A NEW SPECIES OF LATE CRETACEOUS WOOD-BORING BIVALVE FROM NEW ZEALAND

by J. S. CRAMPTON

ABSTRACT. A new species of late Campanian or Maastrichtian (Late Cretaceous) pholadid bivalve, *Pholadidea* (*Hatasia*) wiffenae, is described from shallow marine transgressive Maungataniwha Sandstone, northwestern Hawkes Bay, New Zealand. It represents the earliest confirmed record for both genus and subgenus. The new species is known from exceptionally well-preserved material, which permits detailed knowledge of external morphology, including all accessory plates, and to a lesser degree, internal morphology. It is assigned to *Pholadidea* (*Hatasia*) based largely on the nature of accessory plates. In life-habit and some details of morphology, however. *P.* (*H.*) wiffenae resembles *Opertochasma* and *Martesia*, and may be an evolutionary intermediate between Cretaceous *Opertochasma* and early Tertiary *Pholadidea* and *Martesia*. The present record highlights the need for a comprehensive systematic review of Mesozoic pholadids.

THE late Cretaceous Maungataniwha Sandstone (Moore 1986), outcropping west and southwest of Lake Waikaremoana, northwestern Hawkes Bay, New Zealand (Text-fig. 1), contains the most diverse faunas of this age known from New Zealand. Included are terrestrial and freshwater invertebrates (Craw and Watt 1987; Moore et al. 1988), marine invertebrates (Glaessner 1980; Wiffen 1980; Crampton 1988; Moore et al. 1988; Crampton and Moore 1990), and terrestrial and marine vertebrates (Keyes 1977; Wiffen 1980, 1981, 1983, 1986; Molnar 1981; Scarlett and Molnar 1984; Wiffen and Moisley 1986; Wiffen and Molnar 1988).

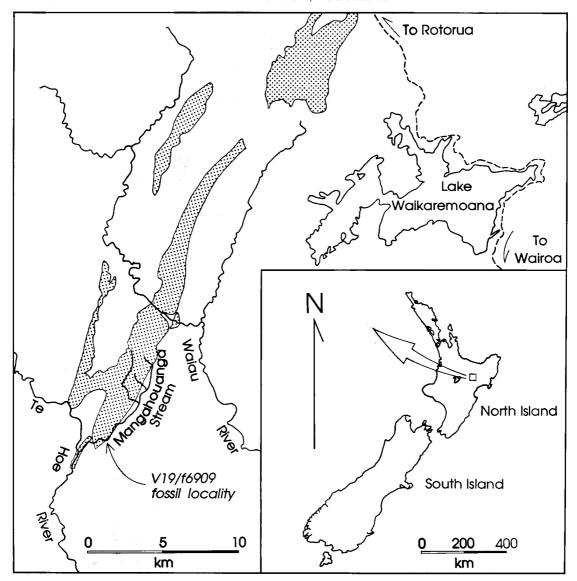
Of special note are some exceptionally well-preserved wood-boring pholadid bivalves. A recent discussion of Antarctic Cretaceous pholadids (Kelly 1988) noted the poorly documented record of these bivalves in the Southern Hemisphere, and the present paper describes the first Cretaceous species known from New Zealand.

The boring bivalves were collected from a single float concretion in Mangahouanga Stream, a tributary of Te Hoe River. Fossiliferous calcareous concretions are concentrated in Mangahouanga Stream, and are derived from fine sandstone of the late Campanian-Maastrichtian Maungataniwha Sandstone which crops out in both banks of the stream. Bored fossil wood is abundant in the concretions, but to date only the single concretion has yielded shells of the bivalves responsible for the borings. The borings themselves have been identified as ichnospecies *Teredolites clavatus* Leymerie (Pl. 3, figs 6–7; see also Kelly and Bromley 1984).

Study of the fauna and sediments in the region of Te Hoe River indicate that the Maungataniwha Sandstone was deposited during a regional marine transgression in a shallow marine nearshore environment on an embayed coastline and in close proximity to a river mouth (Crampton and Moore 1990). Lower Maungataniwha Sandstone includes minor lagoonal sediments, but was deposited mainly on the shoreface or foreshore above fair-weather wave-base. The bulk of this formation was deposited on the lower shoreface to offshore-transition, between fair-weather and storm wave-bases (Crampton and Moore 1990). The stratigraphical position of the fossils described herein is unknown. Fossilized wood occurs as discrete logs and branches which may have borings that enter from all directions, indicating that the wood is probably the same age as the sediment, and was not derived from older, already lithified, lignite beds (see later discussion). The bivalves were collected from araucariacean wood (J. I. Raine, pers. comm. 1989).

