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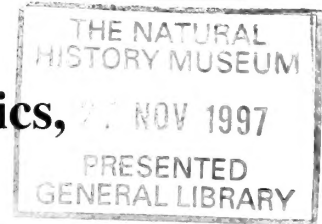
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# The lucinid bivalve genus *Cardiolucina* (Mollusca, Bivalvia, Lucinidae): systematics, anatomy and relationships



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JFR N 30066

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**SYNOPSIS.** The marine lucinid genus *Cardiolucina* (usually known as *Bellucina*) comprises 11 living species of small, heavily ornamented, subspheroidal bivalves. The type species of the genus is the Miocene fossil *C. agassizi* (Michelotti). A new definition and description of the genus is given. All the living species and the type species are redescribed and illustrated. Two species, *C. australopilula* from Western Australia and *C. siquijorensis* from the Philippines, are described as new. Anatomical details are given for two species which both contain chemosymbiotic bacteria in the ctenidia. A preliminary phylogenetic analysis using shell characters and *Parvilucina* as an outgroup, indicates three clades of *Cardiolucina*. Nine species are found in the Indo-W. Pacific and two in the tropical Atlantic. The greatest diversity occurs around Australia where seven species live. The two Atlantic species are similar to the widespread Indo-Pacific species *C. semperiana*. The earliest-known species of *Cardiolucina* is from the Eocene, but the fossil record is very poor.

## INTRODUCTION

Since the discovery of endosymbiotic sulphur-oxidising bacteria contained in the gills, the biology of bivalves in the family Lucinidae has attracted much attention (Fisher & Hand, 1984; Dando, Southward, Southward, Terwilliger & Terwilliger, 1985; Dando, Southward & Southward, 1986; Southward, 1986; Reid & Brand, 1986; Distel and Felbeck, 1987; Cary, Vetter & Felbeck, 1989; Fisher, 1990; Reid, 1990). The symbiosis has so far been recorded in about 25 species of Lucinidae and some species have been shown to be nutritionally dependent on the association (Le Pennec, Beninger & Herry, 1995). The discovery and investigation of the symbiosis has been the key to understanding the many unusual features of lucinoid morphology and habitat distribution (Allen, 1958; Reid & Brand, 1986, Reid, 1990). Despite the burgeoning biological interest in lucinid bivalves, it is unfortunate that the systematics of family are not well understood, with many taxonomic groups, particularly at the supraspecific level, being rather loosely defined. Most recent comprehensive systematic treatments of Lucinidae (Chavan, 1969; Bretsky, 1976) both pre-date the discovery of chemoautotrophy in the family and, moreover, are based entirely on shell characters. As Hickman (1994) points out, there has been no attempt to incorporate the

potential wealth of anatomical and biological characters into systematic studies. Furthermore, following closer attention to lucinid biology and the investigation of new habitats it is now being recognised that there are many undescribed species.

In this paper, we review the species of the lucinid genus *Cardiolucina* (better known as *Bellucina*), which are largely tropical, small, subspheroidal bivalves found in the Indo-Pacific and Atlantic Oceans. The impetus for this revision stems from the discovery of two coexisting lucinids in the shallow waters around the Abrolhos Islands, Western Australia (Glover & Taylor, 1997). Both species appeared to be undescribed and one with unusual periostracal extensions has been assigned to a new genus *Rastafaria* (Taylor & Glover, 1997). The other species, which forms a part of this paper, was evidently a *Cardiolucina* and seemed similar to *C. semperiana* Issel, which is widespread in the Indo-West Pacific. However, preliminary research indicated that there is much taxonomic confusion within the genus, including the priority of the name *Cardiolucina* over *Bellucina*. This led us to revise and redescribe the type species, provide a new diagnosis of the genus, to review the Recent species from the Indo-Pacific and Atlantic Oceans and to describe new species from Western Australia and the Philippines. We have also attempted to identify within the genus *Cardiolucina* those shell and anatomical characters that might be used in a wider study of lucinid systematics.

## ABBREVIATIONS

Institutions: AM – The Australian Museum, Sydney; ANSP – Academy of Natural Sciences, Philadelphia; BMNH – The Natural History Museum, London; MNHN – Muséum National d'Histoire Naturelle, Paris; IRSNB – Royal Belgian Institute of Natural Sciences; NM – Natal Museum; NMW – National Museum of Wales, Cardiff; NSMT – National Science Museum, Tokyo; SAM – South Australian Museum, Adelaide; USNM – National Museum of Natural History, Washington; UMT – University Museum, Tokyo; WAM – Western Australian Museum, Perth; ZMA – Zoological Museum, Amsterdam; ZMC – Zoological Museum, Copenhagen.

Shell measurements: H= height of shell from umbone to ventral margin, L = length of shell from anterior to posterior, T= tumidity of shell i.e. maximum convexity measured on a single valve.

## SYSTEMATIC DESCRIPTIONS

Family LUCINIDAE Fleming, 1828

Genus *CARDIOLUCINA* Sacco, 1901

*Cardiolucina* Sacco, 1901: 89. Published June 30 (see Sacco, 1904; Marshall, 1991).

*Bellucina* Dall, 1901: 806. Published August 22nd (see Keen, 1971: 983). *Lucina eucosmia* Dall, 1901: 806, original designation.

TYPE SPECIES. *Cardium agassizi* Michelotti, 1839 (original designation).

NOMENCLATURE. The species considered in this paper have usually been assigned to the genus *Bellucina* Dall, 1901. However, the Miocene *C. agassizi* Michelotti, the type species of the genus *Cardiolucina* Sacco 1901, has all the characters of Recent *Bellucina* species (see description and figures of *C. agassizi* below). Chavan (1937) recognised this and synonymized the two genera giving *Bellucina* priority. Although published in the same year, Sacco's work appeared in June 1901 (Sacco, 1904, Marshall, 1991) and Dall's in August (see Keen, 1971). *Cardiolucina* therefore has priority over *Bellucina*.

Because the name *Bellucina* has been commonly used, the concept of this genus has to be considered in some detail. Dall (1901, p. 806) erected *Bellucina* as a section of the subgenus *Parvilucina* within the genus *Phacoides*. The genus *Parvilucina* was originally diagnosed as 'Shell small, plump, often inequilateral; sculpture more or less reticulate but not muricate, teeth small, common but all usually present' and the Section *Bellucina* was rather skimpily distinguished as 'Dorsal areas and sculpture strong.' However, Dall (1901) clearly designated *Lucina eucosmia* (= *L. pisum* Reeve) as the type species and the concept of *Bellucina* must be based upon this species. Many authors (e.g. Fischer, 1871, Lamy, 1920; Chavan, 1969; Britton 1972; Bretsky, 1976; Oliver, 1992) have considered *B. eucosmia* to be synonymous with *Bellucina semperiana* (Issel, 1869). Consequently, the characters of the latter species have been taken to represent *Bellucina*. Unfortunately, Reeve (1850) mixed two distinct species in the original description and illustrations of *Lucina pisum* which is clear from the syntype material. Reeve's figure 66a illustrates a specimen from Port Essington, Northern Territory, Australia, and figure 66b shows a shell of another species from Singapore. In the original description of *Lucina pisum* Reeve clearly referred to the deeply incised lunule and fenestrate ornament

which are features of the Port Essington specimens. '*Shell globoseely cordate, solid, thickly latticed with concentric and radiating ribs, of which the interstices are pitted, posterior side grooved, anterior short, lunule small, deeply excavated; whitish.*' For this reason one of the syntypes from Port Essington has been selected as the lectotype of *Lucina pisum* Reeve (see below under description of *Cardiolucina eucosmia*). Because the name *L. pisum* is preoccupied (*L. pisum* Sowerby, 1836) then *C. eucosmia* (Dall, 1901) becomes the valid replacement name. The other Reeve syntypes from Singapore we consider to be *Cardiolucina semperiana* (see below).

DIAGNOSIS. Shells small but solid, usually less than 14mm in height, subcircular (Height/Length ratio around 1.0), moderately inflated to subspheroidal (Tumidity/Length ratio between 0.38 and 0.48). Umbones prosogyrate, more or less central. Anterior sulcus either absent or shallow and narrow. Posterior sulcus always present and either deeply-indented or shallow. Lunule varies in size and depth between species, but where visible it is generally heart shaped. It can be deeply incised and large as in *C. eucosmia*, or very small and hidden under the beaks as in *C. australopilula*. Posterior dorsal area distinct, either concave or convex, usually with concentric ribbing. Ornament of radial ribs and concentric lamellae, relative strength of either varies between species. Concentric lamellae often raised and fluted. Intersection with radial ribs produces a variety of ornament from fenestrate to beaded. Hinge plate thick, dentition of single anterior and posterior lateral and two cardinal teeth in each valve. In the right valve of some species one of the cardinal teeth can be either reduced or absent. Ligament external and varying in length; can extend from beaks to position of posterior lateral tooth, or may be two thirds of this distance. Internal ventral margin finely to coarsely crenulate, corresponding to position of radial ribs. Often small denticles around antero- and postero-dorsal margins. Anterior adductor muscle scar quadrate to elongate, ventral tip only slightly detached from pallial line. Mature individuals of spheroidal species often have the adductor muscle scars located on an internal buttress. Posterior adductor scar short and rounded.

Juvenile shells are thinner, less inflated, more anteriorly extended with radial ribs often visible from interior of shell. Interior ventral margin not thickened.

ANATOMY. Based on observations of *C. australopilula* and *C. semperiana*.

Mantle largely unfused except at posterior exhalant aperture. Mantle margin thick and muscular. Mantle 'gills' absent. No fused inhalant aperture. Exhalant aperture a muscular tube with flared distal end, which can presumably be protracted. Ctenidia consist of inner demibranchs only, filaments elongate and thick. Outer lamella of demibranchs attached to posterior mantle just ventral to the exhalant aperture. Labial palps are small ridges at edge of lips. Foot cylindrical and vermiform with a posterior heel. Body wall muscular, with large hemispherical visceral pouch containing oocytes. Rectum curves around dorsal side of the posterior adductor muscle and opens near the posterior aperture.

Many of the anatomical features, such as the thickened inner demibranchs, reduced labial palps and vermiform foot are similar to those of other lucinids, although some characters may be less widely distributed. A distinctive and possibly functionally important feature is the attachment of the ctenidia to the posterior mantle. It is uncertain how widely this character is distributed amongst the Lucinidae. It was first illustrated by Reid & Brand (1986) for *Parvilucina tenuisculpta*, but not mentioned by Allen (1958) in his general survey of lucinoids, or by Morton (1979) for *Fimbria* and not present in *Rastafaria* (Taylor & Glover, 1997). Large hemispherical

visceral lobes or pouches are not present in most Lucinidae (Allen, 1958), but are found in *Parvilucina* (Reid & Brand, 1986), and species of Thyasiridae have several pouches (Allen, 1958). Most Lucinidae seem to possess both inhalant and exhalant posterior apertures, produced by mantle fusion (Allen, 1958). In *Cardiolucina* there is no inhalant aperture, a state found also in *Parvilucina* (Reid & Brand, 1986).

*Cardiolucina* species share three anatomical characters with *Parvilucina tenuisculpta*, namely; the attachment of the posterior tentacles to the mantle, the hemispherical visceral pouches and the lack of inhalant apertures. These characters may indicate a possible relationship, but the distribution of most anatomical characters amongst the Lucinidae is not well known.

**GEOLOGICAL RANGE.** Eocene (Lutetian) to Recent.

**COMPARISON WITH OTHER GENERA.** There has been a tendency to place small, inflated lucinids with both radial and concentric ornament, rather arbitrarily into a number of genera such as *Phacoides*, *Parvilucina*, *Linga* and *Bellucina*. These decisions have usually been made without reference to the characters of the type species. For instance, the status of *Bellucina* in major taxonomic revisions has varied as follows:

*Phacoides* (*Parvilucina*) section *Bellucina* – Dall, 1901: 806

*Phacoides* (*Bellucina*) – Lamy, 1920: 211

*Linga* (*Bellucina*) – Chavan, 1937: 205; 1969: 496

*Parvilucina* (*Bellucina*) – Britton, 1972: 15

*Lucina* (*Bellucina*) – Bretsky, 1976: 272–3

*Cardiolucina* (as *Bellucina*) has often been considered as a subgenus of *Parvilucina* Dall, 1901, type species *Lucina tenuisculpta* Carpenter, 1864, which ranges from Alaska to Baja California. Hickman (1994) redescribed and illustrated *P. tenuisculpta* and two other west American species. Although they are small, rounded and fairly inflated, *Parvilucina* species are thinner shelled and less tumid (T/L 0.29) than all *Cardiolucina* (T/L 0.38–48) species. Most *Cardiolucina* have a pronounced posterior sulcus, and sometimes a narrow anterior sulcus, compared to the weak, shallow, posterior sulcus of *Parvilucina*. *Parvilucina* has both radial and concentric ribs; the radial ribbing consisting of closely-spaced, low riblets, which are generally weak, but most prominent at the anterior and posterior of the shell. The internal ventral margin of *Parvilucina* is finely denticulate, compared with the coarser crenulations of *Cardiolucina*. The lunule in *Parvilucina* is narrowly lanceolate and asymmetric with the right valve overlapping the left, compared with the shorter, heart-shaped lunule of *Cardiolucina agassizi*. The hinge plate of *Parvilucina* is also thinner and the lateral teeth distant from the cardinals. Although a major reappraisal of the relationships of these genera is necessary, evidence suggests that the *Parvilucina* taxa centred around the type species, represent a clade distinct from *Cardiolucina*.

Another genus which should be considered in relation to *Cardiolucina* is *Radiolucina* Britton, 1972, (type species *Phacoides amiantus* Dall, 1901) from the Caribbean. Dall placed this species and the similar West American species *L. cancellaris* Philippi, 1846 in *Bellucina*. Later, Keen (1971, p.121) recognised that they were only superficially similar to the type species of *Bellucina* and placed them in the subgenus *PleuroLucina* Dall, 1901, remarking that American authors had been slow to recognise Dall's error. Bretsky (1976) confusingly gave an extensive diagnosis of the genus *Bellucina* based on *P. amiantus* rather than the type species *Bellucina eucosmia*. Britton (1972) had previously compared *P. amiantus* with *Bellucina semperiana* (Issel) which he considered the type species of *Bellucina* and recognised that *P. amiantus*

represents a distinct and separate lineage within the Lucinidae. For this reason, he erected a new subgenus *Radiolucina*. The type species, *R. amianta* has a more elongate shell than most *Bellucina* species H/L 0.92 (data from Bretsky, 1976, p. 273) compared with about 1.0 for *Cardiolucina* species, and the shell is less tumid T/L 0.33 compared with 0.43 for *Cardiolucina*. Furthermore, *R. amianta* has 8–12 broad radial ribs crossed by threadlike concentric lamellae, often with intermediate secondary radial ribs in the ventral two thirds of the shell. We agree with Keen (1971) and Britton (1972) that *Radiolucina amianta* belongs to a distinct and separate clade which includes several fossil species from the south western USA. Therefore, Bretsky's (1976, p. 272) diagnosis of *Bellucina* based on *P. amiantus* should be rejected.

Some American palaeontologists (Woodring, 1925; Gardner, 1926) used the generic name *Cardiolucina* for some Miocene lucinids with high beaks and lacking radial ribs. These species are now placed in the genus *Cavilinga* Chavan, 1937 (see Olsson & Harbison, 1953 p. 85; Bretsky, 1976 p. 265).

