a thick periostracum covers the siphons that extend through the wood, while packed faecal pellets surround the siphons in one subclade, perhaps providing a physical barrier. In only one clade are fleshy siphons exposed to the wood.

INTRODUCTION

Deep-sea wood falls are increasingly the focus of research, as they can form sulphide-based chemosynthetic habitats (Bernardino *et al.*, 2010; Bienhold *et al.*, 2013; Fagervold *et al.*, 2014; Kalenitchenko *et al.*, 2016). Although they have served as stepping-stones for lineages that have entered sulphide-dominated habitats such as cold seeps and hydrothermal vents (Distel *et al.*, 2017), they also harbour unique taxa, notably xylophagaid bivalves. These animals use toothed ridges on their anterior valves to scrape and bore into wood that has fallen to the seafloor; the bivalves ingest the scrapings and digest them with the help of enzymes from endosymbiotic bacteria (Distel & Roberts, 1997). Because most animals are unable to digest wood, the ability of these bivalves and their bacteria to convert the wood's energy to a readily available form links terrestrial and marine ecosystems from the intertidal zone to depths of 7,250 m (Knudsen, 1961).

Despite the ecological uniformity of xylophagaids, characteristics of their valves and siphons combine to distinguish three genera: *Xylophaga* Turton, 1822, *Xyloredo* Turner, 1972a and *Xylopholas* Turner, 1972b. Valve morphology (Fig. 1) is as unusual as is their feeding mode. The anterior incision separates the beaks medially, allowing them to rotate anteriorly. Ventral to the incision, the large pedal gape exposes the circular foot that attaches to the wood by suction (reviewed by Voight, 2015). Contraction of the posterior adductor muscle powers the cutting stroke during which the toothed ridges scrape the wood. The number of toothed ridges on the anterior part of the valves (or beaks), although often reported in taxonomic accounts, appears to vary with size and degree of stenomorphy (Clapp, 1925; Turner, 2002). The anterior

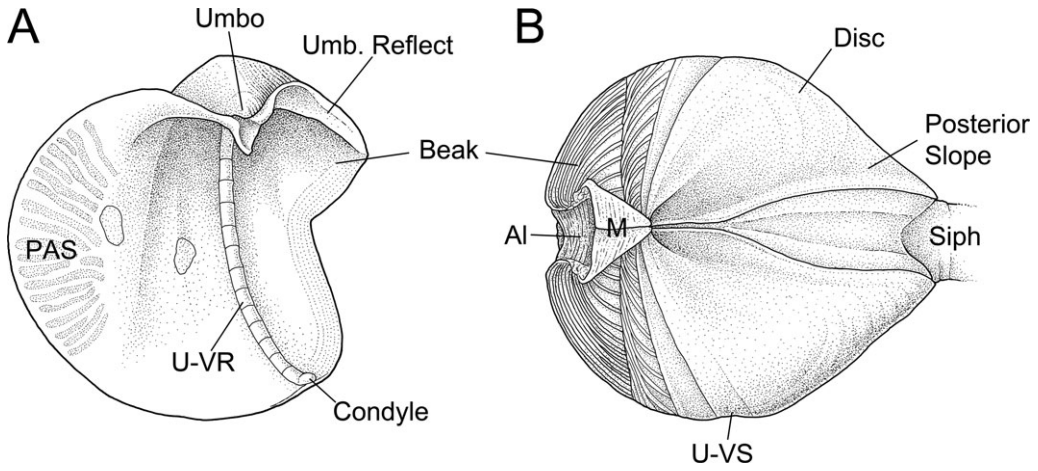

Figure 1. Schematic of lateral view of generic xylophagaid shell. **A.** Inner valve. PAS, posterior adductor scar; Umb. Reflect, umbonal reflection; U-VR, umbonal–ventral ridge. **B.** Outer valve. AI, anterior incision; M, mesoplax; Siph, siphon; U-VS, umbonal-ventral sulcus. In the living animal, the foot would extend through the pedal gape ventral to the anterior incision.

adductor muscles lie under the mesoplax, a pair of calcareous plates (Turner, 2002); in the only known large specimens of *Xylopholas* there is instead a fleshy cover, termed the 'anterior adductor cover' by Voight (2016). Dorsal views of the mesoplax and anterior adductor covers (Fig. 2) are usually given in taxonomic accounts, together with descriptions of the valves, regardless of within-species variation in valve shape (Romano *et al.*, 2014). In fact, characters of the siphons (the muscular tubes that carry water in and out of the valves) may be more important in taxonomy than are those of the valves, as they are in teredinids (Turner, 1966; Borges *et al.*, 2012). The siphons may be of equal or nearly equal length, or 'incomplete' with the excurrent siphon considerably shorter than the incurrent. Their surface may be fleshy (Fig. 3F) or covered in periostracum (Fig. 3A, B, E, G); if the latter, the siphons may open inside structures apparently made of periostracum (Fig. 3A, E, G). Some taxa can fully withdraw their siphons into their valves; others seem to be unable to do so.

Do siphonal characters moderate the high concentrations of sulphide (Yücel *et al.*, 2013; Kalenitchenko *et al.*, 2016, 2018a, b) the animals are exposed to inside the wood? The boreholes of teredinids, the sister taxon of xylophagaids according to a molecular phylogeny (Distel *et al.*, 2011), have a calcareous lining that extends from the valve to the wood–water interface (Turner, 1966). This isolates the woodborer's siphons which, in teredinids, also contain gills and some viscera, from contact with the wood. Among xylophagaids, calcareous linings that could limit sulphide exposure exist only in the genus *Xyloredo*, where they are restricted to the distal borehole. *Xylophaga dorsalis* (Turton, 1819), type species of the genus and with 56 available names (Voight, 2008, 2009; Voight & Segonzac, 2012; Romano *et al.*, 2014), is among the species that line their boreholes with faecal pellets bound together with mucus to form a conspicuous faecal 'chimney' (Purchon, 1941). Yücel *et al.* (2013) suggested that, by increasing the surface area between the wood and seawater, the pellets increase the movement of the potent oxidizers, oxygen and nitrate, into the wood. Other mechanisms that might minimize sulphide absorption by the siphons include a periostracal sheath over the siphons which, in species of *Xylopholas*, carries terminal periostracal plates (Fig. 3A), and a periostracal 'cone' over the siphons, known in a handful of species of *Xylophaga* (Fig. 3B). In most other species, however, the fleshy siphon would be predicted to absorb sulphide readily.

An unusual characteristic of some members of the family is the attachment of miniature, non-boring individuals to autonomously boring ones. These miniature bivalves had been interpreted as brooded young (e.g. Knudsen, 1961), but were recently shown in two species to be dwarf males (Ockelmann & Dinesen, 2011; Haga & Kase, 2013); we consider all such miniatures to be dwarf males.

