

There have been no anatomical studies of Australian material. However, anatomical descriptions and details of functional morphology of some closely related extralimital species have been provided by Hunter (1949), Yonge (1971) and Narchi (1973).

In *Hiatella* the solid shell is whitish in colour with irregular striae, but is phenotypically variable and irregular in shape (Hunter 1949; Yonge 1971; Narchi 1973). The shells of *Panopea* tend to be greyish white, solid and rectangular in shape with smooth regular

curves. The valves are equal and, compared to *Hiatella* species, have fairly regular commarginal ribbing (Noonan 1981). The byssus is absent in adult hiatellids except nestling individuals of *Hiatella* where it is reduced (Yonge 1962); it is absent in boring forms (Hunter 1949). The siphons are particularly large and elongate in *Panopea* species and shell gape is often as wide or wider than the depth of the shell (Yonge 1971, 1982b; Narchi 1973). The foot is digitate and extensible in the young – adapted for locomotion, but reduced in adults (Hunter 1949).

The long, narrow ctenidia are homorhabdic and synaptorhabdic (smooth or plicate) (Yonge 1971; Narchi 1973). The outer demibranch has a short supra-axial extension and is half the width of the inner demibranch. The gills may extend into the basal region of the siphons. The inner demibranch has a marginal groove but the outer demibranch lacks one (Hunter 1949; Yonge 1971; Narchi 1973). Frontal cilia are primarily responsible for the transport of particles (Narchi 1973). The palps are smooth and have several ridges and folds. A long oesophagus leads into the Type IV stomach antero-dorsally. A combined style sac and midgut enter the stomach postero-ventrally. The main typhlosole is sharply curved. The pericardium has an ovate ventricle through which the intestine passes. The paired auricles are large and lobate, and the pericardial gland is auricular (Yonge 1971; Narchi 1973).

The nervous system of hiatellids conforms generally with that of other heterodonts. Hunter (1949) reported a large central, visceral mass of ganglia with smaller cerebral and pedal ganglia, and a pair of siphonal ganglia.

Little is known of reproduction and development in the Hiatellidae. Representatives are gonochoristic and prolonged planktonic development appears to be common (Thorson 1936; Bernard, F.R. 1979).

Hunter (1949) reported the settlement and postsettlement behaviour in *Hiatella* species. The substratum type on which settlement occurs will determine the boring habit or otherwise of the adult. A smooth surface of soft, homogeneous rock or sponge will induce boring whereas hard, creviced rock will result in the adult nestling and anchoring by byssal threads. Hunter (1949) and Ansell & Nair (1969) considered boring in *Hiatella* to occur by mechanical abrasion, without chemical secretions. Trudgill & Crabtree (1987) reported bioerosion of fossil intertidal limestone by *Hiatella* species. Gallardo & Osorio (1978) reported bore holes of *Hiatella* in ascidians (*Polyandrocarpa*, *Phragmatopoma*), gastropods (*Concholepas*, *Fissurella*) and barnacle shells (*Megabalanus*). *Hiatella australis* occurs in similar epibiotic communities in southern Australian waters (Ludbrook & Gowlett-Holmes 1989), but no detailed studies have yet been undertaken.

The northern Pacific *Panopea generosa* ('geoduck') is considered a prized delicacy because of its large size and extensive fleshy siphons. Once common, it is now very rare in shallow waters because of over-collecting (Yonge 1971; Goodwin 1977; Gillingham 1984). In Australia, *P. australis* is not collected for food. Hiatellids are not economically important in Australia although *Hiatella* species may play a minor role in bioerosion and fouling (see Soldatova 1986; Trudgill & Crabtree 1987).

Superfamily PHOLADOIDEA

The Pholadoidea is a superfamily of bivalves comprising the Pholadidae and Teredinidae, all highly specialised for boring into firm substrata such as stiff clay, mudstone, peat, soft or friable rocks, poor-grade cement, shells, woody plant material, or even polyvinyl chloride (PVC) and styrofoam (Pls. 16.2, 16.3). Species of Pholadidae, commonly called piddocks, occur in one or more of these substrata, and are shallow-water, filter-feeders, with the exception of the deep-sea wood borers (Xylophaginae); their primary food source is wood. The Teredinidae, commonly called shipworms, pileworms or, by the Australian Aborigines, cobra (in the north) and warragará (in the south). Pholadoideans have long worm-like bodies (Figs 8.45B, 8.51B) and occur in shallow water,

