

CRETACEOUS WOOD-BORING BIVALVES FROM WESTERN ANTARCTICA WITH A REVIEW OF THE MESOZOIC PHOLADIDAE

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ABSTRACT. Antarctic wood-boring bivalves are described from the Kotick Point Formation, Gustav Group (Early Cretaceous) and the Marambio Group (Late Cretaceous) of the James Ross Island group, and from the Early Cretaceous part of the Fossil Bluff Formation of eastern Alexander Island. They are identified as the pholadid genera *Opertochasma*, *Teredina*, *Turnus*, and *Xylophagella*. All but *Turnus* are recorded here from the Antarctic for the first time. The following new species are described: *Opertochasma psyche*, *Teredina jeffersoni*, *Turnus kotickensis*, and *Xylophagella truncata*. Particularly well-preserved accessory plates occur in *Opertochasma* and *Teredina*. The borings containing the bivalves are referred to the ichnogenus *Teredolites*. Preparation techniques used include serial sectioning and casting in silicone rubbers. The stratigraphical and geographical distributions of the genera and their palaeoecology are briefly discussed. First appearances of world-wide Mesozoic pholadid genera are reviewed and an attempt is made to construct a phylogeny for the early history of the group. *Teredolites* is known from Pliensbachian time, but the earliest body fossil, '*Teredo*' *australis*, is Middle Jurassic in age and of doubtful generic affinity. *Opertochasma* and *Turnus* appeared in the Late Jurassic and *Xylophagella* in the Early Cretaceous. During the Late Cretaceous the group began to flourish and diversify.

HITHERTO the earliest record of the family Pholadidae in the Antarctic was that of Gazdzicki *et al.* (1982) who reported *Penitella* from borings in a lithic hard-ground within Pliocene glaciomarine sediments of King George Island, South Shetland Islands (62° 08' S., 58° 07' W.). However, these specimens belong to the genus *Pholadidea*, which is known to occur in austral regions today (G. Kennedy, pers. comm.). L. R. Cox (in Bibby 1966, p. 23) determined *Turnus*(?) sp. from the Late Cretaceous, Marambio Group (formerly the Snow Hill Island Series), James Ross Island. Although the genus was originally believed to have been a teredinid (Gabb 1864), it is regarded here as a probable pholadid. Taylor *et al.* (1979, p. 20, pl. 8f) figured borings in wood from eastern Alexander Island and illustrated an unlined boring containing a bivalve which they referred to *Teredo*, a member of the Teredinidae. This material has been re-examined and the figured specimen is reidentified as *Opertochasma psyche* sp. nov. Lined borings also are present in the same assemblage and contain *Turnus* sp. Both these taxa are placed in the Pholadidae. Francis (1986) has recently recorded *Teredolites* from Cretaceous wood from Vega Island, and figured further examples from The Naze, James Ross Island, in which traces of shell are still visible. Lined borings associated with wood of Early Tertiary age were described by Sharman and Newton (1898), from Seymour Island, and attributed to *Teredo*.

Although fossil driftwood is widespread in marine deposits of the Cretaceous of Antarctica, associated wood-boring bivalves have hitherto attracted little attention. The situation is similar elsewhere in Gondwanaland. However, Stoliczka (1870-1871) has described Indian forms; the various records from southern Africa are listed by Du Toit (1954) with source references; and examples are also known from South America (Stanton 1901; Wilckens 1905) and from Australia (Skwarko 1972). Elsewhere references are very scattered and there is considerable scope for taxonomic revision of existing collections.

The present article provides the first full descriptions of Antarctic Cretaceous wood-boring bivalves, and furthermore describes the techniques by which they can be prepared for study. The

importance of these Antarctic specimens is that they are particularly well preserved. Many of the specimens show the delicate structures of the hinge, accessory plates, and other structures in place, including apophyses, callum, hypoplax, mesoplax, metaplax, and siphonoplax. All the specimens collected so far appear to belong to the family Pholadidae. Pallets, characteristic of the family Teredinidae (e.g. Elliot 1963, p. 315), were not found in any of the borings in pieces of fossil wood from the Antarctic collections.

Hoagland and Turner (1981) indicated that the fossil record of the Pholadacea was meagre and that the fossilization of marine wood as a borer substrate is relatively rare in comparison to lithic substrates. In the present author's experience, fossil marine driftwood is by no means rare, and when found in Cretaceous deposits in northern Europe commonly contains borings associated with the shells of the original bivalve constructors. The same situation is true of Cretaceous rocks in south-western Madagascar (T. J. Palmer, pers. comm. 1987), and in Antarctica. However, in the Jurassic deposits of all regions of the world the shells of wood-boring bivalves do appear to be genuinely rare, and are generally poorly documented. The present article indicates that there is much potential in the fossil pholadacean record.

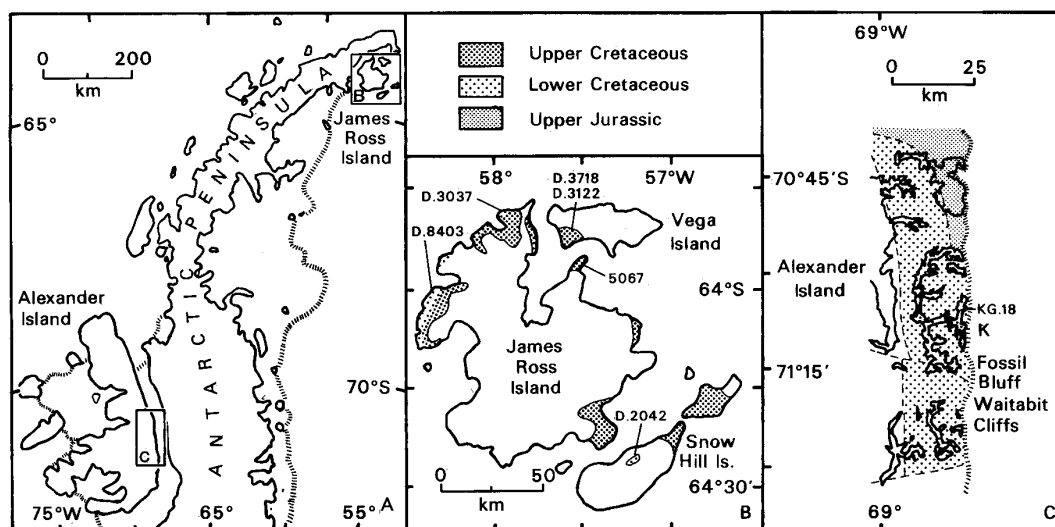
Stoliczka (1870, pp. 17-23) provided the first important taxonomic summary of fossil and Recent Pholadinae. Recent monographs on the family include those of Turner (1954, 1955), Knudsen (1961), and Kennedy (1974). Turner (1969, pp. N702-729) has summarized generic occurrences of both fossil and modern pholadids and Vokes (1980, pp. 187-191, 252) updated the list of known generic names in the family. The phylogenetic relationships of Mesozoic Pholadidae on a world-wide level are still only poorly known, mainly because of the lack of standardized descriptions of material that is well preserved. Considerably more well-preserved material needs to be described before the full Jurassic and Cretaceous history of the pholadaceans is elucidated.

This work was to have formed part of a more comprehensive study of the Cretaceous wood of Antarctica to be undertaken in conjunction with Dr Timothy Jefferson with some notes on the borings by myself. Unfortunately, Dr Jefferson's untimely death prevented the writing of this article in full; however, he had already made important contributions to the palaeobotanical knowledge of Alexander Island (Jefferson 1981, 1982*a, b*). His microphotographs of the wood, along with all the original specimens, including both wood and the bivalves which are illustrated here, are now stored at the British Antarctic Survey (BAS), Madingley Road, Cambridge. The specimen numbers are given as, e.g. KG.18.20a, which indicates that the specimen was collected from Scientific Station KD.18, and that the specimen is number 20 from that station. The suffix 'a' indicates that the original specimen has been prepared into fragments, each designated by a separate letter.

STRATIGRAPHY

Fossil wood associated with wood-boring bivalves occurs in the Early Cretaceous of Alexander Island and the Early and Late Cretaceous of the James Ross Island group, adjacent to the Antarctic Peninsula. The convention of using 'Late' and 'Early' for qualifying chronostratigraphic units and 'Lower' and 'Upper' for formal lithostratigraphic units, as used by Harland *et al.* (1982), is followed here. The localities from which specimens were obtained are shown in text-fig. 1, and the stratigraphical relationships of the deposits are summarized in text-fig. 2.

The specimens from south-east Alexander Island, at Georgian Cliff, occur in the Early Cretaceous part of the Fossil Bluff Formation (text-fig. 1). This formation also contains drifted, scattered plant remains dominated by conifer shoots and robust cycadophytes (Jefferson 1981). The biostratigraphy of the Fossil Bluff Formation was discussed by Taylor *et al.* (1979) and, on the basis of its diverse fauna of ammonites, belemnites, and bivalves, was assigned a Tithonian to Albian age. Bored wood was found in the central part of the section at Georgian Cliff, in highly tuffaceous sandstone units. Associated with the wood is the inoceramid *Anopaea trapezoidalis* (Thomson and Willey), which Crame (1981*b*) believed was as early as Berriasian, but later (Crame 1982, p. 774) assigned to a younger age in undifferentiated Early Cretaceous strata. At Waitabit



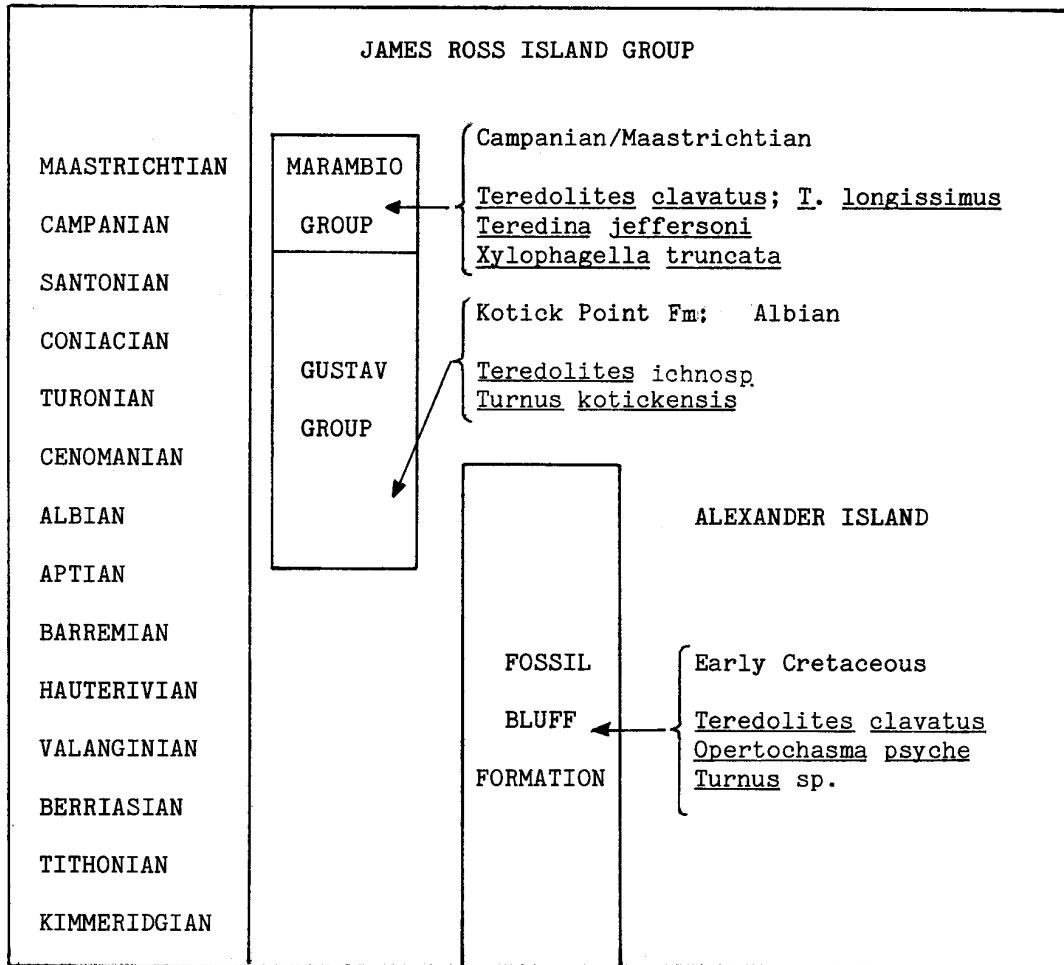
TEXT-FIG. 1. Locality maps for Cretaceous wood-boring bivalves in western Antarctica. K = Locality K, Georgian Cliff.

Cliffs, Taylor *et al.* (1979) also recorded wood from a younger marine sequence which is of Aptian age. The sequence contains a fauna of bivalves, ammonites (including *Sanmartinoceras* and heteromorphs in the lower part and *Eotetragonites* near the top), gastropods, belemnites, brachiopods, and fish fragments.

Most of the specimens from the James Ross Island group come from the Marambio Group (Rinaldi 1982) (formerly the 'Snow Hill Island Series' of Bibby 1966). The lithostratigraphic terminology of the area has been recently revised by Ineson *et al.* (1985). Howarth (1966) regarded the ammonites found throughout the 'Snow Hill Island Series' as indicating an early to mid-Campanian age. However, work on inoceramid bivalves indicated that the sequence covers a much greater time range extending from early Senonian to middle Campanian (Crame 1981a, p. 53). A recent study by Henderson and McNamara (1985) of ammonites from western Australia suggests that some of these assemblages may be Maastrichtian age. Bibby (1966) described assemblages from five localities within the 'Snow Hill Island Series' outcrop. These assemblages contained ammonites, bivalves, serpulids, crustaceans, and fish. Bibby recorded abundant fossil wood on James Ross Island, and although *Turnus* sp. was recorded by Cox (in Bibby 1966, p. 230) there was no further discussion of the specimens. One assemblage from the Lower Kotick Point Formation in the Prince Gustav Group on western James Ross Island, which was collected in association with the ammonites *Silesites* and *Anagaudryceras*, was regarded by Thomson (1984a, p. 87; 1984b, p. 314) as of Albian age.