Phylogenetic studies of the family remain in the early stages. That of Distel *et al.* (2011) strongly supported the teredinids and xylophagaids as sister taxa, based on 18S and 28S ribosomal DNA (rDNA) gene sequences. However, only five xylophagaid species were included; of those, only two were identified to species. Few xylophagaid specimens are available for molecular analyses due to the difficulty and expense of collecting deep-sea animals and to the frequent use of formalin as a preservative. In addition, preservation for molecular work is enhanced if the borers are extracted from the wood before preservation, which can be a difficult and time-consuming process. The use of experimental deployments of wood (e.g. Turner, 1978) has eliminated the problems of unpredictable distribution of wood falls, greatly simplifying research into xylophagaids and wood-fall communities.

Here, we examine the current systematic hypotheses of xylophagaid evolutionary relationships by testing the monophyly of the three named genera. In addition, we assess the taxonomic placement of several species yet to be described, begin to examine the distribution of clades and species in the world oceans and describe the distribution of siphonal protection among taxa.

MATERIAL AND METHODS

Material

We analysed specimens (Supplementary Material Table S1) from the Field Museum of Natural History, Chicago, IL (FMNH), the Museum of Comparative Zoology at Harvard University, Cambridge, MA (MCZ) and the Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington; in addition, material from deployments in the southwestern Atlantic Ocean (Barroso *et al.*, 2018) was included, but without vouchers. Most FMNH specimens had been recovered from experimental deployments (Voight, 2007; Judge & Barry, 2016) and were preserved in 90–95% ethanol. Specimens of *Xylophaga washingtona* from a wild wood fall were preserved in 95% ethanol. The MCZ specimens, collected in 1978 and 1980, were labelled "90% EtOH" without additional preservation information. Material in NMNZ was derived from wild wood falls trawled from off New Zealand and frozen *in situ*; specimens were later removed and preserved in 98%

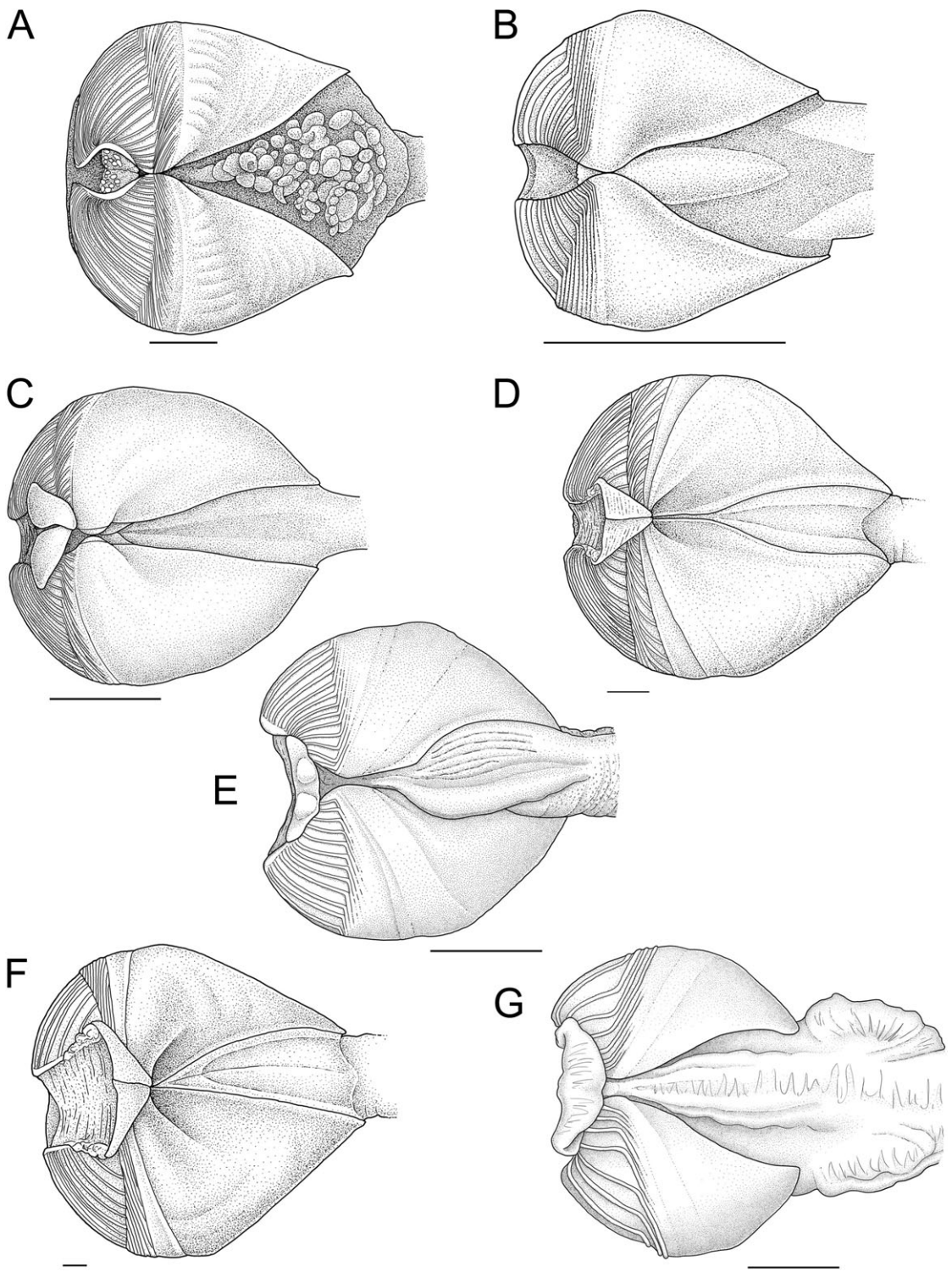

Figure 2. Dorsal views of the mesoplax or anterior adductor cover of seven species in five of the six xylophagaid clades discovered here. **A.** Clade 1 *Xylopholas scrippsorum* from Voight (2009), illustrating the retained faecal mass as in *Xylopholas* sp. NZ. **B.** Clade 3 *Abditoconus heterosiphon* n. comb. from Voight (2007). **C.** Clade 1 *Xylophaga multichela* from Voight (2008) representing the *Xylophaga dorsalis* clade. **D.** Clade 1 *Xylophaga oregona* from Voight (2007). **E.** Clade 2 holotype of *Spiniapex gilsonorum* n. gen., n. sp. **F.** Clade 6 *Xylophaga zierenbergi* from Voight (2007). **G.** Clade 4 *Feaya dostwous* n. gen. from Voight (2016). Scale bars = 1.0 mm.

ethanol. Collection depths ranged from 18 to 4,000 m and collection dates between 1978 and 2014 (Supplementary Material Table S1).

Using a sterile scalpel, tissue samples for DNA extraction and sequencing were removed preferentially from the siphon, although the ventral mantle, posterior adductor muscle and foot also contributed tissue. In total, 59 individuals representing 16 purported species (Supplementary Material Table S1) were successfully sequenced; 12 species were represented by between two and thirteen individuals, the others by a singleton. This research discovered new taxa that are named here; we use these names throughout.

