Redescription of the Deep-sea Wood Borer *Neoxylophaga teramachii* Taki & Habe, 1950 and its Assignment to the Genus *Xyloredo* (Bivalvia: Myoida: Pholadoidea) with Comments on Fossil Pholadoidae

TAKUMA HAGA

Department of Biological Science, Graduate School of Sciences, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan

TOMOKI KASE

Department of Geology and Paleontology, National Museum of Nature and Science [formerly National Science Museum, Tokyo], 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan
(e-mail: haga@kahaku.go.jp)

Abstract. Examination of the type specimens of the Japanese wood-borer *Neoxylophaga teramachii* Taki & Habe, 1950 and additional live and dead intact specimens has revealed that the species should be reallocated to the genus *Xyloredo* Turner, 1972, the third genus of Xylophagainae, because it has: 1) a teredo-like calcareous tube, 2) a greatly reduced calcareous mesoplax, and 3) extended inhalant and exhalant siphonal canals, all features typical of *Xyloredo*. *Mesoxylophaga* Habe, 1977, established for *N. taramachii*, is therefore regarded as the junior synonym of *Xyloredo*. Since the present species is extremely rare and its soft parts never studied, a detailed redescription is given for shell, mesoplax, calcareous tube and soft parts. Two unique organs considered to function in self-fertilization, the accessory genital organ and *vesicula seminalis*, are observed for the first time for *Xyloredo*. The associated calcareous tube shows unique microstructure referred to isolated crystal morphotypes. The mineralogy of the calcareous tube consists entirely of aragonite, and the general morphology of the tube is characterized by remarkably strong, regular growth lines in its surface. These features in the calcareous tube provide useful criteria for identification of the trace fossil *Teredolites* in the Mesozoic and Cenozoic.

INTRODUCTION

The Xylophagainae is a subfamily of Pholadidae and, according to Turner (2002), composed of three genera, *Xylophaga* Turton, 1822, *Xylopholas* Turner, 1972a, and *Xyloredo* Turner, 1972b. All species of this subfamily are obligate borers in sunken woods, mostly in deep seas. Knudsen (1961) described 17 species of *Xylophaga* in the collection obtained during the Galathea Deep Sea Expedition from 1950 to 1952. Subsequently, Turner (2002) revised previously reported species and described seven additional new species. Both authors demonstrated that the soft parts, such as siphons, mesoplax and accompanying external morphology (e.g., 'chimney' and 'tube' seen in their burrows) are important characters for the systematics of this subfamily; shell characters are generally not useful because they share almost homogeneous, simple, spherical, and *Teredo*-like valves. Therefore, detailed examination of intact live animals is indispensable for the systematics of this bivalve group. However, intact live animals are quite difficult to obtain due to their deep-sea occurrence and the fragile nature of the shells.

Japanese authors proposed four subgenera within the genus *Xylophaga* all diagnosed by shell characters alone. These are *Protoxylophaga* Taki & Habe, 1945; *Neoxylophaga* Taki & Habe, 1945; *Metaxylophaga* Taki & Habe, 1945; and *Mesoxylophaga* Habe, 1977. Turner (1969, 2002), Hoagland & Turner (1981), and Hoagland (1983) synonymized all the subgenera with *Xylophaga*. However, such taxonomic treatments need to be confirmed on the basis of detailed examination of soft parts.

Neoxylophaga teramachii Taki & Habe (1950) is a case of such examples. It was described on the basis of specimens from Tosa Bay, Kochi Prefecture in western Japan. Subsequently, Habe (1977) established the monotypic new subgenus *Mesoxylophaga* under the genus *Neoxylophaga* with *N. teramachii* as the type species. Kuroda & Habe (1981) later ranked *Mesoxylophaga* at the genus level, and this taxonomic treatment has been followed by subsequent Japanese authors (e.g., Higo & Goto, 1993; Higo et al., 1999). Okutani (2000) considered *Mesoxylophaga* as a subgenus of *Xylophaga* without any discussion. *N. teramachii* is very rare, and Pailleret et al. (2007: p. 237, fig. 3) documented for the first time since the description by
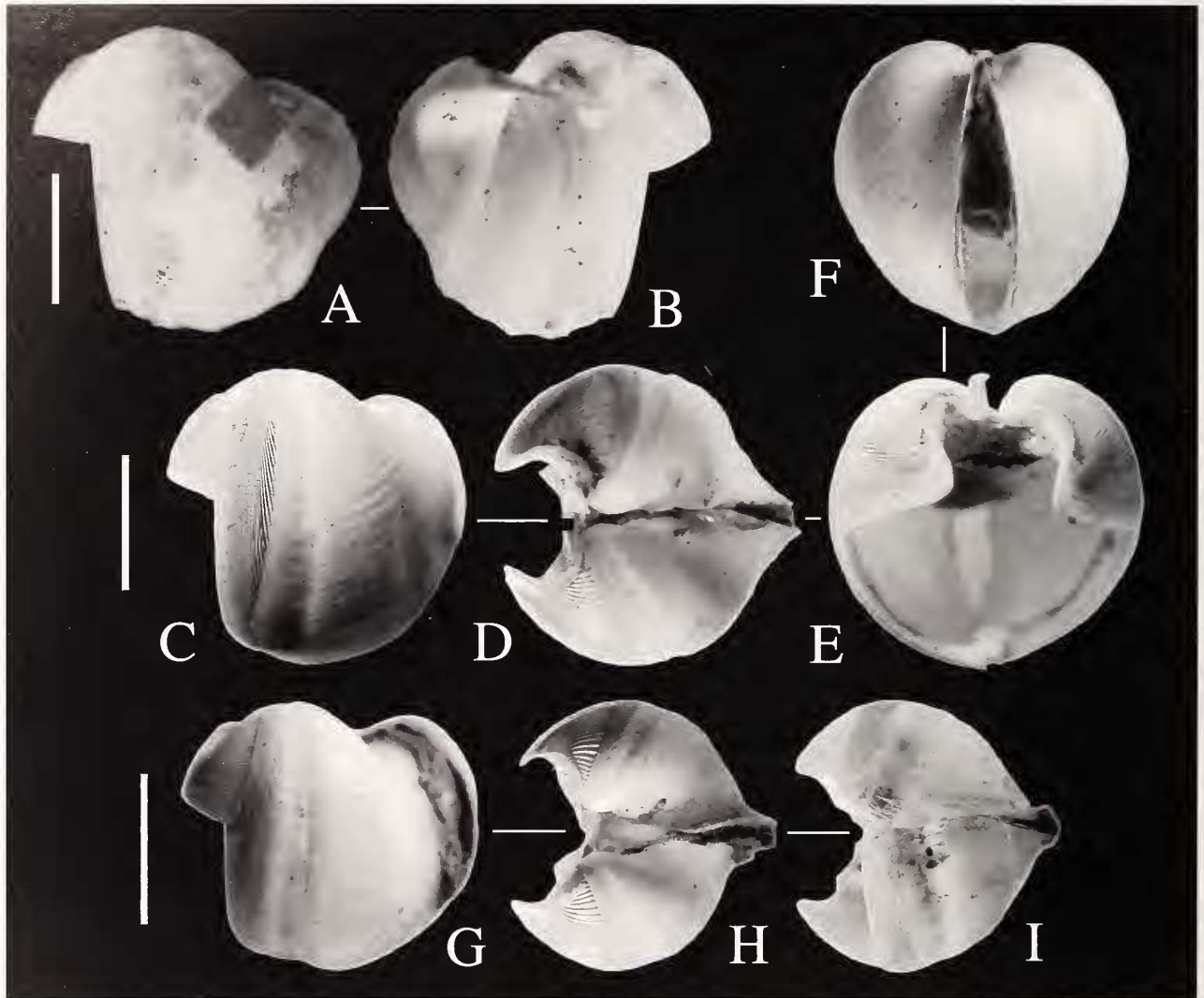
Figure 1.   Type specimens of *Xyloredo teramachii* deposited in the Toba Aquarium labeled as TA-7097. A–B. Holotype. C–F. Paratype #1. G–I. Paratype #2. Scale bars = 5 mm.