PRESERVATION AND PREPARATION

The bivalves are preserved in calcite replacing the original aragonite. The internal growth structures of specimens of *Opertochasma*, which were sectioned, had been mostly destroyed during diagenesis. The periostracum is generally preserved as a distinct dark organic film covering the exterior of the shell, or is unsupported in areas such as the callum which may be completely periostracal. The periostracum may form conspicuous raised lamellae or flaps on the shell posterior that are similar to those found on the posterior slope of modern *Parapholas* and *Lignopholas*. Some recrystallization



TEXT-FIG. 2. Generalized stratigraphy of the strata of eastern Alexander Island and the James Ross Island group, showing distribution of Cretaceous wood-boring bivalves and associated trace fossils.

during diagenesis has been disruptive, causing separation both between the inner and outer shell surfaces and between the shell and the periostracum. Most shell interiors are filled with secondary calcite which has enveloped delicate interior structures and made them suitable for sectioning. Sometimes the shells are incompletely infilled and cement fringes occur as shown in the encrusted apophyses of *Teredina* (see text-fig. 11k). Some weathered specimens are preserved as internal and external moulds. Such specimens were used to construct casts using silicone rubber in the manner described by Kelly and McLachlan (1980).

The serial sectioning technique, using a Capco Annular Saw and described by Joysey and Cutbill (1970), was used here on a single specimen of *Opertochasma* (see text-fig. 8; Pls. 26 and 27). The results were particularly encouraging and the technique is recommended for further studies of this group of bivalves. The technique shows up particularly delicate structures of the hinge and accessory plates, and clearly illustrates the difference between calcitic shell and periostracal tissue. Specimens selected should be robust and secondarily infilled (e.g. with calcite). Delicate and broken

specimens should be impregnated and repaired with epoxy resin. Serial cuts were made at spacings of 0.5 mm and the slices mounted temporarily on glass slides using Canada Balsam. The exposed sides of the slices were ground flat on a glass plate using carborundum powder. The ground surfaces were fixed to microscope slides using 'Araldite' for permanent adhesion, and temporary adhesive and mount were removed by heating and washing in alcohol. The slices were ground further and coverslips attached with Canada Balsam. Acetate peels would also be a satisfactory and economical method for studying such specimens.

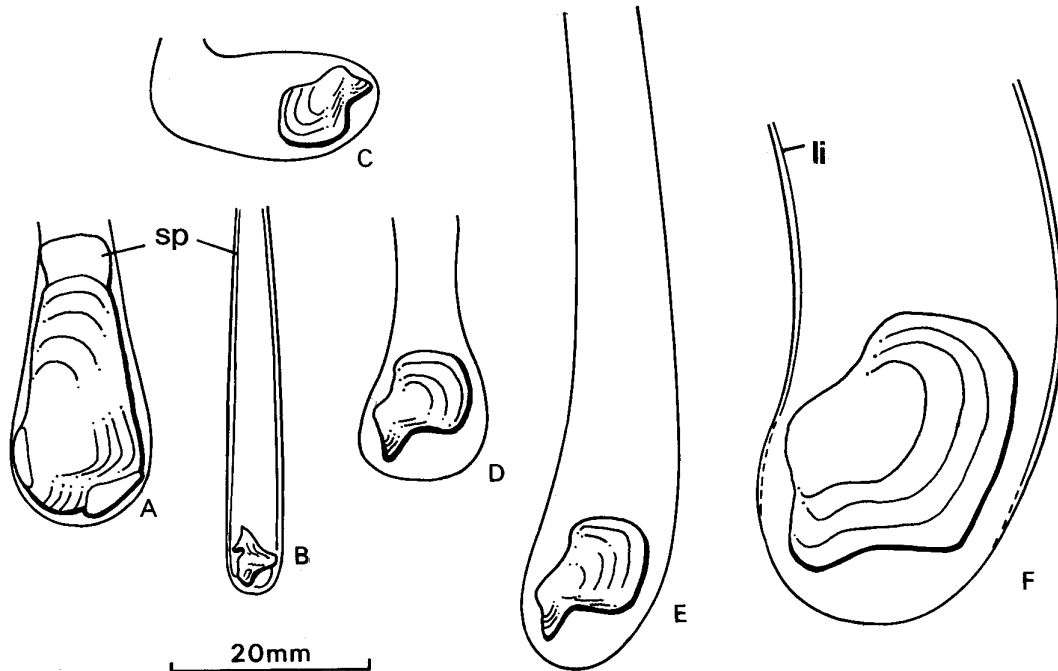
BORINGS

Although club-shaped borings in wood are common in Mesozoic and younger rocks, they are frequently assigned names that should more correctly be applied to the animals which made the borings rather than to the trace fossils themselves. As discussed by Kelly and Bromley (1984), the earliest available suitable ichnogenetic name is *Teredolites* Leymerie, 1842. This name was introduced for Early Cretaceous specimens from eastern France of which the constructor is unknown, and which, in strict zoological terms, are taxonomically indeterminate. *Teredolites* is used here to cover club-shaped borings in a woody substrate regardless of what organism made them. In contrast the ichnogenus *Gastrochaenolites* Leymerie, 1842 is similarly shaped but it has a lithic substrate. Kelly and Bromley (1984) recommend that the ichnospecies *T. clavatus* Leymerie be used for the short borings that are usually perpendicular to the grain of the wood, and *T. longissimus* Kelly and Bromley, for distinctly more elongate borings, usually parallel to the grain (see also Bromley *et al.* 1984).

The size and shape of shells of the bivalves in relation to the borings in which they are found in fossil wood from Antarctica are shown in text-fig. 3. All are club-shaped, approximately circular in cross-section, have a narrow aperture, and swell internally to a bluntly rounded base. The axis of the borings varies from straight to contorted. The neck of the boring is commonly perpendicular or oblique to the outer surface of the wood, but the deeper parts of the boring may be aligned with the long grain of the wood. The dimensions of the borings are discussed in turn with each bivalve species. Most of the borings described here are unlined. However, those of *Turnus* have a thin calcitic lining, not to be confused with the elongate siphonoplax of *Teredina*, which is an extension of the shell proper.

CALCAREOUS LININGS TO BORINGS

The linings of the borings also cause problems in loosely used nomenclature. Strictly speaking, they are secretions of the soft body of the mollusc, rather than a trace which deserves an ichnological name. Thus Kelly and Bromley (1984) have disregarded them with regard to ichnoterminology. However, they are common and need a name. The most useful term is the informal name 'teredolithus', which was introduced by Bartsch (1930). This name, however, is neither a zoological nor an ichnological species or generic name and should not be italicized. The linings are distinct from the siphonoplax because they are not continuous with the shell, whereas the siphonoplax is. The original constructor of teredolithus tubes may be difficult to identify when the original lignic substrate has been destroyed. Such tubes have been commonly misidentified since their description as the worm '*Serpula amphibaena*' by Goldfuss (1831, p. 239, pl. 70, fig. 16), from Cretaceous deposits in Bochum, Westfalia and in Maastricht. These tubes have also been referred without justification to *Cerambycites*, *Fistulana*, *Gastrochaena*, and *Teredo* (Woods 1909, p. 235). However, Frič (1893) and Müller (1898) found associated bivalves and calcareous teredolithus tubes (see also remarks after *Turnus kotickensis* sp. nov. below). Such teredolithus/bivalve associations are rare but significant. The problem is that the *amphibaena* tubes were almost always found in chalk facies without any trace of the original woody substrate which had decomposed completely, either before burial and lithification, or after burial and before compaction preceding lithification. These calcite tubes were readily preserved in contrast to the aragonite shells themselves. The tubes were



TEXT-FIG. 3. Sketch reconstructions showing the variation in the ichnogenus *Teredolites* caused by different wood-boring bivalve genera. A, *Opertochasma* (KG.18.30). B, *Teredina* (D.2042.5). C-E, *Xylophagella* (C, D, D.3122.7; E, D.5067). F, *Turnus* (KG.18.30). Borings of *Opertochasma*, *Teredina*, and *Xylophagella* are unlined; that of *Turnus* has a calcareous lining (li). *Teredina* has a conspicuous siphonoplax (sp) which is calcareous, whereas that of *Opertochasma* is not calcareous.

constructed as a protection against exposure during life of the soft body of the organism as the substrate was broken down by biological degradation and other processes. In teredinids, the tubes serve as muscle attachment following the drastic reduction of the shell. The palaeoecological significance of these linings to the borings has been discussed by Savazzi (1982) and Seilacher (1984).

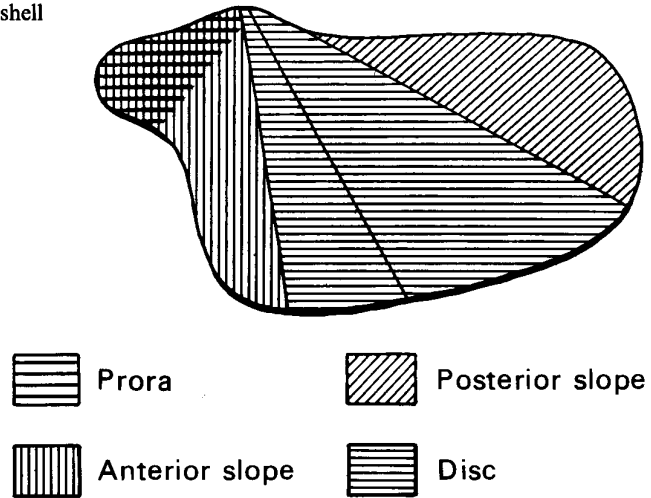
PHOLADID BIVALVE TERMINOLOGY

Some of the general morphological terms used here for pholadid bivalves are illustrated in text-fig. 4. Others are given in text-fig. 5 (*Opertochasma*) and text-fig. 9 (*Teredina*). The terminology of Turner (1954, pp. 11-13, pl. 6; 1969, pp. N702-706) and Kennedy (1974, pp. 11-13) is used below with the following exceptions:

Beak. Used by Turner (1969, p. 704, fig. E163) for the anterior extremity of the shell above the anterior pedal gape or callum. In the more widely used non-pholadid terminology for bivalves, Turner's use of 'beak' causes confusion with the same term used earlier in the volume by Cox (1969, p. N103) for the 'nose-like angle located along or above the hinge margin, marking point where growth of the shell started'. It is preferred here to introduce the new term 'prora' to replace beak *sensu* Turner (1954, 1955, 1969), Knudsen (1961), and Kennedy (1974).

Prora (text-fig. 4); a new term here defined as the anterodorsal part of the anterior slope, which terminates anteriorly either bluntly or acutely above the pedal gape. It may be sharply or obscurely

TEXT-FIG. 4. Some principal features of the shell exterior in pholadid bivalves.



delimited from the posteroventral part of the anterior slope and by the angulation of the commarginal ornament passing around the border of the pedal gape (see 'beak' above).

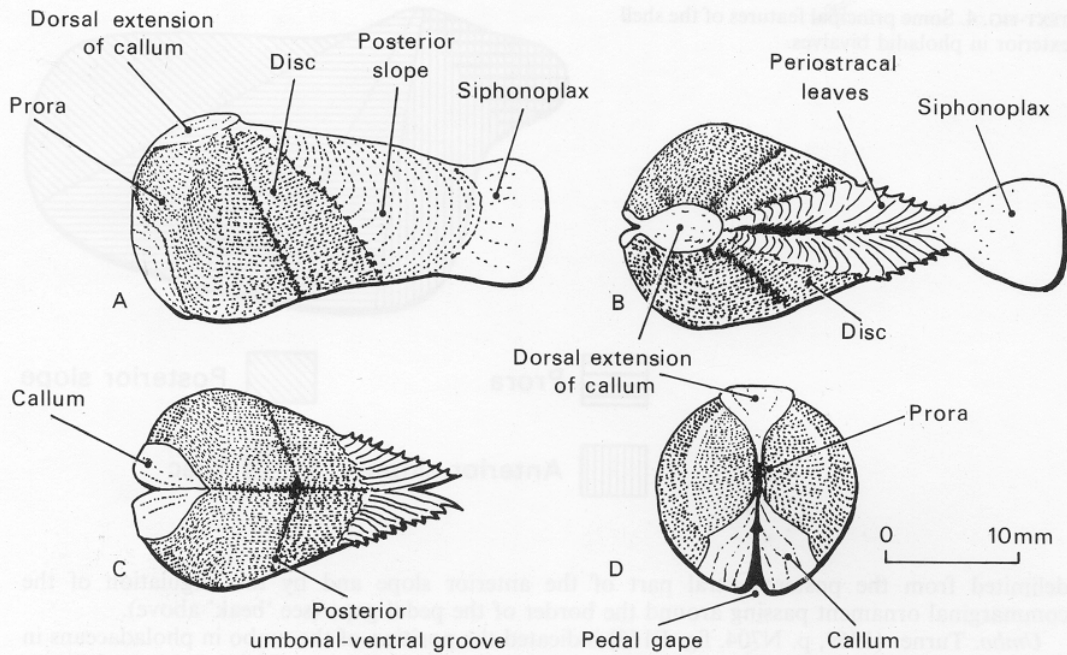
Umbo. Turner (1969, p. N704, fig. E163) indicated the position of the umbo in pholadaceans in the same position as Cox (1969, p. N103) used beak for other bivalves. The definition of Cox is followed here, namely the 'region of valve surrounding point of maximum curvature of longitudinal dorsal profile and extending to beak when not coincident with it'.