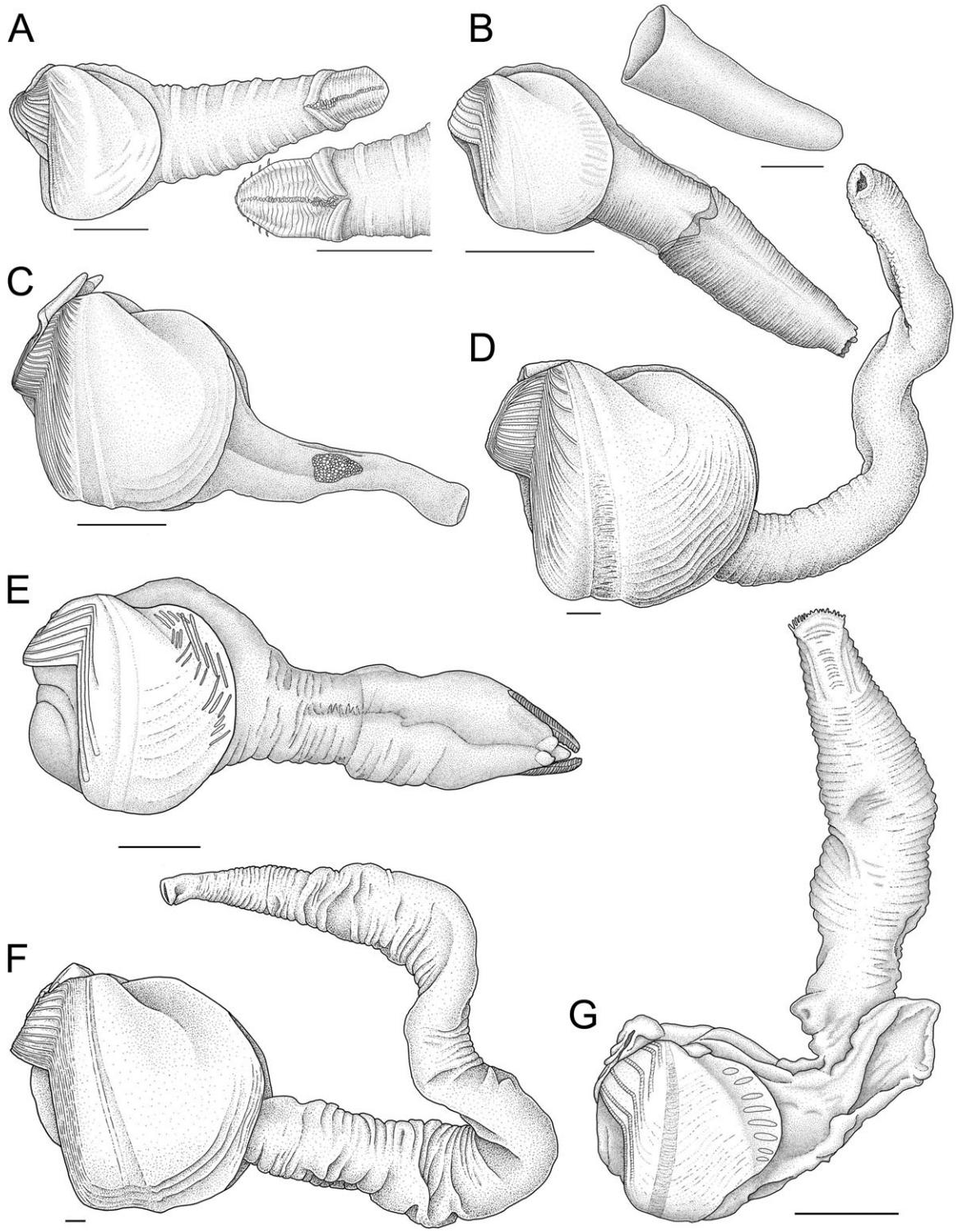

Figure 3. Lateral views of seven species from five of the six xylophagaid clades discovered here. **A.** Clade 1 *Xylopholas crooki* from Voight (2007) with its siphonal plate. **B.** Clade 3 *Abditoconus heterosiphon* n. comb. from Voight (2007) with an isolated siphonal cone. **C.** Clade 1 *Xylophaga multichela* from Voight (2008) representing the *Xylophaga dorsalis* clade. **D.** Clade 1 *Xylophaga oregona* from Voight (2007). **E.** Clade 2 holotype of *Spiniapex gilsonorum* n. gen., n. sp. **F.** Clade 6 *Xylophaga zierenbergi* from Voight (2007). **G.** Clade 4 *Feaya dostwous* n. gen. from Voight (2016). Scale bars = 1.0 mm.

All measurements were made with electronic callipers and illustrations with a camera lucida. We examined the ovals or barbs at the siphon tips of *Spiniaplex gilsonorum* n. gen. n. sp. with the scanning electron microscope (SEM) at FMNH after removing them from the specimen, air-drying and coating with gold.

Molecular data collection

We sequenced both the large (28S) and small (18S) rDNA genes using two approaches: standard Sanger sequencing and next-generation sequencing. At FMNH, DNA of 40 specimens (Supplementary Material Table S1) was extracted from tissue samples using DNeasy Blood & Tissue Kits (Qiagen, USA). We followed the manufacturer's instructions, except for the following modifications that we found increased DNA yield: (1) 20 µl of 1 M dithiothreitol (DTT) was added to the extraction buffer; (2) cell lysis was extended to 48 h; (3) an additional 20 µl of 20 mg/ml proteinase K was added to cell lysis reaction after 24 h and (4) 5 µg of carrier RNA was added to each sample following cell lysis (Shaw *et al.*, 2009). We amplified both genes using primers developed by Distel *et al.* (2011) when possible. As most of our DNA samples were degraded, we developed internal, overlapping primers (Supplementary Material Table S2) to amplify both genes in *c.* 300 bp sections. Internal sections were amplified and sequenced individually. The amplification protocol for all reactions consisted of an initial denaturing step of 94 °C for 12 min followed by 30–35 cycles of 94 °C for 15 s, 60 °C for 15 s, 72 °C for 60 s and a final extension at 72 °C for 10 min. The final concentration of each 10 µl reaction was 1× PCR gold buffer, 0.2 µM dNTPs, 2.5 mM $MgCl_2$, 0.5 µg/µl BSA, 0.5 µM of each primer and 0.5 units of AmpliTaq gold DNA polymerase (Applied Biosystems, USA). The PCR products were then cleaned using ExoSAP-IT (Affymetrix, USA) and Sanger-sequenced using the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, USA) on an ABI 3730xl DNA analyzer (Applied Biosystems, USA). Sequences were trimmed and aligned using Geneious v. 10.0.9 (Kearse *et al.*, 2012).

At Auburn University (AL), DNA was extracted from a further 19 specimens: four of *Xylophaga oregona*, two of *X. washingtona*, one each of *X. corona*, *X. zierenbergi* and an unnamed species, and five each of *Xyloredo nooi* and a second undescribed species. Only specimens of *Xylophaga washingtona* were from a wild wood fall. The DNA was extracted from siphon tissue using the DNeasy Blood & Tissue Kit (Qiagen, USA), following the manufacturer's protocols. Sequencing of genomic DNA was performed by the Genomic Services Laboratory at the Hudson Alpha Institute (Huntsville, AL) on an Illumina HiSeq 2500 platform (San Diego, CA) using PE 125 bp or PE 150 bp paired-end v4 chemistry. Paired-end reads were assembled *de novo* using IDBA-UD (Peng *et al.*, 2012) with default settings. Contigs of interest were identified using Blastn (Altschul *et al.*, 1997) with sequences from Distel *et al.* (2011) serving as bait against the assembled genomic data, followed by manual annotation of gene boundaries.

