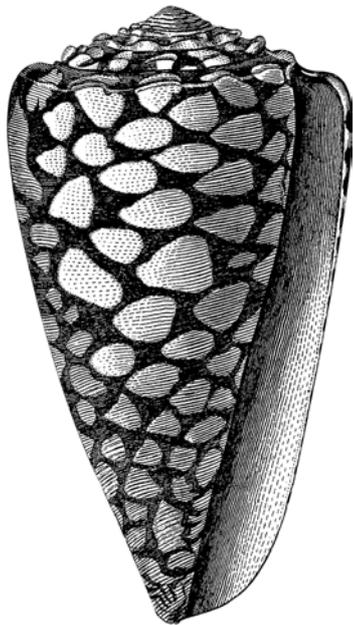


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A review of the Indo-Pacific *Lioconcha* Mörch (Mollusca : Bivalvia : Veneridae), including a description of four new species from Queensland, New Caledonia and the Philippine Islands

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Abstract

The Indo-West Pacific venerid genus *Lioconcha* is reviewed, with special emphasis on species occurring in the Australian and New Caledonian regions. Nineteen species, including four new species, are recognised: *Lioconcha castrensis* (Linnaeus, 1758), *L. macaulayi* n. sp., *L. hieroglyphica* (Conrad, 1837), *L. tigrina* (Lamarck, 1818), *L. fastigiata* (Sowerby, 1851), *L. annettae* Lamprell & Whitehead, 1990, *L. pseudofastigiata* n. sp., *L. ornata* (Dillwyn, 1817), *L. berthaulti* n. sp., *L. sowerbyi* (Deshayes, 1853), *L. polita* (Röding, 1798), *L. schioettei* n. sp., *L. trimaculata* (Lamarck, 1818), *L. philippinarum* (Hanley, 1844), *L. dautzenbergi* (Prashad, 1932), *L. melhartae* Lamprell & Stanistic, 1996, *L. caledonensis* Harte & Lamprell, 1999, *L. richerdeforgesi* Lamprell & Stanistic, 1996 and *L. gordonii* (E. A. Smith, 1885). Colour variation within species ranges from very high (*L. ornata*, *L. castrensis*) to very low (*L. melhartae*, *L. caledonensis*, *L. philippinarum*). All species are figured, diagnosed and discussed and a key is presented. Types of the following taxa are also figured: neotype of *Venus ornata* Dillwyn, 1817; holotypes of *Lioconcha berthaulti* n. sp.; *L. macaulayi* n. sp.; *L. pseudofastigiata* n. sp.; *L. schioettei* n. sp.; *L. annettae* Lamprell & Whitehead, 1990; *Cytherea tigrina* Lamarck, 1818; *Hysteroconcha* (?*Lamellioconcha*) *dautzenbergi* Prashad, 1932 and *Cytherea sulcatina* Lamarck, 1818; lectotypes of *Cytherea hebraea* Sowerby, 1851 and *Circe sowerbyi* Deshayes, 1853. Lectotypes of *Cytherea hieroglyphica* Conrad and *C. fastigiata* Sowerby are based on original figures, in the absence of other undoubted type material. Subdivision of *Lioconcha* into two subgenera (*Lioconcha sensu stricto* and *Sulcilioconcha*), based solely on the presence or absence of concentric ridge sculpture, appears unwarranted.

Introduction

Species of the genus *Lioconcha* Mörch, 1853 are among the more difficult of the Veneridae to identify because of their sometimes wide variation in colour pattern and the vestigial nature of the pallial sinus, the latter structures widely used as a valuable species diagnostic elsewhere within the Veneridae. Species of *Lioconcha* are usually characterised by bright, sometimes intricate shell colour patterns and a smooth shell. Species are known from tropical and subtropical regions of the Indo-West Pacific, but have yet to be reported from the eastern Pacific or the Atlantic. They are infaunal, occurring in clean, muddy or coral sand, typically in sheltered shallow water habitats and, sometimes, in moderately deep water (>100 m; Lamprell and Stanistic 1996). *Lioconcha* shells are commonly collected either as beached specimens or in the vicinity of octopus dens, but living material can usually only be gathered by dredging or digging into the sediment.

Although *Lioconcha* from New Caledonia (Lamprell and Stanistic 1996) and South Africa, Mozambique and the Mascarene and Andaman Islands (Lamprell and Kilburn 1999a,b) have been previously discussed, the genus as a whole has not been reviewed in the modern literature. In the present study, we diagnose or describe all known species of extant *Lioconcha* and take the opportunity to briefly evaluate the relationships within the genus based on shell features and available distribution data. Particular emphasis is given to

recently collected material from Queensland, the Philippine Islands and New Caledonia held in the Australian Museum (Sydney, NSW, Australia), the Queensland Museum (Brisbane, Qld, Australia) and Muséum National d'Histoire Naturelle (Paris, France) in addition to specimens from private collections.

Methods

Shell dimensions

For all material examined, length is the greatest distance between the anterior and posterior extremities, height is measured vertically from the umbo to the ventral margin and total width (inflation or breadth) is the greatest distance between the external surfaces of the paired valves. Unless stated otherwise, measurements are given for the largest specimen examined by the authors.

Abbreviations

lv, left valve
 pv, paired valves
 rv, right valve.

Institutional abbreviations

AMNH, American Museum of Natural History
 AMS, Australian Museum, Sydney
 BMNH, Natural History Museum, London
 KL, Lamprell Collection
 MNHN, Muséum National d'Histoire Naturelle, Paris
 MNHG, Muséum d'Histoire Naturelle, Geneva
 NM, Natal Museum
 NMW, National Museum Wales
 NTM, Northern Territory Museum of Art and Sciences, Darwin
 QM, Queensland Museum, Brisbane
 ZMUC, Zoological Museum, University of Copenhagen, Denmark

Systematics

Superfamily **VENEROIDEA** Rafinesque, 1815

Family **VENERIDAE** Rafinesque, 1815

Subfamily **PITARIINAE** Stewart, 1930

Genus ***Lioconcha*** Mörch, 1853

Type species: *Venus castrensis* Linnaeus, 1758 (by subsequent designation of Stoliczka, 1870).

Diagnosis

Equivalve; resembling *Pitar* but with pallial sinus vestigial; valves rounded to elongate-trigonal, moderately to well inflated with strongly developed veneroid hinge dentition (prominent cardinal and lateral teeth); lunule flat to raised, heart or tear-drop shaped with margin strongly to weakly incised; periostracum usually thin, but sometimes thick peripherally in large adults; externally smooth to glossy with only sculpture consisting of concentric growth lines or striae, often supplemented by variously developed concentric ridges (especially at ventral and /or anterior and posterior margins); exterior coloration typically with zigzag or triangular patterning, sometimes supplemented or replaced by one

or more rays originating umbonally; internal colouration within genus variable, but usually species specific (usually white, but often with yellow, brown or purple patches).

***Lioconcha castrensis* (Linnaeus, 1758)**

(Figs 1A–K, 12A, 15A)

- Venus castrensis* Linnaeus, 1758: 687 (type locality: ‘in O. utriusque Indiae’ (= ‘both East and West Indies’); Chemnitz, 1782: figs 367–370; Chemnitz, 1788: fig. 1662.
Venus fulminea Röding, 1798: 181, no. 295 (based on Chemnitz, 1782: figs 369–370).
Venus lorenziana Dillwyn, 1817: 184 (based on Chemnitz, 1788: figs 1961–2).
Cytherea ornata Lamarck, 1818: 578 (refers Chemnitz, 1782: figs 369–370) (not Dillwyn, 1817); Lamy & Fischer-Piette, 1937: 273.
Cytherea castrensis (Linnaeus). Sowerby, 1851: sp. 103; Lamy & Fischer-Piette, 1937: 273.
Circe castrensis (Linnaeus). Reeve, 1863: pl. 7.
Lioconcha castrensis (Linnaeus). Römer, 1864–69 (1868): 44; Lamy, 1930: 135; Abbott & Dance, 1982: 359, fig. 6; Springsteen and Leobrera, 1986: 297, pl. 85 fig. 2.
Lioconcha lorenziana (Dillwyn). Habe, 1977: 259; Abbott & Dance, 1982: 359, fig. 9.
Lioconcha (Lioconcha) castrensis (Linnaeus). Habe, 1977: 258; Oliver, 1992: 185, pl. 40, fig. 1a,b; Lamprell & Whitehead, 1992: sp. 543; Lamprell & Stanisc, 1996: 30, fig. 1g,h; Lamprell & Kilburn, 1999b: 43, pl. 1, figs a,b.
Lioconcha tigrina. – Eisenberg, 1981: 151, fig. 3-3a (not of Lamarck, 1818).

Material examined

Spengler collection, Ostindien. Specimen figured by Chemnitz (1782: fig. 367; see fig. 1H,I herein), ZMUC; Spengler collection, South Seas. Specimen figured by Chemnitz (1782; specimen named *V. lorenziana* by Dillwyn (1817), fig. 1662; see Fig. 1J,K herein), ZMUC. **Australia: Queensland:** Little Trunk Reef, lagoon, AMNH.303314 (2pv); trawled 10 m off Palm Island, AMNH.303127 (2pv); dredged 8 m, Herald Prong Reef, no. 2, Swains Reef, AMNH. 303936 (1pv); on sand bar, Bowling Green Bay, Townsville, AMNH.303939 (1pv); Batt Reef, AMNH.303272 (1pv); trawled in lagoon Slasher’s Reef no. 1, AMNH.303035 (1pv); 1–2 m, in sandy coral, Opal Reef, north of Cairns, 16°15’S, 145°50’E, AMS C.356686 (3pv) (preserved); Swains Reef, AMS C.148179 (2lv, 1rv); Murray Island, Torres Strait, AMS C.29811 (3pv); Ribbon Reef, 4.5 m, AMS C.137968 (1pv); Macgillivray Cay, Swains Reef, 17 m, AMS C.105190 (1pv); Ellison Reef, AMS C.117393 (1pv); Lady Musgrave Island, AMS C.94051 (1pv); trawled Lady Musgrave lagoon, QM MO.34152 (5pv); Tryon Island (beach), QM MO.31762 (1rv); Darnley Island, Torres Strait, QM MO.8521 (3rv, 2lv); Murray Island, Torres Strait (beach), QM MO.10569 (2rv, 3lv). **Western Australia:** 10 m, Hibernia Reef, Timor Sea, NTM P.7541 (1pv); **Cocos Island:** AMS C.119593 (1lv, 1rv). **Papua New Guinea:** 5–6 m, in sand around coral shoal, between Kranket Island and Madang, 5°12’S, 145°50’E, AMS C.356678 (1pv) (preserved); Shoal to W of Kranket Island, Madang. Bougainville, AMS C.82973 (1pv); Gihili, AMS C.17410 (1pv). **West Irian:** N.Mios, Woendi Island, Padaido Islands, AMS C.96947 (1pv). **New Ireland:** Mangop, Manus Island, AMS C.98254 (4pv); **Admiralty Group,** AMS C.141373 (1pv). **New Hebrides:** Aneiteum, AMS C.1959 (1pv). **Fiji:** KL (1pv) **Suva:** Vitu Levu Island, NTM P.8787 (1rv). **New Hanova Island:** Metelaung Village, NTM P.1663 (1lv). **Loyalty Islands:** Ouvéa Atoll, NTM P.5792 (1lv). **New Caledonia:** Poum Bay, Daomboui Island, 0–3 m, in sand and coral, 20°9’S, 163°59’E, AMS C.356679 (in part) (3pv) (preserved); between Crouy and Abore Reef, 6 m, AMNH.303271 (4pv, 1lv); Crouy Reef, AMNH.303240 (1pv); Anse Vata, Noumea, AMS C.83706 (1pv) (note: for full New Caledonia collecting data, see Lamprell and Stanisc (1996)); Lifou, AMS C.3899 (1pv). **Tonga:** Tongakabu, AMS C.15069 (1pv). **Philippine Islands:** no localised data, AMNH.303128 (1pv); Mactan Channel, Visayas, AMS C.371092 (2rv); off Bunyong Boh, Mactan Island, 10°05’N, 124°00’E, 7–30 m, coral reef face, AMS C.141371 (1 pv, 1lv). **Solomon Islands:** Guadalcanal Island, AMS C.15068 (1pv); AMS C.52243 (1pv). **Indonesia:** Tanimbar Islands, NTM P.2417 (1 rv, 1lv). **Tanzania.** AMS C.368268 (1lv). **Israel:** Nuweiba, Sinai, AMS C.135652 (2rv). **Réunion:** off Souris Chaude, 60 m, sand, NM K.2782 (3lv, 1rv). **Mauritius:** off Trou aux Biches, reef front in 5 m, Sep 1991, NM K.8312 (1rv). **Red Sea:** specimen figured by Oliver (1992), pl. 40, figs 1a,b, NMW.1955.158.02272 (1pv).

Diagnosis

Shell round to ovate, solid and very thick, glossy, moderately to very inflated; umbones slightly to markedly prosogyrate (more so in large adults); lunule heart-shaped to lanceolate, raised, well delineated by incised line; umbones low, slightly prosogyrate; anterodorsal margin sloping, widely convex terminally; ventral margin widely rounded; posterodorsal margin, sloping, widely convex. Sculpture of fine growth striae, supplemented by faintly raised ridges at the anterior and especially posterior extremities (ridges often wrinkled). Colour variable externally, usually white with patches of grey–pink overlain with blue–black to tan zigzag or chevron patterns, some specimens with hieroglyphic patterns (i.e. composed of variously shaped rod or broken chevron markings), umbones white, lunule white (sometimes with one or two lines of pattern), with very small brown–black spots umbonally; shell internally usually white, occasionally with pale peach medially. Shell length to 55 mm.

Distribution and habitat

Indo-West Pacific; loose coral sand, usually in reef lagoons.

Remarks

Lioconcha castrensis is the largest living species of *Lioconcha*, reaching a maximum of 55 mm in length. Because of its marked variability in terms of colour pattern, this species could be confused with species such as *Lioconcha fastigiata* (Sowerby) and *Lioconcha macaulayi* n. sp. However, there are reliable shell features for distinguishing these species from each other and from other members of *Lioconcha*. *Lioconcha castrensis* differs from *L. fastigiata* in its larger, more ovate and considerably thicker shell, a heavier hinge line (with more robust teeth) and a noticeably raised, well-defined lunule. *Lioconcha castrensis* differs from *L. macaulayi* in having a more ovate, heavier shell and in attaining a larger adult size. *Lioconcha castrensis* and *L. macaulayi* occur together in Lady Musgrave lagoon (Great Barrier Reef), New Caledonia (Anse Vata, near Noumea, Crouy Reef) and Saumarez Reef. Based on a consideration of shell features alone, the relationship between *L. castrensis* and *L. macaulayi* appears to be a close one. Although *L. hieroglyphica* (Conrad) has been considered a synonym of *L. castrensis* (Kay 1979; Lamprell and Stanisc 1996), it now seems to be a valid species, judging from Conrad's illustration (herein selected as the lectotype, because no type material of *L. hieroglyphica* has been located to date) and from our examination of three lots of Hawaiian material (held in the Australian Museum) that match Conrad's description and illustration (see also pp. 108–110 for further discussion). Dillwyn (1817) described *V. lorenziana* based on figures 1961 and 1962 in Chemnitz (1788) and remarked that 'The shell in size and form much resembles *V. castrensis*, of which it may perhaps be nothing but a variety; it is of a dirty white colour, with transverse irregular nearly parallel zic-zac reddish brown stripes'. Considering the wide variation in colour patterns among the numerous specimens we have examined and evident in the figures of Chemnitz from his monograph (Chemnitz 1788), we would agree with Dillwyn that this species is probably another variation of *L. castrensis*. However, as with *Lioconcha ornata* (Dillwyn), comparative anatomy and/or molecular studies would greatly assist in determining whether any of the various colour forms of *L. castrensis* deserve formal taxonomic recognition. As a starting point for such future work, we would

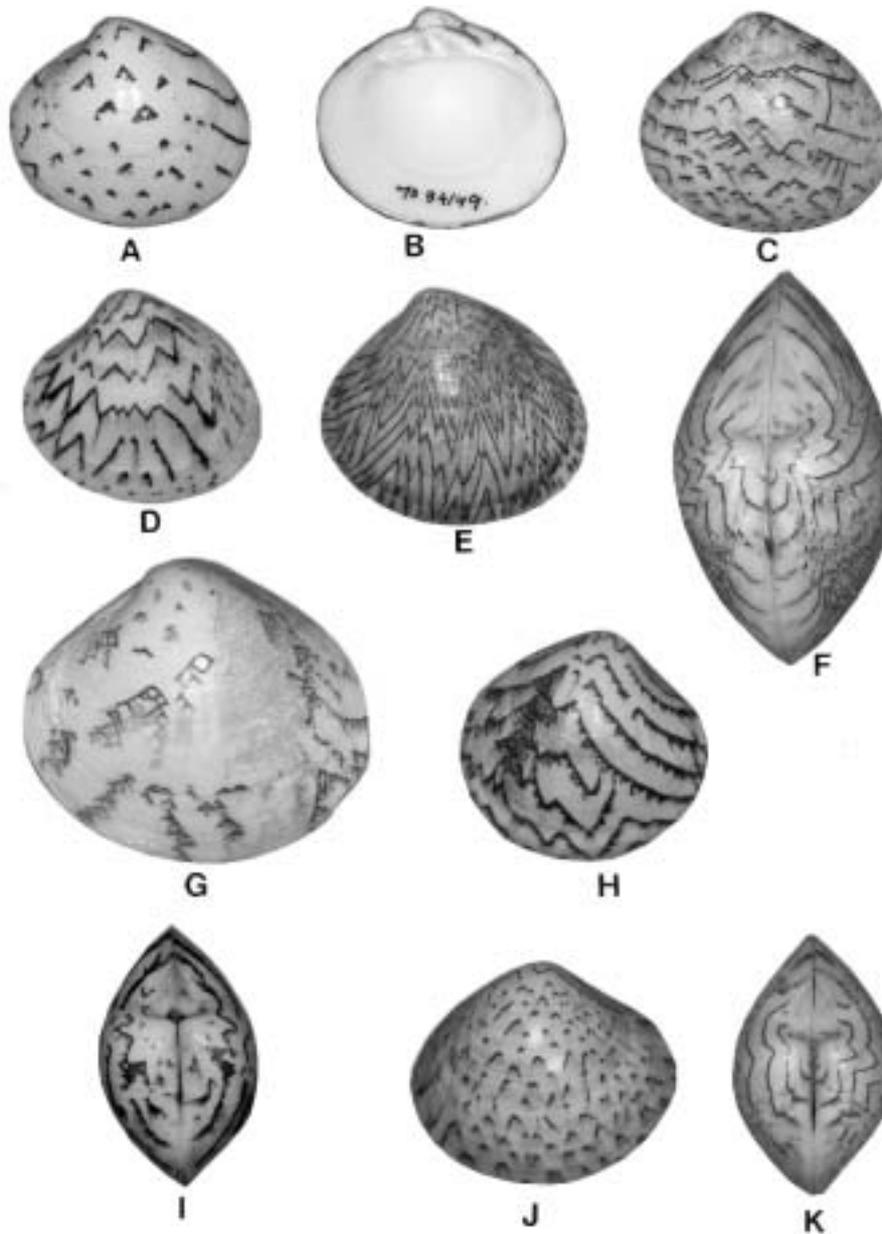


Fig. 1. *Lioconcha castrensis* (Linnaeus, 1758). *A,B*, Lady Musgrave lagoon, QM MO.34149, length 33.9 mm: *A*, external view lv; *B*, internal view rv. *C*, Philippine Islands, AMNH.303128, length 42.3 mm, external view lv. *D*, Little Trunk Reef Qld, AMNH.303314, length 48 mm, external view lv. *E,F*, Suva, Fiji, KL, length 54.5 mm: *E*, external view lv; *F*, dorsal view of pv. *G*, Swains Reef, Qld, AMNH.303936, length 35.2 mm, external view lv. *H,I*, Spengler collection, Ostindien, specimen figured by Chemnitz (1782: fig. 367), length 48 mm, height 45 mm, width of pv 28 mm: *H*, external view rv; *I*, dorsal view pv. *J,K*, Spengler collection, South Seas, specimen figured by Chemnitz (1782: fig. 1662; specimen named *Venus lorenziana* by Dillwyn), length 40 mm, height 35 mm, width of pv 24 mm: *J*, external view rv; *K*, dorsal view pv.

suggest a comparison of the typical *L. castrensis* (heavy zigzag markings) and the hieroglyphic form (of numerous, small, often broken tent markings).