Morphological terminology used in this description follows that of Turner (1969) and Kennedy (1974), as modified by Kelly (1988). Major features of the shell exterior of *Pholadidea* (Hatasia)

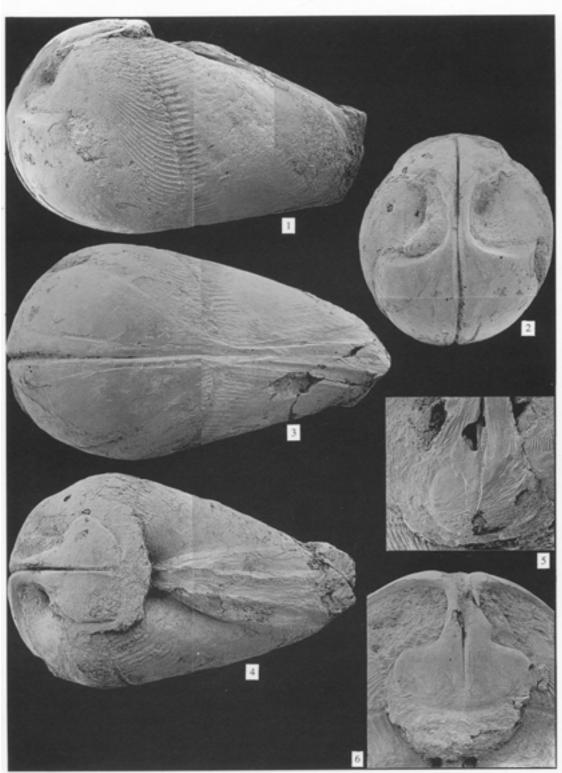
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TEXT-FIG 1. Distribution of Maungataniwha Sandstone (late Campanian-Maastrichtian: shaded) in northwestern Hawkes Bay, New Zealand, showing locality of the fossils described herein (geology after Grindley 1960; Moore 1986; Moore et al. 1988).

EXPLANATION OF PLATE 1

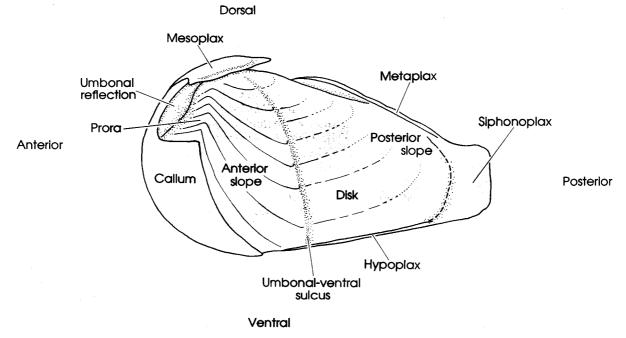
Figs 1-6. Pholadidea (Hatasia) wiffenae sp. nov., V19/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (late Campanian-Maastrichtian). All SEM photographs. Note that apparent variations in dimensions are due to orientation of specimen and parallax distortion of the SEM. 1-4, TM 6942 (holotype), adult; 1, lateral aspect, left valve, ×5·1; 2, anterior aspect, valves in occlusion, ×4·6; 3, ventral aspect, valves in occlusion, ×5·1; 4, dorsal aspect, valves in occlusion, ×5·1. 5, TM 6940, mesoplax showing periostracal folds, anterior up, ×8·7. 6, TM 6951, mesoplax, anterior up, ×8·2.



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wiffenae sp. nov. are illustrated in Text-figure 2. In the following discussion, the bivalves are described as juvenile if the anterior gape is entirely open, immature if the gape is partially closed by callum, and adult if the gape is entirely closed by callum.

Two specimens of the bivalve were transversely serial sectioned (following the recommendation of Kelly 1988) at 500 μ m intervals using a Leitz annular saw. These sections were ground to a thickness of 50 μ m for examination. In the text individual thin sections are referred to by distance (in millimetres) from the anterior margin of the shell.



TEXT-FIG. 2. External morphology of Martesiinae, after Turner (1969), Kennedy (1974), and Kelly (1988).

SYSTEMATIC PALAEONTOLOGY

Family PHOLADIDAE Lamarck, 1809
Subfamily MARTESIINAE Grant and Gale, 1931
Genus PHOLADIDEA Turton, 1819

Type species. Pholadidea loscombiana Turton, 1819 (original designation).