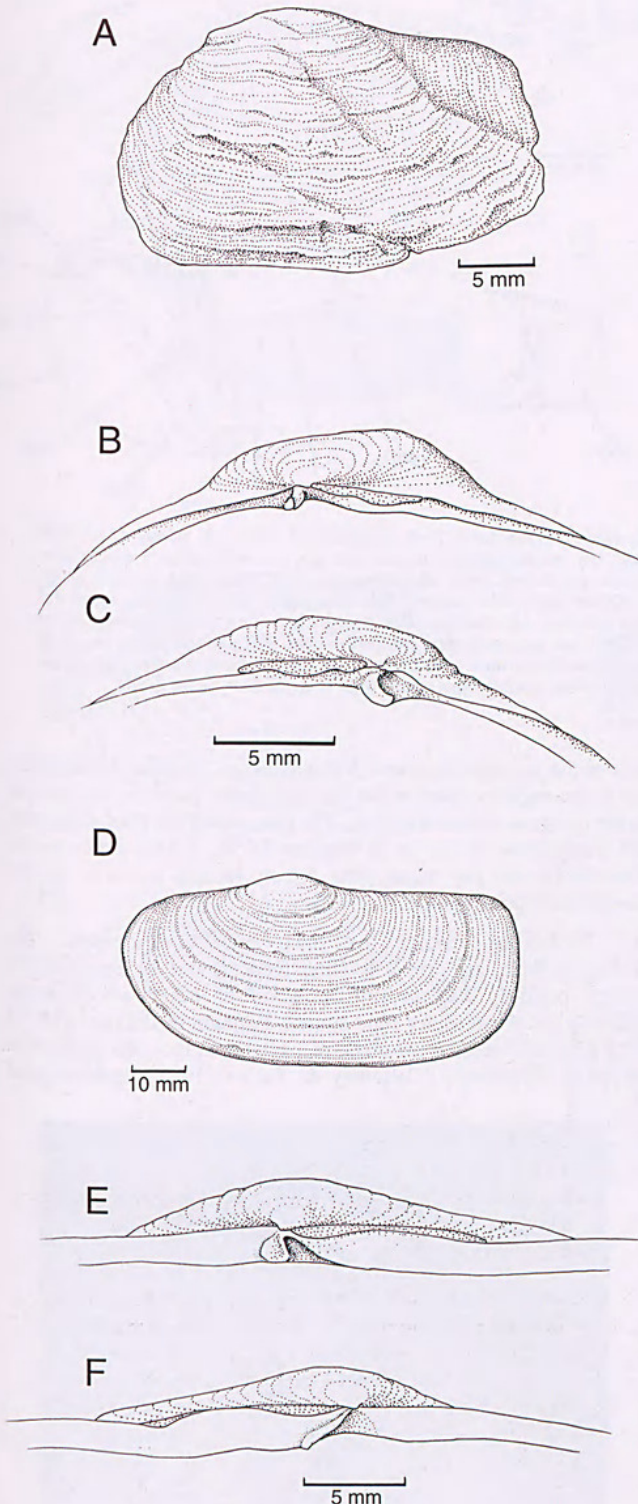


Figure 8.44 Family Hiatellidae. A–C, *Hiattella australis*: A, left shell valve, external view; B, right valve hinge; C, left valve hinge. D–F, *Panopea australis*: D, left shell valve, external view; E, right valve hinge; F, left valve hinge. [S. Weidland]

[R.D. Turner]

The dorsal margins of the valves anterior to the umbones are reflected and form the attachment areas for the anterior adductor muscle which is thus on the outside of the valves. Its contraction brings the valves together against the foot which, during boring, is securely attached to the anterior end of the burrow. The large posterior adductor muscle works antagonistically to the anterior adductor. Its contraction spreads the valves anteriorly, scrapes the denticulate ridges against the end of the burrow and thus enlarges it. The particles removed from the burrow are carried into the mantle cavity and pass out through the inhalant siphon as pseudofaeces in all pholadoideans except those wood borers that utilise the wood as food. The hinge (Figs 8.45D, 8.51C) is reduced to condyles and a small chondrophore for the attachment of the internal ligament which functions to hold the valves in position as they pivot on the condyles when boring. Apophyses, 'ribs', for the attachment of the pedal muscles extend from under the umbones in all pholadoideans

All Pholadidae except the deep sea wood borers, the Xylophagainae, are primarily filter-feeders, and all Teredinidae, except possibly *Kuphus*, utilise wood or other woody plant material as their primary food source. Popham & Dickson (1973) first demonstrated the presence of bacteria in the gills of *Bankia australis*. Waterbury, Calloway & Turner (1983) demonstrated



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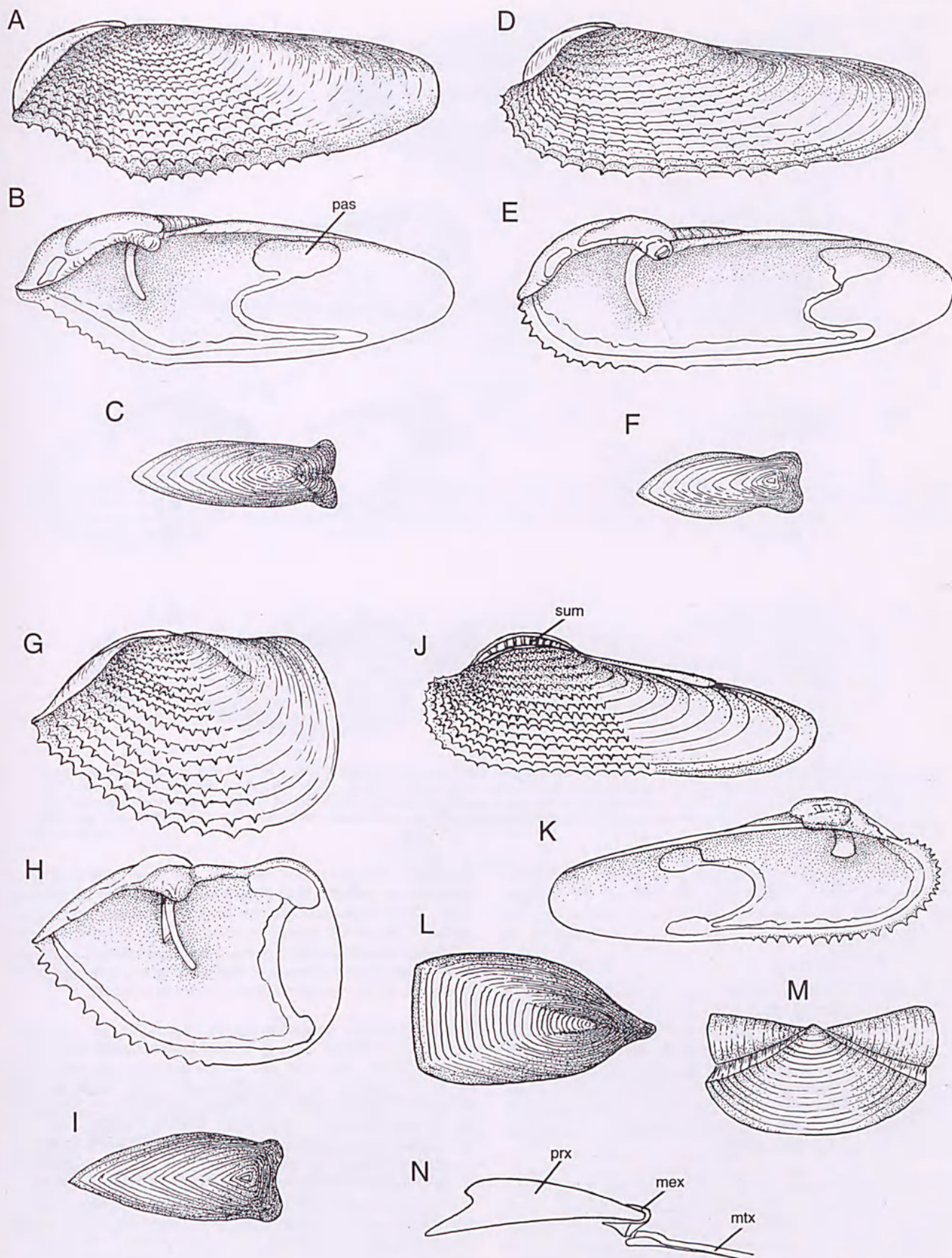