***Lioconcha macaulayi* n. sp.**

(Figs 2A–O, 12B, 15A)

Material examined

Holotype. New Caledonia: Crouy Reef, AMS C.204232 (1pv).

Paratypes. New Caledonia: Anse Vata, Noumea, AMS C.204233 (1pv). Australia: Queensland: trawled Lady Musgrave Island, in lagoon, QM MO.34149 (4pv).

Other material examined. **New Caledonia:** Anse Vata, Noumea, AMS C.37946 (1pv); Ile Signal, off Noumea, 4 m, reef and sand, AMS C.107219 (1pv); Noumea, AMS C.141440 (2lv). **Australia:** Queensland: dredged by 'Kunara', Saumaurez Reef, KL (1pv).

Description and diagnosis

Shell obovate, solid and thick, glossy, well inflated; umbones raised, prosogyrate; lunule heart-shaped, raised, well delineated by incised line; anterodorsal margin long, rounded terminally; ventral margin widely convex; posterodorsal margin moderately convex, steeply sloping, angulate at its posterior termination; lunule raised, elongated heart-shaped, well delineated by incised line. Sculpture of dense concentric striae, with faint to slightly raised ridges at posterior extremity. Hinge of lv with anterior lateral tooth solid, thick, peg-like; anterior cardinal very thin, separated from median cardinal by narrow V-shaped socket; median cardinal thick, oblique, raised; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thick, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, peg-like; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour externally white with irregular, obscure pink and dark to light brown blotches (sometimes extensive), solid tents and occasional short rod-shaped markings, umbones white, lunule white with small pale red–brown spot umbonally; shell internally white. Shell dimensions are given in Table 1.

Distribution and habitat

Known only from Queensland and New Caledonia, dredged in coral reef lagoons.

Remarks

In size, shell thickness and glossy surface texture, *L. macaulayi* most closely resembles *L. castrensis*, with which it occurs sympatrically on the Great Barrier Reef (Lady Musgrave lagoon), Saumarez Reef and New Caledonia. However, the truncate posterior margin, the less ovate valve shape and the irregular, more obscure markings readily and consistently distinguish *L. macaulayi* from *L. castrensis*, even in very juvenile material. *Lioconcha ornata* (Dillwyn), *Lioconcha annettae* Lamprell & Whitehead and *Lioconcha berthaulti* n. sp. also share the same habitat as *L. macaulayi*, but differ from that species in their trigonal shape, lack of posterior margin truncation, smaller size and more complex colour patterns.

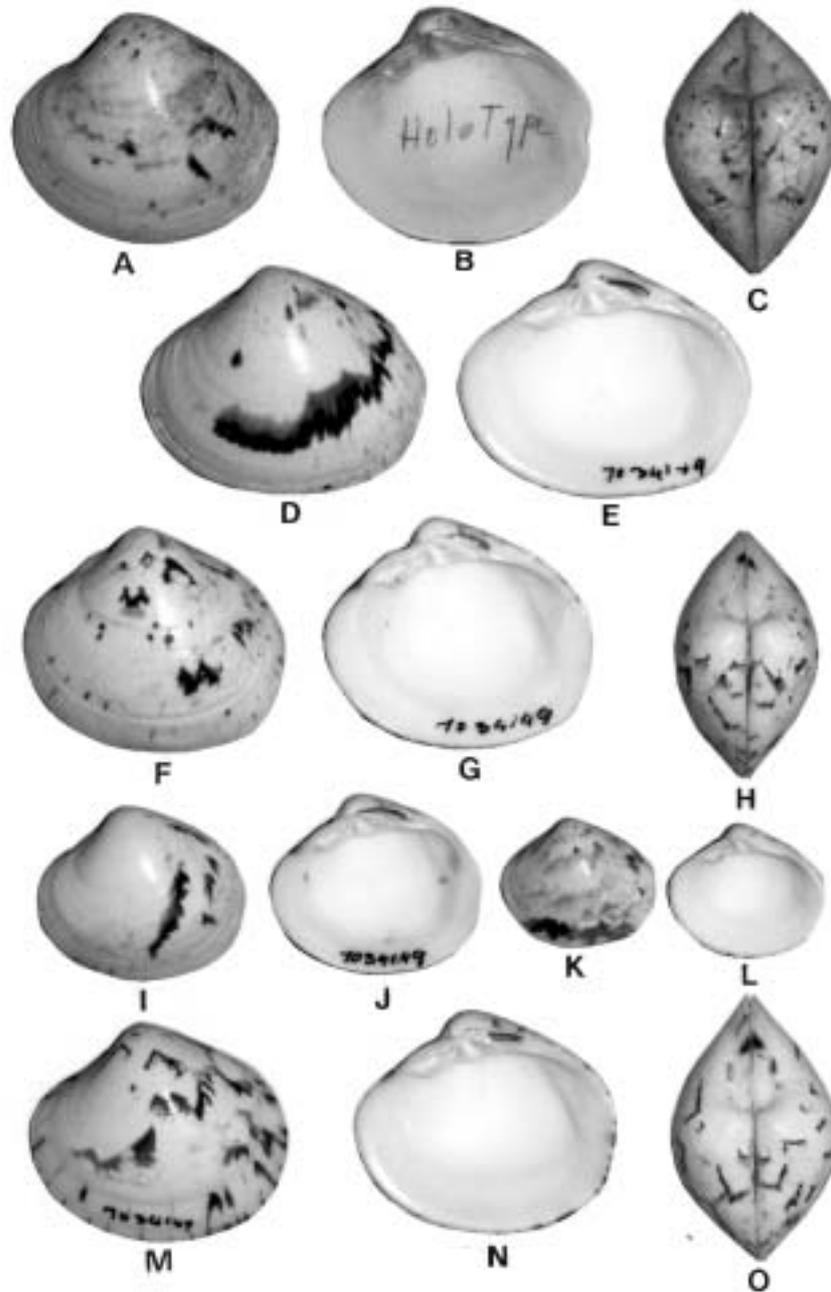


Fig. 2. *Lioconcha macaulayi* n. sp. *A–C*, holotype, Crouy Reef, New Caledonia, AMS C.204232, length 43.5 mm, height 39 mm, width of pv 27.7 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–J, M–O*, paratypes, trawled Lady Musgrave Island, in lagoon, QM MO.34149: *D*, external view lv; *E*, internal view rv, length 37.5 mm; *F*, external view lv; *G*, internal view rv; *H*, dorsal view pv; length 34.2 mm; *I*, external view lv; *J*, internal view rv, length 29.5 mm; *M*, external view of lv; *N*, internal view rv; *O*, dorsal view pv. *K, L*, juvenile, Anse Vata, Noumea, AMS C.204233, length 20.5 mm: *K*, external view lv; *L*, internal view rv.

Table 1. Shell dimensions of type material of *Lioconcha macaulayi* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204232	43.5	39.0	27.7
Paratypes			
AMS C.204233	20.4	18.1	12.1
QM MO.34149 A	47.4	31.6	21.7
B	36.8	32.3	22.1
C	34.3	30.7	19.2
D	29.5	25.8	17.9

Etymology

Named for Dr Geoff Macaulay, in recognition of his generous assistance to the authors through the collecting and for donation of bivalve material used in previous studies.

Lioconcha hieroglyphica (Conrad, 1837)

(Figs 3A–L, 12C, 15A)

Cytherea hieroglyphica Conrad, 1837: 253, pl. 19, fig. 22, (type locality: ‘Sandwich Islands in muddy marshes near Pearl R.’), lectotype here selected (ICZN 74.4; designation by means of an illustration or description); Hanley 1844: 100, pl. 15, fig. 16; Chenu 1859: pl. 14, fig. 4; Sowerby 1851: sp. 105; Lamy and Fischer-Piette 1937: 274.

Circe hieroglyphica (Conrad). Reeve, 1863: pl. 9.

Lioconcha hieroglyphica (Conrad). Römer, 1864–69 (1866): 46; Kay, 1979: 567, fig. 184C,D.

Lioconcha hieroglyphica (Conrad). – Abbott & Dance, 1982: 359, fig. 7 (not of Conrad, 1837) (= *L. castrensis* (Linnaeus)).

Material examined

Hawaii: Kaneohe Bay, Oahu, 21°28'N, 157°48'W, 9 m, AMS C.61304 (4pv); AMS C.38791 (3pv); 21°0'N, 157°0'W, AMS C.96968 (2pv, 2lv); Pearl Harbour, Oahu Island, 21°22.5'N, 157°58'W, AMS C.48240 (1pv, 2rv); AMS C.48240 (3pv); 21°0'N–157°0'W, AMS C.96968 (2pv); Sandwich Island (= Hawaii) AMS C.15084 (2pv); AMS C.47864 (1pv).

Diagnosis

Shell subtrigonal, solid, moderately thick, moderately inflated, smooth to glossy; umbones inflated, elevated, strongly prosogyrate; anterodorsal margin acutely rounded terminally, posteriorly truncate; lunule elongated heart-shaped, raised, well delineated by incised line. Sculpture of fine growth striae, sometimes with faint raised ridges posteriorly. Colour externally white, with dark or tan brown rod-like or angular (hieroglyphic) markings; umbones and lunule white; shell internally white. Shell length to 42 mm.

Distribution and habitat

Known only from Hawaii; Mariana and the Marshall Islands (Kay 1979), in loose coral sand.

Remarks

Lioconcha hieroglyphica has been confused in many collections with the hieroglyphic patterned colour form of *L. castrensis*. Although the type specimen cannot be located, the

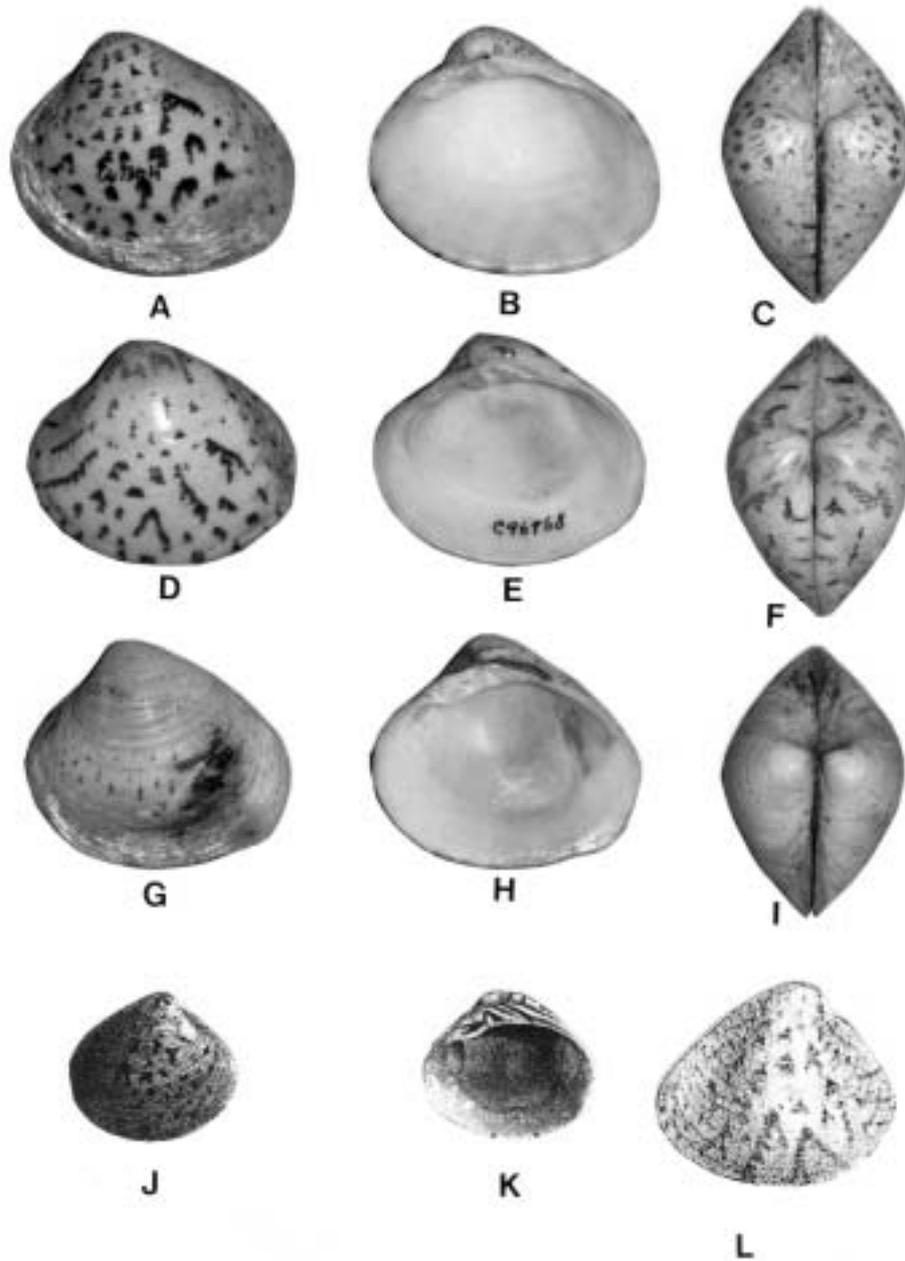


Fig. 3. *Lioconcha hieroglyphica* (Conrad, 1837). *A–C*, Kaneohe Bay, Oahu, length 41.5 mm; AMS C.61304: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F*, Hawaii, length 39 mm; AMS C.96968: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–I*, East Loch, Pearl Harbour, Oahu Island, length 38 mm; AMS C.48240: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J, K*, specimen figured by Chenu (1859) as *Cytherea hieroglyphica* Conrad, 1837: pl. 14, fig. 4: *J*, external view rv; *K*, internal view rv. *L*, Conrad's (1837) original illustration of *Cytherea hieroglyphica* Conrad, 1837: 253, 19, f. 22, external view rv (here selected as lectotype).

description and illustration by Conrad (1837) (see Fig. 3L herein; illustration selected as lectotype) and illustrations in Römer (1866) and Kay (1979) are adequate to establish the identity of the species. The Australian Museum collection has eight lots of *L. hieroglyphica* from Hawaii, most specimens of which agree in every aspect with Conrad's description and illustration (Conrad 1837).

Lioconcha tigrina (Lamarck, 1818)

(Figs 4A–N, 12D, 15A)

Cytherea tigrina Lamarck, 1818: 579; no. 34 (refers to Chemnitz, 1782: figs 374, 375), (type locality: 'mer de l'Inde').

Lioconcha tigrina (Lamarck). Prashad, 1932: 220.

Lioconcha (Lioconcha) tigrina (Lamarck). Lamprell & Whitehead, 1990: 50; Lamprell & Kilburn, 1999a: 22, pl. 1, figs 4, 5, 8; Lamprell & Kilburn, 1999b: 44.

Material examined

Holotype. MNHG.1084/35, 1pv (Fig. 4D–F).

Other material examined. Specimens referred to by Lamarck in Chemnitz Cabinet 'An Chemn. Conch. 6. t. 35. f. 374–375'. Spengler Collection, Copenhagen Museum (Fig. 4G–L). **Mauritius**: QM MO.11230 (1pv) (Fig. 4M–O); Melvill-Tomlin collection, NMW. Z.1955.158 (1pv). **Mozambique**: see NM material listed by Lamprell and Kilburn (1999a).

Diagnosis

Shell solid, moderately thin but very robust, smooth not glossy; triangularly ovate, well inflated; umbones markedly prosogyrate, raised; lunule heart-shaped, flat, weakly outlined by incised line; anterodorsal margin short, moderately sloping; narrowly convex terminally; ventral margin widely rounded; posterodorsal margin straight, steeply sloping, roundly truncate. Sculpture of fine growth striae, supplemented by concentric, flattened ridges at anterior and posterior extremities. Colour externally white with numerous, interconnected, solid triangles of reddish-brown; umbones white, usually with some brown patterning, lunule white or light brown; shell internally white, usually tinged with yellow or orange medially. Shell length to 45 mm.

Distribution and habitat

Western Indian Ocean, in fine littoral sand and mud.

Remarks

This is one of the most poorly understood of all species of *Lioconcha*, due primarily to its close resemblance to *L. castrensis* (another thick, smooth, strongly patterned shell), but also to uncertainties surrounding available type material and its associated locality data ('Oceane Indien'). *Lioconcha tigrina* differs from *L. castrensis* in having posteriorly truncate valves, umbones positioned much closer to the anterior end and a noticeably more compact and better defined lunule. In addition, *L. tigrina* reaches a smaller maximum length (45 mm) than does *L. castrensis* (55 mm). Lamprell and Whitehead (1990) introduced *L. annettae* for a species previously confused with *L. tigrina*. For comparison, they also figured the holotype of *L. tigrina* housed in the Museum d'Histoire Naturelle, Geneva (108/35, no. 34). Although there are some shape and pattern resemblances between *L. tigrina* and *L. annettae*, the closest relationship of the former clearly lies with *L. castrensis* and *L. hieroglyphica*, whereas the latter is associable with the *L. fastigiata* and

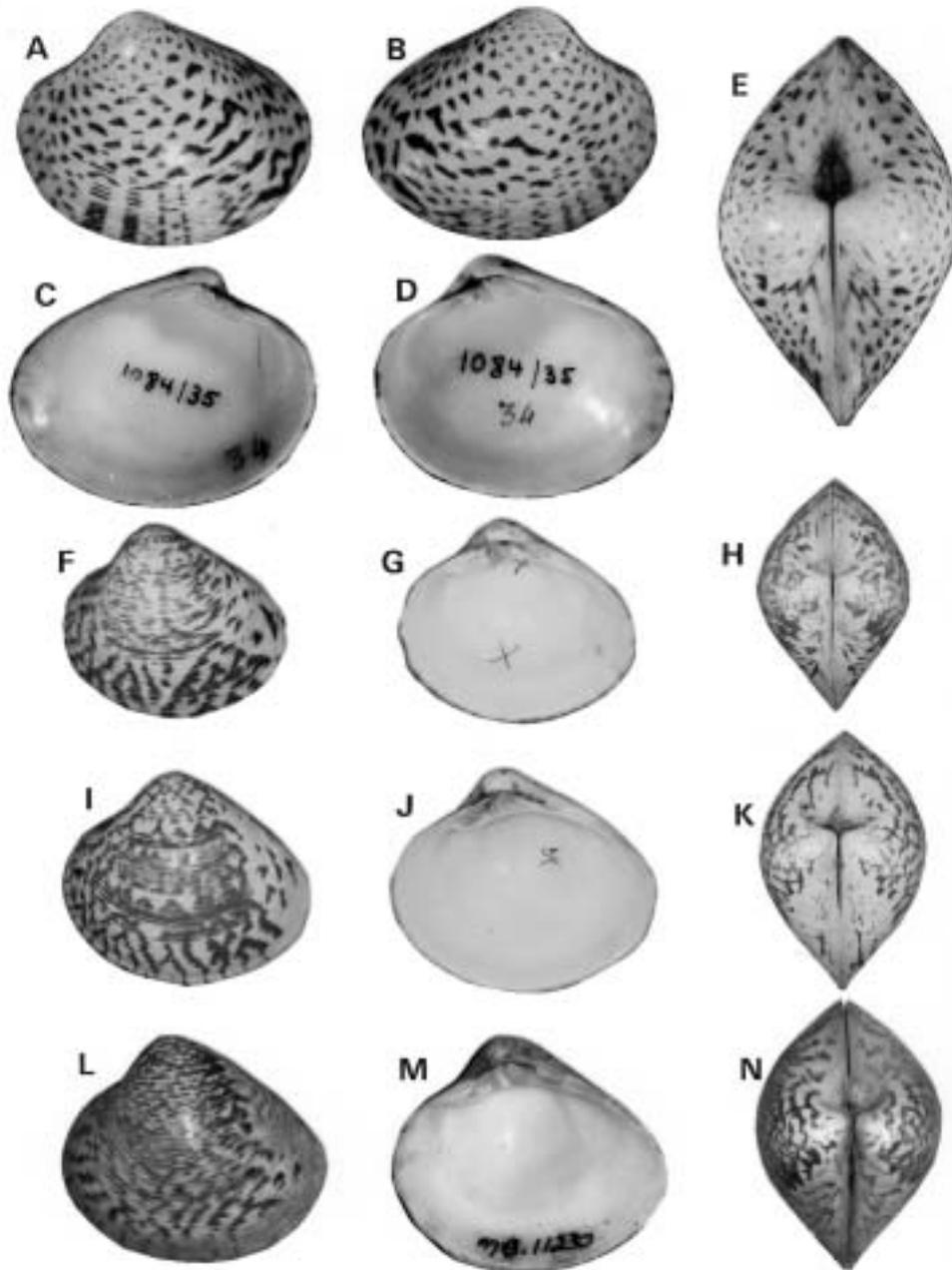


Fig. 4. *Lioconcha tigrina* (Lamarck, 1818). *A–E*, Holotype, ‘mer de l’Inde’, MNHG.1084/35: *A*, external view lv; *B*, external view rv; *C*, internal view lv; *D*, internal view rv; *E*, dorsal view pv. *F–K*, specimens referred to by Lamarck ‘An Chemn. Conch. 6. t. 35. f. 374–375’ but having no type status, from Spengler Collection, species 374: *F*, external view lv; *G*, internal view rv; *H*, dorsal view pv; species 375: *I*, external view lv; *J*, internal view rv; *K*, dorsal view pv. *L–N*, Mauritius, 37.9 mm, QM MO.11230: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

L. ornata species complex. During the present study, we were fortunate to have at our disposal a large series of *L. castrensis* from the Philippine Islands, the Great Barrier Reef and New Caledonia for comparison with *L. tigrina*. We also have had the opportunity to examine and photograph type material of *L. tigrina* from the Geneva Museum. We have examined a specimen from the western Indian Ocean (QM MO.11230), which agrees with the type series. Lamprell and Kilburn (1999b) examined specimens from northern Mozambique that agree with the holotype and figured both the holotype and a typical specimen. Shell length to 45 mm.

