

Systematic Revision of Australian and Indo-Pacific Lucinidae (Mollusca: Bivalvia): *Pillucina*, *Wallucina* and Descriptions of Two New Genera and Four New Species

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ABSTRACT. This taxonomic revision concerns the Australian and Indo-Pacific species of small lucinid bivalves possessing a deeply inset internal ligament. Nine species of *Pillucina* are recognised of which four occur around Australia including the two new species, *P. pacifica* and *P. australis*. Two other new species are described; *P. denticula* from South Africa and *P. mauritiana* from Mauritius. *Pillucina vietnamica* is common along the Queensland coast and *P. symbolica* the only species previously recorded from Australia is considered conspecific with the wide ranging species *P. pisidium*. A new genus, *Chavana*, includes two species; *C. striata* is widely distributed in the Indo-West Pacific including eastern and western Australia, while *C. erythraea* is restricted to the Arabian Peninsula. Two species of *Wallucina* live around Australia, *W. assimilis* is endemic occurring at southerly locations from New South Wales to North West Cape, while the tropical species, *W. fijiensis*, is found in island habitats of Queensland but is widely distributed in the Indo-West Pacific. Another new genus, *Funafutia*, is proposed for the species, *F. levukana*, recorded from Australia for the first time. Details of anatomy are provided for *Pillucina vietnamica*, *W. assimilis* and *C. striata*. Symbiotic bacteria are confirmed for the first time in the lateral zone of gill filaments of *Pillucina vietnamica* and *Wallucina assimilis*.

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The discovery of the symbiotic association between lucinid bivalves and sulphide oxidising chemoautotrophic bacteria has attracted much recent biological interest (Reid, 1990; Distel, 1998). The symbiosis has now been confirmed in at least 30 species of Lucinidae representing 18 different genera from several distinct clades (Taylor & Glover, 2000) and from this may it be extrapolated as present in most, if not all, living taxa. This biological interest highlights the neglect of lucinid systematics at all levels, with most taxa being rather poorly defined (e.g., Chavan, 1969) and known only from shells. The last major taxonomic review (Bretsky, 1976) was largely restricted to north American taxa and no

phylogenetic analyses, either morphological or molecular, provide an evolutionary framework for the group. Additionally, recent studies of tropical lucinids show that the family is much more diverse than has been previously realised (Glover & Taylor, 1997; Taylor & Glover, 1997a,b) and many small species remain undocumented.

During a search for lucinids on the Queensland coast we discovered populations of an abundant *Pillucina* species, not previously reported from Australia, living on the outer fringes of mangroves at Port Douglas. On attempting to identify this species (*Pillucina vietnamica*) it soon became clear that the taxonomy of *Pillucina* and related genera was

in a state of confusion and, moreover, other species, either undescribed or unrecorded from Australia, were present in museum collections. None of these species were considered in the recent synopses of the bivalve fauna of Australia (Lamprell & Whitehead, 1992; Lamprell & Healy, 1998). To identify and assess the status of the Australian species, we embarked on a review of the Australian and Indo-West Pacific species of *Pillucina*. Because of similarities of shell form we also took into account species of *Wallucina* and other genera having an internal ligament with the form described by Allen (1960) for *Loripes lucinalis*. Genera with internal ligaments were briefly reviewed by Oliver (1986) when he introduced a new generic name for West African species. Apart from *Keletistes* from West Africa (Oliver, 1986) and *Loripes* from northeast Atlantic, Mediterranean and western Indian Ocean, the other genera are, at the present day, confined to the Indo-West Pacific province. These genera, *Pillucina*, *Wallucina*, *Sydlorina* are not well defined (e.g., Iredale, 1930) and much confusion concerns the assignment of species (Chavan, 1937, 1938, 1969). Most species are rather small and usually the figures accompanying the original descriptions lack detail, as is the case for *Pillucina spaldingi* Pilsbry, 1921, the type species of *Pillucina*. Additionally, several species, such as *Lucina funafutica* Finlay, 1927, cannot be satisfactorily accommodated within any described genus. A preliminary survey of museum collections also showed that some species have considerably broader distributions within the Indo-West Pacific province than previously realised.

Most species considered in this study are known only from shells and little information is available concerning their biology. However, chemosynthetic bacteria have been previously described from the gills of *Pillucina pisidium* from the Sea of Japan (Rodionov & Yushin, 1991). Also, Barnes & Hickman (1999) record but do not illustrate ctenidial bacteria and provide a detailed habitat description for *Wallucina assimilis* from Western Australia.

The objectives of this study are to describe and review the species of *Pillucina*, *Wallucina* and other genera possessing internal ligaments living around Australia and to review the other species of the Indo-West Pacific province. Virtually all relevant primary type material available has been examined and lucinid collections studied in the museums of Sydney, Melbourne, Adelaide, Perth, London, Cardiff and Paris. Additionally, we describe the anatomy and life habit of some live-collected animals, and confirm the presence of chemosymbiotic bacteria in the ctenidia of two species.

Although we have live-collected material of a few species, most samples in museum collections usually comprise dead shells from beach collections or otherwise picked from sediment samples. It is clear that the frequency of these small white bivalves in collections is a function of the effort devoted by particular museums (notably the Australian Museum) to intensive sediment sorting. Thus, the distribution maps included in this paper probably do not reflect the complete ranges of these species but to some extent are artifacts of the intensity of sampling effort.

Methods

Material for anatomical studies was fixed either in 4% seawater formalin, or in a 2.5% solution of glutaraldehyde in phosphate buffer. For serial thin sections, animals were

decalcified in EDTA, wax embedded, sectioned at 8 μ m and stained with Masson's trichrome. For scanning electron microscopy (SEM), animals were dissected, then critical point dried, mounted on stubs and sputter coated with gold. Most shells were imaged without coating using an environmental SEM.

Most available type specimens have been examined as indicated in the synonymies by the word "seen". The frequently used terms: shell height in mm (H), shell length in mm (L) and tumidity of a single valve (T), have been abbreviated, as have museums and institutions cited in the text:

AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	The Natural History Museum, London
BPBM	Bernice P. Bishop Museum, Honolulu
DK	Henk Dekker, private collection
MCG	Museo Civico, Genoa
MCZ	Museum of Comparative Zoology, Harvard
MNB	Museum für Naturkunde, Berlin
MNHN	Museum national d'Histoire naturelle, Paris
NMSA	Natal Museum, South Africa
NMV	National Museum of Victoria, Melbourne
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
SAM	South Australian Museum, Adelaide
UMUT	University Museum, University of Tokyo
UMZC	University Museum of Zoology, Cambridge, UK
WAM	Western Australian Museum, Perth
ZISP	Zoological Institute, St Petersburg, Russia

Systematic descriptions

In this review, we consider lucinid genera possessing an internal ligament of the form described for *Loripes lucinalis* by Allen (1960). This type of ligament (Fig. 1) has a broad, wedge-like internal portion which broadens to the posterior and is formed within a deep embayment of the mantle epithelium. The groove in the hinge (resilifer) to accommodate the ligament is deeply inset and is aligned obliquely and laterally into the left and right valves. Although no comprehensive phylogenetic analysis of the Lucinidae has yet been attempted it is possible that this internal ligament may prove to be an apomorphy of a clade of genera allied to *Loripes*. In a phenetic analysis, Bretsky (1970, 1976) recognised a distinct "*Loripes* group" based on this form of ligament.

The genera possessing internal ligaments were briefly reviewed by Oliver (1986) when he introduced the new generic name, *Keletistes*, for West African species. In this paper, we redefine some of the genera, based on reinvestigation of the type species and introduce two new genera for species which could not be accommodated into any existing taxa. The Indo-West Pacific genera *Pillucina*, *Wallucina*, and two new genera *Chavania* and *Funafutia* are described and illustrated in the systematic section below and their characters summarised in Table 1. The name *Sydlorina* Iredale is synonymised with *Pillucina* (p. 266). The main characters we have used to discriminate the genera derive from the external sculpture, hinge teeth and shape. Although some characters may appear rather minor, after examination of many specimens from around the Indo-Pacific we feel that the groupings of species probably represent monophyletic clades. The three other genera with internal ligaments *Loripes*, *Keletistes* and the Miocene *Microroripes* are briefly reviewed below and their characters also listed

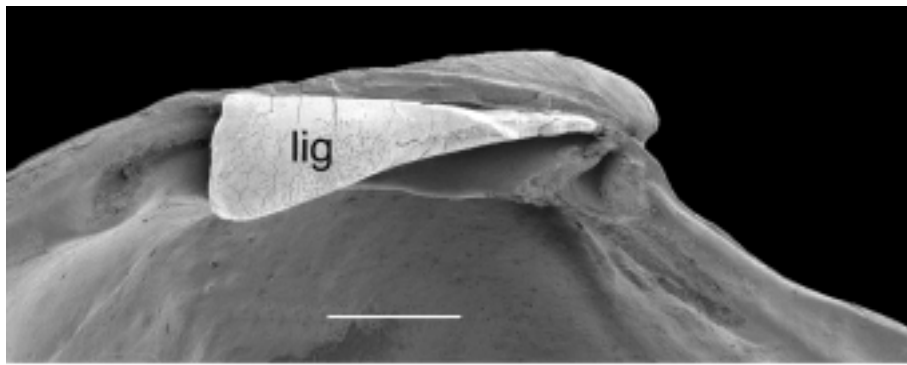


Figure 1. Hinge of left valve of *Pillucina pisidium* showing the deeply inset internal ligament. Scale bar = 1.0 mm.

in Table 1. Chavan (1938) regarded *Microripipes* as a “stem” group from which *Loripes*, *Pillucina* and *Wallucina* were derived, however, a phylogenetic analysis of all these genera is needed to clarify their relationships.

Other genera possessing internal ligaments

Microripipes Cossmann, 1910 (type species: *Lucina dentata* Defrance, 1823 a fossil from the L. Miocene of France

(Burdigalian)). Although Chavan (1938) considered *Microripipes* close to and a likely sister taxon to *Wallucina* and *Pillucina*, he later classified it (Chavan, 1969) as a subgenus of *Parvilucina* despite the possession of an internal ligament. The type species is similar to *Chavanja* (described herein p. 282) in general morphology but possesses a sculpture of rather broad, flat, commarginal lamellae and a strong anterior lateral tooth. *Microripipes* has been applied to a Recent species, *Lucina contrarius* Dunker, 1846, from

Table 1. Summary of shell characters of lucinid genera considered in this review and other genera with internal ligaments.

	shell sculpture		marginal crenulae	ligament	anterior adductor	cardinal	hinge teeth		sulci
	radial ribs	commarginal lamellae					anterior lateral	posterior lateral	
<i>Chavanja</i>	faint riblets to anterior and posterior	fine, low, anastomosing more prominent to posterior	present, fine, margin thickened	internal, very short	short, detached for 1/3–1/5 of length	1 RV large, 2 LV	RV absent or weak, LV absent	RV present, low; LV present, low	shallow, posterior
<i>Funafutia</i>	fine striae between lamellae	prominent, thick	present, fine	internal, short	short, barely detached	1 RV, 2 LV	RV present prominent, LV present prominent	RV present, LV present	absent
<i>Pillucina</i>	fine to coarse ribs often stronger to posterior and anterior	numerous, fine to prominent, fluted in some species	present, fine to coarse	internal, short	short, detached only slightly or for less than 1/2 length	1 RV, 2 LV	RV present or absent, LV present or absent	RV present, LV present	absent
<i>Wallucina</i>	absent or fine striae	numerous, low	very fine	internal, deeply inset	detached, for 1/2 length	1 RV, 2 LV	RV v small to indistinct LV absent	RV present LV present	very shallow posterior
other genera with internal ligaments									
<i>Keletistes</i>	weak riblets towards anterior and posterior	numerous, fine anastomosing	present, fine variable	internal, short	short, detached for 1/2 length	1 RV v low, 2 LV v low	RV low to obsolete LV low to obsolete	low, indistinct	absent
<i>Loripes</i>	weak radial striations	fine growth lines	absent	internal, long deeply inset	long, detached for 2/3 of length	1 RV, 2 LV	RV small LV absent to v small	RV present LV present	present posterior
<i>Microripipes</i>	faint radial striations	broad, slightly raised, anastomosing	fine	internal, very short	very short, barely detached	1 RV, 2 LV	RV present LV present	RV low LV low	present posterior and anterior

West Africa (Chavan, 1937; Dell, 1964), however, von Cosel (pers. comm.) considers this species as part of a broader concept of *Keletistes*.

Keletistes Oliver, 1986 (type species: *Loripes (Keletistes) rhizoecus* Oliver, 1986 from West Africa). This genus was proposed for an unusual species, *K. rhizoecus*, which is subquadrate in shape, with commarginal lamellae, slight radial costae, a denticulate inner margin, and hinge teeth including anterior laterals that become obsolete with age. Another West African species, *K. aberrans* (Dautzenberg, 1910), was an included species and von Cosel (pers. comm.) also considers the other West African species *Lucina contrarius* and *L. legouxi* (Nicklès, 1952) as part of the same group. The relationships of the West African species to the Indo-Pacific *Chavania*, *Wallucina* and *Pillucina* need to be examined in more detail.

Loripes Poli, 1791 (type species *Tellina lactea* Poli, 1791 (non Linnaeus, 1758) = *Amphidesma lucinalis* Lamarck, 1818 from the eastern Atlantic and Mediterranean). The type species has a thin subcircular shell, slightly inflated, smooth, with a sculpture of fine growth lines only, a hinge with strong anterior lateral teeth, an obliquely inset internal ligament, a long anterior adductor muscle scar detached from the pallial line for about 2/3 of its length and a smooth inner shell margin. *Loripes lucinalis* is common in the Eastern Atlantic and Mediterranean and the morphologically rather different, *Loripes clausus* (Philippi, 1850), occurs in the Red Sea, along the east African coast and Madagascar.

Family Lucinidae Fleming, 1828

Genus *Pillucina* Pilsbry, 1921

Pillucina Pilsbry, 1921: 382. Type species: original designation *Pillucina spaldingi* Pilsbry, 1921 (= *P. hawaiiensis* Smith, 1885).

Sydlorina Iredale, 1930: 390. Type species: original designation *Sydlorina symbolica* Iredale, 1930

Diagnosis. Shells small (H to 14), inflated, sculpture of fine to broad radial ribs that often bifurcate, crossed by fine, low, commarginal lamellae. Sculpture usually more prominent on anterior and posterior parts of shell. Hinge with two cardinal teeth in left valve and a single cardinal tooth in right valve. Posterior lateral tooth present in both valves, anterior lateral tooth present or absent. Ligament internal, located on elongate resilifer widening to the posterior. Anterior adductor muscle scar short and detached from pallial line for about 1/4–1/2 of length. Inner shell margin finely to coarsely crenulate.

Remarks. The type species, which possesses relatively fine radial ribs, would seem to be rather different in morphology from some of the other species we regard as congeneric, in particular the coarsely ribbed *Pillucina vietnamica*. However, a complete range in the strength of radial ribbing is seen amongst *Pillucina* species and we have found no objective criteria for separating them. *Pillucina* differs from *Wallucina*, *Chavania* and *Funafutia* in the presence of radial ribs which cross the commarginal lamellae and which are particularly prominent to the anterior and posterior parts of the shell.

Distribution. Indo-West Pacific, Red Sea to Hawaii.

Pillucina hawaiiensis (Smith, 1885)

Fig. 2h,i

Lucina (Codakia) hawaiiensis Smith, 1885: 183–184, pl. 13, figs. 8, 8a. Three syntypes: BMNH 1887.2.9.2780; unrecognisable from serious decay from Byne's disease. Type locality: Honolulu Harbour, Hawaii. Seen

Pillucina hawaiiensis (Smith).—Dall, Bartsch & Rehder, 1938: 134, pl. 36, figs. 9–12.

Loripes (Pillucina) spaldingi Pilsbry, 1921: 381, fig. 17. Lectotype: ANSP 127929; H 8.6, L 7.6. Type locality: Kaneohe Bay, Oahu, Hawaii.

Pillucina spaldingi (Pilsbry).—Dall, Bartsch & Rehder, 1938: 133–134, pl. 36, figs. 7 & 8.

Description. Small, H to 10, robust, inflated shell, higher than long (H/L 1.1), low commarginal growth increments, with fine radial ribs more prominent in the anterior and posterior parts of shell. Lunule, short, broad, slightly impressed. Hinge plate sinuously curved with cardinals located on a downward projection. Right valve with strong, single cardinal tooth under umbo, short anterior lateral tooth lying close to the cardinal tooth and elongate posterior lateral. Left valve with two cardinal teeth, anterior is larger and elongate; anterior and posterior lateral teeth present. Ligament internal, located on elongate resilifer widening to the posterior. Anterior adductor muscle scar short, detached ventrally from pallial line for about 1/5 of length, posterior scar ovate. Inner shell surface with faint radial grooves. Pallial line continuous. Shell outside of pallial line slightly thickened. Shell margin finely and evenly crenulate. Colour white.

Distribution. Endemic to Hawaiian Is (12–20 m), see Kay (1979).

Remarks. Although *P. hawaiiensis* and *P. spaldingi* have been usually considered as separate species (Dall, Bartsch & Rehder, 1938; Kay, 1979), they are similar in most characters except shape and we regard them as variants of a single species. Specimens usually named *P. hawaiiensis* are slightly longer than high compared with the higher *P. spaldingi*. Such shape variation is common within Indo-Pacific *Pillucina* species.

Material examined. Hawaiian Islands: off Waikiki, Oahu (BPBM); entrance to Honolulu Harbour, Oahu (BPBM); Midway, (BPBM).

Pillucina pacifica n.sp.

Figs. 2a–g, 3

Type material. HOLOTYPE: AMS C355685; H 5.5, L 5.5. PARATYPES: AMS C380464, 3 paired valves. PARATYPES: BMNH 2000204, 3 single valves. Type locality: Michaelmas Cay, Great Barrier Reef, Queensland, Australia, 16°36'S 145°59'E, collected by Iredale and Whitley, May 1926.

Description. Shell small (H to 8), robust, inflated, slightly higher than long (H/L 1.1). Juveniles are proportionately more anteriorly extended (Fig. 2f) and outline of adults is variable from much higher than long to more circular in shape. Sculpture of fine radial ribs (>50) that are slightly more prominent in anterior of the shell and are slightly broader posteriorly. Radial ribs are crossed by thread-like,

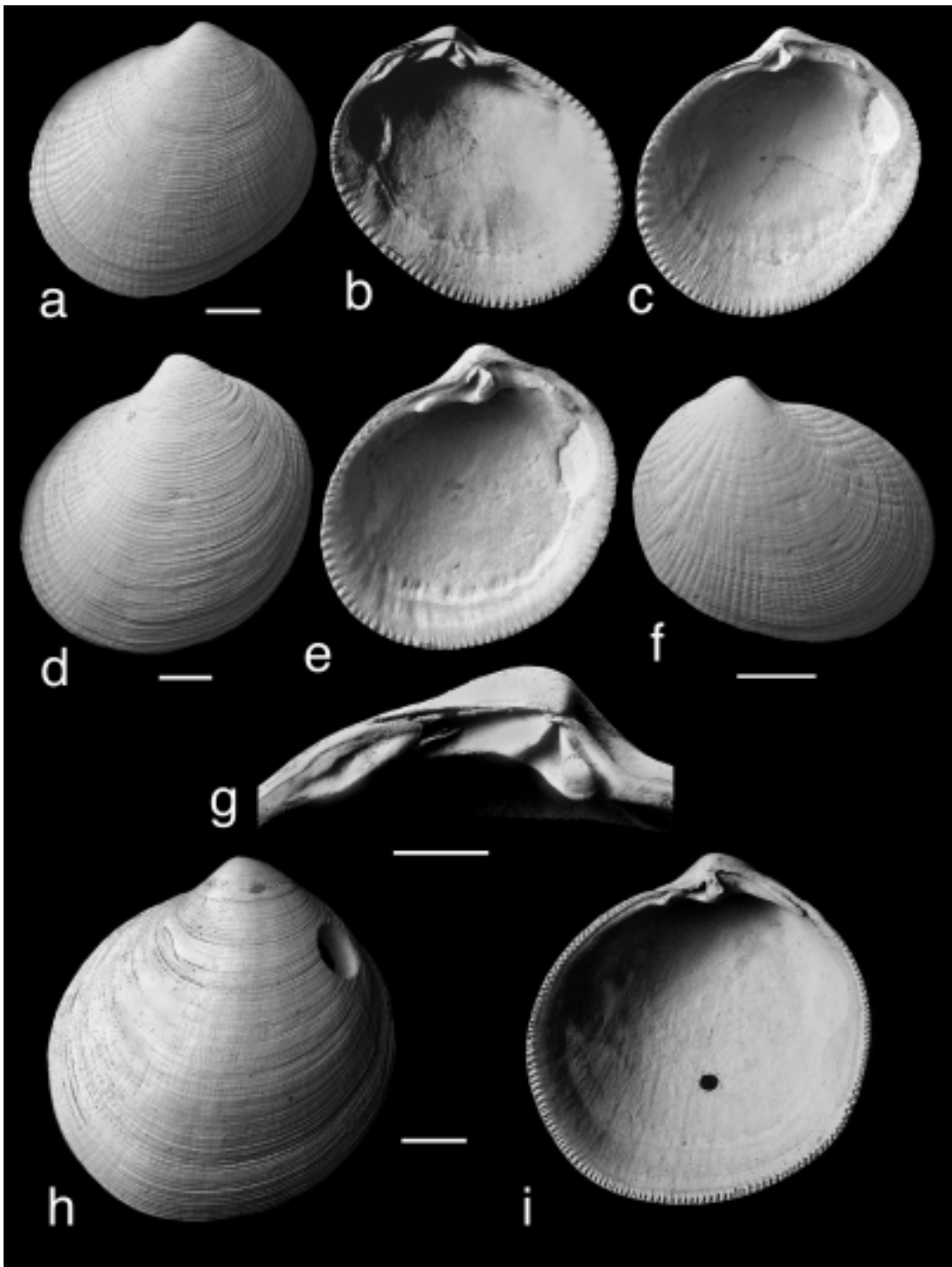


Figure 2. *Pillucina pacifica* n.sp. and *P. hawaiiensis* (Smith). a–c, *Pillucina pacifica* holotype AMS C355685, Michaelmas Cay, Great Barrier Reef, Queensland; a, exterior of left valve; b, interior of left valve; c, interior of right valve. d–f, paratypes AMS C380464; d, exterior of left valve; e, interior of right valve; f, exterior of right valve of juvenile specimen. g, detail of hinge of left valve of holotype. h,i, *Pillucina hawaiiensis* (Smith), off Waikiki, Oahu, Hawaii (BPBM 22068); h, exterior of left valve; i, interior of right valve. Scale bars = 1.0 mm.

commarginal lamellae giving a reticulate ornament. Ribbing is often worn in the middle part of the shell. No sulci present. Lunule is short, broad and slightly impressed. Hinge plate sinuous, with cardinal teeth located on downward projection. Right valve with single prominent cardinal tooth with a thin, elongate, posterior lateral tooth and an indistinct anterior lateral peg. Left

valve with two cardinal teeth of which the anterior is larger. Posterior lateral tooth a thin groove, anterior lateral indistinct. Ligament internal, short. Anterior adductor scar short and barely detached from the pallial line, posterior scar ovate. Pallial line continuous and shell outside pallial line thickened. Shell margin finely and evenly crenulate. Colour white.