Figure 8.47 Family Pholadidae, subfamily Pholadinae. Shell valves and accessory plates of species in the Australian fauna. A–C, *Barnea obturamentum*: A, left shell valve, external view; B, right shell valve, internal view; C, protoplax. D–F, *Barnea australasiae*: D, left shell valve, external view; E, right valve, internal view; F, protoplax. G–I, *Barnea dilatata*: G, left shell valve, external view; H, right shell valve, internal view; I, protoplax. J–N, *Pholas orientalis*: J, left shell valve, external view; K, left shell valve, internal view; L, protoplax; M, mesoplax; N, arrangement of the accessory plates. mex, mesoplax; mtx, metaplax; pas, posterior adductor muscle scar; prx, protoplax; sum, septate umbone reflection.

[R.D. Turner]

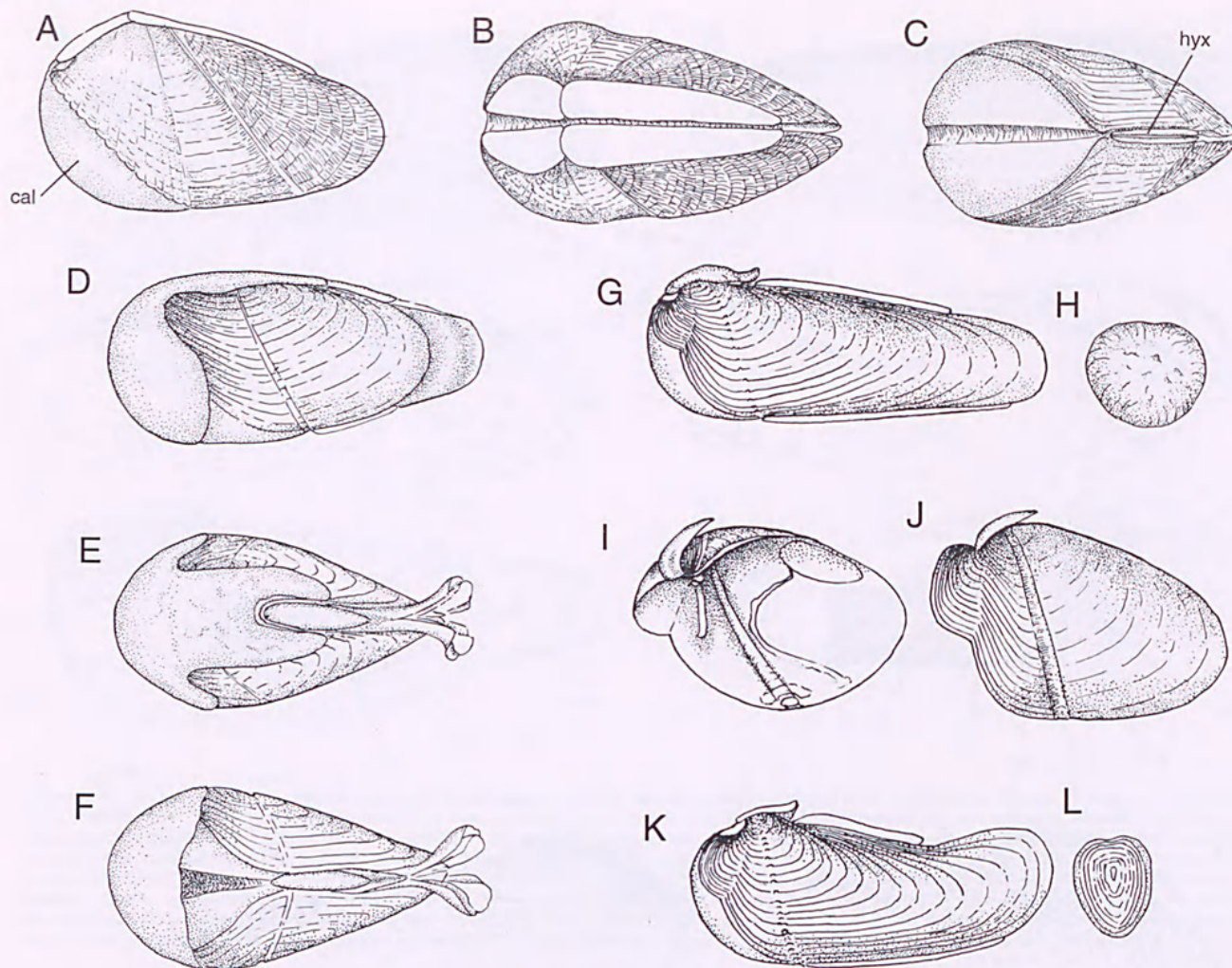


Figure 8.48 Family Pholadidae, subfamily Martesiinae. Shell valves, accessory plates and whole animals of species in the Australian fauna. A–C, *Parapholas quadrizonata*: A, left shell valve, lateral view; B, shell valves, dorsal view; C, closed shell valves, ventral view. D–F, *Aspidopholas obtecta*: D, left shell valve, lateral view; E, shell valves, dorsal view; F, shell valves, ventral view. G–J, *Martesia striata*: G, left shell valve, lateral view; H, mesoplax, dorsal view; I, right shell valve, internal view; J, left shell valve of a young specimen, external view. K, L, *Martesia fragilis*: K, left shell valve, lateral view, L, mesoplax, dorsal view. cal, callus; hyx, hypoplax.