SYSTEMATIC PALAEOONTOLOGY

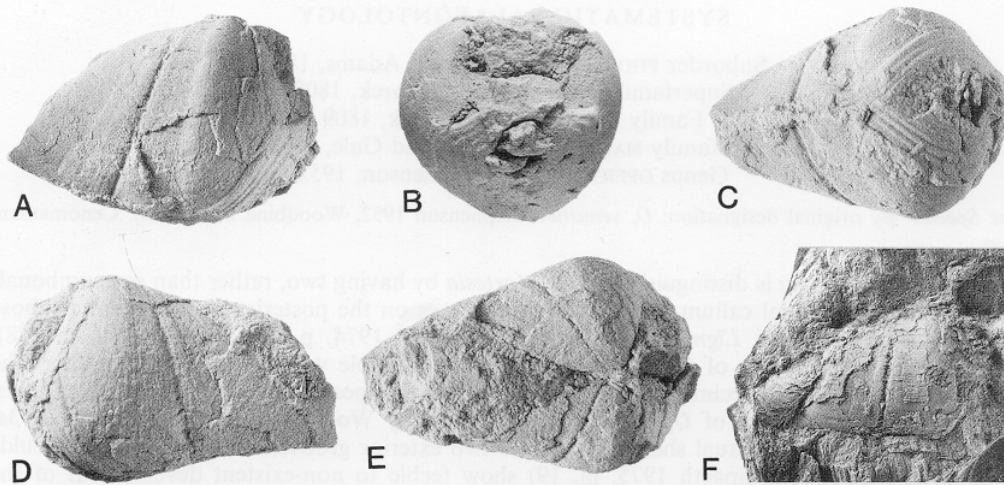
Suborder PHOLADINA Adams and Adams, 1856
 Superfamily PHOLADACEA Lamarck, 1809
 Family PHOLADIDAE Lamarck, 1809
 Subfamily MARTESIINAE Grant and Gale, 1931
 Genus OPERTOCHASMA Stephenson, 1952

Type Species. By original designation: *O. venustum* Stephenson 1952, Woodbine Formation, Cenomanian, Texas.

Remarks. *Opertochasma* is distinguished from *Martesia* by having two, rather than one, umbonal-ventral grooves, a partial callum, and periostracal leaves on the posterior slope similar to those found in *Parapholas* and *Lignopholas* (see also Kennedy 1974, p. 60; Speden 1970, p. 148). Unfortunately, assemblages of *Opertochasma* show considerable variation in the strength of the second groove and some specimens may resemble *Martesia*, especially if they are internal moulds. For example, the specimen of *Opertochasma* illustrated by Woods (1909, pl. 38, fig. 8) as *M. constricta* (Phillips) is an actual shell showing the two exterior grooves, whereas internal moulds of the same species (e.g. Spaeth 1975, pl. 19) show feeble to non-existent development of the anterior groove. There is a prominent strong internal rib under the posterior groove and under the anterior groove almost none. The shell is usually large relative to the size of the boring. *Opertochasma* has a callum, mesoplax, metaplax, and siphonoplax. Although the hypoplax was not recorded in the original description of *Opertochasma*, it was recorded subsequently by Speden (1970, p. 147) and Kennedy (1974, p. 61).



TEXT-FIG. 5. Sketch reconstruction of the exterior of *Opertochasma psyche* sp. nov., Fossil Bluff Formation, Early Cretaceous, Alexander Island. A, left lateral aspect. B, dorsal aspect. C, ventral aspect (without siphonoplax). D, anterior aspect.



TEXT-FIG. 6. *Opertochasma psyche* sp. nov., Fossil Bluff Formation, Early Cretaceous, locality K, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island. A-C, internal mould of paired valves. A, right lateral, B, posterior and C anteroventral aspects, KG.18.30e, $\times 3$. D, E, holotype, internal mould of paired valves. D, left lateral, E, dorsal aspects, KG.18.30f, $\times 3$. F, right valve, internal mould with some shell attached, *in situ*, in wood, KG.18.30c, $\times 2$.

Species ascribed to *Opertochasma* include:

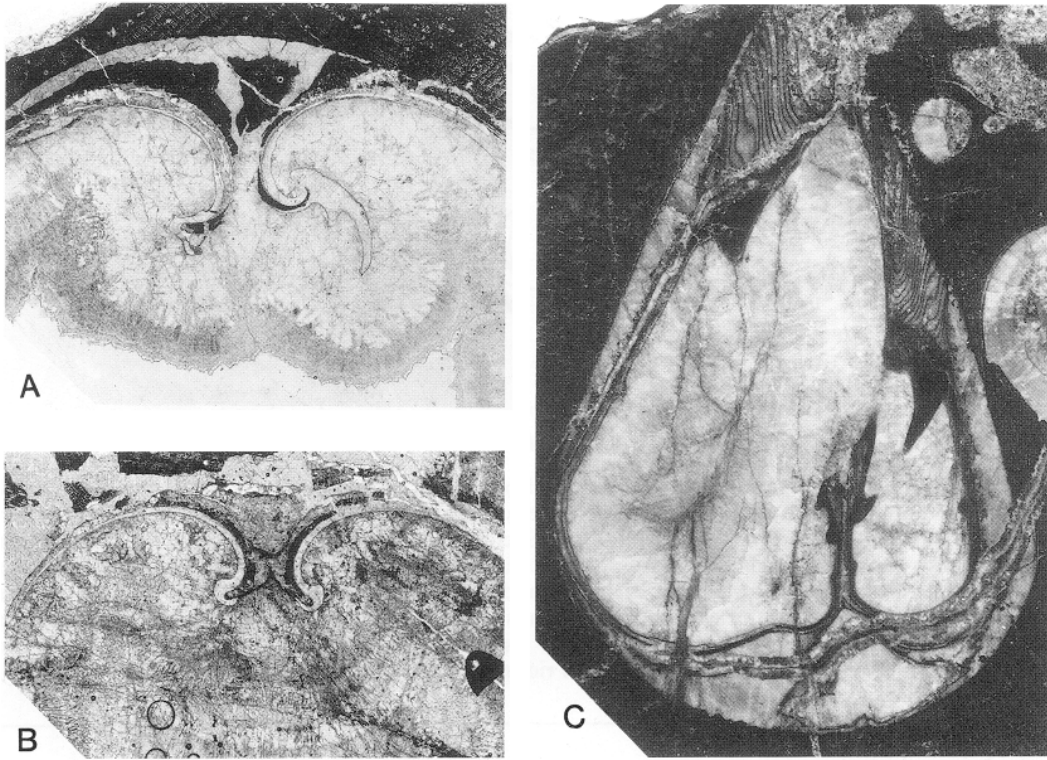
- O. constrictum* (Phillips 1829), Early Cretaceous, England;
- O. malonianum* (Cragin 1905), Late Jurassic, Texas;
- O. mersum* (Stoliczka 1870), Cenomanian, south India;
- O. sanctaerucis* (Pictet and Campiche 1864), Albian, Switzerland;
- O. subconicum* Stephenson 1952, Cenomanian, Texas;
- O. subcylindricum* (d'Orbigny 1845a), Albian, eastern France;
- O. venustum* Stephenson 1952, Cenomanian, Texas;
- O. turneri* (Hickman 1969), Oligocene, Oregon.

Distribution. Kimmeridgian–Tithonian and Cenomanian of Texas; Ryazanian to Cenomanian of north-west Europe; Cretaceous of South Dakota; Cenomanian of southern India; Albian of Mangyshlak and northern Caucasus; Barremian and Campanian–Maastrichtian of Argentina; Early Cretaceous of western Antarctica; Late Cretaceous of California; Palaeocene or Eocene(?) of southern California; Oligocene of Oregon.

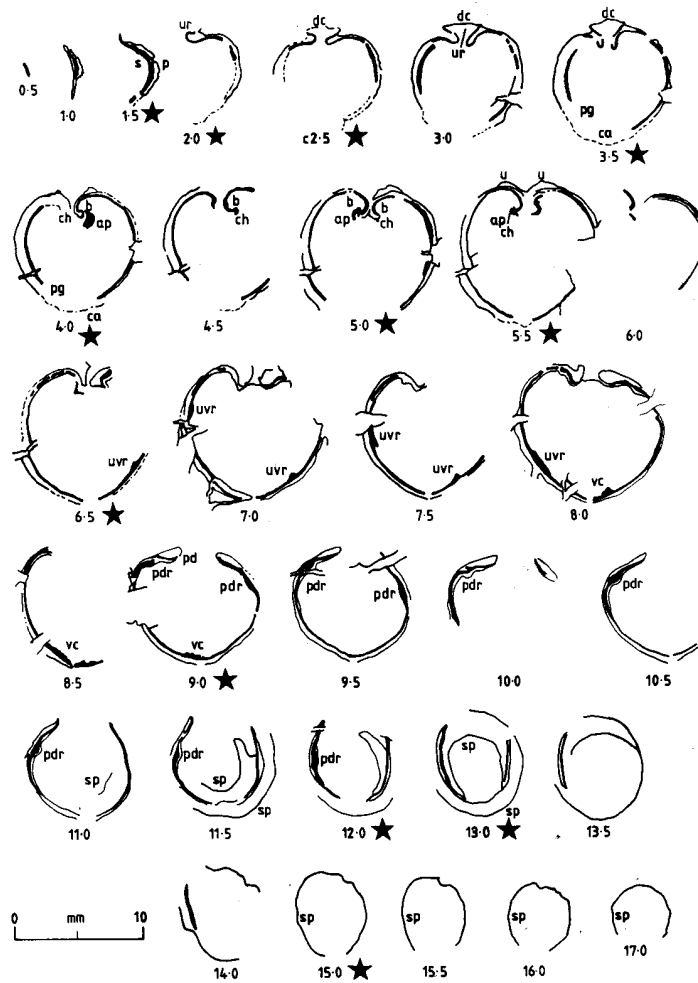
Opertochasma psyche sp. nov.

Plate 26, figs. 1–6; Plate 27, figs. 1–6; text-figs. 3A, 5–8

Derivatio nominis. Psyche (Greek), a maiden beloved by Cupid and made immortal by Jupiter.



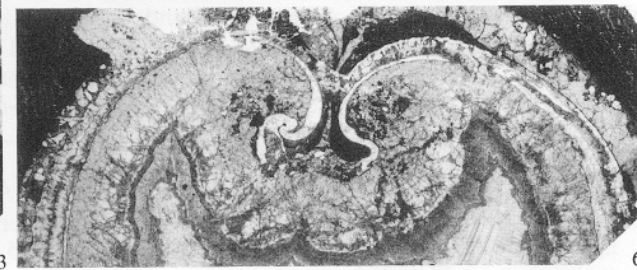
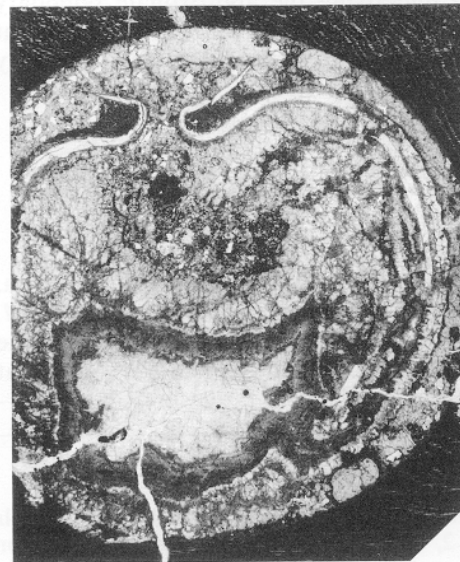
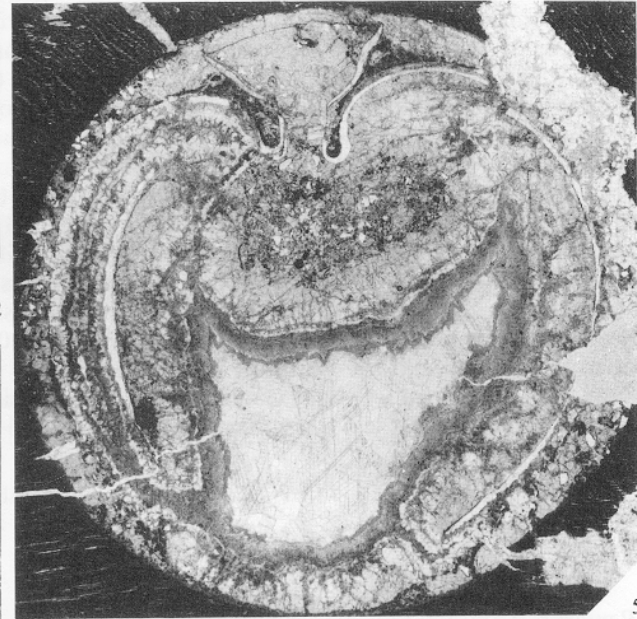
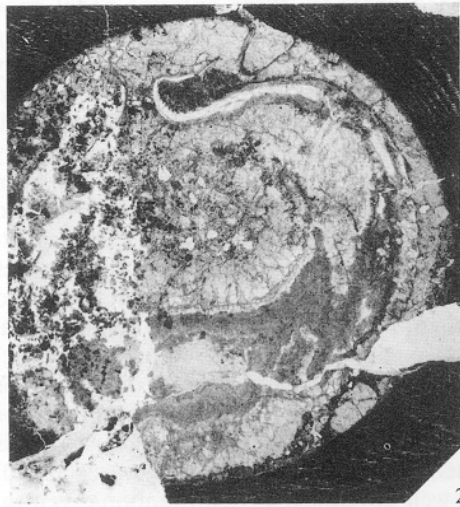
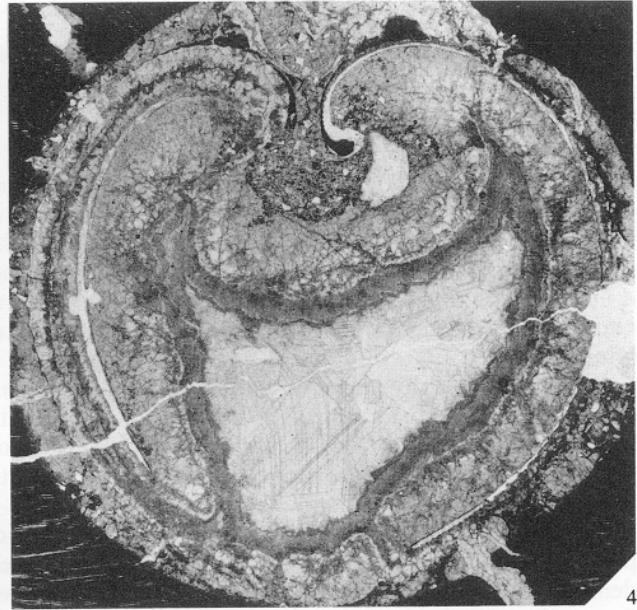
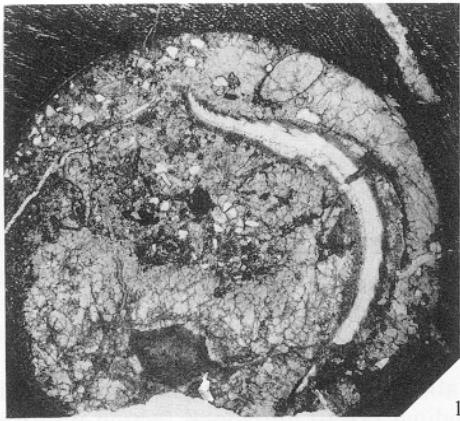
TEXT-FIG. 7. *Opertochasma psyche* sp. nov. Fossil Bluff Formation, Early Cretaceous, locality K, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island, all $\times 5$. A, vertical transverse thin section in region of apophyses, KG.18.30i (original figured by Taylor *et al.* 1979, pl. 8f). B, vertical transverse thin section in region just anterior to apophyses, KG.18.30h. C, horizontal sagittal section through paired valves in occlusion, which shows at anterior (i.e. base of photograph) the infilled mesoplax, and at the posterior (arrowed at top of photograph) raised periostracal leaves of the posterior slope, KG.18.30d.