Taki & Habe (1950) a live animal of this species from a deep-sea bottom off Vanuatu.

This paper reexamines the type specimens of *N. teramachii* deposited in the Toba Aquarium, Toba City, Mie Prefecture, Japan, as well as describes in detail the shell, mesoplax, accompanied calcareous tube, and soft parts of *N. teramachii* on the basis of additional live and dead specimens obtained by the first author from his recent extensive field sampling. We show that this species can be reallocated to *Xyloredo*, another genus of Xylophagainae, and that *Mesoxylophaga* is a junior synonym of *Xyloredo* instead of a subgenus of *Xylophaga*. In addition, this paper first documents the mineralogy and microstructure of the calcareous tube of the genus *Xyloredo*.

Institutional Abbreviations: NSMT—National Museum of Nature and Science, Tokyo, Japan (formerly National Science Museum, Tokyo); OKCAB—Okayama University, Conservation of Aquatic Biodiversity, Okayama, Japan; TA—Toba Aquarium, Mie, Japan.

MATERIALS AND METHODS

Holotype: Left valve (11.62 mm in height, 12.73 mm in length, TA-7097: Figure 1A–B), possibly taken alive. Taki & Habe (1950) described the present species based on a single conjoined specimen and illustrated it with a freehand figure. The 'holotype' deposited in the Toba Aquarium with the registration number TA-7097 consists only of a left valve, although it was 'conjoined'

in the original description, of which Higo et al. (2001) were aware. Its dimensions do not match well with those given in the original description. However, this 'holotype' specimen matches the figure and retains part of the dried-up posterior adductor muscle within the valve, suggesting that it was originally a conjoined valve. Shell dimensions sometimes differ because of varying measuring methologies. We therefore regard TA-7097 as the holotype.

Paratypes: Two conjoined shells (Paratype #1, 11.90 mm in height, 11.15 mm in length: Figure 1C–F; Paratype #2, 8.93 mm in height, 9.91 mm in length: Figure 1G–I), possibly taken alive from the type locality. Although Taki & Habe (1950) did not mention paratypes in the original description, two conjoined specimens were labeled and preserved under the registration number of TA-7097, the same as the holotype (Figure 2). The type specimens deposited in the Toba Aquarium are briefly labeled and holotypes and paratypes are distinguished with red and blue labels, respectively (M. Isowa, personal communication). Although the other two specimens are not marked with blue labels, they are regarded as paratypes.

Other material: JAPAN—Five empty shells, one individual with decayed animal and fragments of tubes inside a sunken wood trunk recovered by a commercial trawler at 200 m deep off Tokai, Ibaraki Prefecture, April 29, 2004, *leg.* T. H. (NSMT-Mo76705); 50 empty shells, two live individuals and nine almost intact tubes, inside a sunken wood trunk recovered by a commercial trawler at a depth of 125 m off Tokai, Ibaraki Prefecture, June 3, 2004, *leg.* T. H. (NSMT-Mo76706; OKCAB M15894); 12 empty shells and fragments of tubes, inside a sunken wood trunk recovered by a commercial trawler at a depth of 500 m off Hitachi, Ibaraki Prefecture, March 10, 2007, *leg.* T. H. (NSMT-Mo76707); three empty shells and four tubes, inside a sunken wood trunk, 250–300 m deep off Atsumi Peninsula, Aichi Prefecture, February 1999, *leg.* S. Kimura (NSMT-Mo76708). VANUATU—two intact specimens; BOA0, from a depth of 560–580 m between Malekula and Epi Island, Vanuatu, inside a sunken wood trunk identified either as *Leucaena* or as *Serianthes*, November, 2004, R/V *Alis* (NSMT-Mo73806, 73807) (Pailleret et al., 2007).

Methods: Since the outer morphology of soft body *in situ* provides characters indispensable for systematics, we exposed the animals by breaking the wood with special care, and then observed and photographed the specimens. We used one of two live individuals (originally prepared for molecular analysis with 99% ethanol, following Ueshima, 2002) recovered from off
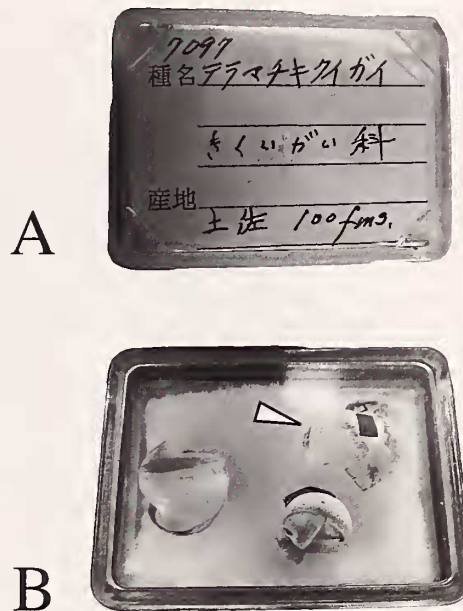

A

B

Figure 2.   Type specimens of *Xyloredo teramachii* with the attached label in the Toba Aquarium, registered as TA-7097. A. The label. Japanese texts mean Japanese name (teramachi-kukui-gai = teramachi xylophagain clam), the family (kikui-gai-ka = Xylophagaidae), and the locality (Tosa 100 fms. = Kochi Prefecture, −100 fathoms deep) from top to bottom, respectively. B. Type specimens. Arrowhead indicates the holotype. Note a boxed seal attaching the holotype.

Tokai, Ibaraki, Japan in June, 2004 for gross anatomy. This material was strongly dehydrated, so that we employed a method improved from Fukuda & Ekawa (1997): (1) the whole animal was immersed in 5% HCl solution for 30 min to rehydrate it sufficiently for dissection, (2) rinsed with tap water for 10 min, and then (3) dissected in 70% ethanol under a binocular microscope. As the dried periostracal sheath was strongly contracted, it was photographed by immersing in 70% ethanol. Scanning electron microscopy (SEM) micrographs were produced on a JOEL-T330A scanning electric microscope after the preparation of material with the standard method: material was cleaned and rinsed with distilled water, hydrated with pure ethanol, dried, mounted on the stages, and then coated with gold. For prodissoconch observation, the shelled structure covering the umbo was removed manually to expose the prodissoconch prior to the preparation. X-ray diffraction analyses were conducted for mineralogical determination of the shell and calcareous tubes. All the specimens used in this study are housed at NSMT (NSMT-Mo 76705–76708).