[R.D. Turner]

that bacteria isolated from the gills of six species representing four teredinid genera both digest cellulose and fix nitrogen. Tereidins have also been shown to utilise phytoplankton and dissolved organics. For a review of feeding in teredinids see Mann (1984, 1988).

All pholadids, with the possible exception of some *Xylophaga*, are oviparous as are all teredinids except *Lyrodus*, *Teredo* and *Zachsisia*. Species in these genera are larviparous, brooding their young in the gills of the parent to the feeding stage (straight-hinge veliger) or the settling stage (pediveliger). Life histories of teredinids are reviewed by Turner (1966, 1971a, 1971b), Turner & Johnson (1971) and Calloway & Turner (1988) and the physiological and biochemical energetics of swimming larvae by Mann & Gallager (1985).

Information on the ecology of the 15 or more Australian pholad species is scattered and often anecdotal except for the coral borer, *Jouannetia cumingii* (see Morton, B. 1986a) and *Martesia striata* (see Moore 1947). *Martesia* species are typically wood borers, but do not utilise the wood as food and may be found in laterite, styrofoam and PVC. All other pholads, except the deep-sea wood borers, *Xylophaginae*, are shallow-water, marine, soft rock, shell and coral borers which live in Queensland and along the north coast, with only *Barnea australasiae*, *B. obturamentum* and *J. cumingii* extending into the temperate southern regions (Cotton 1961). This lack of biological data is probably a reflection of the difficulty in collecting these borers and their minor economic importance.

The major factors in the ecology and local distribution of teredinids are salinity, temperature, tidal height and presence of wood. *Bactronophorus*, *Dicyathifer* and *Nausitora* species are typical of low salinity mangrove areas, and also colonise wharves and boats in low salinity areas, whereas *Bankia*, *Teredo* and *Lyrodus* species are common in higher salinities, boring in boats, wharves and other waterfront structures made of wood.

Though generally considered pests, teredinids are of major importance in littoral ecology as recyclers of wood and woody plant material. They are also a delicacy with an oyster-like flavour, favoured by the Aborigines. The piddocks and shipworms become pests only when structures of interest to people are damaged or destroyed. *Martesia striata*, the only Australian pholad considered a pest, was first reported in Australia by Hedley in 1901 and by 1938 it was considered a menace in Middle Harbour, Sydney (Moore 1947). During the CSIRO marine borer survey of 1970–1973, it was collected from Waipa south to Sydney and on the north west coast in the vicinity of Port Hedland (Marshall & Turner 1974). The cost of protection and repair of wooden boats, wharves and other waterfront structures due to the activity of teredinid borers runs into millions of dollars annually. The enormous body of literature on the subject (up through 1954) was abstracted by Clapp & Kenk (1963) and includes some thirty-four Australian authors among them the biologists E.P. Wright, C. Hedley, C.T. Calman, T. Iredale and D.D. Moore. For further references see Marshall-Ibrahim's (1981) report on seasons of larval settlement conducted as part of the CSIRO marine borer survey.

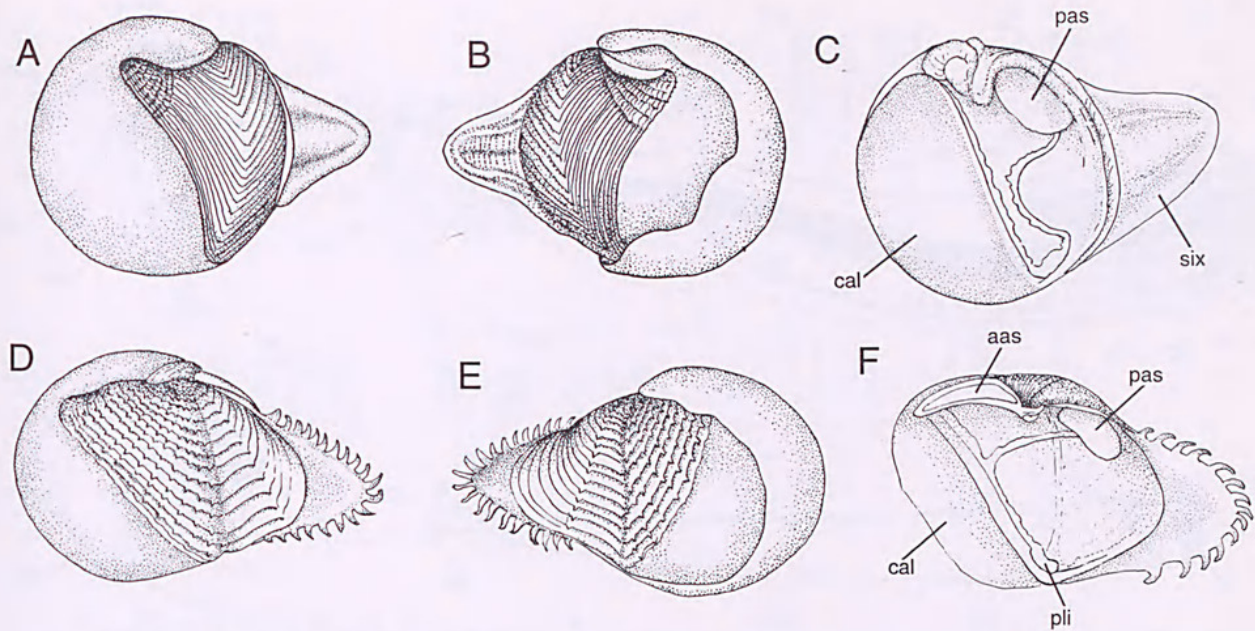


Figure 8.49 Family Pholadidae, subfamily Jouannetinae: shell valves and accessory plates of species in the Australian fauna. A–C, *Jouannetia cumingii*: A, left shell valve, lateral view; B, right shell valve, lateral view; C, right valve, internal view. D–F, *Jouannetia globosa*, shell valves: D, left, lateral view; E, right, lateral view; F, right, internal view. aas, anterior adductor muscle scar; cal, callum; pas, posterior adductor muscle scar; pli, pallial line; six, siphonoplax. [R.D. Turner]