Phylogenetic reconstruction

We combined our DNA sequences (GenBank acc. nos. MK 142554–MK 142671) with sequences from GenBank that represented an additional 18 individuals of 12 taxa (Supplementary Material Table S3), including four teredinids as outgroup taxa following the phylogeny of Distel *et al.* (2011). Only specimens represented by sequences of both marker genes (18S and 28S rDNA) were included in our analysis. Sequences of both markers were individually aligned using the programme MUSCLE (Edgar, 2004) implemented in MEGA v. 7.0.20 (Kumar, Stecher & Tamura, 2016) with default parameters. Poorly aligned regions were eliminated in each matrix using the Gblocks online server (Castresana, 2000), with relaxed settings for DNA allowing 'smaller final blocks', 'gap positions within the final blocks' and 'less strict flanking positions'. Both matrices were concatenated into a final sequence matrix that consisted of 77 specimens in 26 taxa, and 3004 positions, in Sequence Matrix v. 1.8 (Vaidya, Lohman & Meier, 2011) and made available under TreeBase project 22928. Phylogenetic relationships were inferred using maximum likelihood (ML) and Bayesian inference (BI). The ML trees were estimated with the program RAxML v. 8.0.20 (Stamatakis, 2014) implementing the 'GTRGAMMA' model. Nodal support was evaluated by 100 iterations of the fast bootstrapping option (Stamatakis, Hoover & Rougemont, 2008). Exploratory ML analysis of each individual marker resulted in highly similar topologies (not shown). BI was performed using MrBayes v. 3.2.6 (Ronquist & Huelsenbeck, 2003) using the GTR + G model. Trees from two parallel runs with four chains were sampled every 100 from 1,000,000 generations. The first 25% of all sampled trees was discarded as burn-in. The ML tree was drawn with the MEGA v. 7.0.20 tree explorer and BI posterior probabilities manually added to common nodes of the ML and BI trees. Preliminary analyses showed that *X._atlantica*_isolate_26 from GenBank (KJ946317.1 and KJ946342.1) exhibited strikingly odd behaviour in contrast to the other five individuals of that taxon from GenBank. We inferred a possible mislabelling of its 28S sequence and so deleted it and re-ran the analyses.

RESULTS

Both ML and BI approaches returned identical results; six major clades were recovered, all supported by ML bootstrap (BS) values of at least 70% (except Clade 2 with 62% BS support) and BI posterior probability (PP) of 0.99 (Fig. 4). Relationships among the clades were not resolved. The tree revealed an outlier within *Xylophaga zierenbergi*, likely due to its having considerably more indels than did conspecific specimens. Our phylogenetic reconstruction recovered all included species and the genus *Xyloredo* as monophyletic; however, *Xylopholas* was not unequivocally monophyletic. Although basal relationships were generally not resolved, the two OTUs representing the genus *Xylopholas* were basal to the clade containing the species of *Xylophaga* with incomplete siphons (i.e. *X. dorsalis*, *X. washingtona* and *X. oregona*). This strongly supported relationship precludes monophyly of *Xylophaga*.

To begin to resolve the problem of the paraphyly of *Xylophaga*, we opt to erect new genus-level names for three of the six clades (below). We purposely decline to assign a new genus name to Clade 6 (Fig. 4), although it appears to be required, because greater taxonomic sampling should help to resolve that group more completely and determine if it is a single clade.

SYSTEMATIC DESCRIPTIONS

Superfamily PHOLADOIDEA Lamarck, 1809

Family XYLOPHAGAIDAE Purchon, 1941

Spiniapex new genus Voight, 2019

Type species: Spiniapex gilsonorum n. sp.

Etymology: From Latin, *spini-* referring to spine, and *-apex* to tip, in reference to the spiny oval or barb at the siphon tip; gender masculine.

ZooBank registration: urn:lsid:zoobank.org:act:47EF1981-641F-4BB4-A4E6-E64A99B7E4FA

Diagnosis: Short, dark periostracal ovals superficially embedded in external dorsal and ventral siphon tips; inner oval transversely ridged. Siphons long; proximal and distal parts differ in texture, meeting at straight seam. Mesoplax periostracal when small; at larger sizes separate, paired calcareous pieces meet medially.

