The Taxonomic Position of *Hemidonax* Mörch, 1871 with a Review of the Genus (Bivalvia: Cardiacea)

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ABSTRACT

Hemidonax Mörch is considered to be sufficiently distinct to justify the recognition of the group at family level (Hemidonacidae) within the Cardiacea. The first record of the genus is from the late Oligocene or early Miocene of Victoria, Australia, and its subsequent fossil history is traced. Five Recent species and one subspecies are recognised, 4 of which are endemic to Australia. One extinct Australian species (*Donax dixoni* Tate) is also recognised. A new Recent species from northern Australia (*H. arafurensis* nov.) is described.

INTRODUCTION

The genus *Hemidonax* Mörch, 1871 contains only a few named species, several of which are endemic to Australia. The taxonomic position of the genus has been the subject of some controversy and the purpose of this paper is to consider the family position and to review the included species.

Hemidonax has been included by different authors in the Donacidae, the Tancrediidae, the Crassatellidae, the Cardiidae and the Hemidonacidae. Apart from the last, all of these families are included in different superfamilies, which gives some indication of the degree of confusion surrounding the higher classification of this genus.

MATERIAL AND METHODS

The majority of specimens examined in detail are housed in either The Australian Museum or The Western Australian Museum. The anatomy of two species was examined (*H. pictus* (1 specimen) and *H. arafurensis* nov. (several specimens) and several cardiid species dissected for comparative purposes by W.F.P. and C.M.Y.

Specimens were examined by W.F.P. in various museums for locality records. Locality information was compiled from museum material and records by P.H.C.

W.F.P. is responsible for the taxonomic work. Because of the lack of preserved material of most species, the species taxonomy is based entirely on shell characters. Measurements of the shells were made by P.H.C. and analysed by M.H.C.

Methods employed in analysing dimensions

The height (H), length (L) and posterior length (PL) of representative samples of shells were measured using vernier calipers. The ratios H/L and PL/L were calculated for each

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shell and then the means and standard deviations (SD) of each of these dimensions and ratios were calculated for each species. Each pair of samples being compared was tested statistically for equality of the variances by the variance ratio or F test. If the variances were found to be equal then the means were compared using a Student's t-test. If the variances were unequal then an approximation of based on the normal distribution was used. A significance level of $P \leq 0.05$ was used in the tests.

Abbreviations used for institutions

Note: Where the name of institution is not stated the material is housed in The Australian Museum, Sydney.

AMS The Australian Museum, Sydney.
ANSP Academy of Natural Sciences of Philadelphia, Philadelphia.
BMNH British Museum (Natural History), London.
BMR Bureau of Mineral Resources, Canberra.
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Boston.
NHMG Muséum d'Histoire Naturelle de Genève, Geneva.
NHMP Muséum National d'Histoire Naturelle, Paris.
NMV National Museum of Victoria, Melbourne.
SAM South Australian Museum, Adelaide.
WAM Western Australian Museum, Perth.
ZMC Zoological Museum, Copenhagen.
ZML Rijksmuseum van Natuurlijke Historie, Leiden.

CLASSIFICATION

Boss (1971), citing the anatomical description of *Hemidonax* by Pelseneer (1911), argued in favour of the Cardiidae as a location for *Hemidonax* and rejected its assignment by Keen (*in* Moore) (1969) to the Donacidae (Tellinacea). Boss thought that *Hemidonax* did not belong in the Donacidae because it lacks a cruciform muscle and siphons (with which the cruciform muscle is associated), resulting in the absence of a pallial sinus. Although the cruciform muscle is not a universal feature in the Tellinacea, being absent in the subfamily Novaculininae (Yonge, 1949) in which the siphons cannot be completely withdrawn and in *Pharus* where there is extensive ventral fusion of the mantle lobes absent in other Tellinacea (Yonge, 1959), it is a highly characteristic feature of this essentially deposit-feeding superfamily. The separate and highly mobile siphons formed exclusively from the inner mantle folds and with concentric layers of muscle and collagen fibres (Hoffmann, 1914; Graham, 1934; Yonge, 1949, 1959; Chapman & Newell, 1956) which are *the* characteristic feature in the Tellinacea are not present in *Hemidonax*, which is without siphons of any kind.

Hemidonax differs from the Crassatellidae, where it was placed by Pelseneer (1911) and Hedley (1906, 1909, 1923), and also from the Carditacea (the two probably better united within the superfamily Crassatellacea (Yonge, 1969), in possessing an inhalant opening that is structurally separated from the pedal gape. Also, as pointed out by Boss (1971), there is considerable difference in dentition. In addition, the predominantly radial sculpture of *Hemidonax* differs from that of the concentrically sculptured astartids and crassatellids. There is also no trace in *Hemidonax* of the prominent mantle glands present in the crassatellids (Pelseneer, 1911; Allen, 1968; Prezant, 1979) and in the Carditacea (Yonge, 1969) both of which also differ from *Hemidonax* in possessing non-plicate ctenidia. Most significant of all, the Astartacea and the Carditacea (i.e. all of the Crassatellacea *s. l.*) are unique in possessing a mantle crest subdivided into five lobes (Yonge, 1969). The mantle crest has the usual, undivided form in *Hemidonax*.

Boss (1971) maintained that the following features of *Hemidonax* indicated that it should be placed in the Cardiidae rather than the Donacidae:— (1) The shell has relatively strong radial ribs and (2) lacks both pallial sinus and cruciform muscle scars. (3) The hinge is similar to that of the Cardiidae, differing only in detail. (4) The animal lacks pallial siphons (Boss states that the siphons are "simple"), having inhalant and exhalant openings only and, therefore, no siphonal retractor muscles are present. (5) The gills are plicate, with both inner and outer demibranchs and (6) the adductor muscles are subequal.

Boss (1971) also stated that the extensive mantle gape allied *Hemidonax* with the Cardiidae, but *Hemidonax* actually has a smaller pedal mantle opening than is found in either the Cardiidae or the Donacidae. Boss (1971) also pointed out that *Hemidonax* lacked the elongate, geniculate foot, the pedal-byssal groove and the pallial eyes assumed to occur in all cardiids and suggested *Hemidonax* could be placed in a separate subfamily.

Other features which indicate that *Hemidonax* is a cardiacean include:— (1) The ligament is similar to that of cardiaceans in having anterior and posterior secondary (periostracal) extensions to a primarily opisthodetic ligament with accompanying large posterior, and very small anterior, outer layers. (2) As in the Cardiidae and in the siphonal regions in the Tridacnidae (Yonge, 1981), the middle folds of the mantle margins are greatly reduced with sensory tentacles (and eyes where present) on inner folds.

The ctenidia have the typical cardiid form as described by Kellogg (1915) in *Clinocardium corbis* (=*nuttallii* (Conrad, 1837) and Atkins (1937) in *Cerastoderma edule* (Linné, 1767) and *Parvicardium ovale* (Sowerby, 1841) (also observed in the Indo-Pacific species listed below by two of us (W.F.P., C.M.Y.), namely a smaller outer demibranch with a supra-axial extension and a much larger inner demibranch. In *Hemidonax* the free edge of the outer demibranch reaches only to about the middle of the descending surface of the inner demibranch to which it is closely applied. This indicates the probability of direct transfer of food particles for passage to the food groove along the free surface of the inner demibranch. The presence of a second orally directed current along the axis, as in the three species mentioned above, can only be determined in living material.

The evidence thus overwhelmingly favours the placement of *Hemidonax* in the Cardiacea, but we disagree with Boss's (1971) conclusion that *Hemidonax* should be placed in the family Cardiidae.

Comparison of the gross anatomy of *Hemidonax* and of four cardiid species belonging to four genera *Laevicardium lobulatum* (Deshayes, 1855) *Fragum (F) fragum* (Linné, 1758), *Acrosterigma enode* (Sowerby, 1840), *Corculum cardissa* (Linné, 1758) has shown the following anatomical features separating the Cardiidae and *Hemidonax*.

1. Most of the visceral mass in cardiids is contained within a muscular sheath continuous with the ventrally placed foot. This has resulted in the visceral mass being compressed into a dorso-ventral column in the cardiids whereas in *Hemidonax* (fig. 2) it is spread fairly evenly between antero-posterior and dorso-ventral axes. The pedal muscles do not encase much of the visceral mass in *Hemidonax* and they are much thinner over the visceral area than in the cardiids.
2. The foot in *Hemidonax* is wide and relatively thin whereas in the Cardiidae it is geniculate (i.e. elongate and oval in section).

3. The ascending lamellae (fig. 2, aid) of the inner demibranchs are not fused to the visceral mass in either *Hemidonax* or the cardiids but in the latter they are fused to one another behind the visceral mass by a broad, thin but strong septum. In *Hemidonax* they have only ciliary connections.

4. The labial palps (fig. 1, olp, ilp) have migrated ventrally (as seen by their elongated bases) in the cardiids and lie well below the antero-postero ctenidial axis just ventral to the anterior adductor muscle, whereas they are level with the anterior end of the ctenidial axis and with the dorsal side of the anterior abductor muscle in *Hemidonax*. This difference in configuration is presumably associated with the changes in orientation of the body related to the difference in habits (see below). The ctenidial axis is also altered as a result of the different shape of the body and is much more acutely swung downwards towards the posterior end in the cardiids than in *Hemidonax*. The migration of the palps has necessitated the attachment of the anterior edge of the ascending lamellae of each outer demi-branch to the visceral mass over ⅓ to ½ its length in cardiids, whereas it is free in *Hemidonax*.
5. A prominent, muscular, tongue-like structure (or valvule) ventral to the posterior end of the ctenidia arises from the junction between the inhalant and exhalant siphonal openings in most, if not all, Cardiidae (Pelseneer, 1911; our observations), but is not present in the Tridacnidae. A shorter flap arises from the dorsal side of the tongue. No

similar structure was observed in *Hemidonax*, although a probable homologue is a thin, simple fold (fig. 1, fd) between the inhalant and exhalant apertures. The exhalant aperture of *Hemidonax* has a small, muscular flap dorsally which has not been observed in the cardiids examined.