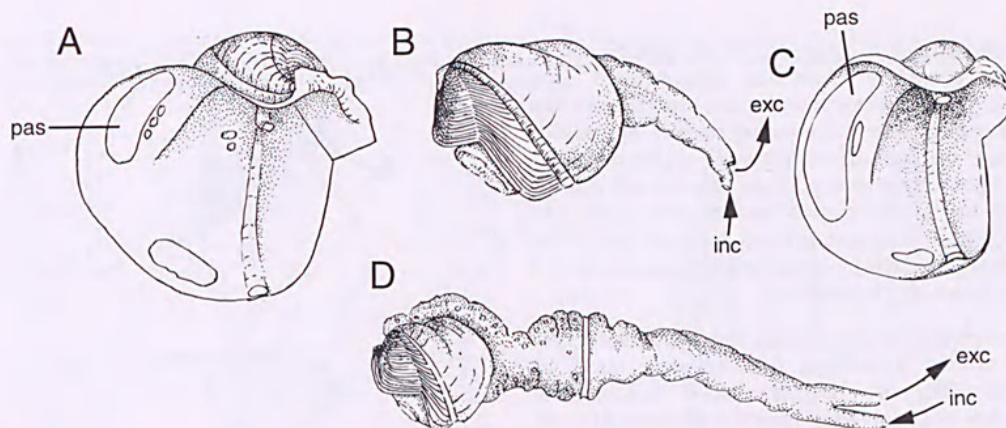


Figure 8.50 Family Pholadidae, subfamily Xylophaginae. Shell valves and whole animals of species in the Australian fauna. A, B, *Xylophaga* sp.: A, left shell valve, internal view; B, animal. C, D, *Xyloredo* sp.: C, left shell valve, internal view; D, animal. exc, exhalant current; inc, inhalant current; pas, posterior adductor muscle scar. [R.D. Turner]

Family Pholadidae

The family Pholadidae, with at least 15 species in Australia, is distinguished from the Teredinidae by lacking siphonal calcareous pallets, by having each gill consisting of two demibranchs (except in the Xylophaginae), and by the presence of accessory plates (hypoplax, mesoplax, metaplax, protoplax, siphonoplax) that cover the exposed anterior adductor muscles and protect the siphons (Fig. 8.45). The animals are capable of retracting into the shell valves. On the basis of the accessory plates, the presence or absence of the apophyses and the number of gill lamellae, the family Pholadidae is divided into four subfamilies (Turner 1969).

The subfamily Pholadinae comprises two fossil and five living genera, two of which, *Barnea* and *Pholas*, occur in Australia. They have elongate shells, apophyses, one to three dorsal accessory plates and grow throughout life (see Fig. 8.47). They live in firm to hard clay, peat or soft rock in the lower littoral or shallow sublittoral. Some live in the lower third of the shore. The siphons of *Barnea dilatata* are shown in Figure 8.47 and those of *Pholas obturamentum* in Plate 16.3.

The subfamily Martesiinae, the largest in the Pholadidae, comprises sixteen genera: eight fossil and eight extant, of which at least three, *Parapholas*, *Aspidopholas* and *Martesia*, occur in Australia. They have apophyses, a mesoplax, metaplax and hypoplax, but the most distinctive feature of the subfamily is the callum, a calcareous structure that closes the pedal gape when boring and growth ceases (see Fig. 8.48). At this stage the foot atrophies and the callum grows forward from the anterior margins of the valves until the two halves meet at the midline and are joined by a periostracal fold. This completely seals the anterior end of the shell except for a small pore in the periostracal connective, probably for water circulation. Some species protect the burrow entrance with a 'chimney' composed of faeces and/or pseudofaeces cemented with mucus from the siphons and shaped to fit snugly into the posterior end of the burrow. They bore into firm mud, mudstone, coral and soft rock, except for the wood-boring *Martesia* species which bore into mangroves, wharves and wooden boats and, because they do not utilise the wood for food, even into styrofoam, and PVC pipes. Martesiines range from low water to depths of about 100 m.