Subgenus HATASIA Gray, 1851

Type species. Pholas melanura Sowerby, 1834 (subsequent designation, Stoliczka 1870).

Discussion. The genus Pholadidea is distinguished from other genera in Martesiinae by its single umbonal-ventral sulcus, complete closure of the anterior gape in the adult by a callum which is extended dorsally to cover the beaks, the presence of a mesoplax which is longitudinally divided at some growth stage, and the presence or absence of a metaplax and a hypoplax which, if present, are not separate plates, but result from the deposition of calcite in the periostracum uniting the valves posterior to the umbos (see Turner 1969, p. 716). Two subgenera have been described; P. (Hatasia)

is distinguished by a relatively closely appressed umbonal reflection, a comparatively large flat mesoplax in the juvenile overlain dorsally in the adult by a longitudinally divided plate, and a variable siphonoplax composed largely of periostracum (Turner 1969, p. 716). Most *Pholadidea* are shale, soft rock, and coral borers (Turner 1969, see discussion below).

Turner (1969) stated that *Pholadidea* is known from the Eocene-Recent, and the subgenus *P*. (*Hatasia*) from the Recent only. In his review of Mesozoic pholadids, Kelly (1988) did not list any Cretaceous or older records of *Pholadidea*. Stephenson (1923, 1941) referred a number of Late Cretaceous species from North America to the genus, but his species are known from incomplete specimens or require reinterpretation in the light of the family taxonomy described by Turner (1969). Campbell *et al.* (in press) list *Pholadidea* n. sp., based on well-preserved material, from Palaeocene strata on the Chatham Islands, New Zealand. Re-examination of their material, however, suggests that this species may belong in *Jouannetia* (*Pholadopsis*) Conrad. *P.* (*H.*) wiffenae sp. nov., therefore, apparently represents the first fossil record for the subgenus, and probably one of the oldest records for the genus.

The genus *Pholadidea* closely resembles both *Martesia* Sowerby and *Opertochasma* Stephenson. *Martesia* are wood-boring pholadids distinguished from *Pholadidea* by an undivided mesoplax, the absence of a dorsal extension of the callum, and by a metaplax and a hypoplax which are separate calcified plates (Turner 1969; Kennedy 1974). Many Cretaceous pholadids formerly assigned to *Martesia* have subsequently been referred to *Opertochasma*, and the earliest confirmed record of *Martesia* is Palaeocene (Speden 1970; Kennedy 1974; Kelly 1988). *Opertochasma* are also woodborers distinguished by the presence of two umbonal-ventral sulci, periostracal flaps on the posterior slope, and incomplete closure of the anterior gape in the adult (Turner 1969; Speden 1970; Kennedy 1974; Kelly 1988). As noted by Kelly (1988), the second umbonal-ventral sulcus shows considerable intra-population variation in strength, and some specimens may be difficult to distinguish from both *Martesia* and *Pholadidea* (for example, see Speden 1970, pl. 38, figs 2, 4). The first record of *Opertochasma* is in the late Jurassic (Kelly 1988).

Pholadidea (Hatasia) wiffenae sp. nov. is referred to the Martesiinae on the basis of its gross morphology, in particular the complete closure of the anterior gape by a calcareous callum in the adult, and by the absence of protoplax. It is referred to Pholadidea because of its dorsally-extended callum, longitudinally divided adult mesoplax, and weakly calcified metaplex and hypoplax within the periostracum uniting valves. The closely appressed umbonal reflection and nature of the mesoplax are consistent with placement in P. (Hatasia).

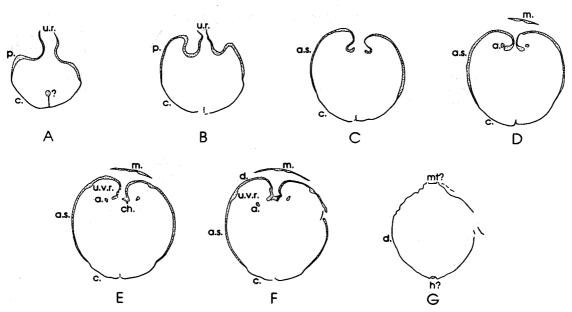
One significant difference between P. (H.) wiffenae and typical Pholadidea is its wood-boring life-habit. This character, and the well-defined prora (see Turner 1969) suggest affinities with Martesia, whereas the life-habit and comparatively narrow commarginal ridges suggest affinities with Opertochasma. P. (H.) wiffenae, therefore may represent an intermediate between Cretaceous Opertochasma, and early Tertiary Pholadidea and Martesia. It should be stressed, however, that morphological similarities will be the result, in part at least, simply of convergent life habits, which may or may not indicate evolutionary relationships. The influence of substrate type, for example, on shell shape and ornament is outlined in Kennedy (1974). Conclusions about evolutionary relationships, therefore, must await a comprehensive revision of all Cretaceous pholadids, a task hampered by the poor fossil record of this group and the typically incomplete nature of the fossils and early descriptions.