Chavan (1937, 1969) classified *Bellucina* as a subgenus of *Linga* de Gregorio 1885, for which the type species is *Lucina columbella* Lamarck, 1818, a Miocene fossil from France. This is a large, very thick-shelled species with concentric ribs only and a strong posterior sulcus unlike *Cardiolucina*.

## SPECIES DESCRIPTIONS

### *Cardiolucina agassizi* (Michelotti, 1839)

Fig. 1

*Cardium agassizi* Michelotti, 1839: 17.

*Lucina agassizi* – Michelotti, 1847: 404 pl. 4 figs 4,5, 7.

*Lucina irregularis* Eichwald, 1853: 82–83, pl. 5 fig. 4.

*Cardiolucina agassizi* (Michelotti) – Sacco, 1901: 89–90, pl. 10 figs 37–39.

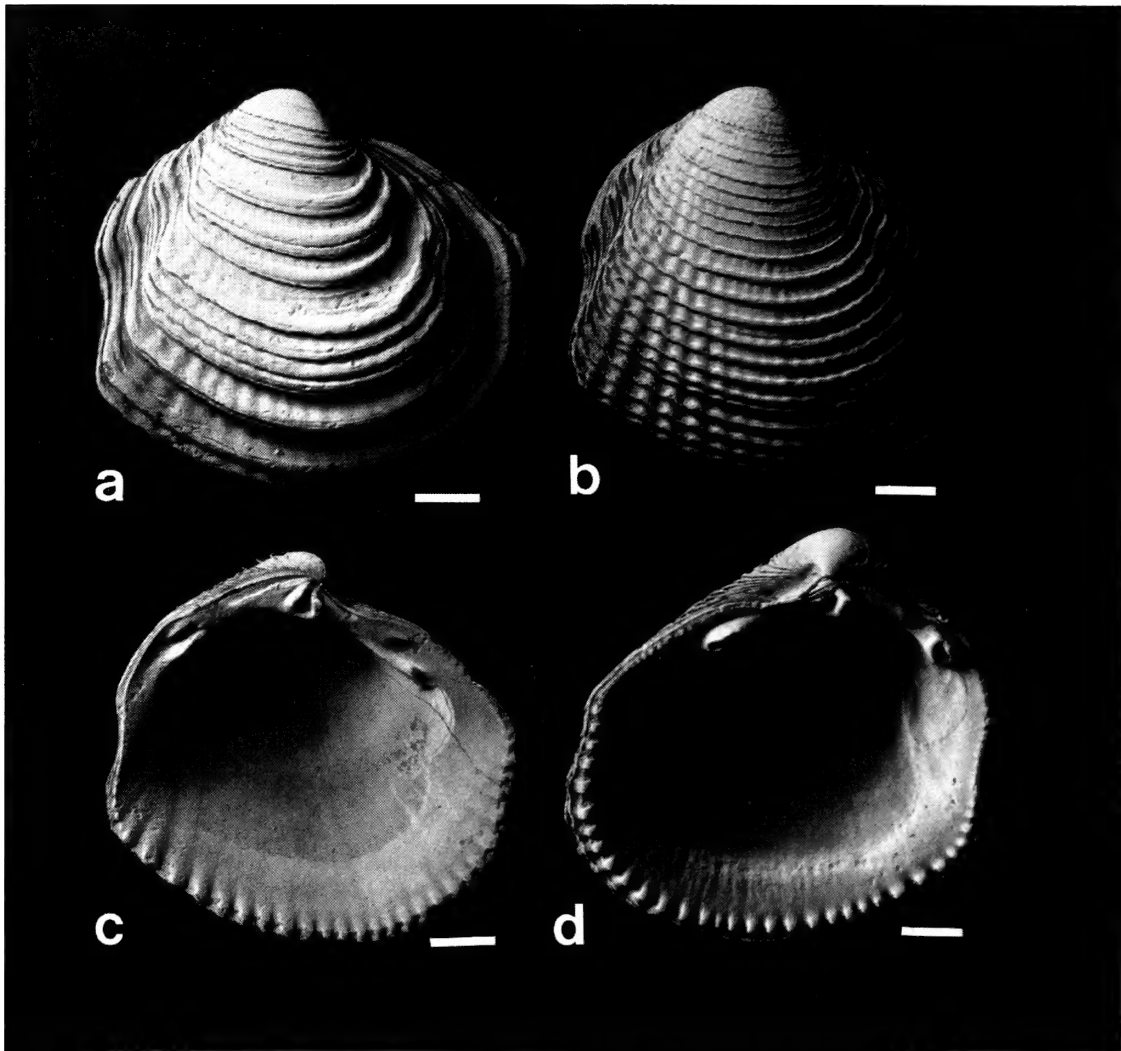
*Phacoides* (*Cardiolucina*) *agassizi* (Michelotti) – Cossmann & Peyrot, 1911: 688–689, pl. 28. figs 83–86.

**TYPE MATERIAL.** ?Museo di Paleontologia, Rome.

**TYPE LOCALITY.** Not given by Michelotti, but Sacco (1901) records several localities in the Miocene of Italy.

**DESCRIPTION.** Shell small, solid, height to 7.4 mm, subcircular, mean H/L 1.03, moderately inflated, mean T/L 0.39, tumidity to a maximum of 2.7 mm on a single valve. Shell inequilateral, extended anteriorly. Deep posterior sulcus with fine concentric lamellae. Shallow anterior sulcus. Lunule heart-shaped, small and shallow. Escutcheon lanceolate with concentric lamellae and a single strong radial ridge. Exterior sculpture of more than 25 faint, radial, rounded ribs with narrow interspaces. There are about 20 prominent, concentric lamellae which are often slightly recurved. Lamellae are extremely variable in thickness, degree of projection, recurvature and width of interspaces. Hinge plate thick. Left valve with single posterior lateral tooth, two cardinal teeth and single anterior lateral. Right valve with single posterior and anterior laterals and single cardinal. Ligament extending two thirds of the distance from umbone to posterior lateral tooth. Inner margin with 28–30 crenulations and small denticles along anterodorsal and posterodorsal margin. Anterior adductor muscle scar elongate, not buttressed, with pallial line attached near to the ventral tip. Posterior muscle scar ovate. Pallial line indistinct. Shell white.

In the material examined from France we found the concentric ornament to be extremely variable from separated, thin lamellae to clusters of thicker lamellae producing a rugose ornament (see Fig.



**Fig. 1** *Cardiolucina agassizi* (Michelotti, 1839), middle Miocene (Langhian), St Jean de Marsacq, Landes, France. (coll Lozouet and Maestrati, MNHN) a, exterior of right valve; b, exterior of right valve; c, interior of left valve; d, interior of right valve. Scale bars a = 750 $\mu$ m, b = 700 $\mu$ m, c = 1.5mm, d = 500 $\mu$ m.

1d). Similar variability of the concentric sculpture is seen in the Recent species *C. crassilirata* and *C. semperiana*.

**DISTRIBUTION.** As well as the records of Sacco (1901), *C. agassizi* is also recorded from the Tortonian of the Aquitaine Basin (Cossmann & Peyrot, 1911) and from the middle Miocene Korytnica Formation of Poland (Friedberg, 1934).

**MATERIAL EXAMINED.** **FRANCE:** Middle Miocene (Langhian), St Jean de Marsacq, Landes, France; ca 100 shells, Lozouet & Maestrati coll (MNHN).

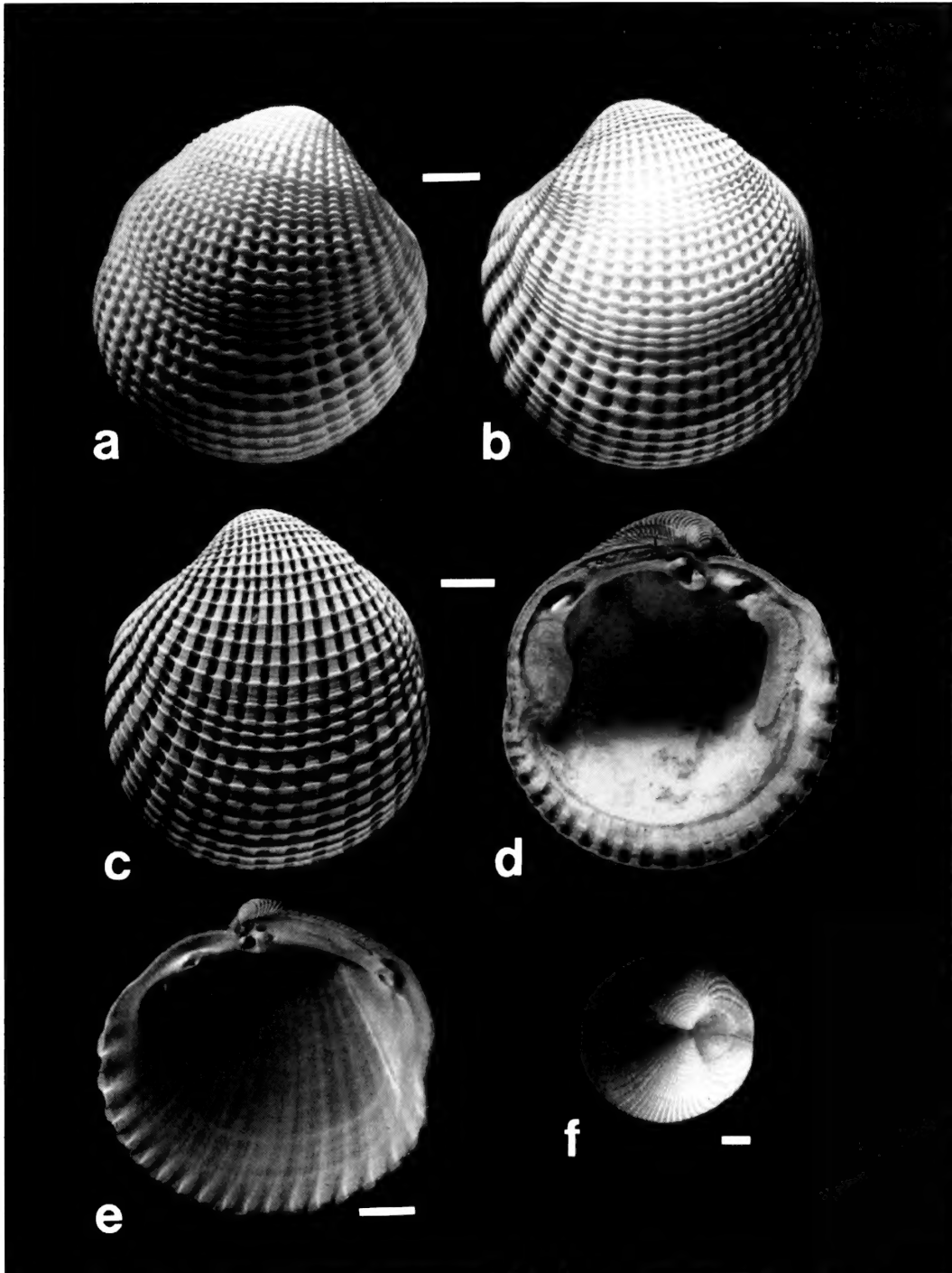
***Cardiolucina australopilula* Taylor and Glover, new species**

Figs 2–6

**TYPE MATERIAL.** Holotype: WAM reg number 110–96: H. 13.6, L. 12.8, T. 6.6 mm. Paratypes: WAM 111–96 2 preserved specimens station 35; AM C.202975 1 preserved specimen, station 23; BMNH 1996086, 1996087, 1996088, 1996089 4 preserved specimens, stations 1, 33, 36, 37; BMNH 1996090 one dry shell station 36. (Station data in Glover & Taylor, 1997).

**TYPE LOCALITY.** 9 km north of Beacon Island, Wallabi Group, Houtman Abrolhos Islands, Western Australia, 113° 46'E, 28° 23'S, depth 39m.

**SHELL DESCRIPTION.** Shell solid, small, height to 13.8 mm, subcircular in outline, H/L mean 1.03, inflated, orbicular, T/L mean 0.47, tumidity to a maximum of 7.5 mm on a single valve. Shell slightly inequilateral, extended anteriorly. Very shallow posterior sulcus. Umbones pronounced, prosogyrate. Lunule extremely small and shallow. Anterodorsal area slightly convex, heart-shaped in outline and with fine concentric ribbing. Escutcheon broadly lanceolate, convex and finely ribbed with concentric and a few radial ribs. Exterior sculpture of about 20 radial ribs, rounded in profile, separated by flat interspaces. Anteriorly, interspaces are as wide as the ribs, elsewhere interspaces are about two thirds of the width of radial ribs. Radial ribs have very fine radial striations (Fig. 3d). Radial ribs are crossed by 34–36 thin, low, concentric lamellae and their intersection produces a finely fenestrate ornamentation. Hinge plate thick, left valve with single posterior lateral tooth, two cardinal teeth, the anterior of these is robust and hooked (Fig. 3c) and a single anterior lateral. Right valve with single posterior lateral



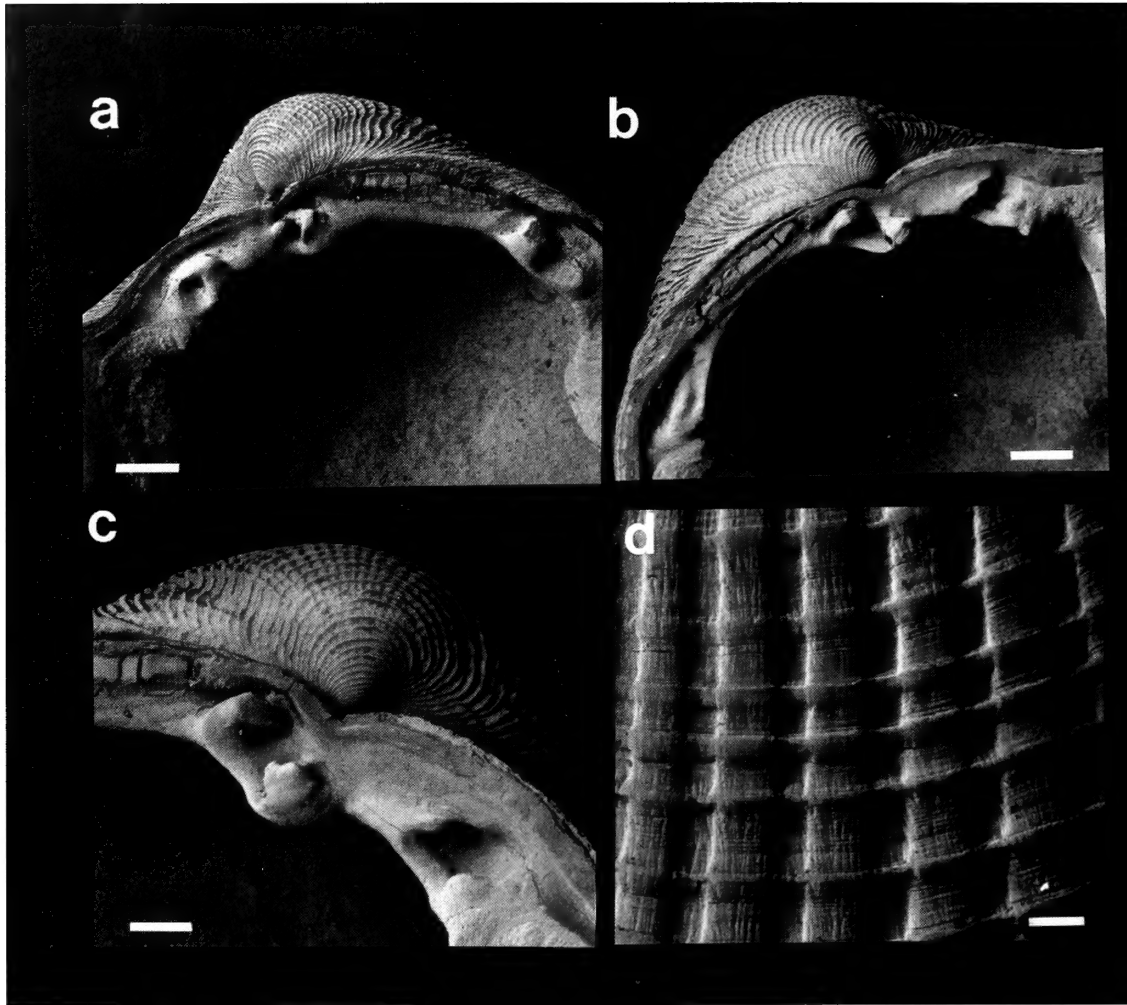
**Fig. 2** *Cardiolucina australopitula* Taylor and Glover new species, Beacon Island, Wallabi Group, Houtman Abrolhos Islands, Western Australia. a, Holotype (WAM 110-96), exterior of right valve; b, Holotype, exterior of left valve; c, Paratype (BMNH 1996090), exterior of left valve; d, Paratype (BMNH 1996090), interior of left valve; e, interior of right valve of juvenile shell, Eagle Bluff, Peron Point, Shark Bay; f, Holotype dorsal area. Scale bars a-d = 2.0mm, e = 2.5mm, f = 2.0mm.

tooth, two cardinal teeth, the posterior larger than the anterior, and a single anterolateral. Cardinal teeth sit on a curved, ventrally projecting buttress. Ligament elongate, extending from beak to posterior lateral tooth. Inner margin of shell thickened with 21 crenulations. Small sinus on posterolateral margin corresponding to the position of the posterior sulcus. Anterior adductor muscle scar narrow, elongate and sited on a buttress with ventral third detached from the

pallial line. Posterior muscle scar ovate. Pallial line continuous. Shell colour white.