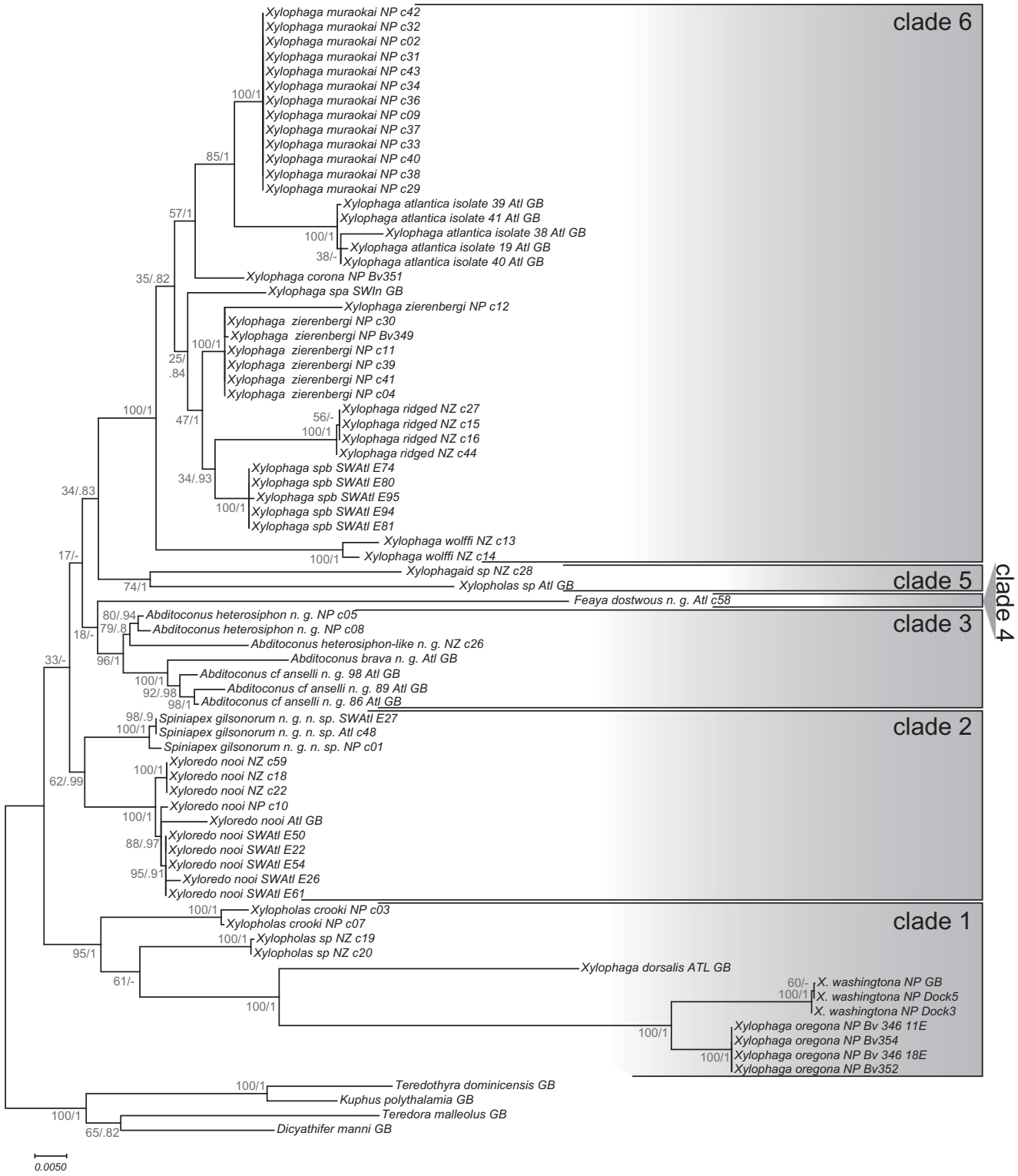

Figure 4. Maximum-likelihood and Bayesian phylogenetic analysis of 18S and 28S rDNA sequences of the Xylophagaidae. Numbers at the nodes of the tree are bootstrap values over posterior probabilities. The unit of branch length is substitution per site. Geographic areas: Atl, North Atlantic, including Gulf of Mexico and Caribbean Sea; NP, North Pacific; NZ, New Zealand; SWIn, Indian Ocean off South Africa; SWAtl, Santos or Espirito Santo Basin, Brazil. Individuals sequenced at FMNH indicated by c; *Xylophaga washingtona* and individuals indicated by E and Bv sequenced at Auburn University; GB indicates GenBank sequences.

Spiniapex gilsonorum **new species Voight, 2019**
(Figs 2E, 3E, 5A, B, 6A, B)

Xyloredo sp. nov. Judge, 2015: 71. Judge & Barry, 2016: 3036.

Types: Holotype FMNH 386321 (shell 2.6 mm height H × 2.9 mm length L; length of oval at siphon tip 1.2 mm) and two paratypes (including remnant of DNA specimen FMNH 386322: shell 3.3 mm H × 2.9 mm L; oval length 1.1 mm) from spicebush wood

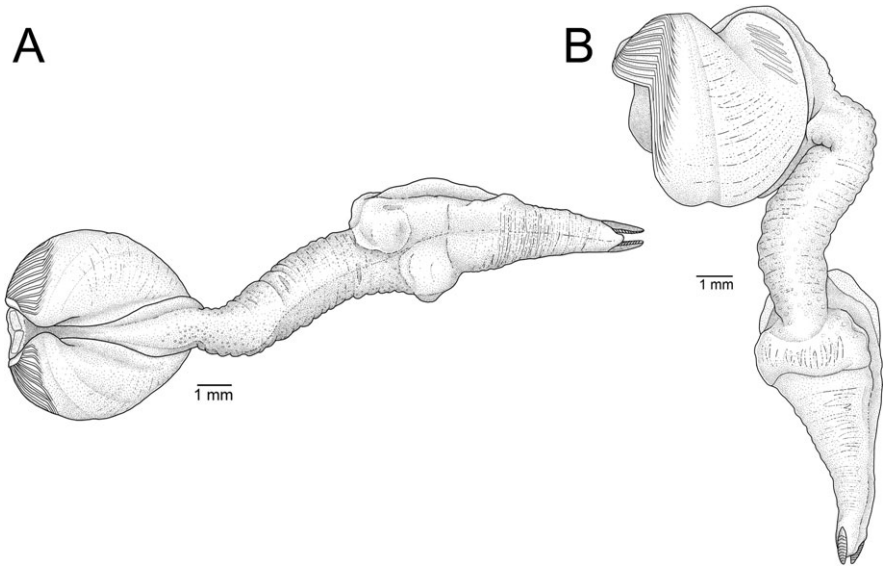

Figure 5. *Spiniapex gilsonorum* n. gen. n. sp. from Caribbean Sea (MCZ M.381893). **A.** Dorsal view. **B.** Lateral view. Scale bars = 1.0 mm.

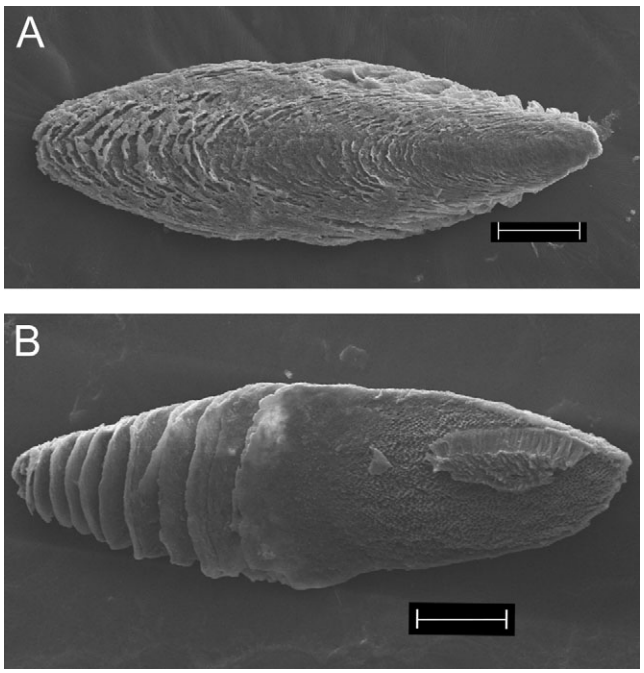

Figure 6. *Spiniapex gilsonorum* n. gen. n. sp. **A.** SEM photo of outer oval or barb from siphon tip; proximal to the left. **B.** SEM of inner surface of oval from siphon tip; proximal to the right.

deployed on sediment near Monterey Canyon ('Deadwood 2' site; 36°15.677′N, 122°40.679′W, 3,100 m depth) by ROV 19–20 Oct., 2011 recovered 25 Oct., 2013; details in Judge (2015).
Five paratypes MCZ M.381893 (size range: shell 3.4–6 mm H × 3.3–5.8 mm L, oval length 0.7–0.8 mm) from Caribbean Sea, north of St Croix, 17° 57.5′N 64° 48.5′W, 4,000 m depth. One paratype MCZ M.381874 with detached cone (shell 5.8 mm H × 6.5 mm L, oval length 0.9 mm), original label "P-4" (see Supplementary Material Table S4 for locality). Paratypes 24 dry valves MCZ M.381868.

ZooBank registration: urn:lsid:zoobank.org:act:29FFFEFF-E31B-4652-9396-65596F2B24DF

Etymology: Named in honour of the Gilsons, Dr Warren Gilson who with son Bob invented and perfected Gilson Pipetman, and daughter Mary Gilson Feay, supporter of FMNH science; gender masculine.

Material examined: Supplementary Material Table S4.

Diagnosis: See characters of genus.