Pholadidea (Hatasia) wiffenae sp. nov.

Plates 1-3; Text-figs 3 and 4

Name. Named after Mrs Joan Wiffen who discovered these bivalves, in recognition of her major contribution to our knowledge of New Zealand late Cretaceous palaeontology.

Type specimens. Holotype: TM 6942, V19/f6909a, GS 14241; entire articulated phosphatized specimen with all accessory plates preserved. Fifteen paratypes: TM 6938-6941, TM 6943-6953, all from V19/f6909a, GS



TEXT-FIG. 3. Interpretive drawings of selected vertical transverse thin sections of *Pholadidea* (*Hatasia*) wiffenae sp. nov., specimen TM 6953. Sections drawn from photographs, all enlarged \times 3·4. Individual drawings oriented dorsal up and arranged with respect to distance from the anterior margin, given below in millimetres. Note that interpretation of sections is hampered by the replacement of originally calcitic shell material by collophane, and the presence of interstitial and cavity-filling collophane. A, 1·5 mm. B, 2·0 mm. C, 2·5 mm. D, 3·0 mm. E, 3·5 mm. F, 4·0 mm. G, 8·0 mm. Legend: a = apophysis; as = anterior slope; c = callum; ch = chondrophore; d = disk; h = hypoplax; m = mesoplax; mt = metaplax; p = prora; ur = umbonal reflection; uvr = umbonal-ventral ridge.

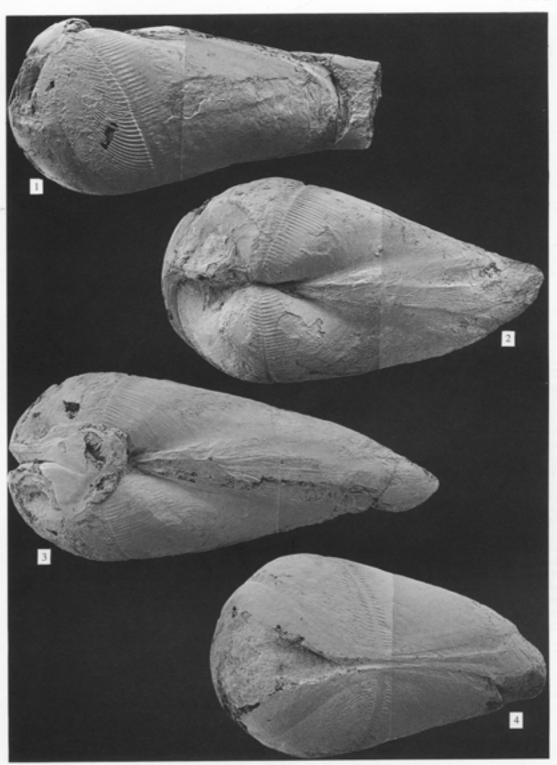
14241. All specimens phosphatized. TM 6952 and TM 6953 serial sections at 0.5 mm intervals through juvenile and adult respectively.

Type locality. Mangahouanga Stream, float concretion 470 m east southeast of Te Hoe forestry road bridge over stream and approximately 200 m downstream from first major true left tributary above bridge, north western Hawkes Bay, New Zealand (see Text-fig 1). New Zealand national Fossil Record locality V19/f6909a, grid reference NZMS 260 sheet V19 42134700. New Zealand Geological Survey collection GS 14241 and Wiffen collection. Collected by J. and M. Wiffen, February 1987.