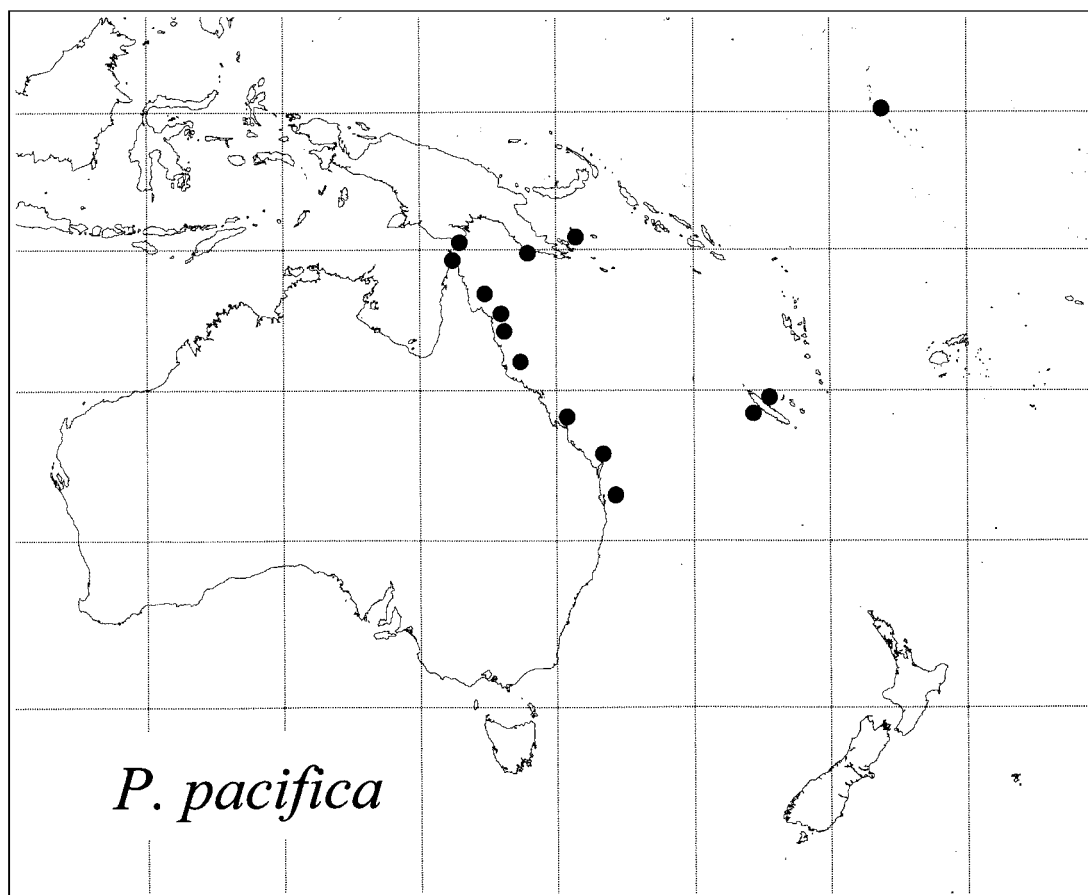


Figure 3. Map showing distribution of *Pillucina pacifica* n.sp.

Habitat. Intertidal to shallow subtidal (20–30 m).

Distribution. Northern Australia on the Great Barrier Reef and offshore islands to Micronesia (Fig. 3).

Remarks. *Pillucina pacifica* is similar to *P. hawaiiensis* but the latter has a longer lunule, a more robust hinge area, and in the right valve a less prominent anterior lateral tooth which is located at a greater distance from the cardinal tooth. The radial ribbing of *P. pacifica* is more prominent compared to *P. hawaiiensis* and the marginal crenulations are coarser.

Material examined. **Australia:** QUEENSLAND, Murray I., Torres Strait (AMS); Thursday I., Torres Strait (AMS); Albany Passage, Cape York (AMS); Flinders I., Princess Charlotte Bay (AMS); Lizard I. (AMS); Eagle I. (AMS); Low Isles, 22 m (AMS); Michaelmas Cay 16°36'S 145°59'E (AMS); Green I., Cairns (AMS); Ellison Reef, near Kurrimine (AMS); Juno Bay, Fantome I., Palm Group (AMS); North East Bay, Great Palm I., 6 m (AMS); Nara Inlet, Hook I., Whitsunday Group (AMS); Heron I., Capricorn Group (AMS); Lady Elliott I., Bunker Group (AMS); Lady Musgrave I., Bunker Group 23°54'S 152°25'E lagoon (AMS); NE of Cape Moreton Light 26°55'S 153°33'E (AMS). **New Guinea:** Lolorua I., Port Moresby, 13–18 m (AMS); SW of Losuia, Kiriwina I., Trobriand Is, mudflats (AMS). **Kiribati:** Tarawa Lagoon (AMS). **New Caledonia:** Baie des Isoles, Ouemo, Magenta mudflats (AMS); Nouméa (MNHN); Touho, 11 m, 20°5'S 165°8'E (MNHN).

Pillucina pisidium (Dunker, 1860)

Figs. 4a–f, 8

Lucina pisidium Dunker, 1860: 227; figured by Dunker, 1861: 28, pl. 3, fig. 9. Two syntypes: badly eroded, MNB. Type locality: Dejima, Nagasaki City, Japan. Seen.

Lucina parvula Gould, 1861: 36. Lectotype: MCZ169284. Type locality: Port Lloyd, Bonin Is (see Johnson, 1964: 122, pl. 28, fig. 5) (non *Lucina parvula* Muenster, 1835).

Codakia pisidium (Dunker).—Hedley, 1914: 699, figs. 25–28.

Sydlorina symbolica Iredale, 1930: 390. Syntypes: AMS C032175; Hedley's figured specimen plus many other syntypes. Type locality: Sydney, NSW, Australia (introduced as new name for Hedley's material and figure). Seen.

Loripes (*Pillucina*) *pisidium* (Dunker).—Chavan, 1937: 226.

Pillucina (*Pillucina*) *pisidium* (Dunker).—Kuroda, Habe & Oyama, 1971: 393, pl. 118, fig. 14; Habe, 1977: 126, pl. 24, figs. 5 & 6.

Description. Shell small, H to 7, moderately inflated, longer than high (H/L 0.98). Sculpture of fine, close set, commarginal lamellae crossed by fine radial ribs which are more distinct at posterior and anterior parts of the shell. Shell surface slightly nodulose at junctions of radial and commarginal sculpture. Posteriorly, there is usually a very shallow sulcus with commarginal sculpture only. Lunule shallowly impressed. Hinge plate sinuous with cardinal teeth located on a downward projecting buttress. Right valve with prominent single cardinal tooth, no anterior lateral, and a low, short, posterior lateral. Left valve with two cardinal teeth, no anterior lateral and a low short, posterior lateral.

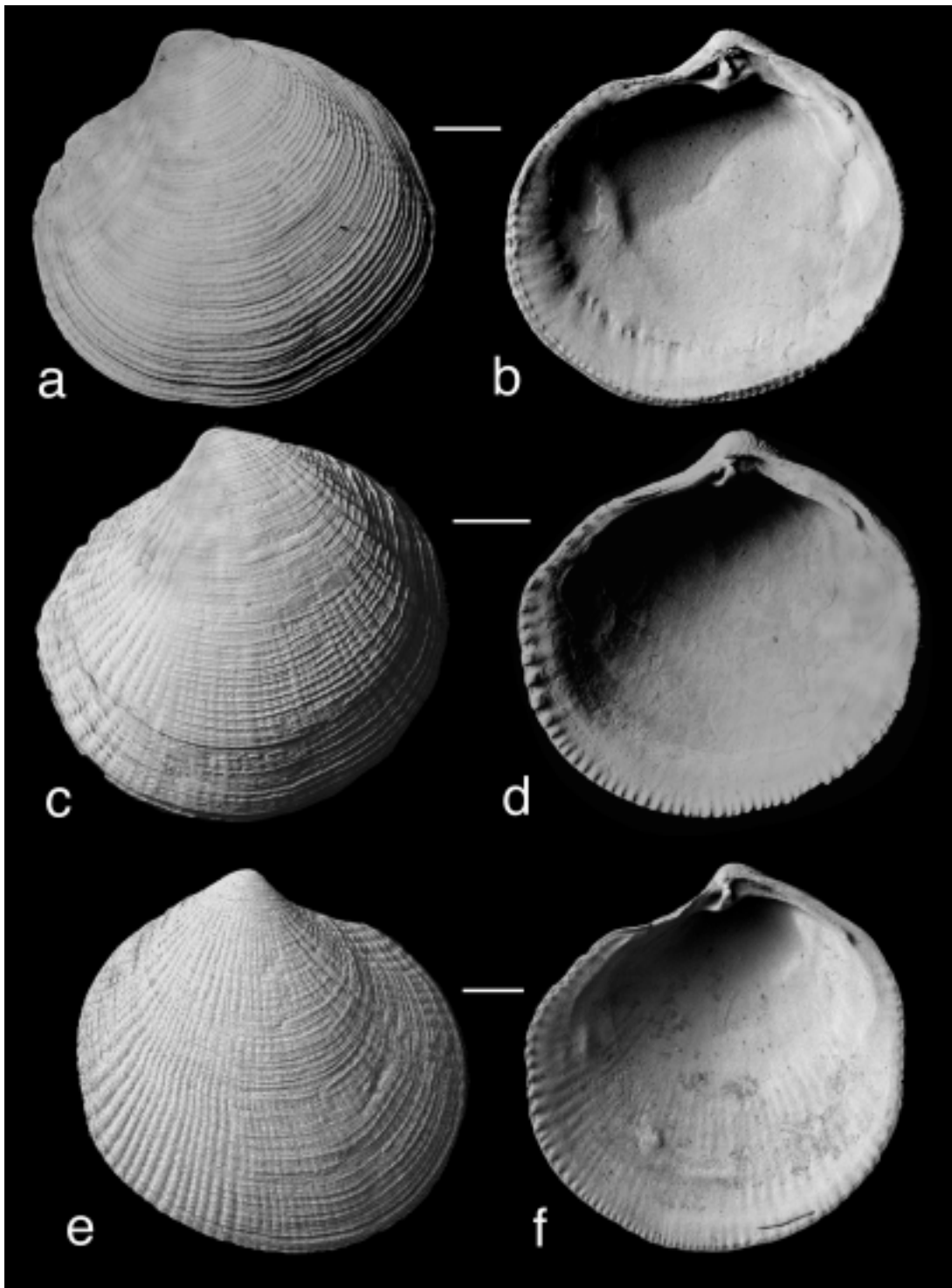


Figure 4. *Pillucina pisidium* (Dunker); a,b, exterior of left valve and interior of right valve of *P. pisidium*, Hizen, Hirado, Kyushu, Japan (BMNH 1009.6.9.60); c,d, exterior of left valve and interior of right valve, Sydney, NSW (BMNH 1963534); e,f, exterior and interior of right valve, a less mature individual than c, Port Jackson, Sydney, NSW (AMS C013982). Scale bars = 1.0 mm.

Ligament internal, sitting on broad, obliquely extended triangular resilifer. Anterior adductor muscle scar short, narrow, detached for about one third of length. Posterior adductor muscle scar ovate. Pallial line patchily discontinuous with ventral margin slightly thickened and finely crenulate. Inner shell surface dull, chalky, pustulate within pallial line. Pallial blood vessel scar visible. Colour white.

Remarks. Hedley (1914) identified the *Pillucina* species from Sydney as *Codakia pisidium* although he had not seen the type and the original illustration is poor (Dunker, 1861). However, Iredale (1930) later considered that the Australian shells were only slightly similar to *L. pisidium* from Japan and introduced a new genus and species, *Sydlorina symbolica*. Despite Iredale's opinion, the Japanese and

Australian shells are very similar and we consider them as conspecific. We have examined the type material of *L. pisidium* Dunker in Berlin, other material from Japan and the Indo-Pacific and conclude that *P. pisidium* is widely distributed species which includes the eastern Australian shells.

Pillucina pisidium can be distinguished from *P. australis* (Fig. 6) from southern and southwestern Australia, by the absence of an anterior lateral tooth in the right valve, by the more numerous and finer radial ribs and its larger size. It is also similar to *P. neglecta*, also from Japan, which is smaller, more inflated and with a strong anterior lateral tooth in the right valve.

Two types of bacteria have been reported in bacteriocytes from the gills of *P. pisidium* from the Sea of Japan (Rodionov & Yushin, 1991). One type resembles the sulphide-oxidising, chemosymbiotic bacteria found in other lucinids, while the other type with cytoplasmic inclusions is dissimilar to other bivalve symbionts.

Habitat. Intertidal and shallow water (to 90 m) in mud and fine sand.

Distribution. Indo-West Pacific, Japan to East Africa and Madagascar (Fig. 8).

Material examined. **Kenya:** Ras Anzuani, near Shimoni (BMNH); Kilifi (NMSA). **Tanzania:** Kunduchi Beach, 6 km N of Dar es Salaam (AMS); Ras Fumba, Zanzibar (DC). **Madagascar:** Tuléar (several lots MNHN). **Mozambique:** Conducia Bay; Bazzaruto Is (ZMSA). **Reunion:** Souris Chaude (ZMSA). **Mauritius:** Le Goulet, Tombeau Bay (ZMSA). **Seychelles:** Aldabra Atoll, Main Channel (BMNH); Cascade, Mahé (BMNH). **Maldives:** Gan lagoon, Addu Atoll (BMNH). **Ceylon:** Trincomali (BMNH). **Andaman Islands:** Aves I. (BMNH). **Thailand:** Ko Chang, Trat Province, Gulf of Thailand (DC). **Australia:** QUEENSLAND: Macoma Inlet, 20°9.6'S 148°55.3'E (AMS); NEW SOUTH WALES: 12 km E of Cakora Point, S of Yamba (AMS); Dudley, Newcastle (AMS); Toowoomba Bay, The Entrance (AMS); Port Stephens, 44 m (AMS); Careel Bay, Pittwater (AMS); Broken Bay, Pittwater (AMS); Broken Bay, Patonga (AMS); Port Jackson (BMNH); Balmoral, Middle Harbour, Sydney, 5 m (AMS); off Morts Dock, Balmain, Port Jackson (AMS); Middle Harbour, Chinaman's Beach (AMS); Narrabeen Lagoon, Sydney (AMS); Quarantine Bay, North Head, Sydney Harbour (AMS); Collaroy Beach Sydney (AMS); Port Hacking, Bundeena, Simpsons Beach (AMS); Port Hacking, Gunnamatta Bay (AMS); Cronulla (AMS); off Montague Is, Narooma (AMS); Boydtown Beach, Twofold Bay (AMS). **Philippines:** 11°43'N 122°34'E, 93 m (MNHN); Magellan Bay, Mactan I., Cebu (BMNH). **New Caledonia:** Bay of Ouanap, 0–2 m, 20°34'S 164°16'E (MNHN). **Japan:** Hirado Hizen, Kyushu (BMNH); Kamakura Beach, Sagami Bay, Honshu (AMS); Okinawa, Ryukyu Is (AMS). **China:** Hoi Ha Wan, Tolo Channel, Hong Kong (NMW).

Pillucina neglecta Habe, 1960

Figs. 5a–d, 8

Pillucina neglecta Habe, 1960: 282, figs. 7–9. Holotype: H 2.4, L 2.2, and paratypes NSMT—Mo38710. Type locality: Tanabe Bay, Wakayama Prefecture, Japan.

Description. Shell very small (H to 2.5) and rather inflated. Sculpture of 30–40 radial ribs which often bifurcate, crossed by fine commarginal lamellae, both of which are more pronounced towards the posterior and anterior. Median part

of shell often worn and sculpture indistinct. Lunule smooth and distinctly impressed. Left valve with two solid cardinal teeth and anterior and posterior lateral teeth. Right valve with a single, solid cardinal tooth, a large peg-like anterior lateral tooth and long, posterior lateral tooth. Anterior adductor muscle scar short and only slightly separated from pallial line. Interior margin finely crenulate.

Remarks. This species is similar to *P. pisidium* but can be distinguished by the smaller size, greater inflation, more deeply impressed lunule and the presence of a strong lateral tooth in the right valve. It is also similar to *P. australis* but is longer, with a shorter, deeper lunule and fewer ribs.

Habitat. Intertidal mud (Habe, 1960).

Distribution. Japan. see Higo, Callomon & Goto (1999).

Material examined. **Japan:** Okinawa, Ryukyu Is (AMS).

Pillucina australis n.sp.

Figs. 6a–f, 8

Type material. HOLOTYPE: NMV F83659; H 2.9, L 3.1. PARATYPE: H 3.3, L 3.2, NMV F87506 (other specimens in lot F87507). Type locality: Port Lincoln, Eyre Peninsula, South Australia, 34°44'S 135°52'E, J. Veitch collection.

Description. Shell very small, H to 4.8, moderately inflated, circular to sub circular in outline (H/L 1.02). Sculpture of fine, closely-spaced commarginal lamellae crossed by 35–45 low radial ribs. Radial ribs sometimes bifurcating particularly at the anterior of the shell, more prominent and slightly broader towards the anterior and posterior. Radial sculpture absent from the umbones. Lunule shallowly impressed and lanceolate in outline. Ligament internal, extremely short. Hinge plate narrow, right valve with single large cardinal tooth and single anterior and posterior lateral teeth. Left valve with two cardinal teeth, anterior slightly larger; posterior lateral is a narrow groove and anterior lateral a shallow socket. Anterior adductor scar short and rounded, only barely detached from pallial line. Shell margin finely crenulate, often coarser towards the posterior. Colour white.

Habitat. Intertidal to shallow water in sand.

Distribution. South Australia to Western Australia as far north as Port Hedland and Scott Reef (Fig. 8).

Remarks. Although specimens of this species from localities in South Australia and Western Australia are present in museum collections (AMS, NMV, WAM) it has not been mentioned in earlier literature (see Cotton & Godfrey, 1938), or even recorded as *Pillucina pisidium* (= *symbolica*) which it resembles. However, it differs from *P. pisidium* in its smaller size, fewer radial ribs, about 35–45 compared to more than 50 ribs on *P. pisidium*, and an anterior lateral tooth in the right valve which is lacking in *P. pisidium*. The two species also have a disjunct distribution with seemingly no *Pillucina* species recorded from Victoria and Tasmania, either in collections or literature.

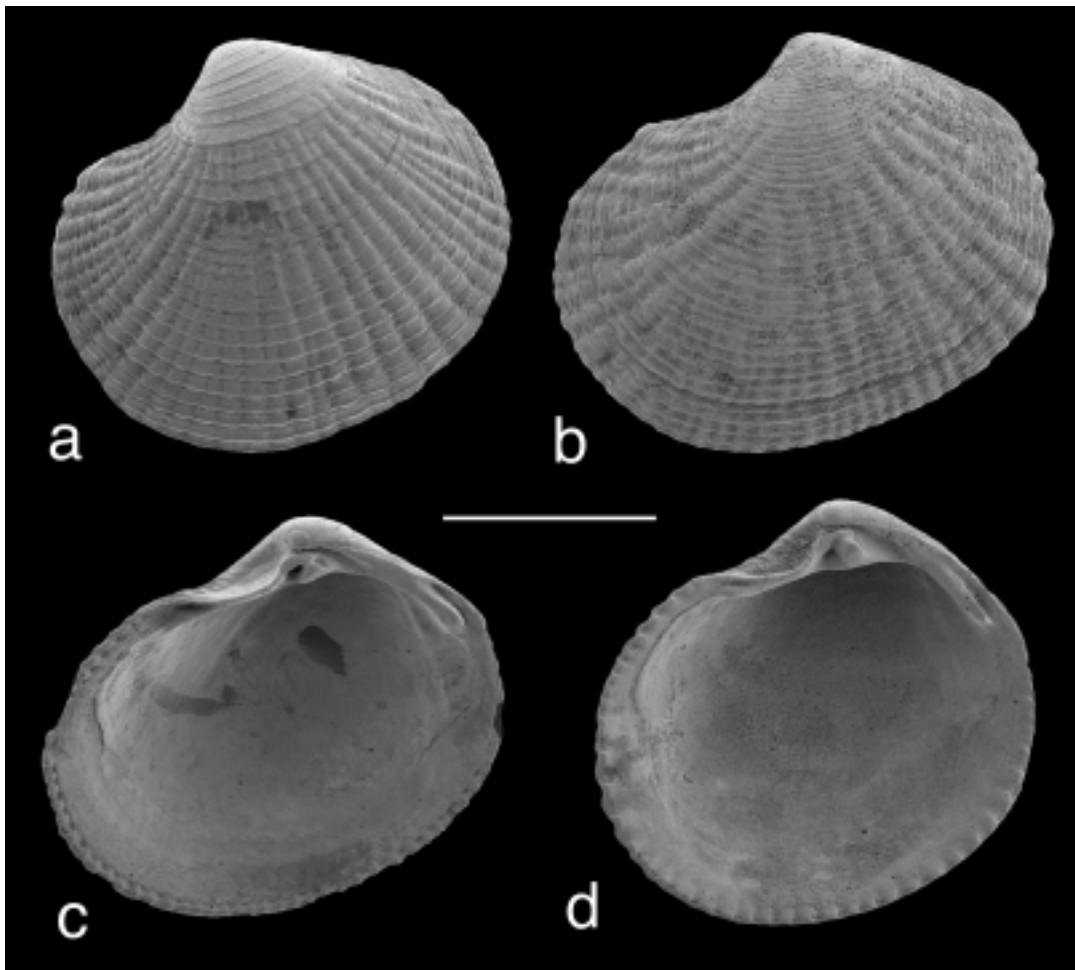


Figure 5. *Pillucina neglecta* Habe, Okinawa, Japan (AMS C355657); a, exterior of left valve; b, exterior of right valve; c, interior of right valve; d, interior of left valve. Scale bar = 1.0 mm.