***Lioconcha fastigiata* (Sowerby, 1851)**

(Figs 5A–J, 6I, 12E, 15B)

Cytherea fastigiata Sowerby, 1851: 643, (type locality: Sydney, Australia), lectotype (here selected, as Sowerby's (1851) illustration 158, pl.; ICZN 74.4; designation by means of an illustration or description; see Fig. 6A herein).

Circe fastigiata (Sowerby). Reeve, 1863: sp. 41.

Lioconcha fastigiata (Sowerby). Römer, 1864–69 (1868): 45, fig. 1a–c; Springsteen & Leobrera, 1986: 298, pl. 85 fig. 4.

Lioconcha (*Lioconcha*) *fastigiata* (Sowerby). Habe, 1977: 258; Lamprell & Whitehead, 1992: no. 546.

Material examined

Type material examined. Possible syntypes (presently labelled as 'syntypes', 'Sydney, Australia') BMNH.20000455 (5pv).

Other material examined. **Australia: Western Australia:** One Arm Point, littoral sand, AMNH.303274 (2pv); Broome, AMS C.141100 (1rv, 1lv); Buccaneer Archipelago, AMS C.42458 (many). **Northern Territory:** Vashon Head, Port Essington, Coburg Peninsula, AMS C.93083 (2pv); Friday Island, Torres Strait. **Queensland:** AMS C.96956 (2lv); Mapoon, AMS C.14238 (5lv, 1rv); Bowling Green Bay, Townsville, AMNH.303036 (1pv); trawled off Palm Island, AMNH.303315 (8pv); Dingo Beach, AMNH.303037 (1pv); Gloucester Passage, Dingo Beach, AMS C.72153 (4pv); Hayman Island, AMS C.97340 (2pv); Bustard Heads, Port Curtis, AMS C.141411 (1pv); Myora, Stradbroke Island, AMNH.303373 (2pv). **Thursday Island:** Torres Strait, AMS C.141413 (1pv). **Philippine Islands:** (no localised data) QM MO.14448 (in part) (1pv).

Diagnosis

Shell ovate–trigonal to trigonal, moderately thin but strong, smooth to glossy, well inflated, posteriorly somewhat attenuate in large adults; umbones prosogyrate (more so in large adults) and raised; lunule heart-shaped, flat, weakly delineated by incised line; anterodorsal margin short, steeply sloping; narrowly convex terminally; ventral margin widely rounded; posterodorsal margin straight, steeply sloping, narrowly rounded at its extremity. Sculpture of growth striae supplemented by slightly raised ridges at anterior and posterior extremities. Colour externally white with heavy, black, ragged chevron patterns, lunule with prominent purple–black blotch; umbones white, lunule white with large brown–black blotch umbonally; shell internally white, sometimes with cream flesh colour centrally. Shell length to 38 mm.

Distribution and habitat

Western Indian Ocean to the West Pacific, in littoral muddy sand (not known from lagoonal or reef areas).

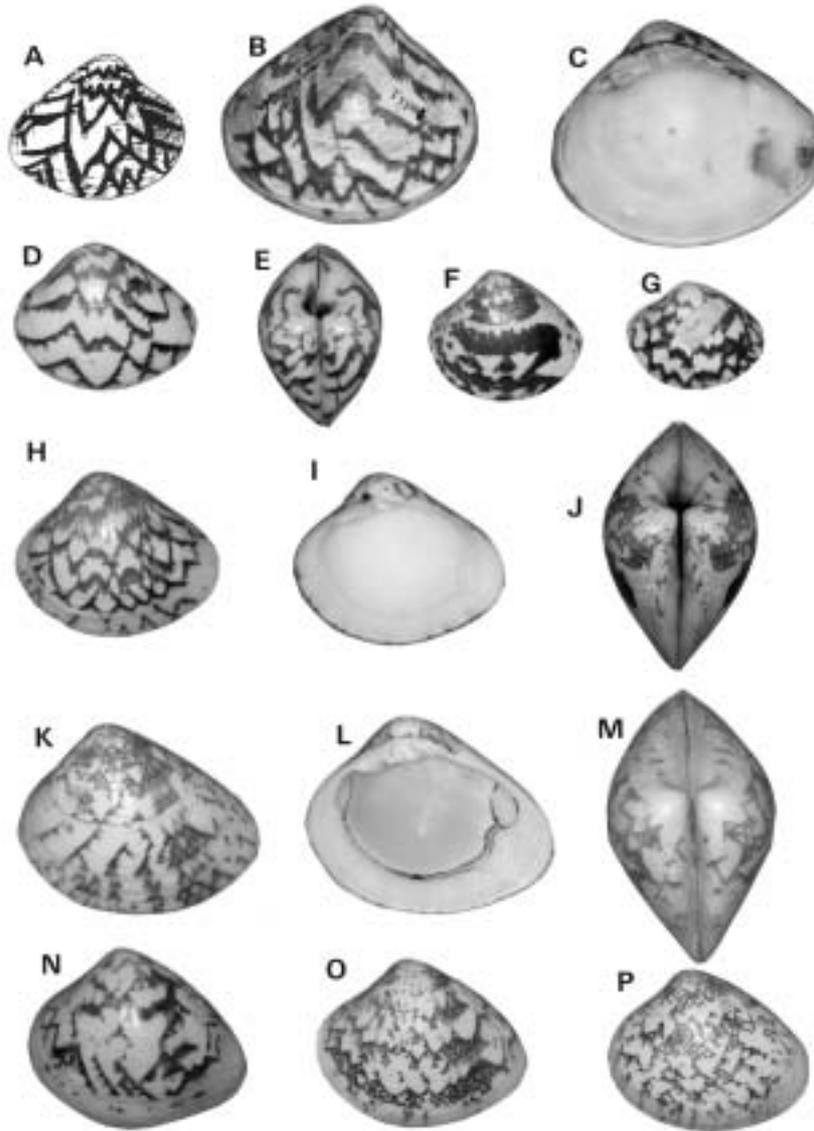


Fig. 5. *A–J*, *Lioconcha fastigiata* (Sowerby, 1851). *A*, *Cytherea fastigiata* (fig. 158 of Sowerby (1851), here selected as lectotype) external view rv; *B*, external view rv of largest specimen presently carded as one of the ‘syntypes’ from Cuming Collection (BMNH.20000455) and marked with the word ‘Type’ glued to the shell (note: designator unknown; neither this specimen nor other material from lot BMNH.20000455 match either fig. 158 or 159 of Sowerby (1851); see also Fig. 6*G* herein for reproduction of fig. 159 from Sowerby (1851)); *C*, internal view rv (same specimen as *B*). *D, E*, Palm Island, N Qld, length 33.5 mm: *D*, external view lv; *E*, dorsal view pv, AMNH.303315; *F*, Philippine Islands, QM MO.14448 (in part), length 22 mm, external view lv; *G*, Philippine Islands, QM MO.14448 (in part), length 15 mm, external view lv; *H–J*, Palm Island, N Qld, AMNH.303315, length 37.8 mm: *H*, external view lv; *I*, internal view rv; *J*, dorsal view pv. *K–P*, *Lioconcha annettae* Lamprell & Whitehead, 1990. *K–M*, Holotype, Swains Reef, QM M0.22852, length 39 mm: *K*, external view lv; *L*, internal view rv; *M*, dorsal view pv; *N*, Lady Musgrave Island, in lagoon, Qld, KL, length 41 mm, external view lv; *O*, Taylor Reef, Qld, KL, 39 mm, external view lv; *P*, Crouy Reef, New Caledonia, KL, length 37.2 mm, external view lv.

Remarks

The five pv from the Natural History Museum (BMNH.20000455) are labelled as 'syntypes'. Although these specimens were from the Cuming collection and the largest specimen has the word 'Type' glued to the shell, none matches either of Sowerby's (1851) illustrations of *C. fastigiata* (his figures 158, 159). There is no indication as to who originally gave the status of syntypes to the material in lot BMNH.20000455 (J. Pickering, personal communication). We have therefore decided to downgrade the status of this material from 'syntypes' to 'possible syntypes' and, in the absence of any definite type material, herein select Sowerby's figure 158 as the lectotype (ICZN 74.4). Sowerby's figure 159 closely resembles *Lioconcha pseudofastigiata* n. sp., based on the external coloration and the attenuate valve shape (see Fig. 6G herein), but, in the absence of any illustration of the interior of the shell by Sowerby (or any matching specimen from the Natural History Museum collection), it is impossible to be absolutely certain of the identity of this specimen. Sowerby gives 'Sydney, Australia' as the locality for *L. fastigiata*, but if his figure 159 represents *L. pseudofastigiata* n. sp. (a species presently recorded only from the Philippine Islands), then it would seem highly likely that some, and possibly all, of his material was collected in the Philippine Islands. We know of no records of this species from Sydney or any locality south of Moreton Bay, southern Queensland.

This is a well known and reasonably common species, recorded from several localities throughout the Indo-West Pacific. The colouration of dark brown zigzag flammules over the valves and the dark brown blotch associated with the lunule, combined with the smooth, inflated shell appear to be constant within the species and help to distinguish it from other species of *Lioconcha*. Superficially *L. fastigiata* may be mistaken for *L. castrensis* (which also shows zigzag flammules), but that species always has a thick, rounded shell featuring a heavy hinge line (and teeth) and a strongly raised lunule. Specimens of *L. fastigiata* from the Philippine Islands differ from those from Australia in having more elongate, slightly thinner shells, which exhibit a diffuse brown band internally. The relationship between *L. fastigiata* and *L. annettae* seems to be a very close one, although the former is chiefly a coastal inhabitant, whereas the latter is always found in reef lagoonal localities. It is possible that *L. annettae* may prove to be a localised reef form of *L. fastigiata*, but until the relevant anatomical and/or molecular data become available to test this suggestion, we continue to recognise both as valid taxa. Certain forms of *L. ornata* (in the rather broad sense adopted herein) examined in the present study, especially material from New Caledonia, also suggest a relationship between this species, *L. fastigiata* and *L. annettae*. Again, this requires clarification based on non-conchological characters. Cernohorsky (1972) illustrates a fairly typical specimen of *L. fastigiata* from Caboni Beach, Fiji, and this represents the most easterly confirmed record of this species within the Pacific. Although Kira (1962) records *L. fastigiata* from Japanese waters ('the Amami Islands and southwards', p. 162) his illustrated specimen is clearly identifiable as *L. ornata*.

***Lioconcha annettae* Lamprell & Whitehead, 1990**

(Figs 5K–P, 12F, 15C)

Lioconcha (Lioconcha) annettae Lamprell & Whitehead, 1990: 49, fig. 4e–h; Lamprell & Whitehead, 1992: sp. 545; Lamprell & Stanisc, 1996: 17: 27–48.

Material examined

Holotype. Australia: Queensland: Swain Reef, dredged coral sand, D. and V. Harris, 1986, QM M0.22852 (1pv).

Paratypes. Australia: Queensland: Lady Musgrave Island, coral sand, 3–7 m, dredged, D. and V. Harris, 1986, AMS C.160474 (1pv), WAM.941–89 (1pv).

Other material examined. **Australia: Queensland:** Lady Musgrave Island, in lagoon, AMNH.303126 (4pv); Herald Prong Reef, Swains Reef, AMNH.303163 (6pv); Kelso Reef, dredged 3–7 m coral sand, MV F.57681 (1pv); Taylor Reef; KL (1pv), AMNH.303029; Kelso Reef, AMNH.303025 (1pv); Swains Reef, AMS C.132082; Queens Beach, Bowen, AMS C.75887 (in part); Rudder Reef, off Port Douglas, AMS C.138072 (4pv); Murray Island, Torres Strait, AMS C.138080. **New Caledonia:** Poum Bay, Daomboui Island, 0–3 m, in sand and coral, 20°9'S, 163°59'E, AMS C.356679 (in part) (1pv) (preserved); Anse Vata, Noumea, AMNH.303031–AMNH.303269 (2pv); Baie des Citrons, Noumea, AMNH.303034 (1pv); Crouy Reef, Noumea, AMNH.303030 (1pv). (For further New Caledonian sites, refer to Lamprell and Stanisic (1996).) **Indonesia:** Wai Island, Sorong, NW Irian Jaya, 5–10 m in rubble on coral slope, AMNH.303045 (1pv). **Philippine Islands:** Bohol Island, Tagbilaran, 9°39.000'N, 123°51.000'E, AMS C.371090 (1lv).

Diagnosis

Shell moderately thin but strong, trigonal, smooth to glossy, well inflated, becoming somewhat attenuate posteriorly in large adults; umbones prosogyrate (markedly so in large adults) and raised; lunule elongate heart-shaped to lanceolate, flat, weakly delineated by incised line; anterodorsal margin short, steeply sloping; narrowly convex terminally; ventral margin convex (slightly sinuate in very large adults); posterodorsal margin straight, steeply sloping, narrowly rounded at its extremity. Sculpture of fine, dense, growth striae supplemented by raised concentric ridges ventrally, anteriorly and posteriorly. Colour externally white, with black, chestnut or dark-brown chevron or hieroglyphic patterns and microscopic dots; umbones and lunule white, with purple spots beneath umbones; shell internally white, yellow centrally. Periostracum straw coloured. Shell length to 41 mm.

Distribution and habitat

Western Pacific and Eastern Indian Ocean (Irian Jaya), in coral sand, lagoonal and reef areas.

Remarks

Lamprell and Whitehead (1990) differentiated *L. annettae* from *L. tigrina* and *L. fastigiata* on the basis of valve profile, sculpture and colouration. They further separated *L. annettae* from *L. fastigiata* using habitat preferences (reef for the former, mainland coastal for the latter), maximum shell length and the length of the teeth. Examination of a more extensive series of specimens (including juveniles) than that available to Lamprell and Whitehead suggests that there are no significant differences between the species as regards teeth length or valve profile. Whereas it is true that mature *L. fastigiata* tend to be smaller (generally 25–30 mm in length) than *L. annettae* (generally 30–40 mm in length), we have examined a number of specimens of *L. fastigiata* comparable in size to average *L. annettae*. The differences between *L. annettae* and *L. fastigiata* in habitat preference, adult sculpture and colouration (including lunule colouration) appear to hold, but the basic patterning of the shells is similar and suggestive of a close relationship. As to the precise nature of this connection, whether that of sister species, subspecies or populational variants, nothing can as yet be concluded. Lamprell and Stanisic (1996) recorded *L. annettae* from several subtidal stations off New Caledonia. We can confirm this, but add that several interesting specimens from this region appear to be intermediate between *L. annettae* and *L. ornata*,

suggestive of occasional hybridisation and, as with *L. fastigiata*, also a close relationship. Lamprell and Stanisc (1996) previously indicated that *L. annettae* and *L. ornata* may eventually prove to be conspecific but, based on shell features alone, the closest relationship of *L. annettae* would seem to lie with *L. fastigiata*.

***Lioconcha pseudofastigiata* n. sp.**

(Figs 6A–H, 13A, 15B)

Material examined

Holotype. Philippine Islands: Leyte, littoral sand, AMS C.204480 (1pv).

Paratypes. Philippine Islands: Cebu, Mactan Island, Punta Engano 10°19.000'N, 124°1.000'E ('90–145 m. Tangle nets' (sic)), AMS C.1633076 (7pv, 1lv); 'Philippines', purchased Sowerby and Fulton, Kew, London, QM MO.14448 (4pv).

Description and diagnosis

Shell ovate–trigonal; thin but strong, smooth; anterior end of shell less than one-third of maximum length; medially inflated; umbones raised, markedly prosogyrate; anterodorsal margin short, rounded terminally; ventral margin widely convex; posterodorsal margin almost straight, steeply sloping, narrowly rounded and attenuate terminally; lunule elongate heart-shaped, flat, obscurely delineated by incised line; ligament impressed. Sculpture of concentric striae and well-defined growth pauses, terminating at postero–umbonal ridge. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal very thin, separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique, joined to anterior lateral at top; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, long, thin; posterior lateral, parallel to nymph. Anterior muscle adductor scars teardrop shaped, posterior adductor scars subovate. Pallial line thin, well defined; pallial sinus diminutive. Colour: externally white with irregularly arranged, solid tents of brown–black (sometimes fused laterally); umbones and lunule white, with purple spots beneath umbones; umbones white or pale pink; lunule white but with large brown–black blotch; shell internally white, sometimes flesh coloured umbonally, always with very wide, diffuse purple–brown ray or blotch medially (darkest at ventral margin). Shell dimensions are given in Table 2.

Distribution and habitat

Known only from the Philippine Islands, in littoral sand and mud.