6. The inhalant (fig. 2, ia) and exhalant (fig. 2, ea) apertures are fringed with short, simple tentacles in the cardiids and, whereas the inner mantle lobe of the pedal and exhalant apertures bears a row of short, simple tentacles in *Hemidonax*, additional complexly branched tentacles supported on thick, trunk-like bases surround the inhalant aperture (fig. 3). Cardiid species possess short siphons but the mantle edge around the apertures of *Hemidonax* (in the living specimen of *H. pictus* examined) scarcely protrudes beyond the shell margin. The ventral portion of the exhalant aperture has an extensile edge which protrudes like a short, thick tentacle.

7. A pair of large elevator pedis muscles is present in cardiids but is absent in *Hemidonax*.

8. The mantle lobes are widely open ventrally in the Cardiidae but united, by fusion of the inner marginal folds, for the posterior third in *Hemidonax*.

9. A byssal groove and gland are found in many cardiids but are absent from *Hemidonax*.

10. Eyes are present on the mantle margins (or tentacles) in most Cardiidae and Tridacnidae, but are absent in *Hemidonax*.

The shells of *Hemidonax* and the Cardiidae differ in the following ways:—

1. The anterior end is shorter than, or equal to, the posterior end in all cardiids but is much longer than the posterior end in some species of *Hemidonax*.

2. Although essentially similar to that of the Cardiidae, the hinge differs in the following details:—

(a) the anterior cardinal tooth in the left valve is somewhat bifid in *Hemidonax* and simple in cardiids.

(b) the lateral teeth are not widely separated from the cardinal teeth as they are in the Cardiidae.

(c) the cardiids have a flat plate which partly encloses the ligament and confines it to the upper margin of the shell. This plate has the appearance of a smooth, flat area between the posterior cardinal tooth and the posterior lateral tooth in both valves and seems to be present in all of the "subfamilies" of cardiids. The ligament in *Hemidonax*, on the other hand, lies well within the dorsal part of the hinge plate (although it is still an external ligament), and the plate-like structure is only rudimentary.

The smooth, anteriorly extended shells of some species of *Hemidonax*, which gives them a superficial resemblance to *Donax*, indicates a similarity in habits. They probably move about just below the surface of clean sand with the posterior apertures flush with the surface. The compressed foot and rather smooth shell surface of most species are probably well adapted for relatively rapid burrowing. Unfortunatley the normally sub-littoral habits of the temperate species have so far prevented direct observation. These probable habits are in sharp contrast to those of the also superficially dwelling but typically globular cardiids, which move over the surface of the substrate with the exceptionally powerful jerking movements of the geniculate foot.

In conclusion it appears that *Hemidonax* shows a sufficient number of differences from the Cardiidae to be placed in a distinct family. No currently recognised family grouping can conveniently accommodate *Hemidonax* which, it is proposed, should be given family status equivalent to that of the Cardiidae and of the Tridacnidae within the superfamily Cardiacea. A full survey of the basic form and adaptions throughout this superfamily is planned by C.M.Y.

TAXONOMY

Family **Hemidonacidae** Iredale & McMichael, 1962.

Diagnosis. As for genus *Hemidonax.*

Genus **Hemidonax** Mörch, 1871.

(*Malak. Blatt.*, 17:121.

Type species (by monotypy): *Donax (Serrula) pictus* Tryon, 1870.

Synonym: *Donacicardium* Vest, 1875 (*Jahr. deuts. Malak. Ges.*, 2:322).

Type species (original designation): *Donax donaciformis* (Schröter, 1786).

Diagnosis. Shell small to moderate in size, usually solid. Anterior end subequal to, or longer than posterior end; shape donaciform; sculpture of weak to strong, simple radial ribs, often weaker or absent on anterior end. Adductor muscle scars subequal, pallial line entire (i.e. lacking a pallial sinus); shell margin with interlocking, coarse crenulations along entire length.

Hinge and ligament generally similar to that of Cardiidae. Right valve with 2 anterior and 2 posterior lateral teeth, the upper lateral teeth fused to shell margin in most species. A very weak anterior cardinal and a strong posterior cardinal tooth present. Left valve with a single anterior and posterior lateral tooth, a prominent, triangular anterior cardinal tooth and a small, usually lamellate, posterior cardinal tooth. Ligament opisthodetic, with anterior and posterior secondary (periostracal) extensions; not partially enclosed by a shelly extension of the resilifer as in Cardiidae.

Animal with no siphons, an extensive pedal gape, a broad foot with no byssal groove, and no pallial eyes. Other anatomic characteristics which separate *Hemidonax* from the Cardiidae are discussed under Classifiction.

Remarks. The features which distinguish this family from the Cardiidae are discussed in detail under Classification.

When introducing his new genus Mörch included only one binomial name (*Donax pictus* Tryon) and two non-binomial names so the selection of the type species is by monotypy.

Lamy (1917) regarded *Hemidonax* as a monotypic genus but Hedley (1923) recognised 5 Australian species, one of which he described as new. Boss (1971) listed the 7 available *nomina* in the genus but did not comment on their validity as species taxa. In the present revision we recognise five Recent species, one on which consists of two subspecies, and one extinct species.

Key to the Recent species and subspecies of *Hemidonax*

Because of the considerable similarity in the shells of species of *Hemidonax* and the changes in form that they undergo during growth, the following key should be used only with subadult and adult specimens.

1. Radial ribs strong over whole surface 2

   Radial ribs weak or absent on anterior end 3

2. Shell large (mean length 25mm), subpolygonal, hinge heavy, radial ribs heavy ..... *donaciformis donaciformis*

   Shell small (mean length 15mm), subtriangular, hinge rather weak, radial ribs usually rather weak ..... *chapmani*

3. Shell with almost straight ventro-posterio margin ..... *dactylus*

Shell with distinctly concave ventro-posterior margin 4

4. Posterior end about ½ length of shell ..... *donaciformis australiensis*

Posterior end about 1/3 length of shell 5

5. Anterior lateral tooth long (about 1/3 length of anterior end of shell) ..... *pictus*

Anterior lateral tooth short (about 1/5 length of anterior end of shell) ..... *arafurensis* nov.

Hemidonax donaciformis donaciformis (Schröter, 1786). Figs 9, 10, 12. Plate 1, figs 1-5.

Cardium medium Lamark var. Chemnitz, 1782, *Conch. Cab., VI*, pl. 16, fig. 165 (non binomial).

Cardium donaciforme (Spengler) Chemnitz, 1782, *Conch. Cab., VI*, p. 171 (non binomial).

Cardium donaciforme (Spengler) Schröter, 1786, *Einleit. Conch., 2*: pl. 7, fig. 14; *3*: 68 (type locality: unknown, subsequently given as Philippine Islands (Römer, 1869, *Syst. Conch. Cab., 10* (3): 100).

Cardium donaceum Spengler, 1798, *Skrivt. Naturh. Selsk, 6*: 37 (type locality: Drontheim, Norway. Error).

Donax cardioides Lamarck, 1818, *Anim. sans Vert., 5*: 550 (type locality: mers de la Nouvelle-Hollande à l'it Saint Pierre-Saint Francois (Nuyts Archipelago, Great Australian Bight)), Delessert, 1841, *Rec. coq. Lamarck*, pl. 6, figs 14a, b, c.

Hemidonax donaciformis. — Lamy, 1917, *J. Conch. (Paris), 62*: 264-270 (gives full synonymy).

Hemidonax donacaeiformis (sic!). — Popenoe & Kleinpell, 1978, *Occas. Pap. Calif. Acad. Sci.*, 129: pl. 14, figs 181, 182.

Shell: Of rather large size, solid, anterior and posterior ends about equal in length, ventral margin convex except for slight indentation near posterior end, beaks high, prominent; posterior end with prominent, rounded, diagonal ridge from umbo to ventral margin. Thirty to 40 flat-topped radial ridges with narrow to equal-sized interspaces, ribs becoming weaker on anterior end of shell. Inner ventral margin coarsely crenulated along entire length; edge of valve also with extremely fine crenulations.

Hinge: Right valve with strong, lower anterior and posterior lateral teeth separated by a deep socket from upper lateral teeth which are fused to hinge margin. Anterior lower lateral tooth moderately long, posterior lower lateral tooth short. Anterior cardinal tooth very weak, fused to inner end of lower anterior lateral tooth. Posterior cardinal tooth narrow, longitudinally grooved, separated from resilifer by a shallow, narrow groove. A very shallow groove separates upper anterior lateral tooth from hinge margin in some specimens. Left valve with strong anterior and posterior lateral teeth, a prominent, triangular anterior cardinal tooth and a small, lamellate posterior cardinal tooth adjacent to edge of resilifer (figs 9, 10).

Colour: White to brown, often with brown to purplish-brown markings, especially on posterior end; interior white, sometimes with small purple or orange blotches.

Dimensions: See table 1

Types. Cardium donaciforme and *C. donaceum* (pl. 3, figs 1,2), ZMC. A reproduction of Schroter's figure of *D. donaciformie* is given in plate 1, fig. 1. *Donax cardioides*. There are two lots marked "type" in the NHMG. In one lot (No. 1083/82) of 3 complete specimens 2

are *H. donaciformis* and 1 is *H. pictus* (Tryon). One of the specimens of *H. donaciformis* agrees fairly well with the specimen figured by Delessert (reproduced in plate 1, figs. 2-4), although there are slight differences in colour pattern. Another lot marked *cardioides* Lamarck *var.* (No. 1083/83) is also *H. pictus*. Two lots in NHMP are marked *cardioides* Lamarck and have probably been identified by the author; one lot of 3 complete specimens is from the Islands St Pierre and St Francois, coll. Peron and Lesueur, 1803, and another lot of 3 complete specimens is from Nouvelle-Hollande, coll. Peron and Lesueur, 1803. All of the specimens in the NHMP are Australian species. In order that this name be stabilized in conformity with the present usage of species names in this group the specimen which appears to be that figured by Delessert in the NHMG, No. 1083.82.1 is chosen as the lectotype. It measures 25.8mm in length and 19.1mm in height. This action retains */dibakx cardioides as a junior synonym of H. donaciformis,* although the type locality cited by Lamarck is not compatable with the distribution of the species.