TEXT-FIG. 8. *Opertochasma psyche* sp. nov. KG.18.30j. Fossil Bluff Formation, Early Cretaceous, Locality K, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island. Vertical transverse serial sections through a single specimen within boring in wood. Sketches are based on photographs of sections. The numbers refer to distance of each section from the anterior of the shell in millimetres. Those figures marked * are also illustrated as photographs on Plates 26 and 27. Key: ap = apophysis, b = beak, ca = callum, ch = chondrophore, dc = dorsal extension of callum, ms = mesoplax, p = periostracum, pd = posterodorsal reflexion, pdr = posterodorsal ridge, pg = pedal gape, sp = siphonoplax, ur = umbonal reflexion, uvr = umbonal-ventral ridge, vc = ventral condyle.

EXPLANATION OF PLATE 26

Figs. 1-6. *Opertochasma psyche* sp. nov. Transverse serial sections of a single specimen, Fossil Bluff Formation, Early Cretaceous, Locality K, Georgian Cliff, about 10 km north of Fossil Bluff, east coast of Alexander Island, KG18.30j, $\times 8$. Distances in millimetres of each figure from the anterior of the shell are as follows: 1, 1.5; 2, 2.0; 3, 2.5; 4, 3.5; 5, 4.0; 6, 5.0. These sections are shown diagrammatically on text-fig. 8, where they are marked with stars. This plate shows the anterior and mesial sections of the series, which is continued on Plate 27.



KELLY, *Opertochasma*

Type specimens. Holotype, KG.18.30f (text-fig. 6D, E) and seven paratypes, KG.18.30c-j. Fossil Bluff Formation, Early Cretaceous, Locality K, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island, Antarctic Peninsula.

Description. The description is based on one specimen which was prepared to show the exterior ornament (text-fig. 6F); two specimens preserved as internal moulds (text-fig. 6A-C, D-E); two polished sections (only one figured, text-fig. 7C); and two thin sections (text-fig. 7A, B). Another specimen was serially sectioned at 0.5 mm intervals. The full set of sections is illustrated in text-fig. 8 as line-drawings, while Plates 26 and 27 show some of the photographs upon which the line-drawings were based. The same serial numbering system (prefix ss) has been used for both plates and text-figures; the distance from the anterior of shell to the section being given in half millimetre intervals.

Shell small, usually about 10 mm in height and up to about 20 mm in length; strongly inflated, sub-circular in vertical sagittal cross-section, but longitudinal (axial) horizontal section piriform to evenly tapering towards posterior from evenly rounded anterior. Wide anterior pedal gape ss 3.0-5.5 (see text-fig. 8), which is diamond shaped (text-fig. 6B) and filled by a callum, but leaving a small ellipsoidal gape in some individuals (ss 3.5, 4.0). Callum appears as dark organic film only and therefore believed to be periostracal; commarginal ridgelike structures are sometimes developed paralleling edge of pedal gape. Anterior slope not well exposed, but prora is moderately well demarcated from it; extends posteriorly to highest and widest point of shell. Slope ornamented by fine commarginal ridges (text-fig. 6F) which parallel anterior margin and become horizontal between the two umbonal-ventral grooves. Umbonal reflection visible in thin sections on both anterior and posterior of beak, but obscured in dorsal aspect by dorsal extension of callum (ss 2.5, 3.5; text-fig. 5) which is periostracal. Incurvature near beak acute (ss 2.5, 3.0). Two umbonal-ventral grooves are present on shell exterior (text-fig. 6D), the anterior of which may be weak and ill-defined, and the posterior one more strongly pronounced. Disc has usually low, well-spaced commarginal growth ornament and is distinct from posterior slope. In two cases (one illustrated on text-fig. 7C) ornament is raised periostracal lamellae which close tightly with wall of boring. At posterior siphonoplax seen as incomplete uncalcified tube (ss 11.5-17.0) which has buckled and overlaps posterior part of shell itself. In ss 11.5 it appears both inside the shell and outside because of this buckling. Shell interior smooth except for distinct posterior umbonal-ventral ridge (ss 5.0-9.0) which terminates at the swollen ventral condyle and a less well-developed anterior umbonal-ventral ridge. There is also a posterodorsal ridge (ss 9.0-12.0) underlying the approximate boundary between the disc and the posterior slope. Near umbo shell strongly incurved with an apparent weak chondrophore (text-fig. 7A) and elongate apophysis below, both structures show very clearly in Plate 26, fig. E, but less so in serial sections (ss 4.0-5.5).

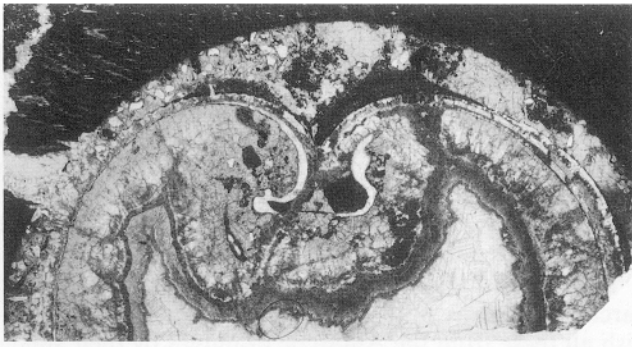
Measurements. In millimetres.

	Length	Length posterior	Height	Height hinge
KG.18.30f, holotype	16.5	12.0	9.5	8.0
KG.18.30e, paratype	18.0	12.0	9.0	—

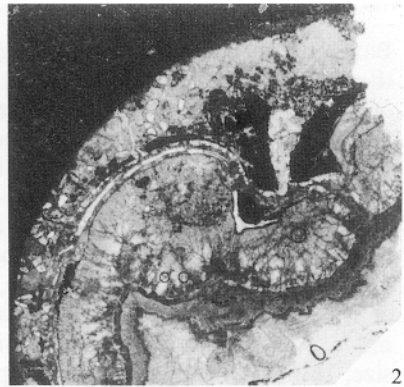
Remarks. Although two species of wood-boring bivalves are recorded as *Martesia* from Argentina, the original figures are not very clear and they are likely to be *Opertochasma*. The first is *M. argentinensis* Stanton (1901, p. 27, pl. 6, figs. 3 and 4), from the Belgrano Beds near Lake Pueyrredon, Argentina. The age was given as Albian, but Thomson (1982, p. 767) has stated that the associated ammonite fauna of *Hatchericeras* post-dates the *Favrella* fauna of Hauterivian-

EXPLANATION OF PLATE 27

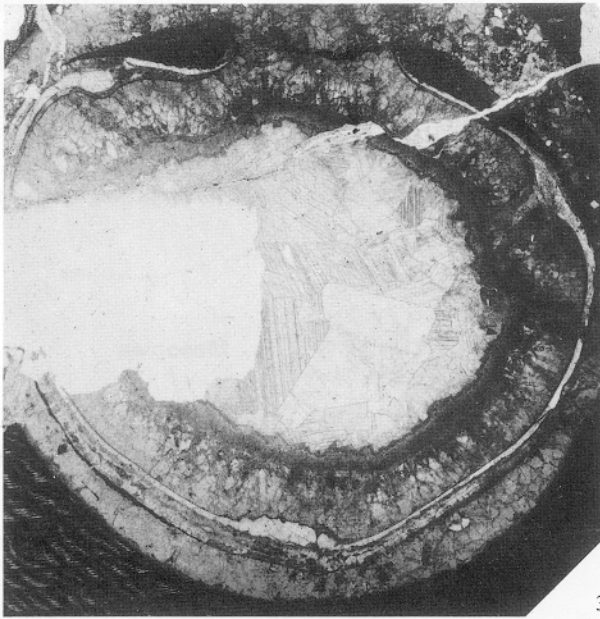
Figs. 1-6. *Opertochasma psyche* sp. nov. Continuation of serial sections. Distances in millimetres of each figure from the anterior of the shell are as follows: 1, 5.5; 2, 6.5; 3, 9.0; 4, 12.0; 5, 13.0; 6, 15.0. (For explanation see Plate 26.)