Remarks

Lioconcha pseudofastigiata n. sp. occurs sympatrically with *L. ornata*, at least based on locality data for certain material of both species from the Australian Museum (*L. pseudofastigiata*, AMS C.163076; *L. ornata*, AMS C.163075). Depth and collection method information associated with these lots ('In tangle nets, 90–145 m') should probably be disregarded, because the holotype of *L. pseudofastigiata* and all examined material of the closely allied species *L. fastigiata*, *L. annettae* and *L. ornata* are from shallow water (in most cases unknown from depths greater than 10 m; *L. ornata* occasionally recorded from up to 50 m). We have examined *L. fastigiata* from the Philippine Islands, which agree in all

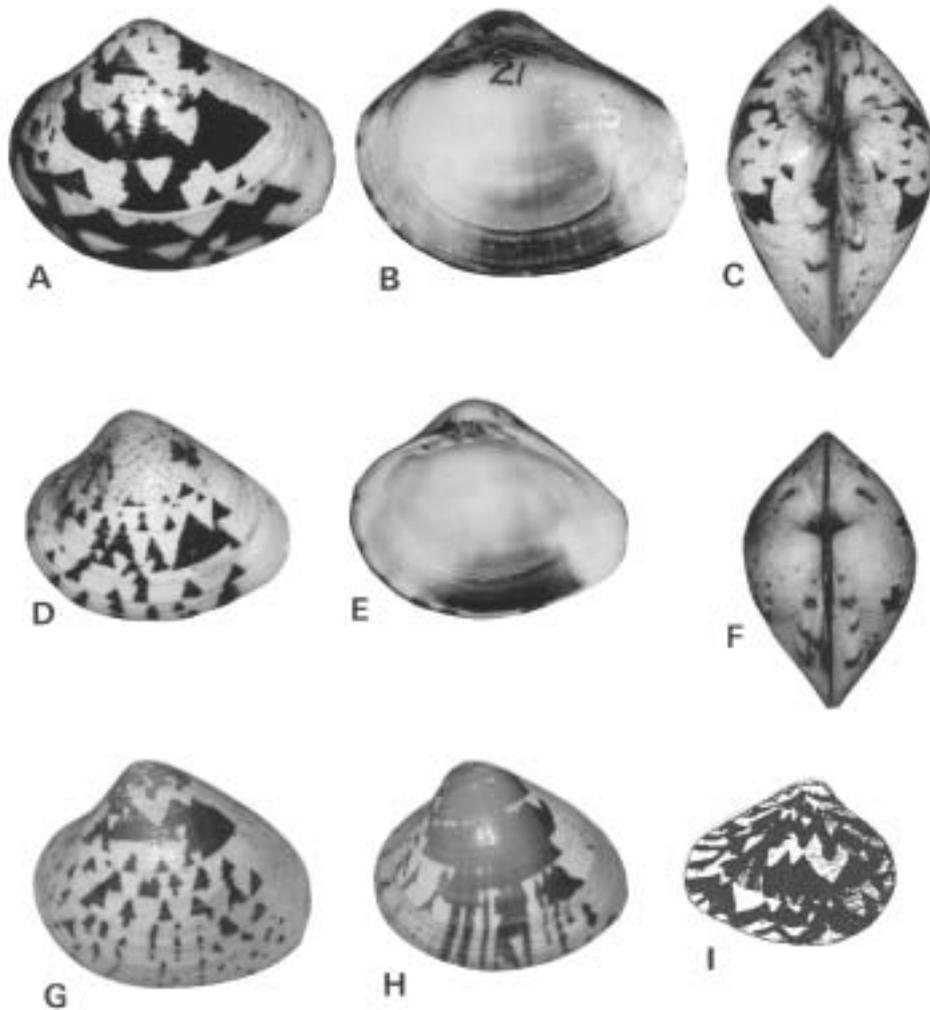


Fig. 6. *A–H*, *Lioconcha pseudofastigiata* n. sp. *A–C*, Holotype, Leyte, littoral sand, Philippines, AMS C.204480, length 34.5 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv; *D–F*, paratype, Cebu, Mactan Island, Punta Engano 10°19.000'N, 124°1.000'E, AMS C.163076, length 30.8 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv; *G,H*, Philippine Islands, QM MO.14448, external views lv (length 43.7 and 40 mm, respectively); *I*, *Cytherea fastigiata*, fig. 159 from Sowerby (1851), external view rv; this figure (= strictly, a paralectotype of *Lioconcha fastigiata*) closely resembles shells of *Lioconcha pseudofastigiata* and is probably a representation of that species.

respects with Australian specimens, but we cannot conclude whether *L. fastigiata* and *L. pseudofastigiata* occur sympatrically. Sowerby's (1851) fig. 159 of *C. fastigiata* (an external view of a rv and, strictly, a paralectotype of *L. fastigiata*; see Fig. 6*I* herein) resembles shells of *L. pseudofastigiata* and is probably a representation of this new species (for further comments on Sowerby's material see remarks under *L. fastigiata*). The moderately thin shell, distinctive external pattern of solid tenting and consistent presence of a wide, purple–brown ray or blotch internally all help to distinguish *L. pseudofastigiata* from *L. fastigiata* and *L. annetae*.

Table 2. Shell dimensions of type material of *Lioconcha pseudofastigiata* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204480	34.5	27.5	20.5
Paratypes			
AMS C.163076 A	27.7	23.0	17.1
B	31.5	18.9	24.5
C	30.8	24.0	17.5
D	29.0	23.3	17.7
E	27.3	21.5	16.8
F	27.7	22.7	17.3
G	25.5	21.6	16.7
H	24.3	19.7	8.1 (1rv)
QM MO.14448 A	40.0	34.5	25.4
B	43.7	36.9	26.2
C	28.2	24.6	18.5
D	24.8	20.2	13.8

***Lioconcha ornata* (Dillwyn, 1817)**

(Figs 7A–I, 13B,C, 15D)

Venus castrensis var., Röding, 1798: 181, no. 294 (refers to Chemnitz, 1782: figs 380, 381).*Venus ornata* Dillwyn, 1817: 184, no. 61 (based on Chemnitz, 1782: figs 380, 381), (type locality: Tranquebar, Mauritius); Wood, 1818: 36, no. 60.*Lioconcha (Lioconcha) ornata* (Dillwyn). Habe, 1977: 258; Oliver, 1992: 185, pl. 40 figs 2; Lamprell & Whitehead, 1992: sp. 544; Lamprell & Stanistic, 1996: 32, fig. 2e,f; Lamprell & Kilburn 1999a: (neotype designated), 22, pl. 1, figs 9–14; Lamprell & Kilburn 1999b: 44.*Lioconcha ornata* (Dillwyn). Prasad, 1932: 219.*Lioconcha (Lioconcha) ornata* (Lamarck) (sic). Abbott & Dance, 1982: 359.*Cytherea picta* Lamarck, 1818: 579, no. 33 (refers to Chemnitz, 1782: figs 373, 376–381) (in part), (type locality: Indian Ocean); Lamy & Fischer-Piette, 1937: 274.*Lioconcha picta* (Lamarck). Lamy, 1930: 135.**Material examined***Venus ornata*. Syntypes lost; neotype (designated by Lamprell and Kilburn (1999a)) Mauritius, Spengler collection (figs 9–11) ZMUC (1pv; see discussion below).

Other material examined. **Australia: Queensland:** trawled between Palm and Curacoa Islands, AMNH.303472 (7pv); trawled lagoon, Little Trunk Reef, AMNH.303471 (4pv); Slashers Reef no. 1, in lagoon, 10 m, AMNH.303284 (6pv); Lizard Island, AMNH.303283 (1pv). **Papua New Guinea:** 5–6 m, in sand around coral shoal, between Kranket Island and Madang, 5°12'S, 145°50'E, AMS C.356678 (5pv) (preserved); northern end Madang, 5°12'S, 145°51'E, AMS C.358000 (5 rv, 4lv). New Britain: Duke of York Island, AMS C.68234 (1pv). **Indonesia:** Kalimantan, 14 km N of mouth of Mahakan R., KL (1lv). **Solomon Islands:** Honiara beach, AMNH.303374 (1pv). **New Caledonia:** Secteur de Koumac, 10–16 m, AMNH.303406–AMNH.303409 (4pv); Anse Vata, AMNH.303285 (1pv); Noumea, AMS C.86251 (many) (full New Caledonia locality data is provided Lamprell and Stanistic (1996)). **New Hebrides:** AMNH.303279 (1pv). Fiji: Nadi Bay, 34.5 m, AMS C.67589 (many). **Philippine Islands:** Tabangao, Batangas Prov, Luzon Island, AMS C.104739 (1pv); Sulu Sea, Cuyo Islands, AMS C.2228 (1rv, 1lv); Luzon Island, entrance to Manila Bay, Corregidor Island, AMS C.138086 (1rv); Luzon Island, Bauang, Perez Beach, AMS C.141441 (1rv, 1lv); Palawan Island, N Hondo Bay, Tanabag Beach, AMS C.371091 (1rv). **Mozambique–Northern Zululand** (for full localities refer Lamprell and Kilburn (1999a), all NM material). **Mauritius:** AMS C.96966 (1pv). **Red Sea:** Dissal Island, off Massana, AMS, no number (3pv); NE of Safaga Town, among coral and sand, NMW. Z.1997.021.100 (1pv). **Israel:** Eilat, KL (6pv).

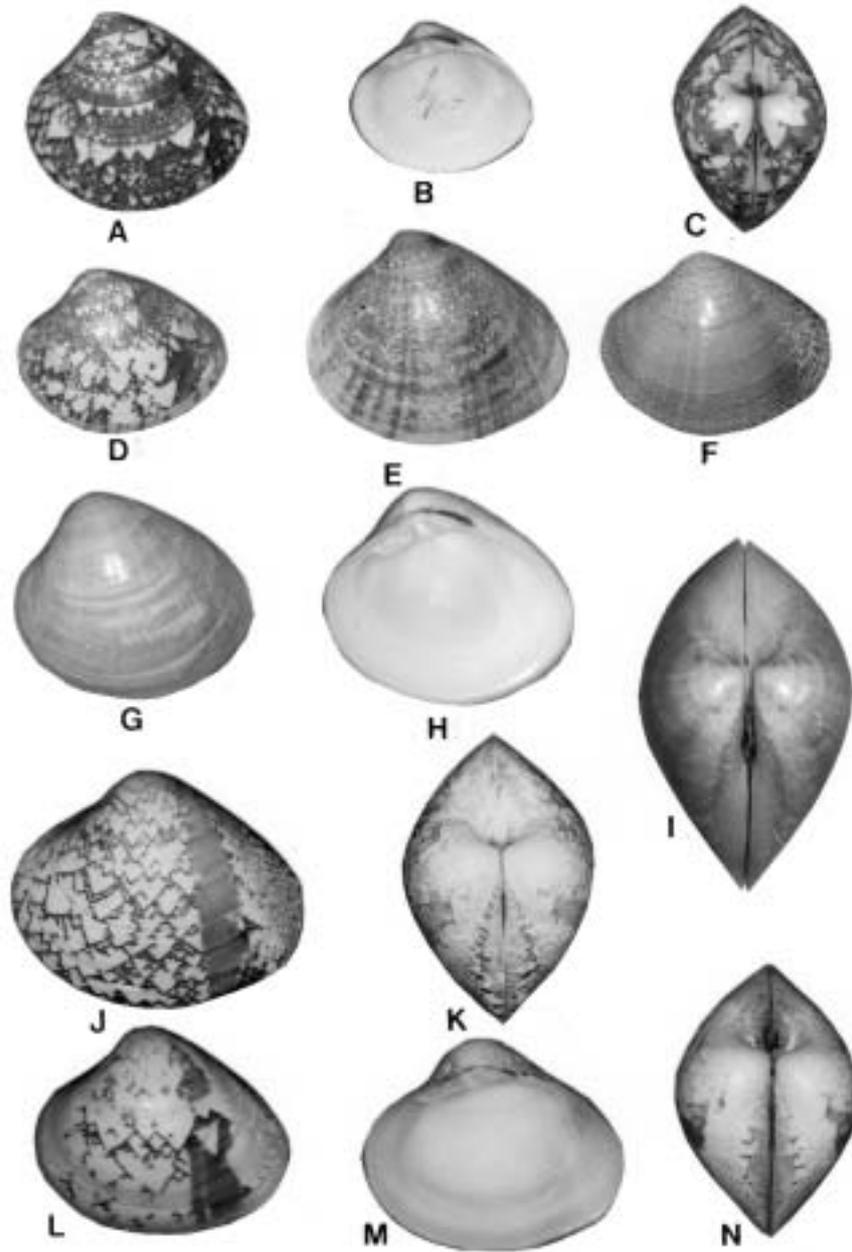


Fig. 7. *A–I*, *Lioconcha ornata* (Dillwyn, 1817). *A–C*, Neotype, Spengler Collection, length 26.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv; *D*, specimen from Spengler Collection, external view lv; *E*, Palm Island, N Qld, QM MO.34141, 38 mm, external view lv; *F*, Honiara, Solomon Islands, AMNH.303038, length 32 mm, external view lv; *G–I*, Slasher's Reef no. 1, AMNH.303284, length 43.3 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J–N*, *Lioconcha berthaulti* n. sp. *J, K*, Holotype, Broadhurst Reef, E of Townsville, AMS C.136078, length 31.7 mm: *J*, external view lv; *K*, dorsal view pv; *L–N*, paratype QM MO.65962, 18°76.7'S, 147°89.9'E, N Qld, length 30 mm: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

Diagnosis

Shell ovate–trigonal to trigonal, solid, smooth to glossy; umbones raised, slightly prosogyrate but markedly so in large adults; lunule elongate heart-shaped to lanceolate, flat, faintly delineated by incised line; anterodorsal margin short, widely rounded terminally; ventral margin widely convex; posterodorsal margin slightly convex, steeply sloping, narrowly rounded at termination. Sculpture of obscure concentric striae, well defined at anterior and posterior margins and stronger growth pauses. Colour externally white with brown blotches forming a dense network of fine chevron markings (tent shaped) over entire surface; umbones white, lunule white often with light-brown staining near umbones; shell internally white usually with yellow or pale orange medially. Dimensions of neotype: length 28.3 mm, height 26.2 mm, width of pv 18.5 mm. Shell length to 48 mm.

Distribution and habitat

Indo-West Pacific (including Japan (Habe, 1977)) in coral sand or loose sand and rubble, littoral to about 50 m.

Remarks

Lamprell and Kilburn (1999a) established a neotype for this species from material in the Spengler Collection. This material is representative of what we may term ‘typical’ *L. ornata*. During the course of the present study, we have examined several specimens, especially from the south-western Pacific, which indicate to us that *L. ornata* (as broadly interpreted herein) either represents a complex of species, subspecies or geographic variants or, as recently suggested by Lamprell and Stanisc (1996), is simply an extremely variable species with the ability to generate a number of distinctive colour and/or morphological forms at any one locality. As indicated elsewhere in this paper, occasional specimens of *L. ornata* may show shape and/or pattern similarities to *L. fastigiata* and *L. annettae* and, by so doing, somewhat blur the boundaries between these three taxa. Unfortunately, examination of the hinge teeth from an extensive range of material has not yielded any characters to help separate these three species, leaving colour pattern, valve shape and sculpture as the only useful means of discrimination. Specimens from Israel often show a patch of purple internally and are trigonal, even in very juvenile specimens. A very attractive form from the Solomons and New Guinea exhibits minute rows of spots, which merge into fine zigzag markings near the dorsal edge. Specimens from the outer region of the Great Barrier Reef are large (45–48 mm), heavy, trigonal and exhibit minute tents in their patterning. The frequent occurrence of intermediates between several of the ‘forms’ suggests that they are all merely variants within a single species. However, it is hoped that future molecular and/or detailed anatomical work will assist in determining whether some of the more distinctive forms here grouped under the name *L. ornata* deserve to be recognised taxonomically.

Lioconcha berthaulti n. sp.

(Figs 7J–N, 13D, 15E)

Material examined

Holotype. Australia: Queensland: 18°57’S, 147°44’E, Broadhurst Reef, off Townsville, subtidal, AMS C.138078 (1pv).

Paratypes. Australia: Queensland: Station 048, 18°76.7'S, 147°89.9'E, 47 m, QM MO.65962 (1pv); Lizard Island, NTM P.12500 (2pv, 1rv (juvenile)).

Other material examined. **Australia: Queensland:** Little Broadhurst Reef, May 1993, Rowse Collection (1pv); Station 031, 18°82.9'S, 147°59.6'E, 53 m, KL (1pv); Lizard Island (1rv), Wistari Reef, Heron Island, Willan Collection (2rv, 3lv). **New Caledonia:** Grand Recif Sud, Stn 552, 22°54'S, 166°55'E, 38 m, MNHN (1rv); Secteur de Belep, Station 1088, 19°46'S, 163°58'E, 23 m, MNHN (1lv, 1pv).

Description and diagnosis

Shell ovate–trigonal; thin but strong, smooth but not glossy; anterior end of shell less than one-third of maximum length; medially inflated; umbones raised, markedly prosogyrate, especially in large adults; anterodorsal margin short, narrowly rounded terminally; ventral margin widely convex; posterodorsal margin almost straight, steeply sloping, narrowly rounded and attenuate terminally; lunule elongate heart-shaped, flat, obscurely delineated by incised line; ligament impressed. Sculpture of concentric striae and well-defined growth pauses, terminating at postero-umbonal ridge. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal very thin, separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique, joined to anterior lateral at top; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, long, thin; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour externally white with a dense network of fine chevron markings (tenting) over entire surface, one broad, orange ray extends from umbones to posteroventral margin, one broad ray composed of fine pale pink dots lies between orange ray and escutcheon; umbones white, lunule usually speckled with brown; shell internally white or very pale flesh colour. Shell dimensions are given in Table 3.

Distribution and habitat

Known only from Queensland and New Caledonia, in coral reef and sand areas to 53 m.

Remarks

This small to medium sized species approaches most closely *L. annettae* and *L. ornata* in size and shape, but can be easily separated from both of these by its more inflated, thinner shell and very distinctive broad orange colour ray posteriorly and narrower hinge plate. In addition, the anterior lateral tooth is smaller and less projecting than in either *L. annettae* or *L. ornata* and, in mature specimens, of *L. berthaulti*, the posterodorsal margin is abruptly

Table 3. Shell dimensions of type material of *Lioconcha berthaulti* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.38078	31.7	27.0	20.5
Paratypes			
QM MO.65962	30.0	25.5	20.5
NTMP.12500 A	30.0	25.4	20.02
B	19.4	16.2	12.2
C	23.8	20.5	9.2 (rv)
D	14.8	12.8	5.3 (rv)

truncate. Mature *L. annettae* and *L. ornata* also normally reach a considerably larger size than *L. berthaulti*. *Lioconcha castrensis* may, in its very juvenile state, show similar tenting of the pattern, but the shell is always more ovate and thicker than *L. berthaulti*, with a much more robust hinge plate and teething. This species has been taken from the same dredge sample as *L. annettae* at one Queensland locality (a complete and fresh juvenile pv, Station 031 18°82.9'S, 147°59.6'E) and as a single dead left valve in the same dredge sample off New Caledonia (Secteur de Belep, Station 1088), together with fresh pv of *L. ornata* and both fresh and single-valve juveniles of *L. castrensis*. Presumably *L. berthaulti* lives sympatrically with one or more other species of *Lioconcha*. The broad orange band may be very faded in dead shells and it is interesting to note that very occasional specimens of *L. ornata* may show a narrow orange band posteriorly, suggesting at least the possibility of some interspecific hybridisation. *Lioconcha berthaulti* appears to be a moderately rare subtidal species, with a known distribution from the Great Barrier Reef off Townsville to New Caledonia.

Etymology

Named for Mr Claude Berthault in recognition of his generous assistance to the authors through the collecting and donation of several lots of *Lioconcha* used in the present study.

Lioconcha sowerbyi (Deshayes, 1853)

Figs 8A–N, 13E, 15E

Cytherea hebraea Sowerby, 1851: sp. 100, figs 143, 144, 148 (not of Lamarck).

Circe sowerbyi Deshayes, 1853: p. 2, sp.7; Reeve, 1863; sp. 29, figs *a,b*.

Lioconcha sowerbyi (Deshayes). Römer, 1864–69 (1866): 46.

Material examined

Lectotype. Figured specimen 148 in Sowerby (1851); figured specimen 29a in Reeve (1863); ex Cuming collection; BMNH.19991518/1 (1pv); here designated (ICZN 74.4; designation by means of an illustration or description); (type locality: Manila, Philippine Islands). Measurements of lectotype: length 31.4 mm, height 27.4 mm, width of paired valves 20.2 mm.

Paralectotypes. Figured specimen 29b in Reeve (1863), BMNH.19991518/2 (1pv); not figured; ex Cuming collection, BMNH.19991518/3 (1pv).

Possible syntypes. Ex Cuming collection, not figured, BMNH.19991519/1 (1pv); ex Cuming collection, not figured, BMNH.19991519/2 (1pv).

Other material examined. **Philippine Islands**: Manilla Bay, QM MO.14505 (2pv).

Diagnosis

Shell ovate–trigonal, moderately thin but strong, smooth but not glossy, moderately inflated; anterior and posterior margins convex and attenuate, ventral margin evenly convex; umbones only slightly projecting, slightly prosogyrate; lunule heart-shaped, flat, weakly delineated by incised line. Sculpture of fine growth striae supplemented by dense, concentric, raised ridges and stronger, irregular growth pauses. Colour externally white with red–brown pattern of small zigzags, often intersected by radial rays of white or red–brown; umbones white, lunule white or brownish; shell internally white, with varying expanses of dark red–brown medially. Shell length to 41.2 mm.

Distribution and habitat

Known only from the Philippine Islands in sandy mud.