Additional Material Examined. Philippines: Luzon Is.,Cataoyan Reef, S.E. Polillo Is. (WAM); Matabungkay; Subic Bay (MCZ); Marivales, Bataan (MCZ); Nasasa Bay, San Antonio (MCZ); Tabaco (ANSP, NMV); San Juan; Awazan Beach, Tegoawayan; Macabunki, *Lubang Is.*, Tilic Beach (MCZ); Tilic Bay (MCZ); *Mindoro Is.* Balatero Bay, Galera (MCZ); Calapan (MCZ). *Palawan Is.*, Dumaran Is (MCZ); Cuyu Is., (MCZ); Puerto Princessa (ANSP). *Negros Is.* (ANSP). *Cebu Is.*, Cebu City (MCZ, ANSP). *Bohol Is.*, Tagbilaran (MCZ). *Mindanao Is.*, Placer (MCZ). *Sulu Archipelago*, Natalio Odon, Laminusa (ANSP); Bongao Channel, SW end Sanga Sanga Is. (ANSP); South Lagoon, Sibutu (WAM). *Malaysia-Sabah*: Bohaydulong Is. (ANSP); Semporna (NMV). *Indonesia*: *Moluccas*, Ambon (MCZ); Kasiruta Is. (MCZ); Manipa Is. (MCZ). *Java-Madura*, Bali. *West Irian*, Jefman Is. (ZML); Mios Woendi Atoll, Padaido Ids. (2 lots, ANSP); Manokwari (ZML).

Fossil Record. Late Pliocene-early Pleistoecene, Vigo Group, Bondoc Peninsula, Luzon, Philippines (Dickerson, 1922 (as *Cardium donaciformis* Cuming), Popenoe & Kleinpell, 1978). (California Academy of Sciences, Dept. Paleont., No. 2426). One immature left valve.

Remarks. This species is restricted to the Philippines, eastern Indonesia and western West Irian and is easily distinguished from the Australian subspecies. Lamy (1917) reduced *Donax pictus* Tryon and *Cardium australiensis* Reeve to synonyms of *H. donaciformis* but his revision was based on very limited material. Differences ij shell shape, sculpture and hinge details noted below indicate that *australiensis* can be regarded as a geographically isolated subspecies of *H. donaciformis* and that *H. pictus* is a separate species.

Quoy and Gaimard (1834) described and figured *"Cardium cardioides"* from New Guinea and their figure is of a specimen of *H. donaciformis donaciformis*. The only records of the species in this area are from north-western West Irian; there are none from Papua-New Guinea. However, it is probably more widespread than is indicated by the available material.

Dickerson (1921, 1922) recorded this species from the "Miocene" (=Upper Pliocene — early Pleistocene, Popenoe & Kleinpell, 1978) of the Philippines. Comparison of the single fossil specimen with the living species shows it to be identical. It is figured by Dickerson (1922, pl. 6, figs. 9a, 9b) and Popenoee & Kleinpell (1978, pl. 14, figs 181, 182) and is immature, being only 18.8mm in length.

Hemidonax donaciformis australiensis Reeve, 1844). Fig. 12. Plate 1, figs 6-9.

Cardium australiense Reeve, 1844, *Conch. Icon., 2, Cardium,* Pl. 5, fig. 24 (type locality: Port Lincoln, South Australia. Error for North (Western) Australia); Reeve, 1845, Proc. Zool. Soc. Lond., 1844: 168.

Donacicardium australiense — Vest, 1876, *Jahr. deuts. Malak. Ges., 3*: 291, pl. 10. fig. 1.

Hemidonax donaciformis.— Wilson & Stevenson, 1977, *West. Aust. Mus. Spec. Publ., 9*: 10 (*non* Schröter, 1786).

Shell: Of moderate size, rather solid, anterior end slightly longer to slightly shorter than posterior end, ventral margin convex except for slight indentation near posterior end;

beaks high, prominent; posterior end with prominent, rounded, diagonal ridge from umbo to ventral margin. About 20 weak, flat-topped radial cords with narrow interspaces on posterior half of shell, anterior half with weak radial scratches; whole surface sculptured with concentric growth lines. Internal ventral margin coarsely crenulated along entire length, anterior end of some specimens very finely crenulated on edge of valve.

Hinge: Right valve with moderately long anterior and posterior lateral teeth, each pair separated by a deep socket; upper lateral tooth very weak and almost merged with shell margin, lower lateral tooth strong. Anterior cardinal tooth very weak, fused to inner end of anterior lateral tooth and appearing to be a continuation of it. Posterior cardinal tooth thin, weakly grooved in lectotype, sometimes single, separated from edge of resilifer by a narrow, rather shallow groove. A narrow groove separates upper anterior lateral tooth and anterior cardinal tooth. Left valve with strong, anterior and posterior lateral teeth; a strong, triangular anterior cardinal tooth and a small, lamellate posterior cardinal tooth. Hinge line rather strong.

Colour: White, sometimes with purple markings on shell margins above lateral teeth and zig-zag brown or purple markings on posterior margin and, in some specimens, on body of shell. Interior white.

Dimensions: See table 1.

Type. None of the material in the BMNH agrees with Reeve's figure. The several specimens labelled *australiense* include several species. A single specimen in the NMV agrees with Reeve's figure and originated from the H. Cuming collection. It is labelled with Reeve's name and the locality given is "N. Australia". A specimen of *H. donaciformis donaciformis* from the Cuming collection, also in the NMV, is labelled *australiense* and the locality given is "Port Lincoln, S. Australia". It is probable that labels have been mixed, possibly even by Cuming or Reeve. The specimen labelled "N. Australia" is likely to be the specimen figured by Reeve and is here selected as the lectotype (NMV No.. 19128). There are several other Reeve types in the NMV amongst specimens purchased from Reeve and Cuming (B. J. Smith, *pers. comm.*)

Dimensions of Lectotype. Length 25.8mm, height 17.9mm.

Additional Material Examined. Western Australia: Dampier Archipelago (WAM, 3 lots); Monte Bello Is.; Barrow Is. (WAM, 4 lots; AMS).

Fossil Record. Pleistocene, Barrow Is., north Western Australia, beach deposit in S.E. corner, approx. 2.5m above H.W.M.,3 specimens (WAM, 74.1110, a-c).

Remarks. The only material examined that agrees closely with the lectotype are a few lots from north Western Australia. Other specimens from north Western Australia have a shorter posterior end and brighter coloration and these are here regarded as a separate taxon which is described and contrasted below.

Although similar to *H. pictus* in most features, *H. donaciformis australiensis* is easily distinguished from that species in having much shorter anterior lateral teeth in both valves and in usually having a relatively longer posterior end. It differs from the typical subspecies in having fewer radial ribs, the anterior end being almost smooth instead of ribbed, a significantly lower height/length ratio and relatively longer posterior lower lateral teeth.

The fossil material of this subspecies agrees closely with the Recent form in shape but has stronger radial ribbing which extends further anteriorly than in most Recent shells. This suggests that the Pleistocene north Western Australian population of *H. donaciformis* had a greater resemblance to *H. donaciformis donaciformis* than do the Recent populations.

Hemidonax pictus (Tryon, 1870) Figs 6, 7, 12. Plate 2, figs 1-5.

Cardium australiense.— Angas, 1867, *Proc. zool. Soc. Lond.* (1867): 925 (*non* Reeve, 1844).

Donax (Serrula) pictus Tryon, 1870, *Amer. J. Conch*, 6: 23, Pl. 1, fig. 1 (no locality given; = eastern Australia).

Hemicardia donaciformis — Brazier, 1880, *Proc. Linn. Soc. N.S.W.* 5,847 (*non* Schröter, 1786).

Cardium donaciforme.— Whitelegge, 1889, *Proc. R. Soc. N.S.W., 23:* 241 (*non* Schröter, 1786).

Hemidonax donaciforme. — Hedley, 1909, *Proc. Linn. Soc. N.S.W.,* 34: 425 (*non* Schröter, 1786).

Hemidonax australiensis.— Hedley, 1918, *Jl. R. Soc. N.S.W. (Suppl.),* 51: M16 (*non* Reeve, 1844).

Shell: Of large size, solid, anterior end slightly longer than posterior end, ventral margin convex except for an indentation near posterior end; beaks high, prominent; posterior end with prominent, rounded, diagonal ridge from umbo to ventral margin. Numerous, weak, narrow radial ridges on posterior half of shell, interspaces of about equal width to ridges and each sculptured with 1-2 weak radial striae. Anterior half of shell with radial ribs of most specimens becoming subobsolete towards anterior end and having, usually, extremely fine radial striae. Internal ventral margin strongly crenulated along entire length and finely cenulated on outer edge of valve at anterior end.

Hinge: Very similar to that of *H. donaciformis donaciformis* but lateral teeth slightly weaker, anterior lateral teeth relatively longer and hinge line narrower (Figs 6, 7).

Colour: White to brown, with brown to purple radial or zig-zag markings on exterior surface of most specimens, especially on radial ribs. Interior white, with purple blotches on some specimens.

Dimensions: See table 1.

Holotype. ANSP, No. 51562.

Dimensions of holotype. Length: 37.5 mm, height 28.88 mm.