Juvenile shells (Fig 2e) less inflated, more anteriorly extended. External radial ribs visible on interior of shell.

**ANATOMY.** The mantle margin is thick and fused only at the posterior exhalant aperture (Fig. 4), and there is no fused inhalant



**Fig. 3** *Cardiolucina australopilula* new species. a, Holotype, hinge in the right valve; b, Holotype, hinge in the left valve; c, Paratype, left valve, detail of cardinal teeth; d, outer shell surface showing radial striations on radial ribs. Scale bars a=2.0mm, b=2.5mm, c=1.0mm, d=500µm.

aperture. The exhalant aperture consists of a muscular tube with a flared distal end, which is inverted in preserved specimens, but can presumably be protracted. The ctenidia comprise inner demibranchs only. These have large, thick filaments which are fused between the ascending and descending lamellae. To the posterior, the outer lamellae are attached to the mantle margin just ventral to the exhalant aperture. The attachment area forms a thin, muscular septum. The labial palps consist of small folds at the edge of the thin, ridge-like lips. The foot is cylindrical and vermiform, tapering to a blunt point and extending posteriorly with a rounded heel. The visceral mass is covered by a muscular wall with a single, large, hemispherical visceral lobe on each side. The rectum runs around the dorsal side of the posterior adductor muscle and opens into the mantle cavity close to the exhalant tube.

**COMPARISON WITH OTHER SPECIES.** This species is similar in size, shape and sculpture to *C. quadrata* (Prashad, 1932) (Fig. 16) but differs in the greater prominence of the radial ribs and thinner, concentric lamellae. *C. australopilula* is also more tumid and spherical. This species has been referred to as *Bellucina* cf. *semperiana* by Slack-Smith (1990), but *semperiana* is smaller, with different ornamentation and hinge teeth.

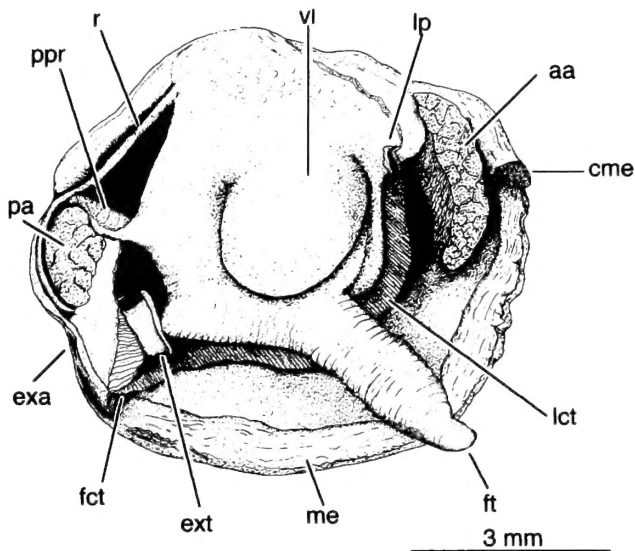
**HABITAT.** Fine, well-sorted, calcareous sand between 30–40m, in association with other bivalves *Amusium balloti*, *Mimachlamys australis* and *Rastafaria thiophila* (Glover & Taylor 1997).

**DISTRIBUTION.** Western Australia, Houtman Abrolhos Islands to Broome (Fig. 6).

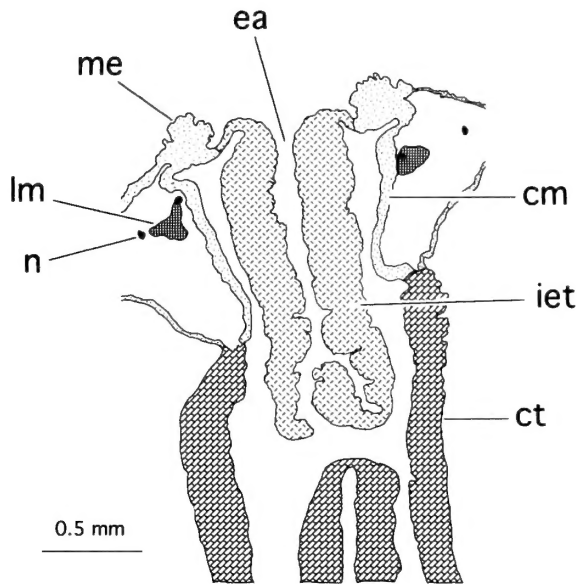
**ETYMOLOGY.** *australopilula* meaning 'Australian little ball'.

**MATERIAL EXAMINED.** **WESTERN AUSTRALIA:** Broome (AM C.309449); Roebuck Bay, Broome (BMNH 1892.1.29.121); Montebello Islands, Bunsen Channel, N. end of Trimoville I. 20° 23.8'S; 115° 32.43'E 3m (WAM); Barrow Island 20° 53'S, 115° 20'E (WAM); Exmouth Gulf (WAM 3461–3468); Mauds Landing, N.W. Cape, 3m (WAM); Turtle Beach, off N.W. Cape (AM C.309456); Carnarvon (AM C.309455); Dirk Hartog Island, 10–20m (WAM 3475.68); Bernier Islands 24° 53.3'S 113° 17.5'E. (WAM); Shark Bay, Peron Peninsula (WAM 249.94); Shark Bay, 5 km E.S.E. Cape Heirisson, 18m (WAM); Shark Bay, Freycinet Estuary (WAM 252–94). Houtman Abrolhos Islands: N. of Wallabi Islands, 40m (BMNH acc 2384); Easter Group, 50m (WAM N–2777); Zeewyk Channel, 40m (WAM N–2822); Little North Island, Easter Group, 40m (WAM); Rat Island, 30m (WAM wet material); East of Good Friday Bay, 28° 39.5'S – 113° 49.5'E, 40m (WAM).

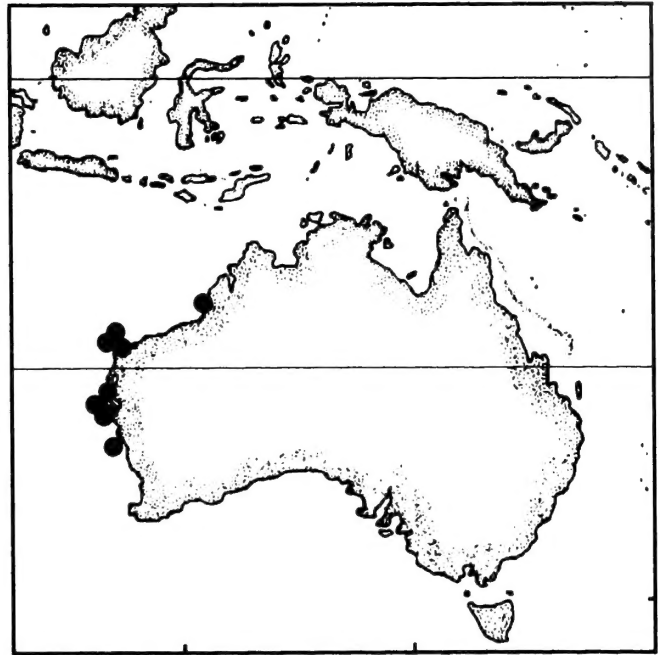




**Fig. 4** *Cardiolucina australopilula* anatomy. Right mantle and ctenidium removed. Abbreviations aa – anterior adductor muscle, cme – cut mantle edge, exa – exhalant aperture, ext – exhalant tube, fct – fused ctenidium to mantle, ft – foot, lct – left ctenidium, lp – labial palps, me – mantle edge, pa – posterior adductor muscle, ppr – posterior pedal retractor muscle, r – rectum, vi – visceral lobe.



**Fig. 5** Semidiagrammatic transverse section through the posterior exhalant area of *C. australopilula* showing the inverted exhalant tube and the connection of the ctenidium to the mantle. Abbreviations: cm – connection between mantle and ctenidium, ct – ctenidium, ea – exhalant aperture, iet – inverted exhalant tube, lm – longitudinal muscle, me – mantle edge, n – nerve.



**Fig. 6** Geographical distribution of *Cardiolucina australopilula* new species.

### *Cardiolucina civica* (Yokoyama, 1927)

Figs 7–9

*Cardium civica* Yokoyama, 1927: 179. pl. 48, figs 3 & 4.

*Dentilucina (Bellucina) hedleyi* Prashad, 1932: 163–164, pl. 5, figs 17 & 18.

*Bellucina civica* (Yokoyama, 1927) – Kuroda, Habe & Oyama, 1971: 394, pl. 118 figs 17 & 18.

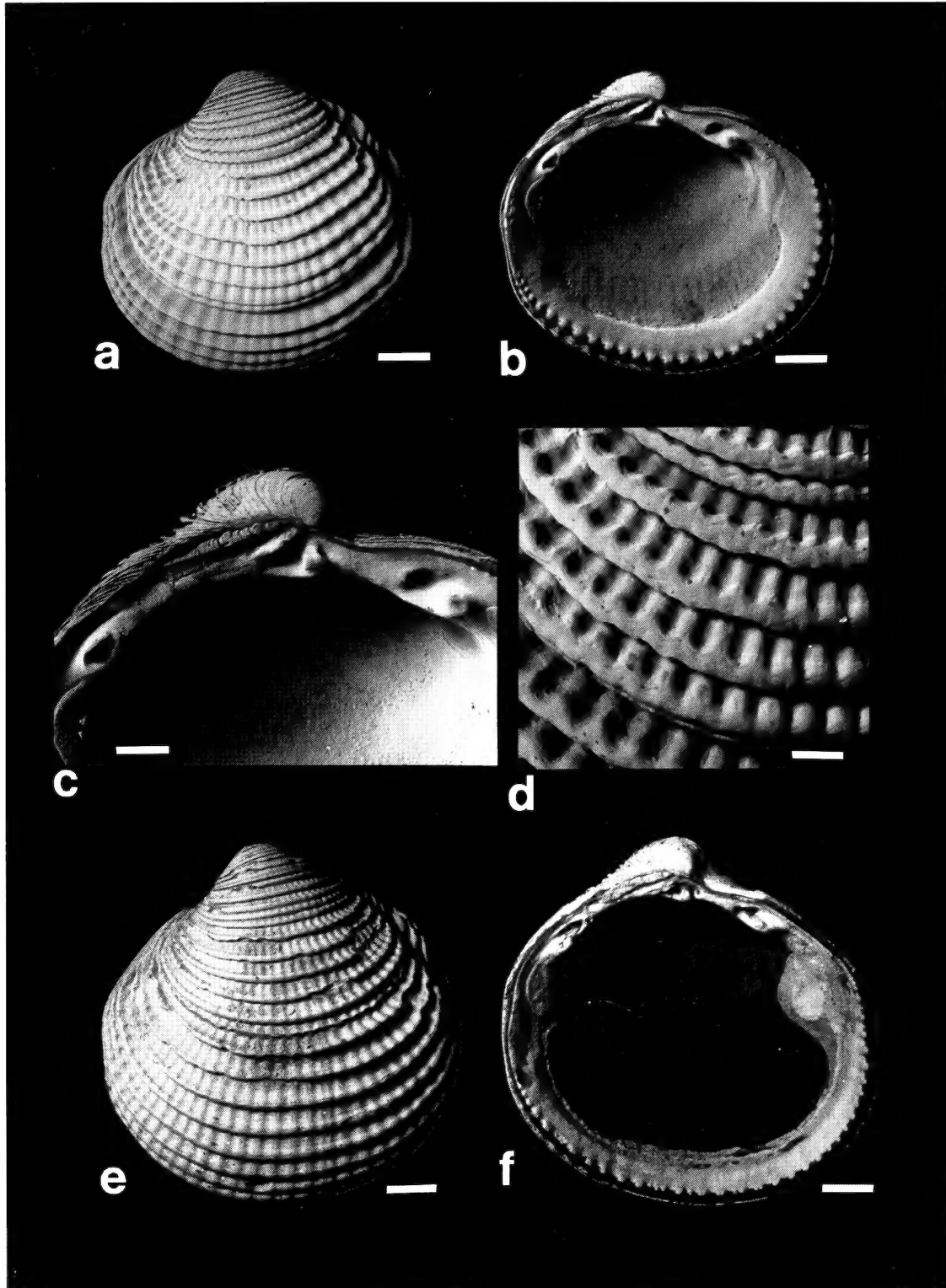
*Lucina (Codakia) semperiana* (Issel, 1869) – Melvill & Sykes, 1898: pl. 3, fig. 1.

**TYPE MATERIAL.** *C. civica* syntypes, University Museum, Tokyo, CM 24913–24914, see Makiyama (1959); *C. hedleyi* holotype, 1 individual 2 valves (ZMA).

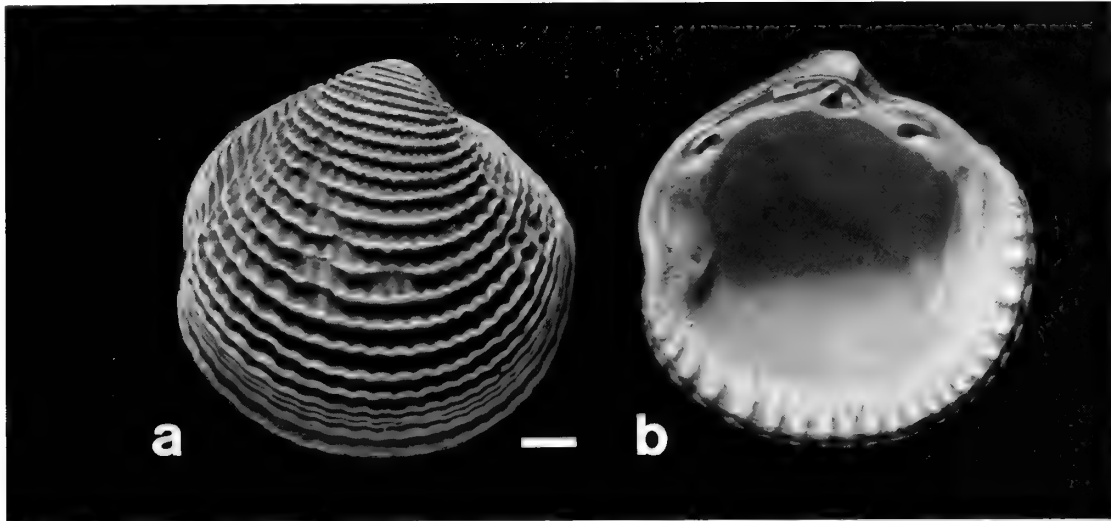
**TYPE LOCALITIES.** *C. civica* was described as a Pliocene fossil from Nagaya and Kakuma in Kaga Province, Japan. *C. hedleyi* from the Philippines, Sulu Archipelago, Siboga station 105 (6° 8'N, 121° 19'E), depth 275 m.