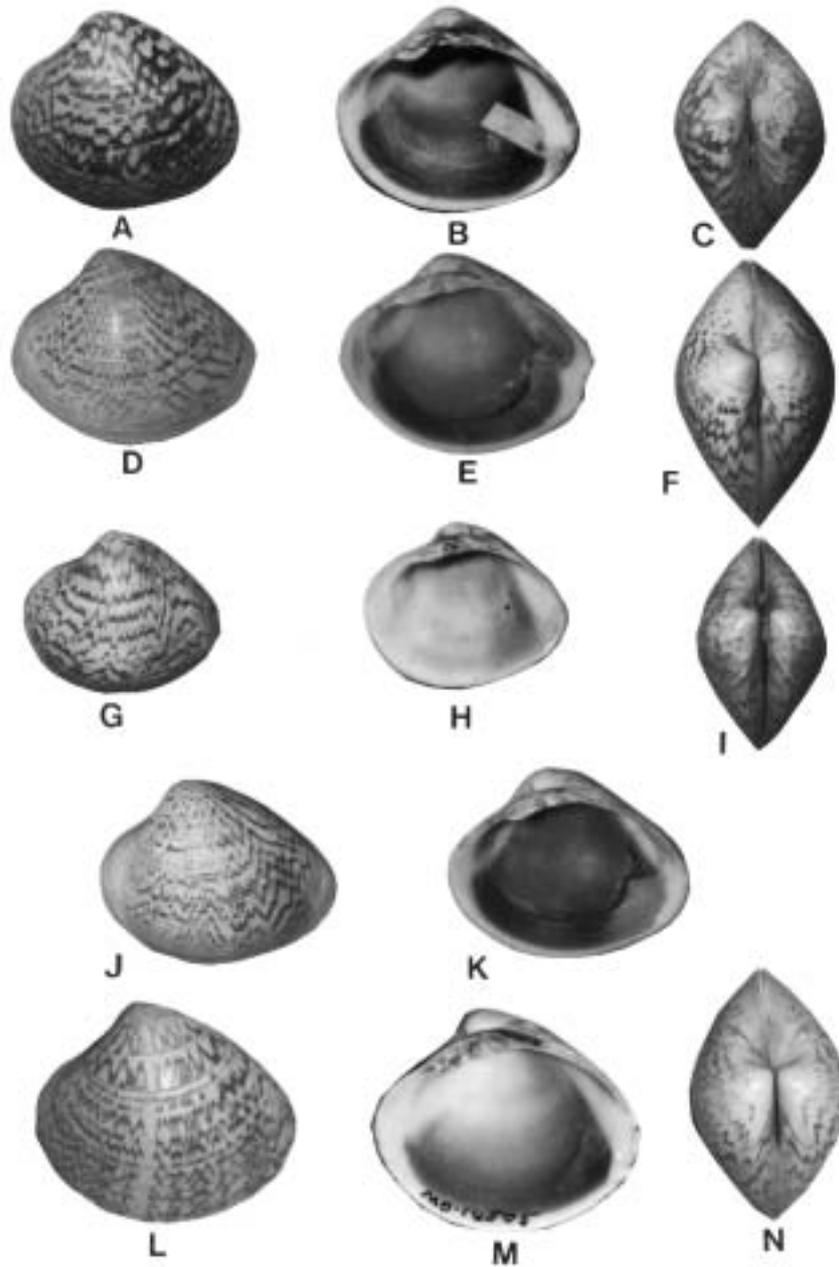


Fig. 8. *Lioconcha sowerbyi* (Deshayes, 1853). *A–C*, Lectotype, here designated BMNH.19991518/1, length 31.4 mm, height 27.4 mm, width of pv 20.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F*, Fig. spec. 29b (Reeve 1863), BMNH.19991518/2, length 41 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–I*, Probable syntype, ex Cuming collection, Manila, Philippine Islands, BMNH.19991519/1, 31.5 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J,K*, ex Cuming collection, BMNH.19991518/3, 39.5 mm: *J*, external view lv; *K*, internal view rv. *L–N*, Manilla Bay, Philippine Islands, QM MO.14505, length 32 mm: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

Remarks

Although *L. sowerbyi* closely resembles *L. schioettei* n. sp. in shape and colour, it lacks the sinuate posteroventral margin of that species and differs in internal colouration (brown staining medially in *L. sowerbyi*, mauve–purple staining posteriorly in *L. schioettei*). *Lioconcha sowerbyi* and *L. schioettei* show a remarkable, but convergent, resemblance in colour pattern to *Pitar (Pitarina) abbreviata* (Krauss) (fine red–brown zigzags interrupted by growth pauses and by rays of white extending from the umbones). The presence of a well-developed pallial sinus in *P. abbreviata* clearly shows that this species is not a member of the genus *Lioconcha*. *Lioconcha trimaculata* differs from *L. sowerbyi* and *L. schioettei* in its smaller size, more regular and better developed concentric ridges, external colouration (emphasising rays, lacking zigzags), purple-brown lunule and escutcheon and in the internal colouration (typically muscle scars with brown staining).

The syntypes of *C. hebraea* Sowerby, 1851 (not of Lamarck, 1818 = *Circe sowerbyi* Deshayes, 1853) have been located in the BMNH. The specimen illustrated by Sowerby (1851; figure 148, BMNH.9991518/1) has been isolated and is here designated as the lectotype in order to fix the type. Sowerby's figured specimens 143 and 144 from the Gubba collection have not been located. Other specimens from the Cuming collection and associated with the lectotype (BMNH.19991518/1–2) are here designated as paralectotypes, whereas two other specimens (BMNH.19991519/1–2), also from the Cuming collection, are possible syntypes.

Lioconcha polita (Röding, 1798)

Figs 9A–J, 13F, 15E

Venus polita Röding, 1798: 181, (type locality not given (= Nicobar Islands, Chemnitz, 1782: 371–372).

Cytherea sulcatina Lamarck, 1818: 568, (type locality: 'l'Océan indien' nr. 29), (refers to Chemnitz, 1782: 371–372); Lamy & Fischer-Piette, 1937: 273.

Circe (Lioconcha) sulcatina (Lamarck). Lynge, 1909: 233 (early references).

Lioconcha sulcatina (Lamarck). Melvill & Sykes, 1898: 48; Lamy, 1930: 135; Oliver, 1992: 186, pl. 40, fig. 3.

Lioconcha polita (Röding). Prashad, 1932: 218.

Lioconcha (Lioconcha) polita (Röding). Lamprell & Kilburn 1999a: 21, pl. 1, figs 1–3 (= *L. schioetti* n.sp. herein, see p. 126).

Material examined

Type material examined. The specimen illustrated by Chemnitz (1782; figs 371, 372; Nicobar Island, Spengler collection ZMUC), used as the basis for Röding's (1798) description of *L. polita*, has been isolated and is here figured and designated as the lectotype in order to fix the type. Dimensions of lectotype: length 41.5 mm, height 35 mm, width of paired valves 27 mm.

Other material examined. Specimen from MNHN, marked on associated label '*Cytherea sulcatina* Lamarck var 2, Individual named by Lamarck. No status'.

Diagnosis

Shell solid, trigonal, smooth to glossy, moderately inflated, posteriorly attenuated; umbones strongly prosogyrate; lunule heart-shaped, flat, delineated by well-incised line. Sculpture of flattened concentric ridges posteriorly and growth pauses. Colour externally white with dark, radial, brown or orange rays, often interacting with rays composed of zigzag or chevron patterns; umbones white or light brown, lunule brownish; shell internally white, sometimes brown or orange medially. Shell length to 41.5 mm.

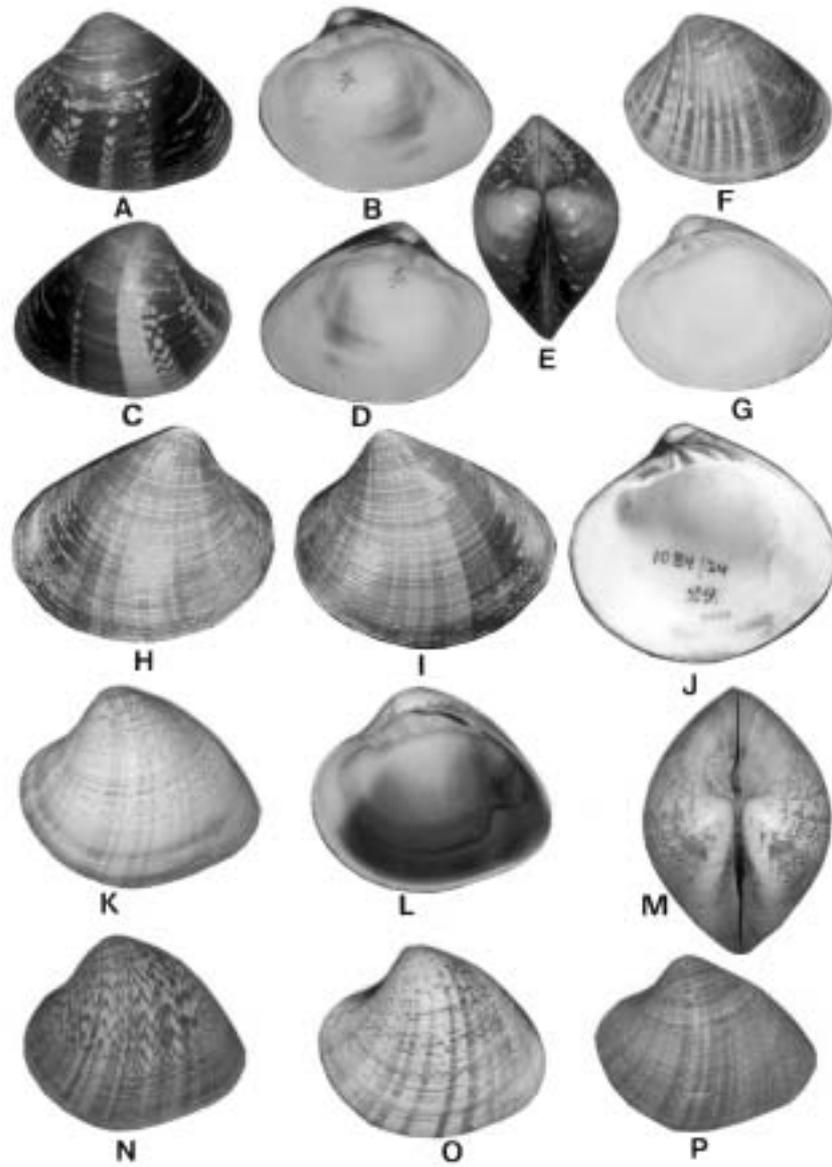


Fig. 9. A–J, *Lioconcha polita* (Röding, 1798). A–E, Specimen illustrated by Chemnitz (1782), figs 371 and 372, Nicobar Island, Spengler collection ZMUC, length 41.5 mm, height 35 mm, width of pv 27 mm: A, external view lv; B, internal view rv; C, external view rv; D, internal view lv; E, dorsal view pv; F, G, specimen from MNHN, marked *Cytherea sulcatina* Lamarck var 2, individual named by Lamarck, no status, length 40 mm, height 33 mm, width of pv 25 mm: F, external view lv; G, internal view rv; H–J, *Cytherea sulcatina* Lamarck, 1818, holotype MHNG.1084/24, length 42.2 mm, height 39 mm: H, external view rv; I, external view lv; J, internal view rv. K–P, *Lioconcha schioettei* n. sp. K–M, Holotype, Taylor Reef, north Queensland, AMS C.204296, dredged 10 m, height 35 mm, length 42 mm, width of pv 28 mm: K, external view lv; L, internal view rv; M, dorsal view pv; N, 20°35'S, 164°12'E, New Caledonia, AMNH.303408, 14–15 m, length 39 mm, external view lv; O, P, Palm Passage off Palm Island, AMNH.303412, 10–15 m: O, external view lv, length 35.5 mm; P, external view lv, length 39.5 mm.

Distribution and habitat

Northern Indian Ocean, littoral areas, in sandy mud.

Remarks

Lioconcha polita can best be compared with *L. sowerbyi*, but the strong groove surrounding the lunule, greater inflation, broad radial colour bands and internally orange or light brown centrally (weak lunule groove, moderate inflation, thin zigzag patterns and deep brown internal colour in *L. sowerbyi*) distinguish the two species. Compared with *L. annettae*, which is also attenuated posteriorly, the broad external radial colour bands, internal orange or light brown colour (sparse tent patterns and yellow internal colour in *L. annettae*) separate the species. The lectotype of *L. polita* is an interesting specimen in that the right and left valves show marked differences in colour patterns, this caused some authors (Lamprell and Whitehead 1992; Lamprell and Stanisic 1996; Lamprell and Kilburn 1999a, 1999b) to deal with the two Chemnitz (1782) figures (371 and 372) as two separate species. Examination of the specimen from the ZMUC and the Lamarck specimen from the MNHN also show this colour variation; however, the specimen MHNG.1084–24 marked '*Cytherea sulcatina* Lamarck, 1818 holotype' does not. Figure 4J, showing the internal rv of MHNG.1084–24, indicates a less elongate shell, but this is due to visual distortion created by the camera angle.

Lioconcha schioettei n. sp.

(Figs 9K–P, 13G, 16A)

Lioconcha (Lioconcha) polita (Röding). Lamprell & Whitehead, 1992: sp. 547; Lamprell & Kilburn, 1999a: 21; Lamprell & Kilburn, 1999b: 44 (not Röding, 1798).

Material examined

Holotype. Taylor Reef, north Queensland, dredged 10 m, 1995, AMS C204296 (1pv).

Paratypes. Queensland: 19°02.7'S, 147°62.2'E, 52 m, AMS C.204297 (47pv); trawled off Loadstone Reef, 30 m, QM MO.66997 (2pv).

Other material examined. **Australia: Queensland:** 14°40'S, 145°28'E, on surface of fine, clean sand, offshore from 'Chinaman's Ridge', Watson's Bay, NW coast of Lizard Island, 16 m, NTM P.000975 (1pv, 1lv); 14°40'S, 145°28'E, on fine, clean sand with siphonaceous algae, offshore from 'Chinaman's Ridge', Watson's Bay, NW coast of Lizard Island, 20 m, NTM P.000976 (1rv); Palm Passage off Palm Island, 10–15 m, AMNH.303412 (2pv, 1rv). **New Britain:** Duke of York Island, AMS C.68247 (in part) (1pv). **New Caledonia:** 20°35'S, 164°12'E, 14–15 m, AMNH.303408 (2pv); Noumea (further material listed by Lamprell and Stanisic (1996) under '*Lioconcha (Lioconcha) polita*'), AMS C.141449 (1pv). **Philippine Islands:** 12°0.000'N, 122°0.000'E, 1935; NMW. Z.1955.158 (9pv) Melville-Tomlin Collection, AMS C.141450 (3pv). **East Timor:** 08°20'S, 125°21'E, in beach drift, Tibar Beach, near Dili, NTM P.000963 (1rv). **Vanuatu** (New Hebrides): Port Vila, AMS C.141448 (3rv, 1lv). **Madagascar:** Nosey-Be, AMNH.303411 (1pv)-AMS C.88985 (1pv). **Tanzania:** Kunduchi Beach, Dar es Salaam, AMS C.124788 (in part) (1rv). **Sri Lanka:** AMS C.107978 (1rv). **Mozambique:** (see Lamprell and Kilburn (1999a) for a listing of material and locality data, under '*Lioconcha (Lioconcha) polita*'). Shell dimensions are given in Table 4.

Description and diagnosis

Shell ovate-trigonal, moderately thin but strong, well inflated, chalky to smooth; umbones raised, slightly to moderately prosogyrate (more so in large adults); anterodorsal margin short, narrowly rounded terminally; anterior margin widely rounded; ventral margin widely convex, slightly but still conspicuously sinuate posteriorly; posterodorsal margin widely

rounded, steeply sloping, narrowly rounded and attenuate terminally; with well-defined postero-umbonal furrow; lunule heart-shaped, flat, obscurely delineated by incised line. Sculpture of fine growth striae supplemented by numerous, slightly raised, concentric ridges, especially over ventral half of valves, and also of well-defined, but irregular, growth pauses. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique; posterior cardinal free, moderately thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, oblique, short; median cardinal, moderately thick, peg-like; posterior cardinal thick, bifid, oblique; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour: externally cream to red-brown with white and red-brown radial rays and diffuse red-brown zigzag markings (the latter stronger umbonally becoming obscure medially); umbones white, lunule light brown or diffuse mauve; shell internally white to yellow, typically stained with mauve posteriorly (mauve staining sometimes extending to median region of valves but often absent in juvenile specimens). Shell dimensions are given in Table 4.

Distribution and habitat

Indo-West Pacific, in clean sand and rubble to 52 m.

Remarks

Examination of several specimens of *L. schioettei* n. sp. from Madagascar, Papua New Guinea, northern Queensland and New Caledonia reveal that *L. schioettei* is reasonably constant in its distinctive valve shape (slightly but consistently sinuate on the ventroposterior margin) and in its colour pattern of intersecting, broken rays and small, somewhat diffuse, zigzag lines. However, the degree of development of the concentric ridges is quite variable, with many specimens observed by us exhibiting pronounced sculpture and others showing very subdued development of the ridges. *Lioconcha sowerbyi* is very similar to *L. schioettei* in shape, surface sculpture and aspects of the external colouration (e.g. also exhibiting fine zigzags of red-brown interrupted by growth pauses and white rays from the umbones) but differs from that species in not having a sinuate posteroventral margin and in being stained brown internally (v. mauve posteriorly in *L. schioettei*). *Lioconcha trimaculata* Lamarck, 1818 shows some resemblance to *L. schioettei* in shell shape, but has more extensive patches of brown colouration externally (not containing fine zigzag lines) and a brown to purple-brown dorsal margin. Internally, *L.*

Table 4. Shell dimensions of type material of *Lioconcha schioettei* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204296	42.1	35.9	27.5
Paratypes			
AMS C.204297 A	31.7	28.8	20.0
B	30.2	26.6	19.5
C	25.8	21.1	16.3
D	18.6	15.7	11.5
QM MO.66992 A	34.8	30.5	22.2
B	27.8	24.0	18.0

trimaculata typically exhibits a patch of light brown on both the anterior and posterior margins (including the adductor scars), whereas, in *L. schioettei*, purple staining is usually confined to a broad band posteriorly (but not in the region of the anterior adductor scar).

Etymology

Named for Mr Tom Schiotte in recognition of his difficult work in isolating the bivalve species from the Spengler and Moltke collections housed in the ZMUC and figured by Chemnitz (1782).

***Lioconcha trimaculata* (Lamarck, 1818)**

(Figs 10A–F, 14A, 16A)

Cytherea trimaculata Lamarck, 1818: 571, sp. 41; Sowerby, 1851: sp. 102; Lamy & Fischer-Piette, 1937: 273.

Circe trimaculata (Lamarck). Reeve, 1863: pl. 8, sp. 33.

Lioconcha sphaeragitis Römer, 1868: 162, pl. 43 fig. 3 (*syn. sensu* Hidalgo, 1903: 221), (type locality unknown).

Lioconcha trimaculata (Lamarck). Römer, 1868: 166, pl. 46, fig. 2; Melvill & Sykes, 1898: 172; Habe, 1977: 259; Springsteen & Leobrero, 1986: 304, pl. 86 fig. 18.

Circe (Lioconcha) trimaculata (Lamarck). Lynge, 1909: 233 (References).

Lioconcha (Lioconcha) trimaculata (Lamarck). Lamprell & Kilburn, 1999b: 45 (Discussion and References).

Material examined

Andaman Islands: Port Blair area, 1858–71, E Man, NMV F.8441 (2 pv, 1rv). **Philippine Islands:** AMNH.303252 (1pv). **New Caledonia:** Nea-Magenta, MNHN, ECOTROPE Expedition. Station (lot 84) (1 pv (juvenile)), littoral collected.

Diagnosis

Shell solid but not thick, ovate, smooth but not glossy, moderately inflated; anterodorsal margin extended anteriorly; posterodorsal margin rounded or slightly attenuate, posteroventral margin showing slight flexure in adults; umbones prosogyrate, more so in adults; lunule flat, heart-shaped, delineated by weakly incised line. Sculpture of fine growth striae supplemented by numerous, fine, concentric, raised ridges over most of valve surface, becoming definable as ribs in ventral half of valve and stronger, irregular growth pauses. Colour externally white, with variously developed rays of brown; lunule and dorsal margin purple or purple–brown; shell internally white or pale peach, usually with light brown associated with adductor. Shell length to 28.5 mm.

Distribution and habitat

Western Pacific, in littoral sand.