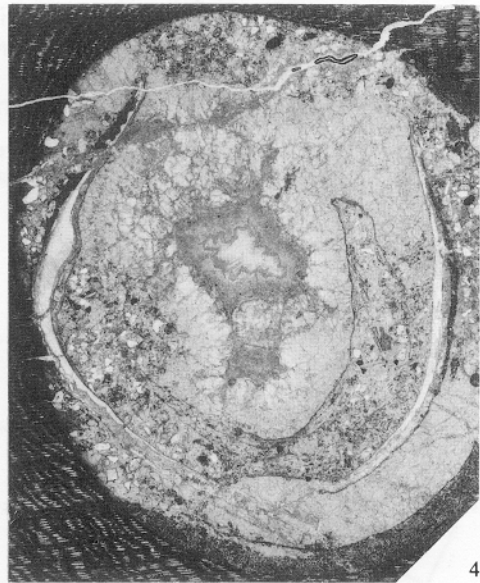
1



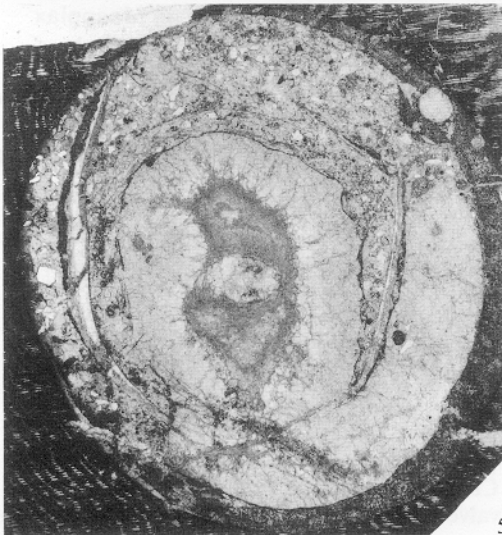
2



3



4



5

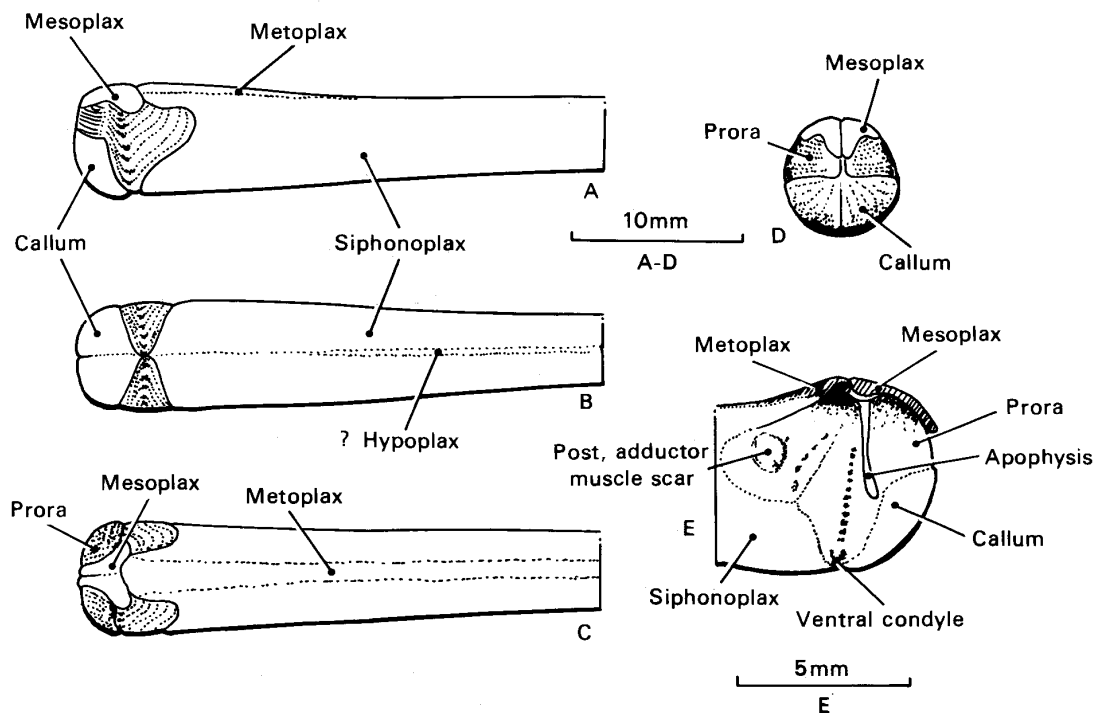


6

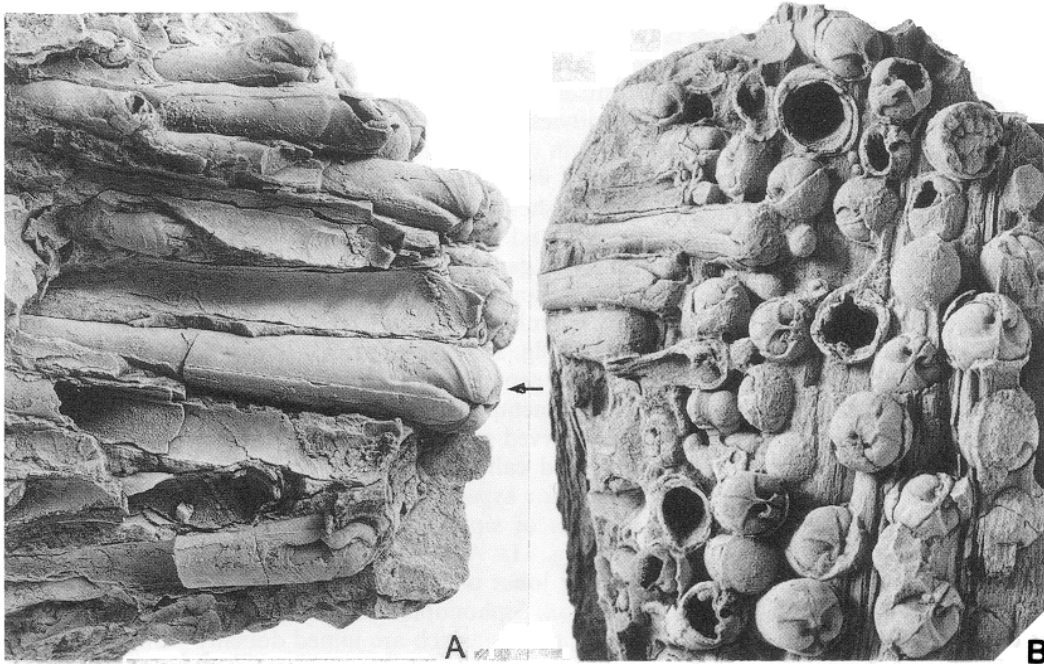
Barremian age, and pre-dates the *Sanmartinoceras* fauna of late Barremian–Aptian age. Therefore the age of the Belgrano beds is likely to be Barremian. *O. psyche* sp. nov. differs from *O. argentinensis* by being twice as large and having less prosogyrate beaks. The accessory plates of *O. argentinensis* are unknown. The second species is *M. cazadoriana* Wilckens (1905, p. 51, pl. 8, fig. 11) from the Cerro Cazador Formation of Patagonia, which Riccardi and Rolleri (1980, p. 1227) regarded as of Campanian–Maastrichtian age. Wilckens's illustration is a drawing, which shows an individual bearing only a single radial groove, a damaged posterior, a raised portion to the shell (just posterior to the umbo), and a possible callum. Several other species of *Opertochasma* exist in North America, Europe, Asia, and India. It is not yet possible to make a detailed comparison of these taxa with the Antarctic specimens until a thorough systematic revision is made. Although it is possible to distinguish all these from the Antarctic examples by their smaller size, this criterion is poor for separating species of wood-boring bivalves because of the likely occurrence of stenomorphism (Turner 1954, p. 6; Kennedy 1974, p. 14). One distinctive feature of the Antarctic examples is the commarginal ridges on the edges of the callum, it has not been recognized on any other species of *Opertochasma*.

Genus TEREDINA Lamarck, 1818

Type species. By subsequent designation: *Fistulana personata* Lamarck (1806, p. 429; 1808, pl. 43, figs. 6 and 7); Children (1823), Tertiary, Paris Basin, France.



TEXT-FIG. 9. Sketch reconstruction of *Teredina jeffersoni* sp. nov., based on type series specimens D.2042.5, Marambio Group, Coniacian–Maastrichtian, Sanctuary Cliffs, Snow Hill Island. A, left lateral aspect. B, ventral aspect. C, dorsal aspect. D, anterior aspect. E, left valve interior aspect with most of the siphonoplax not shown.



TEXT-FIG. 10. Assemblage of *Teredina jeffersoni* sp. nov. infesting lignic substrate. The holotype is arrowed. D.2042.5, Marambio Group, Coniacian–Maastrichtian, Sanctuary Cliffs, Snow Hill Island. A, specimens mainly in dorsal or lateral aspect, $\times 2$; B, specimens mainly in anterior aspect, $\times 2$.

Remarks. Shell is reduced and small relative to the size of the borings which are unlined. Siphonoplax very elongate and calcified, commonly five times the length of the shell. Mesoplax distinctly divided into four lobes.

Distribution. Late Cretaceous(?) to Middle Miocene of Europe; Campanian–Maastrichtian of western Antarctica; Palaeocene of North America.

Teredina jeffersoni sp. nov.

Text-figs. 3B, 9–11

Derivatio nominis. After the late Dr Timothy H. Jefferson.

Types. Holotype (text-figs. 10A, B, 11A–C, Q) and about forty-five visible paratypes from a single block of fossil wood D.2042.5 (text-fig. 10A, B), Marambio Group, Campanian or Maastrichtian, Sanctuary Cliffs, Snow Hill Island, James Ross Island group.

Description. Shell small, up to height *c.* 6 mm, and length 8 mm, but with siphonoplax 35 mm+; widely gaping at anterior and posterior ends, almost circular in sagittal cross-section (text-fig. 11C, Q) throughout length. Prora clearly demarcated from rest of anterior slope (text-fig. 11C, D, P, Q) with commarginal ridges (text-fig. 11L, N) which angle sharply towards venter at junction with posterior part of anterior slope. Ribs spaced further apart on anterior of anterior slope but become finer and more closely packed on its posterior. Umbonal-ventral groove marked by abrupt formation of coarse ridges, which weaken towards posterior, where fine commarginal growth lines continue. Valves in contact along ventral surface only at ventral condyles (text-fig. 11M). Posterior to condyles, ventral margin swings dorsally in sigmoidal manner to produce a flared posterior. As

growth lines swing towards dorsal margin, they disappear under metaplast (text-fig. 11E, J, O). There is no exterior differentiation between posterior slope and disc (text-fig. 11N, O) (but see shell interior below). Beaks and umbonal region are obscured by mesoplast. Shell interior smooth (text-fig. 11I, M), but bears distinct umbonal-ventral ridge, corresponding to external groove. Umbonal-ventral ridge formed by succession of condyles which become progressively larger towards the ultimate ventral condyle at the ventral margin (text-fig. 11M). Posterior to ridge, another groove runs upward to posteroventral margin (text-fig. 9E). This groove approximates to boundary between disc and posterior slope which is not clear on shell exterior. Details of hinge line not seen clearly, but bases of apophyses visible in text-fig. 11I, and complete structures with drusy encrustation in text-fig. 11K. In all examples examined, anterior gape is filled by callum, which appears uncalcified and divided (text-fig. 11C, D, P, Q). Dorsal extension of callum is small projection extending towards large mesoplast. Four-lobed mesoplast covers umbonal region and part of anterodorsal margin in dorsal aspect; shown as internal mould in text-fig. 11F-H, and as cast in exterior aspect in text-fig. 11E, J, O. Mesoplast has medial axial division separating it into two symmetrical portions; two anterior lobes separate near anterior end of metaplast; two posterior lobes spread outwards in posteroventral direction, but terminate in recurved structure which swings back towards postero-dorsal margin (text-fig. 11F, P). Mesoplast and callum may have been attached by periostracal tissue. Metaplast elongate and shown in exterior aspect in text-fig. 11E, and in internal aspect in text-fig. 11J. It connects with dorsal margins of siphonoplast. Metaplast thin and may not be calcified; a broken edge can be seen in text-fig. 11J. Anterior end of metaplast raised and swollen (text-fig. 11A, B) and nestles between anterior lobes of mesoplast; to posterior, metaplast forms a tapering tube with siphonoplast and ?hypoplast. Siphonoplast calcified, continuous with posterior part of shell, comprising two lateral tapering gutters which are joined dorsally with metaplast and ventrally with ?hypoplast; stretches as narrow tapering band along ventral margins of siphonoplast; it may or may not be calcified. Shell small relative to size of boring which may be commonly about five times length of shell; borings are all very straight and perpendicular to grain and surface of the wood, belonging to the ichnotaxon *Teredolites clavatus* Leymerie.

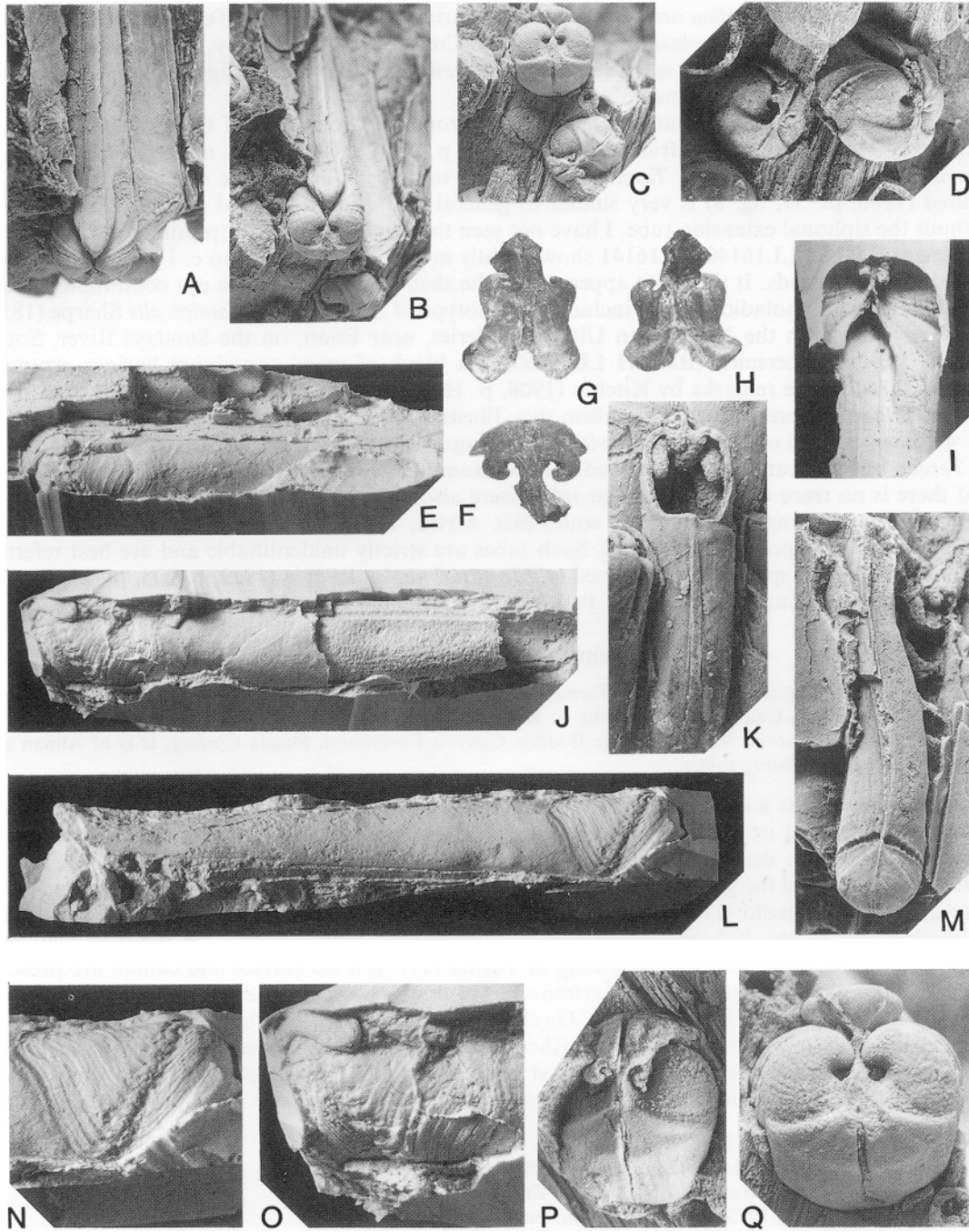
Measurements. In millimetres.

	Length	Length posterior	Height	Height hinge
D.2042.5 (holotype)	9.0*	8.0	6.0	4.5

* 35 mm including siphonoplast.