Material examined. **Australia:** SOUTH AUSTRALIA: Outer Harbour Beach, Adelaide (AMS); Largs Bay, St Vincents Gulf (AMS); Point Sinclair (AMS); Tumby Bay, Spencer Gulf (AMS); Arno Bay, Eyre Peninsula, Spencer Gulf (AMS); Hardwicke Bay, Spencer Gulf (AMS); Henley 34°56'S 138°31'E (AMS); WESTERN AUSTRALIA: E of Observatory Point, Recherche Archipelago (AMS); Esperance (AMS); Oyster Harbour, Emu Point, Albany (AMS); South Point, Two Peoples Bay, Albany (AMS); Yallingup 33°39'S 115°1'E, intertidal; Dunsborough 33°36'S 115°6'E (AMS); Peppermint Grove beach near Capel, 6 m (AMS); Mandurah, 32°32'S 115°43'E (AMS); Point Peron, S of Perth (AMS); Ricey Beach, Rottneest I. (WAM); E of Buller I., Grey, 6 m (WAM); Cervantes, Hansen Bay (WAM); W of Green Head 29°50'S 114°7'E, 50 m (AMS); Dongara 29°9'S 114°43'E (AMS); Jurien, Murchison River (WAM); Hamelin Pool, Shark Bay (WAM); 10 km SE of Faure I., Shark Bay (AMS); Freycinet Reach, Shark Bay, intertidal sand (WAM); Bernier I., S of Redcliff Point, Shark Bay, 10 m (WAM); Carnarvon, 6 m (AMS); North West Cape 21°44'S 114°19'E (AMS); North West Cape, S of Vlamingh (WAM); Port Hedland (AMS).

***Pillucina denticula* n.sp.**

Fig. 7a–g

Type material. HOLOTYPE: NMSA B310/T1758; H 3.5, L 3.5. PARATYPES: NMSA V8402/T1759; H 2.8, L 2.9; H 2.9, L 2.8; H 3.1, L 3.1. BMNH 2000377; H 3.7, L 3.5; H 3.5, L 3.5. Type locality: Durban Bay, South Africa.

Description. Shell small (H to 3.7), robust, inflated (H/L 1.0). Circular in outline. Sculpture of fine, closely spaced, commarginal lamellae crossed by low, rounded radial ribs that are prominent and broader towards anterior and posterior. Ribs inconspicuous in central part of shell. Lunule long, shallowly impressed and lanceolate in outline. Ligament internal, short. Right valve with single cardinal tooth and prominent anterior and posterior lateral teeth. Left valve with two cardinal teeth, and anterior and posterior lateral teeth. In addition to the major teeth the hinge plate between the internal ligament and posterior lateral tooth bears subsidiary denticles and sockets. Left valve has 6–8 sawtooth-like denticles and a posterior narrow ridge overlying the lateral tooth (Fig. 7f), and right valve has corresponding series of irregular sockets (Fig. 7g). Anterior adductor scar short and barely detached from the pallial line. Shell margin crenulate, with crenulations more widely spaced to anterior and posterior of shell. Colour white.

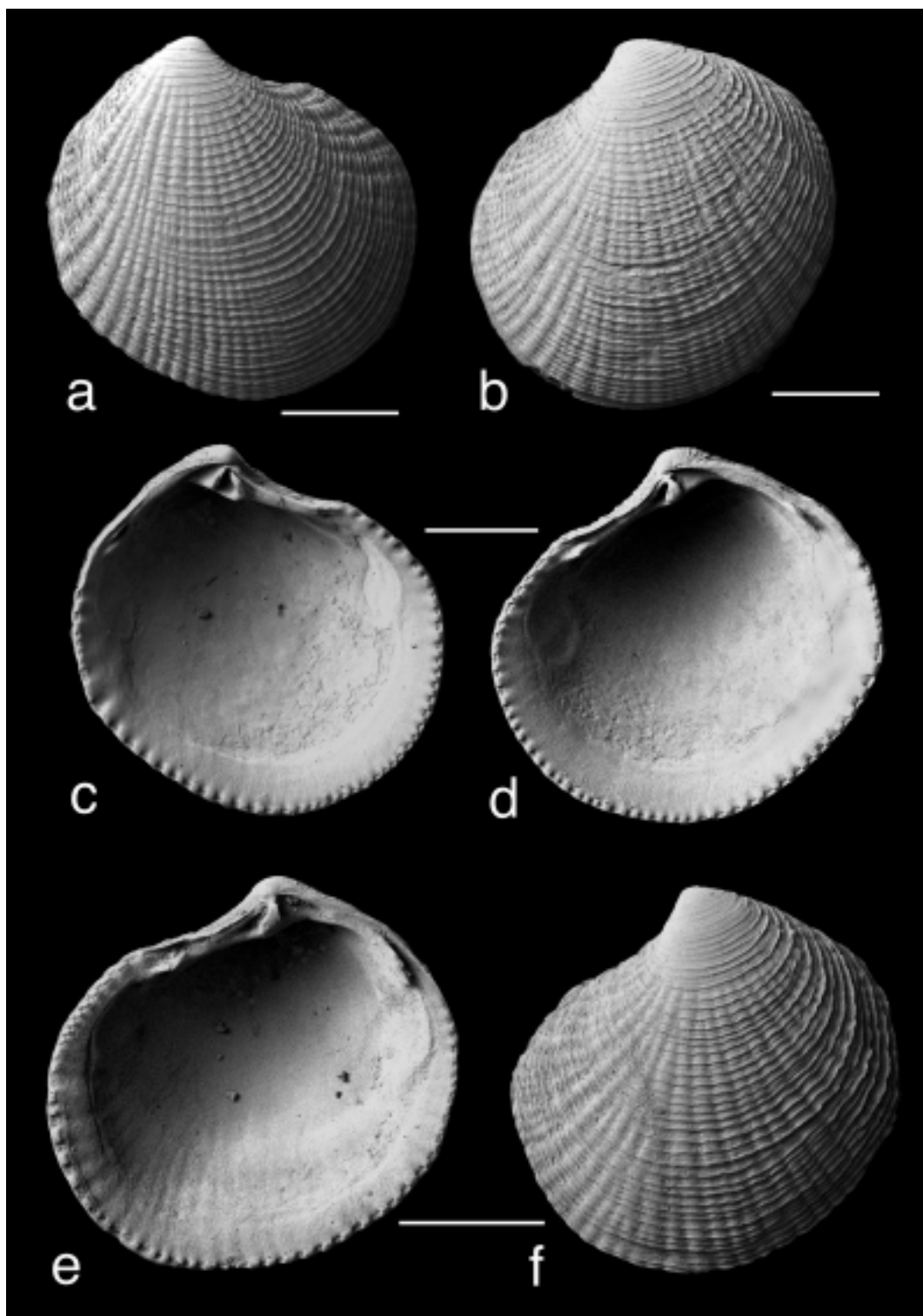


Figure 6. a–f, *Pillucina australis* n.sp.; a, exterior right valve, holotype NMV F83659, Port Lincoln, South Australia; b, paratype NMVF 87506, exterior of left valve; c,d, interior of left and right valves of holotype; e,f, interior of right valve and exterior left valve of specimen from Jervoise Groyne, 1.5 km south of Woodmans Point, Cockburn Sound, Western Australia (AMS C355475). Scale bars = 1.0 mm.

Etymology. The name denticula refers to the denticles on the hinge plate.

Habitat. Subtidal sand 18–50 m.

Distribution. Eastern South Africa (Fig. 8).

Remarks. *Pillucina denticula* is similar in shell form to *P.*

australis from southern and western Australia but easily distinguished by the presence of the unusual denticles on the hinge plate.

Material examined. **South Africa:** KWAZULU NATAL, St Lucia Lighthouse, 50 m (NMSA); Durban Bay Head, 18–22 m (NMSA).

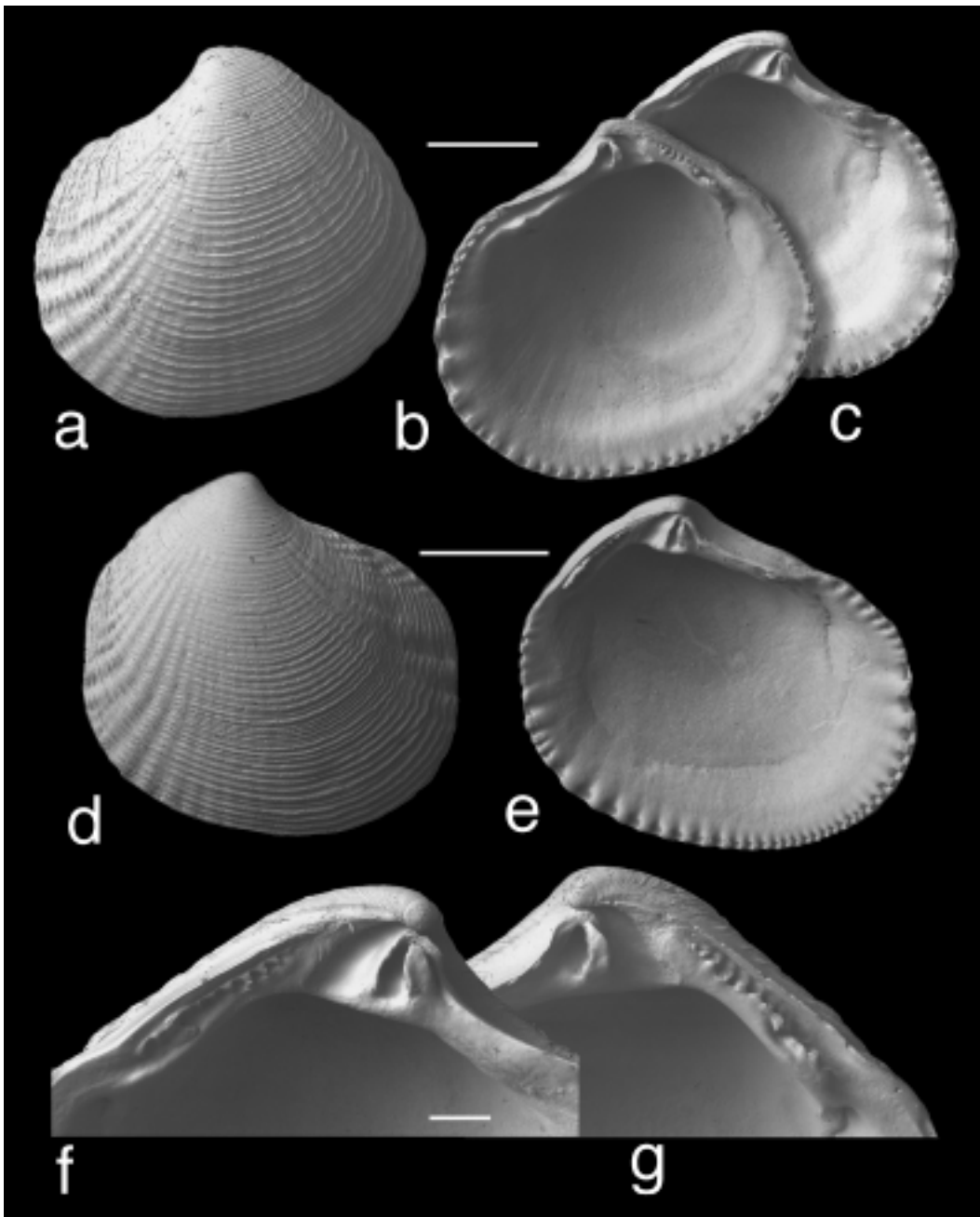


Figure 7. a–g. *Pillucina denticula* n.sp.; a,b,c, exterior of left valve and interior of right and left valves, holotype NMSA, Durban Bay, South Africa; scale bar = 1.0 mm. d,e, exterior of right valve and interior of left valve, paratype NMSA; scale bar = 1.0 mm. f,g, detail of hinges of left and right valves of holotype showing the unusual denticles on the hinge plate; scale bar = 250 μ m.

***Pillucina vietnamica* Zorina, 1978**

Figs. 9a–g, 10–13, 14a–d,f, 15a,c,d, 16

Pillucina vietnamica Zorina, 1978: 195, figs. 3 & 6 (fig. 6 seems to be the interior of fig. 3 rather than the cited fig. 4 which is the inside of fig. 5). Syntypes: ZISP, 13 whole shells and 1 valve, L 5.5–8.9. Type locality: intertidal, south coast of Hainan, China. Seen

Lucina fischeriana Issel, 1869: 83–84, pl. 1, fig. 8 (non *L. fischeriana* Orbigny, 1845, a Jurassic fossil). Five syntypes: MCG, possible figured syntype, H 10.7, L 12.1. Type locality: Suez, Egypt. Seen.

Lucina concinna H. Adams, 1871: 791, pl. 48, fig. 14 (non *L. concinna* Deshayes, 1857, Eocene fossil). Holotype: ZMC; H

9.1, L 9.2. Type locality: Gulf of Suez, Red Sea. Seen. *Pillucina fischeriana* (Issel).—Oliver, 1992: 98, pl. 20, fig. 4; Oliver, 1995: 236, fig. 1026.

Description. Shell small, H to 14, moderately inflated, shell longer than high (H/L 0.9–0.95). Shell slightly translucent and waxy in appearance. Extended anteriorly. Sculpture of many, fine, low commarginal lamellae and fine radial ribs which are broader and more prominent towards the anterior and posterior. Intersection of commarginal and radial ribs is finely cancellate in central part of shell and conspicuously fluted where commarginal lamellae cross the broader radial ribs towards anterior and posterior. Shell margin can appear “scalloped” towards anterior and posterior. Lunule elongate,

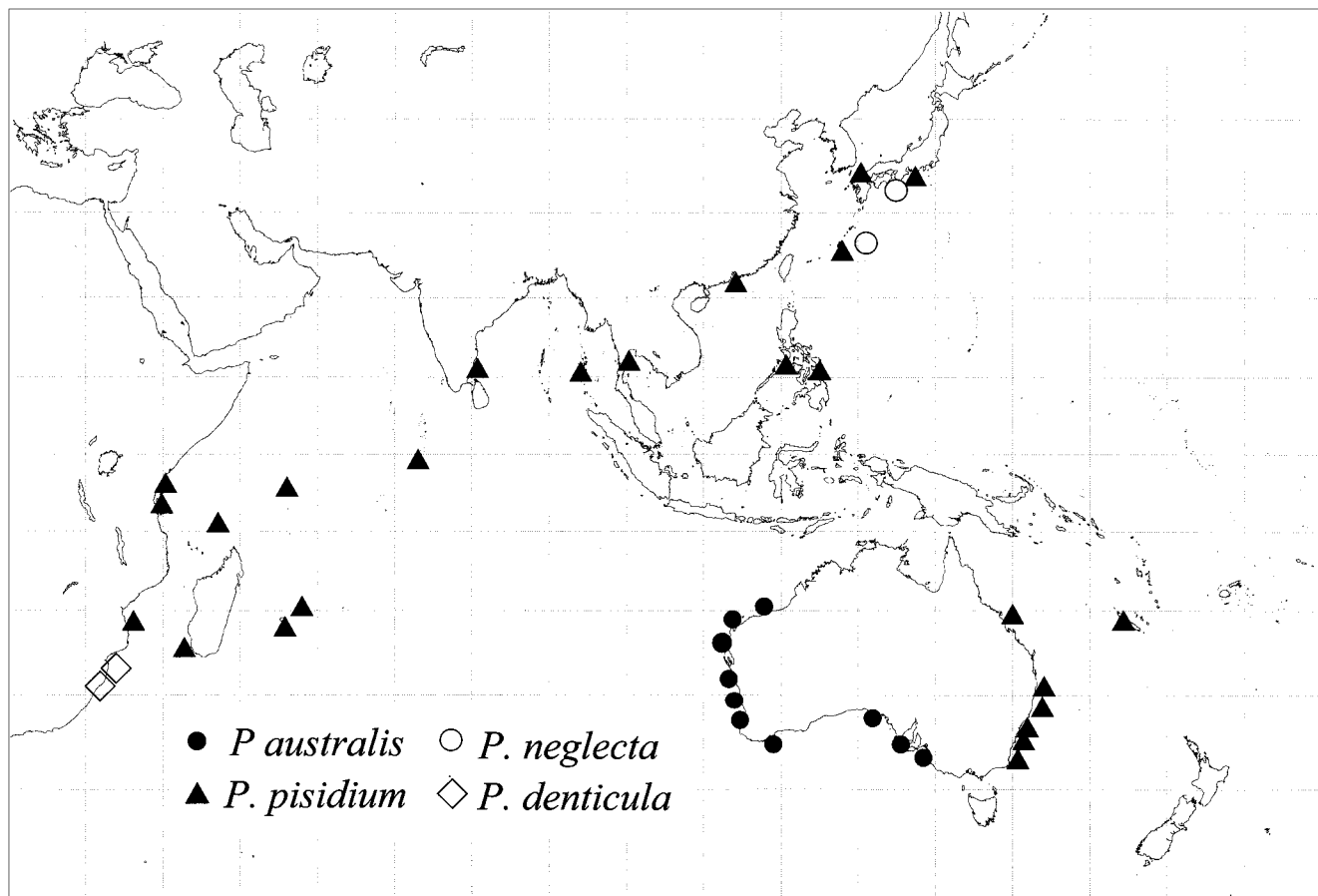


Figure 8. Map showing distribution of *Pillucina pisidium* (Dunker), *P. neglecta* Habe, *P. australis* n.sp. and *P. denticula* n.sp.

lanceolate and impressed, slightly asymmetrical, with right valve overlapping left. Hinge plate slightly sinuous, right valve with single, narrow, cardinal tooth, anterior and posterior lateral teeth short and peg-like. Left valve with two narrow cardinal teeth, small, anterior lateral tooth and posterior lateral tooth comprises a low, short ridge. Ligament internal, short, situated on a broadly triangular resilifer. Anterior adductor muscle scar medium-long, but narrow, detached for slightly more than half of its length from pallial line. Posterior scar ovate. Inner shell surface is fluted from impressions of radial ribs especially in younger specimens. Shell margin slightly thickened and crenulate, with crenulations coarser towards anterior and posterior. Colour yellowish to white.

Anatomy. The anatomy of *P. vietnamica* from Port Douglas, Queensland was studied by dissection (Fig. 11), serial thin sections and by SEM of critical point dried specimens. The gross anatomy is generally similar to other species of Lucinidae (Allen, 1958; Taylor & Glover, 2000).

Mantle. Three main folds of the mantle edge are present (Fig. 12). There is a small outer fold, divided by the periostracal groove from a middle fold which is composed of two unequal lobes, the outer surface of the smaller outer lobe forms the edge of the periostracal groove, whilst the innermost lobe is large and muscular. Some distance back from the mantle margin there is a small inner fold forming a narrow, low ridge. Within the outer fold there is a large blood space and within the inner part of the mantle edge

just below the line of pallial attachment there are groups of large, blue-staining, subepithelial gland cells. Groups of gland cells in this position within the inner mantle are seen in other lucinids (Allen, 1958, fig. 2; Taylor & Glover, 2000, fig. 7).

Mantle gills (putative respiratory structures situated near the anterior adductor muscle) or a mantle septum as described for lucinids such as *Codakia*, *Phacoides*, *Lucina* and *Anodontia* (Taylor & Glover, 2000) are absent. However, the inner surface of the mantle in the area surrounding the anterior and ventral end of the anterior adductor muscle and also the surface of the muscle itself are covered by abundant ciliary tufts (Fig. 15c).