We followed Purchon (1941) and Turner (2002) for the terminology of anatomical and conchological characters, respectively, except for 'dorsal portion of
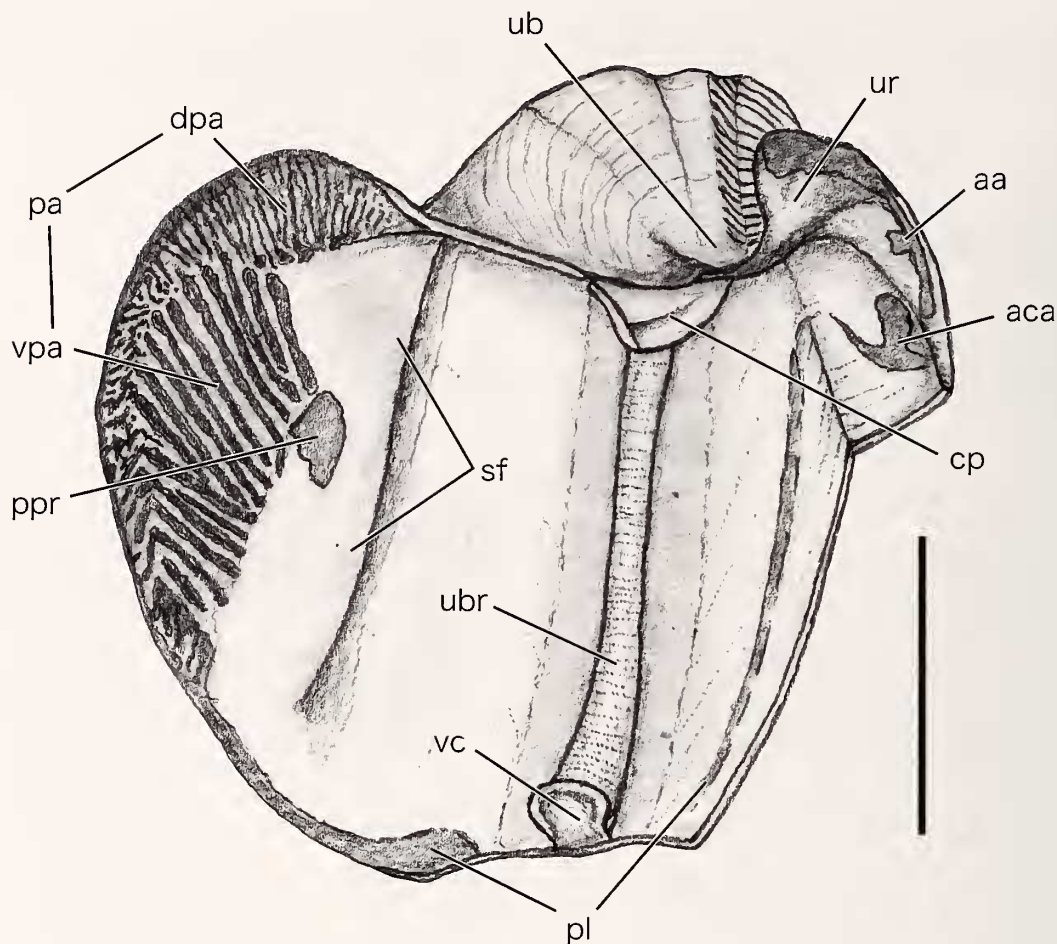
Figure 3. Internal left valve of *Xyloredo teramachii*. Abbreviations: aa = anterior adductor scar, aca = accessory anterior adductor scar, cp = chondrophore, dpa = dorsal portion of posterior adductor scar, pa = posterior adductor scar, pl = pallial line, ppr = posterior pedal retractor scar, sf = shelf, ub = umbo, ubr = umbonal-ventral ridge, ur = umbonal reflection, vc = ventral condyle, vpa = ventral portion of posterior adductor scar. Scale bar = 5 mm.

posterior adductor,' 'ventral portion of posterior adductor' and 'accessory anterior adductor,' which are newly introduced herein.

SYSTEMATICS

Superfamily Pholadoidea Lamarck, 1809

Family Pholadidae Lamarck, 1809

Subfamily Xylophagainae Purchon, 1941

Genus *Xyloredo* Turner, 1972b

Xyloredo Turner, 1972b, p. 3. Type species: *Xyloredo nooi* Turner, 1972b, by original designation.
Mesoxylophaga Habe, 1977, p. 295. Type species: *Neoxylophaga teramachii* Taki & Habe, 1950.

Remarks: Turner (1972b) established the genus *Xyloredo* by distinguishing it from all the other xylophagines in having 1) a long, teredinid-like burrow with a calcareous lining, 2) a thin periostracal border of the tube, and 3) extended inhalant and exhalant canals. *Xyloredo* superficially resembles genera of the Teredinidae, but its anatomical features indicate placement in Xylophagainae; these features are: 1) the U-shaped wood-storing caecum, 2) the internal visceral mass completely covered by the shell, 3) the presence of mesoplax, and 4) the absence of apophysis and pallet (Turner, 1972b, 2002). Aside from the type species, Turner (1972b, 2002) included *Xyloredo ingolfia* Turner, 1972b and *Xyloredo naceli* Turner 1972b in this genus. We here include *Neoxylophaga teramachii* Taki & Habe, 1950 as the fourth species of this genus. Therefore, *Mesoxylophaga* is a junior synonym of *Xyloredo*.
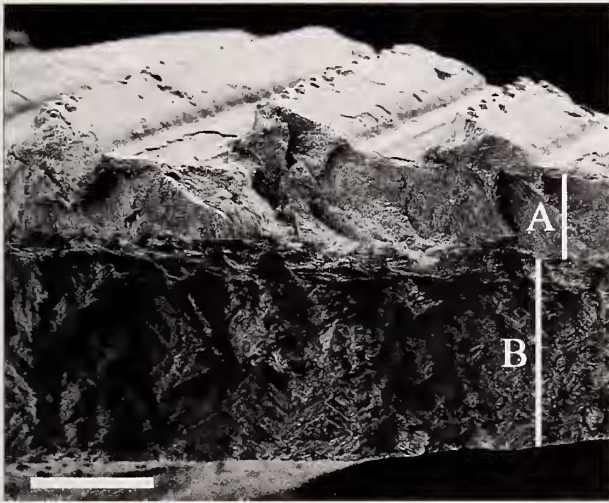
Figure 4. *Xyloredo teramachii*, enlarged view of sagittal section of the anterior slope. NSMT-Mo76706. Prismatic layer and crossed lamellar layer are indicated as A and B, respectively. Scale bar = 100 μm.

Xyloredo teramachii (Taki & Habe, 1950) [new combination]

(Figures 1–11)

Neoxylophaga teramachii Taki & Habe, 1950, p. 46, fig. 3; Kuroda et al., 1971, p. 715 (Japanese text), 471 (English text), pl. 121, fig. 11; *non* Okutani, 1968, p. 23, pl. 2, fig. 3.

Neoxylophaga (*Mesoxylophaga*) *teramachii*. Habe, 1977, p. 295.

Xylophaga teramachii. Hoagland & Turner, 1981, p. 44; Hoagland, 1983, p. 7; Turner, 2002, p. 227 (written as *Xylophaga teramachi* [*sic*]); Pailleret et al., 2007, p. 236, fig. 3.

Mesoxylophaga teramachii. Kuroda & Habe, 1981, p. 179, pl. 7, fig. 6; Higo & Goto, 1993, p. 670; Higo et al., 1999, p. 520; Higo et al., 2001, p. 181.

Xylophaga (*Mesoxylophaga*) *teramachii*. Okutani, 2000, p. 1031, pl. 513, fig. 3.

Shell: The valve is globose, up to 16.5 mm in height, 17.9 mm in length in the largest specimen, and has a shape typical of the subfamily, consisting of an anterior slope, disc and posterior slope (Figures 1–2). The valve surface is originally pearly white in color and glossy, and covered with a thin, dark golden brown periostracum over the whole surface (Figures 1, 8A). Finely denticulated bunches are regularly distributed over the anterior slope from the umbonal-ventral sulcus forwards, and fine growth lines extend over the disc and posterior slope. The posterior slope is widely reflected dorsally and its ventral midline, where the shelf terminates with the posterior slope and forms a blunt angulation (Figure 3). Since the margin of posterior
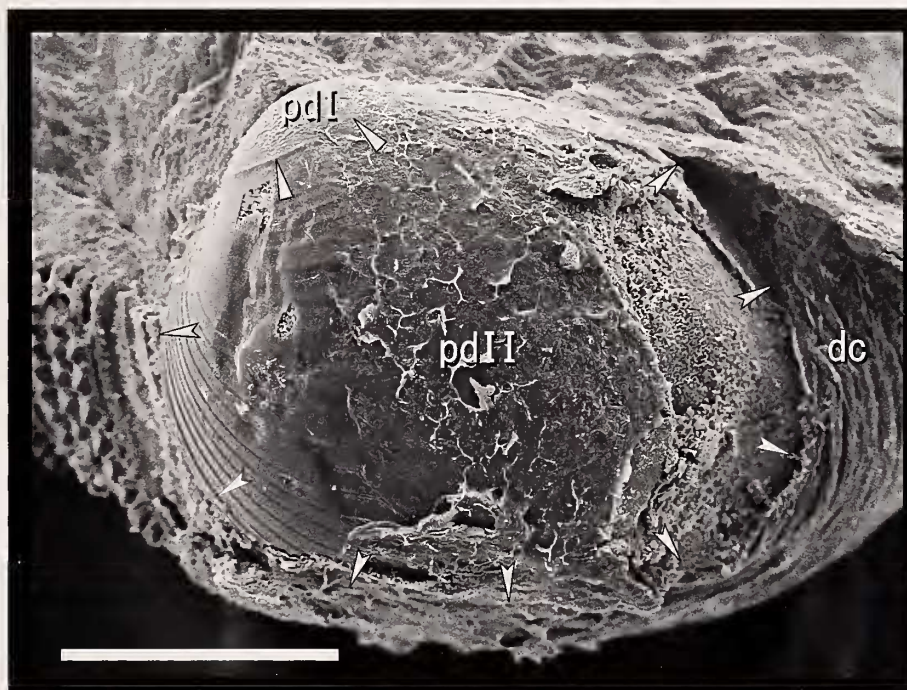