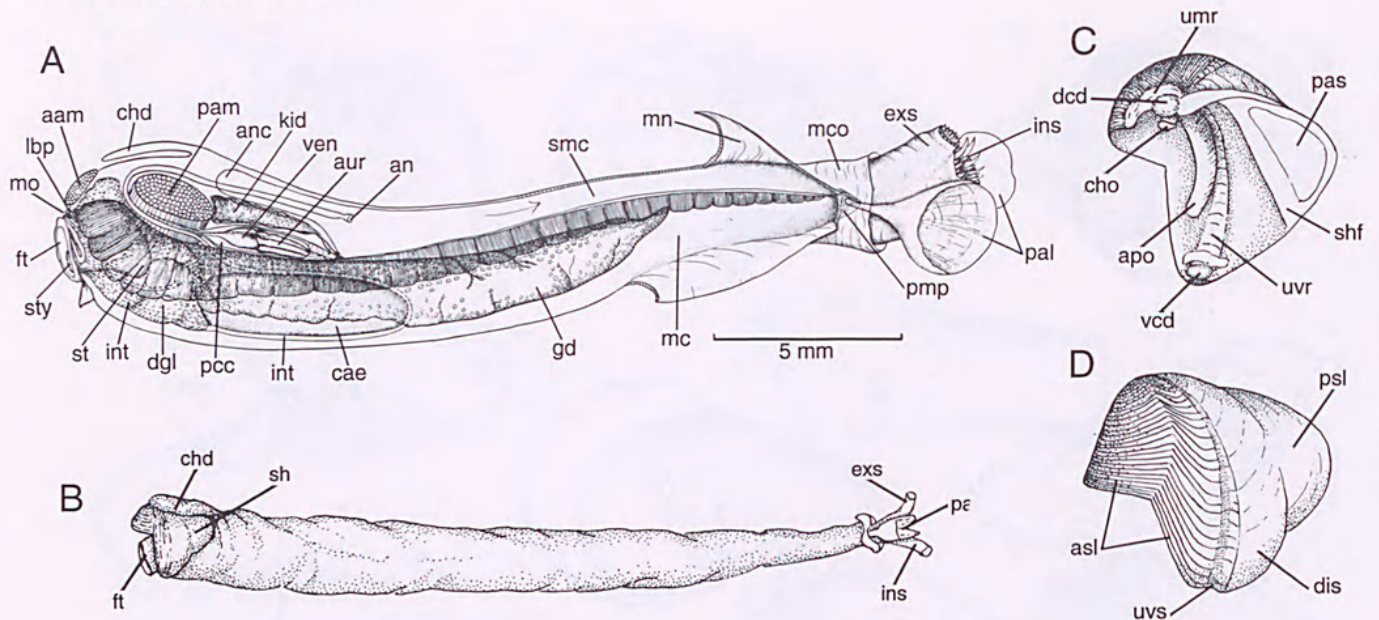


Figure 8.51 Family Tereidinidae. A, internal anatomy of an adult *Teredora malleolus*, one of the least specialised teredinids. B–D, morphological features: B, animal; C, right shell valve, internal view; D, left shell valve, external view. aam, anterior adductor muscle; an, anus; anc, anal canal; apo, apophysis; asl, anterior slope; aur, auricle; cae, caecum; chd, cephalic hood; cho, chondrophore; dcd, dorsal condyle; dgl, digestive gland; dis, disc; exs, exhalant siphon; ft, foot; gd, gonad; ins, inhalant siphon; int, intestine; kid, kidney; lbp, labial palp; mc, mantle (or infrabranchial) cavity; mco, mantle collar; mn, mantle; mo, mouth; pal, pallet; pam, posterior adductor muscle; pas, posterior adductor muscle scar; pcc, pericardial cavity; pmp, protractor muscle of pallet; psl, posterior slope; sh, shell; shf, shelf; smc, suprabranchial (or epibranchial) cavity; st, stomach; sty, crystalline style sac; umr, umbonal reflection; uvr, umbonal-ventral ridge; uvs, umbonal-ventral sinus; vcd, ventral condyle; ven, ventricle. (A, after Turner 1966) [R.D. Turner]

The subfamily Jouannetiinae is composed of two genera, one of which, *Jouannetia* occurs in Australia. Jouannetiines lack apophyses and the pedal retracter muscles are inserted near the posterior adductor muscle. The active boring stage is equivalved, the pedal gape large; the adult nonboring stage of *Jouannetia* is inequivalved, the right siphonoplax is larger than the left and the enlarged callum of the left valve overlaps that of the right (see Fig. 8.49). The mesoplax, if present, is fused to the left half of the callum and displaced to the left by its growth. *Jouannetia* species burrow in coral, soft rock and sandstone.

The subfamily Xylophaginae includes one fossil and three living genera, two of which, *Xylophaga* and *Xyloredo* occur in Australian waters. They are deep-sea wood borers, with teredo-like shells that lack apophyses, have a small mesoplax, and do not produce a callum, and in which the gill consists of a single inner demibranch (see Fig. 8.50). They have a large wood-storing caecum, utilise the wood as food, and have been found in wood dredged from depths of 1051 and 4530 m off Sydney, New South Wales. Examination of wood dredged at other localities around Australia will no doubt produce additional material.

Family Tereidinidae

The family Tereidinidae, with at least 32 species in Australia, is distinguished by having a long worm-like body, a reduced shell with an angled anterior margin (Fig. 8.51D), a large pedal gape, a truncate foot, and calcareous siphonal pallets that close the burrow when the siphons are retracted (Fig. 8.52). The pallets may be in one piece (Fig. 8.53) or composed of numerous elements called cones (Fig. 8.54). Major vital organs are posterior to the shell and the long gills consist of inner demibranchs only (Fig. 8.51A). In *Teredora* and *Uperotus* species the gills extend from the mouth to the siphons (Fig. 8.51A); in all other genera they extend from the posterior end of the pericardium to the siphons. The burrow has a calcareous lining, which is thickened where the siphon and pallet muscles are attached. If the walls of the burrow become thin due to external erosion of the wood or the proximity of other borers, the tube is thickened (see Pl. 16.2). Consequently, a healthy borer may be found in a tube that is better than 60% exposed or the end of which protrudes from the eroded surface of the wood. Following settlement and metamorphosis, all teredinids except *Kuphus* and possibly some

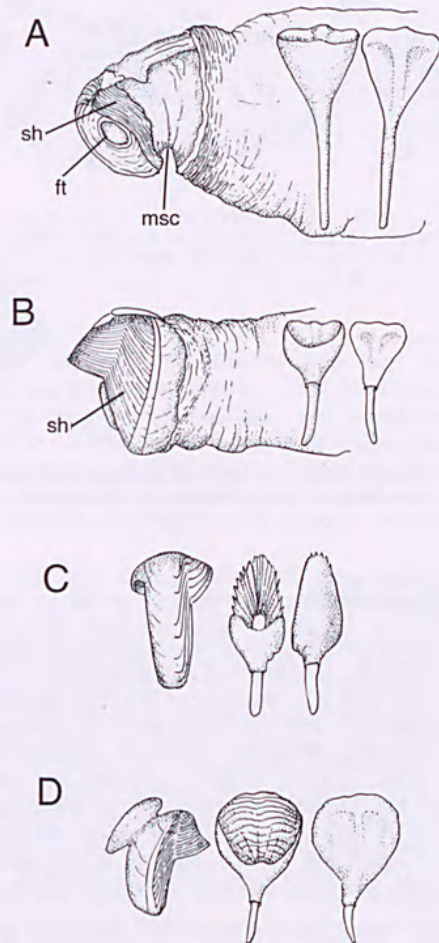


Figure 8.52 Family Tereidinidae. A, subfamily Kuphinae, *Kuphus polythalamia*, anterior end of animal and outer and inner face of pallet. B–D, subfamily Tereidininae: B, *Dicyathifer manni*, anterior end of animal and outer and inner face of pallet; C, *Uperotus clavus*, shell valve, exterior and inner face of pallet; D, *Teredora princepsae*, shell valve, exterior and inner face of pallet. ft, foot; msc, muscular collar sh, shell. [R.D. Turner]

