



RESEARCH NOTE

PROGENETIC DWARF MALES IN THE DEEP-SEA WOOD-BORING  
GENUS *XYLOPHAGA* (BIVALVIA: PHOLADOIDEA)

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Sunken plant debris (sunken wood, hereafter) in deep-sea environments harbours an idiosyncratic fauna that is based directly or indirectly on wood decomposition (Turner, 1973, 1978). This resource is ecologically comparable with deep-sea whale-falls, because of its ephemeral nature (Distel *et al.*, 2000). The obligate wood-boring and wood-consuming (xylophagous) bivalve genera *Xylophaga*, *Xylopholas* and *Xyloredo*, all belonging to the family Xylophagaidae (Turner, 2002; we here regard it as an independent family based on unpublished molecular phylogenetic data of TH), occur primarily in the deep sea, extending down to the hadal zone, from polar to tropical regions (Knudsen, 1961; Schiøtte, 2005). They have been recognized as the most important organisms that convert refractory sunken wood into a food source available to other members of the community (Turner, 1973; Distel & Roberts, 1997; Distel, 2003). However, Xylophagaidae remain little studied, as they are difficult to find due to their patchy distribution at great depths. Therefore, many species are known only from the type localities (see Voight, 2007).

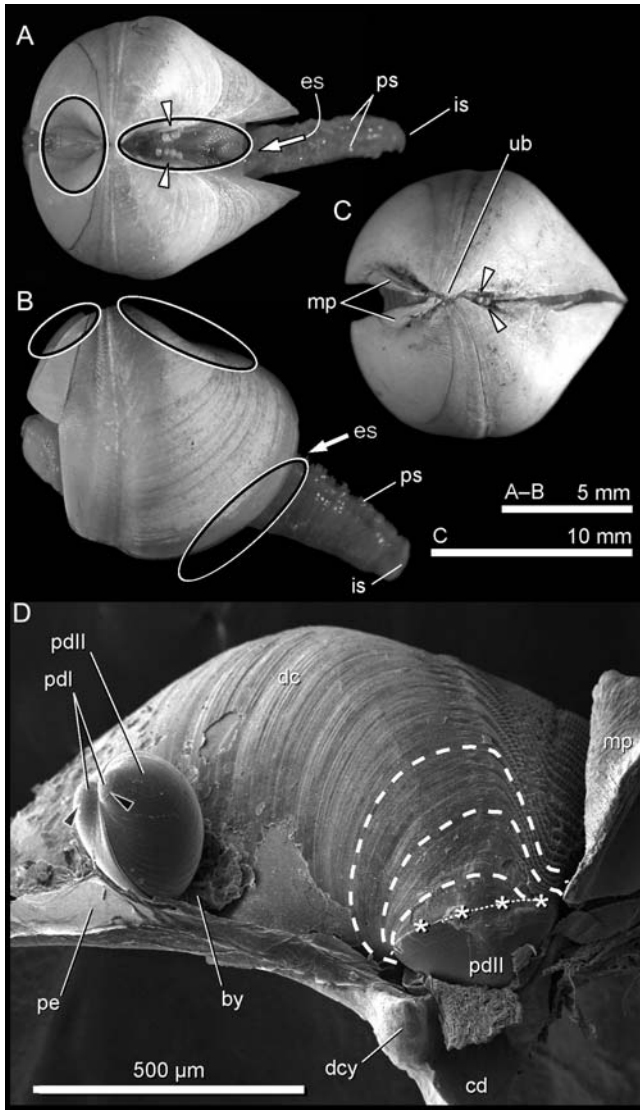
The reproduction of Xylophagaidae is poorly known so far. Purchon (1941) reported protandric hermaphroditism in *Xylophaga dorsalis* (Turton, 1819), but this interpretation was recently corrected by Tyler, Young & Dove (2007) to gonochoristic based on a reanalysis of Purchon's (1941) data. Tyler *et al.* (2007) also showed gonochorism with a fast growth rate and rapid gametogenesis (in addition to very few examples of simultaneous hermaphroditism) in *X. depalmai* Turner, 2002. Purchon (1941) and Culliney & Turner (1976) suggested self-fertilization for *X. dorsalis* and *X. atlantica* Richards, 1942, because both species have paired seminal vesicles (i.e. vesicles in which spermatozoa discharged from the same individual are stored) beneath the pedal retractor in the suprabranchial cavity. Such reproductive patterns have been regarded as a resource adaptation to their deep-sea ephemeral habitats (Purchon, 1941; Culliney & Turner, 1976; Tyler *et al.*, 2007). On the other hand, extended parental care in the form of 'juvenile brooding' has often been suggested based on the occurrence of tiny individuals with pediveliger morphologies that are byssally attached to the shell or the soft parts of large *Xylophaga* individuals (Knudsen, 1961, 1967; Harvey, 1996; Turner, 2002; Voight, 2007, 2008, 2009). However, this proposed developmental mode remained puzzling, because the