Figure 5. Prodissoconch of *Xyloredo teramachii*. NSMT-Mo76706. Arrowheads indicate the boundaries among prodissoconch I, II, and dissoconch. Abbreviations: dc = dissoconch, pdI = prodissonconch I, pdII = prodissoconch II. Scale bar = 100 μm.
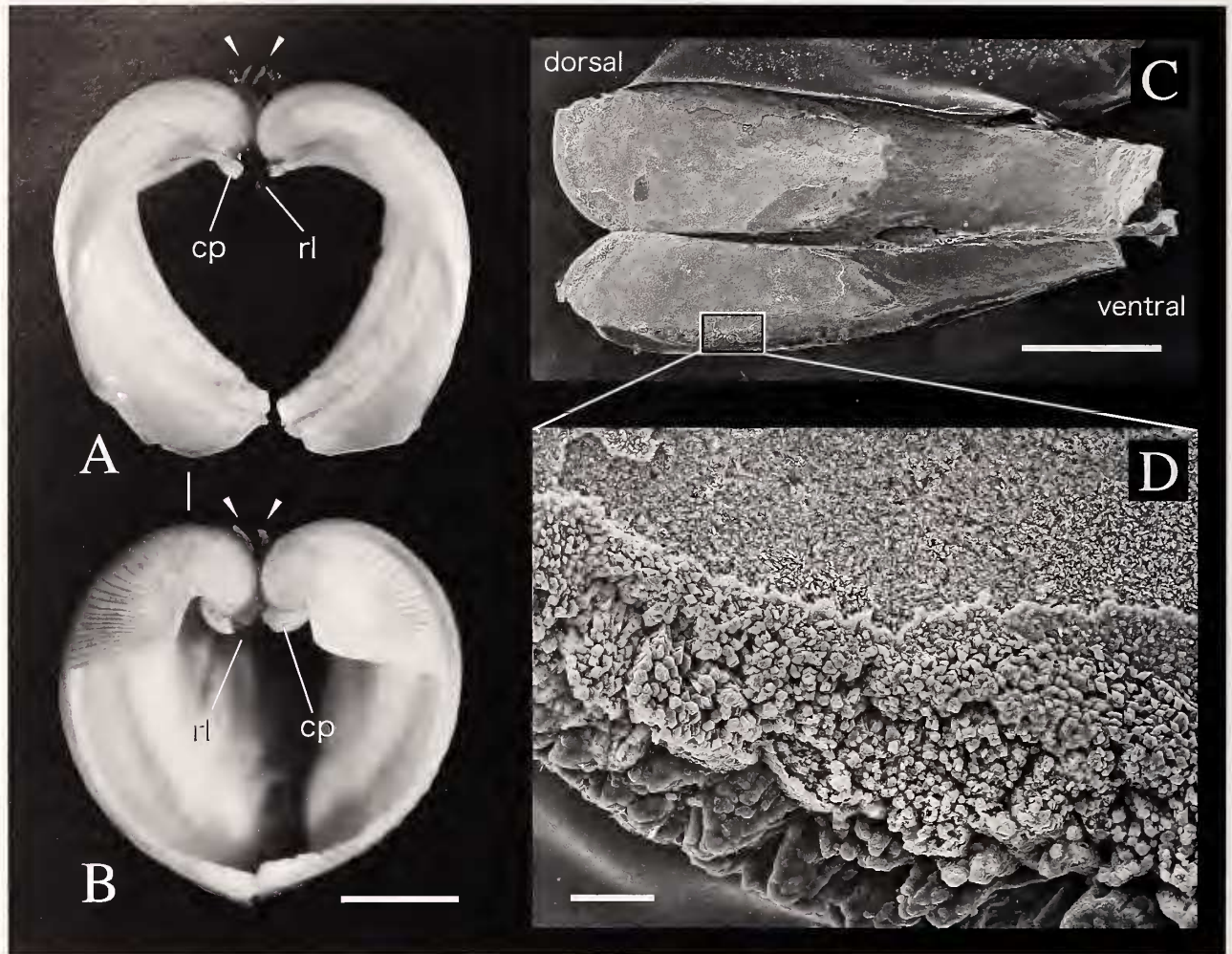
Figure 6.   Mesoplax of *Xyloredo teramachii*. NSMT-Mo76706. A–B. Mesoplax *in situ* attached to the extended periostracum at the umbonal reflection indicated by arrowheads. C–D. Enlarged ventral view of the mesoplax. Abbreviations: cp = chondrophores, rl = rod-shaped ligament. Scale bars = A–B: 2 mm; C: 500 µm; D: 20 µm.

slope reflects laterally, the posterior end opens widely and large siphonal canals extend from it (Figure 6A). The umbonal-ventral sulcus (Figure 1A, C, G) is wide and concave without the crenate varix. The umbonal reflection largely develops and reflects dorsally, so that it is ear-shaped in anterior view (Figures 1E, 6B)

The internal valve surface is smooth, also pearly white and glossy. The shelf largely develops at the middle of the posterior slope and is impressed deeply to form a bump similar to that in teredinids (sf: Figure 3). The umbonal-ventral ridge (ubr: Figure 3) is wide, laterally depressed, irregularly marked with rough lines, descends from the umbo along the middle of the disc, and forms the large spherical ventral condyle (vc: Figure 3). In the left valve, the large, cuneiform and flat chondrophore is prominent beneath the umbo (cp: Figure 3), but in the right valve, the brown-