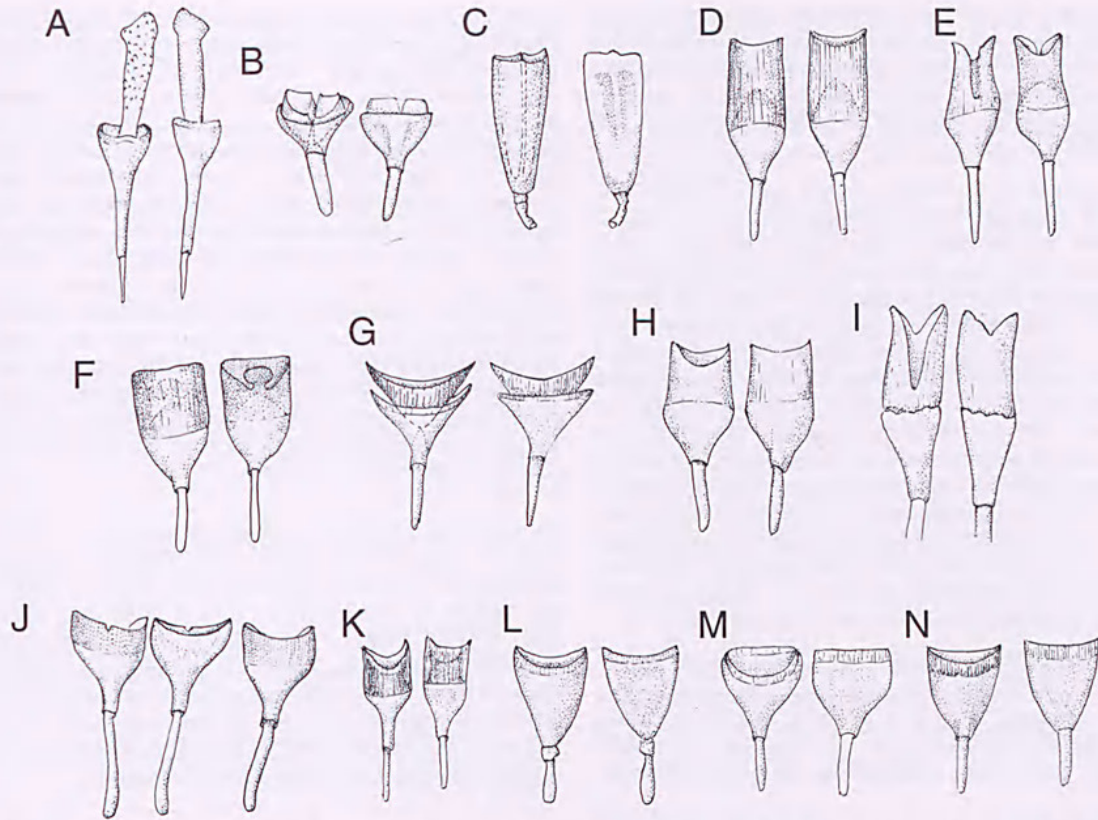


Figure 8.53 Family Teredinidae, subfamily Teredininae, pallets, outer and inner face. A, *Bactronophorus thoracites*; B, *Teredothyra matacotana*; C, *Teredothyra dominensis*; D, *Lyrodus pedicellatus*; E, *Lyrodus bipartitus*; F, *Lyrodus medilobatus*; G, *Lyrodus massa*; H, *Teredo navalis*; I, *Teredo furcifera*; J, *Teredo clappi*; K, *Teredo bartschi*; L, *Teredo mindanensis*; M, *Teredo poculifer*; N, *Teredo triangularis*. [R.D. Turner]