absence of pelagic larval development implies a low capacity for dispersal and for finding ephemeral resources in the deep sea (Knudsen, 1961; Scheltema, 1994; Voight, 2009).

An alternative hypothesis concerning the association of tiny individuals with larger conspecifics in many *Xylophaga* species is that, instead of externally-brooded offspring, they represent mating partners in the form of dwarf males. Dwarf males are, in general, tiny individuals (50% or less of the normal body size) that attach to large individuals in gonochoristic organisms. They are believed to have evolved among species whose population size is small and/or in which the female is sedentary or hard to find (e.g. Ghiselin, 1974; Vollrath, 1998).

The goal of our study was critically to test these two hypotheses by performing a detailed ultrastructural and histological study of tiny conspecifics attached to large individuals of *X. supplicata* (Taki & Habe, 1950). This species is found in the Western Pacific from Japan to the Philippines at depths of 200–5050 m (Higo, Callomon & Goto, 1999; Haga, 2011). Adults attain a maximum shell length (SL) >15 mm. *Xylophaga supplicata* can colonize a wide range of submerged wooden substrates, ranging from tree trunks to bamboo branches and even individual mangrove seeds and it exhibits a low population density (T. Haga, unpubl.). Materials examined in this study included the holotype (National Museum of Nature and Science, Tokyo; Mo-39891) in addition to 54 large specimens that had bored into wooden substrates retrieved from waters around Leyte and Bohol, Philippines ( $n = 38$ ) and Espiritu Santo, Vanuatu ( $n = 16$ ). Live animals were carefully removed from the sunken wood by hand, anaesthetized, fixed in 10% seawater-diluted formalin, stored in 70% ethanol, then examined either by freeze-dried scanning electron microscopy (SEM) or by paraffin-embedded serial sectioning.

The tiny conspecifics of *X. supplicata* attach byssally to the surface of the autonomously boring larger conspecifics, either singly or in multiples up to a maximum of 29. There are three areas of attachment: the periostracal extension on the dorsal and ventral side of the posterior slope, and the anterior umbonal area around the mesoplax (Fig. 1; circles). The holotype bears two tiny conspecifics (Fig. 1C); 45 out of the 54 autonomously boring individuals from the West Pacific (83.3%) carried tiny conspecifics. The number of the attached tiny conspecifics increased with host size ( $R = 0.54$ ,  $P < 0.001$ ), suggesting that



**Figure 1.** *Xylophaga supplicata* carrying dwarf males. **A, B.** Specimen with siphon extended. **C.** Holotype (National Museum of Nature and Science, Tokyo, Mo-39891). **D.** SEM micrograph of left umbral area of autonomously boring specimen. Symbols: circles, approximate attachment areas of dwarf males; white arrowheads, dwarf male; white arrow, exhalant siphonal opening; dotted line, postlarval growth lines in dissoconch; black arrowheads, boundary of prodissoconch I/prodissoconch II; asterisks, boundary of prodissoconch II/dissoconch. Abbreviations: by, byssus; cd, chondrophore; dc, dissoconch; dcy, dorsal condyle; es, exhalant siphon; is, inhalant siphon; mp, mesoplax; pdI, prodissoconch I; pdII, prodissoconch II; pe, periostracum; ps, papillae at inhalant siphon; ub, umbo.