Ctenidia. As in most lucinids, the ctenidia consist of inner demibranchs only, these are large and thick. The posterior end of each ctenidial demibranch is joined laterally and ventrally to the mantle edge by a thin tissue connection which effectively partitions the inhalant and exhalant apertures (Fig. 11). The gill filaments are each around 20–25 µm in width. In section, there is a short outer ciliated zone with the usual bands of frontal, laterofrontal and lateral cilia (Fig. 14a,b). This is followed inwards by a narrow intermediate zone of 2–3 cells, and then the thick lateral zone comprising bacteriocytes and intercalary cells which compose the greater part of the filament. The symbiotic bacteria in *P. vietnamica* are contained in bacteriocytes and have the form of elongate rods 6–8 µm long and 1.5–2 µm in width (Fig. 14c,d). The bacteriocytes also contain spherical granules around 5–7 µm in diameter which are

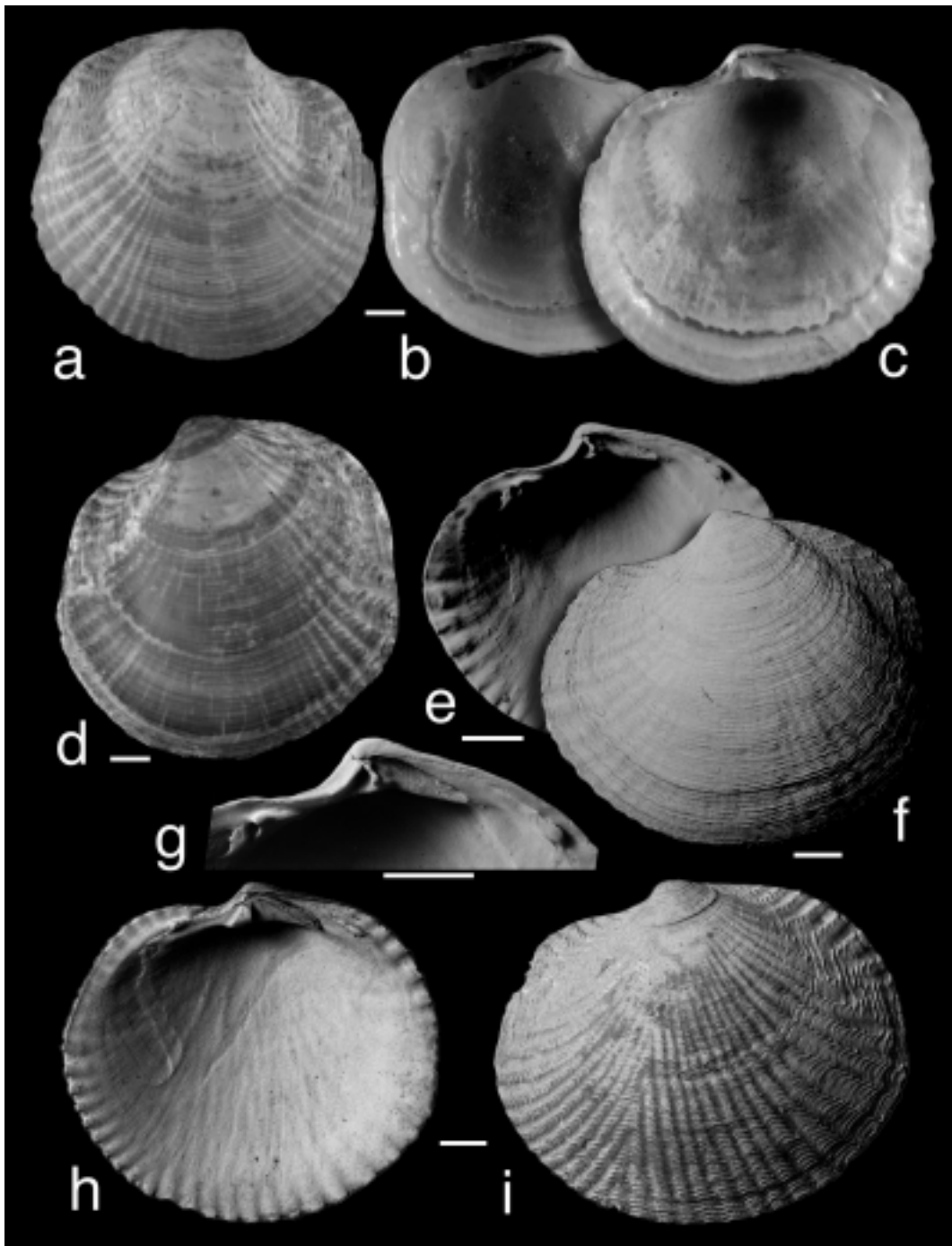


Figure 9. *Pillucina vietnamica* Zorina and *P. angela* (Melvill). a–d, *P. vietnamica* syntypes south coast of Hainan, China, ZISP; a, exterior of right valve; b, interior of left valve; c, interior of right valve; d, exterior of left valve. e–g, *P. vietnamica*, Jazirat as Sa’ diyat, Abu Dhabi BMNH; e, interior of left valve; f, exterior of left valve; g, detail of hinge of left valve. h,i, *Pillucina angela* (Melvill) figured syntype. Gwadur, Pakistan, BMNH 1899.12.18.20; h, interior right valve; i, exterior of left valve. Scale bars = 1.0 mm.

known in other lucinids to be sulphur-rich (Fig. 14f). The labial palps of *Pillucina* are very small, as in most Lucinidae, and consist of small, ciliated folds at the edge of the elongate ciliated lips (Fig. 15d).

Foot. The foot is long and subcylindrical and lacks the heel present in some lucinids. In section, it is composed of layers of longitudinal, radial and circular muscles surrounding a central blood space and is capable of considerable protraction. The distal end of the foot is ciliated with abundant subepithelial gland cells similar to those described for other

lucinids (Allen, 1958; Taylor & Glover, 1997a).

Mantle fusion and the posterior apertures. Characters of the posterior apertures vary considerably between lucinid genera (Allen, 1958, fig. 9) and may have value in phylogenetic analysis. One of these characters is the extent of mantle fusion ventral to the inhalant aperture and this may vary from very short as in *Codakia*, to long as in *Anodontia*. In *Pillucina vietnamica*, the fused section of mantle is relatively long with only the inhalant aperture edged with 6 papillae on either side (Fig. 15a), similar to

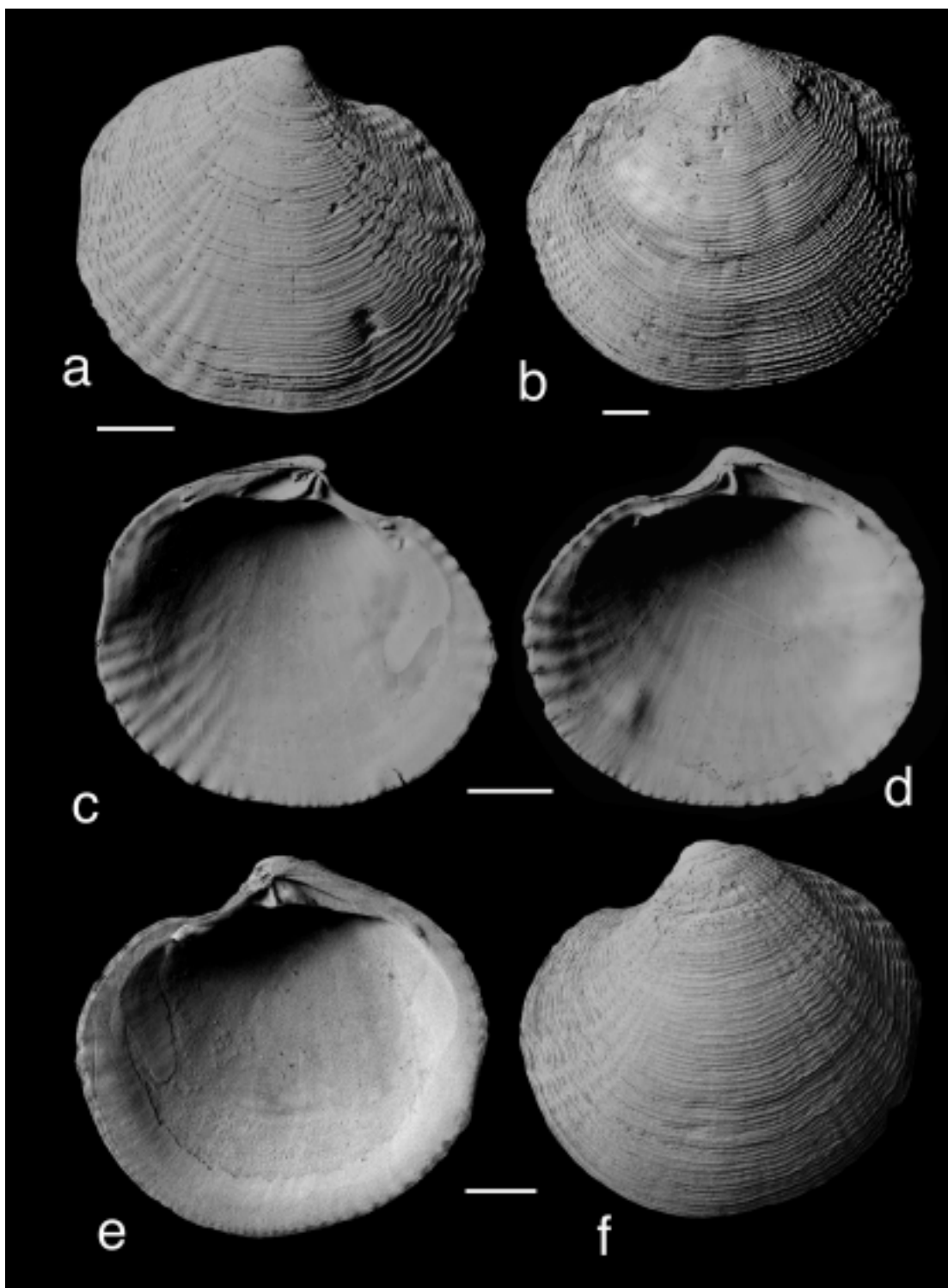


Figure 10. *Pillucina vietnamica* Zorina from Queensland, Australia. a–d, from Port Douglas, Queensland BMNH accession 2394; a, exterior of right valve; b, exterior of left valve; c, interior of right valve; d, interior of left valve. e, f, specimen from Redland, Moreton Bay, Queensland (BMNH accession 2394); e, interior of right valve; f, exterior of left valve. Scale bars = 1.0 mm.

the condition in *Lucinoma borealis* (Allen, 1958, fig. 9c). Sections of the fused mantle near the inhalant aperture (Fig. 13b) show the extent of mantle fusion involving both the inner and most of the middle mantle folds. The large blood spaces indicate that this part of the mantle may be considerably expanded and contracted. The exhalant aperture comprises a thin-walled retractable tube which in

sections was seen inverted into the suprabranchial space between the two inner demibranchs (Fig. 13b).

Distribution. Tropical Indo-West Pacific from Red Sea to China and southern Queensland (Fig. 16).

Habitat. Intertidal to shallow water, sand and silt on the

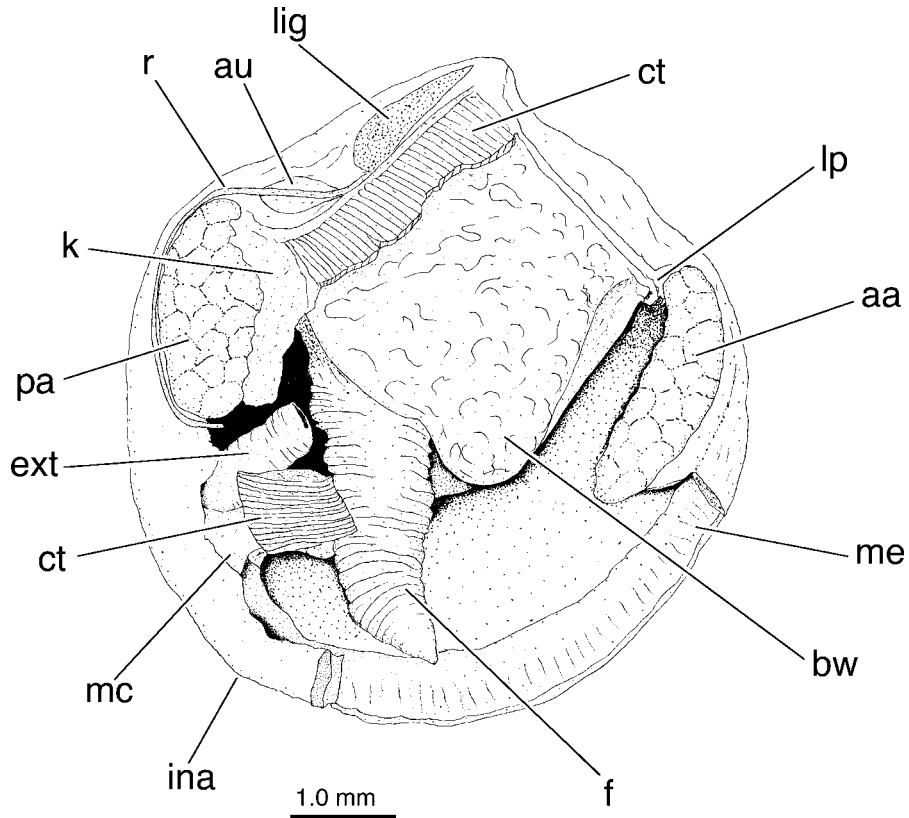


Figure 11. *Pillucina vietnamica* Zorina from Port Douglas, Queensland, general anatomy with right gill demibranch nearly completely removed. Abbreviations: aa, anterior adductor muscle; au, auricle; bw, body wall; ct, ctenidia; ext, exhalant tube; f, foot; ina, inhalant aperture; k, kidney; lig, ligament; lp, labial palp; mc, mantle connection to gill; me, mantle edge; pa, posterior adductor muscle; r, rectum.

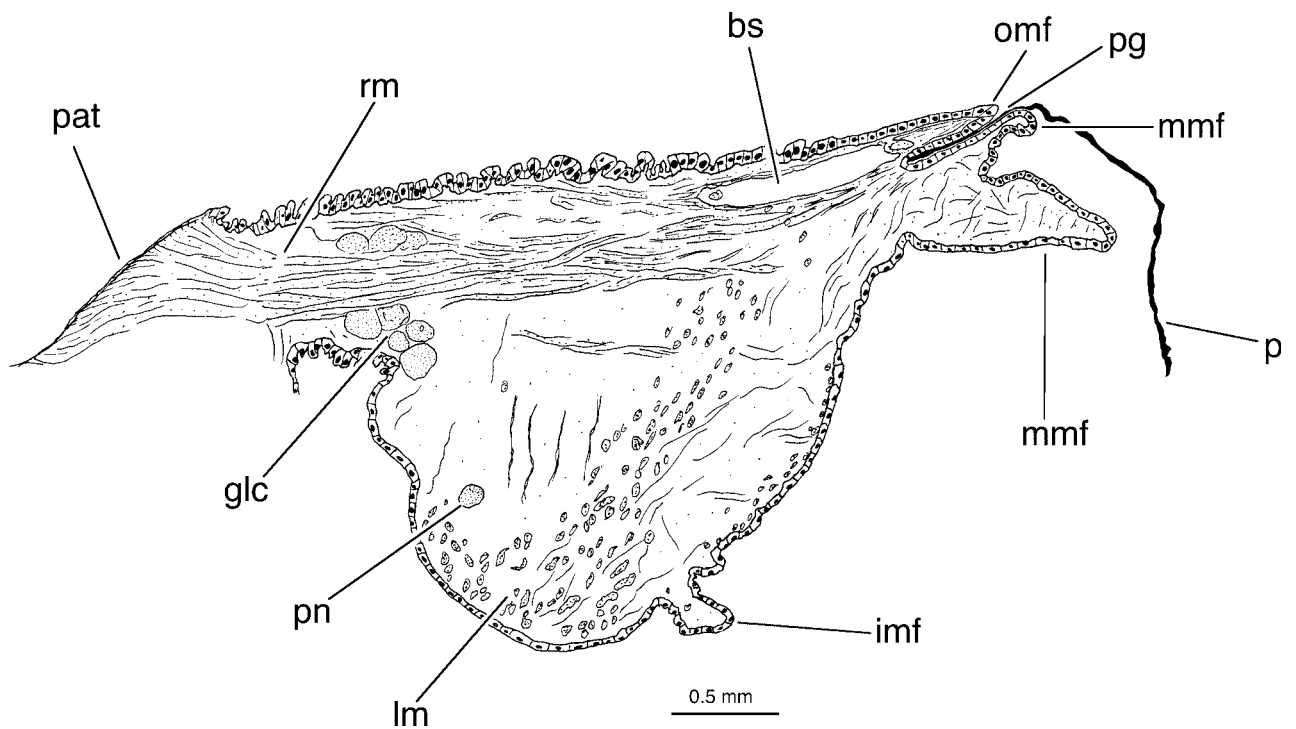


Figure 12. *Pillucina vietnamica* Zorina from Port Douglas, Queensland, section through the mantle edge showing the structure of the mantle folds. Abbreviations: bs, blood space; glc, subepithelial gland cells; imf, inner mantle fold; lm, longitudinal muscles; mmf, middle mantle fold; omf, outer mantle fold; p, periostracum; pat, pallial attachment; pg, periostracal groove; pn, pallial nerve; rm, radial muscles.

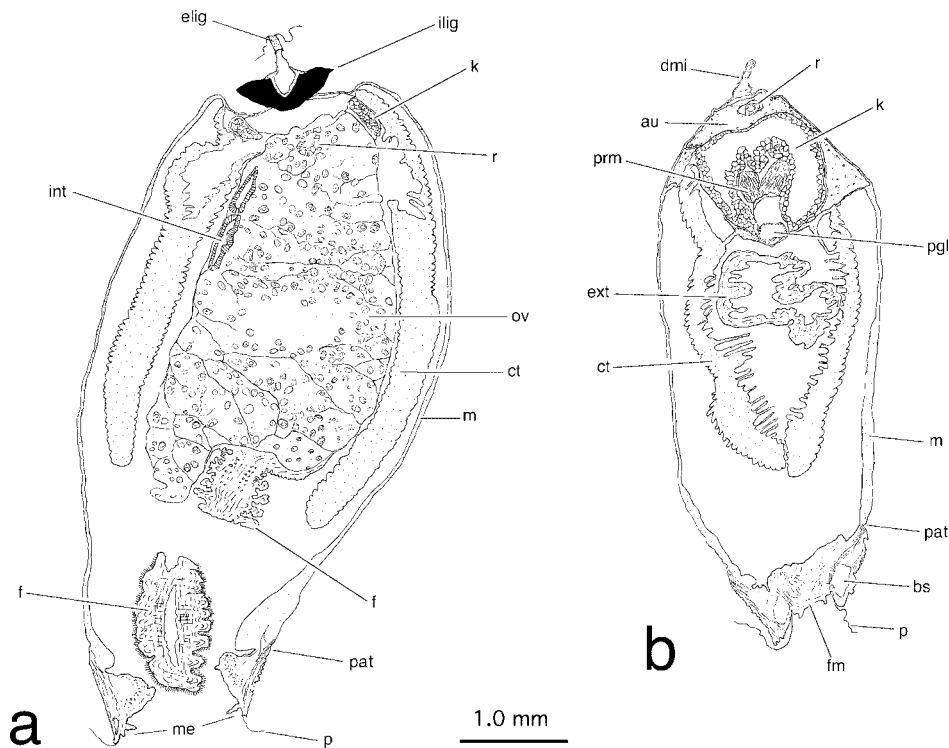


Figure 13. a,b, *Pillucina vietnamica* Zorina from Port Douglas, Queensland; a, semi-diagrammatic drawing of transverse serial section through median part of the body; b, semi-diagrammatic drawing of transverse section through the posterior of body. Abbreviations: au, auricle; bs, blood space; ct, ctenidia; dmi, dorsal mantle isthmus; elig, external ligament; ext, exhalant tube; f, foot; fm, fused mantle; ilig, inner ligament; int, intestine; k, kidney; m, mantle; me, mantle edge; ov, ovary; pat, pallial attachment; pedal ganglion; prm, pedal retractor muscle; r, rectum.

fringes of mangroves; a species of continental margins rather than offshore islands.

Remarks. This species is usually known from localities around the Arabian Peninsula as *Pillucina fischeriana* (Issel, 1869) (see Oliver, 1992; 1995), however, the name is unfortunately preoccupied, as is the name *L. concinna* H. Adams, 1871. The next available name appears to be *Pillucina vietnamica* Zorina, 1978 with the type locality of Hainan I., China. We have examined the syntype series of this species and they are similar in shell morphology to samples from the Arabian Peninsula, Southeast Asia and northern and eastern Australia and we regard them as conspecific. Oliver (1992) regarded *Pillucina concinna* as a distinct species from the Red Sea, however, we have examined the type material and consider it a slightly more inflated variant of *P. vietnamica*.

Individuals of *P. vietnamica* from the northern Red Sea are larger than those from other localities as are shells from Moreton Bay, Queensland at the southern edge of its range.

Pillucina vietnamica has never previously been recorded from Australia although unidentified shells in museum collections and our own sampling of live animals from mangroves show that this species is widely distributed on the Queensland coast.