**NOMENCLATURE.** We have examined the holotype of *C. hedleyi* from Indonesia, which is very similar to both Recent specimens of *C. civica* from Japan and the fossils figured by Yokoyama (1927) and consider them conspecific.

**SHELL DESCRIPTION.** Shell solid, small, height to a maximum of 10.6 mm; subcircular, mean H/L 1.02, inflated, mean T/L 0.40, tumidity to a maximum of 4.5 mm on a single valve. Shell slightly extended anteriorly. There is a shallow posterior sulcus which has concentric ribs. Lunule small and shallow. Anterodorsal area weakly defined. Escutcheon slightly convex and finely ribbed. Exterior sculpture of numerous (more than 30) fine, slightly rounded, radial ribs with narrow interspaces. Radial ribs are crossed by many (more than 25) conspicuous concentric lamellae, which are rounded in profile and slightly recurved. Left valve with a single posterior lateral, two cardinal teeth and a single posterior lateral; right valve with a single posterior lateral, two cardinal teeth, the posterior



**Fig. 7** a–d *Cardiolucina civica* (Yokoyama, 1927) southern Honshu, Japan BMNH 1878.10.16.191 and e–f *Dentilucina (Bellucina) hedleyi* Prasad, 1932 Holotype, Sulu Archipelago, Philippines. a, exterior of left valve; b, interior of left valve; c, hinge in left valve; d, outer surface of shell showing concentric and radial ribs; e, Holotype *C. hedleyi* exterior of left valve; f, Holotype *C. hedleyi* interior of left valve. Scale bars a=2.5mm, b=1.2mm, c=500 $\mu$ m, d=500 $\mu$ m, e=2.0mm, f=2.5mm.



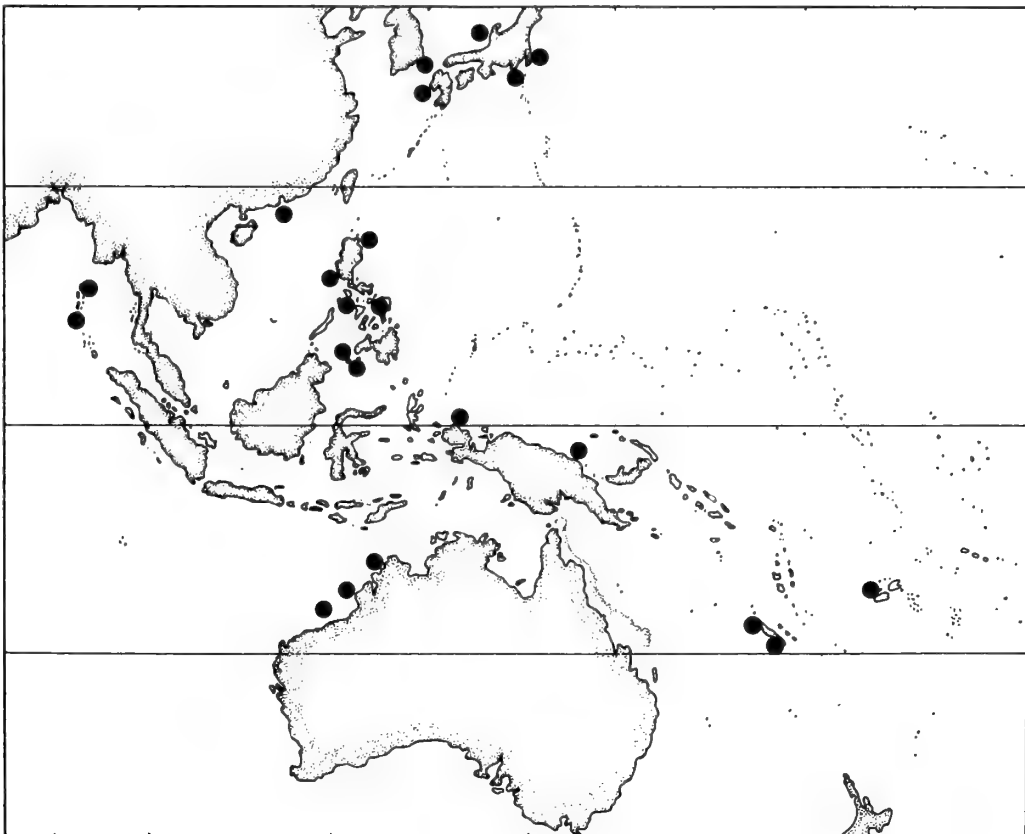
**Fig. 8** *Cardiolucina civica* from Andaman Islands. Large specimen illustrated by Melvill and Sykes (1897, fig.1) as *Lucina (Codakia) semperiana* Issel (BMNH 1898.4.30.7) a, Right valve exterior; b, Left valve interior. Scale bar a-b = 1.0mm.

cardinal large and the anterior very small. There is a single anterior lateral tooth. Ligament short, extending from the beak to about half way to posterior lateral tooth. Inner margin of shell thickened and with 30 crenulations. Small denticles on anterodorsal margin. Anterior adductor muscle scar elongate and not buttressed, pallial line attached near ventral tip. Posterior adductor scar small and rounded. Pallial line continuous. Shell grey white.

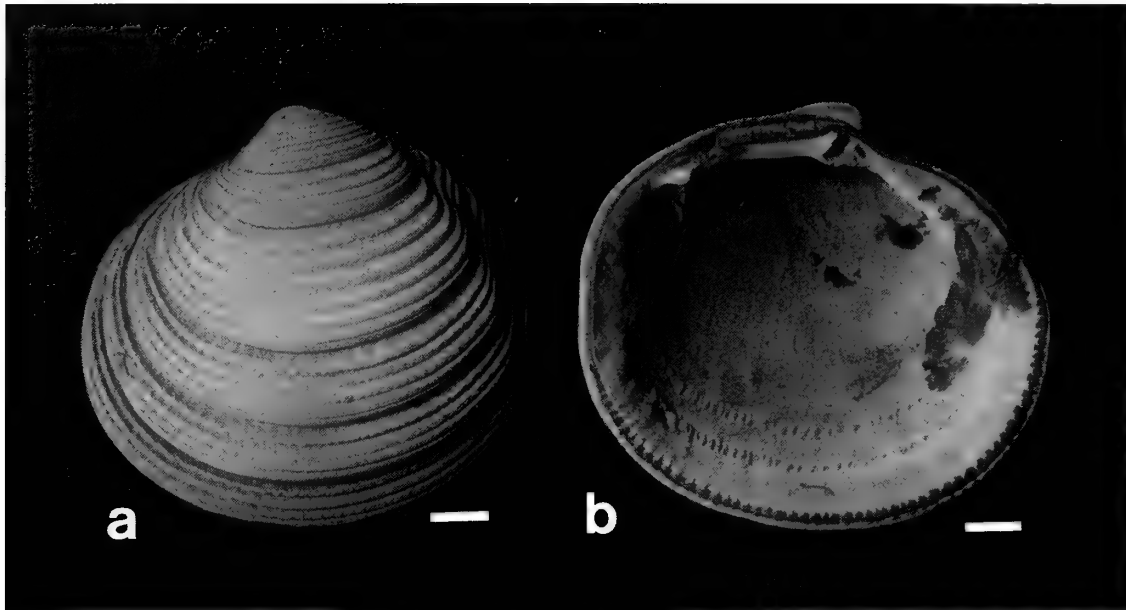
Juveniles less inflated and more extended anteriorly. Posterior

sulcus more pronounced and anterodorsal shell margin markedly convex. Shell thinner with radial riblets visible from interior of shell.

A large specimen (BMNH 1898.4.30.7) from the Andaman Islands, figured by Melvill and Sykes (1898 pl.3, fig.1) as *Lucina (Codakia) semperiana*, has many of the characters of *C. civica*, although larger than specimens from other localities. Other specimens in the BMNH from Port Blair, Andamans are similarly large.



**Fig. 9** Geographical distribution of *Cardiolucina civica* (Yokoyama).



**Fig. 10** *Cardiolucina crassilirata* (Tate, 1886), Western Port, Victoria, Australia. BMNH 1963200. a, exterior of left valve; b, interior of left valve. Scale bars a = 2.0mm, b = 2.5mm.

**COMPARISON WITH OTHER SPECIES.** *C. civica* is most similar to *C. crassilirata*, but it has a shorter ligament and coarser marginal crenulations.

**HABITAT.** Fine sandy and shelly bottoms mainly from shallow water to 200m, with a few dead shells recorded up to 600 m.

**DISTRIBUTION.** Andaman Islands, North Western Australia, South East Asia, Japan, to Fiji (Fig. 9).

**MATERIAL EXAMINED.** **ANDAMAN ISLANDS:** 11°37'N, 92°56'E, 357m (ANSP 292239); Port Blair, BMNH 1953.1.30.199–201; BMNH 1898.4.30.7. **AUSTRALIA:** Western Australia, N.W. of Port Hedland 19°13'S, 116°6'E, 271m & 19°24'S, 115°52'E, 238m (AM C.309458 & C.309453); N.W. Beagle Island, 29°43'S, 114°17'E, 274–283m (AM C.309465); N.W. Roebuck Bay, Broome 17°34'S 120°22'E, 188m (AM C.309457). **PHILIPPINES:** Luzon, off Matocot Pt W., 370m (USNM 295697); Tayabas Bay, off Tayabas Lt, 200m (USNM 297745); Ragay Gulf, off North Burias, 185m (USNM 246286); off Balanja Pt, S.E. Mindoro, 280m (USNM 295581); Adyagan I. E. Masbate, 190m (USNM 298134); off Pt Dumurug, Masbate, 273m (USNM 298227); Linapacan Strait, 90m (USNM 301994); off Pt Lauis, E. Cebu, 280m (USNM 300493); off Gigantangan I., N.W. Leyte, 210m (USNM 298317); off Dammi I., Sulu Archipelago, 446m (USNM 299036); off Simaluc Island, Tawi Tawi Is, 600m (USNM 299195); off Jolo, Jolo I., 283m (USNM 294618) & 37m (USNM 294584); 14°01'N 120°18'E, 192m (MNHN). **CHINA:** off Pratas Islands., China Sea, 272m, (USNM 296724). **JAPAN:** off southern Honshu 34°13'N, 136°13'E, 90–100m (BMNH 1878.10.16.191); Kumano-Nada, off Kii Peninsula, 93m (NSMT 70534); off Jyogashima I., Miura Peninsula (NSMT 70535); off Goto Islands, 168m (NSMT 56297); off Tsushima Islands, 112m (NSMT 56298); Usibuka, Anakusa Island (NSMT 70533); Sagami Bay (USNM 708071). **IRIAN JAYA:** Aeri I., Geelvink Bay, 1–40 (ANSP 275808, 280332); Japen I., Geelvink Bay, 30–40m (ANSP 277817, 276638, 279725); Schouten I., 18m (ANSP 280204). **NEW CALEDONIA:** 19°07'S 163°22'E, 110–200m (MNHN); 22°02'S 165°57'E 135–150m (MNHN); Grande

Récif Sud, 22°42'S 157°22'E, 35m (MNHN). **FIJI:** Viti Levu Bay 0–5m near shore (USNM 878321).

#### *Cardiolucina crassilirata* (Tate, 1887)

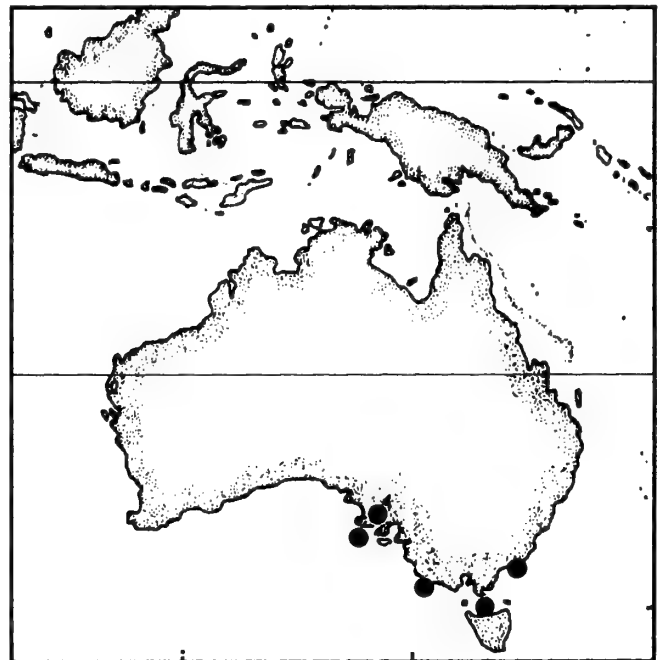
Figs 10–11

*Lucina crassilirata* Tate, 1887a: 6–7, pl. 4 fig. 2.

*Codokia crassilirata* (Tate) – Cotton & Godfrey, 1938: 206 fig. 218.

*Loripes crassilirata* (Tate) – Pritchard & Gatliff, 1903: 139.

*Bellucina crassilirata* (Tate) – Macpherson & Gabriel, 1962: 327.



**Fig. 11** Geographical distribution of *Cardiolucina crassilirata* (Tate).

*Linga (Bellucina) crassilirata* (Tate, 1887) – Lamprell & Whitehead, 1992: pl. 21 figs 128a & b.

**HOLOTYPE.** South Australian Museum No. D.12957. L = 8.5 mm, H = 8.3 mm, T = 7.0 mm.

**TYPE LOCALITY.** Streaky Bay, near Ceduna, South Australia.

**SHELL DESCRIPTION.** Shell small, solid, height to 8.4 mm, outline circular, H/L mean 0.98; shell moderately inflated with T/L mean 0.41, tumidity of a single valve to a maximum of 3.4 mm. Shell slightly inequilateral, extended anteriorly. Shallow sulcus posteriorly, with concentric lamellae. Lunule small and shallow. Escutcheon slightly convex, with fine concentric ribs. Exterior sculpture of more than 30 fine concentric lamellae, clustered in groups of 4–6 with broader interspaces between the clusters. Radial sculpture of many fine ribs visible in the interspaces of the concentric ribs. Hinge plate narrow; left valve with single posterior lateral, two cardinal teeth and single anterior lateral. Right valve with a single posterior and anterior laterals and two cardinal teeth, posterior cardinal larger than anterior cardinal tooth. Ligament long, extending from beaks to posterior lateral tooth. Inner margin with around 60 fine crenulations. Anterior adductor muscle scar, elongate, not buttressed, with ventral quarter detached from pallial line. Posterior adductor muscle scar ovate and not buttressed. Pallial line discontinuous. Shell greyish white.