Additional Material Examined. New South Wales: Port Jackson, Sydney; Collaroy area (4 lots); Palm Beach (WAM); Broken Bay area (9 lots); Blacksmiths Beach, Swansea; Port Stephens area (7 lots); Byron Bay (2 lots). *Queensland:* Coolangatta; Southport; Stradbroke Is. (2 lots); Moreton Is. (WAM); Caloundra (3 lots); Bargara, near Bundaberg; Tannum Sands (2 lots); Keppel Bay (2 lots); Port Curtis area (4 lots, 1 lot 18 m); Pialba, Hervey Bay; River Don delta Bowen (WAM); Innisfail (2 lots); Annan River near Cooktown.

Fossil Records. Upper Pliocene — Lower Pleistocene: Era River, Gulf of Papua, Papua New Guinea (BMR, O.S./NK6) (1 valve). Cape Possession, Gulf of Papua, Papua New Guinea (BMR,F. 7237) (2 valves).

Remarks. This species is restricted to eastern Australia, being more common, and reaching a larger size, in New South Wales than in Queensland. It differs from *H. donaciformis* in attaining a larger size, having a relatively longer anterior end, and having a slightly narrower hinge line, weaker lateral teeth and more elongate anterior lateral teeth. The external radial sculpture differs in being weaker and is confined to the posterior end in most specimens of *H. pictus* which is also more brightly coloured than is usual in *H. donaciformis.* Some specimens from north Queensland have strong radial sculpture persisting over the whole exterior surface but they show the other differentiating features of *H. pictus* and so can readily be separated from *H. donaciformis* and *H. chapmani.*

Upper Pliocene — Lower Pleistocene specimens are known from Papua New Guinea in the Gulf of Papua area (pl. 2, figs. 4, 5). These records represent a northern extension of the known present range. The specimens agree in most respects with Recent material but are of ligher build and have slightly weaker sculpture.

Hemidonax chapmani Gatliff & Gabriel, 1923, Fig. 12. Plate 1, figs 10-14.

Donax cardioides.— Tate, 1887, *Trans. R. Soc. S. Aust.,* 9: 86; Pritchard & Gatliff, 1903, *Proc. R. Soc. Vict., 16:* 119 (*non* Lamarck, 1818).

Hemidonax australiense.— Gatliff & Gabriel, 1914, *Vict. Nat., 31:* 83 (*non* Reeve, 1844).

Hemidonax chapmani Gatliff & Gabriel, 1923, *Vict. Nat.*, *40*: 10, pl. 2 (type locality: San Remo, ocean beach, Victoria, Australia).

Deltachion chapmani.—Cotton, 1961, *South Australian Mollusca* — Pelecypoda: 285, fig. 313.

Shell: small, rather solid, anterior end about twice as long as posterior end, ventral margin convex except for a very slight indentation near posterior end, beaks rather low, rounded; posterior end with prominent, rounded, diagonal ridge from umbo to ventral margin. Whole surface except extreme anterior end had close, weak, flat-topped radial ribs. Inner ventral margin coarsely crenulated along entire length.

Hinge: Right valve with short lateral teeth, the posterior lateral tooth about ½ length of anterior tooth, outer lateral teeth fused to margin and weak. Anterior cardinal tooth very thin, fused to inner end of outer anterior lateral tooth. Posterior cardinal tooth rather thin, separated from edge of resilifer by a distinct furrow and well separated from upper posterior lateral tooth. Left valve with single, strong anterior cardinal tooth and a small, very weak, lamella-like posterior cardinal tooth.

Colour: White with purple tinge near umbos and brown to purple zig-zag and radial markings on exterior surface in most specimens. Interior white with purple blotches that are extensive in most specimens; pallial line diffuse pale-orange in some specimens.

Dimensions: See table 1

Types. Lectotype (here chosen) (F512a) (1 valve) and 2 paralectotypes (F 512eb(1 valve) and F513 (2 valves), NMV. 5 paralectotypes (single valves), AMS, C.117896.

Dimensions of Lectotype. Length 21.66mm, height 15.5 mm.

Additional Material Examined. Western Australia: Cottesloe; Thomson Bay, Rottnest Is.; Pt. Peron; Garden Is., Rockingham Bay (2 lots); off Fremantle, 15m (WAM); Safety Bay; Windy Harbour (3 lots) (WAM); E. of Cheyne Bay, 75m; Malimup, Black Point (WAM): off Hood Point, 79 m; Hopetoun. *South Australia:* 80 km SE of Kangaroo Is., 77m; Spencer Gulf; Royston Head (3 lots). *Victoria*: Phillip Is. (WAM); Western Port Bay (2 lots); San Remo (2 lots).

Fossil Records. Western Australia. Pliocene. All Ascot beds, central Perth Basin: Kewdale (5, WAM); Redcliffe (6, 3 lots, WAM); Thornlie (several, 4 lots, WAM); Muchea (1, WAM). *Early Pleistocene.* Early Pleistocene beds of the Perth Basin, mostly from bores. Paulik's bore, Jandakot (46 lots, WAM); Jandakot Cement Works bore (13 lots, WAM), Adrians Nursery bore, Jandakot (many, 2 lots, WAM); Jandakot exploratory bores (4, 3 lots, WAM); Success (2, WAM); Wanneroo (several, WAM); Atwell (4, 2 lots, WAM); Pinjarra West (5, WAM); West Coolup (1, WAM); Myalup (1, WAM). *Late Pleistocene.* Tamala Limestone: Coogee, S. of Fremantle, from quarry (1, WAM); Lake Clifton, from quarry, S. of Mandurah (2, WAM); Singleton (2, WAM); Ocean Reef, Beenyup (8, WAM).

The ages of the material listed above are given on the authority of Mr. G. W. Kendrick, of the Western Australian Museum.

Remarks. Hemidonax chapmani can be distinguished from the other two temperate Australian species by its small size and by having prominent radial sculpture over the whole surface. A new species possibly related to *H. chapmani* is found in northern Australia and is described below.

A south Western Australian Pliocene-Pleistocene ancestral form of *H. chapmani* is represented by a large amount of material, mainly from bores. It has fewer, broader ribs (11-20, mean 15.6)* than Recent shells (Pl. 1, fig. 14). Specimens with few ribs also tend to have a shorter posterior end than most Recent shells. There is, however, considerable variation in rib numbers within the material examined and we can make no satisfactory consistent distinction between Recent and fossil series on this or other characters. Upper Pleistocene — Holocene material has a similar rib count to Recent specimens (18-30, mean 21.8; Recent 15-24, mean 20) whereas Pliocene specimens, while having a lower mean rib-

Foot note

* *Rib counts exclude those ribs posterior to the posterior angulation.*

count than Recent specimens, have a higher number than those from the lower Pleistocene (13-20, mean 17.3).

Hemidonax arafurensis sp. nov. Figs 1-5, 11, 12. Plate 1, figs 6-9.

Hemidonax donaciforme.— Hedley, 1918, *Proc. R. Geog. Soc. S. Aust., 18*: 271 (*non* Schröter, 1786).

Shell: Small, solid, anterior end about 1½ times as long as posterior end, ventral margin weakly convex except for slight indentation near posterior end; beaks rather low, rounded, posterior end with prominent, rounded, diagonal ridge from umbo to ventral margin. About 20 moderately strong, rounded, radial ribs with narrow interspaces on posterior half of shell, anterior half with weak radial striae; whole surface with concentric growth lines. Inner ventral margin crenulated along entire length; edge of valve with very fine crenulations in some specimens.

Hinge: Right valve with moderately long anterior lateral teeth and short posterior lateral teeth, both pairs of lateral teeth separated by a deep socket; upper lateral teeth almost completely fused to shell margin; lower lateral teeth strong. Anterior cardinal tooth small, separated from lower anterior lateral tooth by a shallow groove. Posterior cardinal tooth thin, simple, separated from edge of resilifer by a deep, narrow socket. Upper anterior lateral and anterior cardinal teeth not completely separated by a groove, surface of area between them, and above inner part of upper anterior lateral tooth, finely granular. Left valve with single, strong, anterior and posterior lateral teeth; posterior tooth short. Anterior cardinal tooth strong, triangular; posterior cardinal tooth small, lamellate. Hinge line rather long (figs 4, 5).

Colour: White, with some purplish-brown, zig-zag, radial or dot-like markings over the exterior surface of most specimens. Interior white, typically with pale-purplish blotches.

Dimensions: See table 1.

Types. Holotype (C.117895) and many paratypes(C.72967, C.72970 (wet), C.90614), AMS: 2 paratypes WAM, 1 paratype NMV, 1 paratype Auckland Institute and Museum, Auckland, New Zealand, 1 paratype Museums and Art Galleries of the Northern Territory.

Dimensions of Holotype. Length 24.4 mm, height 16.2 mm.

Type locality. Sandbar off Emery Point, Darwin, Northern Territory, Australia, 26 Oct. 1969, coll. P.H. Colman; alive at low tide in sand.

Additional Material Examined. Northern Territory: Off Point Charles, 14-17 m; Darwin area (3 lots). *Western Australia*: Buccaneer Archipelago; Broome, 13 m; Lagrange Bay; Dampier Archipelago (WAM, 2 lots); North West Australia (WAM).

Remarks. This species can be distinguished easily from *H. pictus* by its much shorter anterior lateral teeth, the lack of a distinct groove between the upper anterior lateral tooth and the anterior cardinal tooth in the right valve and the simple (not grooved) right posterior cardinal tooth. In addition *H. pictus* is much larger and only a very few specimens develop purple blotches internally. The southern *H. chapmani* has a more triangular shell and has well-developed radial sculpture over the whole surface. *H. dactylus* Hedley differs in its larger, lighter shell and evenly-convex ventral margin as well as in hinge details. *H. donaciformis australiensis* can be distinguished by its longer posterior end and white interior. The hinge of *H. donaciformis australiensis* differs from that of *H. arafurensis* in having longer posterior lateral teeth, an indistinct anterior cardinal tooth in the right valve and a narrow groove in the area between the inner end of the upper anterior lateral and anterior cardinal teeth. In *H. arafurensis* this area is not grooved.