Remarks. *Teredina personata*, the type of the genus, differs from *T. jeffersoni* by having a siphonoplast which is a complete cylindrical tube without continuation of a metaplast on its dorsal side. Kennedy (1974, p. 72, fig. 99) illustrated a specimen labelled '*Martesia*(?)' sp., from the Palaeocene of California. The anterior region of the shell is not clear, but the posterior is obviously

TEXT-FIG. 11. *Teredina jeffersoni* sp. nov. D.2042.5, Marambio Group, Coniacian-Maastrichtian, Sanctuary Cliffs, Snow Hill Island. A-C, Q, internal mould of holotype. A, dorsal aspect, $\times 2$. B, anterodorsal aspect, $\times 2$. C, anterior aspect, $\times 2$. Q, anterior aspect, $\times 5$. D, paratypes, details of anterior ends of internal moulds showing divided callum and anterior portion of mesoplast, $\times 3$. E, paratype, silicone rubber cast of left valve showing mesoplast, siphonoplast, and metaplast, $\times 2.5$. F-H, paratype, detail of mesoplast internal mould in dorsal, ventral, and anterior aspects respectively, $\times 6$. I, paratype, silicone rubber cast of dorsal region of paired valves viewed from the venter, showing posteroventral ridges and metaplast, $\times 2.5$. J, O, paratype. J, silicone rubber cast of left valve showing mesoplast, siphonoplast, and internal mould of posterior portion of metaplast, $\times 2.5$. O, detail of left valve, $\times 5$. K, paratype, ventral aspect of internal mould with region of callum broken away showing drusy encrusted apophyses, $\times 2.5$. L, N, paratype. L, silicone rubber cast of right valve, showing siphonoplast and impression of ?hypoplast, $\times 2.5$. N, detail of right valve, $\times 5$. M, paratype, natural internal mould showing impressions of ?hypoplast and slightly twisted siphonoplast, $\times 3$. N, see L. O, see J. P, paratype, internal mould, anterior aspect showing mesoplast and callum, $\times 5$.



fused with the divided siphonoplax, and the metaplast is swollen near its anterior end. The specimen is almost certainly a *Teredina* and is probably the earliest recorded in the Tertiary. Roemer (1841, pl. 10, fig. 10) described *T. clavata* from the Late Cretaceous of Germany. Pictet and Campiche (1865, p. 23) believed that the specimen was *Clavagella*, but the original figures are poor and the original generic allocation seems unlikely.

Teredina was recorded by Bailey (1855, p. 462) from the Cretaceous of the Umzambani River district of Natal, southern Africa. Woods (1906, p. 309) reviewed the material and was not convinced that it belonged to *Teredina*, preferring to call it *Teredo*. The specimen that Woods figured (1906, pl. 37, fig. 8) is very similar in general shape to an isolated valve of *Teredina* but without the siphonal extension tube. I have not seen the original shell, but (presumably) associated specimens BMNH LL16140, LL16141 show slightly meandering tubes up to c. 1 cm diameter with closed innermost ends. It therefore appears that the shell and the lining are not continuous. Other southern African pholadid records include the holotype of *Gastrochaena dominicalis* Sharpe (1856, pl. 23, fig. 4a) from the Neocomian Uitenhage Series, near Enon, on the Sundays River, South Africa. The type specimen (BMNH LL16060) is a block of wood containing borings arranged radially. Despite the remarks by Kitchin (1908, p. 162), the borings appear to contain pholadids, but are in need of preparation to confirm this. Illustration of a specimen by Newton (1909, pl. 8, fig. 4) shows a piece of bored wood, with the borings lined with a tube. He referred the specimens to *Teredo* but this cannot be confirmed. I have examined the original specimen, BMNH L22064, and there is no trace of a shell. Similar tubes were also reported by Griesbach (1871, p. 68) from the 'Inzinhluwabalu' deposits of south-east Africa, and Etheridge (1907, p. 83) from the Umsinene River deposits of Zululand. Such tubes are strictly unidentifiable and are best referred to 'teredolithus'. A specimen determined as *Martesia?* sp. by Rennie (1929, p. 205, pl. 23, figs. 13 and 14), from the Late Cretaceous of Pondoland is probably *Girardotia* or *Jouannetia*.

Genus TURNUS Gabb, 1864

Type species. By original designation: *Turnus plenus* Gabb, 1864, originally described as from 'Upper Cretaceous', northern California. According to Kennedy (pers. comm. 1986) the type probably came from the Chickabally Mudstone Member of the Budden Canyon Formation, Shasta County. It is of Albian age and lacks calcareous lining tubes.

Remarks. *Turnus* has a shell that is moderate to large in size relative to the lined borings. Linings were not recognized in the original descriptions of the type species, but have been found in the Antarctic specimens described below and were also recorded by Stewart (1930, p. 296). Turner (1969, p. 471) placed the genus as subfamily uncertain within the Teredinidae, but Kennedy (1974) considered it a pholadid. The shape of the anterior gape is broadly lanceolate, unlike that found in all members of the Xylophaginae and the Teredinidae, whose gapes are more angular and diamond-shaped. Following the reasoning of Turner (1971), if apophyses and callum are present, specimens should be referred to the Martesiinae, but if apophyses are present and callum is absent, they should be placed in the Pholadinae. On the balance of evidence gathered so far, *Turnus* should be probably referred to the Pholadinae rather than the Martesiinae, because of the apparent lack of callum, but more information is needed concerning the absence or presence of apophyses. Accessory plates and palletal structures are unknown.

Species included within the genus include:

- T. argonnensis* (Buvignier, 1852), Albian, Ardennes, E. France;
- T. dallasi* (Walker) (Woods 1909), Aptian, England;
- T. inclusus* Spaeth, 1975, Hauterivian/?Barremian, N. Germany;
- T. rhodani* (Pictet and Campiche, 1864), Albian, Switzerland;
- T. waldheimi* (d'Orbigny, 1845b), Volgian, Russian Platform.

Distribution. Volgian of the Russian Platform; Hauterivian-Barremian and ?Senonian of Germany; Albian of western Antarctica and California; Aptian to Albian of England, France, and Switzerland; Cenomanian of southern India?

Turnus kotickensis sp. nov.

Text-figs. 12-14

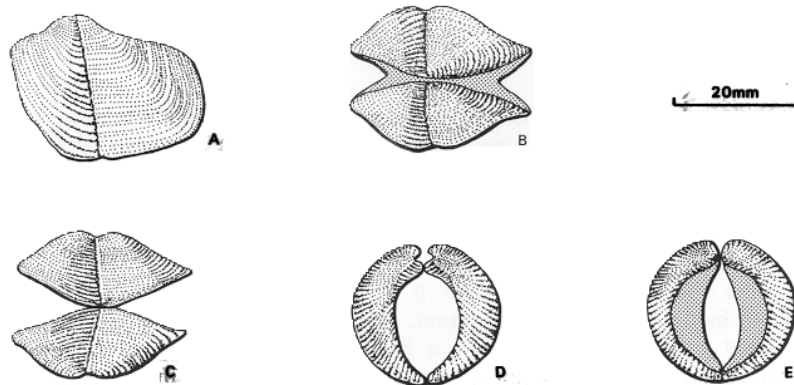
Derivatio nominis. After Kotick Point, the type locality. Kotick was a baby white seal in Kipling's 'The White Seal' (*Jungle Book*).

Type specimens. Holotype: D.8403.71o (text-fig. 13J-N), and twenty-five paratypes: D.8403.71a (six individuals), b (two individuals), c (four individuals), g, h (three individuals), i (three individuals), j-m, Kotick Point Formation, Gustav Group, Albian, Kotick Point, western James Ross Island.

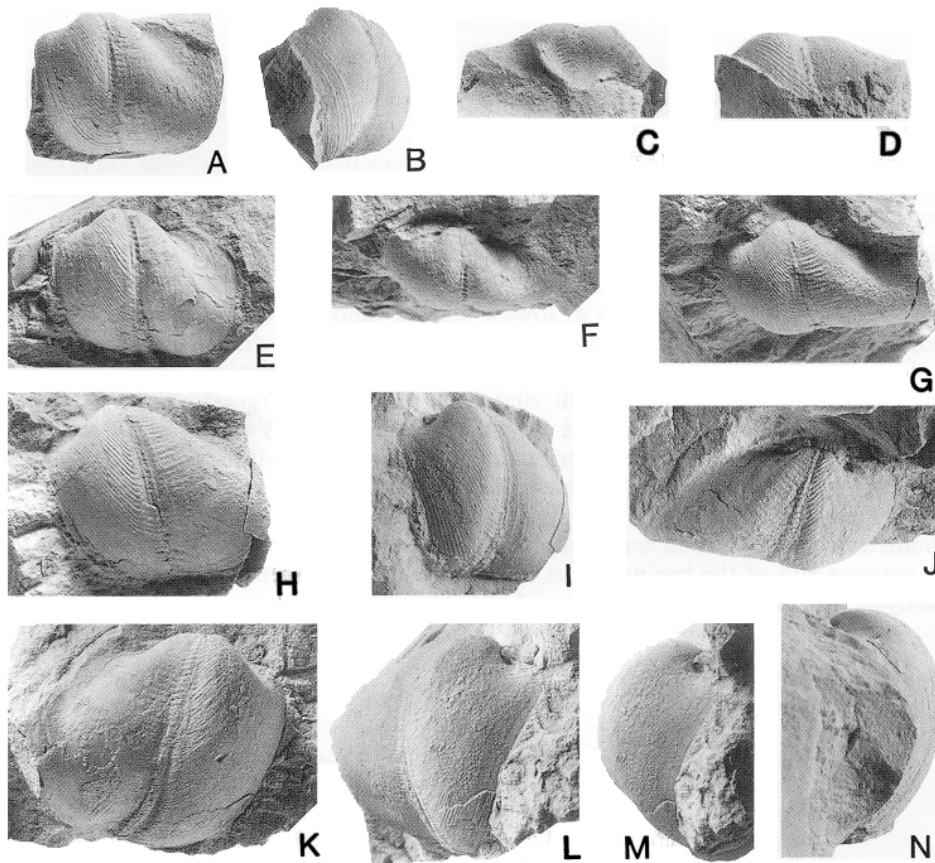
Description. Shell globular, inflated, up to 18 mm length and 17.5 mm height. Umbones rounded and projecting, with weakly prosogyrate beaks. Valves strongly gaping at anterior and posterior, with ventral margins only contiguous at lowest part of umbonal-ventral groove. Anterior slope undivided, with fine regular commarginal ornament. Prora feebly demarcated from posterior of anterior slope. Shell widest just to anterior of umbonal-ventral groove, where slightly swollen radial zone occurs. Posterior slope with slightly coarser commarginal ornament than on the anterior. Posterior margin truncate, but broadly rounded toward dorsal and ventral margins. Dorsal margins of the anterior and posterior slopes are slightly produced, but shell is not strongly recurved. Shell interior not seen clearly; however, the posterodorsal interior rib appears to be only weakly developed. Shells associated with lined *Teredolites* (text-fig. 14), whose tubes are from 3 to 13 mm diameter, up to 60 mm in length, and vary from straight or arcuate to twisted. No examples show the anterior end of the borings, thus no closure has been seen. As almost all the wood has been destroyed, and only the calcareous teredolithus remain, this suggests that the closure was not calcified.

Measurements. In millimetres.

	Length posterior	Length	Height	Height hinge
D.8403.71o holotype	17.0	11.0	16.0	14.5
D.8403.71a paratype	9.0	5.5	8.5	—
D.8403.71h paratype	15.5	10.0	12.0	11.0
D.8403.71l paratype	12.5	8.5	11.0	9.5
D.8403.71m paratype	5.0	3.5	4.5	—
D.8403.71n paratype	13.0	8.0	10.0	8.5
D.8403.47 paratype	18.0	11.5	17.5	15.0



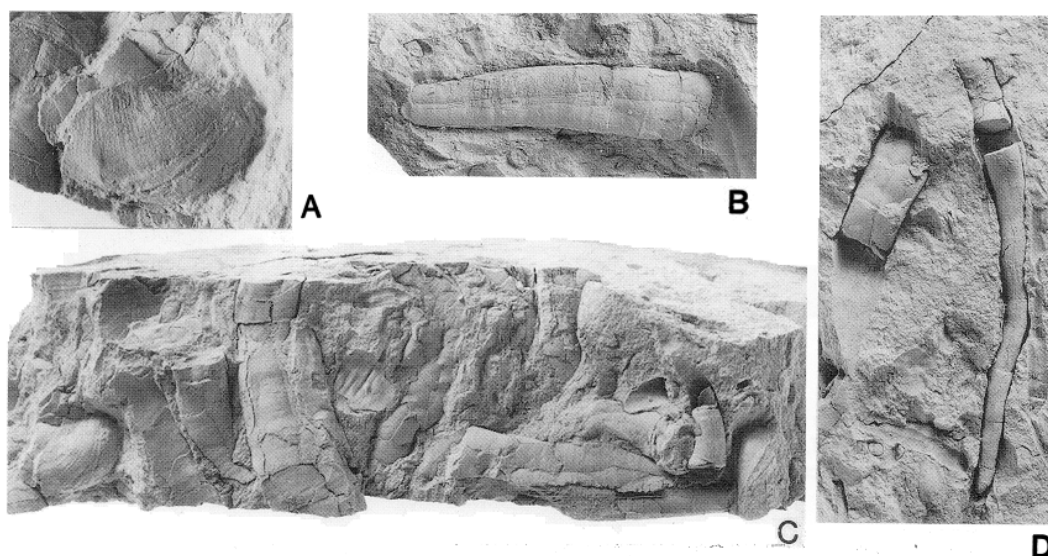
TEXT-FIG. 12. Sketch reconstruction of exterior of *Turnus kotickensis* sp. nov., based on specimens from D.8403, Kotick Point Formation, Albian, Kotick Point, James Ross Island. A, left lateral aspect. B, dorsal aspect. C, ventral aspect. D, anterior aspect. E, posterior aspect.



TEXT-FIG. 13. *Turnus kotickensis* sp. nov., Kotick Point Formation, Albian, Kotick Point, James Ross Island. A–D, paratype, left lateral, anterolateral (showing pedal gape), dorsal and ventral aspects respectively, D.8403.71i, $\times 2$. E, F, paratype, left lateral and dorsal aspects respectively, D.8403.71h, $\times 2$. G–I, paratype, dorsal, left lateral, and anterolateral aspects respectively, D.8403.71n, $\times 2$. J–N, holotype, dorsal, right lateral, anterolateral, anterior, and posterior aspects respectively, D.8403.71o, $\times 2$.