**COMPARISON WITH OTHER SPECIES.** See *C. civica*.

**HABITAT.** Shallow subtidal to 70m.

**DISTRIBUTION.** South Australia, Victoria and Tasmania (Fig. 11).

**MATERIAL EXAMINED.** **AUSTRALIA:** **Victoria**, BMNH 1906.9.19.70–2; Western Port (BMNH 1963200); BMNH 1911.12.19.11–12; Western Port (WAM); Western Port (AM C.303440); Western Port, 15–18m (AM C.309469); Port Fairy, beach (ANSP 135488); **New South Wales**, Between Eagle and Crawfish Rock (AM); **South Australia**, Spencers Gulf (BMNH 1893.12.12.352–54); Hardwicke Bay (AM C.13463); Neptune I., 70m (AM); South Australia (AM C.6677); **Tasmania**, Geography Strait, 27m (AM C.38180).

### *Cardiolucina eucosmia* (Dall, 1901)

Figs 12–13

*Lucina pisum* Reeve, 1850 (in part): pl. 11 fig. 66a (non *Lucina pisum* Sowerby, 1836: 341).

*Phacoides (Bellucina) eucosmia* Dall, 1901: 806 (replacement name for *L. pisum* Reeve).

*Phacoides eucosmia* Dall. – Hedley, 1909: 426, pl. 37 fig 16.

**TYPE MATERIAL.** Lectotype here selected BMNH 1963194/1 (Figs 12a–d). Paralectotypes BMNH 1963194/2–3; 1845.825.210–212; 1963552 (this is *C. semperiana* see p. 107)

**TYPE LOCALITY.** Restricted to Port Essington, Northern Territory, Australia (modified from Reeve, 1850).

**NOMENCLATURE.** Many authors, for example Fischer (1871), Lamy (1920), Chavan (1969), Britton (1972), Bretsky (1976) and Oliver (1992) have considered *Lucina semperiana* Issel, 1869 a senior synonym of *P. eucosmia*. However, *Lucina pisum* Reeve, for which Dall gave the replacement name *Phacoides eucosmia*, is based on a syntype series composed of two distinct species. For the reasons given above in the generic section, we consider the specimens from Port Essington to conform most closely with Reeve's description

and concept of *Lucina pisum* and one of these has been selected as a lectotype. The other syntypes from Singapore, now become paralectotypes and we consider these to be the eastern Indian Ocean form of *C. semperiana* (Fig. 21 a & b).

**SHELL DESCRIPTION.** Shell solid, small, height to 7.8 mm, subcircular in outline, slightly extended in an anterolateral direction, H/L mean 1.05; inflated, T/L mean 0.49, tumidity to a maximum of 3.8 mm on a single valve. Posteriorly, there is deep sulcus extending from hinge to ventral margin. The sulcus and the posterior portion of the shell has fine concentric ribbing with no radial ribs. The lunule is 'U'-shaped and deeply incised to the ventral edge of the hinge plate. Anterodorsal area is slightly convex, ovate in outline with fine concentric sculpture. Posterior dorsal area broadly lanceolate in outline, convex, with fine concentric ribbing. Exterior sculpture of about 12 broad, radial ribs with rounded profile, somewhat flattened on upper surface. Ribs narrower towards umbos. Interspaces between ribs deep, narrower than ribs. Radial ribs crossed by 13–14 thin, low, concentric lamellae which project slightly above radial ribs. The intersection of concentric and radial sculpture gives a distinctive fenestrate ornament. Hinge plate thick. Left valve has a single, strong lateral tooth posteriorly, two thin, cardinal teeth, the posterior tooth much larger than the anterior. Cardinal teeth are denticulate (see Fig. 12d). A single anterior lateral lies close to perimeter of the lunule. Right valve has a single posterior lateral, a large single cardinal tooth and a single anterior lateral. Both valves have small denticles around the dorsal margin of valve. Ligament elongate, extending from beak to posterior lateral tooth. Inner shell margin thickened, with 12 coarse crenulations. Small sinus on posterior lateral margin corresponding to position of sulcus. Anterior adductor muscle scar elongate, sitting on a shallow buttress with the only the ventral tip detached from the pallial line. Posterior adductor scar ovate on a shallow buttress. Pallial line is thin and continuous. Shell colour creamy white.

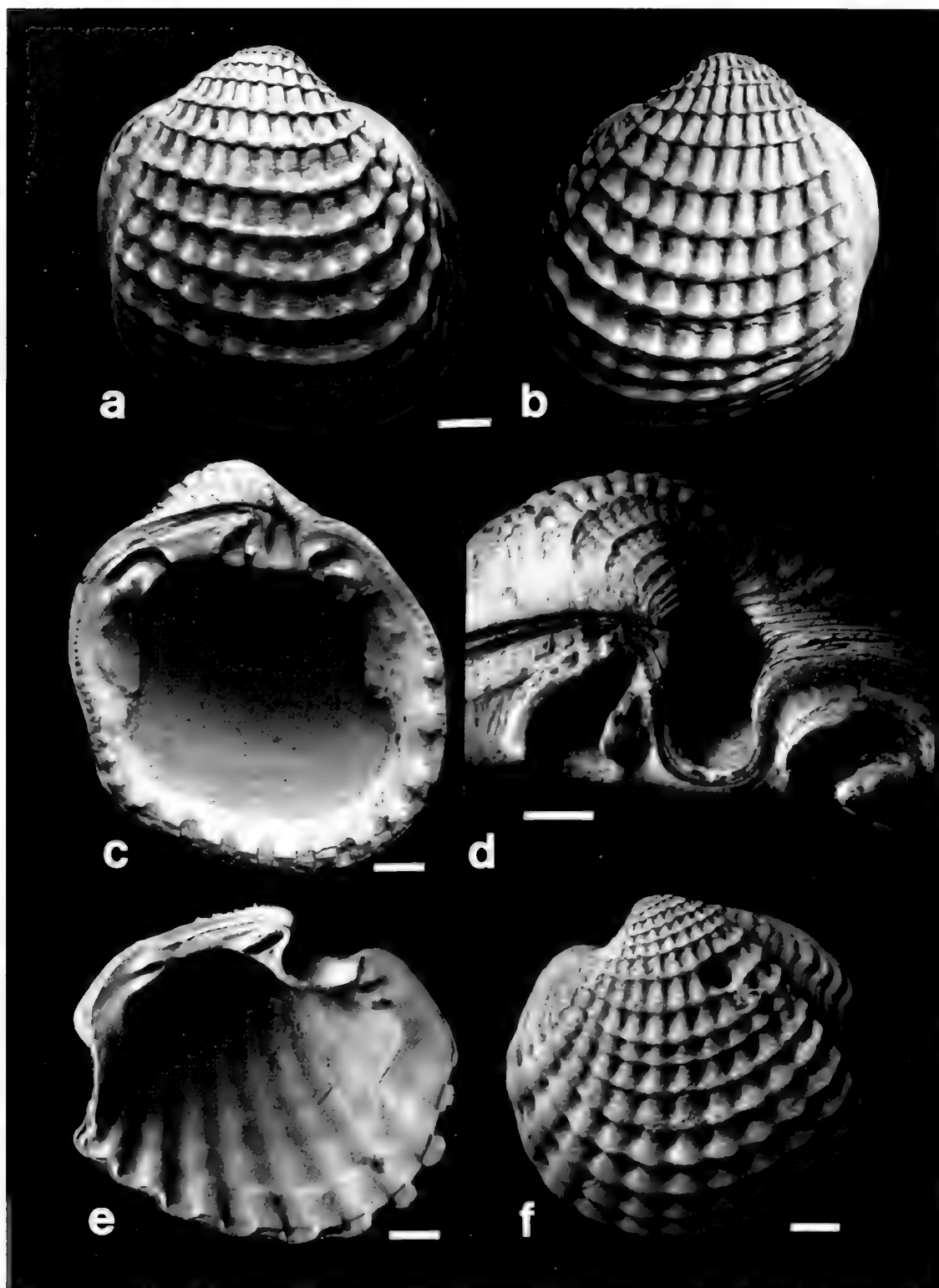
Juvenile shells (Figs 12 e & f) are less inflated and more extended anteriorly. The lunule is widely opened in younger stages. Denticles are absent on the dorsal inner margins. Radial ribs begin narrow and broaden ventrally between each concentric rib. Radial ribs are visible on interior of shells.

**COMPARISON WITH OTHER SPECIES.** Although *C. pisiformis*, *C. siquijorensis* and *C. australopilula* have a similar fenestrate ornament, *C. eucosmia* can be easily distinguished from all other species by the deeply incised lunule.

**HABITAT.** Low intertidal to 100 m in fine sand and mud. Hedley (1909) reports dredging the species in the Gulf of Carpentaria from about 10 m in soft black mud, where it was abundant.

**DISTRIBUTION.** Northern Australia (Fig. 13).

**MATERIAL EXAMINED.** **AUSTRALIA:** **Northern Territory and Queensland**, BMNH 1963490, 1963236, 1910.9.28.77–8; W. of Cape York, 8m (BMNH 1887.2.9.2776–7); Gulf of Carpentaria (NMW 1955.158); Sweers I. (AM C.75249, 78223); Forsyth I. (AM C.14892); Horsey River mouth, 9m (AM C.15152), Karumba (AM C.14963); Mapoon (AM C.14281); off Bountiful Islands (AM); Gulf of Carpentaria (AM C.100498); mid-Gulf of Carpentaria, 66m (AM); off Albany River (AM); Karumba Point (AM 1909); Albany Passage, 8–25m (AM C. 36172); Port Essington (BMNH); off Point Charles, Darwin, 27–37 m (AM C.309468); Van Diemen's Inlet (NMW 1955.158); Van Diemen's Inlet (AM C.15273); 100 miles N. of Croker Island, Arafura Sea, 124m (AM C.309454); 150 km N. of Coburg Peninsula, 108m (AM); Dinah Beach, Darwin (AM); Crocodile Research Station, Manningrida, Arnhem Land (AM);



**Fig. 12** *Cardiolucina eucosmia* (Dall, 1901) Port Essington, Northern Territory, Australia. Figured specimens a–d are the lectotype of *Lucina pisum* Reeve, BMNH 1963194/1. & Figure e–f *C. eucosmia*, Arafura Sea, Northern Territory, Australia, AM C.309454. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, hinge and lunule in left valve; e, juvenile, interior of left valve; f, juvenile, exterior of left valve. Scale bars a–c = 1.0mm, d = 500µm, e = 650µm, f = 1.0mm.

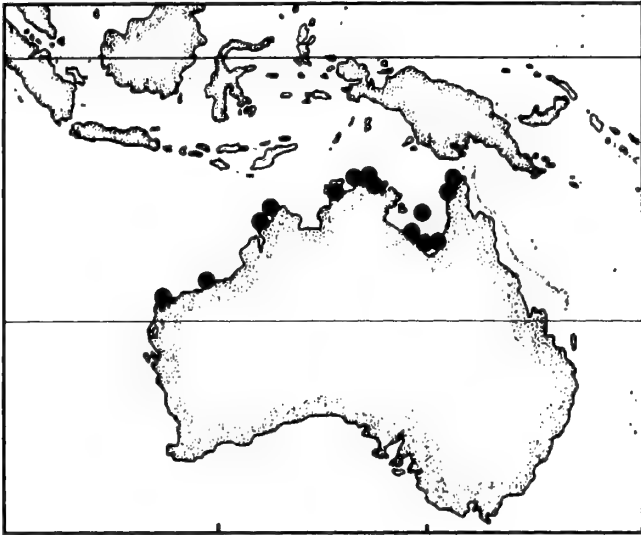


Fig. 13 Geographical distribution of *Cardiolucina eucosmia* (Dall).

**Western Australia**, Prince Frederick Harbour (WAM); Cape Leveque (AM); Port Hedland (AM); Direction Island, off Onslow (AM C.69334).

***Cardiolucina pisiformis*** (Thiele, 1930)

Figs 14–15

*Phacoides* (*Parvilucina*) *pisiformis* Thiele, 1930: 592.

*Phacoides* (*Parvilucina*) *pisiformis* Thiele – Ponder, 1978: 439, pl. 2 figs 3 & 9.

*Bellucina pisiformis* (Thiele) – Slack-Smith, 1990: 135.

**HOLOTYPE**. Museum für Naturkunde, Berlin. Reg. no. 67726. L=3 mm, H=2.9 mm (details from Ponder, 1978).

**TYPE LOCALITY**. 5 km N.W. of Denham, Shark Bay, Western Australia, 3 m.

**SHELL DESCRIPTION**. Shell very small, to a maximum height of 4.4 mm, outline circular, H/L mean 0.97; inflated, T/L mean 0.42, tumidity of single valve to 2.0 mm. Inequilateral, slightly extended anteriorly. Shallow posterior sulcus with concentric lamellae. Lunule heart-shaped, slightly excavated, smooth. Anterodorsal area indistinct. Posterodorsal area with concentric lamellae. Exterior sculpture of 13–17 low, flattened, radial ribs with broad interspaces. Ribs broader and more rounded towards anterior of shell. About 20 thin, concentric lamellae project slightly above radial ribs. Sculpture distinctly fenestrate in appearance. Hinge plate strong. Left valve with single posterior lateral, two cardinal teeth, the posterior of these large and robust, the anterior small. Single anterior lateral tooth. Right valve with a single, strong, posterior lateral tooth, two cardinals, the anterior large and the posterior very small and a single anterior lateral. Ligament extends from beak to posterior lateral tooth. Inner margin with about 13 coarse crenulations, which are sometimes bifurcate with occasional small denticles in the interspaces. Small, rounded denticles around anterior and posterior dorsal margins. Anterior adductor muscle scar elongate, slightly buttressed with only the ventral tip detached from the pallial line. Posterior adductor muscle scar rounded. Pallial line continuous. Shell white.

Juvenile shells (Fig. 14 e) are more extended both anteriorly and posteriorly, with a prominent convex anterodorsal area.

**COMPARISON WITH OTHER SPECIES**. This is a small distinctive species with an exterior ornament similar to *C. eucosmia* and *C. siquijorensis*. It is smaller, more circular in shape and lacks the deeply-excavated lunule of *C. eucosmia*. *C. siquijorensis* has fewer and broader radial ribs, a shallower lunule and a different dentition.

**HABITAT**. Shallow water to 240 m.

**DISTRIBUTION**. Western Australia (Fig. 15).

**MATERIAL EXAMINED**. **AUSTRALIA: Western Australia**, W. of Rottne Island, 110m (WAM 262–94); Point Peron Peninsula, Shark Bay (WAM 257–94, 258–94, 259–94, 260–94.); Carnarvon (WAM); N. of Homestead Point, Dirk Hartog Island (WAM 250–94); Ningaloo Reef, N.W. Cape (WAM); Mangrove Bay beach, N.W. Cape (WAM); Yardie Creek to Tantibiddi, N.W. Cape (WAM wet material); N.W. of Port Hedland, 112m (AM C.309462); N.W. Shelf, W. of Roebuck Bay, 238m (AM C.309464); Broome (ANSP 233737); **Northern Territory**, N. of Cobourg Peninsula, 55m (AM); 200km N. of Melville Island, 215m (AM).

***Cardiolucina quadrata*** (Prashad, 1932)

Figs 16–17

*Dentilucina* (*Bellucina*) *hedleyi* var. *quadrata* Prashad, 1932: 164, pl. 5 figs 19 & 20.