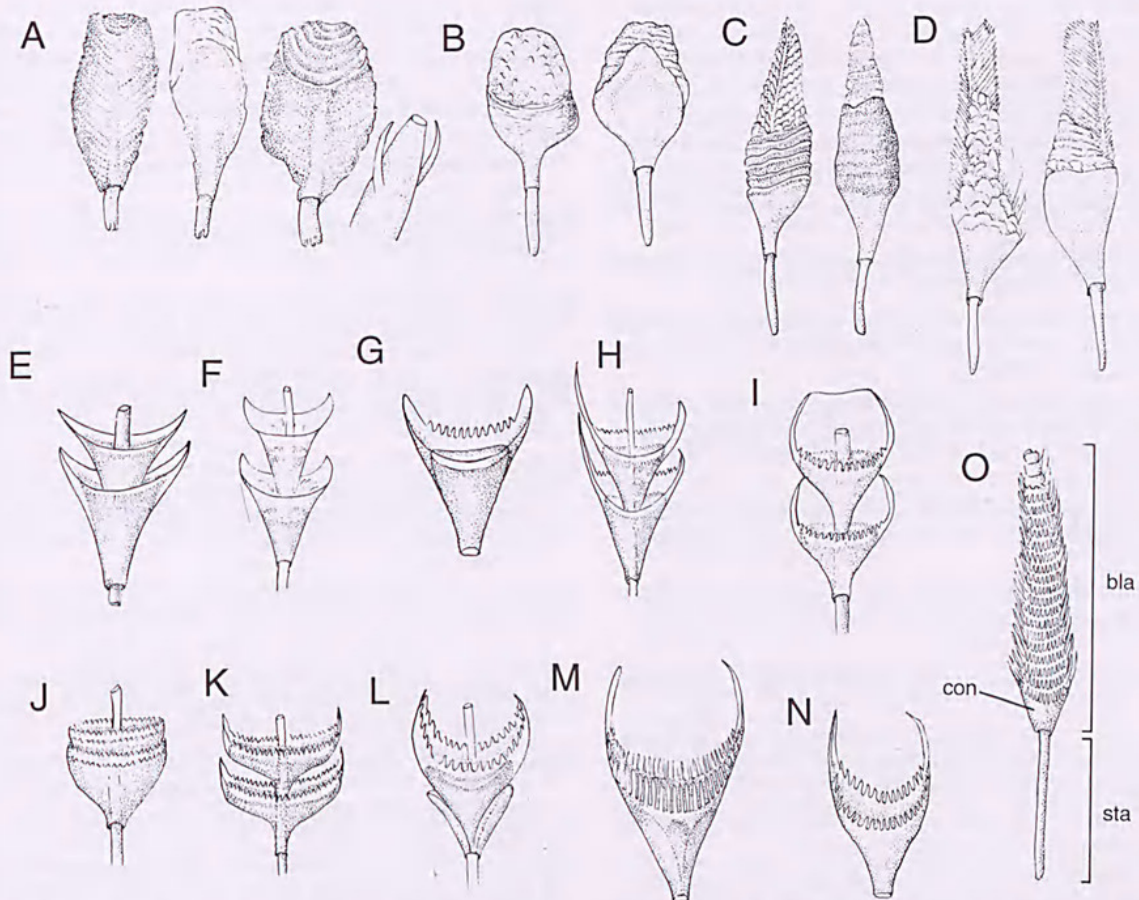


Figure 8.54 Family Teredinidae, subfamily Bankiinae, pallets and cones. A, *Nototerredo edax*, pallet, outer and inner face, and exhalant siphon with lateral tentacles. B, *Spathoterredo obtusa*, pallet, outer and inner face. C, *Nausitora hedleyi*, pallet, outer and inner face. D, *Nausitora dunlopei*, pallet, outer and inner face. E–M, cones or sets of cones from pallets: E, *Bankia carinata*; F, *Bankia campanellata*; G, *Bankia nestalia*; H, *Bankia bipalmulata*; I, *Bankia barthelowi*; J, *Bankia nordi*; K, *Bankia johnsoni*; L, *Bankia rochi*; M, *Bankia gracilis*. N, *Bankia australis*: N, one of the cones of the pallet; O, the stalk and the blade that compose the pallet. bla, blade; con, cone; sta, stalk. [R.D. Turner]

species of *Uperotus*, utilise wood or other plant material as food and bore throughout life or until no further space is available. If this happens they cap the tube anteriorly and, depending on the richness of the phytoplankton, live at a subsistence level or die. On the basis of the pallets and characters of the soft anatomy the family is divided into three subfamilies.

The subfamily Kuphinae comprises a single genus, *Kuphus*, and, on the basis of tubes only, has been reported from the middle Eocene. *Kuphus polythalamia* (Fig. 8.52A), the only living species, is not known in Australia, but is mentioned here because of its confusion with *Dicyathifer manni* (Fig. 8.52B) and because it might well be found on the north coast. Hedley (1895) observed *Kuphus* tubes in Papua New Guinea. Sivickis (1928) described a colony of sand-borers which he called *K. dubia* and said were closely related to *Kuphus arenarius* (= *K. polythalamia*). Anatomical studies by Turner (1966) on *Kuphus* show it to have a small shell, reduced adductor muscles, a muscular collar binding the valves posteriorly, long separate siphons, simple pallets, a reduced visceral mass largely posterior to the shell, and a long pericardium with the ventricular bulb traversed by the intestine. The large tube of an adult may reach 1.5 m in length, 55–60 mm in diameter, and the wall 8 mm in thickness. These enormous tubes are in many museum collections, but most lack data.

The subfamily Teredininae includes ten genera, seven known from Australia. All species bore into wood or woody plant material, have simple pallets, a large posterior adductor muscle, a moderate to large wood-storing caecum, and an intestine that does not traverse the pericardium. Identification of the 24 Australian

species is based largely on the pallets and reproductive mode. Pallets of a selection of Australian species are illustrated in Figures 8.52B–D, 8.53. *Dicyathifer* (Fig. 8.52B) and *Kuphus* (Fig. 8.52A) species have similar pallets, but differ anatomically; the former are always found in wood. *Bactronophorus thoracites* (Fig. 8.53A) and *Dicyathifer manni* (Fig. 8.52B), the largest species in the subfamily, live in mangroves. Species of *Teredothyra* (Fig. 8.53B, C) are relatively rare, and are usually found in fully marine conditions from subtidal to depths of 100 m. *Uperotus* species (for example, Fig. 8.52C) in Australia are nut borers, generally found in old floating *Xylocarpus moluccensis* (a mangrove) as a cluster of closely packed tubes usually with the anterior ends closed, suggesting that they are filter-feeders. *Teredora* species (for example, Fig. 8.52D) typically bore into the underside of floating wood and so are not exposed by a receding tide. All are oviparous except species in *Teredo* (Fig. 8.53H–M) and *Lyrodus* (Fig. 8.53D–G) which are not only larviparous, but also the smallest of the teredinids.

The subfamily Bankiinae includes four genera, all known from Australia. They differ from the Teredininae in having pallets composed of numerous segments which may be closely packed and indistinct in *Nototerodo* (Fig. 8.54A) and *Spathoterodo* (Fig. 8.54B) species; distinct, but with fused segments in *Nausitora* species (Fig. 8.54C, D); or with individual segments (cones) set on a long stalk as in *Bankia* species (Fig. 8.53E–O). Species of *Spathoterodo* and *Nausitora* often have calcareous encrustations at the distal end of the pallets. They are all oviparous wood borers; many are found in brackish water.

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