This species is apparently sympatric with *H. donaciformis australiensis* in the Dampier Archipelago, north Western Australia because both species are represented by fresh specimens in two samples in the WAM.

Hemidonax dactylus, Hedley, 1923. Fig. 12. Plate 2, figs 9-11.

Hemidonax dactylus Hedley, 1923, *Proc. Linn. Soc. N.S.W., 41*: 303, pl. 31, fig. 13 (type locality: Kiama, New South Wales, Australia).

Shell: Of moderate size, rather thin, anterior end slightly longer than posterior end with low diagonal ridge running from umbo to ventral margin. Weak radial ribs on posterior half of shell become obsolete on anterior half but are replaced by extremely fine radial striae. Internal margin crenulated along entire length, anterior end with coarse crenulation on inside edge and very fine crenulation on outer edge.

Hinge: Right valve with long anterior lateral teeth and short posterior lateral teeth, both pairs separated by a deep socket; upper lateral teeth very weak and fused to shell margin, lower lateral teeth moderately strong but weaker than in other species of genus. Anterior cardinal tooth small, lamella-like, fused to inner end of lower anterior lateral tooth. Posterior cardinal tooth rather strong, grooved, separated from edge of resilifer by a narrow, shallow groove. Inner end of upper anterior lateral tooth well separated from anterior cardinal tooth which meets shell margin only. Left valve with relatively weak lateral teeth, a strong triangular or sub-bifid anterior cardinal tooth and a weak, lamellate, posterior cardinal tooth attached to edge of resilifer. Hinge plate narrow.

Colour: White to fawn, with brown to purplish-brown markings externally. Interior white to pinkish, orange or purple.

Dimensions: See table 1.

Type. Holotype, AMS, C.47619 (2 valves).

Dimensions of holotype. Length 27mm, height 16.7 mm.

Additional Material Examined. New South Wales: Twofold Bay (2 lots); Batemans Bay; Sussex Inlet, Wreck Bay; Gerringong; Seven Mile Beach, Wollongong; Botany Bay area (5 lots); E. of Sydney, 75-150 m; Sydney area (7 lots); Manly; Collaroy Beach (3 lots); Broken Bay area (7 lots); Tuggerah Lakes; Port Stephens (5 lots); off Cape Hawke, 82 m; Laurieton Beach; Pt. Macquarie (WAM); South West Rocks; Angourie (2 lots); Clarence River mouth; Ballina (WAM); Byron Bay (2 lots); Tweed Heads. *Queensland:* Coolangatta (2 lots); Nerang River, Southport; Southport; North Stradbroke Is. (3 lots) (1 lot, WAM); Hervey Bay; Port Curtis area (5 lots, 1 lot 13 m); Mackay; Buchans Point, near Cairns (WAM); Albany Passage, Cape York Peninsula, 7-26 m.

Remarks. This species differs from the others in the genus by its light build, elongate shape and narrow hinge line. There are also differences in coloration and hinge details. It is sympatric with *H. pictus* and seems to share a similar habitat, shells being found washed up mostly on open coastal beaches.

Wilson & Stevenson (1977: 10) indicate that they believe this species to be synonymous with *H. chapmani*. We cannot agree with this conclusion for the reasons advanced above.

Hemidonax dixoni (Tate, 1887). Plate 1, figs 15, 16.

Donax dixoni Tate, 1887, *Trans. R. Soc. S. Aust.*,*9*: 169, pl. 16, fig. 15 (Lower beds, Muddy Creek, Victoria, Australia); Dennant & Kitson, 1903, *Rec. Geol. Surv. Vict., 1* (2): 125.

Shell: Small, of rather light build, anterior end only slightly longer than posterior end, ventral margin evenly convex; beaks rather low but somewhat pointed; posterior end with very weak to absent diagonal ridge. Anterior ¼ of exterior with subobsolete radial lines, remainder of shell with rounded, low radial ribs with linear interspaces. Internal margin coarsely crenulated along entire length.

DIMENSIONS OF TYPES

	Length	height	length of posterior end
Lectotype	12.3 mm	9.1 mm	5.7 mm
Paralectotypes	10.2	6.6	4.5
	11.3	8.4	4.6

Hinge: Similar to that of *H. arafurensis* nov. but somewhat weaker, with slightly longer anterior lateral teeth. Right valve with a stronger, thicker posterior cardinal tooth; left valve with upper lateral teeth very weak and fused to shell margin, the groove between upper and lower laterals being almost obsolete.

Types. Lectotype (here chosen) and 9 paralectotypes, SAM (T1201). The dimensions given by Tate best fit a small specimen, a right valve, whereas his figure agrees with the specimen here chosen as the lectotype.

Additional Material Examined. Middle Miocene. Muddy Creek Formation, lower beds, Muddy Creek, Hamilton, Victoria (topotypes, NMV). Fyansford Formation, Shelford (probably = Red Hill), Victoria (NMV). *Lower Pliocene.* Grange Burn Formation, upper beds, Muddy Creek, Hamilton, Victoria (NMV). (?) *Early Pleistocene.* Glenelg River, W. Victoria, Werrikoo Limestone (WAM).

Remarks. Apart from the type series, the material available of this species, is immature and mostly worn. The early pliocene material consists of two juveniles and the Early Pleistocene record is based on a single juvenile, all of which compare much more closely with *H. dixoni* than with Pliocene specimens of *H. chapmani.* The very coarse radial ribbing seen in the Pliocene material of *H. chapmani* is in sharp contrast to that of *H. dixoni.*

This species lacks the long anterior lateral tooth and fine anterior radial striae of *H. pictus* and *H. dactylus* and appears to have only one series of crenulations on the ventro-anterior valve margin. For these reasons *H. dixoni* is not considered to be ancestral to *H. dactylus* and *H. pictus.*

Three small valves (fig. 5) from the late Oligocene or early Miocene of Maude, Victoria (Lower Maude Limestone) in the NMV (P. 58000-58002) appear to represent an undescribed form which is probably ancestral to both *H. chapmani* and *H. dixoni.* These specimens are triangular in outline and rather coarsely ribbed over almost the entire surface. The available material is not adequate for a name to be provided for this form. These specimens were recorded by Dennant & Kitson (1903) as *H. dixoni.*

Results of Analysis of Dimensions

The analysis of the shell dimensions showed that all the taxa could be separated. For the height/length (H/L) ratio there were significant differences between all taxa except between *H. pictus* and *H. donaciformis australiensis, H. pictus* and *H. arafurensis,* and *H. donaciformis australiensis* and *H. chapmani.* For the posterior length/length (PL/L) ratio there were significant differences between all taxa except between *H. donaciformis donaciformis* and *H. donaciformis australiensis* and *H. pictus* and *H. chapmani* (see tables 2 and 3).

DISCUSSION

The Evolution of the Species of Hemidonax

The fossil record of *Hemidonax* is sparse but sufficient to build a speculative model for the evolution of the group. Its earliest origins are unknown, the first appearance being in the late Oligocene or early Miocene of Victoria, southern Australia where it is known from 3 immature, poorly-preserved specimens (fig. 5). The genus is not known in the rich Miocene faunas of Indonesia but is first seen in the tropical Indo-pacific in the late Pliocene early Pleistocene of the Philippines. It is postulated that, probably in the late Miocene, this tropical element was derived from a stock present in tropical Australia but not represented in the Australian Miocene fossil record because of the absence of suitable fossil deposits in northern Australia. A south-western Pacific derivative of this northern form probably became adapted to burrowing in fine substrate by developing an almost smooth, elongate, anterior end. This form may have evolved in eastern Australia (as the ancestor of *H. dactylus*) and may have been able to spread south during a warm period. It may have become isolated in the temperate to warm-temperate waters of the east coast, because of the development of some sort of barrier to dispersal. This possibly came about during a period of low sea level in the Pliocene which may have greatly reduced suitable

habitats along most of the Queensland coast. A further invasion of the tropical western Pacific isolate, which evolved into *H. pictus*, probably occured in the late Pliocene or Pleistocene (*H. pictus* is known from the late Pliocene —Pleistocene of the Gulf of Papua), and resulted in the spread of *H. pictus* along the eastern coast of Australia to become sympatric with *H. dactylus*. These two forms are similar in their elongate shape, long anterior lateral teeth and fine radial striae on the anterior end of the shell.

The tropical *H. donaciformis donaciformis* is apparently adapted to living in coarse coral sand, probably in environments of lower energy than those of *H. pictus* and *H. dactylus*. Consequently the shell is more cardiform, the anterior and posterior ends being about equal in length, and its whole surface is sculptured with coarse radial ribs. This species may have been derived from a north-western Australian form now represented by *H. arafurensis*. A southwards invasion of *H. donaciformis* may have occurred during the Pleistocene and, subsequently, a break-down in dispersal allowed the differentiation of *H. donaciformis australiensis*. *Hemidonax arafurensis* and *H. donaciformis australiensis* are now sympatric in at least one locality in north-western Australia. They are both more elongate than *H. donaciformis donaciformis* and their shells have relatively smoother anterior ends. One form (*H. arafurensis*) is donaciform with a short posterior end and the other (*H. donaciformis australiensis*) has a relatively elongate posterior end.

The southern Australian Oligocene or early Miocene species appears to have given rise to two species, *H. dixoni* in western Victoria ranging from Miocene to Pliocene (and possibly Pleistocene), and *H. chapmani* in south Western Australia, first appearing in the Pliocene. *Hemidonax chapmani* subsequently invaded southern Australia, including Victoria, probably in the Pleistocene.

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REFERENCES

Allen, J.A., 1968. The functional morphology of *Crassinella mactraea* (Linsley) (Bivalvia: Astartacea). *Proc. Malac. Soc. Lond.*, 38: 27-40.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part III. Types of lamellibranch gills and their food currents. Quart J. Micr. Sci., 79: 375-421.