Material examined. **Egypt:** Suez (BMNH). **Yemen:** Aden (BMNH). **Kuwait:** (BMNH). **Bahrain:** Tubli Bay (NMW). **Emirate of Abu Dhabi:** Dhafra Beach, Jebel Dhanna (BMNH). **Emirate of Ras Al Khaymah:** Rams (BMNH). **Saudi Arabia:** Tarut, Arabian Gulf

(BMNH). **Oman:** Masirah I. (BMNH); Umm Rusays, Masirah; Quriyat, Gulf of Oman (NMW); Qurm, Muscat. **Somalia:** Loyada Beach (MNHN). **Pakistan:** Karachi (BMNH). **India:** Madras (BMNH); Krusadai, Kutical Bay (BMNH); Kunugal Bay (BMNH). **Sri Lanka:** Trincomalee (BMNH & MNHN). **Malaysia:** Kuantan, intertidal sandflats 3°48'N 103°20'E (AMS); Country Club, Pulau Langkawi, NW Malaysia (AMS). **Cambodia:** 5 km E of Port Sihanoukville (BMNH). **Australia:** WESTERN AUSTRALIA: Parry Harbour, Kimberley 13°58'S 126°05'E (WAM); Mission Bay, Napier Broome Bay, Kimberley; intertidal (WAM). NORTHERN TERRITORY: East Point, Darwin (BMNH); Snake Bay, near Timarambu Creek, Melville I. (BMNH); Cape Consor, Melville I. (AMS); Crocodile Research Station, Maningrida, Arnhemland (AMS); Port Essington (AMS); Crab Cay, Boucot Bay (AMS); Gove (NMV); Groote Eylandt, Gulf of Carpentaria (AMS). QUEENSLAND: Forsyth I., Gulf of Carpentaria; Friday I., Torres Strait 10°36'S 142°10'E (AMS); Somerset, Cape York (AMS); Seisia, Bamaga, Cape York (NMV); Cairns Reef lagoon, 9–18 m, 14°42'S 145°30'E, N of Cooktown (AMS); Craiglie, Port Douglas (BMNH); Buchans Point, N of Cairns 16°44'S 145°40'E (AMS); Halfmoon Bay, Yorkeys Knob (AMS); Michaelmas Cay, Cairns (AMS); Port Denison, Bowen (AMS); Mission Beach, N of Tully (AMS); Lucinda (AMS); Kings Beach, Bowen (AMS); Seaforth, Mackay (AMS); Sarina beach (AMS); Yeppoon (AMS); Quoin Is, Port Curtis, 2–5 m (AMS); Pialba, Hervey Bay 25°17'S 152°50'E (AMS); Dundowran Beach, Hervey Bay (AMS); Point Vernon, Hervey Bay (AMS); Tin Can Bay, NE of Gympie (AMS); Noosa Heads (AMS); Redland Bay (BMNH); Nudgee Beach, Moreton Bay (BMNH); Coochiemudlo I., SW of Cleveland, Moreton Bay (AMS); Sandgate, Moreton Bay (NMV); Woody Point, Moreton Bay (NMV); Peel I., Moreton Bay (AMS); Southport, 27°58'S 153°25'E (AMS). **China:** Hong Kong (BMNH); Daya Bay, Guangdong Prov (BMNH); Hainan (MNHN).

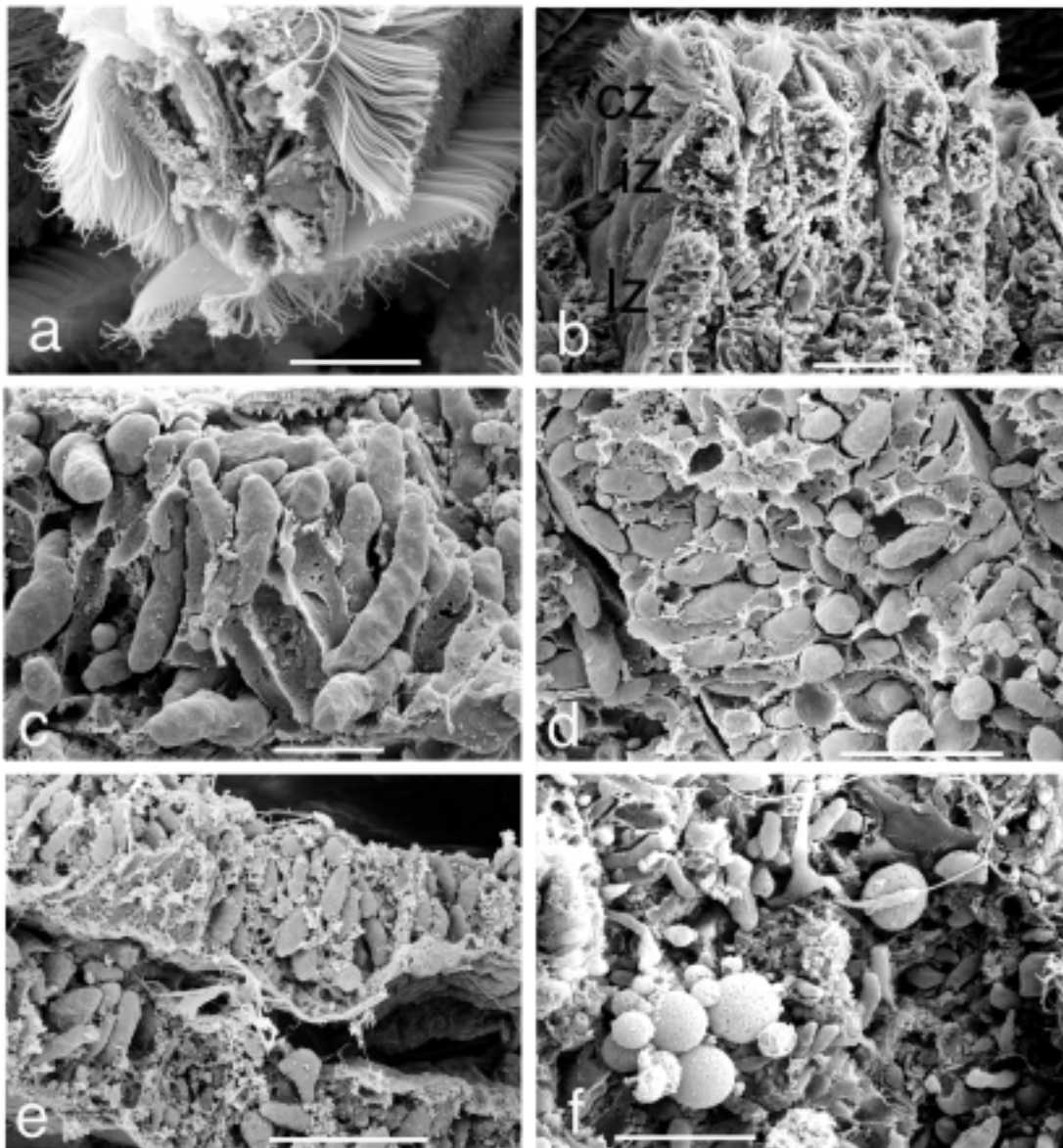


Figure 14. a–d. *Pillucina vietnamica* Zorina from Port Douglas, Queensland, all SEMs of critical point dried preparations; a, distal tip of gill filament showing frontal, laterofrontal and lateral cilia, scale bar = 10 μ m; b, section through three gill filaments showing ciliated zone, intermediary zone and bacteriocyte zone, scale bar = 20 μ m; c, section through bacteriocyte showing rod shaped bacteria, scale bar = 5 μ m; d, section through gill filament showing bacteria in vacuoles within bacteriocytes, scale bar = 10 μ m. e, *Wallucina assimilis* Jervis Bay, NSW, section through gill filaments showing bacteria in bacteriocyte zone, scale bar = 10 μ m. f, *Pillucina vietnamica* spherical granules in bacteriocytes, scale bar = 10 μ m. Abbreviation: cz, ciliated zone; iz, intermediate zone; lz, lateral zone.

***Pillucina angela* (Melvill, 1899)**

Fig. 9h,i

Lucina (*Codakia*) *angela* Melvill, 1899: 98, pl. 2, fig. 8. Two syntypes: BMNH 1899.12.18.20–21; figured syntype: H 7.9, L 8.1, T 1.9 (1v); 1 syntype: NMW 1955.158.684. Type locality: Gwadar, Pakistan, 8 fathoms. Seen.

Divaricella cypselis Melvill, 1918: 156, pl. 5, fig. 33. Holotype: BMNH 1921.1.28.42; H 5.1, L 5.2, T 3.5 (2v). Type locality: Karachi, Pakistan. Seen.

Pillucina angela (Melvill).—Oliver, 1995: 236, fig. 1025.

Description. Shells small (H to 8.0), subcircular (H/L 0.91), inflated. Sculpture of strong radial ribs which are broader

and more widely spaced to the anterior and posterior. Ribs steeply divaricate in anterior third of shell. Ribs crossed by fine, closely spaced, commarginal lamellae which curve over ribs producing a scalloped appearance. Anterodorsal area extended above hinge line. Right valve with single large cardinal tooth and short anterior and posterior lateral teeth. Left valve with two cardinal teeth and anterior and posterior lateral teeth. Ligament, internal, short. Anterior adductor scar narrow, elongate, detached from pallial line for about half of length. Inner shell margin coarsely crenulate.

Distribution. Oman, northern Arabian Sea.

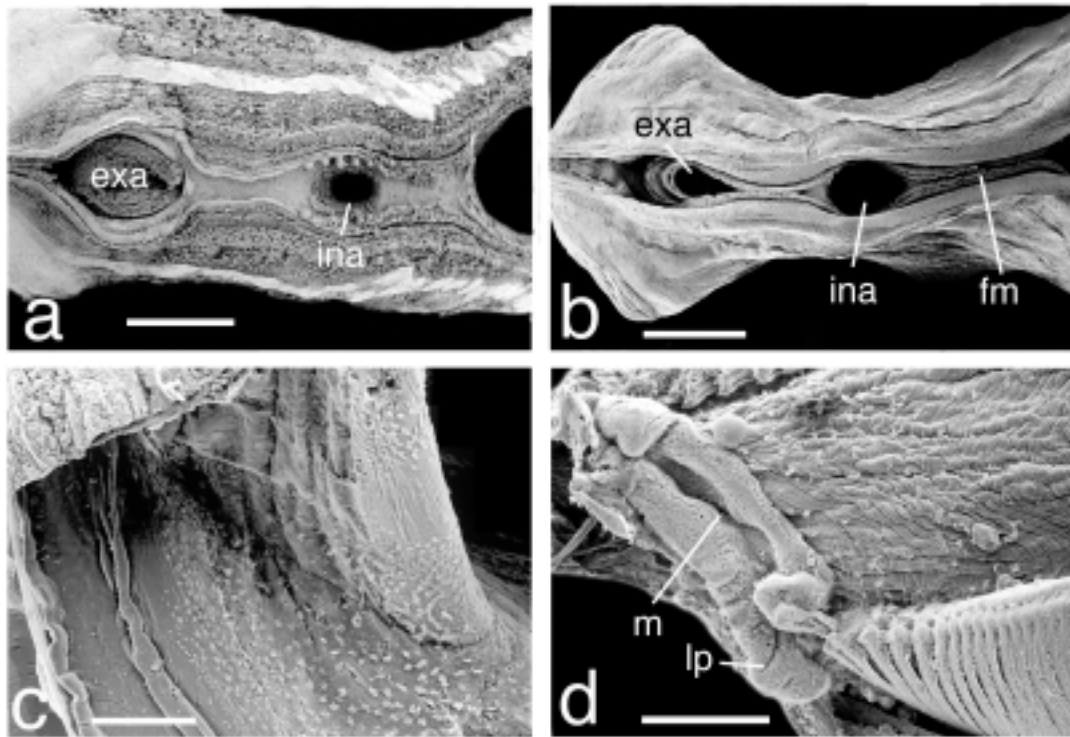


Figure 15. a, *Pillucina vietnamica* Zorina, Port Douglas, Queensland, posterior apertures showing mantle fusion, scale bar = 1.0 mm. b, *Wallucina assimilis*, Jervis Bay, NSW posterior apertures, scale bar = 1.0 mm. c,d, *Pillucina vietnamica*; c, inner surface of anterior mantle showing ciliary tufts and ciliated surface of anterior adductor muscle, scale bar = 200 μ m; d, ventral view of mouth, lips and labial palps, scale bar = 200 μ m. Abbreviations: exa, exhalant aperture; fm, fused mantle; ina, inhalant aperture; lp, labial palps; m, mouth.

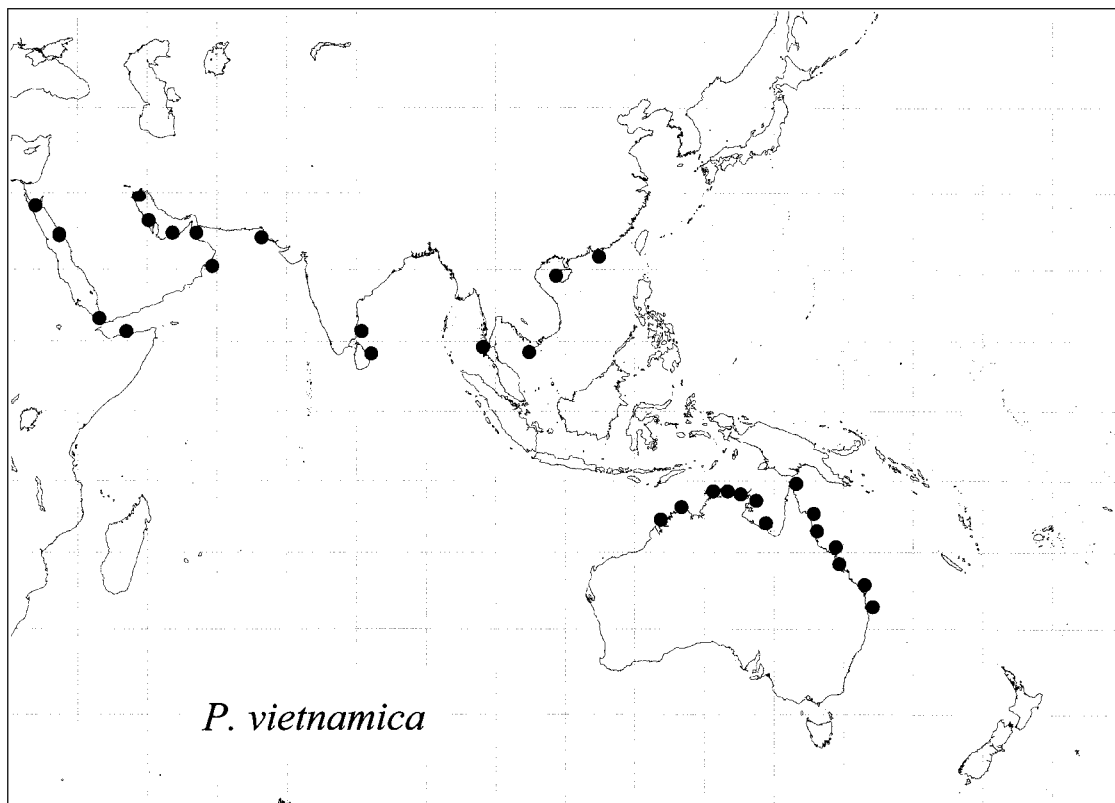


Figure 16. Map showing distribution of *Pillucina vietnamica* Zorina.

Remarks. This species is similar to *Pillucina vietnamica* and may represent an extreme morphological variant of that species. However, from the evidence of the few shells we have seen it differs from *P. vietnamica* in the stronger divaricate radial ribbing, the extended anterodorsal area, the more robust cardinal teeth and the longer and more detached anterior adductor muscle scar. The holotype of *Divaricella cypselis* Melvill, 1918 from Karachi is similar.

Material examined. **Oman:** Sur Masirah, sand flats (NMW 1993, figured in Oliver, 1995) plus 5 other lots from Masirah (NMW). **Pakistan:** Gwadur (BMNH, NMW); Karachi (BMNH).

Pillucina mauritiana n.sp.

Fig. 17

Loripes erythraeus (Issel, 1869).—Viader, 1951: 132, pl. 3, fig. 12.

Type material. HOLOTYPE: BMNH 20000079 paired valves H 11.6, L 11.2, T. 4.0 (single valve). Type locality: dredged Grande Passe, Cannoniers Point, Mauritius, 1947, Viader collection. PARATYPES: BMNH 20000080/1–7. Six paired valves and single left valve, locality as holotype.

Etymology. Named for the island of Mauritius.

Description. Shell small (H to 11.6), thin, subcircular in outline (H/L 1.0), some individuals slightly higher than long, not inflated (T/H 0.3), although larger individuals tend to be more inflated than juveniles. Sculpture of extremely fine, low, commarginal lamellae with variable, fine, radial striae that are slightly broader and more prominent near the dorsal margin on both sides of the shell. Lunule narrow, lanceolate to heart-shaped, slightly impressed. Hinge plate shallow. Right valve with a single prominent cardinal tooth, an elongate, posterior lateral tooth and a peg-like anterior lateral tooth. Left valve with two cardinal teeth, a low posterior lateral tooth and a socket for the anterior lateral tooth of the right valve. Ligament internal, fairly short, deeply impressed into each valve. Anterior adductor muscle scar short, broad and detached from the pallial line for about 1/2 of its length; the posterior scar is reniform. Pallial line discontinuous and impression of pallial blood vessel faint. Shell outside of the pallial line glossy with fine radial striations. Shell margin finely denticulate.

Remarks. Viader placed this species from Mauritius in what we now call *Chavania erythraea* (see below) but it differs in shape, hinge and external sculpture. Although the type material is slightly worn the shells are distinctive and differ from other *Pillucina* species. The species is most similar to *Pillucina hawaiiensis* and *P. pacifica*, but it is larger, less

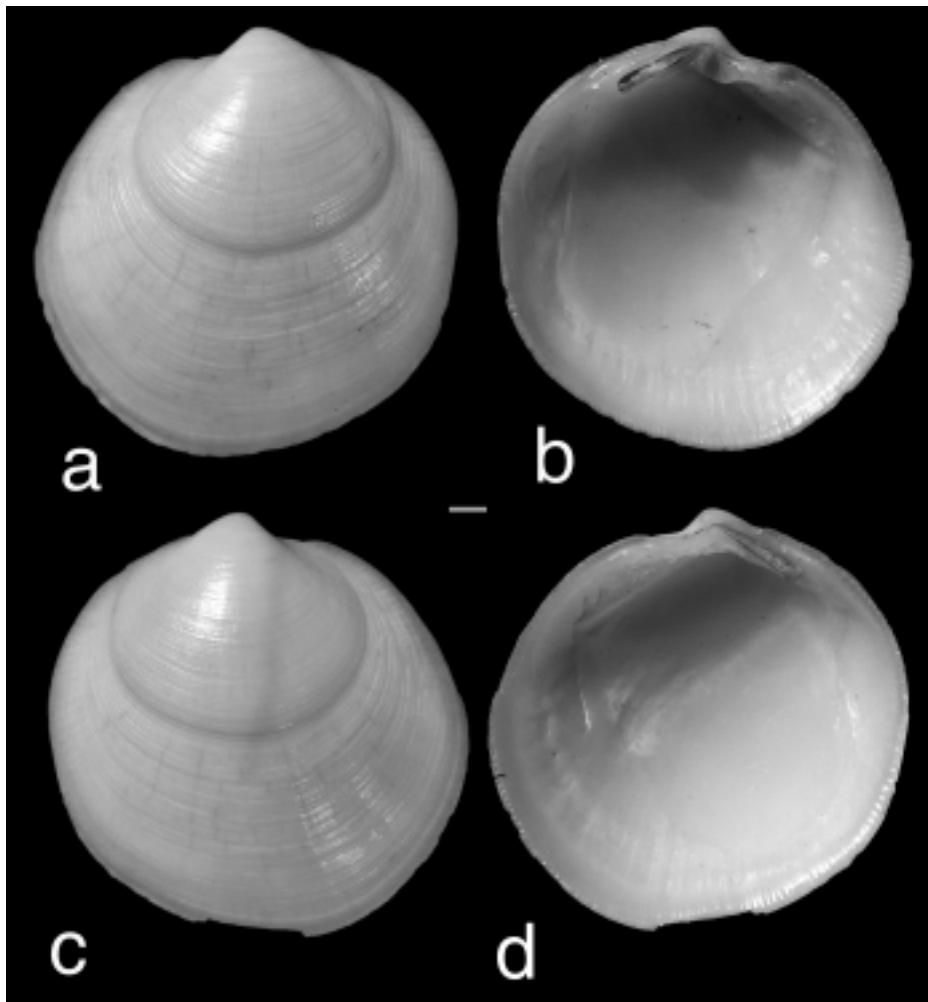


Figure 17. *Pillucina mauritiana* n.sp., holotype BMNH 20000079, Grande Passe, Cannoniers' Point, Mauritius: a, exterior of left valve; b, interior of left valve, c, exterior of right valve; d, interior of right valve; scale bar = 1.0 mm.

inflated, with a prominent anterior lateral tooth in the right valve, a longer anterior adductor muscle scar and finer radial ornament.

Distribution. Known only from Mauritius.

Material examined. Mauritius: Mauritius (MNHN).

Chavania n.gen.

Type species. *Lucina erythraea* Issel, 1869.

Diagnosis. Shells small, robust, H to 12. Outline generally circular to slightly higher than long but rather variable. Sculpture of fine, closely-spaced, low commarginal lamellae which anastomose occasionally (Fig. 18), fine riblets sometimes visible on anterior and posterior of shell and also fine radial striations visible within the outer shell layer. Shallow posterior sulcus present on both valves (Fig. 18). Cardinal teeth large, with a single projecting tooth in the right valve and two cardinal teeth in left valve of which the anterior is larger. Anterior lateral teeth absent or vestigial ridge. Ligament internal and short, deeply inset into valve. Anterior adductor scar short and rounded and detached from pallial line for about 1/5 to 1/3 of length. Shell margin broad, thickened with the inner margin finely crenulate.

Remarks. Differs from *Pillucina* in the lack of prominent radial ribs (Table 1), from the Miocene *Microloripes* in form of the commarginal lamellae and the absence of an anterior lateral tooth, and from *Wallucina* in having a more robust, inflated shell, and coarser and anastomosing, commarginal sculpture.

Etymology. Named in recognition of André Chavan for his work on lucinid systematics.

Distribution. Indo-West Pacific (Fig. 21)

Chavania erythraea (Issel, 1869)

Figs. 18i–k, 21

Lucina erythraea Issel, 1869: 84, pl. 1, fig. 9. Three syntypes: MCG, largest H 4.1, L 4.5. Type locality Suez. Some Byne's disease but identifiable. Seen.

Lucina crosseana Issel, 1869: 255, pl. 3, fig. 3. Types: ?Turin Museum, not located.

?*Lucina elegans* H. Adams, 1871: 791, not figured. Types: not located ?BMNH or ?MZC.