colored, rod-shaped ligament protrudes laterally (Figure 6B). The umbo strongly curves antero-ventrally (ub: Figure 3), and the prodissoconch is completely enclosed in the anterior reflection. The posterior muscular scar (pa: Figure 3) is large, deeply impressed with many lines, and divided into two areas: one with numerous irregular narrow lines that spread inward along the dorsal part of posterior slope (dorsal portion of posterior muscular scar: dpa, in Figure 3), and the other with a few wide lines that obliquely spread ventro-internally and are chevron-shaped ventrally (ventral portion of posterior muscular scar: vpa, in Figure 3). The pallial line (pl: Figure 3) is narrow and located along the valve margin, and is rather obscure near the ventral condyle. The accessory anterior adductor muscle scars (aca: Figure 3) and anterior adductor scars (aa: Figure 3) are rather obscure and
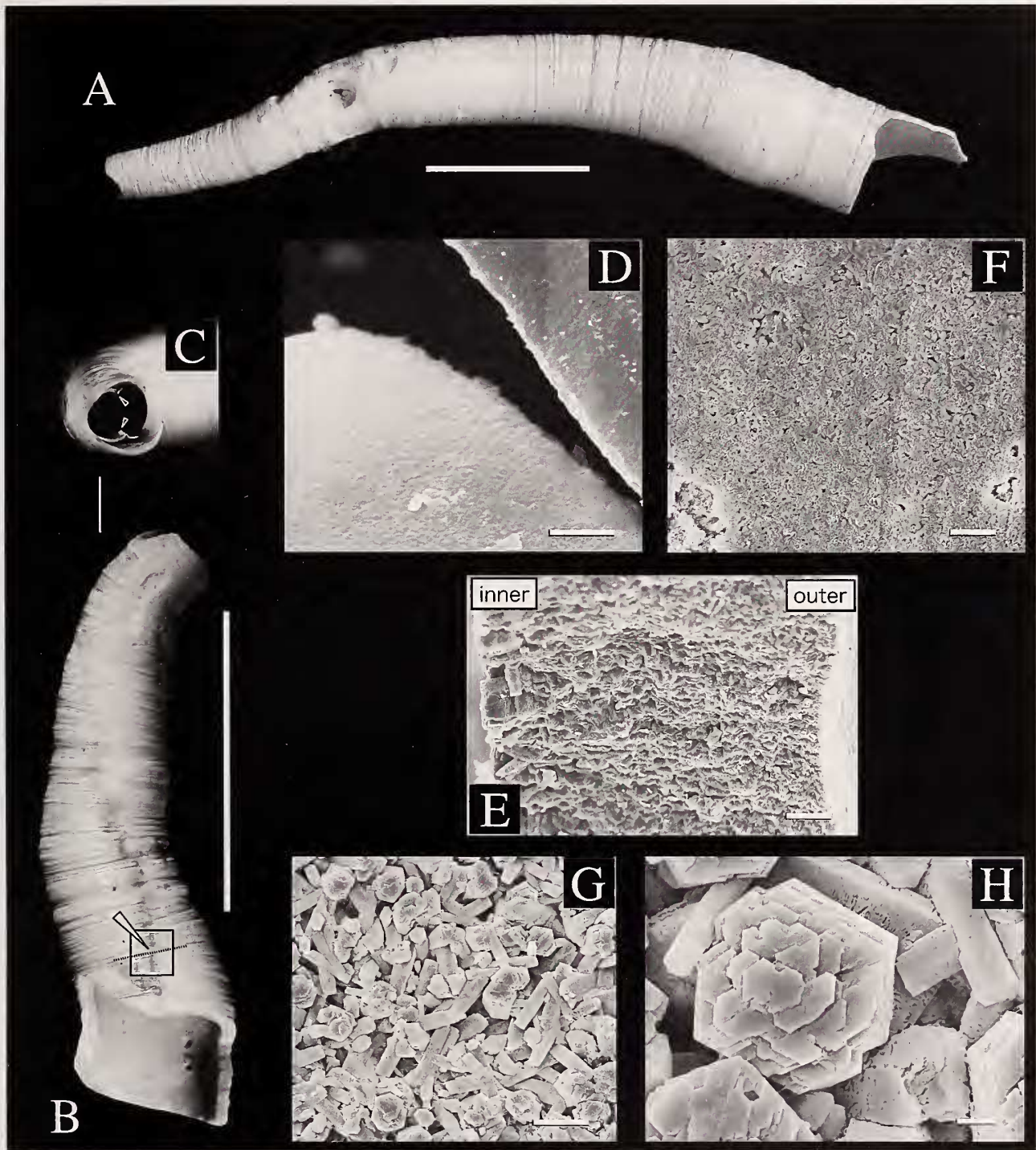
Figure 7.   Calcareous tubes of *Xyloredo teramachii*. NSMT-Mo76706. A–B. Posterior end of the tube. Arrrowhead, dotted line, and box indicate the enlarged views of D–H. C. posterior tip of the tube. Arrowheads indicate the lateral 'blades'. D. Enlarged view of periostracum which externally covers the tube. E. Enlarged view of sagittal section. F. Enlarged view of the outer surface. G–H. Enlarged view of the inner surface. Scale bars = A–B: 10 mm; D, F: 3 μm; E, G: 10 μm; H: 2 μm.

Figure 8. Periostracal sheath of *Xyloredo teramachii* which covers the siphonal canals. NSMT-Mo76706. A. Intact specimen *in situ* with the complete periostracal sheath fully extended. B–C. Enlarged view of microscopic pores, indicated by arrowheads. Scale bars = A: 20 mm; B: 100 µm; C: 10 µm.

Figure 9. A–C. Animal *in situ* of *Xyloredo teramachii*. NSMT-Mo76706. Arrowhead indicates the boundary of the calcareous tube and the periostracal sheath. B. A sunken wood trunk *in situ* bored by *Xyloredo teramachii*. Abbreviation: ct = calcareous tube. Scale bars: A–C = 5 mm; D = 20 mm.
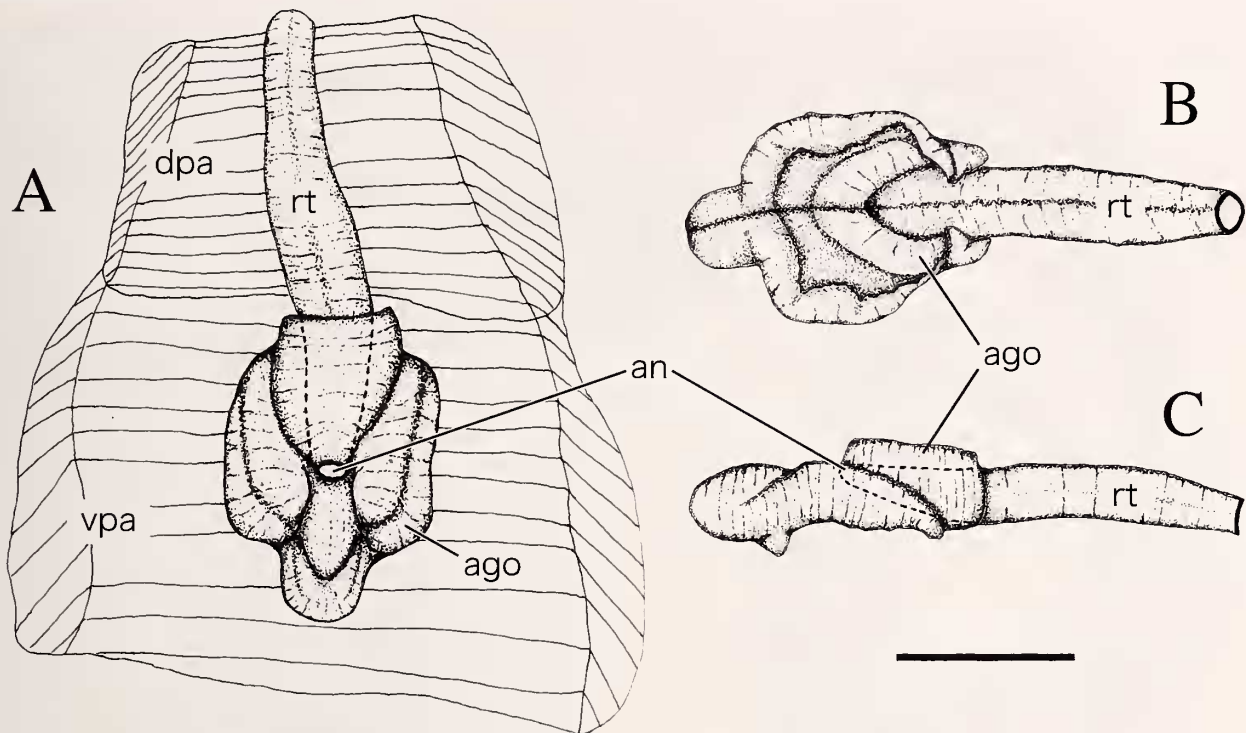
Figure 10.   Accessory genital organ of *Xyloredo teramachii*. A. Posterior view. B. Anterior view. C. Lateral view. Abbreviations: ago = accessory genital organ, an = anus, dpa = dorsal portion of posterior adductor, rt = rectum, vpa = ventral portion of posterior adductor. Scale bar = 1 mm.

fuse with the pallial line; the former lies at the anterior margin of the anterior slope, and the latter are small and are located in the middle of the umbonal reflection. The posterior pedal retractor scar (ppr: Figure 3) is large, located close to the ventral portion of the posterior adductor scar, and positioned in the middle of the shelf. The anterior pedal retractor scar is situated beneath the anterior reflection. The ventral adductor scars and siphonal retractor scars are absent.