Boss, K.J., 1971. Familial affinities of *Hemidonax* (Bivalvia). *Nautilus*, 85 (1): 9-12

Chapman, G. & G.E. Newell, 1956. The role of the body fluid on the movement of soft-bodied invertebrates. II. The extension of the siphons of *Mya arenaria L.* and *Scrobicularia plana* (da Costa). *Proc. Roy. Soc. Lond.*, B, 145: 564-580.

Dennant, J. & A.E. Kitson, 1903. Catalogue of the described species of fossils (except Bryozoa and Foraminifera) in the Cainozoic fauna of Victoria, South Australia, and Tasmania (with locality plan). *Rec. Geol. Surv. Vict.*, 1 (2): 89-147.

Dickerson, R.E., 1921. A fauna of the Vigo Group: its bearing on the evolution of marine molluscan faunas. *Philipp. J. Sci.*, 18 (1): 1-21, 2 plts.

_____1922. Review of Philippine Paleontology. *Philipp. J. Sci.*, 20 (2): 195-229.

Graham, A. 1934. The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proc. Roy. Soc. Edinb.*, 54: 158-187.

Hedley, C., 1906. Studies on Australian Mollusca. Part IX. *Proc. Linn. Soc. N.S.W.*, (1905) (4): 520-546.

_____1909. Mollusca from the Hope Islands, North Queensland. *Proc. Linn. Soc. N.S.W.*, 24 (3): 429-466.

_____1923. Studies on Australian Mollusca. Part XIV. *Proc. Linn. Soc. N.S.W.*, 48: 301-316.

Hoffmann, F., 1914. Beiträge zur Anatomie und Histologie von *Tagelus dombeyi* (Lamarck). *Jena Z. Naturw*, 52: 521-561.

Keen, A.M. (*in* R.C. Moore edit), 1969. *Treatise on Invertebrate Paleontology.* Part N, vol. 2 (of 3), Mollusca 6, Bivalvia, pp. N 491-951.

Kellogg, J.L., 1915. Ciliary mechanisms of Lamellibranchs with descriptions of anatomy. *J. Morph.*, 26: 625-701.

Lamy, E., 1917. Révision des Crassatellidae vivants du Museum d'Histoire Naturelle de Paris. *J. Conch. (Paris)*, 62: 197-270.

Pelseneer, P., 1911. Les lamellibranches de l'expedition du *Siboga.* Partie Anatomique. *Siboga Exped. Repts.*, 29, Mollusca 125 pp., 25 pls.

Popenoe, W.P. & R.M. Kleinpell, 1978. Age and stratigraphic significance for Lyellian correlation of the fauna of the Vigo Formation, Luzon, Philippines. Occas. Pap. Calif. *Acad. Sci.*, 129: 1-73, 18 plts, 1 table.

Prezant, R.S., 1979. The structure and function of the radial glands of *Lyonsia hyalina (Bivalvia: Anomalodesmata). J. Zool. Lond* (187): 505-516.

Quoy, J.R.C. & J.P. Gaimard, 1832-1835. *Voyages de découvertes de l'Astrolabe,...sous le commandement de M.J. Dumont d'Urville. Zoologie: Mollusca.* Vol. 2 and atlas. Paris.

Wilson, B.R. & S.E. Stevenson, 1977. Cardiidae (Mollusca, Bivalvia) of Western Australia. *West. Aust. Mus. Spec. Publ.*, 9: 1-114.

Yonge, C.M., 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Phil. Trans. Roy. Soc.*, B, 234: 29-76.

_____1959. On the structure, biology and systematic position of *Pharus legumen* (L.). *J. Mar. biol. Ass. U.K.*, 38: 277-290.

_____1969. Functional morphology and evolution within the Carditacea (Bivalvia). *Proc. malac. Soc. Lond.*, 38: 493-527.

_____1981. Functional morphology and evolution in the Tridacnidae (Mollusca: Bivalvia: Cardiacea). *Rec. Aust. Mus.* (in press).

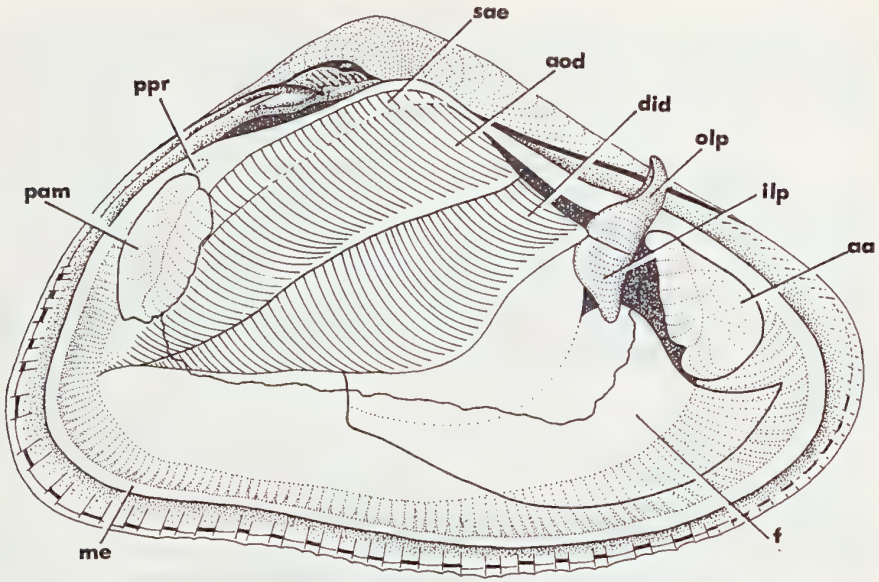


Figure 1. Right valve and inner part of mantle removed.

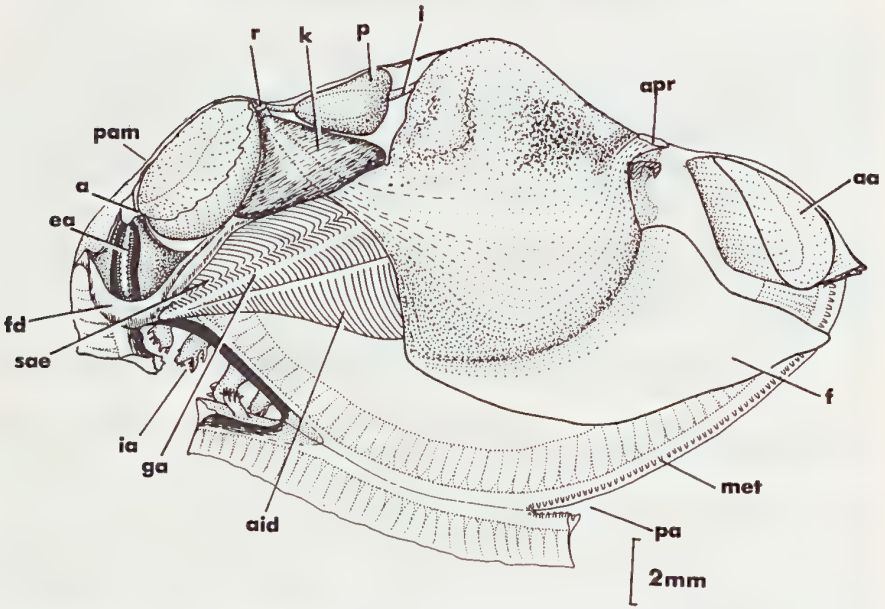


Figure 2. Animal removed from shell and most of right mantle cut away; right ctenidia and palps also removed.

Key to abbreviations used in figures 1-2.

a anus
aa anterior adductor muscle
aid ascending limb of inner demibranch
aod ascending limb of outer demibranch
apr anterior pedal retractor muscle
did descending limb of inner demibranch

dod descending limb of outer demibranch
ea exhalant aperture
f foot
fd fold between exhalant and inhalant apertures
ga ctenidial axis
i intestine
ia inhalant aperture
ilp inner labial palp
k kidney
me mantle edge
met mantle edge tentacle
olb outer labial palp
p pericardium
pa pedal aperture
pam posterior adductor muscle
ppr posterior pedal retractor muscle
sae supra-axial extension of ascending limb of outer demibranch.