Remarks

Lioconcha trimaculata shows similarities to several other *Lioconcha* species, including *L. philippinarum* (Hanley), *L. gordonii* (E. A. Smith), *L. dautzenbergi* (Prasad), *L. schioettei* n. sp. and *L. sowerbyi*. *Lioconcha trimaculata* shares with *L. philippinarum*, *L. gordonii* and *L. dautzenbergi* a purple–brown, clearly incised lunule and a purple–brown escutcheon and predominance of rays in the external colouration. It differs from these three species in lacking the highly glossed surface, in having a much finer ridge sculpture and in

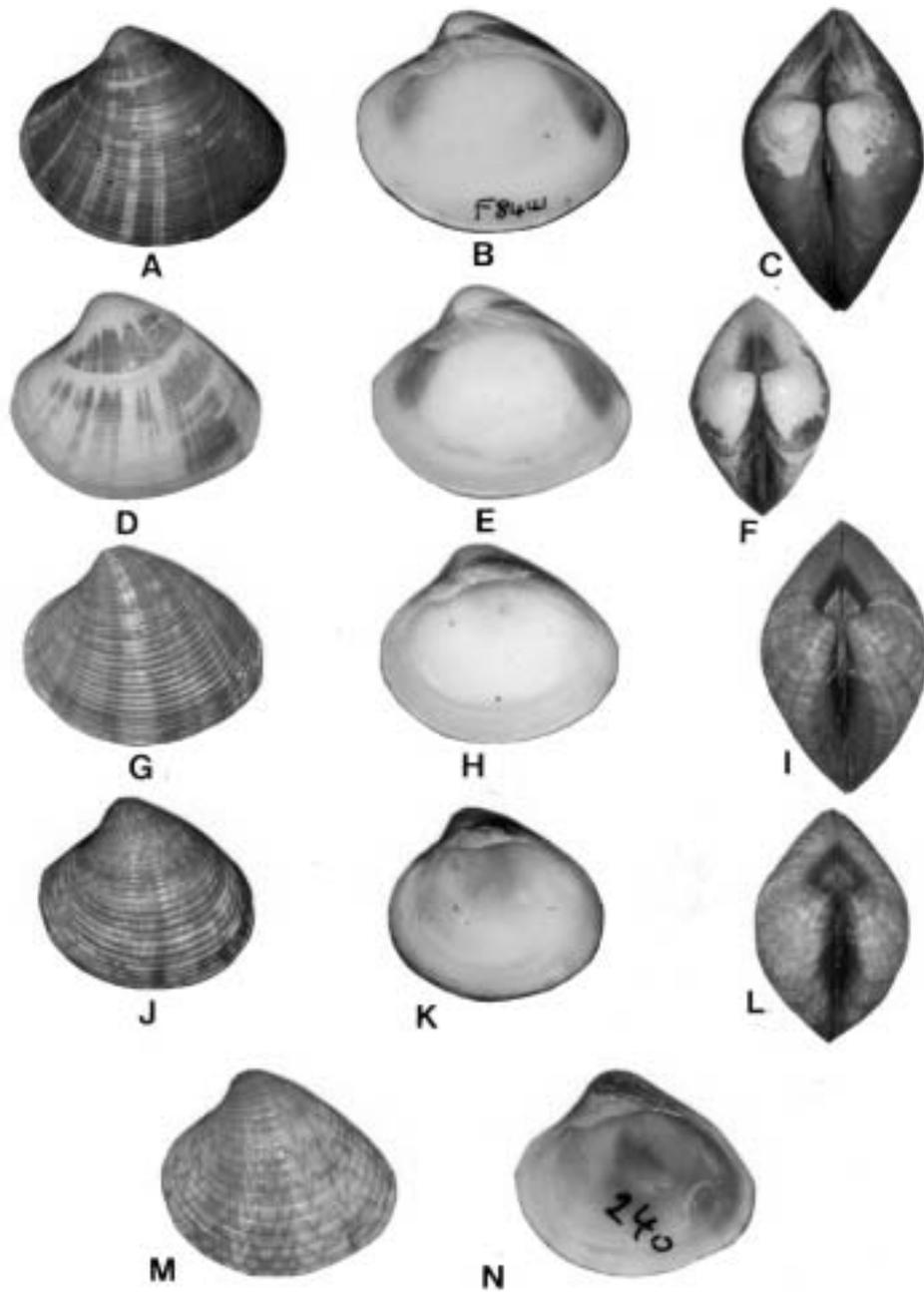


Fig. 10. *A–F*, *Lioconcha trimaculata* (Lamarck, 1818). *A–C*, Philippine Islands, NMV F.8441: *A*, external view lv; *B*, internal rv; *C*, dorsal view pv; *D–F*, Philippine Islands, KL, length 27.6 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–I*, *Lioconcha philippinarum* (Hanley, 1844). *G–I*, New Guinea, AMNH.303252, 24.5 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv; *J–L*, New Guinea, P. Pecker coll.: *J*, external view lv; *K*, internal rv; *L*, dorsal view pv. *M, N*, *Lioconcha dautzenbergi* (Prasad, 1932), holotype, ZMA.3.32.112, length 15.9 mm: *M*, external view lv; *N*, internal view rv.

the positioning of internal staining of the valves (typically anterior and posterior staining in *L. trimaculata* v. subumbonal staining in *L. philippinarum* and *L. gordonii* and median–posterior staining in *L. dautzenbergi*). *Lioconcha trimaculata* shares with *L. sowerbyi* and *L. schioettei* the fine concentric ridge sculpture (although better developed and more regular in *L. trimaculata*), but differs from both these species in external colouration (predominantly rays in *L. trimaculata* v. fine zigzags in *L. sowerbyi* and *L. schioettei*), lunule and escutcheon colouration (purple–brown in *L. trimaculata* v. tan, patterned or white in *L. sowerbyi* and *L. schioettei*) and internal colouration typically anterior and posterior blotches in *L. trimaculata* v. median–posterior mauve staining in *L. schioettei*, median brown staining in *L. sowerbyi*). Lamprell and Kilburn (1999b) confirmed the occurrence of this rare species in the Andaman Islands and we can here substantiate Lyngé's (1909) New Caledonian record based on our examination of a recently collected juvenile from the Ecotrope Expedition (L'institut Francais de Recherche Scientifique pour le Développement en Coopération), this specimen exhibiting a completely white interior but otherwise agreeing with typical *L. trimaculata*.

Lioconcha philippinarum (Hanley, 1844)

(Figs 10G–L, 14B, 16B)

Cytherea philippinarum Hanley, 1844: 110, (type locality: Philippine Islands); Hanley, 1844: pl. 15. fig. 36; Deshayes, 1863: 12.

Cytherea mendance Philippi, 1851: 72.

Cytherea (Dione) philippinarum (Hanley). Smith, 1885: 141.

Hysteroconcha (?*Lamelliconcha*) *philippinarum* (Hanley). Prashad, 1932: 217 (References), pl. 6, figs 7–10.

Lioconcha (Sulcilioconcha) philippinarum (Hanley). Habe, 1951; Lamprell & Stanisic, 1996: 35; Lamprell & Kilburn 1999b: 45.

Callista amirantium Melvill, 1909: 132, pl. 4, fig. 12, (type locality: Amirantes Is., 61.2 m, among Polyzoa and shell rubble).

Material examined

Lectotype. *Cytherea philippinarum* Hanley, 1844, H. Harvey Coll., ex Hanley, designated by Lamprell and Kilburn (1999b): 45, BMNH.1912.6.18.20.

Paralectotypes. BMNH.1966346/1–7; *Callista amirantium* lectotype designated by Lamprell and Kilburn (1999b) three paralectotypes from same lot, BMNH.1910.3.17.14.17.

Other material examined. **Australia:** Murray Island, Torres Strait, AMS C.36345 (1pv); Arafura Sea, 115 m, AMS C.358022 (1rv); Lindeman Island, AMS C.358023 (1lv). **Papua New Guinea:** (ex P. Pecker, no localised data), AMNH.303252 (4pv). **New Britain:** Duke of York Island, AMS C.68244 (in part) (1pv). **Philippine Islands:** AMS C.34910 (2pv). **New Caledonia:** Baie de St Vincent (Lagon: stn 186) (1lv) Secteur de Canala (Lagon: stn 703) (1pv) 40 m; Grand Recif Mengalia (Lagon: stn 839) (2pv, 1lv) 37 m; (stn 849) (1pv, 1lv, 1rv) 41 m; Secteur des Belep (Lagon: stn 1213) (1pv, 1rv) 32 m (MNHN, ORSTOM Expeditions). **Andaman Island:** AMS C.34486 (3pv). **Réunion:** Cap la Houssaye (1lv) 8–17 m, 1984, NM K.4548 (1lv); Saint Paul Bay; 3–30 m, J. Drivas, NM K.2780 (3pv, 14lv, 14rv). **Mauritius:** Off Black R., 24–30 m, NM K.7547 (1pv).

Diagnosis

Shell robust but not thick, elongate–ovate, glossy, moderately inflated; anterior margin rounded; posterior margin rounded, becoming slightly attenuate and truncate in large adults, ventral margin rounded; umbones markedly prosogyrate, more so in adults; lunule heart-shaped, flat, well delineated by incised line. Sculpture of fine growth striae dominated by many coarse, concentric raised ridges developed as rounded ribs; interstices

approximately equal in width to ribs. Colour externally flesh to light brown, with several rays of darker brown and sometimes underlying broad zigzags; lunule and dorsal margin purple-brown; shell internally white with mauve-brown staining subumbonally (staining dominating in small juveniles). Shell length to 27.7 mm.

Distribution and habitat

Indo-West Pacific, in sand and rubble, to 115 m.

Remarks

This is a very distinctive species that is easily differentiated from other heavily ridged *Lioconcha* by a combination of a glossy, flesh to light brown shell (featuring darker brown rays) and a comparatively large adult size. Habe (1951) used this species as the type of his subgenus *Sulcilioconcha* but, as discussed later in the present account, his defining features are inadequate. Habe's reference to a 'purplish' shell appears to apply more so to the inside colouration of the valves rather than the overall external colouration (excepting the lunule area). However, we have not examined Japanese material of *L. philippinarum* and it is possible that geographic variation in external colouration may occur in this species. Although not mentioned by Lamprell and Kilburn (1999b), the lectotype of *L. philippinarum* (selected by them) also shows broad, fine zigzag markings. In most specimens examined herein, only faint traces of zigzags could be discerned, largely due to the predominance of brown rays in the colour pattern. On external appearance, *L. philippinarum* is possibly more likely to be confused with certain other heavily ridged venerids, such as various *Callista* species, but these taxa all have a deep, well-developed pallial sinus. The closest relatives to *L. philippinarum* within the genus *Lioconcha* appear to be *L. gordonii* and *L. dautzenbergi*, which, likewise, have glossy shells and exhibit a well delineated lunule tinged with purple-brown (however, in *L. gordonii*, colour is limited to the periphery of the lunule). These species differ from each other in external colour patterns and degree of rib development, irrespective of the size of the individual. In addition, neither *L. gordonii* nor *L. dautzenbergi* reaches the maximum size attained by *L. philippinarum*. *Lioconcha trimaculata* also exhibits a purple-brown lunule, but has a decidedly non-glossy surface and a tendency to show slight sinuation of the posteroventral margin. Lamprell and Kilburn (1999b) have recently confirmed Deshayes' (1863) record of this species from Réunion in their survey of venerids from the South African and Mozambiquan region. Lamprell and Kilburn (1999b) also note that all specimens from the syntype series of *C. amirantium* are paler than typical Philippine Islands shells, but agree in all other characters.

***Lioconcha dautzenbergi* (Prashad, 1932)**

(Figs 10M–N, 14C, 16B)

Hysteroconcha (?*Lamelliconcha*) *dautzenbergi* Prashad, 1932: 217, pl. 6, figs 11–12, (type locality: Siboga station 240, Banda Sea).

Lioconcha (*Sulcilioconcha*) *dautzenbergi* Prashad. Habe, 1977: 259.

Material examined

Holotype. *Hysteroconcha dautzenbergi* (ZMA 3.32.112).

Diagnosis

Shell robust; ovate-trigonal, glossy; lunule heart-shaped, flat, well delineated by an incised line. Sculpture of fine growth striae largely obscured by wide, rounded concentric ridges

developed as ribs; interstices very narrow compared with width of ribs. Colour externally white-tan, with brown chevron pattern intersected with wide tan rays; umbones, lunule and dorsal margin purple-brown; shell internally white, mauve-purple medially, brown posteriorly. Shell length to 15.8 mm.

Distribution and habitat

Known only from the type locality Siboga stn 240, Banda Sea, habitat unknown (dredged at anchorage in sand).

Remarks

Lioconcha dautzenbergi is a small, distinctive, little known species that is differentiated from other concentrically ridged *Lioconcha* by the fewer stronger concentric ridges, developed as ribs, and very narrow rib interstices. The colouration and shape of the lunule are similar to *L. philippinarum* and, indeed, *L. dautzenbergi* could potentially be confused with that glossy surface species. However, *L. philippinarum* only occasionally exhibits the zigzag lines observed in *L. dautzenbergi*, reaches a larger size and has much narrower, more widely spaced ridges. *Lioconcha gordonii* is similar in size and surface gloss to *L. dautzenbergi*, but the ribs are much narrower, the external colour pattern features zigzags only (no rays of colour), the mauve-purple internal staining is limited to the median portion of the valve and the lunule is primarily white with only a faint tinge of purple peripherally.

***Lioconcha melhartee* Lamprell & Stanisic, 1996**

(Figs 11A–C, 14D, 16C)

Lioconcha (Sulcilioconcha) melhartee Lamprell & Stanisic, 1996: 35, (type locality: New Caledonia, Grand Recif Sud (Lagon) stn 361, 22°36'S, 167°02'E, 78 m).

Material examined

Holotype. New Caledonia: Grand Recif Sud (Lagon: (1pv) stn 361, 22°36'S, 167°02'E, 29 Nov 1984, 78 m, MNHN.

Paratypes. New Caledonia: Grand Recif Sud (1pv, 3lv, 1rv) stn 370, 22°38'S, 167°06'E, 30 Nov 1984, 127 m; Lagon: (2pv, 2rv) stn 397, 22°39'S, 167°11'E, 23 Jan 1985, 125 m; (1pv, 1lv, 1rv) stn 429, 22°40'S, 167°15'E, 25 Jan 1985, 95 m); Sud Nouvelle-Caledonie (Lagon SMIB: (6pv, 2rv) stn DW81, 22°38'S, 167°35'E, 9 Sep 1989, 110 m); Lagon Nord (Lagon: (1pv) stn 484, 19°00'S, 163°35'E, 2 Mar 1985, 35 m; (5pv) stn 517, 19°09'S, 163°35'E, 5 Mar 1985, 42 m; (1pv) stn 522, 19°08'S, 168°38'E, 5 Mar 1985, 42 m, MNHN; (Lagon: Stn 361, 22°36'S, 167°02'E, 29 Nov 1984, 78 m, AM C.305574 (3pv).

Other material examined. Other New Caledonian (ORSTOM) material is listed by Lamprell and Stanisic (1996), but note that some of these specimens now form the type series for *L. caledonesis* Harte & Lamprell, 1999.

Diagnosis

Shell thin but strong, ovate-triangular, smooth but not glossy, lunule heart-shaped, outlined by deeply incised line. Sculpture of dense (approximately 80) raised, concentric, rounded ridges developed as fine ribs, which become wrinkled at the anterior and posterior extremities. Colour externally translucent white, with orange ray extending from umbones to posteroventral margin; dorsal margin and lunule also orange; umbones white; internally glossy white with blue-white growth pauses showing through shell surface. Shell length to 21 mm.

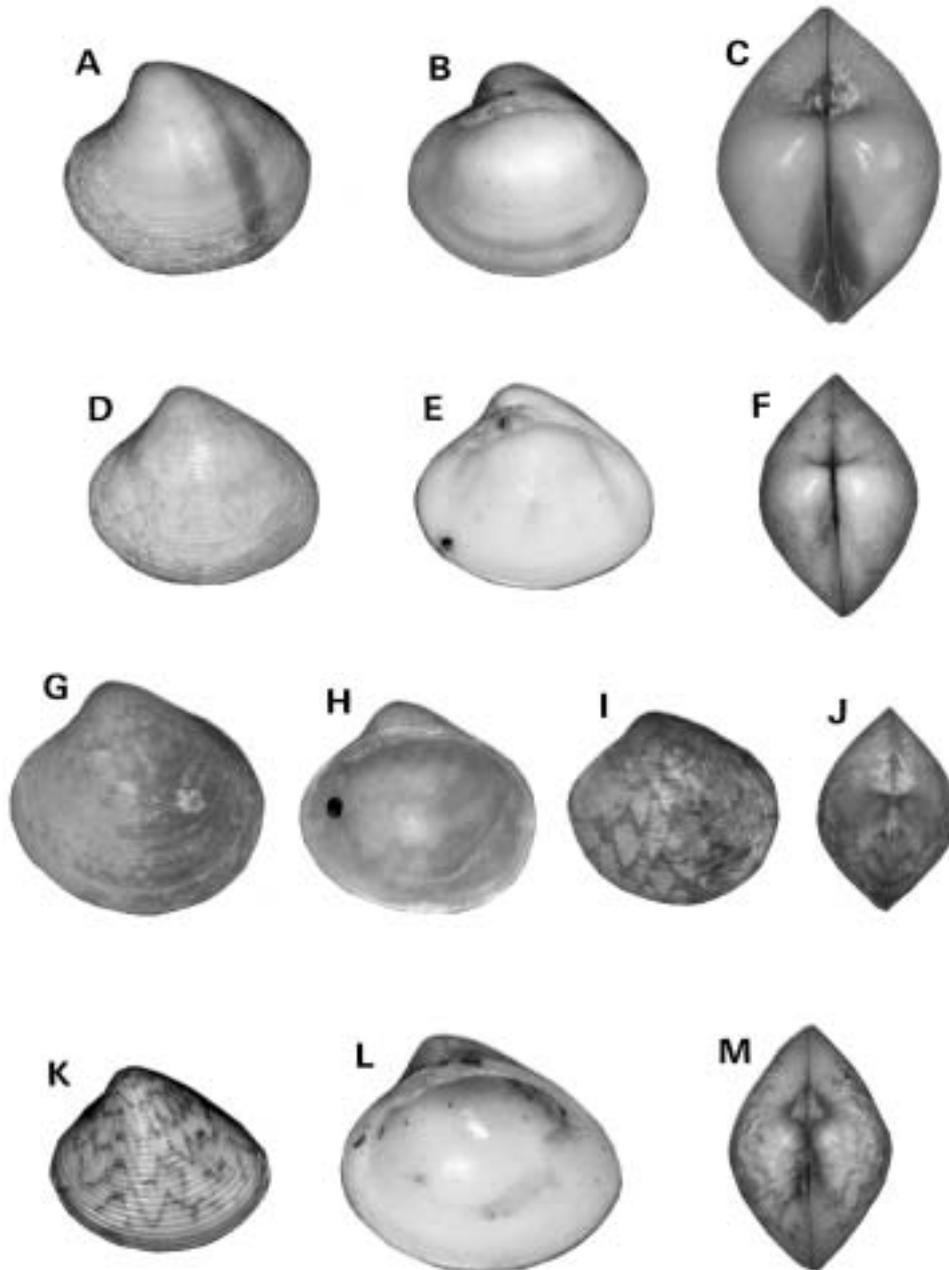


Fig. 11. *A–C*, *Lioconcha melhartae* Lamprell & Stanisc, 1996, New Caledonia, KL, 78 m, length 20.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F*, *Lioconcha caledonensis* Harte & Lamprell, 1999, Secteur de Belep, New Caledonia, KL, length 21 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–J*, *Lioconcha richerdeforgei* Lamprell & Stanisc, 1996, Secteur de Pouebo, KL: *G*, length 9.9 mm, external view lv; *H*, length 9.18 mm, internal view rv; *I, J*, length 8 mm: *I*, external view lv; *J*, dorsal view pv. *K–M*, *Lioconcha gordonii* (E. A. Smith, 1885), Nada Bay, Viti Levu, Fiji, KL, length 14.6 mm: *K*, external view lv; *L*, internal view rv; *M*, dorsal view pv.

Distribution and habitat

Known only from New Caledonia, in sand to 127 m.