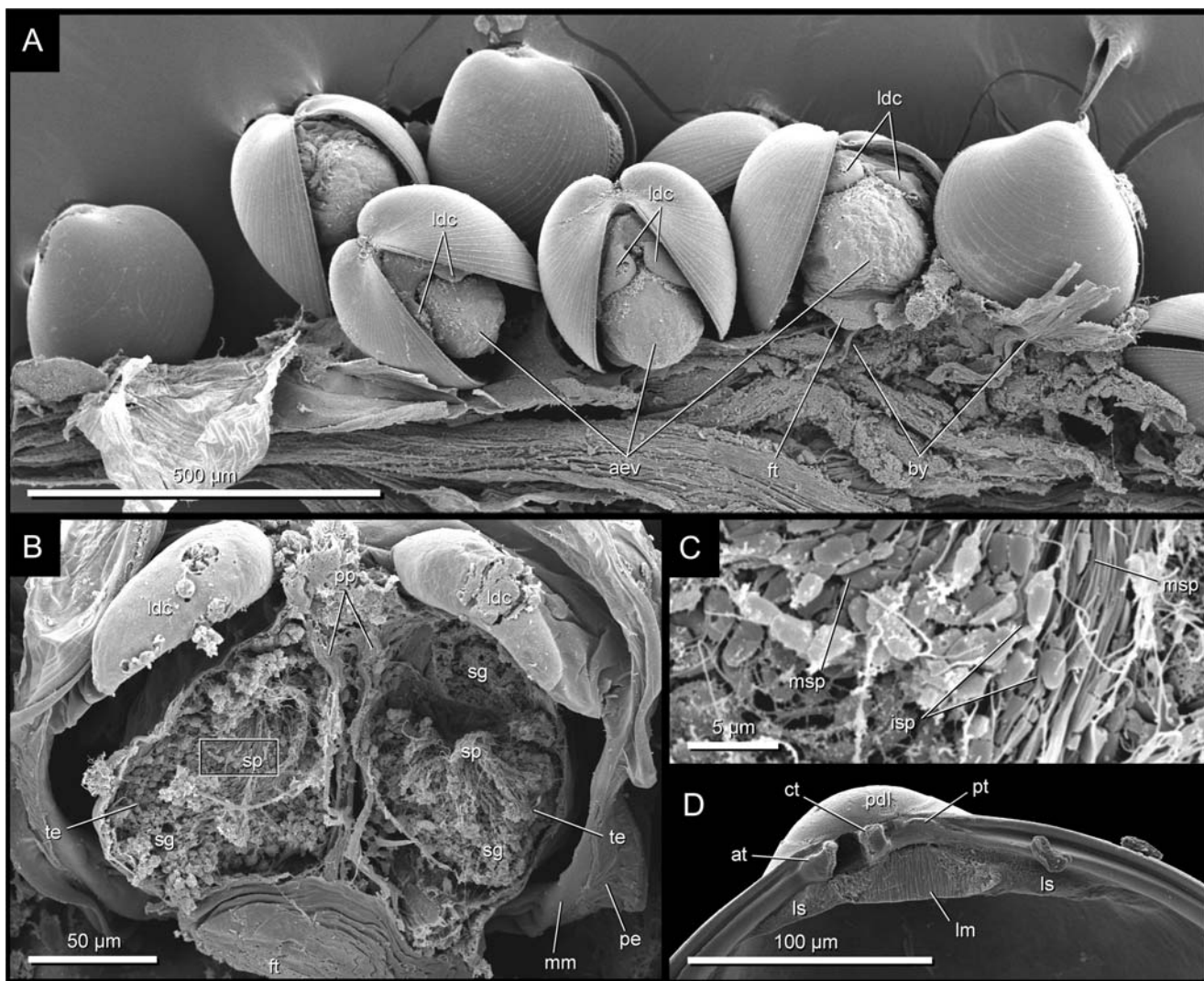
the tiny conspecifics tend to settle on the larger individual when the latter reaches *c.* 2.15 mm in SL, estimated from a regression line ( $y = 1.246x - 2.674$ ,  $R^2 = 0.29$ ,  $P < 0.001$ ).

The tiny conspecifics exhibit paedomorphy; for example, the valve is composed only of an externally oblong prodissoconch, in contrast to that of the autonomously boring larger conspecifics which develop a *Teredo*-like valve immediately upon settlement (Fig. 1D; dotted lines). The valve of the tiny conspecifics consists of a finely punctate prodissoconch I (*c.* 40  $\mu\text{m}$  in length) and an almost smooth, slightly inequivalve prodissoconch II (average SL of larger right valve 309.5  $\mu\text{m}$ ; range = 299.8–320.0  $\mu\text{m}$ , SD =  $\pm 5.57$ ,  $n = 39$ ) (Figs 1D and 2A).