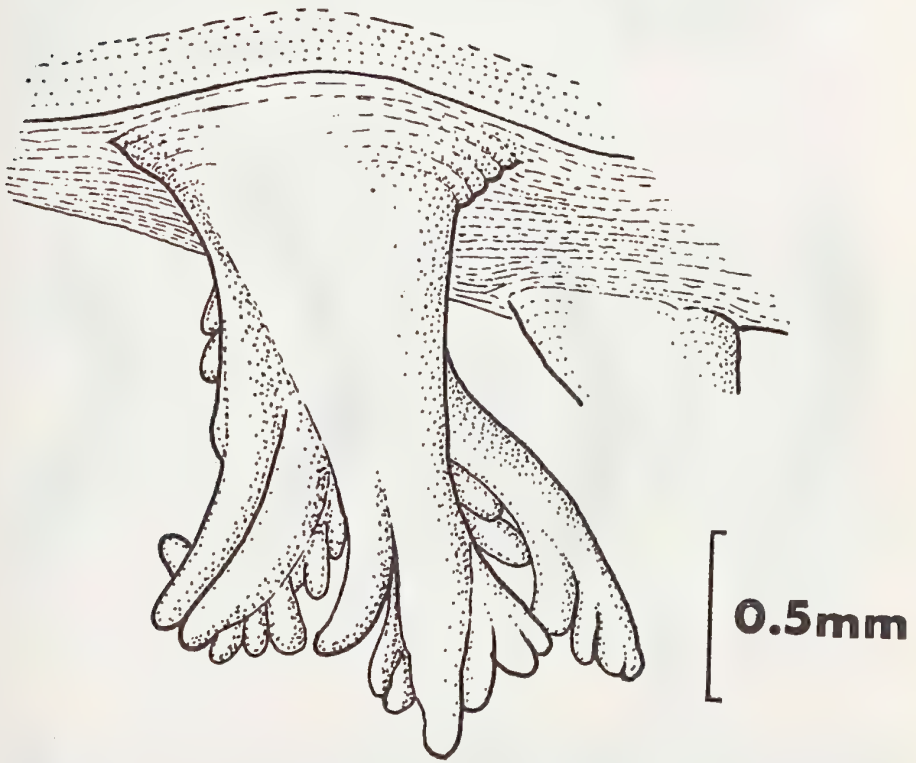
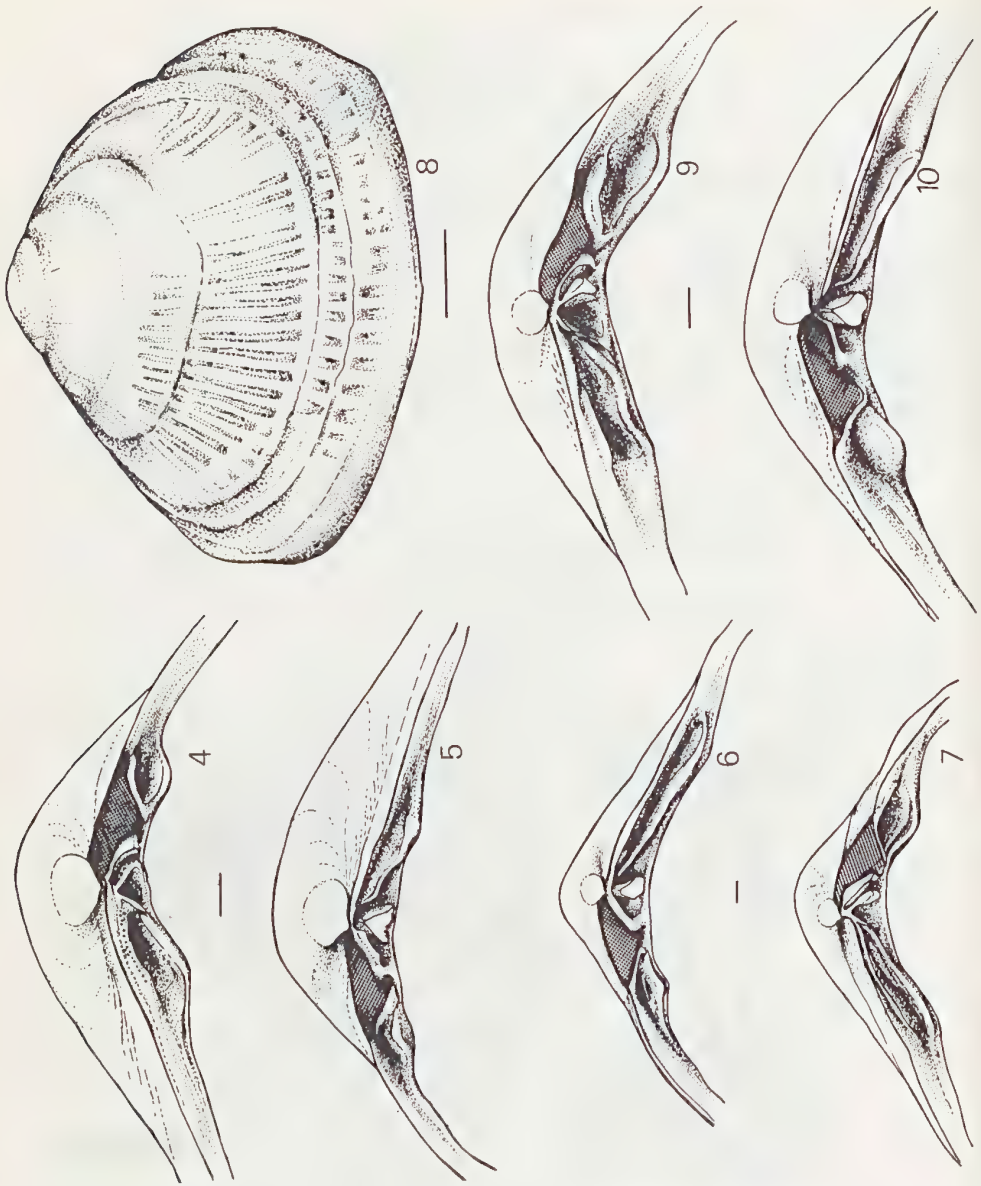


Figure 3. Tentacle from inhalant aperture.

Figures 1-3. *Hemidonax arafurensis* nov.



Figs 4-10. 4, 5. *Hemidonax arafurensis* sp. nov. Hinge of right (4) and left (5) valves. Paratype (C.72967). 6, 7. Hemidonax pictus (Tyron). Hinge of left (6) and right (7) valves. Caloundra, Queensland (AMS, C. 91610). 8 *Hemidonax* sp., cf. *dixoni* (Tate). LOwer Maude Limestone, Maude, Victoria (Upper Oligocene — early Miocene) (NMV, P.58000). 9, 10. *Hemidonax donaciformis donaciformis* (Schröter). Hinge of right (9) and left (10) valves. Cataoyan Reef, S.E. Polillo Is., E. Quezon, Philippines (WAM, 333.73).

Scale line × 1 mm. The ligament is represented by coarse stipple.

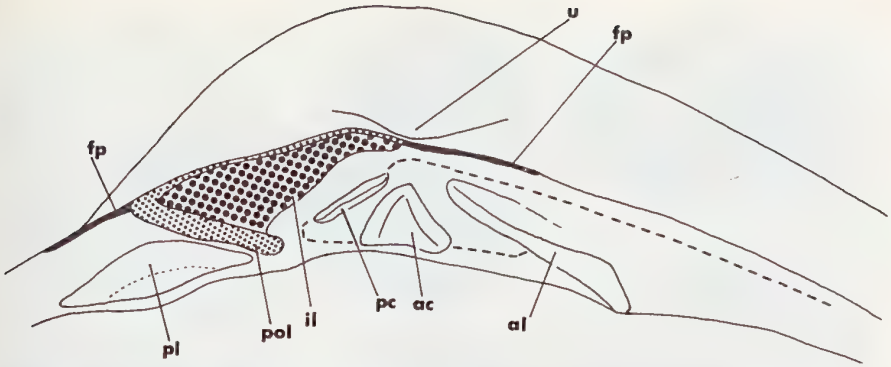


Fig. 11. The hinge and ligament of *Hemidonax*; a diagrammatic representation to show the main structures (based on *H. arafurensis* sp. nov).

ac anterior cardinal tooth
al anterior lateral tooth
fp fused periostracum (secondary extension to primary ligament)
il internal ligament
pc posterior cardinal tooth
pl posterior lateral tooth
pol posterior outer ligament layer
u umbo

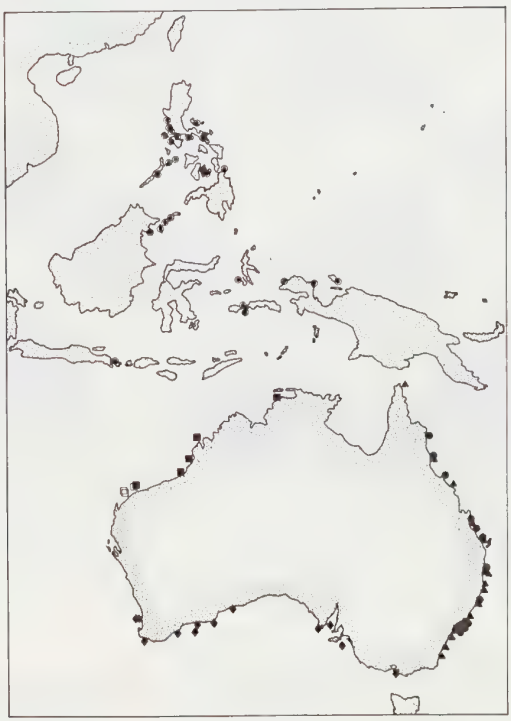


Fig. 12. Distribution of the Recent specis of *Hemidonax*.