Remarks. The specimens of *Turnus kotickensis* appear to have a more truncate posterior than *T. dallasi* (Walker) from the English Aptian (Woods 1909, p. 238) and also lacks the ribs on the interior under the position of the posterior carina—by which it also differs from *Turnus* sp. from Alexander Island (see below). It also differs from *T. plenus* Gabb by its narrower umbones. However, the refigured lectotype of that species (Stewart 1930, p. 296, pl. 4, fig. 3) is a much larger specimen than those from Kotick Point. *T. dubius* Stanton (1901) from the ?Barremian of Argentina is almost certainly a *Xylophagella*. Frič (1893, p. 96, fig. 112) described *Teredo ornatissimus* from the Gastropoden Schichten of Pfeisen, Bohemia, and compared it to '*Gastrochaena amphisbaena*'. But the shell of that specimen appears to be a *Xylophagella* with a clearly defined prora. Müller (1898, p. 78) figured *Turnus* n. sp.? from the Lower Senonian of Braunschweig, Germany, which was found in association with '*T. amphisbaena*'. The shell could be *Turnus*, but cannot be identified with certainty from the figure.

The Kotick Point specimens are important because of their occurrence in association with their teredolithus tubes. Stoliczka (1870, p. 23) described *T. lapidarius* also associated with calcareous



TEXT-FIG. 14. *Turnus kotickensis* sp. nov. with associated teredolithus. Kotick Point Formation, Albian, western James Ross Island. A, detail of *T. kotickensis* sp. nov. from *in situ* at left end of D, D.8403.43, $\times 2$. B, internal mould of teredolithus, D.8403.42, $\times 1$. C, internal and external mould of teredolithus, D.8403.43, $\times 1$. D, mass of teredolithus tubes with *T. kotickensis* *in situ*, D.8403.5, $\times 1$.

tubes from the Ootatur Group, Cenomanian, of southern India. However, his drawing of the shell shows a much more prominent prora than in *T. kotickensis*, and therefore the specimen may not be a true *Turnus*.

Turnus sp.

Text-figs. 3F and 15

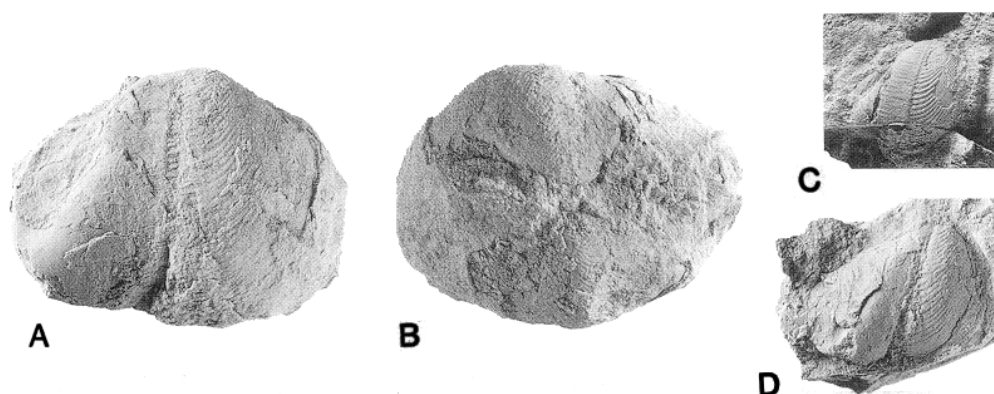
Material. KG.18.23a, b, KG.18.30b, Fossil Bluff Formation, Early Cretaceous, Locality K, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island.

Description. Shell squat and inflated, up to 30 mm in length, and *c.* 20 mm in height. Anterior slope undivided, but ornamented by strong regular commarginal ridges which curve gently around weak anterior gape. Callum, if present, unknown. Single umbonal-ventral groove. Disc short and ornamented by finer growth lines than on anterior slope, and separated by abrupt change in slope from posterior slope. Posterior slope bears traces of lamellose ornament. Posterior margin truncate. Shell interior smooth, with strong radial rib running from interior of beak to posteroventral margin. Shell length ranges from about a quarter to three-quarters the length of the boring, which has a thin calcareous lining.

Measurements. In millimetres.

	Length posterior	Length	Height	Height hinge
KG.18.23a	11.5	8.5	10.0	—
KG.18.23b	23.0	13.0	17.0	—
KG.18.30b	8.5	5.0	7.5	—

Remarks. The borings tend to be convoluted and have the greatest diameters of any other wood-boring bivalves described herein. Some tubes have a maximum diameter of 20 mm and a calcareous



TEXT-FIG. 15. *Turnus* sp. Fossil Bluff Formation, Early Cretaceous, Georgian Cliff, about 10 km north of Fossil Bluff, eastern Alexander Island. A, B, paired valves in occlusion, KG.18.23b, $\times 2$. A, right lateral aspect. B, dorsal aspect. C, right lateral aspect, KG.18.23a, $\times 1.5$. D, right lateral aspect, KG.18.30b, $\times 1.5$.

lining. Comparison with other *Turnus* would not be productive because of the poor preservation of the Antarctic specimens.

Subfamily XYLOPHAGAINAE Purchon, 1941

Genus XYLOPHAGELLA Meek, 1864

Type species. By original designation: *Xylophaga elegantula* Meek and Hayden, 1858, Meek, 1864, Taylor Group, Campanian, Montana. According to G. Kennedy (pers. comm. 1984), the types must have come from Montana, not Idaho as understood today. Idaho Territory, as organized on 3 March 1863, included all of the present states of Idaho, Montana, and Wyoming. On 26 May 1864, Montana Territory was split off from Idaho territory. Meek and Hayden (1858) were quite specific about the occurrence on Muscle Shell [i.e. Musselshell] River. Because this river is east of the continental divide, which separates Idaho and Montana, the specimens could not have come from Idaho.

Remarks. Shell globular, small relative to size of unlined borings (c. 25% of length). Anterior gape wide, but posterior gape narrow. A strong internal rib follows the approximate line of demarcation between disc and posterior slope, although not externally expressed. According to Turner (1971) a mesoplax is present in the subfamily, but apophyses and callum are absent.

Species in the genus include:

- X. dubius* (Stanton, 1901), ?Barremian, Argentina;
- X. zonata* Casey, 1961, Aptian-Albian, S. England.

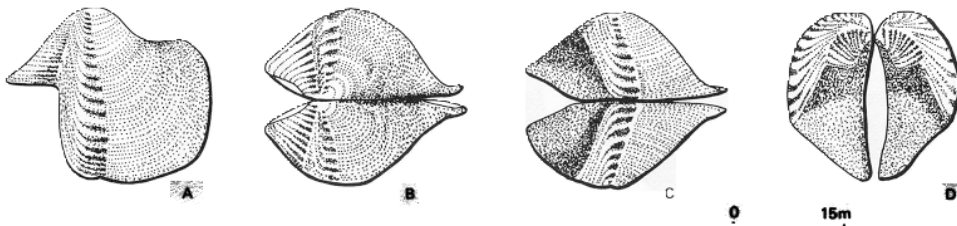
Distribution. ?Barremian of Argentina; Late Aptian to Albian of southern England; Campanian of southern California; Campanian-Maastrichtian of western Antarctica; Late Cretaceous of Montana; Maastrichtian of Alberta.

Xylophagella truncata sp. nov.

Text-figs. 3C-E, 16, 17

Derivatio nominis. Named for the truncate aspect of the posterior margin.

Type specimens. Holotype D.3122.7b and thirty paratypes D.3122.7a (twenty-three individuals), b-h, associated with borings from a single block of lignite (D.3122.7), Marambio Group, Campanian-Maastrichtian, Cape Lamb, south-west Vega Island; paratype 5067: single valve with associated boring, 'Snow Hill Island Series', Campanian, The Naze, north-east James Ross Island.



TEXT-FIG. 16. Sketch reconstruction of *Xylophagella truncata* sp. nov., based on several specimens from a single piece of fossil wood D.3122.7, Marambio group, Campanian-Maastrichtian, Cape Lamb, south-west Vega Island. A, left lateral aspect. B, dorsal aspect. C, ventral aspect. D, anterior aspect.

Description. Shell small, height up to 15 mm and length up to 17 mm, circular in sagittal cross-section; paired valves globular; pedal gape large (text-figs. 16E and 17F) and posterior gape narrow. Prora (text-figs. 16, 17A, B, G) prominent, ornamented with strong, smooth, commarginal ridges that are reflexed along dorsal margin. These ridges angle sharply downwards and diverge ventrally on narrow posterior part of anterior slope. Ridges on umbonal-ventral sulcus intercalate with those on anterior slope. Disc and posterior slope undifferentiated externally, ornamented by low commarginal ribs which again are reflected at dorsal margin. Posterodorsal margin strongly flared in posterodorsal direction. Shell interior smooth, but with notched umbonal-ventral ridge that corresponds to umbonal-ventral groove on exterior. A second broad internal rib is located approximately at projected boundary between disc and posterior slope (text-fig. 17A, B, G). Siphonal area bears fine radial grooves and riblets (text-fig. 17B) near posterior margin. Accessory plates, if present, have not been observed. Associated borings vary from being fairly straight (text-fig. 17I) to irregularly bent (text-fig. 3C, D, E), are unlined, and usually show gentle constrictions that correspond to periods of boring (cf. Röder 1977, fig. 20). They belong to forms ranging between *Teredolites clavatus* Leymerie and *T. longissimus* Kelly and Bromley. Shell small in relation to size of borings, which are commonly three to six times longer. Deeper parts of borings of larger specimens tend to be aligned with grain of wood, with axes which range from straight to curved.

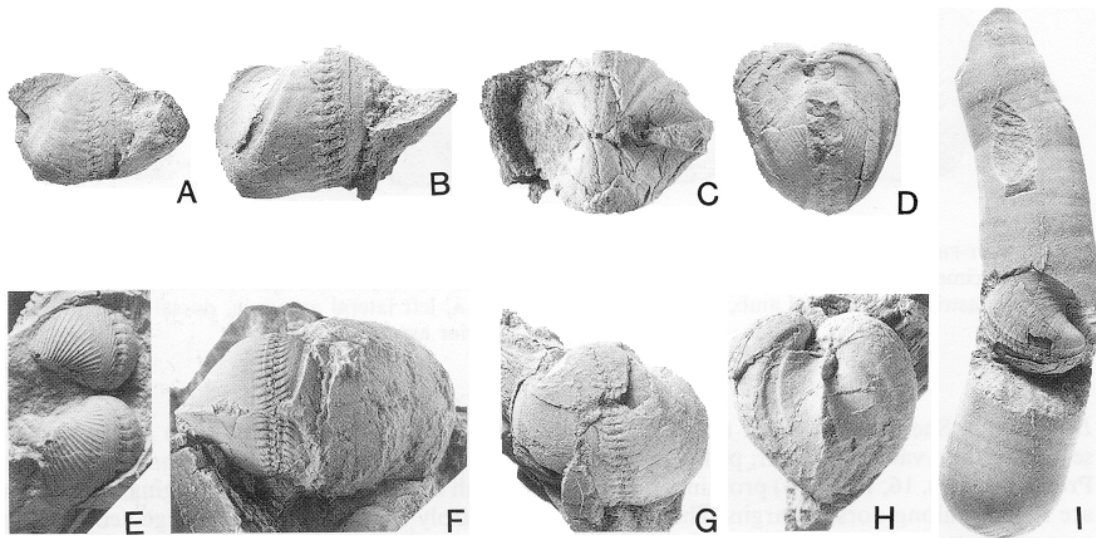
Measurements. In millimetres.

	Length	Length	Height	Height
D.3122.7c holotype	11.5	9.0	10.5	9.5
D.3122.7b paratype	13.5	9.5	12.5	9.5
D.3122.7d paratype	8.5	6.0	8.5	7.5
5067 paratype	16.5	10.5	15.0	—

Remarks. *X. truncata* sp. nov. is very similar in outline and inflation to *X. zonata* Casey, 1961 from the Upper Aptian to Albian of southern England, but it is more flared and recurved at the posterior border. *X. elegantula* (Meek and Hayden, 1858) from the Upper Cretaceous of Montana has an even shorter posterior slope than *X. zonata*. *X. dubius* (Stanton, 1901) from the ?Barremian of Argentina is distinguished by having a larger posterior gape.

PALAEOECOLOGY

The fragmentary nature of the pholadid-bearing fossil wood from all the Antarctic Peninsula localities and the associated marine faunas indicate that the substrate of the borings was marine driftwood. Without more detailed field observations it is not possible to determine if the wood was infested while floating or when waterlogged on the sea floor. All the *Teredolites* appear to have been constructed by bivalves, and they are found commonly in association together.



TEXT-FIG. 17. *Xylophagella truncata* sp. nov. A, internal mould of paratype with paired valves in occlusion, right lateral aspect, D.3122.7d, $\times 2$. B-D, internal mould of holotype, showing paired valves in occlusion, D.3122.7c, $\times 2$. B, right lateral aspect, C, dorsal aspect, D, posterior aspect. E, silicone rubber cast of paratype, showing shell exterior of anterodorsal region, D.3122.7h, $\times 2$. F, internal mould of paratype, showing wide pedal gape, ventral aspect, D.3122.7a, $\times 2$. G, H, internal mould, with some shell adhering, of paratype showing paired valves in left lateral and posterior aspects respectively. Marambio Group, Campanian-Maastrichtian, Cape Lamb, Vega Island, D.3122.7b, $\times 2$. I, right valve of paratype exposed in boring of ichnotaxon *Teredolites clavatus* Leymerie, Marambio Group, Coniacian-Maastrichtian, The Naze, James Ross Island, 5067, $\times 1$.

The palaeoecology of wood-boring bivalves can be inferred by comparison with their modern counterparts. Röder (1977) gives considerable detail concerning the autecology of a number of members of Recent Pholadidae. According to Turner and Johnson (1971) feeding habits of Recent wood-boring Bivalvia fall into two categories, which are of considerable palaeoecological significance:

1. Bivalves having a wood-storing caecum digest wood with the aid of bacteria. These bivalves tend to be the forms with an extremely elongate boring which is long relative to the length of the shell, e.g. Teredinidae and Xylophaginae.
2. Bivalves lacking a wood-storing caecum do not digest wood, but are filter feeders. These tend to have borings which are short relative to the length of the shell.