Phacoides malcolmensis Melvill, 1918: 156–157, pl. 5, fig. 32. One syntype: BMNH 1921.1.28.41, Malcolm Inlet, Arabian Gulf, 35 fathoms; 1 syntype: NMW Z.1955.158.686. Seen.

Wallucina erythraea (Issel).—Oliver, 1992: 98, pl. 20, fig. 3; Oliver, 1995: 236, fig. 1027.

Description. Shell small, H to 12, sub-circular, anterior and posterior shell margins straight, posterior slightly concave. Sculpture of fine, low, closely-spaced, commarginal lamellae which occasionally intersect and divide; fine radial riblets sometimes visible to anterior and posterior. Posterior dorsal area demarcated by broad shallow sulcus and less prominent commarginal lamellae. Lunule heart shaped and impressed. Hinge plate narrow, right valve with single cardinal tooth, elongate posterior lateral tooth and no anterior lateral tooth. Left valve with two cardinal teeth, an elongate posterior lateral tooth and no anterior lateral.

Ligament internal, short, deeply inset into the valve. Anterior adductor scar short, rounded and detached from pallial line for about 1/3 of its length. Inner shell margin finely denticulate. Colour white.

Habitat. Shallow water to 200 m.

Distribution. Red Sea, Arabian Gulf, Arabian Sea (Fig. 21).

Remarks. This species is similar to *Chavania striata* (Tokunaga) but can be distinguished by the less inflated shell and the quadrate anterior and posterior shell margins. Issel's original description was based on three specimens from Suez and Savigny's figure (1817, pl. 8, fig. 8). Bouchet & Danrigal (1982, fig. 20) illustrate a shell from Savigny's collection, but this is a *Ctena* species whereas Issel's specimens (MCG) match the original description. We have not seen the type material of *L. crosseana* (Issel) but follow Lamy (1916) and Oliver (1992) in synonymising this species with *C. erythraea*. Evidence from the description suggests that *Lucina elegans* H. Adams may be a junior synonym but there was no original figure and the type material has not been located.

Material examined. Egypt: Suez (BMNH); Gulf of Suez (NMW); Tubya al-Bayda, Safaga Bay. **Kuwait:** (BMNH). **Oman:** Urf, Masirah (NMW); Sur Masirah, Masirah (NMW). **Yemen:** al-Murk island, Red Sea (DC); Aden (MNHN); Ra's Qusay'ir, Hadramawt (DC). **Djibouti:** (MNHN).

Chavania striata (Tokunaga, 1906)

Figs. 18a–h, 19, 21

Lucina contraria Dunker, 1882: 215, pl. 13, figs. 12–14. Holotype: MNB Type locality: Japan (non *Lucina contraria* Dunker, 1846 a West African species). Seen.

Lasaea striata Tokunaga, 1906: 53–54, pl. 3, fig. 14. Twenty-one syntypes: UMUT CM13599 and CM13753–13772 size range H 7.1–9.0, L 7.0–9.4. Type locality: Oji, Tokyo City (Pleistocene fossil). Seen.

Phacoides minutus Thiele, 1930: 592, pl. 4, fig. 72. Three syntypes: MNB 67727, H 2.5. Type locality: Warnbro Sound, Western Australia. Seen, with Byne's disease.

Wallucina lamyi Chavan, 1938: 227, fig. 19. A replacement name for *L. contraria* Dunker, 1882. Habe, 1977: 126, pl. 24, figs. 1 & 2.

Pillucina (*Wallucina*) *striata* (Tokunaga, 1906).—Kuroda, Habe & Oyama, 1971: 392, pl. 118, fig. 15.

Wallucina aff *jacksoniensis* (Smith, 1885).—Hickman & Barnes, 1999: 240, fig. 1a–e.

Description. Shell small, H to 12, sub-circular, but shape variable (mean H/L 1.02), posterior margin often somewhat truncate. Sculpture of fine, low, closely-spaced, commarginal lamellae which occasionally intersect and divide; commarginal lamellae slightly higher on posterior dorsal margin. Fine radial riblets sometimes visible on anterior ventral margin. Posterior dorsal area demarcated by a narrow sulcus. Lunule heart shaped and impressed. Hinge plate narrow, right valve with single cardinal tooth, elongate posterior lateral tooth and no anterior lateral. Left valve with two cardinal teeth, an elongate posterior lateral tooth and no defined anterior lateral although there is sometimes a vestigial ridge in that position. Ligament internal, short, deeply inset into the valve. Anterior adductor scar short,

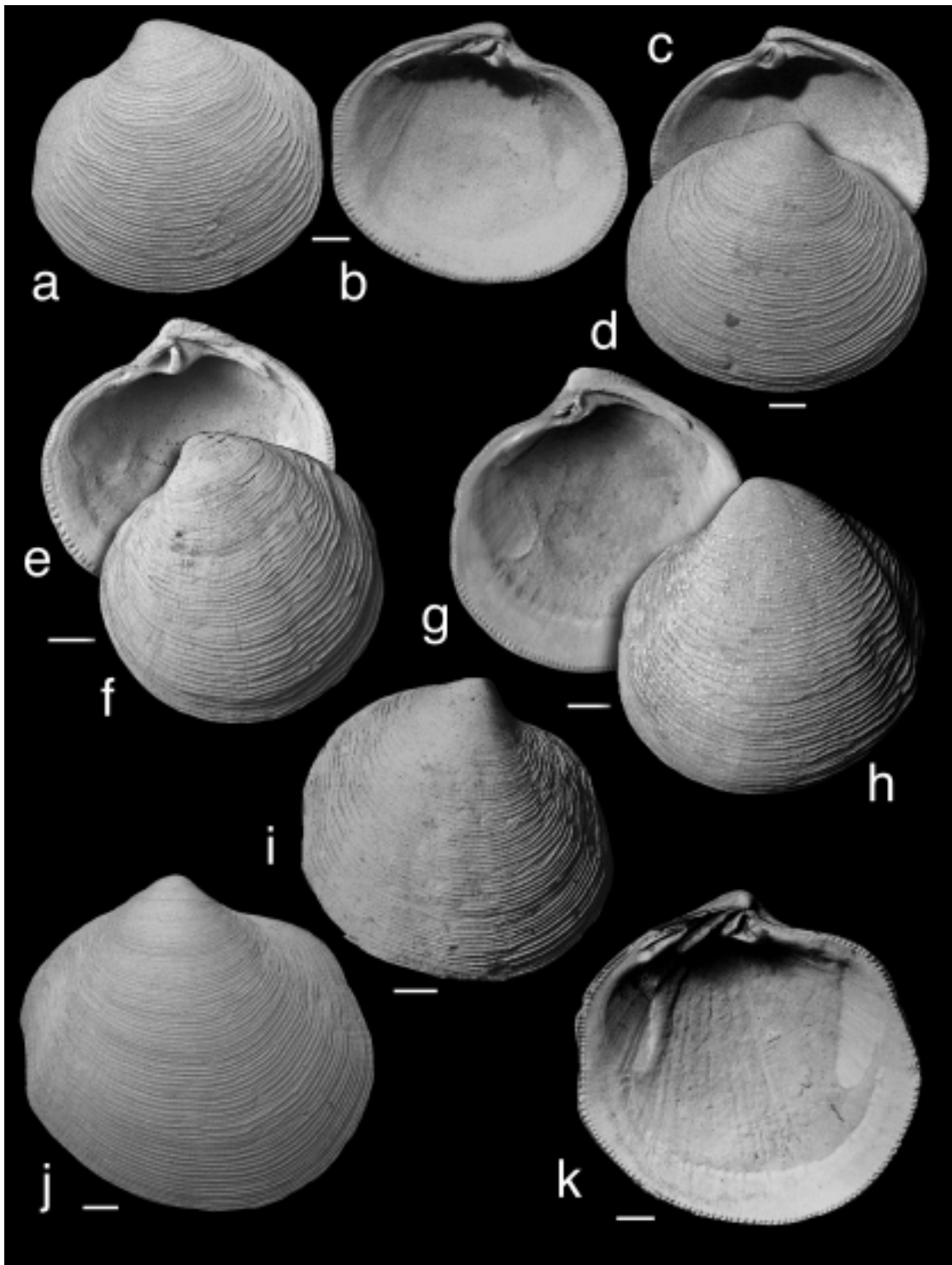


Figure 18. *Chavania striata* (Tokunaga) (a–h) and *C. erythraea* (Issel) (i–k). a,b, *Lasaea striata* Tokunaga syntype UMUT CM13754, exterior and interior of left valve. c,d, *Lasaea striata* syntype UMUT CM13763, interior and exterior of right valve. e–f, *Chavania striata* Japan, BMNH 1873.8.6.196; e, interior of right valve; f, exterior of left valve. g,h, *C. striata* Atoll de Huon, New Caledonia, station 439, 39 m, MNHN; g, interior of right valve; h, exterior of left valve. i, *Chavania erythraea*, Suez, Red Sea, exterior of right valve BMNH. j,k, *C. erythraea* Sur Masirah, Masirah, Oman, NMW 1993.061.00425a; j, exterior of right valve; k, interior left valve. Scale bars = 1.0 mm.

rounded and detached from pallial line for about 1/5 of its length. Inner shell margin finely crenulate. Colour white.

Anatomy. The only material available for study was a single poorly-fixed individual from the Easter Group, Houtman Abrolhos Is, Western Australia (BMNH). With a cylindrical

foot, large gill and tiny labial palps, the gross anatomy of the animal (Fig. 20) is similar in most respects to *Pillucina vietnamica*. A tissue connection occurs between the demibranchs and posterior mantle margin. The fused mantle anterior to the inhalant aperture is shorter than in *P. vietnamica* or *Wallucina assimilis* and papillae are lacking

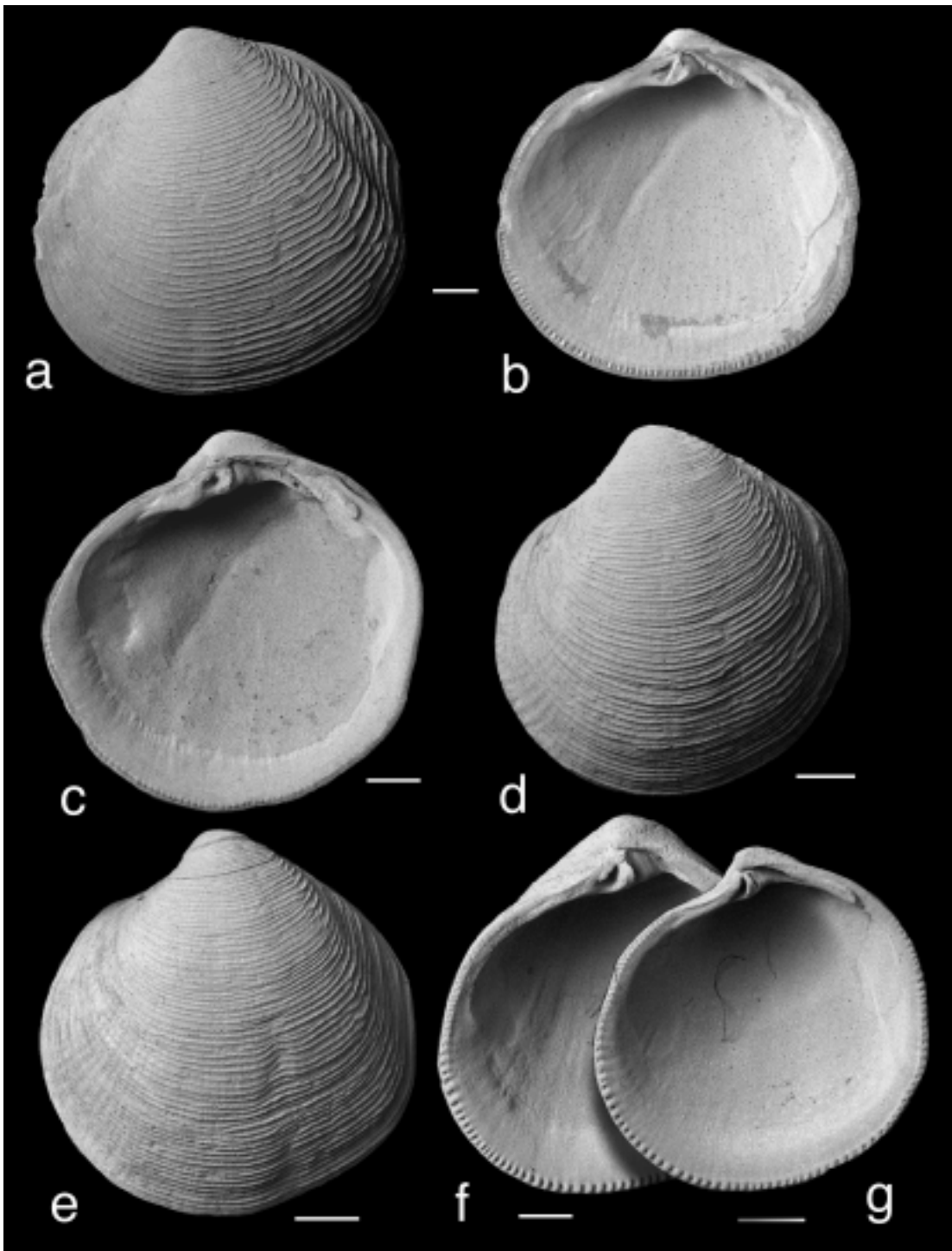


Figure 19. *Chavania striata* (Tokunaga) from Australia. a–c, Watsons Bay, Lizard I., Queensland, 10.5 m, AMS C355806; a, exterior of left valve; b, interior of right valve; c, interior of right valve. d–g, Fremantle, Western Australia, 18–22 m, NMV TD15644; d, exterior of left valve; e, exterior of left valve; f, interior of right valve; g, interior of right valve. Scale bars = 1.0 mm.

around the aperture. An elongate glandular strip is located along the mantle margin ventral to the anterior adductor muscle.

Distribution. Central Indo-West Pacific—India to Japan, Marshall Is, intertidal to 250 m (Fig. 20).

Remarks. The earliest available name is *Lasaea striata* Tokunaga, a Pleistocene fossil from Japan. We have

examined 21 syntypes of this species that are similar to living shells from the Indo-West Pacific. This species has been known as *Wallucina lamyi* Chavan (a replacement name for the preoccupied *L. contraria* Dunker) but Chavan (1938) was apparently unaware of the earlier name. *Phacoides minutus* Thiele seems to be the same species although the original figure is poor and the syntypes are corroded by Byne's disease.

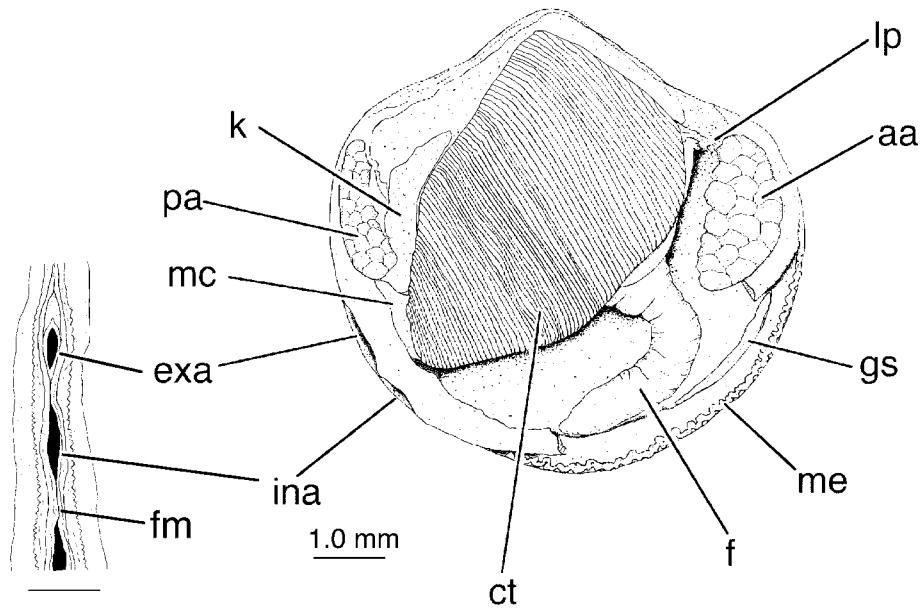


Figure 20. *Chavania striata* (Tokunaga) from the Houtman Abrolhos Is, Western Australia, showing general anatomy and detail of exhalant and inhalant apertures. Abbreviations: aa, anterior adductor muscle; ct, ctenidia; exa, exhalant aperture; f, foot; fm, fused mantle; gs, glandular strip; ina, inhalant aperture; k, kidney; lp, labial palp; mc, mantle connection; me, mantle edge; pa, posterior adductor muscle.

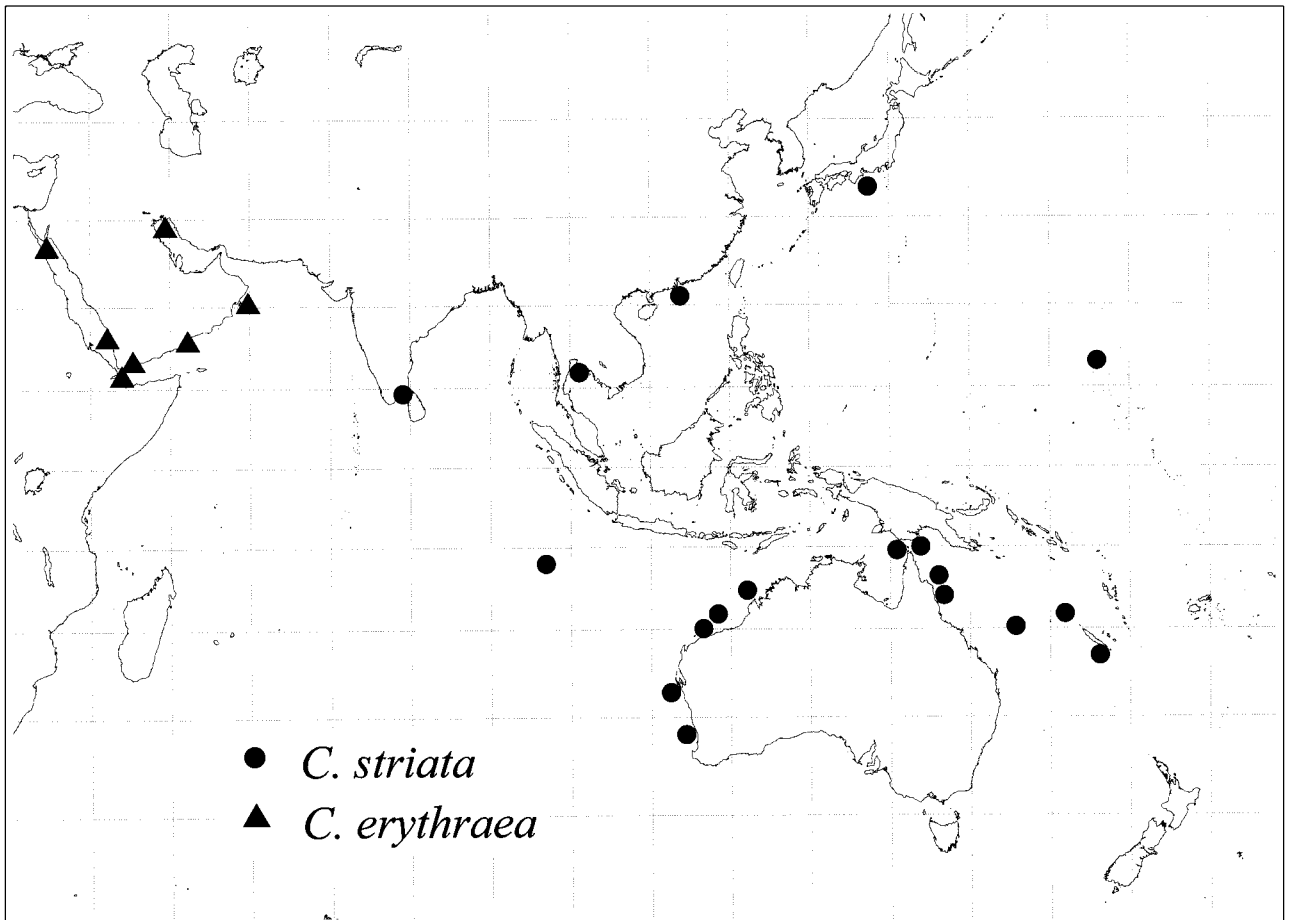


Figure 21. Map showing distribution of *Chavania striata* (Tokunaga) and *C. erythraea* (Issel).

Where larger samples from single localities (for example a few sites from northern Queensland) are available, *Chavania striata* shows considerable shape variation and this is likely typical of the species throughout its range. However, most of our records listed below comprise only single or few dead shells.

This is the species referred to by Hickman & Barnes (1999, fig. 1a–e) as *Wallucina* aff. *jacksoniensis* (Smith) from the Late Quaternary Herschell Limestone of Rottneest I., Western Australia. They suggest that the species is now extinct in the area but shells are frequent in offshore sediment samples and live animals have been dredged around the Abrolhos Is.