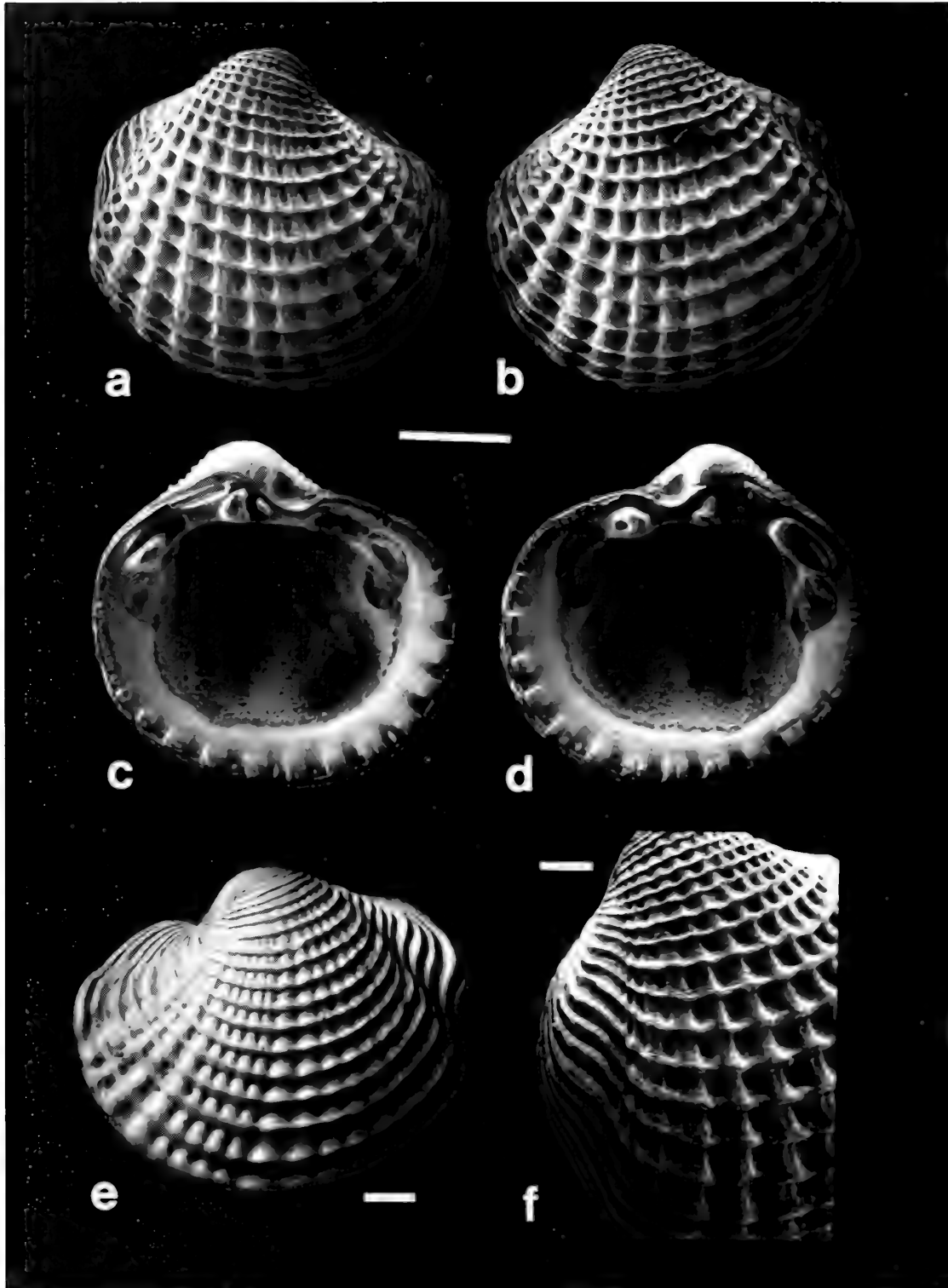
**TYPE MATERIAL**. Holotype, one individual two valves, L=10.5 mm, H=10.5 mm. Also 4 paratype valves. (ZMA).

**TYPE LOCALITY**. Siboga Expedition station 212 (5° 54.5'S, 120° 19.2'E), west of Salayar, Sulawesi, Indonesia, 462 m.

**SHELL DESCRIPTION**. Shell solid, small, height to 12.9 mm, subcircular, H/L mean 0.97, moderately inflated, mean T/L 0.38, tumidity to a maximum of 5.3 mm on a single valve. Shell inequilateral, extended anteriorly. Shallow posterior sulcus with concentric lamellae; umbones prominent. Lunule extremely small and shallow. Anterodorsal area heart-shaped, slightly convex with fine concentric lamellae. Escutcheon lanceolate, with fine concentric lamellae and a few radial ribs. Exterior sculpture of about 25 fine, closely spaced, radial ribs which are rounded in profile. Radial ribs crossed by 25–30 low, broad, concentric lamellae, the intersection giving a finely beaded appearance. Hinge plate thick. Left valve with an single posterior lateral tooth, two cardinal teeth, the anterior of which is hooked and sits on a rounded buttress, and a single anterior lateral tooth. Right valve with single posterior lateral, two cardinal teeth with the posterior larger and a single anterior lateral tooth. Ligament elongate extending from beak to two thirds of distance to the posterior lateral tooth. Inner margin with about 25 crenulations, some of those to the posterior bifurcating. Shallow sinus on posterior margin. Anterior adductor muscle scar elongate, not buttressed, slightly detached at the ventral tip from the pallial line. Posterior adductor muscle scar ovate. Pallial line continuous. Shell colour white.

**COMPARISON WITH OTHER SPECIES**. Although this species name was first introduced by Prashad (1932) as a variety of *Dentilucina* (*Bellucina*) *hedleyi* (= *C. civica*) it is clearly distinct. In many characters, such as hinge teeth, it resembles *C. australopilula*, but differs in shape and external sculpture, the latter having a fenestrate ornament compared with the finely beaded sculpture of *C. quadrata*.

**HABITAT**. A deeper water species from muds at 230–1280 metres.



**Fig. 14** a–d, f *Cardiolucina pisiformis* (Thiele, 1930) Bandicoot Bay, Barrow Island, Western Australia, WAM 268–94 and Fig. e *C. pisiformis*, Peron Peninsula, Shark Bay, Western Australia WAM 258–94. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, interior of right valve; e, juvenile, exterior of shell; f, exterior of shell surface showing posterior sulcus. Scale bars a–d = 1.0mm, e = 500 $\mu$ m, f = 300 $\mu$ m.



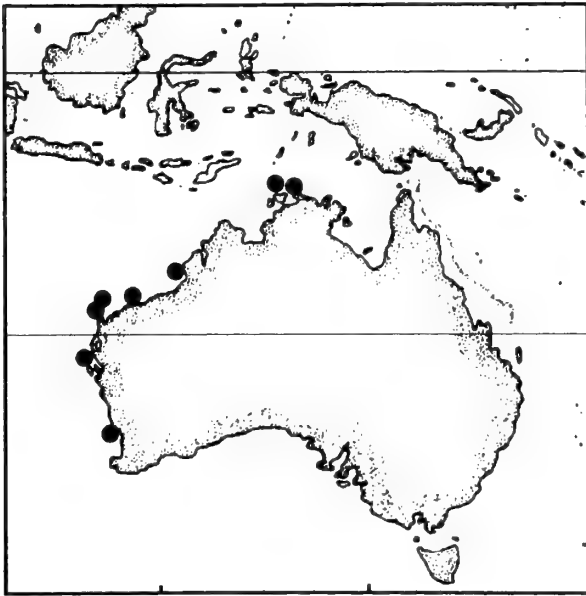


Fig. 15 Geographical distribution of *Cardiolucina pisiformis* (Thiele).

DISTRIBUTION. Indonesia and Philippines (Fig. 17).

MATERIAL EXAMINED. **INDONESIA:** Kai Islands, 05°23'S 132°37'E, 436–413m & other stations in same area between 250–450m (MNHN, Bouchet and von Cosel manuscript). **KALIMANTAN:** Sibuko Bay, 762 & 589m (USNM 302240). **PHILIPPINES:** 11°58'N 122°02'E, 486–551 m (MNHN) (see Cosel & Bouchet, ms.); off Baliscasag I., S. Bohol, 812m (USNM 298742); Iligan Bay, N. Mindanao, 500m (USNM 298616) & 505m (USNM 298660); off Claveria, Burias, 390m (USNM 2800546); off N. Ticao I., 420m (USNM 298025); off Ponson I., Camotes Islands, 650m (USNM 298468); off Apo I., S. Negros, 460m (USNM 298759); Sogod Bay, Leyte, 1280m (USNM 298560).

### *Cardiolucina rugosa* (Hedley, 1909)

Figs 18–19

*Lucina* (*Myrtea*) *seminula* Gould, 1862: 174 (non *Lucina seminulum* Deshayes, 1858: 673).

*Lucina* (*Codakia*) *seminula* (Gould) – Smith, 1885: 180–181, pl. 13, figs 5 & 5a.

*Phacoides rugosus* Hedley, 1909: 427.

*Lucina seminula* Gould – Johnson, 1964: 148, pl. 28 fig. 3.

TYPE MATERIAL. Lectotype selected by Johnson (1964, pl 28 fig. 3) (USNM 553). Hedley (1909) introduced the replacement name *P. rugosus* because *L. seminula* is preoccupied. The specimen from the type locality illustrated in Fig. 18 was given by Gould to Cumings.

TYPE LOCALITY. Hong Kong Harbour, 9–18 m.

SHELL DESCRIPTION. Shell solid, small, height to a maximum of 3.1 mm, subcircular in outline, H/L mean 0.92; moderately inflated, T/L mean 0.38, tumidity to a maximum of 1.2 mm on a single valve. Shell inequilateral and extended towards anterior. Pronounced posterior sulcus with concentric lamellae. Anteriorly, there is a narrow sulcus. Lunule small, heart-shaped. Anterodorsal area shallowly concave with fine concentric lamellae. Escutcheon lanceolate and slightly convex. Exterior sculpture of about 20 thick, slightly recurved, concentric lamellae. Interspaces between concentric la-

mellae are variable in width. Concentric lamellae often extended into short flanges at margin of posterior sulcus. Radial ribs indistinct, flattened and closely spaced. Hinge plate thick. Left valve with single posterior lateral, two cardinal teeth, the anterior of which is thicker and triangular and a single anterior lateral. Right valve with a single posterior lateral tooth, two cardinal teeth, the posterior large and the anterior a thin plate, with a single anterior lateral tooth. Ligament very short, extending from beak to less than half way to posterior lateral tooth. Inner margin with 20–21 sharp crenulations. Small denticles on posterior and anterior dorsal margin. Shallow sinus on posterior margin corresponding to the position of the posterior sulcus. Anterior adductor muscle scar elongate, not buttressed, detached from the pallial line only at the ventral tip. Posterior adductor muscle scar ovate. Pallial line continuous. Shell colour creamy white.

COMPARISON WITH OTHER SPECIES. *Cardiolucina rugosa* is closely similar to *C. semperiana*, but it is smaller, less tumid with more prominent, recurved concentric lamellae and greater anterior extension.

HABITAT. 10–250 m with a few dead shells from 540 m, sublittoral silts and muds.

DISTRIBUTION. Queensland, Australia to Hong Kong (Fig. 19).

MATERIAL EXAMINED. **HONG KONG:** North Lantau (BMNH; BMNH 1963233; NMW acc. 55.158; AM C.33806; 9–18m (USNM 611842, 2 paratypes); (USNM 24252); (USNM 714821). **CHINA:** off Pratas Islands, 268m (USNM 296955). **KALIMANTAN:** off Silungan I., 539m (USNM 291027). **PHILIPPINES:** (USNM 21109); Pescador I. Tanon Straits, 412m (USNM 293876); Bohol (BMNH); off Sombrero I., Balayan, 216m (USNM 312342); S.E. of Bantayan I., 60m (USNM 293115); Destacado I., 218m (USNM 298090); off N. Cebu, 125m (USNM 293266); Pujada R., E. Mindanao, 253m (USNM 294765); off Tochanhi Pt. Tawi Tawi Islands, 90m (USNM 292997) & 35m (USNM 283372); 11°43'N, 122°34'E, 93–99m (MNHN). **AUSTRALIA:** Queensland, Cape York (BMNH 1887.2.9.2772–5); Hope Islands, 10–18m (BMNH 1910.9.28.68–71 and BMNH 1963259); Palm Island (NMW acc. 55.158); Gulf of Carpentaria 16°58'S 140°53'E, 9m (AM C.015275); Albany Passage, Torres Strait, 9–30m (AM C.36171); Palm Island (AM C.1049); Low Isles, 27m (AM); Cape Sidmouth (AM C.2594); Endeavour Reef, 40m (AM C.44668); Hervey Bay (AM); Barney Point, Port Curtis (AM C.21805); Facing Island (AM C.4428); Quoin Island, Port Curtis (AM); **Northern Territory**, Darwin (AM). **PAPUA NEW GUINEA:** 0.5 mile off Fairfax Harbour, Port Moresby, 15–18m (AM C.309466).

### *Cardiolucina semperiana* (Issel, 1869)

Figs 21–24

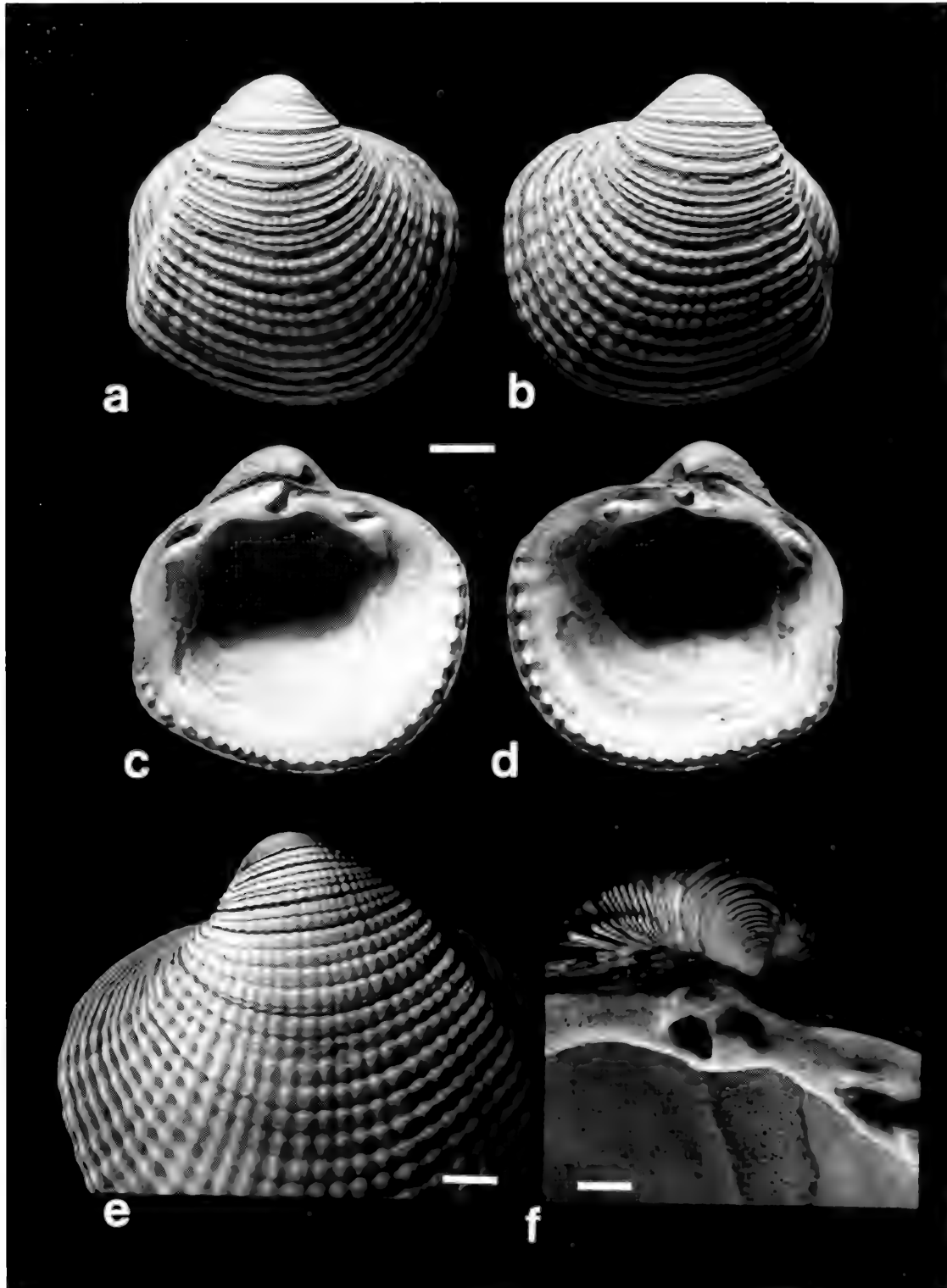
*Lucina pisum* Reeve 1850 (part), pl. 11, fig. 66b (non *L. pisum* Sowerby 1836).