Description: Shell: tall, fairly fragile; posterior edge reflected laterally (Fig. 2E); beak projecting at small sizes. Umbonal reflection rather square. Slightly swollen posterior to narrow umbonal–ventral sulcus. Inner shell: umbonal–ventral ridge moderate, slightly flattened; most ventral section suddenly enlarged beginning at odd angle; continuous with undifferentiated condyle. Deep groove ('shelf' *sensu* Haga & Kase, 2008) between posterior slope and disk fades ventrally. Posterior adductor scar large, complex, variable; typically 3–5 linear elements consistently ventral to round, well-marked pedal retractor scar. Additional shorter linear elements may lie at 90° to longer ones at posterior shell edge. Linear elements may continue dorsally at an acute angle, or overlapping scars may give leopard-spot appearance.

Mesoplax: anterior to umbos (Fig. 5A); when small, primarily soft tissue; paired calcified shapes (broad triangles, rectangles, comma-shapes) often, but not always, present. With growth, spots become triangular, abutting medially without ventral extensions.

Siphons: complete, openings with cirri; long, never retracted into valves (Fig. 3E). Proximal and distal parts usually differentiated. Typically yellow, bumpy, translucent periostracum present proximally; distally more muscular, ringed texture becomes more pronounced toward tip, perhaps due to preservation (Fig. 5A, B). These parts meet at straight seam of variable definition (see below). Siphon sometimes appears inflated, either partially or completely (Fig. 5A, B).

Ovals: paired, dark brown to yellowish brown, 0.5–1.2 mm long, lanceolate. Superficially embedded, dorsal and ventral to siphon openings; parallel to siphon (Fig. 3E). Outside generally smooth; curved lines seen under magnification (Fig. 6A); inside with 'steps' or transverse ridges (Fig. 6B). Present in smallest available specimen (shell L 1.3 mm); no clear relationship with shell or siphon lengths.

Periostracum: long, smooth, transparent, yellowish periostracal cones associated with some specimens, rare *in situ*. Cone appears

to originate at mid-siphon seam. Preserved cone soft, even billowy proximally, increasing in rigidity and darker in colour distally. Two opposing, small U-shaped gaps or slits in distal cone roughly correspond to ovals.

Intestine: sometimes terminates in broadly oval, flat glandular structure with smooth outer surface.

Distribution: North Pacific Ocean: Deadwood 2 site, off Monterey Canyon, 36° 15.677′N, 122° 40.679′W, 3,100 m depth; near Northern Escanaba Trough, Gorda Ridge 41° 00′N, 127° 29′W, 3,305 m depth, wild wood fall recovered by ALVIN Dive 2034, R. A. Zierenberg pers. comm. (MCZ M.381895). South Atlantic Ocean: Santos Basin, 28° 01.706′S, 43° 31.780′W, 3,358 m depth. Caribbean Sea: DOS 3 (*sensu* Turner, 1978), 17° 57.01′N 64° 48.01′W, 3,995 m depth, from a wild wood fall (1978) and 2 year-old deployments (ALVIN Dive 1082) (Supplementary Material Table S4). Known only from below 3,100 m depth. The species was recovered only from wood of *Calycanthus occidentalis* (spicebush) and *Lyonothamnus floribundus* (Catalina ironwood) near Monterey (Judge & Barry, 2016); wood types in other collections unknown.

Remarks: Ovals superficially embedded at dorsal and ventral siphon tips are unique in the family; they may be continuous with the periostracal cone over the siphons. The cone readily disassociates from the animal and, once removed, can easily be overlooked, but cones were recovered with Caribbean and South Atlantic specimens.

Variation in the posterior adductor scar, and presumably in the muscle itself, is unusual in the family, but the molecular data indicate that differences are minor. The two-parted posterior adductor scar, reflected shell, the long siphon with two parts that meet at a straight line and molecular evidence (Fig. 4) all ally this genus with *Xyloredo*. Regardless of these shared characters, *Xyloredo*, diagnosed by a calcareous borehole lining, cannot accommodate this taxon. The mesoplaxes of the two genera differ in that the calcareous pieces in those of *Xyloredo* are long longitudinally and narrow, whereas those of *Spiniapex* n. gen. are wide rather than long. The present genus is distinguished from species in *Xylopholas* by the presence of lanceolate ovals rather than flat plates at the siphon tips. In addition, the ovals are positioned dorsal-ventrally rather than laterally as are the plates in *Xylopholas*.

The siphon and mantle cavity of specimen MCZ M.381863 and paratype MCZ M.381874 carry numerous and fairly large parasites; what may be their eggs are present inside the siphon. The parasites may be polychaetes of Oenonidae such as *Pholadiphila turnerae*, described from a specimen of *Xyloredo* collected at 38° 17.5′N 69° 35.2′W, at 3,602 m depth (Dean, 1992).

Abditoconus **new genus Voight, 2019**

Type species: *Xylophaga heterosiphon* Voight, 2007.

Etymology: Latin, *abditus*, hidden, concealed, + *conus*, cone; in reference to the difficulties in finding the cone *in situ*; gender masculine.

ZooBank registration: urn:lsid:zoobank.org:act:D7C2A700-8A14-4458-9772-8CAA60F37ED7

Diagnosis: Siphons differentiated into proximal and distal parts; gold periostracum over proximal siphons stops near midpoint, meeting much more muscular distal siphon at scalloped line; incurrent and excurrent siphons open terminally inside single ring of cirri. Simple, thick, readily detached cone covers siphons *in situ*; easily lost. Mesoplax poorly calcified. Shell fragile.

Referred species: *X. heterosiphon*; *X. anselli* Harvey, 1996; *X. brava* Romano, Pérez-Portela & Martin, 2014.

Distribution: North Pacific and Atlantic Oceans. Depth range: 900 m for *A. brava* (Romano *et al.*, 2014) to 2,750 m for *A. heterosiphon* (Voight, 2007).

Remarks: Morphological characters and 18S and 28S sequences support monophyly of the genus (Figs 3, 4). Dwarf males are unknown.

Feaya **new genus Voight, 2019**

Type species: Xylopholas dostwous Voight, 2016.

Etymology: Named in honour of Bruce and Mary Gilson Feay who as generous long-time backers of FMNH science, provided essential support to the senior author and to this study in particular; gender masculine.

ZooBank registration: urn:lsid:zoobank.org:act:10FFC760-C63D-499C-97CA-7E1F3C9BEAA2

Diagnosis: Ventral shell margin uneven; gills and viscera extend slightly into proximal siphon. Periostracum loosely covers proximal siphon, terminating in poorly defined plate without collar over siphonal openings. Mesoplax may be all muscular; calcification uncertain.

Distribution: Known only from type locality of single included species, northwestern Atlantic Ocean, 38° 18.4′ N 69° 35.6′W; 3,506 m depth.

Remarks: The type species was originally attributed to *Xylopholas* by Voight (2016), based on the siphons' periostracal cover and siphonal plates, despite the latter being comparatively poorly defined (Figs 2G, 3G); molecular data demonstrate this was in error. Dwarf males are unknown in the genus.