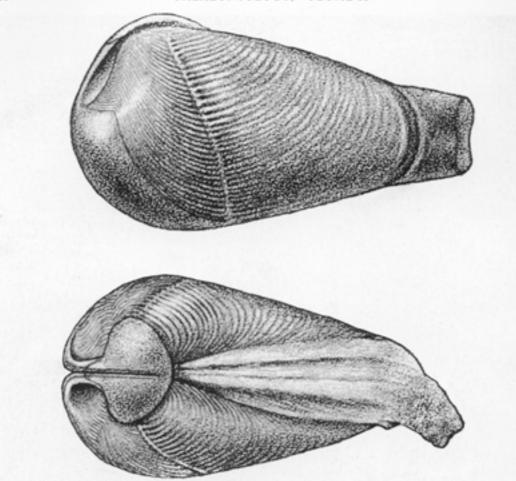
Description. Small, less than 20 mm long, equivalve, inequilateral. Subconical in lateral and vertical profiles, tapering evenly to posterior; subcircular in transverse profile (Pl. 1, figs 1–4; Pl. 2, figs 1–4). Prora well-defined, antero-ventral margin with sharp re-entrant (with sides at approximately 100°) resulting in Teredo-like anterior (Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, fig. 1). Posterior-dorsal margin gently convex, posterior margin bluntly rounded, posterior-ventral margin straight to weakly concave. Umbo low, strongly incurved, prosogyrous, at approximately anterior fifth of shell (Pl. 2, fig. 2). Umbonal reflections lower than umbones. Prominent anterior conical cavity beneath umbonal reflection (Pl. 3, figs 1 and 3). Anterior pedal gape confined to ventral

EXPLANATION OF PLATE 2

Figs 1-4. Pholadidea (Hatasia) wiffenae sp. nov., V19/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (Campanian-Maastrichtian). All SEM photographs. Note that apparent variations in dimensions are due to orientation of specimens and parallax distortion of the SEM. 1 and 3, TM 6941, adult; 1, lateral aspect, left valve, ×4.9; 3, dorsal aspect, valves in occlusion, ×4.9. 2 and 4, TM 6938, immature; 2, dorsal aspect, mesoplax removed, valves in occlusion, ×5.1; 4, ventral aspect, ×5.1.



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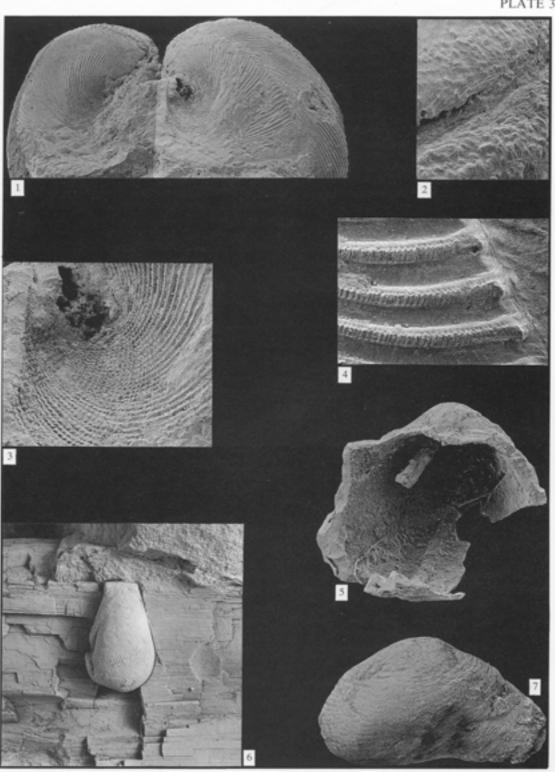


TEXT-FIG. 4. Reconstruction of *Pholadidea (Hatasia) wiffenae* sp. nov. Note that juvenile mesoplax (omitted here) may underlie longitudinally divided adult mesoplax shown, and may extend posteriorly well beyond adult mesoplax (see discussion in text). (Drawn by R. C. Brazier.)

half of height, subtriangular, dorsal margin of gape concave, almost perpendicular to commissure. Anterior gape entirely closed in adults by a callum, the two halves of which are inferred to have been connected by periostracum medially, are slightly raised above level of anterior slope, and extend dorsally over the umbonal reflection (Pl. 1, figs 2 and 3). A few prominent commarginal growth lines present on callum of all specimens examined. Protoplax lacking. Mesoplax of two pear-shaped plates which cover umbones and become fused

EXPLANATION OF PLATE 3

Figs 1–7. Pholadidea (Hatasia) wiffenae sp. nov., V10/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (Campanian-Maastrichtian). All SEM images except Fig. 6. 1 and 3, TM 6950, juvenile, anterior aspect of prora and umbonal reflection, dorsal up; 1, ×10·5; 3, ×34·7. 2, TM 6940, detail of callum at commissure, showing texture resulting from incorporation of clastic grains into periostracum, ×22·4. 4, TM 6941, denticulate ornament on anterior slope immediately adjacent to umbonal-ventral sulcus, dorsal up, anterior to left, ×41·6. 5, TM 6949, interior of juvenile, showing apophysis and umbonal-ventral ridge, anterior to right, ×19·1. 6, TM 6942 (holotype) in life position in araucariacean wood, ×1·7. 7, TM 6954, ichnospecies Teredolites clavatus Leymeric, resulting from boring by Pholadidea (Hatasia) wiffenae sp. nov., aperture to right, ×3·6.