*Lucina semperiana* Issel, 1869: 82–83.

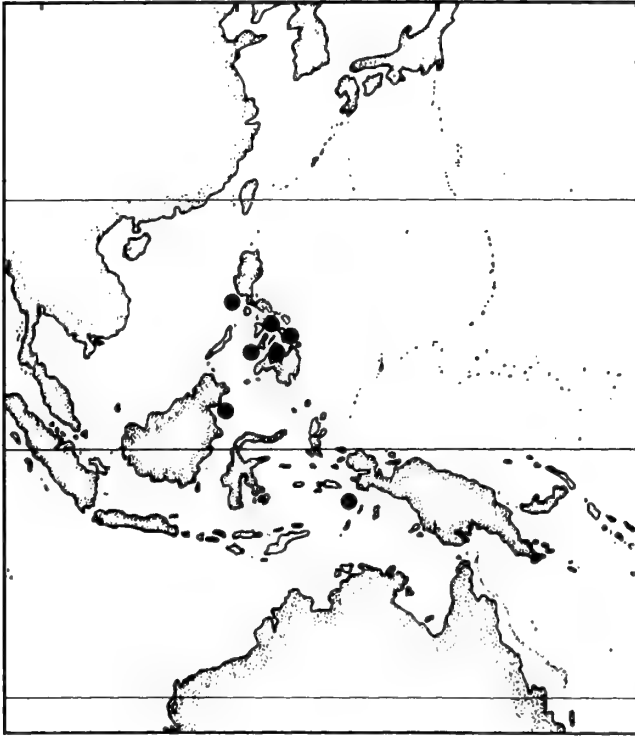
*Phacoides* (*Bellucina*) *semperiana* (Issel) – Lamy 1920: 211–213. *Denitilucina* (*Bellucina*) *macassari* Prasad 1932: 163 pl. 5 figs 13–16.

*Lucina semperiana* (Issel) – Bouchet & Danrigal 1982: 16, fig. 19. *Bellucina semperiana* (Issel) – Oliver 1992: 99, pl. 19 fig. 7.

TYPE MATERIAL. The species concept of *C. semperiana* was based on the figure in Savigny (1817, pl. 8, fig 12) and one specimen from Suez in the Issel Collection (now lost); the single shell of this species in the Savigny collection (MNHN) illustrated by Bouchet & Danrigal



**Fig. 16** *Cardiolucina quadrata* (Prashad, 1932). a–d, holotype of *Dentilucina (Bellucina) var. quadrata* Prashad, 1932, Salayar, Sulawesi, Indonesia and e–f, *C. quadrata*, Kai Islands, Indonesia, BMNH. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, interior of right valve; e, exterior shell surface; f, hinge showing hooked anterior cardinal tooth in the left valve. Scale bars a–e = 2.0mm, f = 1.0mm.

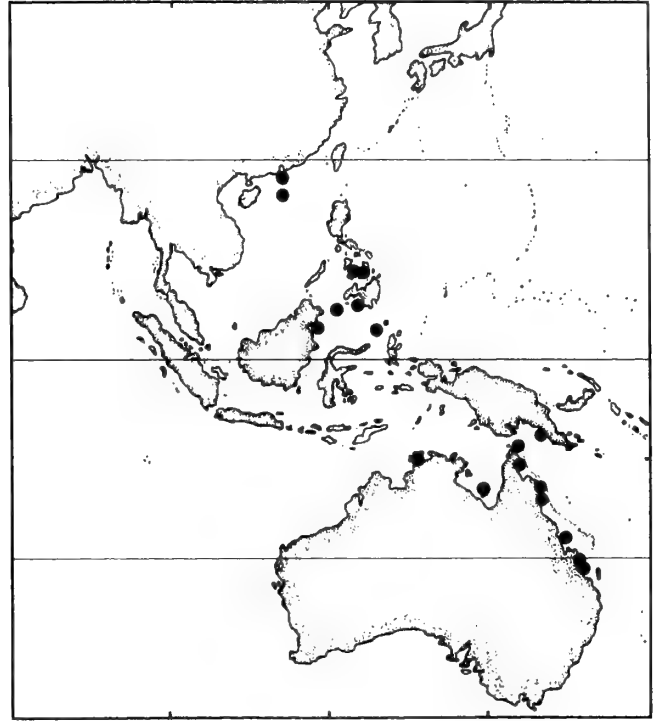


**Fig. 17** Geographical distribution of *Cardiolucina quadrata* (Prashad).

(1982, fig. 19) is here designated as lectotype. The holotype of *Dentilucina* (*Bellucina*) *macassari* Prashad is located at ZMA, reg. number 3.32.090 (Fig. 21 c & d).

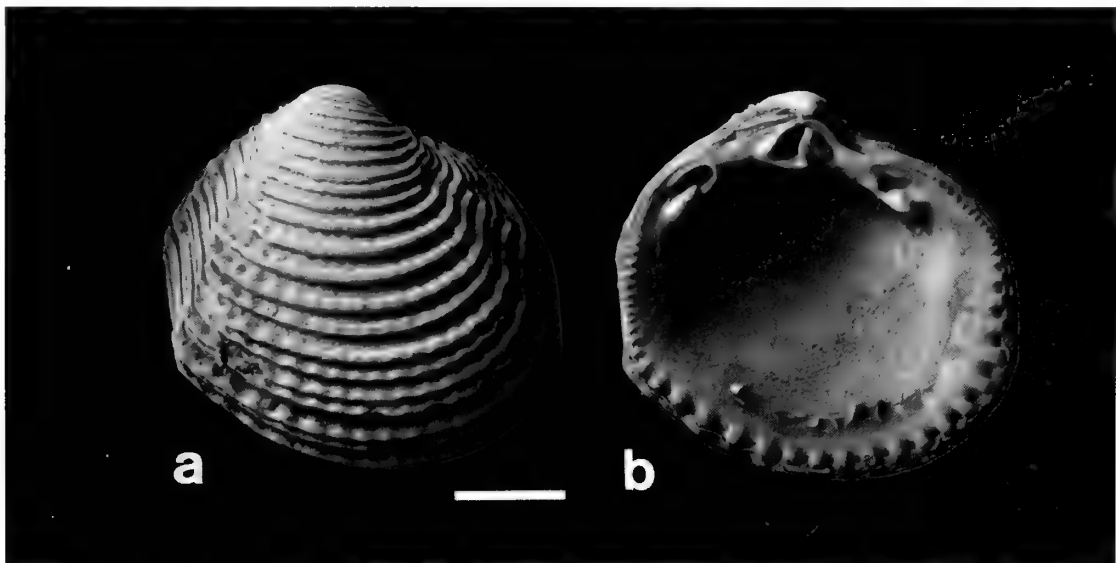
**TYPE LOCALITY.** *C. semperiana* from Suez, Red Sea. *C. macassari* from Makassar, South Sulawesi, Indonesia (Siboga Expedition station 71).

**SHELL DESCRIPTION.** Shell solid, small, height to a maximum of 7.7 mm, sub-circular in outline H/L mean 0.98; inflated, T/L mean 0.46, tumidity of single valve to 4.6 mm. Inequilateral, extended

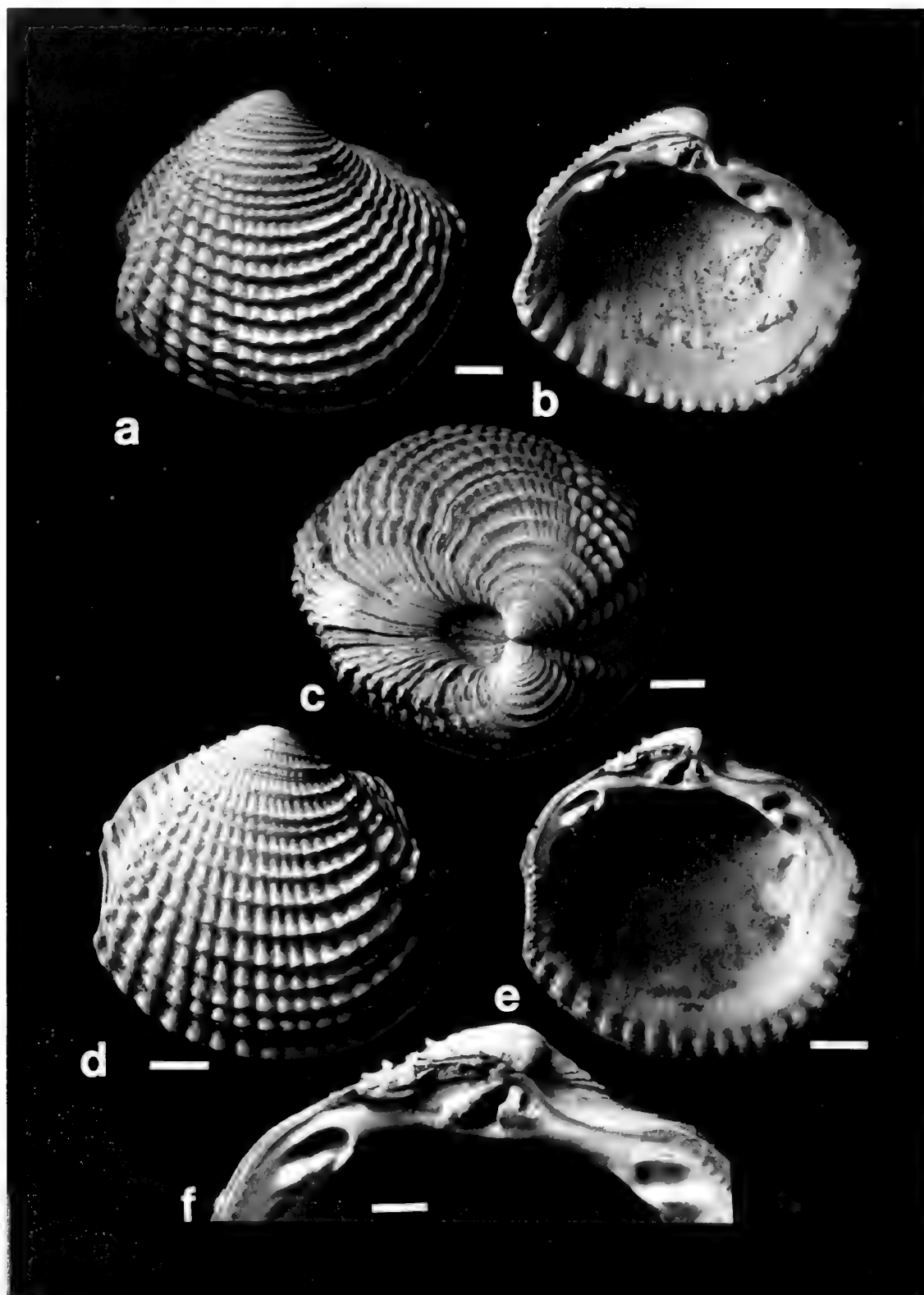


**Fig. 19** Geographical distribution of *Cardiolucina rugosa* (Hedley).

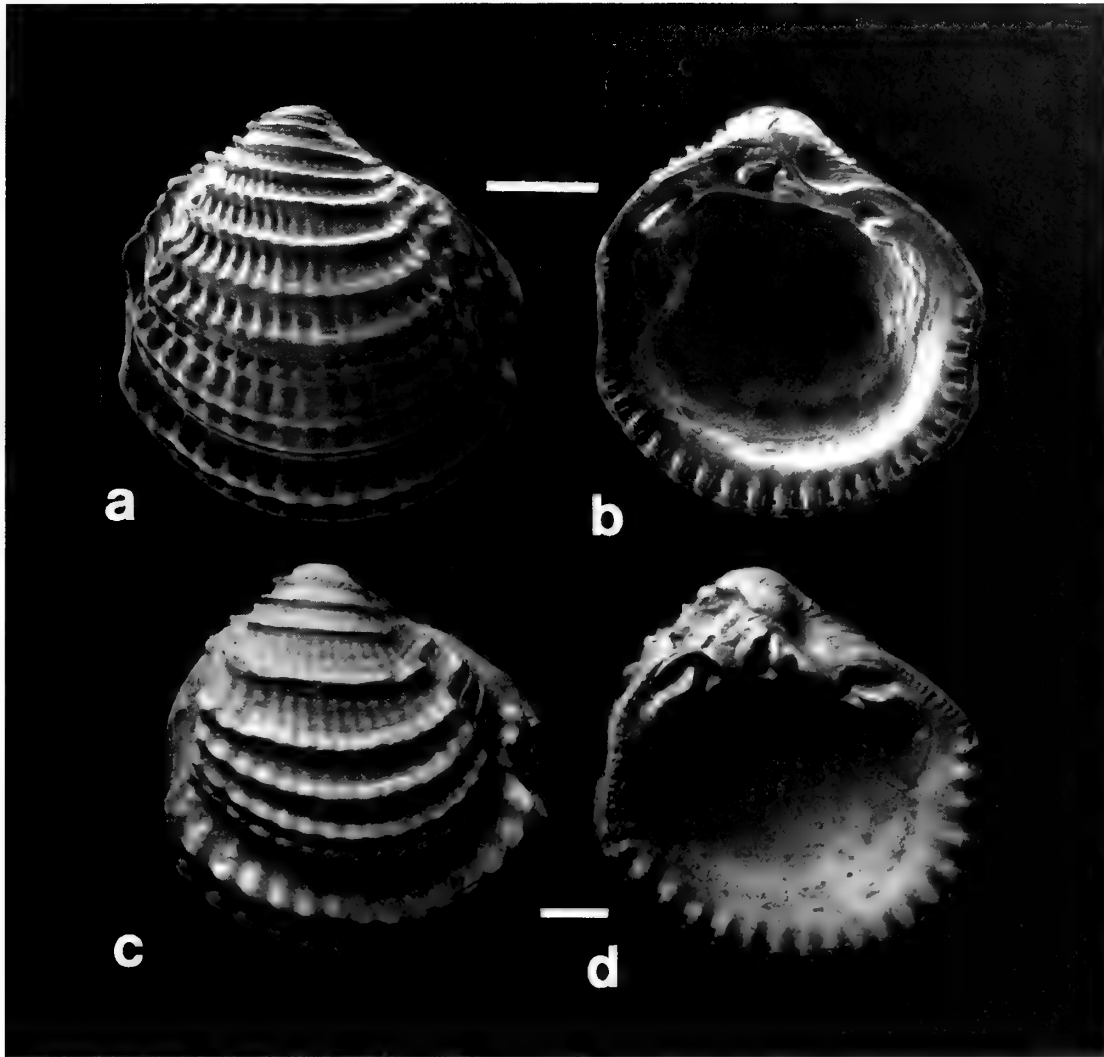
anteriorly. Deep sulcus posteriorly with prominent concentric lamellae. Posterodorsal margin of the sulcus marked by a ridge with prominent short lamellae. Lunule heart-shaped, shallow. Anteriorly, there is a narrow sulcus. Escutcheon lanceolate with fine concentric sculpture. Exterior sculpture of 20–30 low, rounded radial ribs with narrow interspaces. These are crossed by 15–24 projecting, concentric lamellae which are often irregularly spaced. In some specimens, concentric lamellae are thickened with steep, ventral edges, giving a stepped appearance to the shell. Hinge plate thick. Left valve with single posterior and anterior lateral teeth and two cardinal teeth, of



**Fig. 18** *Cardiolucina rugosa* (Hedley, 1909), Hong Kong Harbour, BMNH 1963233. Specimen of *Lucina seminula* Gould 1862 from type locality, given by Gould to Cuming. a, exterior of left valve; b, interior of right valve. Scale bar a–b = 1.0mm.