DISCUSSION

Our results lead us to focus on reconciling the tree that results from our phylogenetic analysis (Fig. 4) with taxonomic understanding. Here, we consider the 22 species of Xylophagaidae included to fall into six genera (*Xylophaga*, *Xylopholas*, *Xyloredo*, *Abditoconus* n. gen., *Spiniapex* n. gen. and *Feaya* n. gen.) and two additional, as yet unnamed taxa (Clades 5 and 6). Below, we discuss each clade in reference to morphology and taxonomy, except for Clade 5, which had very limited taxon sampling. We also consider the presence of dwarf males in the clades in which they are known. We address biogeographic patterns of the clades and, finally, the distribution of potential protection from high sulphide concentrations.

Morphological characters of the clades

Unique shared morphological characters support the monophyly of each clade, except Clade 1. Clade 1 contains *Xylophaga dorsalis* (type species of *Xylophaga*), *X. oregona* and *X. washingtona* and two species assigned to *Xylopholas* (Fig. 4). In the three Clade 1 species of *Xylophaga* a faecal chimney develops around the siphons inside their borehole; Haga (2013: fig. 4) also showed a large faecal chimney around the siphon of a specimen of *Xylopholas*. The three Clade 1 species of *Xylophaga* share a truncated excurrent siphon, a periostracum restricted to the basal and lateral siphon, and a furrow on the dorsal incurrent siphon distal to the excurrent opening. The sister taxa *X. washingtona* and *X. oregona* share a simple triangular mesoplax of two calcareous plates (Fig. 2D), each with a vertical extension, and a posterior adductor scar with herringbone markings. Combined, these species range in depth from 18 to over

2,200 m (Voight, 2007). Not included in the analysis were *Xylophaga praestans*, *X. rikuzenica*, *X. aurita*, *X. turnerae*, *X. siebenalleri*, *X. nidarosiensis* and *X. pacifica*. Because they share these features, they likely are members of the *X. washingtona–oregona* clade, following Turner (2002). Combined, these species are known from the tropical and North Pacific Ocean and from the North Atlantic Ocean.

GenBank sequences of *X. dorsalis* in this analysis are also hypothesized to represent a larger clade. It is united by a somewhat ear-shaped mesoplax with two layers and posterior coiling made of two calcified plates (e.g. *X. multichela* Fig. 2C), a periostracum of variable conspicuousness that contains white or glass-like spots on the lateral incurrent siphon (Fig. 3C) and a fringe or lateral lobes—interpreted as sensory in nature (Reft & Voight, 2009)—distal to the excurrent opening on the dorsal incurrent siphon. Turner (2002) cited these characters as uniting *X. globosa*, *X. indica*, *X. mexicana*, *X. japonica*, *X. guineensis*, *X. bayeri*, *X. depalmai* and *X. tipperi* with *X. dorsalis; X. multichela* is also likely a member of the clade. This hypothesized clade shares an unusually shallow-water distribution for the family, typically above 380 m with only exceptional records to 2,500 m depth (Voight, 2008) and is known from the Pacific, Atlantic and Indian Oceans.

The trichotomy the above species of *Xylophaga* form with the two assigned to *Xylopholas* is startling. (This analysis found that *Xylopholas dostwous* was misplaced in the genus; see Clade 4, below.) The characters that unite *Xylopholas*—terminal siphonal plates, thick periostracum tightly adhering to the siphon, and a minimally calcified mesoplax (Figs 2A, 3A)—are present in both *Xylopholas* species included and absent from the other species in Clade 1. The intestine of the unnamed species of *Xylopholas* included is dilated between the posterior dorsal valves and holds abundant faecal pellets, as does that of *X. scrippsorum* (Fig. 2A).

The tree topology motivated re-examination of the type series of *Xylopholas crooki* (FMNH 308182, FMNH 308679), the single lot of large specimens of that species (FMNH 328003) and the type series of *Xylopholas scrippsorum* (FMNH 312303, FMNH 306660, FMNH 312304). The intestine of *X. crooki* lacks the dilation.

In Clade 1, dwarf males attach to the ventral mantle and/or siphon of the autonomously boring individuals (Turner, 1972b; Romano *et al.*, 2014; Voight, 2008, 2009, 2016). The two species of *Xylopholas* included are from the Pacific off New Zealand and Washington State, USA (Supplementary Material Table S1); the type species, *Xylopholas altenai*, occurs on both sides of the tropical Atlantic (Turner, 1972b) from 41 (Berg *et al.*, 1987) to 2,550 m depth.

Clade 2 contains two morphologically distinct species that both have extraordinarily large geographic ranges with minimal within-species genetic divergence (Fig. 4). The first corresponds to the genus *Xyloredo*. We use the species name *nooi* (type species of *Xyloredo*) here, pending further study. As noted above, it is the only xylophagaid with a calcareous lining of the distal borehole; this lining is ridged and abuts the proximal periostracal sheath over the siphon. Members of the genus also share a straight, well-defined seam where the two parts of the fleshy siphon meet and a mesoplax made of two elongate calcareous strips embedded in transparent tissue. Haga & Kase (2008) illustrated *Xyloredo teramachii* in excellent detail. It and the other named species of *Xyloredo*, *X. ingolfia* and *X. nacelli*, should be considered members of this clade, but their status needs confirmation.

Spiniapex gilsonorum n. gen., n. sp., defined by distinct ovals embedded at the dorsal and ventral siphon tips (Fig. 3E), is the other species in Clade 2. Specimens from off Monterey, CA, off Brazil and the Caribbean Sea were all collected at or below 3,100 m depth (Supplementary Material Table S1).

Despite the low BS value of 62% (Fig. 4), both the PP of 0.99 and morphological characters unite the above species as members of Clade 2. These characters include the subtle lateral reflection of the valves' posterior disc; a posterior adductor scar with two separate, distinct types of marks; a shelf between the posterior slope and disc; a siphon with two parts that meet at a straight seam (which can be subtle in *Spiniapex gilsonorum* n. gen., n. sp.); a mesoplax primarily of soft tissue (Fig. 2E) and their very large areal ranges. Dwarf males are unknown.

Clade 3 contains the morphologically uniform group formally recognized here as *Abditoconus* n. gen (Figs 2B, 3B). It includes *A. heterosiphon* from the northeastern Pacific, an unnamed species from off New Zealand, *A. anselli* and *A. brava* from the eastern Atlantic and Mediterranean Sea, respectively. The species share a detachable cone over the siphons, a small fleshy mesoplax and two-part siphon in which the parts meet at a scalloped edge. Dwarf males are unknown.

Clade 4 is monotypic, containing only '*Xylopholas*' *dostwous* (Figs 2G, 3G), here assigned to the new genus *Feaya*. Superficially similar to *Xylopholas*, but with the gills and viscera extending into the base of the incurrent siphon, the taxon is known only from its type locality in the North Atlantic (Voight, 2016). Dwarf males had been unknown, but appear to be present, loosely associated, in two specimens preserved *in situ* (MCZ M.381884, M.381885); two miniatures attach to the dorsal siphons about midway between the valve and the siphon tips.