Material examined. **India:** Tuticorin (BMNH). **Sri Lanka:** Mannar (BMNH). **Thailand:** Ko Samui, Gulf of Thailand (DC). **Australia:** WESTERN AUSTRALIA: Cockburn Sound, 20 m (AMS); Rottneest I., 18 m (BMNH); Fremantle, 25 m (NMV); Houtman Abrolhos Is, (many lots) (WAM); North West shelf 230 m, 14°50'S 121°49.4'E (AMS); North West Shelf, north of Port Hedland, 150 m, 18°25'S 119°0'E (AMS); North West Shelf, NNW of Dampier, 110 m, 19°29'S 116°E (AMS); North West Shelf, N of Cape Leveque, 194 m, 14°12'S 123°2'E (AMS). QUEENSLAND: Murray I., Torres Strait (AMS); Albany Passage, Cape York Peninsula (AMS); Palfrey I., Lizard I. (AMS); Bird Islet, Lizard I. (AMS); Rocky Point, Lizard I. (AMS); SE of Lizard I., 35 m (AMS); Carter Reef (AMS); Low Isles (AMS). **New Caledonia:** Ile St Marie, Nouméa (AMS); Atoll de Surprise 18°25'S 163°11'E (MNHN); Atoll de Huon 18°07'S 162°55'E (MNHN); Plateau de Chesterfield, 56 and 51 m, 19°25'S 158°22'E (MNHN); Secteur de Belep 19°43'S 163°57'E (MNHN); Isle des Pins, 31 m (MNHN). **Marshall Islands:** Kwajalein Atoll (MNHN). **China:** Mirs Bay, Hong Kong (AMS). **Japan:** Sea of Japan, 34°13'N 136°13'E (BMNH); Bungo Strait, between Shikoku & Kyushu, dredged (BMNH).

Literature record. **Cocos Keeling Atoll:** lagoon as ?*Wallucina* sp. Maes, 1967: 59, pl. 22D.

Funafutia n.gen.

Type species. *Lucina levukana* Smith, 1885 (= *L. oblonga* Hedley, 1899).

Diagnosis. Shells small, anteriorly extended, ornament of prominent commarginal lamellae with finely striated interspaces. Umbones prominent, lunule lanceolate, impressed. Ligament internal, short, triangular. Two cardinal teeth in left valve, one in right valve; anterior and posterior lateral teeth prominent in both valves. Shell margin finely crenulate.

Comparison with other genera. This genus is distinguished from others with an internal ligament by the anteriorly extended shell, the prominent, rounded commarginal lamellae and the strong anterior and posterior lateral teeth in both valves.

Etymology. Named for Funafuti Atoll, the type locality of *L. oblonga*.

Funafutia levukana (Smith, 1885)

Figs. 22a–d, 23

Lucina levukana Smith, 1885: 181, pl. 13, fig. 6. Holotype: BMNH 1887.2.9.2778 (type with extreme Byne's disease). Type locality: Levuka, Fiji.

Lucina (*Codakia*) *oblonga* Hedley, 1899: 497, fig. 51. Two syntypes: AMS C6157 2 right valves, H 3.1, L 4.5. Type locality: Lagoon beach, Funafuti Atoll, Tuvalu. (non *Lucina oblonga* Philippi, 1836).

Lucina funafutica Finlay, 1927: 529. Replacement name for *L. oblonga* Hedley.

Description. Small, H to 6, longer than high (H/L 0.89) and extended anteriorly. Sculpture of prominent, rounded commarginal lamellae that are irregularly spaced. Within the relatively wide interspaces, fine radial striations (Fig. 22a,b) may be more prominent in eroded specimens. Lunule long, lanceolate and impressed; umbonal area prominent. Right valve with single large cardinal tooth and prominent posterior and anterior lateral teeth. Left valve with two cardinal teeth and prominent sockets for the lateral teeth of the right valve. Ligament internal, with short, narrow, triangular resilifer. Anterior adductor scar short and rounded and barely detached from the pallial line, posterior scar ovate. Pallial line continuous. Shell margin outside the pallial line finely and evenly crenulate. Colour white or pink.

Habitat. Shallow water to 40 m.

Distribution. Indian Ocean and West Pacific, ?Japan (in Higo *et al.*, 1999 as *Anodontia oblonga*). A species of offshore island habitats, not found on continental margins (Fig. 23).

Remarks. The two syntypes of *Lucina levukana* Smith, 1885 have entirely decayed from Byne's disease and the figures do not illustrate the distinctive hinge teeth or sculpture. However, in the detailed description Smith highlights the extreme anterior extension of the shell, the prominent commarginal sculpture, the deep internal ligament and the strong cardinal and lateral teeth. These are all features shared by *Lucina oblonga* Hedley.

Material examined. **Seychelles:** Mahé, off Anse aux Pins, 20 m (BMNH); Aldabra Atoll, Main Channel (BMNH). **Madagascar:** Tuléar (MNHN). **Reunion:** 310 m, 21°22'S 55°47'E (MNHN). **Mauritius:** Riambel Lagoon; off Trou aux Biches; Pointe Radeau (NMSA). **Australia:** QUEENSLAND: Murray I., Torres Strait, 9–15 m (AMS); Friday I., Torres Strait (AMS); Euston Reef, 21 m, 16°40'S 146°13'E (AMS); Lindeman I., 37 m (AMS); North West I., Capricorn Group (AMS); Masthead I., Capricorn Group 31–37 m (AMS); Lady Elliott I. (AMS); Lady Musgrave I., Bunker Group (AMS). **New Caledonia:** Loyalty Is, Lifou (AMS); Touho, Grand Récif (MNHN); Passe de Koumac, 20°39'S 164°14'E; Chesterfield Bank (MNHN). **Kiribati:** Aباing lagoon (AMS). **Tuvalu:** Funafuti Lagoon Beach, Funafuti Atoll (AMS). **Wallis Islands:** 13°19'S 176°17'W (MNHN).

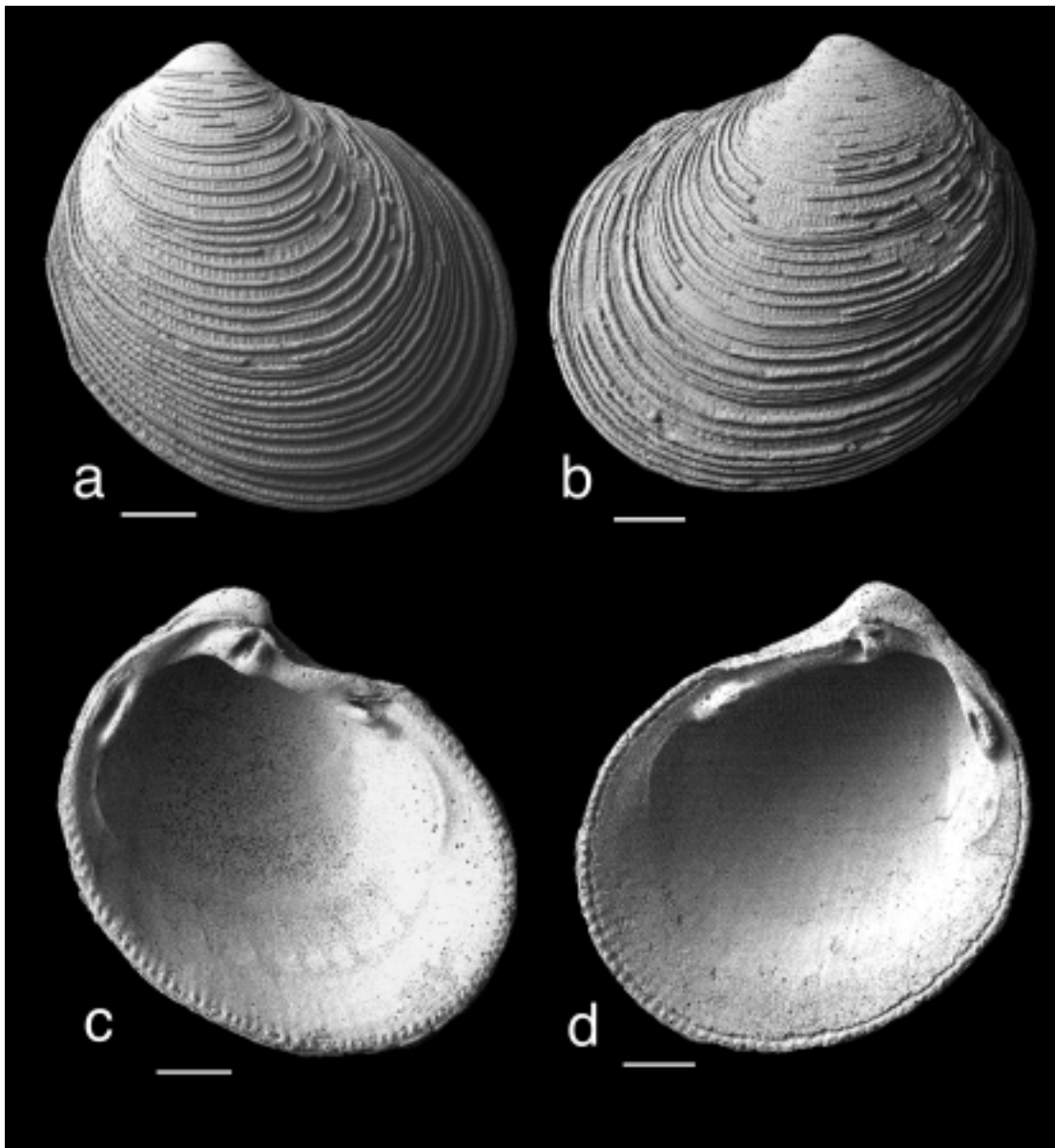


Figure 22. *Funafutia levukana* (Smith). a–d, Masthead I., Capricorn Group, Queensland, 23°32'S 151°45'E AMS C019420, 31–37 m, Hedley collection; a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, interior of right valve. Scale bars = 0.5 mm.

Genus *Wallucina* Iredale, 1930

Wallucina Iredale, 1930: 390.

Type species. *Wallucina jacksoniensis* Smith, 1885 (= *W. assimilis* Angas, 1867).

Diagnosis. Shells small, subcircular in outline. Moderately inflated, relatively thin shelled. Sculpture of fine closely spaced commarginal lamellae, sometimes slightly raised to posterior, fine radial striations sometimes present. Hinge plate narrow. Right valve with single cardinal tooth and posterior lateral tooth, anterior lateral absent or very small. Left valve with two cardinal teeth and a posterior lateral tooth. Ligament internal, set in elongate, oblique resilifer. Anterior adductor muscle scar elongate, detached from pallial line for about 1/2 to 1/3 of length. Pallial line discontinuous. Inner shell margin finely crenulate.

Distribution. Central Indo-West Pacific and southern and western Australia.

Comparison with other genera. *Wallucina* differs from *Pillucina* in absence of radial ribs and from *Chavania* by the much thinner shell, narrow hinge and absence of anastomosing commarginal lamellae.

Wallucina assimilis (Angas, 1867)

Figs. 24c–g, 25, 26

Loripes assimilis Angas, 1867: 910, pl. 44, fig. 8. Two syntypes: BMNH 1870.10.26.34; H 11.6, L 11.8, T 3.8; H 11.0, L 11.1, T 4.8. Type locality: as cited in original description, New South Wales and Hobson's Bay, Port Phillip, Victoria. Seen.

Lucina jacksoniensis Smith, 1885: 185, pl. 13, figs. 11 & 11b. Two syntypes: BMNH 1887.2.9.2784–5, (2 complete shells); larger shell H 9.3, L 9.2, T 3.2. Type locality: Port Jackson,

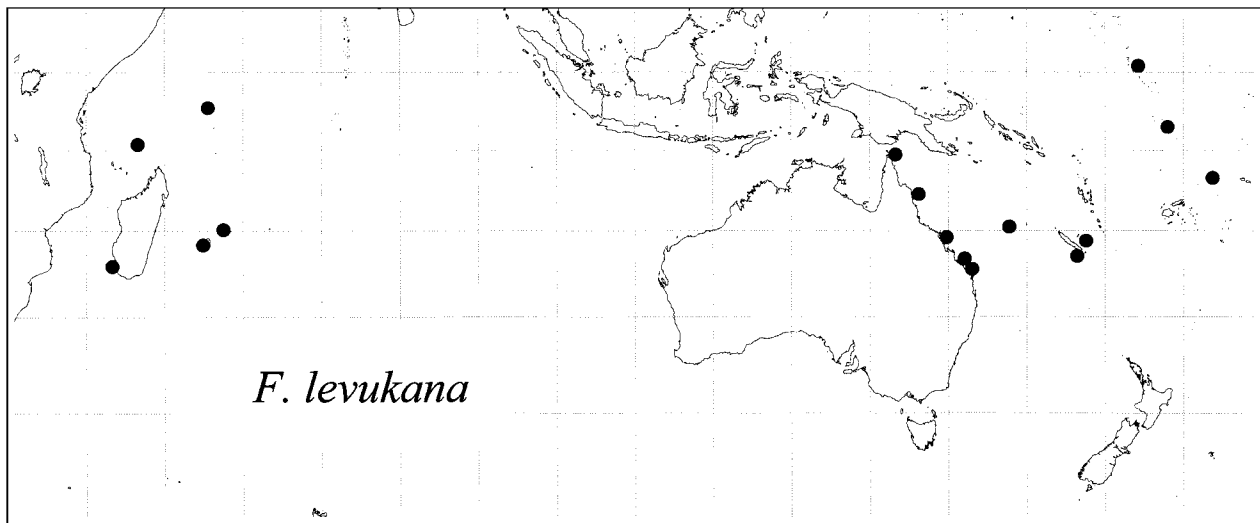


Figure 23. Map showing distribution of *Funafutia levukana* (Smith).

NSW, 6–15 fathoms. Seen.

Wallucina jacksoniensis (Smith).—Iredale, 1930: 390.

Wallucina icterica (Reeve, 1850).—Cotton & Godfrey, 1938: 203, fig. 214. *Lucina icterica* Reeve, 1850 is a *Semele* (BMNH 1998170—see Ludbrook, 1955: 51).

Description. Shells small (H to 15), subcircular, anteriorly extended, not inflated and rather thin-shelled. Sculpture consists of extremely fine, low concentric growth increments with variable, faint, fine radial folds between the commarginal lamellae. Microscopically, shells often have fine radial striations which have been described as external sculpture but are in fact the internal shell microstructure of the outer radial composite prismatic layer. Lunule narrow, lanceolate to heart-shaped, not impressed (in type) and slightly asymmetrical. Anterior dorsal area demarcated by narrow, often indistinct sulcus. Hinge plate shallow, right valve with single prominent cardinal tooth and two smaller posterior laterals, anterior lateral tooth tiny to indistinct. Left valve with two cardinals, of which anterior cardinal is trigonal and pronounced, posterior lateral small and anterior lateral indistinct. Ligament internal, short and deeply impressed into each valve, resilifer oblique. Anterior adductor muscle scar short, rounded and detached for about 1/2 of its length. Pallial line usually discontinuous with pallial blood vessel impression often faint. Shell margin finely crenulate. Typically interior of shell chalky with narrow radial ridges inside pallial line, whilst outside pallial line shell margin is often glossy with fine radial striations. Shell white.

Anatomy. The anatomy was studied from dissections and SEM of critical point dried specimens from Jervis Bay, New South Wales (BMNH). In general anatomical features (Fig. 25), *W. assimilis* is similar in most respects to *Pillucina vietnamica* including the posterior mantle connection to the ctenidia. The fused mantle ventral to the inhalant aperture is relatively longer and the inhalant aperture lacks the papillae of *P. vietnamica* (Fig. 15b). Sections of the lateral zone of the gill filaments confirm the presence of abundant rod-shaped bacteria (about 3–5 µm long and 1–1.5 µm wide) contained in bacteriocytes (Fig. 14e).

Remarks. Samples of *W. assimilis* from Western Australia, South Australia and NSW all show considerable variation in shell outline, lunule depth and thickness of the hinge and size of cardinal teeth. The shells are often rather irregularly shaped with a crumpled appearance. Because of the high variation in shell morphology we can see no reason to support Cotton & Godfrey's (1938) separation of the southern and western Australian shells as a separate species *W. icterica*.

Distribution. From northern NSW to southern Western Australia as far north as Ningaloo (Fig. 26). Barnes & Hickman (1999) highlight the association of this species with seagrass beds around Rottneest I., Western Australia where they recorded densities of up to 1048 m⁻² amongst *Posidonia* and *Amphibolis*. We have also collected living *W. assimilis* from shallow seagrass beds at various localities along the New South Wales coast.

Material examined. **Australia:** NEW SOUTH WALES: Port Stephens (AMS); Pittwater (BMNH); Middle Harbour, Sydney (NMV); Narrabeen lagoon (BMNH); Gunnamatta Bay, Port Hacking (AMS); Jervis Bay (BMNH); Gerringong (AMS); Kiama (AMS); Sussex Inlet (AMS); Lake Conjola (AMS); Twofold Bay (AMS); Bendalong, Ulladulla (AMS); Narooma (NMV); Merimbula (NMV); Pambula Lake (AMS). **VICTORIA:** Mallacoota (NMV); Point Nepean (NMV); Cable I., Bass Strait (NMV); Flinders (NMV); Corio (NMV); Lakes Entrance, 20 fathoms (NMV); Frankston (NMV); Port Albert (NMV); off Wilsons Promontory (NMV); Point Cook, Port Philip Bay (NMV); Point Leo, Mornington Peninsula (NMV). **TASMANIA:** Adelaide Bay, Flinders I. (AMS); Logan's Lagoon, Flinders I. (AMS); Tinderbox, Derwent Estuary (AMS); Randalls Bay, Houn Estuary (NMV); Eaglehawk Bay (AMS); Long Bay (AMS); Cremorne, Frederick Henry Bay (AMS); Pittwater, Cambridge (AMS). **SOUTH AUSTRALIA:** Normanville, St Vincents Gulf (AMS); Outer Harbour, Adelaide (SAM); St Vincents Gulf (SAM); Edithburg, 9 fathoms (SAM); Point Germein (SAM); Boston I. 10 fathoms (NMV); St Francis I. (SAM). **WESTERN AUSTRALIA:** Kalgan Bridge (AMS); Two Peoples Bay, Albany (AMS); E of Hood Point, 79 m, 34°21'S 121°16'E (AMS); King George Sound, Albany (SAM); Windy Harbour (AMS); Nornalup inlet (AMS); Cowaramup (AMS); Eagle Bay, W of Dunsborough (AMS); Yallingup (SAM); Bunbury (SAM); Hopetown beach (SAM); Swan River estuary (AMS); Cockburn Sound (AMS); Rottneest I.

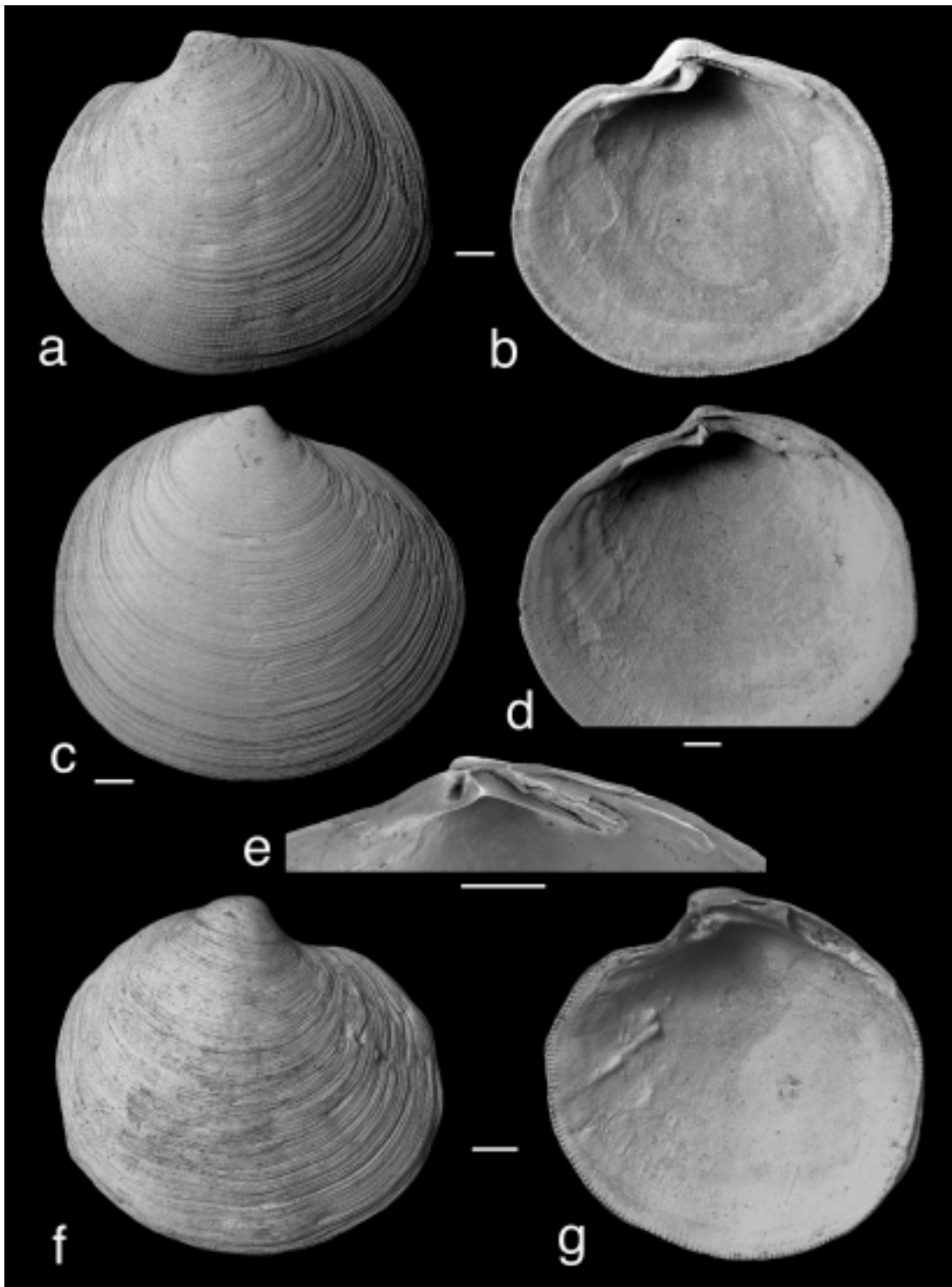


Figure 24. *Wallucina fijiensis* (Smith) and *W. assimilis* (Angas). a,b, *Wallucina fijiensis* Eclipse I., Claremont Group, Queensland, 13°29'S 143°43'E, AMS 007256; a, exterior of left valve; b, interior of right valve. c,d, *W. assimilis* Narrawallee lagoon, Ulladulla (BMNH); c, exterior of right valve; d, interior of right valve. e, hinge of right valve of *W. assimilis* Pittwater, New South Wales (BMNH). f,g, *W. assimilis* Robe, South Australia (SAM D15648); f, exterior of right valve; g, interior of right valve. Scale bars = 1.0 mm.