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posteriorly (Pl. 1, figs 2, 4-6; Pl. 2, fig. 3). Mesoplax closely associated with, and possibly partially fused to, dorsal projections of the callum. The juvenile portion of the mesoplax characteristic of subgenus Hatasia (see above), is not clearly visible on any specimens, but may be represented by the flow flange surrounding and possibly underlying the longitudinally divided portion of the mesoplax (Pl. 1, figs 4-6). In thin section, specimen TM 6953, interpreted as an adult on the basis of its complete callum, displays a single large flat plate which extends 3.0-4.0 mm behind the umbo, and which is interpreted as the juvenile mesoplax (Text-fig. 3). This specimen apparently lacks the divided mesoplax observed on other individuals. Metaplax and hypoplax comprising anteriorly tapering, partially calcified periostracum, uniting valves across dorsal and ventral gapes respectively (Pl. 1, figs 3 and 4; Pl. 2, figs 2-4). Umbonal-ventral sulcus well-defined, narrow. Matched on shell interior by narrow upstanding umbonal-ventral ridge (Pl. 3, fig. 5; Text-fig. 3). Sculpture on prora and anterior slope of between 50 and 70 sharply-defined, narrow, rounded commarginal ridges and broader, flat-floored troughs. Ridges finely denticulate on anterior slope (Pl. 3, fig. 4). Ridges broader and weaker on disc, fading out over posterior slope of many specimens. Periostracum present over entire shell, thicker on disc and posterior slope than elsewhere. In some specimens clastic grains incorporated into periostracum over callum (Pl. 3, fig. 2) and, more commonly, over posterior slope. Siphonoplax short, composed of periostracum or partly calcified periostracum (Pl. 2, fig. 1; Pl. 3, fig. 6). Apophysis relatively short, rod-like, not markedly spatulate at distal end (Pl. 3, fig. 5; Text-fig. 3).

Dimensions (undistorted specimens, mm).

| , , , | Length | | |
|---------------------------|--------------|---------|---------------|
| | (excluding | | Width |
| Specimen | siphonoplax) | Height | (both valves) |
| TM 6938 (immature) | 17.6 | 10.8 | 11.0 |
| TM 6941 (adult) | 17.1 | 9.7 | 10.4 |
| TM 6942 (adult, holotype) | 17.6 | 11.3 | 11.3 |
| TM 6943 (adult) | 17·2+ | 10.7 | 10.6 |
| TM 6944 (adult) | ? | 8.9 | 8.8 |
| TM 6945 (?) | ? | c. 11·0 | 11.1 |
| TM 6946 (adult) | 15.5 | 9.0 | 8.9 |
| TM 6947 (juvenile) | 14.7+ | 9.8 | 9∙7 |
| TM 6948 (adult) | 18.9 | 10.1 | 11.0 |
| TM 6953 (adult) | c. 12·6 | 8·1 | c. 8·0 |

Discussion. A number of late Cretaceous pholadids have been described from the Southern Hemisphere, but incomplete knowledge of these, in most cases, prevents detailed comparison with the present species. Martesia leali Stinnesbeck, 1986 (pp. 185–186, pl. 5, fig. 9) from the Maastrichtian of Chile, resembles P. (H.) wiffenae in gross form and life habit, but possesses a coarser ornament (although, as mentioned above, the nature of the substrate can have a marked effect on ornament, see Kennedy 1974). The nature of the accessory plates in M. leali is unknown. Martesia cazadoriana Wilckens, 1907 (pp. 10–11, pl. 8, fig. 11), from the Campanian-Maastrichtian (Riccardi 1988) of Patagonia, is known only from a single internal mould; and Martesia? sp. of Rennie (1930, pp. 205–206, pl. 23, figs 13 and 14) from the late Cretaceous of South Africa, is known from a single incomplete and distorted specimen, and probably does not belong in Martesiinae (Kelly 1988). Many late Cretaceous pholadids have been described from the Northern Hemisphere, and although superficially some of these resemble P. (H.) wiffenae, detailed comparisons should be made within the framework of a comprehensive systematic review of the family.

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