The valve is entirely of aragonite and consists of an outer, seemingly irregular simple prismatic layer, and an inner crossed-lamellar layer (Figure 4). Very thin prismatic sublayers, possibly of mycostracal prisms, are occasionally inserted into the inner layer. This sublayer is also observed underneath the inner layer where the muscles adhere. The outer prismatic layer becomes thicker and forms denticles particularly in the anterior slope, and the crossed lamellar layer is prominent particularly in the strongly curved regions such as the umbo and the shelf. The umbonal-ventral ridge consists only of simple prisms.

Prodissoconch: The prodissoconch (Figure 5) is typical of planktotrophic development and composed of ca. 80 μm-long prodissoconch I (pdI: Figure 5) and ca. 205 μm-long prodissonconch II (pdII: Figure 5). It is totally concealed within the umbo due to the anterior

reflection and subsequently developed dissoconch in full-grown individuals. The surface is rather rough in prodissoconch I, while it is smooth and marked with regularly spaced concentric growth lines in prodisso-conch II. The boundary between prodissoconch I and II is clearly marked with thin crenations (Figure 5, arrowheads).

Mesoplax: The mesoplax (Figure 6) is paired, tiny, long, subquadrangular (widening posteriorly), and slightly calcified. It is situated beneath the posteriorly ascended periostracum that covers the large and oval anterior incision latero-anteriorly (Figure 6A–B). The mesoplax consists of granular prisms with ca. 20 μm-wide subunits (Figure 6C–D). This structure is difficult to observe in live specimens because of their tiny size and the complete coverage with mucous debris (Figure 9B).

Burrow and calcareous tube: The long burrow (Figure 9D) is typical of teredinids, but does not produce 'nodules,' indicative of the switch-backed drilling behavior observed in teredinids. The approximate posterior two thirds of the burrow is lined with a calcareous tube (Figure 7) that is marked with distinct, regularly spaced growth rings (Figure 7A–B). The external surface of the tube is totally covered with a
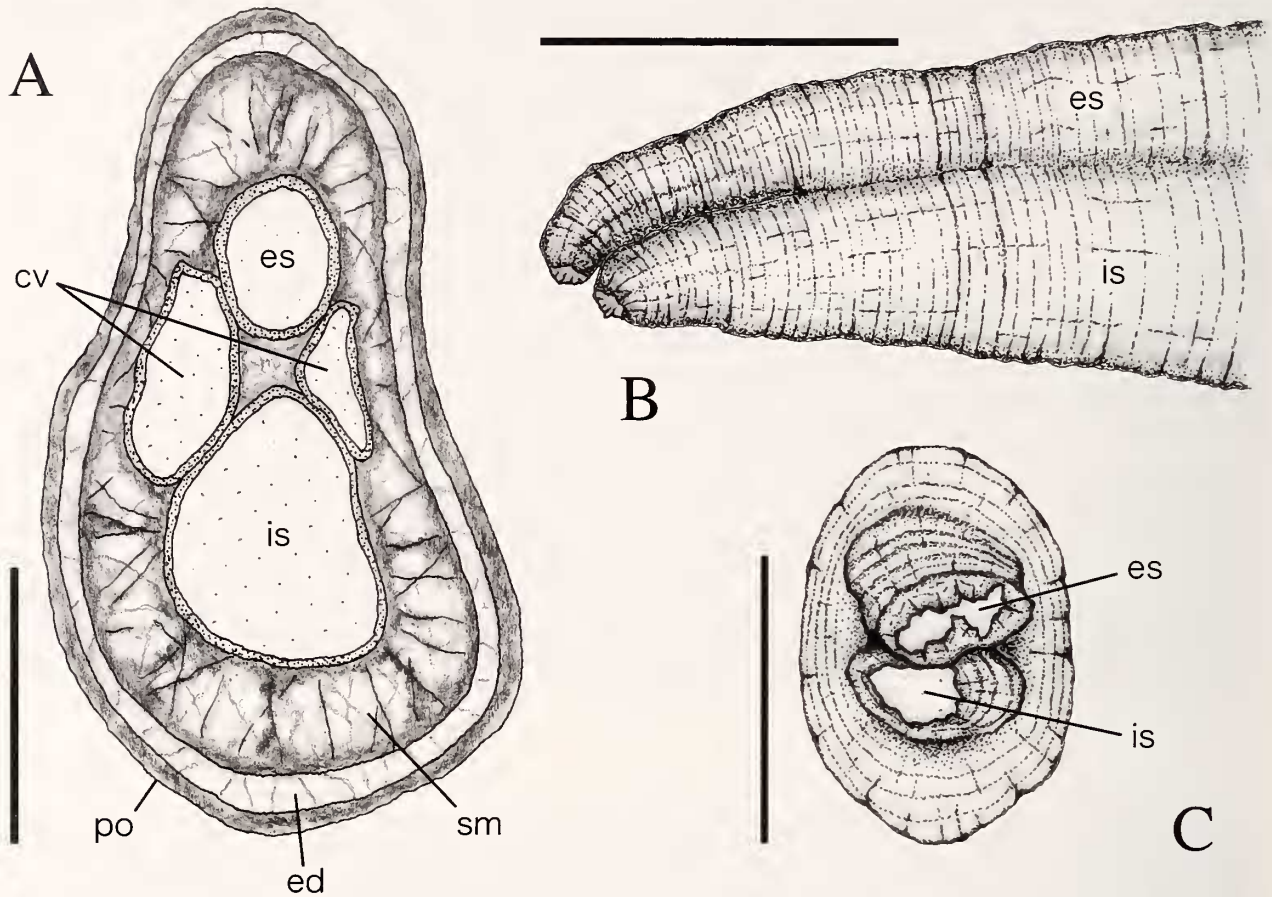
Figure 11. A. Sagittal section of the siphonal canals. B–C. Enlarged view of the siphons. Abbreviations: cv = cavity, ed = epidermis, es = exhalant sihonal canal and siphon, is = inhalant siphonal canal and siphon, po = periostracum, sm = sigmoid mesenchyme. Scale bars = 1 mm.

thin, smooth, and golden-glossy periostracum extending from the valve via a periostracal sheath (Figure 7D). The posterior portion of the tube is rather thick, and bears a lateral 'blade' internally at the tip in full-grown individuals (Figure 7C). From the posterior tip to the midpoint, the calcareous tube becomes significantly thinner, and is terminated with a dark-brown, strong demarcation (Figure 9A, arrowhead). The periostracal sheath extended from the valve also terminates at this demarcation (Figure 8A). The siphonal canal between the valve and calcareous tube is therefore solely covered with a periostracal sheath. The surface of periostracal sheath is smooth, but with microscopic holes (inside of pore is ca. 50 μm in length) all over the surface (Figure 8B–C). These tiny pores are limited in distribution in the extended periostracal sheath. The tube is composed mostly of periostracum in very young individuals; however, calcification of the tube occurs first at the base of the siphon with simple prismatic structure as well as on the internal surface of the full-grown tubes. The calcareous tube is of aragonite, and consists of alternating fine and coarse hexagonal prismatic fibers, oriented either vertically or horizontally (Figure 7G–H) which gradually become smaller in diameter and length towards the outer portion (Figure 7E–F). The vertical prismatic fibers are usually less than 10 μm in diameter, and larger and more abundant than the horizontal prismatic fibers.

Soft parts: The animal is long as in teredinids, but differs in having a completely internal visceral mass, a mesoplax at the anterior incision, and in the absence of apophysis and pallet (Figure 9A–C). The anatomical features are generally identical to xylophagaines (e.g., Purchon, 1941; Turner, 2002): the posterior adductor muscle is large, divided into two parts, and the ventral part consists of chevron-shape fibers and occupies two thirds of the posterior adductor, while the dorsal part consists of irregularly arranged fibers and descends along the posterior slope. The anterior adductor is small, depressed dorso-ventrally and sinuous in the anterior reflection. The accessory anterior adductor is

small, situated beneath the anterior adductor, and consists of stout muscular fibers. The posterior pedal retractor is large and closely inserted into the midpoint of the posterior adductor. The anterior pedal retractor is attached within the deeper portion of the umbo. The ventral adductor and the siphonal retractor are absent. The foot is large, discoid, and is surrounded by circular muscles around its margin (Figure 9C). The gills are narrow, thick, laterally stout, and consist only of inner demibranchs.