The valve is clearly marked by regular growth lines (Figs 1D and 2A) and is identical with the prodissoconch of the larger conspecifics (Fig. 1D). The small size of prodissoconch I and the significant size difference between prodissoconch I and II suggest a planktotrophic larval development for a long period in the water column, when applying the empirical prodissoconch measurement criteria established by Jablonski & Lutz (1983). Based on these criteria, brooded bivalves are proposed to have a large prodissoconch I in which SL exceeds 230  $\mu\text{m}$ . Hence, prodissoconch morphologies in the tiny conspecifics are inconsistent with the ‘juvenile brooding’ hypothesis. The external features and hinge system of the tiny conspecifics match Culliney & Turner’s (1976) description of *X. atlantica* pediveligers, except for the presence of a prominent ligament on the central part of a ligament shelf (Fig. 2D). Development of the ligament proves that metamorphosis has been completed, as found in other pholadoidean species (e.g. Tan *et al.*, 1993; Ito, 1998). The soft parts of the tiny conspecifics are also comparable with newly metamorphosed juveniles of *X. atlantica*, for example in the short fused siphon, functional digestive tracts, a foot with a byssal gland, and the absence of the velum, mesoplax and wood-storing caecum in the stomach (Culliney & Turner, 1976). However, the presence of a pair of lobes on the anterodorsal area into which the digestive caecum projects (Fig. 2A, B; ldc) appears unique to the tiny conspecifics (Fig. 2A, B). In addition, the anterior expansion of the visceral mass above the foot in the tiny conspecifics (Fig. 2A: aev) is a distinctive feature easily recognized under a binocular microscope. Full-grown tiny conspecifics cannot close the valves due to the increase of visceral volume, and probably cannot crawl away actively, and may even be immobile, when alive (Fig. 2A). Testes that are divided laterally by the pedal protractors are present in the anterior expansion of the visceral mass (Fig. 2B). The mature spermatozoon comprises a conical head *c.* 2.2  $\mu\text{m}$  in length, a midpiece *c.* 1.1  $\mu\text{m}$  in length and a long tail (msp in Fig. 2C). The sperm morphology is characterized by having a relatively long midpiece and is referable to the type found in Teredinidae (Popham, 1974; Yakovlev, Drozdov & Ferraguti, 1998).

From these observations, we can conclude that the tiny conspecifics are not juveniles, but progenetic dwarf males, ruling out the previously proposed ‘juvenile brooding’ hypothesis. Male dwarfism of this kind, achieved in newly metamorphosed juveniles, is rare in the Bivalvia, and very few examples are known, for example the montacutid *Peregrinamor ohshimai* commensal with a mantis shrimp (Lützen *et al.*, 2001).

To examine whether *X. supplicata* exhibits sex change, we performed paraffin-embedded sectioning of six autonomously boring specimens ranging in size from 1.1 to 14.9 mm in SL, with or without dwarf males attached. The sections revealed a protandric transition from male to female: the smallest specimen (SL 1.1 mm, no dwarf males) lacked gonadal development; a 3.6-mm SL specimen lacked dwarf males and had immature testes, but a 3.7-mm SL specimen carrying a dwarf male had mature spermatozoa in its testis (Fig. 3A); a 5.7-mm SL specimen carrying five dwarf males was an hermaphrodite with vitellogenic oocytes, *c.* 31  $\mu\text{m}$  in diameter, and mature spermatozoa (Fig. 3B); two female specimens of SL 3.7 and 11.9 mm carrying 8 and 26 dwarf males, respectively, had ovarian tissue only. Neither seminal vesicles nor embryos in the branchial cavities, believed to be evidence of self fertilization (Purchon, 1941), were identified in any of the sectioned individuals. These observations indicate that autonomously boring *X. supplicata* are protandrous, first developing as a male and changing into a female, via a temporary simultaneous hermaphroditic stage, as it becomes a host for complemental (when host is hermaphrodite) and dwarf (when host is female) males (Fig. 4A).