Clade 5 contains two taxa, actually two specimens, which remain poorly understood. The sequenced specimen from off New Zealand is small and had been damaged before tissue of its foot was sampled. The second, represented by sequences from GenBank, was collected in the Gulf of Mexico and had been attributed to *Xylopholas*. Our specimen has an exceptionally large, robust, thick siphon relative to its 3.5 mm shell length, a projecting beak, and 4–5 large cirri around the siphon openings. The mesoplax contains a calcareous rectangle embedded in the periostracum. Orange-yellow staining of its siphon contributes to its unusual appearance. Dwarf males, the presence or extent of any siphonal protection and other aspects of the animal are unknown.

Clade 6 contains 38 individuals assigned to eight species. Three species are unnamed and five have been named in *Xylophaga*. However, *X. dorsalis* (Clade 1) is the type species of the genus, so the genus is currently paraphyletic. Species of Clade 6 share a mesoplax of paired calcareous single-ply plates and equal (or subequal) siphons covered by at most a thin layer of periostracum (Fig. 3F). Although faeces may accumulate in the borehole of these species, the large faecal chimney characteristic of members of Clade 1 does not develop.

Relationships among members of Clade 6 are generally poorly resolved—not unexpected given that only five of an estimated 33 nominal species were included. A sister-taxon relationship was discovered between *X. atlantica* and *X. muraokai* from off the western coast of the US at depths of 1,500 to over 3,100 m. *Xylophaga atlantica* ranges across the North Atlantic from as shallow as 15 m in higher latitudes (Turner, 2002) to abyssal depths (Knudsen, 1961) without genetic divergence, despite considerable variation in mesoplax and shell shape (Romano *et al.*, 2014). These two species share similar subequal siphons and mesoplax that are to some degree variable, a condition also seen in members of Clade 1 (Dons, 1928, 1929; Turner, 2002; Romano *et al.*, 2014).

Additional species that we hypothesize belong to Clade 6 are those sharing fleshy siphons that are equal or subequal and a mesoplax composed from its earliest stages of paired calcareous plates one layer thick. The included species are from off New Zealand and South Africa, and the North Pacific and Atlantic Oceans. Of the 33 species we consider might belong to Clade 6, 17 are known to have dwarf males (data not shown). In 14 of these, the males attach to the dorsal shell, posterior to the umbo. In the three exceptions (*X. concava*, *X. tubulata* and *X. wolffi*), they reportedly attach to the mantle or the ventral siphon (Knudsen, 1961).

Biogeographic patterns

None of the xylophagaid clades with at least two species are endemic to an ocean basin. The four clades with a minimum of seven specimens all have representatives from off New Zealand, the North Pacific and the Atlantic Oceans. The nine North Pacific species are members of four clades. The ten Atlantic species are members of all six clades.

None of the clades is restricted to the Southern Hemisphere. The six New Zealand species included are members of five of the six clades. Of the three species from the southwestern Atlantic off Brazil, *Xyloredo nooi* and *Spiniapex gilsonorum* n. gen., n. sp. have extraordinarily large ranges. Specimens of *Xyloredo* from the Gulf of Mexico (GenBank), the northeastern Pacific off California, the southwestern Atlantic off Brazil and off New Zealand from 540 to 3,100 m depth (Table S1) show only modest genetic divergence, visible in Figure 4 as extremely short branch lengths. The three specimens of *S. gilsonorum* n. gen., n. sp. from off California, Brazil and St Croix at depths at and below 3,100 m, show even less within-species genetic divergence. As Southern Hemisphere species had been very poorly known, we anticipated that their inclusion in the phylogenetic analysis would reveal entirely novel lineages. It did not. Given that xylophagaid survival depends on their locating sunken wood, a resource with an ephemeral existence and a patchy distribution, perhaps a wide geographic distribution is predictable. *Xyloredo nooi* and *Spiniapex gilsonorum* n. gen., n. sp. take this characteristic to extremes, occurring as single species at least from New Zealand to Brazil to California and from California to Brazil to the Caribbean Sea, respectively. Such distributions are not unprecedented in deep-sea animals. Species of foraminifera range well beyond single ocean basins (Pawlowski *et al.*, 2007) and abyssal bivalves, such as *S. gilsonorum* n. gen. n. sp., may show less genetic divergence than do bathyal bivalves (Etter *et al.*, 2005). However, divergence is also limited in the generally bathyal *Xyloredo nooi*. Perhaps the narrow geographic separation of the Mediterranean *Abditoconus brava* and the North Atlantic *A. anselli* (Fig. 4; Romano *et al.*, 2014) should be seen as more enigmatic.

Life in wood

Our analysis of 18S and 28S rDNA sequences from 77 specimens of 22 xylophagaid species (including those from GenBank) found that siphonal coverings are present in most clades, although the homology of the covers remains unknown. These coverings may relate to the sulphide-rich habitat inside wood. Sulphide concentrations inside wood that had been experimentally deployed at 500 m depth reached several hundred μM after 35 days (Yücel *et al.*, 2013). Another study found that hydrogen sulphide reached concentrations as high as 2,000 μM within 45 days of deployment (Kalenitchenko *et al.*, 2018a, b). Both studies attributed subsequent reductions in sulphide levels to xylophagaid activity. Yücel *et al.* (2013) found that an unidentified xylophagaid tolerated sulphide levels comparable to those in low temperature hydrothermal vents (e.g. Urcuyo *et al.*, 2003). Although sulphide concentration declined over time, it remained detectable through the 200-day experiment (Yücel *et al.*, 2013).

Periostracum, which protects against acids (Nakayama *et al.*, 2013), may shield the fleshy siphon from sulphide, and allow the animals to survive in high sulphide areas. The siphons of members of four of our five well known clades are covered in periostracum. Although the siphons of most members of Clade 1 are only partially covered, the faecal chimney produced by these taxa may form a barrier, or facilitate sulphide oxidation (Yücel *et al.*, 2013). Fagervold *et al.* (2012) detected sulphide-oxidizing bacteria only in wood that had been immersed for relatively short periods. If wood generally floats for a long time before sinking (Voight, 2015), deep-sea wood falls may have fairly low sulphide levels; they could then provide a safe habitat for '*Xylophaga*' species of Clade 6 in which the siphon appears to have minimal periostracal covering. Although the faecal chimney may limit movement of sulphide, the surprising relationship between the chimney-building taxa and the faeces-retaining *Xylopholas* species in Clade 1 might indicate that faecal and/or intestinal bacteria play a role in wood digestion, as Betcher *et al.* (2012) suggested in teredinids.

Ornaments at the otherwise vulnerable siphon tips have been suggested to protect from predators (Voight, 2007). In *Xylopholas* (Clade 1) and *Feaya dostwous* n. gen. (Clade 4) periostracal plates cover the siphon tips; spiny ovals project from the siphon tips in *Spiniapex gilsonorum* n. gen., n. sp. (Clade 2) and detachable cones cover the siphons in species of *Abditoconus* n. gen. (Clade 3) and in *S. gilsonorum* n. gen., n. sp. (Clade 2). As Kalenitchenko *et al.* (2018a, b) showed that sulphide also reaches high levels at the wood surface, perhaps they also protect from the chemical environment.

Paired, calcareous mesoplax plates appear to be convergent between Clades 1 and 6. Species without paired calcified plates, at least in specimens of the sizes available, have siphon covers, an inverse correlation not previously recognized.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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