The digestive tract, also typical of xylophgaines, has a large U-shaped wood-storing caecum that is connected to the stomach on its left side. The intestine ascends along the anterior margin of the posterior adductor, penetrates the heart, then terminates as a simple anus, which is surrounded by the accessory genital organ (Figure 10). The accessory genital organ is well-developed, glandular, free from any adhesion to the posterior adductor, and superficially composed of two components: a blade surrounding the end of the rectum (Figure 10A), and a peduncle whose ventral end protrudes like a proboscis and is situated below the rectum (Figure 10B–C). A pair of *vesicula seminalis*, a flattened small lobule visible in pale yellow, is present laterally on the thin suspensory membrane of the ctenidium close to the posterior end of the pedal retractor.

The siphons (Figure 11B) are short, simple, and both tips are usually aligned with the same length; however, the tip of the exhalant siphon appears to be slightly longer in some individuals. The apertures in both siphons are roughly serrated (Figure 11C). The siphonal canals are long and are connected to the posterior part of the visceral mass and siphons. The inhalant and exhalant siphonal canals are supported by well-developed sigmoid mesenchymes (sm: Figure 11A). A pair of cavities (cv: Figure 11A), that probably act as a haemocoel, are situated laterally between the siphonal canals, and continuously extends antero-posteriorly from the bases of siphons and visceral mass.

Type locality: Tosa Bay, Kochi Prefecture, western Japan, ca. 100 fathoms deep.

Distribution: West Pacific along the Japanese mainland from Ibaraki Prefecture to Kochi Prefecture and Vanuatu in the south Pacific. Depth ranges from 125 to 580 m.

DISCUSSION

Our detailed study on the shells and soft parts shows that *N. teramachii* can be reallocated to the genus *Xyloredo*. *Xyloredo nooi*, *X. ingolfia* and *X. naceli* are all less than 10 mm in maximum shell length (Turner, 1972b), while the present species reaches up to ca. 18 mm. In addition to the large shell size, the present species is easily distinguished from the above three

species in having a laterally reflected and developed posterior slope and dark golden brown periostracum. Okutani (1968: p. 23) identified a specimen from a sunken timber obtained at a depth of 1,510 m in Sagami Bay as *Neoxylophaga teramachii* (but in the figure caption he indicated it as '?*Neoxylophage teramachii*' [*sic*]). We suggest however that this specimen seems to belong to another, yet undescribed species because it differs from the present species in having a large and thick mesoplax, a flatted umbonal-ventral sulcus, and a varix-like crenation in its posterior portion. Habe (1977) allocated *Neoxylophaga lobata* (Knudsen, 1961) and *N. knudseni* Okutani, 1975 to his subgenus *Mesoxylophaga*. These two species do not have the calcareous tube in the burrow and therefore cannot be referred to *Xyloredo*. Generic positions of these species still remain uncertain until anatomical details are clarified.

The present species is the first record of the genus *Xyloredo* in the West Pacific. *Xyloredo nooi*, *X. ingolfia* and *X. naceli* were reported from the Atlantic, East Pacific, and South Pacific, respectively, from depths of more than 1,500 m, and they were heretofore known only from their type localities (Turner, 1972b, 2002). Hoagland (1983) suggested oviparous development for the above three species, but the present species appears to undergo planktotrophic development judging from the size (ca. 80 μm in length) of prodissoconch I (see Jablonski & Lutz, 1980). The wide distribution from Japan to Vanuatu of the present species is likely due to its planktotrophic larval transport.

Teredinidae and Xylophagainae have unique reproductive strategies. Turner (1968) and Turner & Johnson (1971) stated that Teredinidae and Xylophagainae studied so far exhibit protandrous hermaphroditism, and suggested self-fertilization for Xylophagainae. Purchon (1941) extensively studied the mechanism of self-fertilization in *Xylophaga dorsalis* (Turton, 1819), and observed spawned sperms deposited in the seminal receptacle via the accessory genital organ that functions to tangle flooded sperms. Hoagland (1983) mentioned that all species of *Xyloredo* lack the accessory genital organ. We nevertheless recognized this organ in the present species (Figure 10) and an undetermined species of *Xyloredo* from Japan. Therefore, our study confirms the presence of the accessory genital organ in *Xyloredo*. It seems likely that the present species also undergoes self-fertilization because of the presence of *vesicula seminalis* and an accessory genital organ. However, this conclusion must be confirmed by detailed histological study on individuals with different developmental stages.

We show that the calcareous tube of *Xyloredo* is composed of hexagonal prismatic fibers, composed of aragonite. The prisms are vertically and horizontally oriented across each other (Figure 7G–H), and its

Table 1

Mineralogical and morphological features of the calcareous tubes in *Xyloredo*, *Teredina*, and Teredinidae. Note that *Teredina* is extant genus.

Family	Genus	Mineralogy	Gross morphology	Surface morphology
Pholadidae	*Xyloredo*	aragonite[1]	long, winded[1,2,3]	maked by regular growth lines[1,2,3]
	Teredina	aragonite[4]	long, straight[5,6]	smooth, gaped at dorsal and ventral[5,6]
Teredinidae		calcite and/or aragonite[4,7]	long, winded[5,8]	smooth[5,8]

References: [1]this study; [2]Turner (1972b); [3]Turner (2002); [4]Bøggild (1930); [5]Turner (1969); [6]Kelly (1988); [7]Carter (1980b); [8]Turner (1966).

structure is referable to 'isolated crystal morphotypes' as defined by Carter (1980a) and Carter & Clark (1985). Carter (1980a) reported that this microstructure is seldom observed in bivalves, since it has rarely been discussed in detail (e.g. Boggild, 1930). As far as we are aware, the aragonitic isolated crystal morphotypes in *Xyloredo* reported herein is a characteristic microstructure among the accessory calcareous tubes in bivalves.

In Pholadoidea, only wood-borers produce long calcareous tubes: those are the genus *Xyloredo* (Turner, 1972b, 2002), fossil genera *Teredina* Lamarck, 1818 and *Turnus* Gabb, 1864 (Turner, 1969; Kelly, 1988) in Pholadidae, and all members of the family Teredinidae (Turner, 1966, 1969). Their fossilized burrows were described under the ichnogenus *Teredolites* Leymerie, 1842, which is characterized by a large club-shaped morphology with a single aperture, and occurs in xylic substrata since the Mesozoic (Leymerie, 1842; Hatai, 1955; Turner, 1966; 1969; Bromley et al., 1984; Plint & Pickerill, 1985; Kelly, 1988). Identification of the trace makers for *Teredolites* is, however, generally difficult because the burrows usually do not preserve internally embedded body fossils such as valves and/or palletal structure (Plint & Pickerill, 1985). Polychaetes and boring isopods produce similar burrows in xylic substrata, but they never secrete calcareous tubes in their burrows (Gingras et al., 2004). Therefore, *Teredolites* with the calcareous tubes can be attributed to pholadoidean boring bivalves.

We suggest that *Teredolites* associated with fossilized calcareous tubes can be referred to a specific family or genus within Pholadoidea by analyzing the mineralogy and external tube morphology (Table 1). Namely, *Xyloredo* is characterized by having a winding, aragonitic tube with remarkably strong, regular growth lines on the surface. In *Teredina* (an odd tube-bearing fossil genus of Pholadidae with morphology convergent to Teredinidae), the tube is mostly straight and aragonitic in composition but its surface is smooth with two gapes at the dorsal and ventral portions in some individuals (Bøggild, 1930; Turner, 1969; Kelly, 1988). On the other hand, Teredinidae has a strongly winding, calcitic and/or aragonitic tube with a smooth

tube surface (Turner, 1966, 1969; Carter, 1980). *Turnus* is a poorly known fossil genus originally placed in Teredinidae (Gabb, 1864; see also Turner, 1969) mostly from the Cretaceous. Kelly (1988) reported a lined calcareous *Teredolites* associated with valves of *Turnus kotickensis* Kelly, 1988, and tentatively referred the genus to Pholadidae. However, the systematic position of *Turnus* remains unclear until mineralogical and microstructural information is available. In conclusion, the mineralogy and external morphology of calcareous tube provide useful criteria for identification of *Teredolites* from the Mesozoic and Cenozoic.