The probable mode of life of *Teredina*, *Turnus*, and *Xylophagella* thus appears to have been as potential wood-digesting forms because of their short shell length relative to the length of the boring. In contrast, modern wood-boring Martesiinae and Pholadinae lack a wood-storing caecum, and filter feed. These latter forms generally have short borings relative to the length of the shells and are represented in the Cretaceous of the Antarctic only by *Opertochasma*. The length of the *Teredolites* is therefore of ecological significance. The shorter *T. clavatus* Leymerie would have been occupied mainly by (but not restricted to) the filter feeding wood-boring bivalves, whereas *T. longissimus* Kelly and Bromley would have been occupied largely by (but not restricted to) wood-digesting forms.

Only some modern Pholadinae are wood-boring in habit, thus it is often difficult to compare directly fossil examples. However, Savazzi (1982, p. 286) has briefly discussed the mode of life of

Teredina, comparing it closely to that of members of the Teredinidae, although it is not a member of that family. The secretion of a secondary thickening of the siphonal tube may have enabled survival of the organism after decay of the surrounding wood. He believed that the siphonal tubes were secreted as a lining to the boring, and in adulthood became fused to the shell. All the antarctic specimens show the siphonal tubes clearly attached to the shell suggesting that the specimens are mature. Secondary thickening of the siphonal tube has not taken place.

Martesia is typical of fully marine environments, and is found today in shallow marine environments. *Lignopholas* occurs in brackish to almost fresh water. Both genera occur in warm temperate to tropical areas (Turner and Johnson 1971), Plint and Pickerill (1985) identified *Teredolites* in Hampshire, from Eocene fluvial facies which has been taken to represent a completely fresh-water environment. Wrigley (1929) noted *Teredina* in wood and associated with *Unio* in coarse sands from French Eocene deposits which he inferred to represent a fresh- or brackish-water environment.

Modern *Xylophaginae* have been recorded live in water depths of 2–7,290 m (Knudsen 1961; Turner 1972). They are world-wide in distribution, but generally replace Teredinidae in deep seas. Thus *Xylophagella* may indicate fairly deep water for the Marambio Group in the region of The Naze, James Ross Island, and Cape Lamb on adjacent Vega Island. Note, however, that some Recent species tend to live in shallow sublittoral depths of high latitudes. Material may also be reworked and is known to be carried ashore during storms (Knudsen 1961; Turner 1971).

The fossil examples of wood-boring bivalves described here from James Ross Island would have been originally at approximately 65° S in the Santonian and those from Alexander Island 70° S in the Hauterivian (Smith *et al.* 1981), assuming the present day configuration of Antarctica in Mesozoic time. Allowing for the more equable Mesozoic climates and the absence of polar ice-caps, both these sites were probably originally temperate, and have been included by Kauffman (1973) in a South Temperate Realm.

One boring (D3718.2) from the Marambio Group, of Cape Lamb, Vega Island, contains fairly uniform-sized oval pellet-like structures whose individual dimensions are approximately 0.3 × 0.2 mm. These appear to be faecal in origin and may have been deposited in a vacant boring, perhaps by some crustacean or worm.

STRATIGRAPHIC DISTRIBUTION OF MESOZOIC PHOLADIDAE

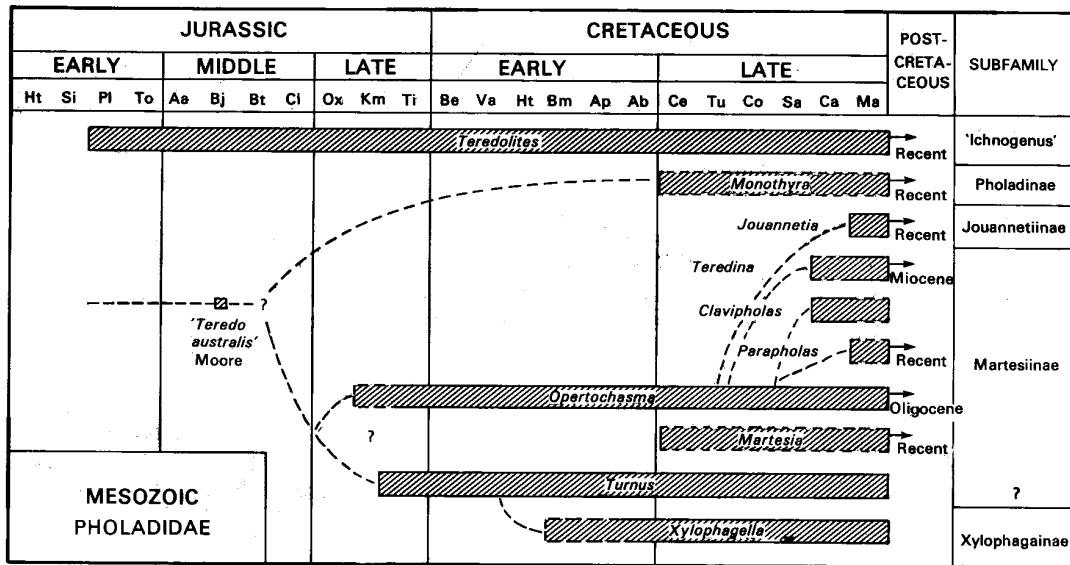
Examination of the Cretaceous pholadid bivalves of the Antarctic and review of literature on related forms elsewhere in the world have enabled a general stratigraphic review of Mesozoic pholadid bivalves to be compiled (text-fig. 18), including both lithic and lignic borers. The most recent compilations of such data was by Kennedy (1974, p. 22, table 1) who reviewed western North American occurrences, and Turner (1954, 1969) who examined world-wide occurrences. The data of these authors were arranged at the period level, and detail of the Mesozoic records was very generalized. The present compilation attempts to reach the stage level of stratigraphy wherever possible. The following list is an attempt to establish the first occurrences of Mesozoic genera and subgenera and is based as much as possible on figured specimens and/or the author's experience together with important observations by G. L. Kennedy (pers. comm. 1986). Entries in square brackets indicate generic names that are probably not appropriate for Mesozoic pholadids.

Family Pholadidae

Subfamily Pholadinae

Pholas (*Monothyra*) Tryon, 1862; earliest: *P?* (*M?*) *scaphoides* Stephenson, 1952, Woodbine Formation, Cenomanian, Texas (septate umbonal reflection and septate area between umbonal reflection and umbo are not recognized in Stephenson's illustrations or descriptions); continues to Recent.

[*Barnea* Leach, 1826; Turner (1954) gave the range as Early Cretaceous to Recent, but later (1969) restricted its range from the Miocene only. Kennedy (1974) recorded from Pliocene only in west North America.]



TEXT-FIG. 18. Distribution of the genera of the Pholadidae in the Mesozoic, showing suggested origins within the group.

Subfamily Martesiinae

[*Martesia* (*Martesia*) J. Sowerby, 1824; earliest: possibly *M. (M?) tundens* (Stoliczka, 1870), Cenomanian, Ootator Group, Moraviator, India; Hallam (1977, p. 73) recorded the genus in the Aalenian/Bajocian based on Skwarko (1972), but see *Particoma* below; Mesozoic records are unconfirmed; Palaeocene to Recent.]

[*Martesia* (*Particoma*) Bartsch and Rehder, 1945; ?Carboniferous, Jurassic, (Turner 1969). Skwarko (1972) recorded it from the Bajocian of Australia, but this is not confirmed, see discussion of earliest wood-boring pholadid below; ?Recent only.]

Clavipholas Conrad, 1868; earliest: *C. pectorosa* Conrad 1853), Campanian, New Jersey; note the specimen figured by Turner (1969, fig. e 171.1 is not the type, which is stated by Richards (1968, p. 73) to be Academy of Natural Science, Philadelphia, No. 16272); may include *Ramsetia* Stephenson, see below, but needs revision; latest: Maastrichtian (Stephenson 1941).

[*Goniochasma* Meek, 1864; perhaps a juvenile *Martesia* (Turner 1969), but needs revision; Late Cretaceous, North America.]

Opertochasma Stephenson, 1952; earliest *O. maloniana* (Cragin 1905), Kimmeridgian or Tithonian, Malone Formation, Texas; continues to Oligocene of Oregon (Kennedy 1974).

Parapholas Conrad, 1848; earliest: *Parapholas* sp. A. Speden (1970), Fox Hills Formation, Maastrichtian, South Dakota (G. L. Kennedy, pers. comm. 1986, considers this record to be *Clavipholas*); or *P. tumidifrons* (Whiteaves 1889), North Saskatchewan River (Speden 1970), Kennedy (1974) placed other Cretaceous records (White 1876, *vide* Kennedy; Stanton 1893; Schuchert 1905) of *Parapholas* in *Opertochasma*; continues to Recent.

[*Ramsetia* Stephenson, 1941; only record: *R. whitfieldi* Stephenson, Maastrichtian, Navarro Group, Texas. This may be a junior synonym of *Clavipholas*, but not confirmed here; needs revision, see above.]

Teredina Lamarck, 1818; earliest: *T. jeffersoni* sp. nov., Campanian or Maastrichtian, Marambio Group, James Ross Island group, Antarctica; continues to Middle Miocene of Europe (Turner 1969).

Turnus Gabb, 1864; *T. waldheimi* (d'Orbigny 1845b), despite original records as Oxfordian age, Moscow region, Gerasimov (1955) has only recorded it from the Early (= Middle of current usage) Volgian; continues to Campanian-Maastrichtian of Antarctica.

[*Xylophomya* Whitfield, 1902; only record: *X. laramiensis* Whitfield, Maastrichtian, Wyoming, USA; the original line-drawings are misleading and this genus may be included within *Turnus* or *Xylophagella*.]
Subfamily Jouannetiinae

Jouannetia Desmoulins, 1828; earliest; *J. supracretacea* (Ryckholt 1852), Late Senonian, Belgium (Stoliczka 1870); continues to Recent.

Subfamily Xylophaginae

[*Xylophaga* Turton, 1822; earliest: Tertiary (Stoliczka, 1870); Cretaceous records reidentified: *X. stimpsoni* Meek and Hayden = *Goniochasma* Meek, 1864 (see above); *X. elegantula* Meek and Hayden = *Xylophagella* Meek, 1864 (see below); continues to Recent.]

Xylophagella Meek, 1864; earliest: *X. dubius* (Stanton, 1901), ?Barremian, Argentina; or *X. zonata* Casey (1961), Early Albian, Lower Gault, England; continues to *X. elegantula* (Meek and Hayden 1858), Taylor Group, Campanian, Montana; or *X. truncata* sp. nov., Marambio Group, Campanian-Maastrichtian, Antarctica; Kennedy (1974, p. 20) recorded *Xylophagella* sp. from Campanian of California, redated (pers. comm. 1986) as Maastrichtian, *catarinae* Zone, Rossario Group, Point Loma Formation, San Diego; possibly includes *Terebrimya*.

[*Terebrimya* Stephenson, 1952; only record *T. lamarana* Stephenson, Woodbine Formation, Cenomanian, Texas. Photographs suggest it should be included in *Xylophagella*.]

THE EARLIEST PHOLADID BIVALVE

It is commonly stated that the earliest pholadid bivalve is Carboniferous (e.g. Turner 1969). This is probably based on the statement by Stoliczka (1870, p. 22): 'The first reliable records of fossil species of *PHOLADINAE* are from the mesozoic strata, (triassic and jurassic), though, as I have already noticed, traces of their borings in fossil-wood and stone have been found already in carboniferous beds, and some of these hollows most likely have been excavated by molluscs belonging to this sub-family.'

Pre-Jurassic records remain unsubstantiated. However, the present author has collected wood containing *Teredolites longissimus* Kelly and Bromley from the Lias of Portugal (Sedgwick Museum Cambridge, X.2643) of probable Late Pliensbachian age. The earliest recorded actual shell of a wood-boring bivalve was first described as *Teredo australis* Moore (1870), from the Bajocian of Western Australia. Skwarko (1972) re-examined the species and identified it as *Martesia (Particoma) australis* (Moore). The specimens associated with *Teredolites* in wood in a limestone matrix are not well preserved. They show short, quadrangular valves with commarginal ornament and strong umbonal-ventral grooves; anterior slope has radial ribs and distinct gape. The specimens superficially resemble *Girardotia*, but the present author believes that the generic allocation is still uncertain. The specimens are at present being further prepared and studied by Dr N. J. Morris (BMNH). The next well-substantiated record is *Turnus waldheimii* (d'Orbigny 1845b), which appears in the Late Jurassic, Middle Volgian, *panderi* Zone, of the Russian Platform (Gerasimov 1955). *Opertochasma* was well established in the Early Cretaceous and first appeared in the Kimmeridgian or Tithonian of Texas (Cragin 1905). *Xylophagella* appeared in the ?Barremian or Albian and was possibly derived from *Turnus*. Relationships between some of the Mesozoic genera have been suggested by Hoagland and Turner (1981, fig. 5) based on derived character states in modern forms; however, these do not take into account time-related events. New tentative relationships between the Mesozoic genera are proposed in text-fig. 18.

The problem of the ancestry of the Pholadidae still remains. This cannot be resolved here, but there are several members of the Pholadomyoidea whose strong ornament suggest homeomorphy if not true relationship, such as *Girardotia* and *Cortinia*. Initial facultative wood-boring by normally rock or consolidated mud-boring genera perhaps gave way to obligate wood-boring in Late Triassic or earliest Jurassic time in some genera. It appears that the now largely sediment-boring bivalves of the superfamily Pholadinae were established by Cenomanian times. They may have been derived secondarily from obligate wood borers in latest Early Cretaceous time, or they may have been established in earlier times than the wood-borers, but have remained unrecognized.

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