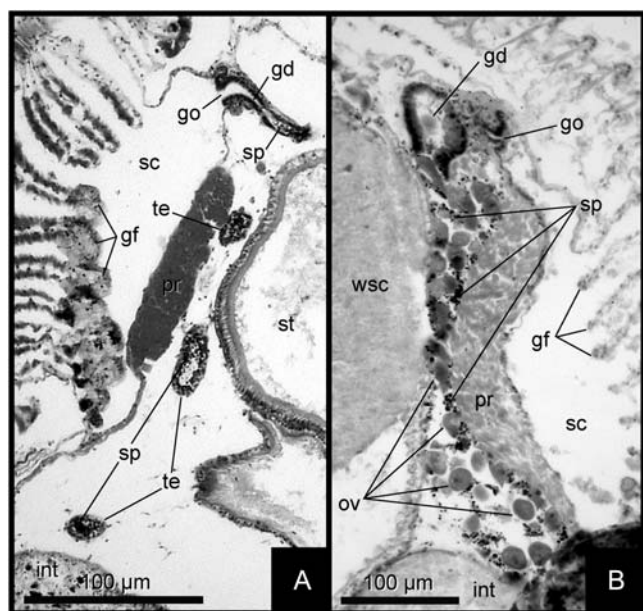
**Figure 2.** Dwarf male of *Xylophaga supplicata*, SEM micrographs. **A.** Dwarf males *in situ* on host's periostracum at posterior slope; freeze-dried material. **B.** Anterior view of mature dwarf male showing testes, shell and anterior portion of visceral mass partially removed; freeze-dried material. **C.** Spermatozoa, magnified from a boxed region in **B**; freeze-dried material. **D.** Right hinge region of mature dwarf male showing ligament. Abbreviations: aev, anterior extension of visceral mass; at, anterior tooth; by, byssus; ct, central tooth; ft, foot; isp, immature spermatozoon; ldc, lobe of digestive caecum; lm, ligament; ls, ligament shelf; mm, mantle margin; msp, mature spermatozoon; pdI, prodissoconch I; pe, periostracum; pp, pedal protractor; pt, posterior tooth; sg, spermatogonium; sp, spermatozoon; te, testis.

It is an intriguing question whether dwarf males can grow into autonomously boring animals. Although our observations do not give an unequivocal answer, they show that autonomously boring males mature at a considerably larger size than do dwarf males. It is therefore unlikely that dwarf males develop into autonomous animals.

How might the ova of *X. supplicata* become fertilized? We suggest that the morphology of the siphon of the host individual, together with the settled position of the dwarf male(s), play an important role in fertilization. Turner (2002: 226) noted that the siphon morphology of *X. supplicata* is "... nearly the same length and usually with small cirri on both openings" but such an arrangement is observed only in small individuals. Large, autonomously boring *X. supplicata* possess an unusually short exhalant siphon and a long, contractile inhalant siphon bearing tentacular papillae on the dorsolateral margins (Fig. 1A, B). The dorsum of the inhalant siphon thus resembles a gutter. Shortening of the exhalant siphon occurs, most probably synchronized with the settlement of dwarf males. The

considerable size difference between the two siphons is probably related to the way fertilization takes place. Moreover, the immature dwarf males attach anywhere on the host shell surface, whereas the mature dwarf males are only present at the dorsal margin of the posterior slope and most mature dwarf males are aligned with their siphons turned towards the dorsum of the host (Figs 1A, D, 2A). Because *X. supplicata* can achieve complete siphonal retraction as well as complete valve closure at the posterior margin during the autonomously boring stage (Fig. 1C), it seems reasonable to assume that the dorsal margin of the posterior slope is the only place where mature dwarf males can settle without being obstructed by the continuous boring locomotion of the host. Also, the discharged ova from the exhalant siphon of the host can therefore be externally fertilized by the dwarf males positioned adjacent to the siphon.

Such a siphonal arrangement and the presence of 'juveniles' at the dorsal margin of the posterior slope are known in eight species of *Xylophaga* (Knudsen, 1961; Harvey, 1996; Turner,