Remarks

The thin, strongly inflated, closely ridged valves, featuring a single orange ray posteriorly and an orange dorsal margin and lunule make this a very distinctive species. *Lioconcha melhartae*, as now redefined, is unlikely to be confused with any other species of *Lioconcha*. In their original description, Lamprell and Stanisic (1996) included, together with typical *L. melhartae*, less inflated specimens that lacked the orange colouration of ray, dorsal margin and lunule. Subsequently, Harte and Lamprell (1999) described these specimens as *L. caledonensis*. Although *L. caledonensis* shows a similar ridged sculpture to *L. melhartae*, it differs in having less inflated valves (narrowed posteriorly) and a pattern of widely scattered brown flecks on its white shell. The two species occur sympatrically off New Caledonia, but have yet to be collected outside this region. Sculptural and, especially, colour pattern and valve profile differences easily separate *L. melhartae* from other species within the heavily ridged *Lioconcha* group, such as *L. philippinarum*, *L. richerdeforgesi* and *L. trimaculata*.

***Lioconcha caledonensis* Harte & Lamprell, 1999**

(Figs 11D–F, 14E, 16D)

Lioconcha (Sulcilioconcha) caledonensis Harte & Lamprell, 1999: 97, (type locality: New Caledonia, Secteur des Belep, stn 1103, 19°43'S, 163°57'E).

Material examined

Holotype. New Caledonia: Secteur des Belep: stn 1103, 19°43'S, 163°57'E (1pv) 32 m, MNHN.

Paratypes. New Caledonia: Secteur des Belep: same data as holotype (2pv, 2 rv, 1lv); stn 1129, 19°29'S, 163°49'E (7pv); stn 1117, 19°38'S, 163°54'E (5pv) 40 m; stn 1168 (1lv); Lagon Nord: stn 484, 19°00'S, 163°35'E (1pv) 35 m; stn 517, 19°09'S, 163°35'E (2pv) 42 m; stn 522, 19°08S, 163°38'E (4pv) 42 m, MNHN; stn 1129, 19°29'S, 163°49'E, 40 m, AMS C.312630 (1pv).

Diagnosis

Shell solid, ovate–trigonal, moderately inflated, solid, glossy; umbones strongly prosogyrate; lunule heart-shaped to lanceolate, raised, well delineated by incised line; shell with a weakly defined fold extending from umbones to the posteroventral margin. Sculpture of fine growth striae dominated by crowded, raised concentric ridges developed as rounded ribs, which become slightly wrinkled or disjunct at the anterior and posterior extremities; rib interstices narrow, shallow. Colour externally cream-white with sparse, obscure, irregularly spaced lines and small triangles; umbones and lunule white; shell internally white. Shell length to 18.5 mm.

Distribution and habitat

Known only from New Caledonia, in coarse sand to 42 m.

Remarks

This species is most similar to *Lioconcha melhartae*, especially in relation to size (maximum 20 mm) and the structure of the close-set concentric ridges (see also Remarks for *L. melhartae*). However, *L. caledonensis* differs in having valves that are markedly

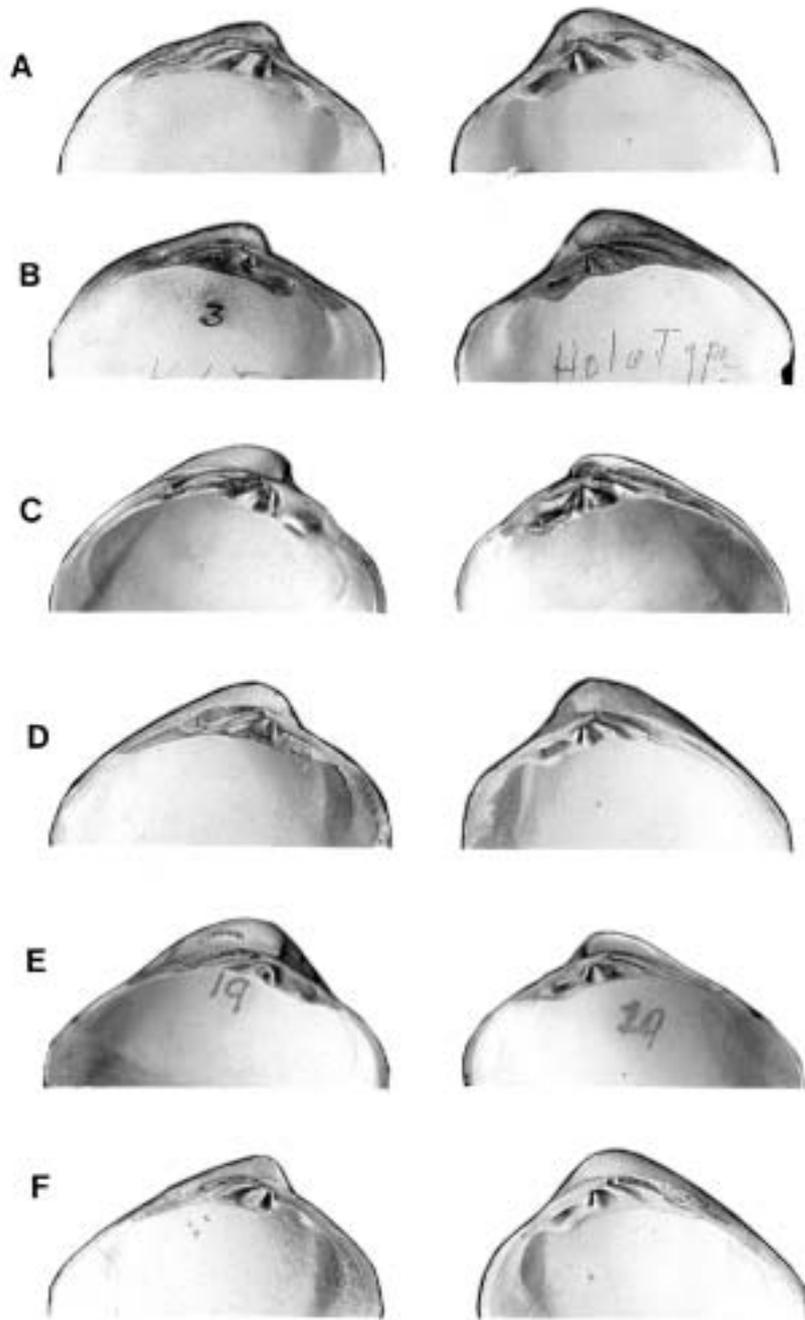


Fig. 12. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A*, *Lioconcha castrensis* (Linnaeus, 1758) Little Trunk Reef, KL, length 49.5 mm. *B*, *L. macaulayi* n. sp., holotype Crouy Reef, New Caledonia, AMS C.204232, length 43.7 mm. *C*, *L. hieroglyphica* (Conrad, 1837), Kaneohe Bay, Oahu, AMS C.061304, length 41.5 mm. *D*, *L. tigrina* (Lamarck, 1818), Mauritius, QM MO.11230, 37.9 mm. *E*, *L. fastigiata* (Sowerby, 1851), Palm Is., KL, length 27.7 mm. *F*, *L. annettae* Lamprell & Whitehead, 1990, Lady Musgrave Island, in lagoon, KL, length 37 mm.

thicker, less inflated and more angulate in shape than those of *L. melhartae*. Moreover, the brown-flecked, poorly developed colour pattern of *L. caledonensis* contrasts with the predominantly white shell of *L. melhartae*, which is coloured by a single, large orange ray posteriorly and an orange dorsal margin and lunule. Other heavily ridged *Lioconcha* species (*L. philippinarum*, *L. richerdeforgesi*, *L. trimaculata* and *L. gordonii*) differ substantially in colour pattern, size and valve shape from *L. caledonensis* and are unlikely to generate any confusion.

***Lioconcha richerdeforgesi* Lamprell & Stanisc, 1996**

(Figs 11G–J, 14F, 16E)

Lioconcha (Sulcilioconcha) richerdeforgesi Lamprell & Stanisc, 1996: 36, (type locality: New Caledonia, Secteur de Pouebo, Lagon, stn 876, 20°35'S, 164°51'E, 30–70 m).

Material examined

Holotype. New Caledonia: Secteur de Pouebo, Lagon (1pv) stn 876, 30–70 m, 20°35'S, 164°51'E, 30–70 m, 13 Jan 1987, MNHN.

Paratypes. New Caledonia: Secteur de Poindimie Lagon (9lv, 8rv many juveniles), stn 830, 105–110 m, 20°49'S, 165°19'E, 10 Jan 1987, MNHN; Secteur de Pouebo, Lagon: stn 876, 30–70 m, 20°35'S, 164°51'E, 13 Jan 1987, AMS C.305575 (2pv, 1 rv, 1lv).

Other material examined. **Australia: Queensland:** Lindeman Island, AMS C.358028 (2rv); off Cairns, 192 m, AMS C.358030 (1lv); Michaelmas Cay 20 m, AMS C.358024 (5 rv, 2lv); St Crispins Reef, AMS C.46277 (6 rv, 1lv). **New Caledonia:** Plateau Chesterfield-Bellona, Chalcal 1, stn D21 MNHN (1lv); Grand Recif Sud, Lagon, stn 324 MNHN (1rv); Secteur des Belep, Lagon, stn 1104 MNHN (1rv).

Diagnosis

Shell very thin, ovate, smooth but not glossy; lunule lanceolate, raised, well delineated by incised line; sculpture of crowded, flattened concentric ridges tending to anastomose at margins; rib interstices narrow, shallow. Colour externally tan with a network of white solid triangular markings; umbones pink, lunule white; shell internally white with external colour patterns visible through shell surface; dorsal margin with external pattern crossing both valves. Shell length to 11.25 mm.

Distribution and habitat

New Caledonia and Queensland, in sand to 110 m.

Remarks

This is the smallest known species of *Lioconcha* and its combination of greatly reduced size, heavy triangle patterning, ovate valves and poorly projecting umbones easily separates it from other heavily ridged members of the genus. *Lioconcha gordonii* is also small, but can be distinguished from *L. richerdeforgesi* by having much coarser ridges, a zigzag pattern and a glossy surface. Of the other small, ridged species of *Lioconcha*, *L. caledonensis* is larger, less patterned and exhibits a longer lunule than *L. richerdeforgesi*, whereas *L. melhartae* has thin, very inflated valves and a distinctive colour pattern featuring a single large ray of orange and an orange dorsal margin. *Lioconcha philippinarum* varies little in valve shape or colour from juvenile to adult and is unlikely to be confused with *L. richerdeforgesi*.

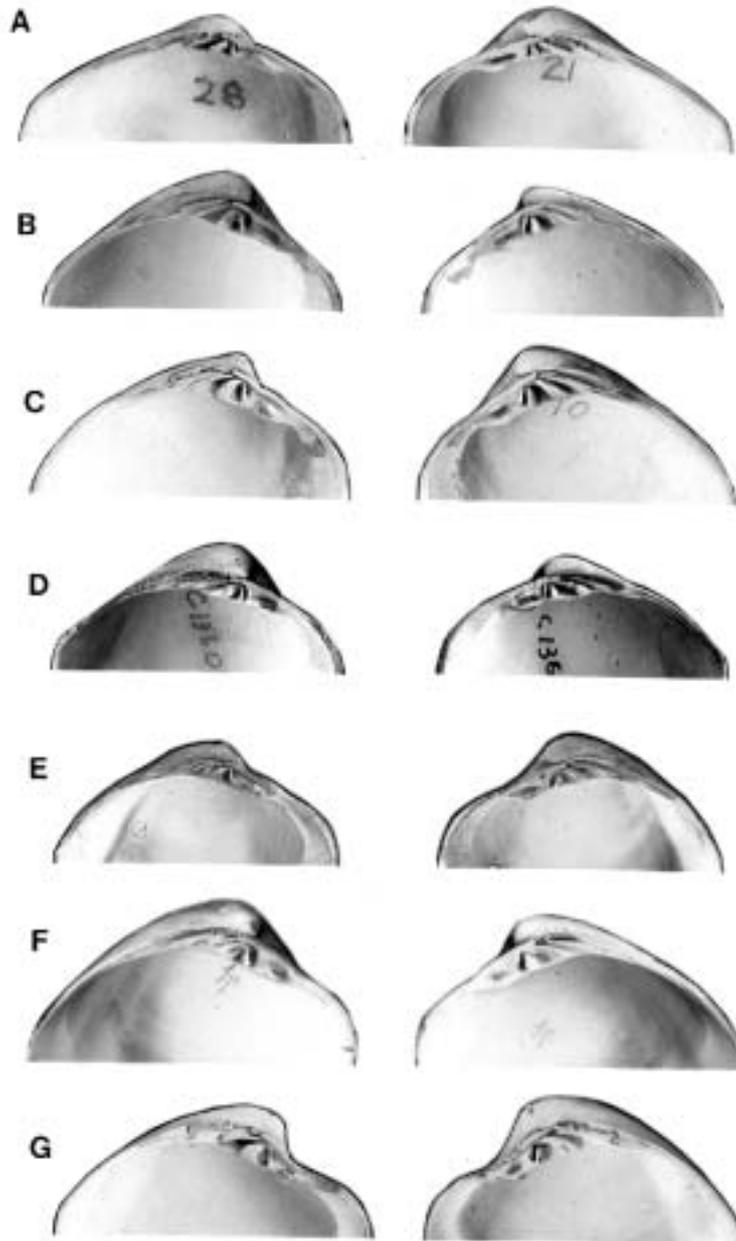


Fig. 13. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A*, *Lioconcha pseudofastigiata* n. sp., holotype, Leyte, Philippines, AMS C.204480, length 34.5 mm. *B*, *L. ornata* (Dillwyn, 1817) Palm Passage, KL, length 33.7 mm. *C*, *L. ornata* (Dillwyn, 1817), Slasher's Reef, KL, 10 m, length 40.3 mm. *D*, *L. berthaulti* n. sp., holotype, Broadhurst Reef, E of Townsville, AMS C.136078, length 31.7 mm. *E*, *L. sowerbyi* (Deshayes, 1853*a*), Manilla Bay, Philippine Islands, QM MO.14505, length 32 mm. *F*, *L. polita* (Röding, 1798), MNHN, marked *Cytherea sulcatina* Lamarck var 2, specimen named by Lamarck, *C. sulcatina* Lamarck, 1817, holotype, MHNG 1084/24, length 42.2 mm. *G*, *Lioconcha schioettei* n. sp., Shelbourne Bay, KL, 52 m, length 32.7 mm.

Lioconcha gordonii (E. A. Smith, 1885), n. comb.

(Figs 11K–M, 14G, 16E)

Circe gordonii E. A. Smith, 1885: 146, (type locality: 22 m off Levuka, Fiji).*Material examined*

Fiji: 16°57'S, 178°47'E, Nadi Bay, 9–35 m, AMS C.338106 (many); 5–19 fathoms, Nadi Bay, AMS C.67583 (in part) (3lv, 3rv). **Society Islands:** AMS C.379959 (1pv). **Sri Lanka:** 9–307 m, AMS C.379960 (1pv, 2lv).

Diagnosis

Shell trigonal, moderately inflated, moderately thin but strong, glossy; umbones strongly progyrate, projecting well above dorsal margins; extended and slightly rostrate posteriorly; moderately inflated; lunule heart shaped, well delineated by incised line. Sculpture of fine growth striae, usually dominated by numerous raised but rounded, concentric ridges developed as ribs (stronger marginally, of sometimes variable coarseness). Colour externally white with transverse zigzag red-brown lines; umbones white; lunule white with purple or mauve tinge peripherally; shell internally white, stained with large median blotch of mauve. Shell to length to 16.3 mm.

Distribution and habitat

Indo-West Pacific (but sporadic), in sand to 110 m.

Remarks

Examination of an extensive series of *Lioconcha gordonii* reveals that the strength and extent of the ribbing may vary and that specimens with poorly developed sculpture can occur in strongly ribbed populations. *Lioconcha melhartae* and *L. caledonensis* are both pale coloured, like *L. gordonii*, but both grow larger than *L. gordonii* and have a proportionately larger lunule. These species also differ from *L. gordonii* in their colour pattern: in *L. melhartae*, a posterior orange ray and orange dorsal margin; in *L. caledonensis*, two to three loosely defined speckled rays. *Lioconcha richerdeforgesi* is much thinner and usually considerably smaller than *L. gordonii* and, although also showing zigzag colour pattern, has ovate valves and low umbones. *Lioconcha dautzenbergi* is similar in size and zigzag colour pattern to *L. gordonii*, but has very thick ribs, less prosogyrate umbones and also exhibits tan rays externally. The compact, mauve-purple lunule of *L. gordonii* is also shared with *L. philippinarum* (a larger species showing a brown colouration with six to eight rays of darker brown), *L. dautzenbergi* and *L. trimaculata* and presumably indicates a close relationship between these species. Although originally placed in *Circe* Schumacher, 1817, by Smith (1885), *L. gordonii* is clearly referable to *Lioconcha*, and is herein transferred to that genus.

Discussion

The genus *Lioconcha* Mörch, 1853 has been divided into two subgenera: *Lioconcha sensu stricto* and *Sulcilioconcha* Habe, 1951. In erecting *Sulcilioconcha*, Habe (1951) gave the following diagnosis for the subgenus: ‘... shell purplish, thick, with remarkable, commarginal ribs’ (English translation of the original Japanese text). He included only the type species *L. philippinarum* within *Sulcilioconcha*. Keen (1969) recognised both subgenera in the ‘Treatise on Invertebrate Paleontology’, but only cited the presence of

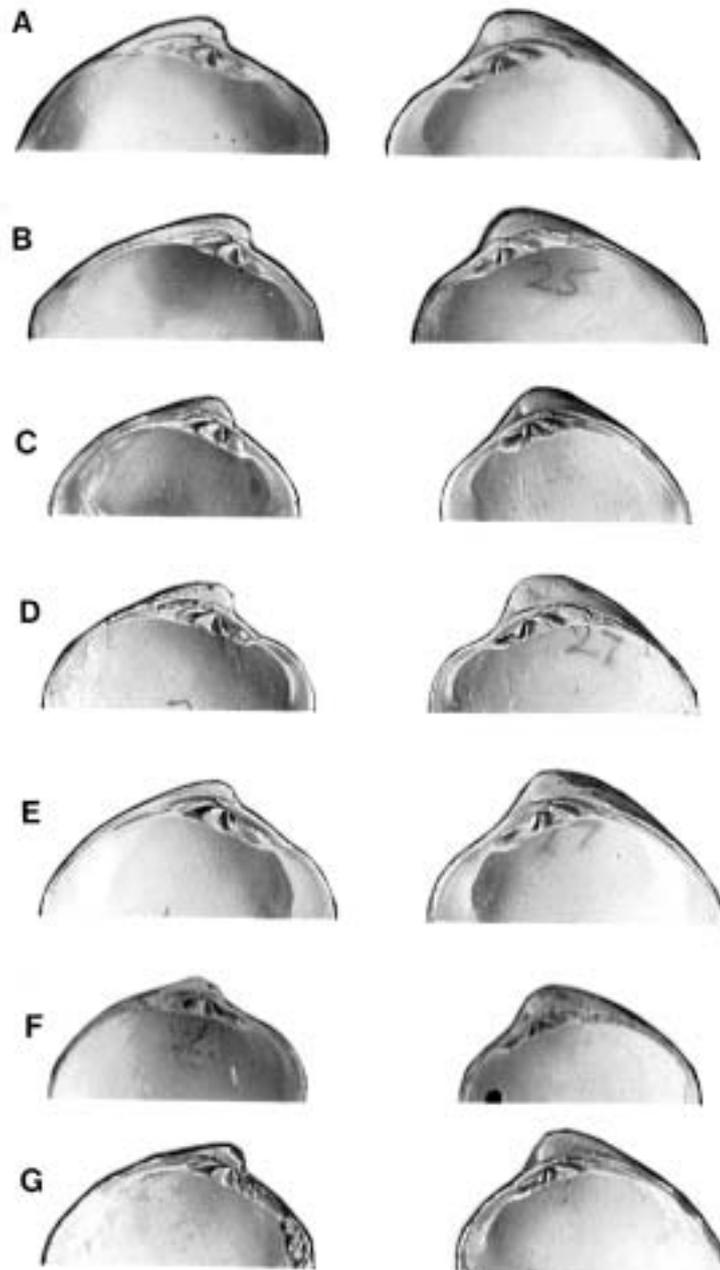


Fig. 14. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A.* *Lioconcha trimaculata* (Lamarck, 1817), Philippines, KL, length 27.6 mm. *B.* *L. philippinarum* (Hanley, 1844), New Guinea, KL, length 29.2 mm. *C.* *L. dautzenbergi* (Prasad, 1932), holotype, ZMA.3.32.112, length 15.9 mm. *D.* *L. melhartae* Lamprell & Stanisc, 1996, New Caledonia, KL, 78 m, length 20.2 mm. *E.* *L. caledonensis* Harte & Lamprell, 1999, Secteur de Belep, New Caledonia, KL, length 21 mm. *F.* *L. richerdeforgesi* Lamprell & Stanisc, 1996, Secteur de Pouebo, KL, length 9.9 mm. *G.* *L. gordonii* (E. A. Smith, 1885), Nada Bay, Viti Levu, Fiji, KL, length 14.6 mm.

concentric ridges (and not shell colouration) in her diagnosis of *Sulcilioconcha*. As we have demonstrated in the present study, the external and often the internal colour of *Lioconcha* shells may vary considerably within and between species. Undoubtedly, valve colouration (both external and internal) is very useful in determining species identity within *Lioconcha*, but not as a key defining character for a subgenus (Habe's reference to a purplish shell for *L. philippinarum* is vague). Several species of *Lioconcha s.s.* may show varying degrees of development of concentric commarginal ridges, to the point that certain highly sculptured specimens of *L. annettae*, *L. schioettei* and *L. sowerbyi* would qualify for inclusion within *Sulcilioconcha* rather than *Lioconcha s.s.* Comparison of *L. schioettei* with *L. trimaculata* provides an excellent example highlighting the rather superficial nature of the subgeneric division. These two species show many conchological similarities (suggesting a close relationship) but, based on the stronger and more consistent development of concentric ridges in *L. trimaculata*, the two would have to be placed into different subgenera. In the case of the normally heavily ridged species *L. gordonii*, we have observed a marked degree of variation in the strength of the ridges, once again suggesting that any subgeneric division of *Lioconcha* based solely on external sculpture has no validity.