H. pictus, H. chapmani, H. dactylus, H. donaciformis donaciformis, H. donaciformis australiensis, H. arafurensis

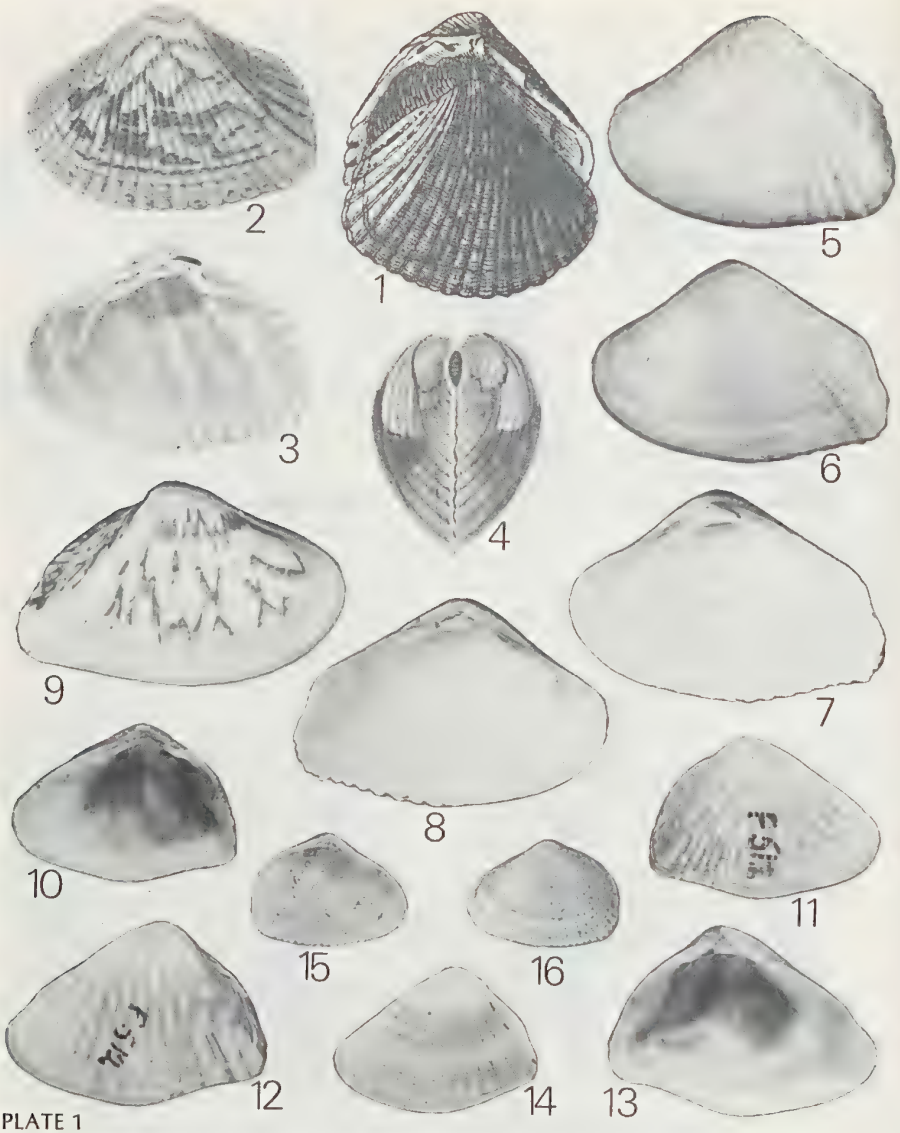


PLATE 1

1-5 *Hemidonax donaciformis donaciformis* (Schroter).
(1) Original figure from Schröter, 1786, *Einleit, Conch.*, 2, pl. 7, fig. 14.
(2-4) Original figures from Delessert, 1841, *Rec. coq. Lamarck*, pl. 6, figs 14a-c.
(5) Cataoyan Reef, S.E. Polillo Is., E. Quezon, Philippines (WAM, 333-73) 2510 x 18.6 mm

6-9 *Hemidonax donaciformis australiensis* (Reeve).
(6-8) Lectotype 25.8 x 17.9 mm
(9) Rosemary Island, Dampier Archipelago, northwest Australia (WAM, 773-68) 27.8 x 17.8 mm

10-14 *Hemidonax chapmani* Gatliff & Gabriel.
(10,11) Paralectotype (NMV, F. 513). 11.9 x 9.3 mm.
(12, 13) Lectotype. 21.6 x 15.5 mm.

(14) Jandakot, W.A., Paulik's Bore, 41.6 — 41.8 m deep, Pleistocene (WAM, 74.269). 14.2 x 10.2 mm.

15, 16 *Hemidonax dixoni* (Tate). Lecotype. 12.3 x 9.1 mm.

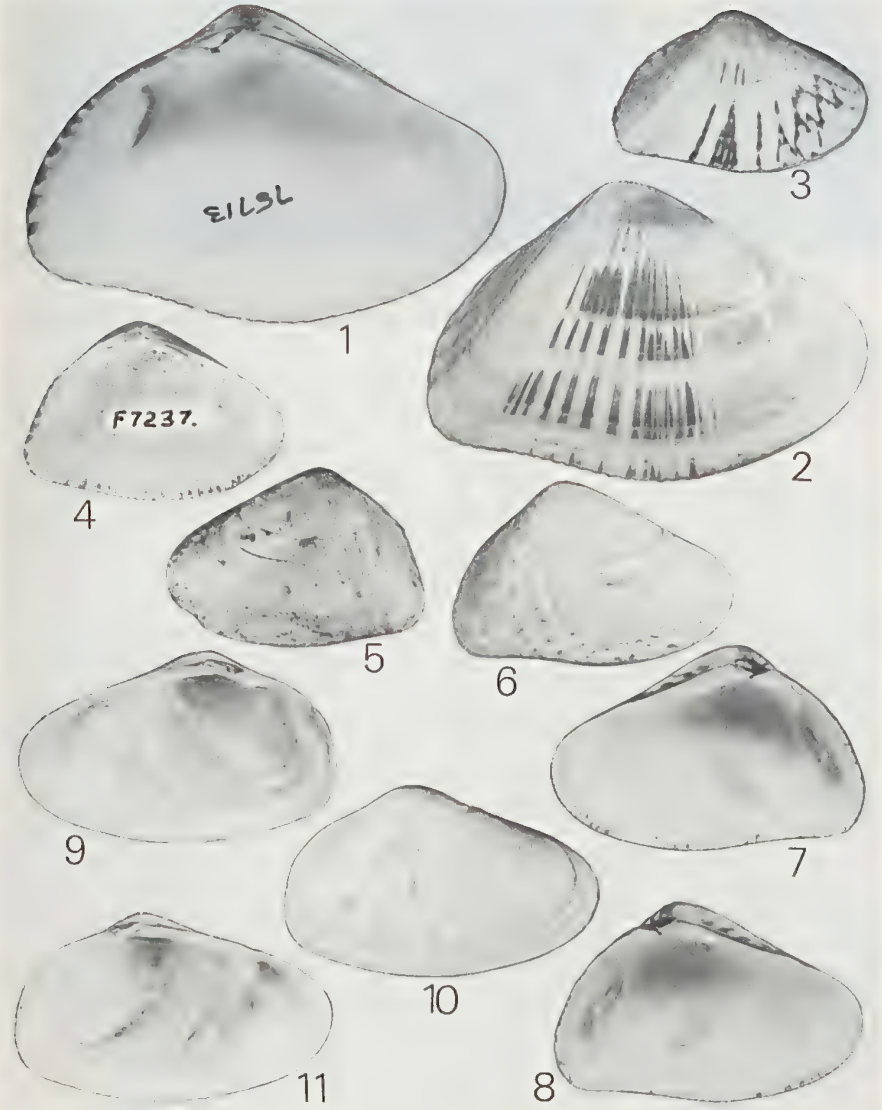


PLATE 2

1-5 *Hemidonax pictus* (Tyron).

(1-2) Hawks Nest Beach, Port Stephens, N.S.W. (AMS, C.75713). 38.2 x 25.5 mm
(3) Innisfail, Queensland (AMS, C. 96295). 21.5 x 14 mm.
(4-5) Cape Possession, Papua New Guinea (Pliocene?) Bureau of Mineral Resources, Canberra, F.7237).

6-8 *Hemidonax arafurensis* sp. nov. Holotype. 24.4 x 16.2 mm.

9-11 *Hemidonax dactylus* Hedley. Holotype. 27 x 16.7 mm.

PLATE 3

1-2 *Hemidonax donaciformis donaciformis* (Schröter). Left valve of holotype Cardium donaceum Spengler. Length 27 mm.

Table 1. Dimensions of *Hemidonax* species and subspecies.
Note: figures in brackets give maximum & minimum dimensions for specimens measured.

Species	Number in Sample	Length (L) mm Mean	Length (L) mm SD	Height (H) mm Mean	Height (H) mm SD	Posterior Length (PL) mm Mean	Posterior Length (PL) mm SD	H/L Mean	H/L SD	PL/L Mean	PL/L SD	Number of Localities	Typical large specimen Length mm	Typical large specimen Height mm
donaciformis donaciformis	69	25.03 (35.2-14.4)	4.60	18.68 (25.5-11.3)	3.22	11.92 (17.8-6.0)	2.54	0.748	0.031	0.475	0.040	5	35.2	25.5
donaciformis australiensis	14	18.71 (27.8-10.5)	5.21	12.75 (17.7-7.3)	3.33	9.25 (13.3-4.8)	2.89	0.683	0.024	0.492	0.032	5	27.8	17.7
pictus	118	25.76 (48.0-2.6)	13.95	16.64 (29.4-2.0)	6.51	10.59 (20.3-1.3)	4.08	0.675	0.026	0.430	0.027	22	47.8	32.3
chapmani (Typical form Recent & Upper Pleistocene)	40	15.71 (22.3-3.9)	5.52	10.90 (15.0-2.9)	3.73	6.47 (12.2-2.1)	2.10	0.699	0.029	0.421	0.037	10	22.3	15.0
chapmani (Lower Pleistocene — Pliocene)	38	15.46 (17.4-3.0)	5.54	10.69 (12.4-2.1)	3.71	6.42 (11.0-1.7)	2.14	0.696	0.026	0.424	0.036	8	17.4	10.0
arafurensis	26	17.20 (22.1-10.2)	3.22	11.44 (14.6-6.8)	2.14	6.81 (9.3-3.8)	1.37	0.665	0.0175	0.398	0.026	5	22.1	14.6
dactylus	43	17.10 (29.3-8.0)	4.98	10.27 (17.6-4.8)	2.92	7.54 (11.7-3.7)	1.93	0.600	0.022	0.447	0.030	8	29.3	17.6

Table 2. Probabilities of significant differences between taxa in their height/length ratios (NSD = no significant difference).

	pictus	*dactylus*	*chapmani*	*arafurensis*	*donaciformis donaciformis*	*donaciformis australiensis*
pictus						
dactylus	P<.001					
chapmani	NSD	P<.001				
arafurensis	NSD	P<.001	P<.001			
donaciformis donaciformis	P<.001	P<.001	P<.001	P<.001		
donaciformis australiensis	NSD	P<.001	P<.05	P<.05	P<.001	

Table 3. Probabilities of significant differences between taxa in their posterial length/length ratios (NSD = no significant difference).

	pictus	*dactylus*	*chapmani*	*arafurensis*	*donaciformis donaciformis*	*donaciformis australiensis*
pictus						
dactylus	P<.01					
chapmani	NSD	P<.01				
arafurensis	P<.001	P<.001	P<.01			
donaciformis donaciformis	P<.001	P<.001	P<.001	P<.001		
donaciformis australiensis	P<.001	P<.001	P<.001	P<.001	NSD	