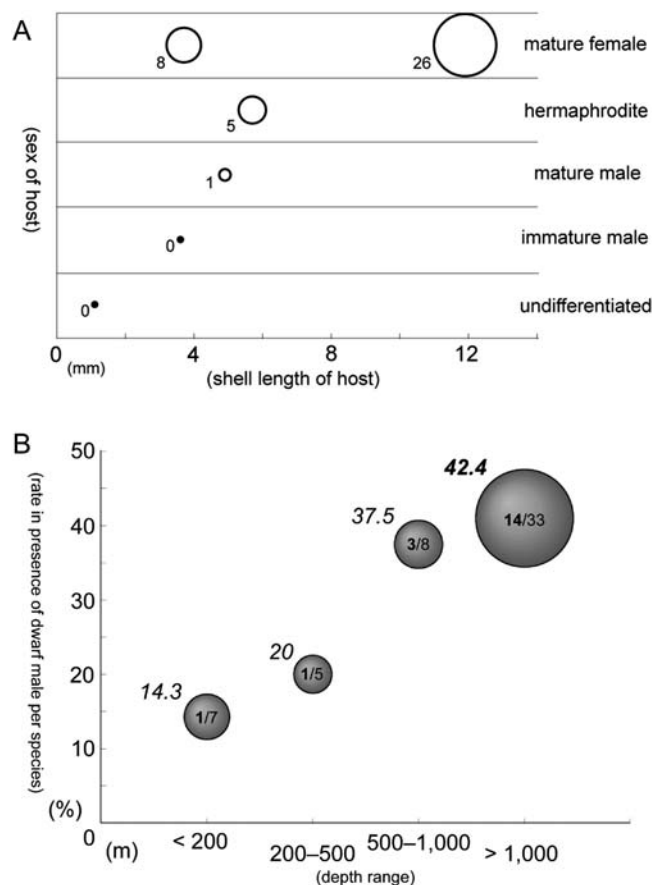


**Figure 3.** Transverse section of autonomously boring *Xylophaga supplicata*. **A.** Male phase. **B.** Hermaphroditic phase. Abbreviations: gd, genital duct; gf, gill filament; go, genital opening; int, intestine; ov, ovum; pr, pedal retractor; sc, suprabranchial cavity; sp, spermatozoon; st, stomach; te, testis; wsc, wood-storing caecum.

2002). We suspect that these ‘juveniles’ are also dwarf males, especially in the case of *X. tubulata* Knudsen, 1961, in which Knudsen (1961: 191, fig. 34) reported ‘juveniles’ characterized by smooth oval valves, short siphon and ventrally projecting inflated foot (interpreted as the anterior expansion of the visceral mass), as in *X. supplicata*.

Among the 53 known nominal species of *Xylophaga*, 19 species (35.8%) carry ‘juveniles’ on the host (data from personal observation by TH and from Purchon, 1941; Knudsen, 1961, 1967; Kudinova-Pasternak, 1975; Okutani, 1975; Santhakumaran, 1980; Harvey, 1996; Turner, 2002; Voight, 2007, 2008, 2009). We propose that these ‘juveniles’ are all dwarf males. Histological and light microscopic examination by Ockelmann & Dinesen (2011), in which they clarified that the ‘brooding juveniles’ of *X. clenchi* Turner & Culliney, 1971 (they identified the specimens as *Xyloredo ingolfia* Turner, 1972), were functional dwarf males, strongly supports our assertion. If we are correct, the dwarf male phenotype is more common in deep-water species, reaching a frequency of 42.4% for taxa below 1000 m depth (Fig. 4B). This pattern of distribution is possibly due to the availability of sunken wood. Sunken wood is a common feature in near-shore benthic habitats, close to river mouths, woody swamps and wooded coastlines (Bruun, 1959), but probably much less common in deeper offshore environments. The sporadic distribution of woody substrata may have promoted the development of dwarf males in the deep-water species of *Xylophaga*.

Recent serial surveys by French deep-sea expeditions in the southwestern Pacific have recorded the distribution of *X. supplicata* for the first time in Vanuatu and have shown that this so-called ‘brooding’ species is much more widely distributed in the West Pacific than previously thought (Higo *et al.*, 1999; Haga, 2011). This discovery suggests that *X. supplicata* can disperse widely by planktotrophic larvae, irrespective of its ephemeral habitat. Although available knowledge on larval development is very limited in Xylophagidae, all species previously examined are reported to have planktotrophic



**Figure 4.** **A.** Sexual modes in relation to host's shell length and number of carried dwarf males in *Xylophaga supplicata*. Size of circle reflects number of carried dwarf males. **B.** Relationship between depth range and ratio of presumed dwarf-male-bearing *Xylophaga*. Numbers in circles are of species with dwarf males (left) and of total species (right). Numbers in italics are rate of dwarf-male-bearing species. Size of circle reflects number of species. Depth range is based on average of records reported in literature (see text).

development. For example, Culliney & Turner (1976) directly observed planktotrophic veligers in *X. atlantica*. Haga & Kase (2008) inferred planktotrophic development based on their SEM observation of the morphology of the prodissococonch of *Xyloredo teramachii* (Taki & Habe, 1950) that is comparable with that observed in *X. supplicata*. Culliney & Turner (1976) further observed delayed metamorphosis of pediveligers for up to 6 months in laboratory-reared *X. atlantica*. Such larval idiosyncracies might be common among the Xylophagidae. We suggest that the Xylophagidae have the ability to distribute widely in the deep sea, being capable of exploiting ephemeral wood falls by means of long-distance dispersal with planktotrophic larvae and by the delay of metamorphosis.

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