(SAM); Cervantes (AMS); Port Denison near Dongara (AMS); Geraldton (SAM); Horrocks (AMS); West Wallabi I., Houtman Abrolhos (AMS); Kalbarri (AMS); Dirk Hartog I. (AMS); Point Peron (AMS); Ningaloo Reef (AMS).

***Wallucina fijiensis* (Smith, 1885)**

Figs. 24a,b, 26

Lucina (*Codakia*) *fijiensis* Smith, 1885: 184, pl. 13, fig. 9.
Holotype: single valve with severe Byne's disease BMNH 1887.2.9. Type locality: off Levuka, Fiji, 12 fathoms. Seen.

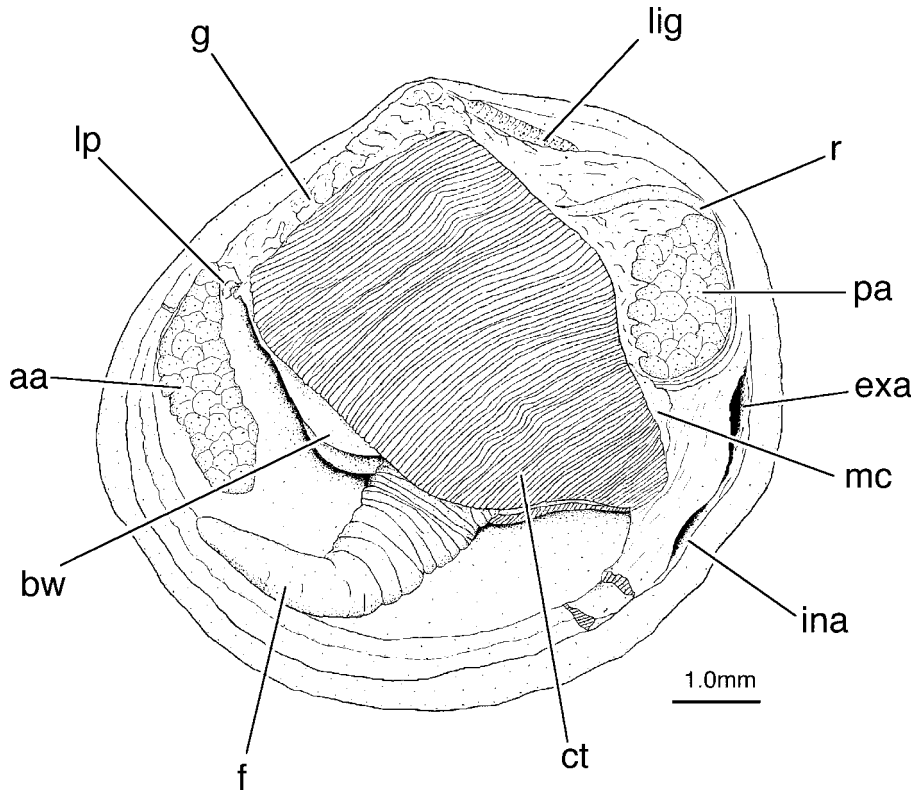


Figure 25. *Wallucina assimilis* (Angas) from Jervis Bay, NSW, showing general anatomy with the gill intact. Abbreviations: aa, anterior adductor muscle; bw, body wall; ct, ctenidia; exa, exhalant aperture; f, foot; g, gonad; ina, inhalant aperture; lig, ligament; lp, labial palp; mc, mantle connection to gill; pa, posterior adductor muscle; r, rectum.

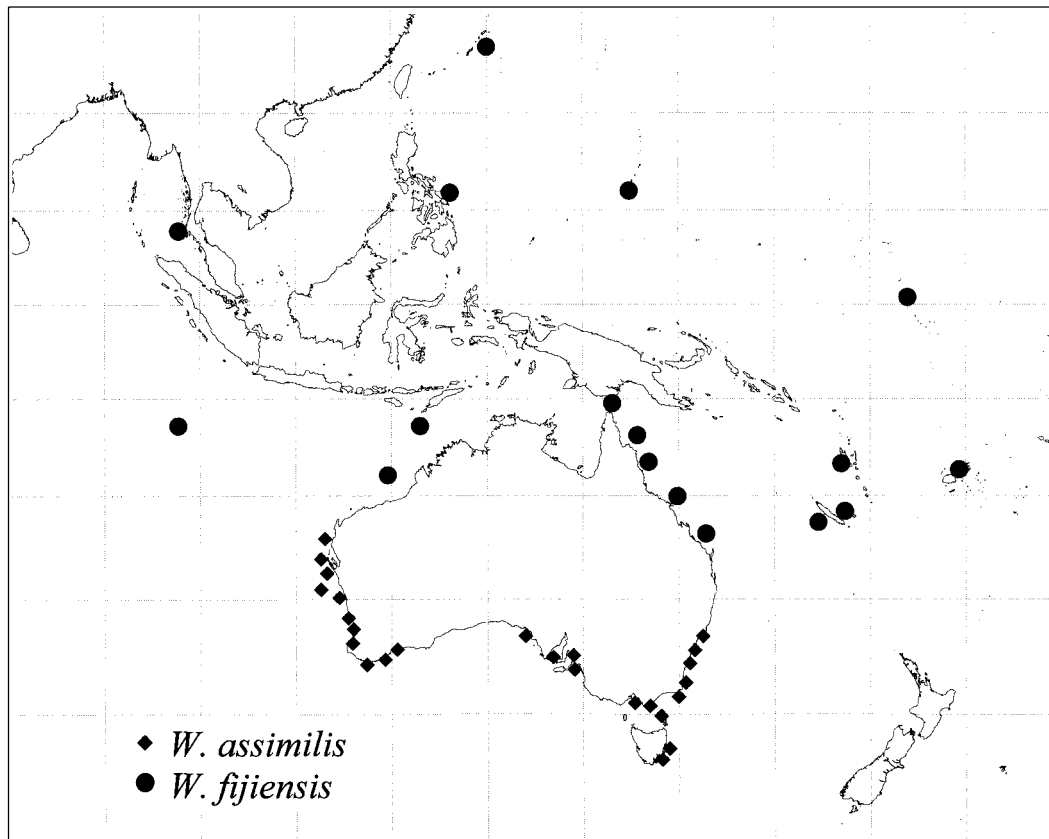


Figure 26. Map showing distribution of *Wallucina fijiensis* (Smith) and *W. assimilis* (Angas).

Lucina (?*Loripes*) *gordoni* Smith, 1885: 186, pl. 13, fig. 12. Holotype: BMNH 1887.2.9.2786 single valve (with Byne's disease). Type locality: off Levuka, Fiji, 12 fathoms. Seen. *Loripes haddoni* Melville & Standen, 1899: 200, fig. 12. Holotype: BMNH 1899.2.23.12; H 12.6, L 13.1, T 13.5. Type locality: Warrior I., Torres Strait, Australia. Seen. *Wallucina gordoni* (Smith).—Maes, 1967: 159, pl. 22, fig. e.

Description. Shell small, thin, H to 15, circular to subcircular in outline; posterior shell margin slightly truncate. Sculpture of extremely fine, low concentric growth increments with variable, faint, fine, radial striae between commarginal lamellae. Commarginal lamellae are slightly broader and more elevated near dorsal margins. Lunule narrow, lanceolate to heart-shaped and slightly excavated. Anterior dorsal area often with irregular folds. Hinge plate narrow; right valve with prominent cardinal tooth, two small posterior lateral teeth and tiny anterior lateral tooth. Left valve with two cardinals, anterior cardinal is trigonal and larger, posterior laterals are low and anterior lateral absent. Ligament internal, deeply impressed into each valve. Anterior adductor muscle scar short, broad and detached from the pallial line for about 1/2 of length. Pallial line discontinuous and pallial blood vessel impression faint. Inner surface of shell inside pallial line with indistinct narrow, radial ridges, shell outside the pallial line glossy with fine radial striations. Shell margin finely denticulate. Colour white.

Distribution. Northern Queensland, Great Barrier Reef islands, western Pacific, tropical southeast Asia, shoals and islands on the north Western Australian shelf (Fig. 26).

Remarks. This species is similar to *W. assimilis*. The shells are larger, with a more quadrate posterior margin and the commarginal lamellae often elevated on the posterodorsal margin. The lunule is deeper and shorter than in *W. assimilis* and the ligament is longer. The two species have non-overlapping ranges; *W. assimilis* has temperate southerly distribution ranging from NSW to Ningaloo in Western Australia whilst *W. fijiensis* is a tropical species (Fig. 26). The specimens from Cocos Keeling are larger, H to 17.5, and have a yellow interior but in other respects are closely similar.

Material examined. **Cocos Keeling Islands:** Pulo Bras, 2 m (BMNH); Prison I., Cocos Keeling (WAM); reef slope off North West I. (WAM). **Australia:** WESTERN AUSTRALIA: Bedwell I., Rowley Shoals (WAM); Eastern I., Ashmore Reef (WAM). QUEENSLAND: Yorke I. (AMS); Bramble Cay (AMS); Friday I., Torres Strait (AMS); Cairncroft I., Torres Strait (BMNH); Thursday I. (AMS); Murray I. (AMS); Hope I. (AMS); Lizard I. (AMS); Two Isles, south of Cape Flattery (AMS); Eagle I., N of Cooktown, 5.5 m (AMS); Low Isles (AMS); Wonga Beach (BMNH); Opal Reef, N of Cairns (AMS); Green Is (AMS); Ellison Reef off Kurrimine (AMS); Palm I. (AMS); Eclipse I. (AMS); Hayman I. (AMS); Michaelmas Cay (AMS); Lady Elliott I. (AMS); Facing I., Port Curtis (AMS). **Thailand:** Ban Thap Lamu, Thai Muang, Phangna province (BMNH). **Philippines:** Magellan Bay, west side of Punta Engaño, Mactan I., Cebu (BMNH). **New Caledonia:** Touho, Grand Récif Mengalia, 20°45'S 165°16'E (MNHN). **New Hebrides:** (MNHN). **Kiribati:** Tarawa lagoon, Kiribati 1°25'N 173°00'E (AMS); Kingsmill I. (BMNH); Teirio Abaiang Atoll (AMS). **Guam:** East Agana Bay (AMS). **Japan:** Edatekujima I., Anami Is, Japan. (BMNH).

Species excluded from *Pillucina* and *Wallucina*

Pillucina yamakawai (Yokoyama, 1920)

Lucina yamakawai Yokoyama, 1920: 135, pl. 10, fig. 9. Type locality: Plio-Pleistocene fossil, Shimo-Miyata, Yokosuka City, Honshu. *Pillucina* (*Sydlorina*) *yamakawai* (Yokoyama).—Kuroda, Habe & Oyama, 1971: 393, pl. 118, fig. 16; Habe, 1977: 126, pl. 24, figs. 3 & 4.

This species probably belongs to the genus *Parvilucina* and can be easily distinguished from *Pillucina* by the absence of an internal ligament.

Wallucina izuensis Okutani & Matsukuma, 1982

Wallucina izuensis Okutani & Matsukuma, 1982: 174–175, pl. 10, figs. 7 & 8, text fig. 2.

This species from Japan has an external ligament and cannot be included in our concept of the genus *Wallucina*.

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References

- Adams, H., 1871. Descriptions of twenty-six new species of shells collected by Robert McAndrew, Esq., in the Red Sea. *Proceedings of the Zoological Society of London* 1870: 788–793.
- Allen, J.A., 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philosophical Transactions of the Royal Society of London B* 241: 421–484.
- Allen, J.A., 1960. The ligament of the Lucinacea. *Quarterly Journal of Microscopical Science* 101: 25–37.
- Angas, G.F., 1867. Descriptions of thirty-two new species of marine shells from the coast of New South Wales. *Proceedings of the Zoological Society of London* 1867: 110–117.
- Barnes, P.A.G., & C.S. Hickman, 1999. Lucinid bivalves and marine angiosperms: a search for causal relationships. In *The Seagrass Flora and Fauna of Rottnest Island, Western Australia*, ed. D.I. Walker & F.E. Wells, pp. 215–238. Perth: Western Australian Museum.
- Bouchet, P., & F. Danrigal, 1982. Napoleon's Egyptian campaign (1798–1801) and the Savigny collection of shells. *Nautilus* 96: 9–24.
- Bretsky, S.S., 1970. Phenetic and phylogenetic classifications of the Lucinidae (Mollusca, Bivalvia). *Bulletin of the Geological Institute of the University of Upsala*, new series 2: 5–23.
- Bretsky, S.S., 1976. Evolution and classification of the Lucinidae (Mollusca; Bivalvia). *Palaeontographica Americana* 8(50): 219–337.
- Chavan, A., 1937–1938. Essai critique de classification des lucines. *Journal de Conchyliologie* 81: 237–281; 82: 215–241.
- Chavan, A., 1969. Superfamily Lucinacea Fleming, 1828. In *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia*, vol.

- 2, ed. R.C. Moore, pp. N491–N518. Boulder, Colorado: Geological Society of America and University of Kansas.
- Cotton, B.C., & F.K. Godfrey, 1938. *The Molluscs of South Australia. Part I. The Pelecypoda*. Adelaide: South Australian Branch of the British Science Guild.
- Dall, W.H., P. Bartsch & H.A. Rehder, 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. *Bulletin of the Bernice P. Bishop Museum* 153: 1–233.
- Dell, R.K., 1964. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. *Discovery Reports* 33: 93–250.
- Distel, D.L., 1998. Evolution of chemoautotrophic endosymbioses in bivalves. *Bioscience* 48: 277–286.
- Dunker, W., 1860. Neue japanische Mollusken. *Malakozoologische Blätter* 8: 150–154.
- Dunker, W., 1861. *Mollusca Japonica Descripta et Tabulis Tribus Iconum*. Stuttgart, 1–36.
- Dunker, W., 1882. Index Molluscorum Maris Japonici. *Novitates Conchologicae, Supplement* 7: 1–301.
- Finlay, H.J., 1927. New specific names for Austral Mollusca. *Transactions of the New Zealand Institute* 57: 488–533.
- Glover, E.A., & J.D. Taylor, 1997. New species and records of *Rastafaria* and *Megaxinus* from the western Indian Ocean and Red Sea, with a reappraisal of *Megaxinus*. *Journal of Conchology* 36: 1–18.
- Gould, A., 1861. Descriptions of shells collected in the North Pacific Exploring Expedition under Captains Ringgold and Rodgers. *Proceedings of the Boston Society of Natural History* 8: 33–40.
- Habe, T., 1960. Eleven new bivalves from Tanabe Bay, Wakayama Pref., Japan. *Publications of the Seto Marine Biological Laboratory* 8: 281–288.
- Habe, T., 1977. *Systematics of Mollusca in Japan, Bivalvia and Scaphopoda*. Tokyo: Hokuryukan.
- Hedley, C., 1899. The Mollusca of Funafuti. Part II. Pelecypoda and Brachiopoda. *Memoirs of the Australian Museum* 3: 491–510.
- Hedley, C., 1914. Studies on Australian Mollusca. Part XII. *Proceedings of the Linnean Society of New South Wales* 39: 695–755.
- Hickman, C.S., & P.A.G. Barnes, 1999. Fossil lucinid bivalves of Rottneest Island: anomalous Late Quaternary geographic distributions. In *The Seagrass Flora and Fauna of Rottneest Island, Western Australia*, ed. D.I. Walker & F.E. Wells, pp. 239–245. Perth: Western Australian Museum.
- Higo, S., P. Callomon & Y. Goto, 1999. *Catalogue and bibliography of the marine shell-bearing Mollusca of Japan*. Osaka: Elle Scientific Publications.
- Iredale, T., 1930. More notes on the marine Mollusca of New South Wales. *Records of the Australian Museum* 17: 384–407.
- Issel, A., 1869. *Malacologia del Mare Rosso, recherche zoologique e paleontologique*. Pisa, Italy.
- Johnson, R., 1964. The Recent Mollusca of Augustus Addison Gould. *Bulletin of the United States National Museum* 239: 1–182.
- Kay, E.A., 1979. Hawaiian marine shells. *Bernice P. Bishop Museum Special Publication* 64 (4): 1–652.
- Kuroda, T., T. Habe & K. Oyama, 1971. *The Seashells of Sagami Bay*. Tokyo, Maruzen.
- Lamprell, K., & J. Healy, 1998. *Bivalves of Australia* Volume 2. Leiden: Backhuys Publishers.
- Lamprell, K., & T. Whitehead, 1992. *Bivalves of Australia*, Bathurst, Australia: Crawford House Press.
- Lamy, E., 1916. Les Lucines et les Diplodontes de la Mer Rouge (d'après les matériaux recueillis par M. le Dr Jousseume). *Bulletin du Muséum d'Histoire naturelle* 22: 145–155, 183–190.
- Ludbrook, N.H., 1955. The molluscan fauna of the Pliocene strata underlying the Adelaide plains. *Transactions of the Royal Society of South Australia* 78: 18–87.
- Maes, V.O., 1967. The littoral marine mollusks of Cocos Keeling Islands (Indian Ocean). *Proceedings of the Academy of Natural Sciences of Philadelphia* 119: 93–217.
- Melville, J.C., 1899. Notes on Mollusca from the Arabian Sea, Persian Gulf, and Gulf of Oman, mostly dredged by Mr. F.W. Townsend, with descriptions of twenty-seven species. *Annals and Magazine of Natural History*, series 7, 4: 81–101.
- Melville, J.C., 1918. Descriptions of thirty-four species of marine Mollusca from the Persian Gulf, Gulf of Oman and Arabian Sea, collected by Mr. F.W. Townsend. *Annals and Magazine of Natural History* series 9, 1: 137–158.
- Melville, J.C., & R. Standen, 1899. Report on the marine Mollusca obtained during the first expedition of Professor A.C. Haddon to the Torres Strait in 1888–89. *Journal of the Linnean Society, Zoology* 27: 150–206.
- Okutani, T., & A. Matsukuma, 1982. Some interesting molluscs dredged from the shelf around the southern coast of the Izu peninsula, Honshu, with descriptions of two new species. *Memoirs of the National Science Museum* 15: 163–180.
- Oliver, P.G., 1986. A new lucinid bivalve from the Niger Delta and an appraisal of the *Loripes* group (Bivalvia, Lucinacea). *Basteria* 50: 47–64.
- Oliver, P.G., 1992. *Bivalved seashells of the Red Sea*. Wiesbaden & Cardiff, Verlag Christa Hemmen & National Museum of Wales.
- Oliver, P.G., 1995. Bivalvia. In *Seashells of Eastern Arabia* ed. S.P. Dance. Dubai, Motivate Publishing.
- Pilsbry, H.A., 1921. Marine Mollusks of Hawaii—XIV, XV. *Proceedings of the Academy of Natural Sciences of Philadelphia* 72: 360–382.
- Reeve, L.A., 1850. Monograph of the genus *Lucina*. *Conchologica Iconica* vol 6. London: Reeve, Benham & Reeve.
- Reid, R.G.B., 1990. Evolutionary implications of sulphide-oxidising symbioses in bivalves. In *The Bivalvia—Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*, ed. B. Morton, pp. 127–140. Hong Kong: Hong Kong University Press.
- Rodionov, I.A., & V.V. Yushin, 1991. Prokaryotic symbionts in gill cells of the bivalve mollusc *Pillucina pisidium*. *Biologia Morya* N 1: 39–46 (in Russian).
- Smith, E.A., 1885. Report on the Lamellibranchiata collected by H.M.S. Challenger during the years 1873–76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76*. 13: 1–341.
- Taylor, J.D., & E.A. Glover, 1997a. A chemosymbiotic lucinid bivalve (Bivalvia: Lucinoidea) with periostracal pipes: functional morphology and description of a new genus and species. In *The Marine Flora and Fauna of the Houtman Abrolhos, Western Australia*, ed. F.E. Wells, pp. 335–361. Perth: Western Australian Museum.
- Taylor, J.D., & E.A. Glover, 1997b. The lucinid bivalve genus *Cardiolucina* (Mollusca, Bivalvia, Lucinidae): systematics, anatomy and relationships. *Bulletin of the Natural History Museum, London (Zoology)* 63: 93–122.
- Taylor, J.D., & E.A. Glover, 2000. Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In *The Evolutionary Biology of the Bivalvia*, ed. E.M. Harper, J.D. Taylor & J.A. Crame, *Geological Society Special Publication* 177: 207–225.
- Thiele, J., 1930. Gastropoda und Bivalvia. In *Die Fauna Sudwestaustraliens*, ed. W. Michaelson & R. Hartmeyer, pp. 561–596. Jena: Gustav Fischer.
- Tokunaga, S., 1906. Fossils from the environs of Tokyo. *Journal of the College of Science, Imperial University, Tokyo* 21: 1–96.
- Viader, R., 1951. New or unrecorded shells from Mauritius and its dependencies. *Mauritius Institute Bulletin* 3: 127–153.
- Yokoyama, M., 1920. Fossils from the Miura Peninsula and its immediate north. *Journal of the College of Science, Imperial University, Tokyo* 39: 1–198.
- Zorina, I.P., 1978. New species of bivalve molluscs (Bivalvia) of the Gulf of Tonkin (South China Sea). *Trudy Zoological Institut, Leningrad* 61: 193–203 (in Russian).

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