LITERATURE CITED

Bøggild, O. B. 1930. The shell structure of the mollusks. Det Kongelige Danske Videnskabernes Selskabs Skrifter. Naturvidenskabelig og Mathematisk Afdeling 9:231–326; 14 pls.

Bromley, R. G., S. G. Pemberton & R. A. Rahmani. 1984. A Cretaceous woodground: the *Teredolites* ichnofacies. Journal of Paleontology 58(2):488–498.

Carter, J. G. 1980a. Controls of bivalve mineralogy and microstructure. Pp. 69–113 in D. C. Rhoads & R. A. Lutz (eds.), Skeletal Growth of Aquatic Organisms. Plenum Press: New York & London.

Carter, J. G. 1980. Selected mineralogical data for the Bivalvia. Pp. 627–643 in D. C. Rhoads & R. A. Lutz (eds.), Skeletal Growth of Aquatic Organisms. Plenum Press: New York & London.

Carter, J. G. & G. R. Clark. 1985. Classification and

phylogenetic significance of molluscan shell microstructure. Pp. 50–71 in T. W. Broadhead (ed.), Mollusks. Notes for a short course. University of Tennessee Studies in Geology 13: Florida.

FUKUDA, H. & K. EKAWA. 1997. Description and anatomy of a new species of the Elachisinidae (Caenogastropoda: Rissoidea) from Japan. The Yuriyagai 5(1/2):69–88.

GABB, W. M. 1864. Description of the Cretaceous fossils. California Geological Survey, Paleontology 1:57–243.

GINGRAS, M. K., J. A. MACEACHERN & R. K. PICKERILL. 2004. Modern Perspectives on the *Teredolites* ichnofacies: observations from Willapa Bay, Washington. Palaios 19: 79–88.

HABE, T. 1977. Systematics of Mollusca in Japan. Bivalvia and Scaphopoda. Hokuryukan: Tokyo, Japan. 372 pp. (in Japanese)

HATAI, K. 1955. A lower Cretaceous *Teredo*. Short Papers from the Institute of Geology and Paleontology, Tohoku University 3:29–32.

HIGO, S. & Y. GOTO. 1993. A systematic list of molluscan shells from the Japanese Is. and the adjacent area. Elle Publishing Co. Ltd.: Yao, Osaka, Japan. 5+3+23+693+13+148+2 pp. (in Japanese)

HIGO, S., P. CALLOMON & Y. GOTO. 1999. Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Elle Scientific Publications: Osaka, Japan. 749 pp.

HIGO, S., P. CALLOMON & Y. GOTO. 2001. Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Type Figures. Elle Scientific Publications: Osaka, Japan. 208 pp.

HOAGLAND, K. E. 1983. Characters, character states, and taxa used in multivariate analysis of the Pholadacea. Tryonia 8:1–51.

HOAGLAND, K. E. & R. D. TURNER. 1981. Evolution and adaptive radiation of wood-boring bivalves (Pholadacea). Malacologia 21(1/2):111–148.

JABLONSKI, D. & R. A. LUTZ. 1980. Chapter 9. Molluscan larval shell morphology. Ecological and paleontological applications. Pp. 323–377 in D. C. Rhoads & R. A. Lutz (eds.), Skeletal Growth of Aquatic Organisms. Plenum Press: New York & London.

KELLY, S. R. A. 1988. Cretaceous wood-boring bivalves from western Antarctica with a review of the Mesozoic Pholadidae. Palaeontology 31(2):341–372.

KNUDSEN, J. 1961. The bathyal and abyssal *Xylophaga* (Pholadidae, Bivalvia). Galathea Report 5:163–209.

KURODA, T. & T. HABE. 1981. A catalogue of molluscs of Wakawama Prefecture, the Province of Kii. I. Bivalvia, Scaphopoda and Cephalopoda. Based on the Kuroda's manuscript (*sic*.) and supervised by Tadashige Habe. Seto Marine Biological Laboratory, Kyoto University, Special Publication Series 7(1):20+301+3 pp.

KURODA, T., T. HABE & K. OYAMA. 1971. The sea shells of Sagami Bay. Maruzen: Tokyo, Japan. 19+741+489+51 pp. 121 pls.

LEYMERIE, A. 1842. Suite du mémoire sur le terrain Crétacé du Département de l'Aube: Mémoires de la Société Géologique de France, sér. 1, 5:1–34, pls. 1–18.

OKUTANI, T. 1968. Bathyal and abyssal mollusca trawled from Sagami Bay and the south off Boso peninsula by R/V *Soyo-Maru*, 1965–1967. Bulletin of the Tokai Regional Fishery Research Laboratory 56:7–56.

OKUTANI, T. 1975. Deep-sea bivalves and scaphopods collected from deeper than 2,000 m in the northwestern Pacific by the R/V *Soyo-Maru* and the R/V *Kaiyo-Maru* during the years 1969–1974. Bulletin of the Tokai Regional Fisheries Research Laboratory 82:57–87.

OKUTANI, T. 2000. Family Xylophaginidae. Pp. 1030–1031 in T. Okutani (ed.), Marine Mollusks in Japan. Tokai University Press: Tokyo, Japan. (in Japanese)

PAILLERET, M., T. HAGA, P. PETIT, C. PRIVÉ-GILL, N. SAEDLOU, F. GAILL & M. ZBINDEN. 2007. Sunken woods from the Vanuatu Islands: identification of wood substrates and preliminary description of associated fauna. Marine Ecology 28:233–241.

PLINT, A. G. & R. K. PICKERILL. 1985. Non-marine *Teredolites* from the middle Eocene of southern England. Lethaia 18:341–347.

PURCHON, R. D. 1941. On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). Journal of the Marine Biological Association of the United Kingdom 25: 1–39.

TAKI, I. & T. HABE. 1945. 'Nihon-san niogai- choka no bunrui' (Systematics of superfamily Pholadoidea in Japan *trans. auct.*). Venus 14(1/4):108–117. (in Japanese)

TAKI, I. & T. HABE. 1950. Xylophaginidae in Japan. Pp. 45–47 in T. Kuroda (ed.), Illustrated Catalogue of Japanese Shells vol. 1(7). 1949–1953. Kyoto, Japan.

TURNER, R. D. 1966. Survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia). The Museum of Comparative Zoology, Harvard University. 265 pp.

TURNER, R. D. 1968. The Xylophagainae and Teredinidae – A study in contrasts. Annual Reports for 1967. American Malacological Union: 46–48.

TURNER, R. D. 1969. Superfamily Pholadacea Lamarck, 1809. Pp. N702–741 in R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Part N. Mollusca 6. Bivalvia. Vol. 2 (of 3). Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas.

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

TURNER, R. D. 1972b. *Xyloredo*, a new teredinid-like abyssal wood-borer (Mollusca, Pholadidae, Xylophagainae). Breviora 397:1–19.

TURNER, R. D. 2002. On the subfamily Xylophagainae (Family Pholadidae, Bivalvia, Mollusca). Bulletin of the Museum of Comparative Zoology 157(4):223–307.

TURNER, R. D. & A. C. JOHNSON. 1971. Biology of marine wood-boring mollusks. Chapter 13. Pp. 259–301 in E. B. G. Jones & S. K. Elteingham (eds.), Marine Borers, Fungi and Fouling Organisms of Wood. Proceedings of the OECD workshop organized by the committee investigating the preservation of wood in the marine environment, 27th March–3rd April, 1968. Organization for Economic Co-operation and Development: Paris.

UESHIMA, R. 2002. Simple methods for DNA preservation in molluscan specimens. Venus 61(1/2):91–94. (in Japanese with English abstract).