Although the precise relationship of *Lioconcha* to other pitarine genera remains to be clarified, in terms of general shell shape, teeth and hinge plate morphology, colour pattern and sculptural range, the group appears closest to *Pitar* Römer, 1857 and *Callista* Poli, 1791. However, *Lioconcha* differs markedly from these two genera in the extent of the pallial sinus, this feature being almost absent in *Lioconcha* and deep and clearly marked in *Pitar* and *Callista*.

The present study has shown that whereas most *Lioconcha* species, such as *L. philippinarum*, *L. melhartae* and *L. berthaulti* n. sp., show low or at least moderately low levels of external colour and pattern variation, others, such as *L. castrensis* and *L. ornata*, show very wide variation. In the latter examples, there is a real possibility that some variants may be worthy of taxonomic recognition and, alternatively, some nominal taxa (e.g. *L. annettae*) may prove to be colour variants of other species. The presence of occasional specimens seemingly intermediate between two sympatric species suggests the possible occurrence of local hybridisation (e.g. between *L. ornata* and *L. annettae* in waters off New Caledonia). Unfortunately, at present, comparative anatomical, reproductive and molecular data are lacking to probe the significance of colour and/or pattern variations within species of *Lioconcha*. Internal colouration can also vary within populations, sometimes more than external colour and/or pattern, but often such variation is associated with increasing age. Juvenile *L. schioettei* n. sp., for example, are often white to light yellow internally and only acquire the mauve posterior colouring with advanced adulthood (and, even then, the valves may occasionally retain their juvenile colour).

In terms of structural variation, we have observed that the umbones often become increasingly prosogyrate with age in a number of species (e.g. *L. ornata*, *L. annettae*, *L. fastigiata* and *L. castrensis*). Usually this occurs as the result of the posterior extremity becoming more attenuated. However, in adults of *L. castrensis* of the 'hieroglyphic' pattern, large individuals have more circular valves (height and length almost equal) compared with the anteriorly–posteriorly elongate juveniles from the same population (valves longer than high). In addition, we have seen evidence of stunting of the posterior extremity, presumably through interaction of the living animal with a less than optimal sediment type. Such valve shape changes reduce the value of length : height ratios for taxonomic discrimination if the primary goal is to unequivocally define a species throughout all its growth stages (unless one is comparing similar sized specimens of different species).

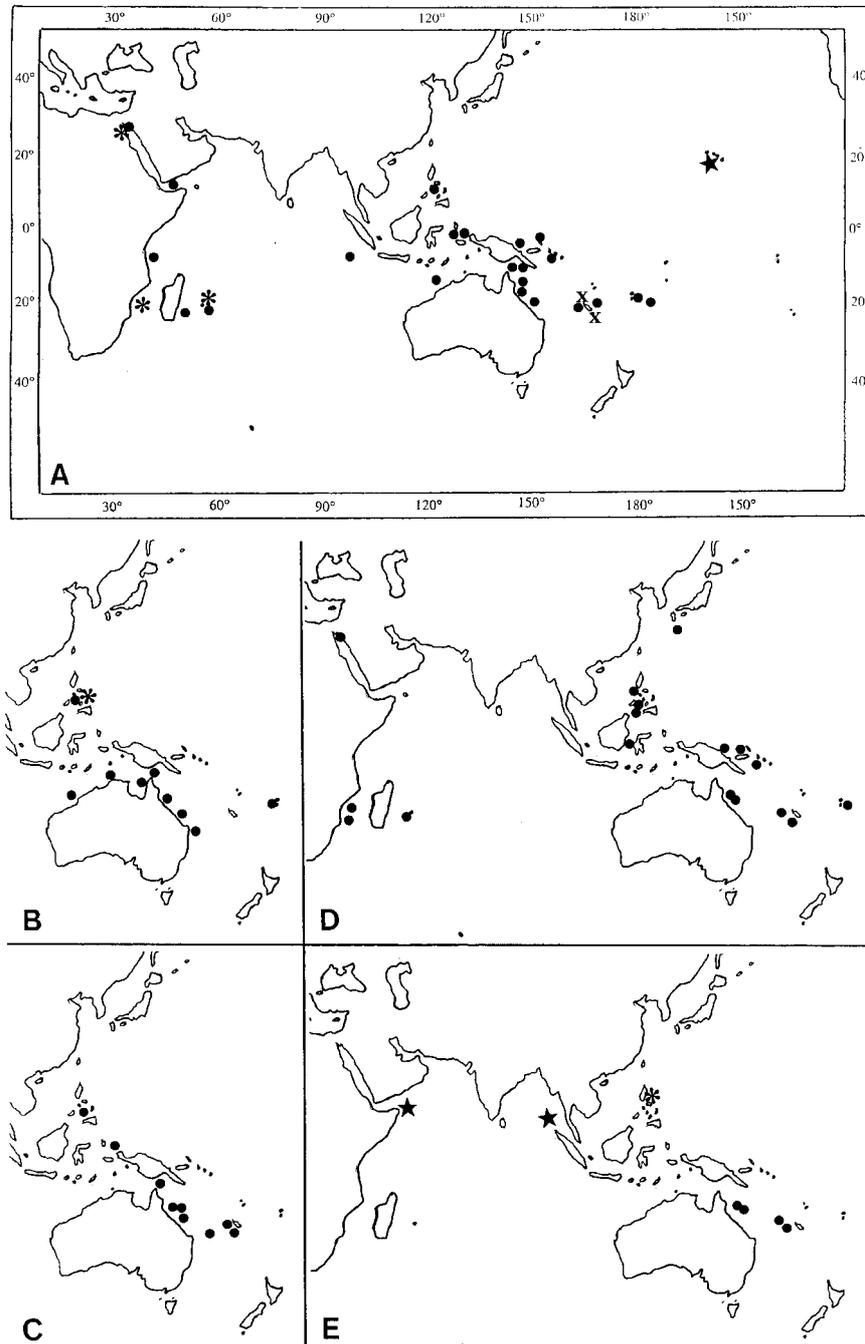


Fig. 15. Distribution. A, *Lioconcha castrensis* (Linnaeus, 1758) (●); *L. macaulayi* n. sp. (X), *L. hieroglyphica* (Conrad, 1837) (★), *L. tigrina* (Lamarck, 1818) (*). B, *L. fastigiata* (Sowerby, 1851) (●), *L. pseudofastigiata* n. sp. (*). C, *L. annettae* Lamprell & Whitehead, 1990 (●). D, *L. ornata* (Dillwyn, 1817) (●). E, *L. sowerbyi* (Deshayes, 1853) (*), *L. polita* (Röding, 1798) (★), *L. berthaulti* n. sp. (●).

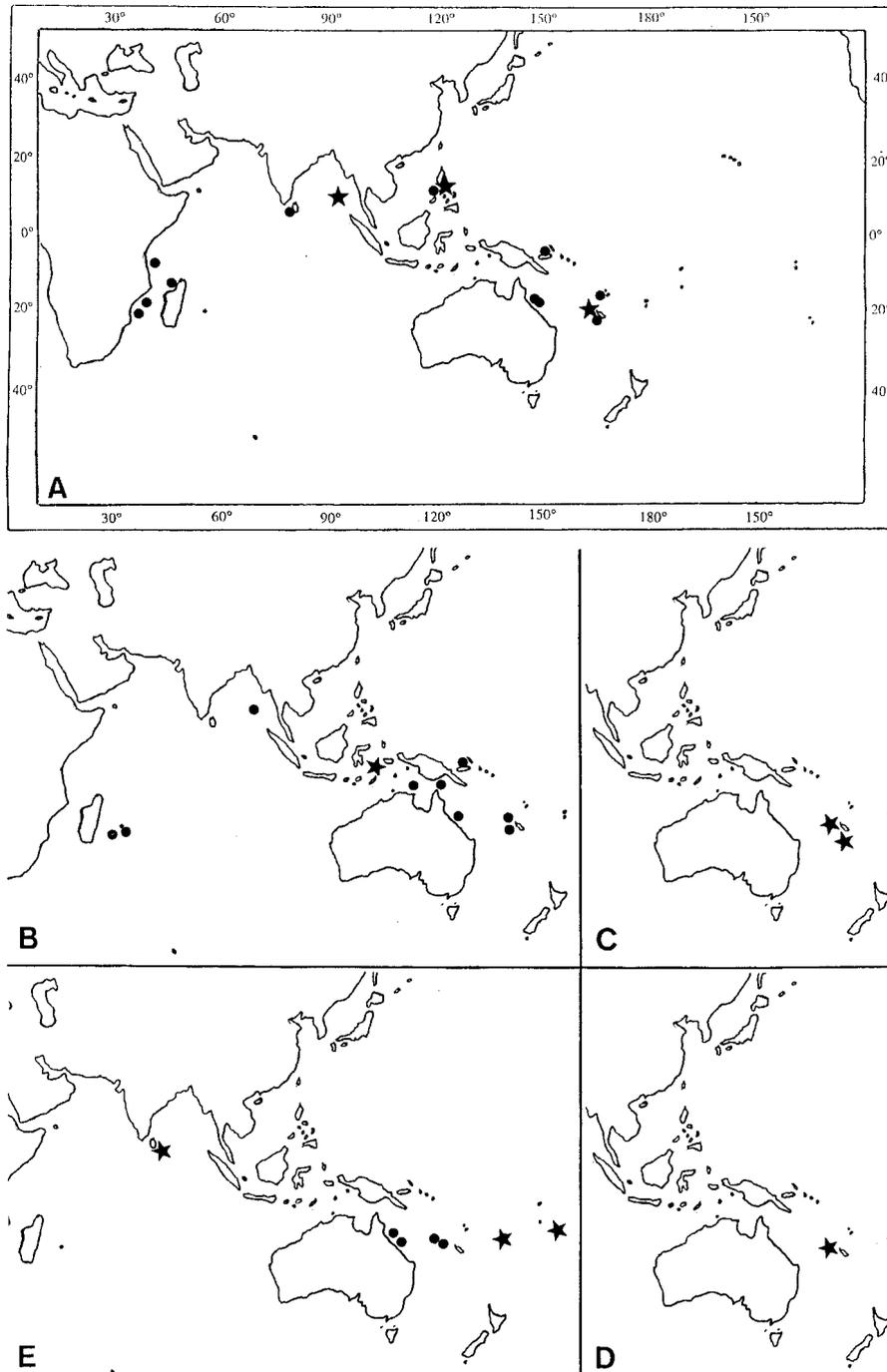


Fig. 16. Distribution. A, *Lioconcha schioettei* n. sp. (●), *L. trimaculata* (Lamarck, 1817) (★). B, *L. philippinarum* (Hanley, 1844) (●), *L. dautzenbergi* (Prashad, 1932) (★). C, *Lioconcha melharteeae* Lamprell & Stanisc, 1996 (★). D, *L. caledonensis* Harte & Lamprell, 1999 (★). E, *L. richerdeforgei* Lamprell & Stanisc, 1996 (●), *L. gordonii* (E. A. Smith, 1885) (★).

The restricted distribution of several species, such as *Lioconcha macaulayi* n. sp., *L. melhartae*, *L. richerdeforgesi* and *L. berthaulti* n. sp., invites discussion. We are unaware of any studies of the length of time spent by larval *Lioconcha* in the water column prior to settlement. However, it would be of considerable interest to determine whether the seemingly high degree of endemism exhibited by several *Lioconcha* species is due to a very abbreviated pre-settlement time (i.e. drifting time spent by veligers in the water column and under the dispersal influence of water currents) or is simply the product of patchy collection effort (many areas of the Western Pacific remain unsampled or poorly sampled). Conceivably, both factors are involved but, if sediment type plays any significant role in settlement success (and the effects of valve stunting, and variation in sculpture strength both hint that this may be so), then there would be a clear selective advantage in having a short larval pre-settlement time. Short pre-settlement times, combined perhaps with localised current eddies, would enhance the prospects of speciation by limiting genetic exchange between populations, as opposed to long pre-settlement times, which would enhance genetic exchange and expand species ranges (see, for example, Scheltema 1971, 1986). High levels of endemism appear to be characteristic of the Australian Veneridae in general, with endemics making up 43% of all venerid species recorded in the fauna (Harte 1998). We anticipate that future studies, especially molecular genetics and field observations on live animals, in combination with comparative work on reproductive habits (including comparative larval settlement studies), will aid greatly in resolving taxonomic difficulties within the genus *Lioconcha*. Controlled breeding experiments between conspecifics and between nominal taxa would also prove a worthwhile exercise, if only to determine the level of colour and pattern variation possible from a single mating pair. Attention for future work should be focused particularly on the variable *L. castrensis* and the exceedingly variable *L. ornata*, with special attention being paid to distinct colour and shape variants.

Key to extant species of *Lioconcha*

Although most species of *Lioconcha* are relatively constant in colour pattern, some of the larger-sized (30–55 mm) species may exhibit significant variation, even at a single collection site. Certain structural features also alter with age, such as the position of umbones in relation to the anterior and posterior extremities and the size of hinge teeth. External colour pattern and internal colour also often vary to some extent between size classes in some species. The following key is intended to be used in conjunction with the plates and text. It should be expected that occasional specimens may prove difficult or impossible to determine accurately, especially in the case of extremely juvenile or worn and bleached material. The key is largely intended for the identification of late juvenile to mature specimens (the size ranges given for each species are indicative of adult specimens). In general, we have emphasised the most accessible and constant shell features, but have also attempted to accommodate any variation in features based on the material available for study.

1. External colouration of shell with a single, broad orange ray posteriorly 2
 External colouration of shell lacking a single, broad orange ray..... 3
2. Shell smooth; tented-reticulate background colour; lunule white or pink; dorsal margin speckled *L. berthaulti* (20–30 mm) (Figs 7J–N, 13D, 15E)
 Shell with raised, concentric ridges; white background colour; orange lunule and dorsal margin *L. melhartae* (10–15 mm) (Figs 11A–C, 14D, 16C)
3. Raised ridges present over all or most of valve surface..... 4
 Raised ridges absent or evident only on marginal regions of valves 9
4. Lunule or perilunular area (and usually dorsal margin) purple-brown in colour 5
 Lunule and perilunular area white, patterned or brown/black; dorsal margin white or patterned 7

5. Shell smooth but not glossy; fine raised ridges externally; internally usually with brown blotch associated with each adductor scar *L. trimaculata* (20 mm) (Figs 10A–F, 14A, 16A)
 Shell glossy; coarse raised ridges externally; internally, colour patches not associated with one or either adductor scars 6
6. Shell externally chestnut brown, with two to five darker brown rays and sometimes faint zigzags; dorsal margin brown or purple-brown; internally white with light brown blotch under umbones *L. philippinarum* (20–30 mm) (Figs 10G–L, 14B, 16B)
 Shell externally white overlain with zigzag reticulations; dorsal margin white or with some line patterning; internally white with brown/purple blotch mid-valve *L. gordonii* (10–15 mm) (Figs 11K–M, 14G, 16E)
 Shell externally white overlain with broad bands or brown and zigzag reticulations; dorsal margin purple-brown; internally white with purple patch mid-valve and brown on posterior adductor scar *L. dautzenbergi* (10–15 mm) (Figs 10M,N, 14C, 16B)
7. Shell minute; rounded; thin and fragile; fine, concentric raised ridges developed as fine ribs; white tented reticulate pattern on tan externally *L. richerdeforgesi* (5–8 mm) (Figs 11G–J, 14F, 16E)
 Shell small, robust, well developed, concentric raised ridges developed as ribs; externally white with small, scattered, faint tent markings *L. caledonensis* (10–20 mm) (Figs 11D–F, 14E, 16D)
 Shell moderately to very large (20–55 mm), robust to moderately thin; concentric raised ridges clearly marked or subdued; externally tan to brown, pattern of fine, diffuse zigzags 8
8. Posterior–ventral margin showing sinuation; umbones slightly to moderately prosogyrate; lunule weakly delineated by incised line; internally white to yellow, usually with mauve-purple staining posteriorly *L. schioettei* (30–40 mm) (Figs 9K–P, 13G, 16A)
 Posterior–ventral margin evenly convex; umbones slightly to moderately prosogyrate; lunule weakly delineated by incised line; internally white with extensive postero-ventral brown staining *L. sowerbyi* (25–35 mm) (Figs 8A–N, 13E, 15E)
 Posterior–ventral margin evenly convex; umbones strongly prosogyrate; lunule well delineated by incised line; internally white, often with some median brown staining *L. polita* (30–40 mm) (Figs 9A–J, 13F, 15E)
9. Lunule raised, well delineated by deeply incised line 10
 Lunule flat, poorly delineated by incised line 12
10. Shell with abruptly truncate posterior margin; heart-shaped lunule; valves externally white overlain with sparse, irregular tents or blotches, most of which appear smudged and diffuse *L. macaulayi* (40–50 mm) (Figs 2A–O, 12B, 15A)
 Shell with rounded posterior margin; heart-shaped to lanceolate lunule; valves externally white to grey-white with well-defined markings 11
11. Shell circular to ovate; umbones slightly progyrate; externally valves with variable pattern of tents, zigzags or rods (or a mixture of these) *L. castrensis* (30–55 mm) (Figs 1A–K, 12A, 15A)
 Shell ovate–triangular; umbones markedly prosogyrate; externally valves with rod or angular markings *L. hieroglyphica* (40–50 mm) (Figs 3A–L, 12C, 15A)
12. Ridges clearly marked on ventral third of valve 13
 Shell lacking or essentially lacking ridge sculpture (i.e. growth striae only) 14
13. Colour pattern composed of many, open brown tents of varying sizes (pointing away from the umbones), often diffuse (and with patches of grey); umbones not markedly raised above hinge line *L. annettae* (30–40 mm) (Figs 5K–P, 12F, 15C)
 Colour pattern composed of solid tents (pointing towards the umbones) of reddish-brown on a white background, the tents often amalgamating ventrally into coarse, angled rays; umbones markedly raised above hinge line *L. tigrina* (30–40 mm) (Figs 4A–N, 12D, 15A)
14. Colour pattern externally of heavy, open black-brown tents often interconnected; rays of colour never present externally; lunule with black-brown blotch umbonally; shell internally white often flesh coloured umbonally *L. fastigiata* (20–40 mm) (Figs 5A–J, 12E, 15B)
 Colour pattern externally of solid black-brown tents sometimes connected; rays of colour never present externally; lunule with black-brown blotch umbonally; shell internally white, often flesh coloured umbonally, always with broad, diffuse purple-brown ray or blotch medially *L. pseudofastigiata* (25–34 mm) (Figs 6A–G, 13A, 15B)
 Colour pattern externally of small to minute open tents of brown, very commonly intersected by rays of brown or white; lunule lacking black-brown blotch umbonally; shell internally white to orange *L. ornata* (25–45 mm) (Figs 7A–I, 13B,C, 15D)

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