**Fig. 20** a–b *Cardiolucina semperiana* (Issel, 1869), Gulf of Suez, Red Sea BMNH 1870.1.19.4, c–f *C. semperiana*, Tuléar, Madagascar, BMNH. a, exterior of right valve; b, interior of left valve; c, dorsal view articulated shell; d, exterior of right valve; e, interior of left valve; f, hinge showing details of the dentition with denticulate posterior cardinal tooth. Scale bars a–b = 1.0mm, c = 750 $\mu$ m, d–e = 1.0mm, f = 500 $\mu$ m.



**Fig. 21** *Cardiolucina semperiana* (Issel, 1869). Figure a–b Paralectotype of *Lucina pisum* Reeve, 1850 BMNH 1963552. Singapore and c–d Holotype of *Dentilucina (Bellucina) macassari* Prasad, 1932, Makassar, Indonesia, ZMA. a, exterior of right valve; b, interior of left valve; c, exterior of right valve; d, interior of left valve with attempted drill hole on the posterior part of the umbo. Scale bars a–d = 1.0mm.

which the anterior is the smaller. Right valve with single posterior and anterior laterals and two cardinals, the posterior being the larger. Cardinal teeth have small denticles. Ligament extends two thirds of the distance from the beak to the posterior lateral tooth. Inner margin with 20–21 crenulations and there are also small, rounded denticles along anterodorsal and posterodorsal margins. Both anterior and posterior shell margins have shallow sinuses corresponding to the sulcii. Anterior adductor muscle scar elongate, buttressed in the more tumid specimens, detached from the pallial line only at the ventral tip. Small pedal retractor muscle scar at dorsal tip of anterior adductor scar. Posterior adductor muscle scar ovate. Pallial line continuous. Shell creamy white.

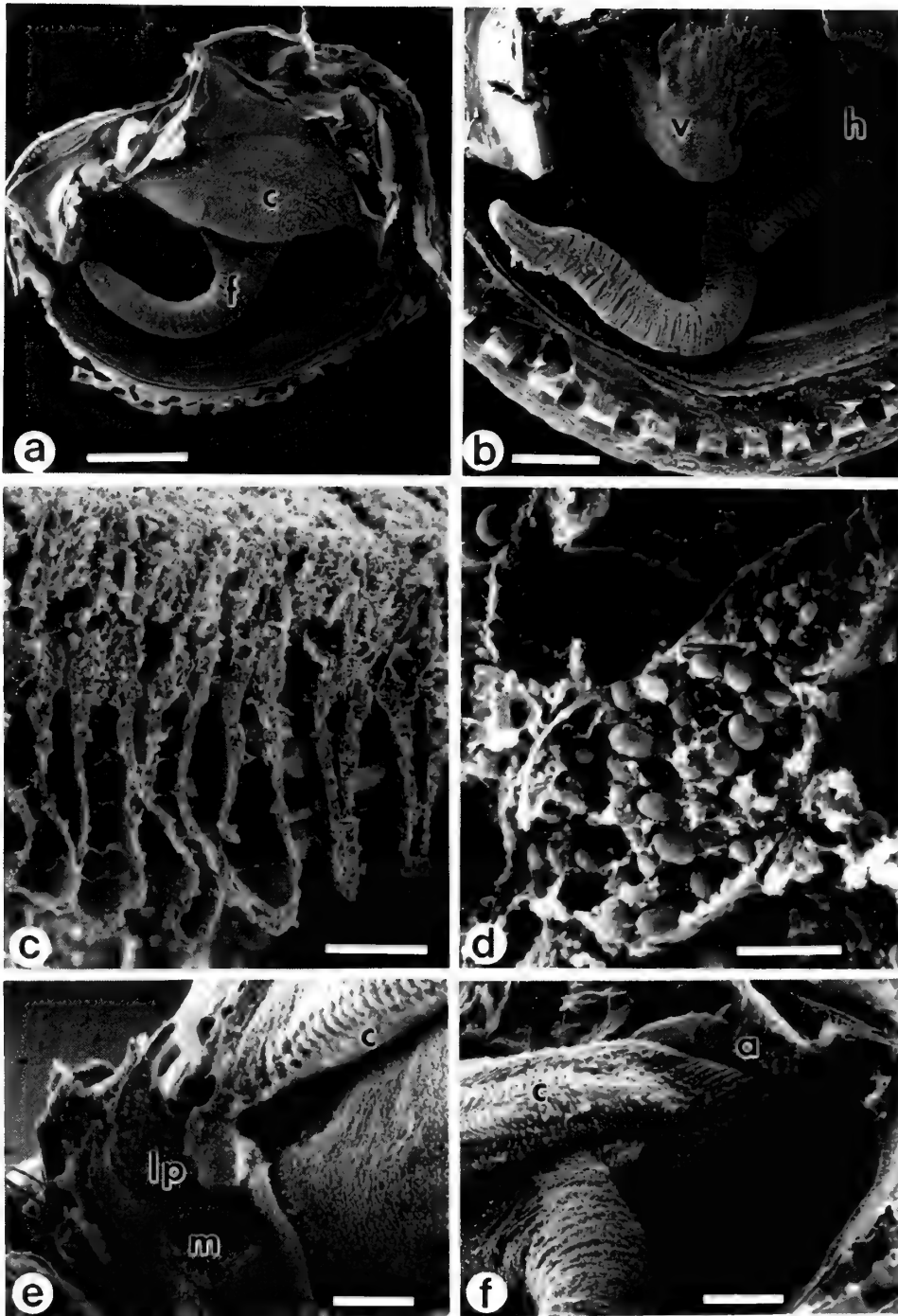
**ANATOMY.** (Fig. 22) Posterior inhalant aperture absent, exhalant aperture a small inverted tube. Ctenidia large and thick, inner demibranchs only, with a thin, shallow, ventral food groove. Gill filaments long and broad, with large central space crossed by transverse muscle strands (Fig. 22 c). Bacteriocyte zone packed with ovoid bacteria about 2.0–2.5  $\mu\text{m}$  in length (Fig. 22 d). Labial palps consist of small papilla at edge of lips. Foot cylindrical, vermiform,

with a much-corrugated outer surface, a pointed tip and a small rounded heel to the posterior. Ctenidia attached to posterior mantle by a thin muscular sheet (Fig. 22 f). Body wall with a large irregular visceral pouch in the antero-ventral position.

**GEOGRAPHICAL VARIATION.** This species is extremely variable both within populations and across its range from the northern end of the Red Sea to the Philippines. In Southeast Asia *semperiana* are generally smaller, but relatively more tumid, as shown in Fig. 23, which plots ratio of length over tumidity against mean height of specimens from Red Sea, Madagascar, India, South East Asia. The holotype of *macassari* is the most tumid of all the specimens measured, but is probably an abnormal individual which has survived attempted drilling at the posterior dorsal margin. *C. semperiana* from Southeast Asia also tend to have fewer, but heavier, concentric lamellae (Figs. 21).

**HABITAT.** Live material collected from shallow water (up to 50 m), a few dead shells from up to 350 m, mud and sand.

**COMPARISON WITH OTHER SPECIES.** *C. semperiana* is similar to *C. rugosa* but is larger, more tumid and has more prominent radial ribs.



**Fig. 22** *Cardiolucina semperiana* (Issel, 1869), Sinai Coast, Gulf of Suez, Egypt. NMW 1982.068. a, interior of right valve showing thick inner demibranch of the ctenidium and cylindrical, vermiform foot; b, right valve showing pronounced visceral pouch and the foot with strongly corrugated surface and small, rounded heel; c, section showing broad gill filaments and transverse muscle strands crossing the spaces within the filaments. d, bacteriocyte zone with ovoid bacteria; e, labial palps (lp) and mouth (m); f, ctenidia attached to the posterior mantle by a thin muscular sheet. Abbreviations: c=ctenidium, f=foot, v=visceral pouch, h=heel, lp=labial palps, m=mantle, a=attachment of ctenidium to mantle. Scale bars a = 1.0mm, b = 500 $\mu$ m, c = 40 $\mu$ m, d = 5 $\mu$ m, e = 150 $\mu$ m, f = 250 $\mu$ m.

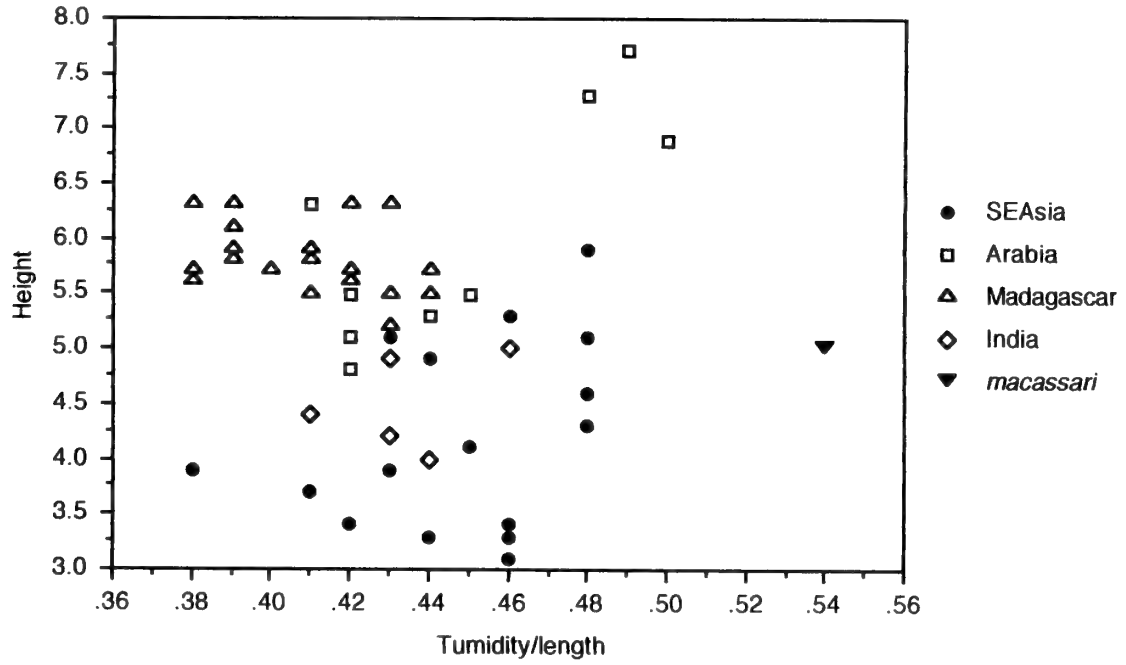


Fig. 23 Geographical shape variation of *Cardiolucina semperiana*. The specimen of *C. macassari* is the holotype.

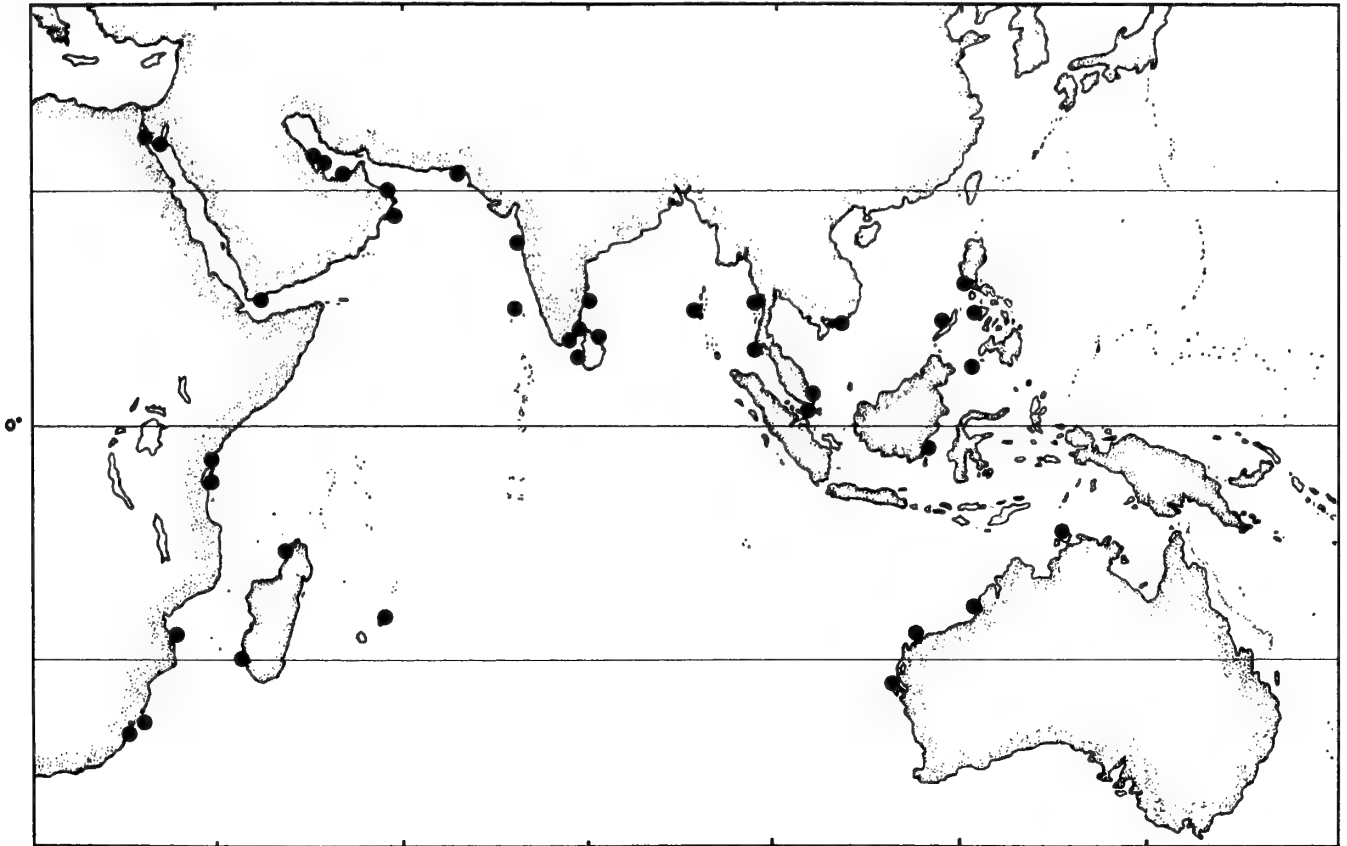
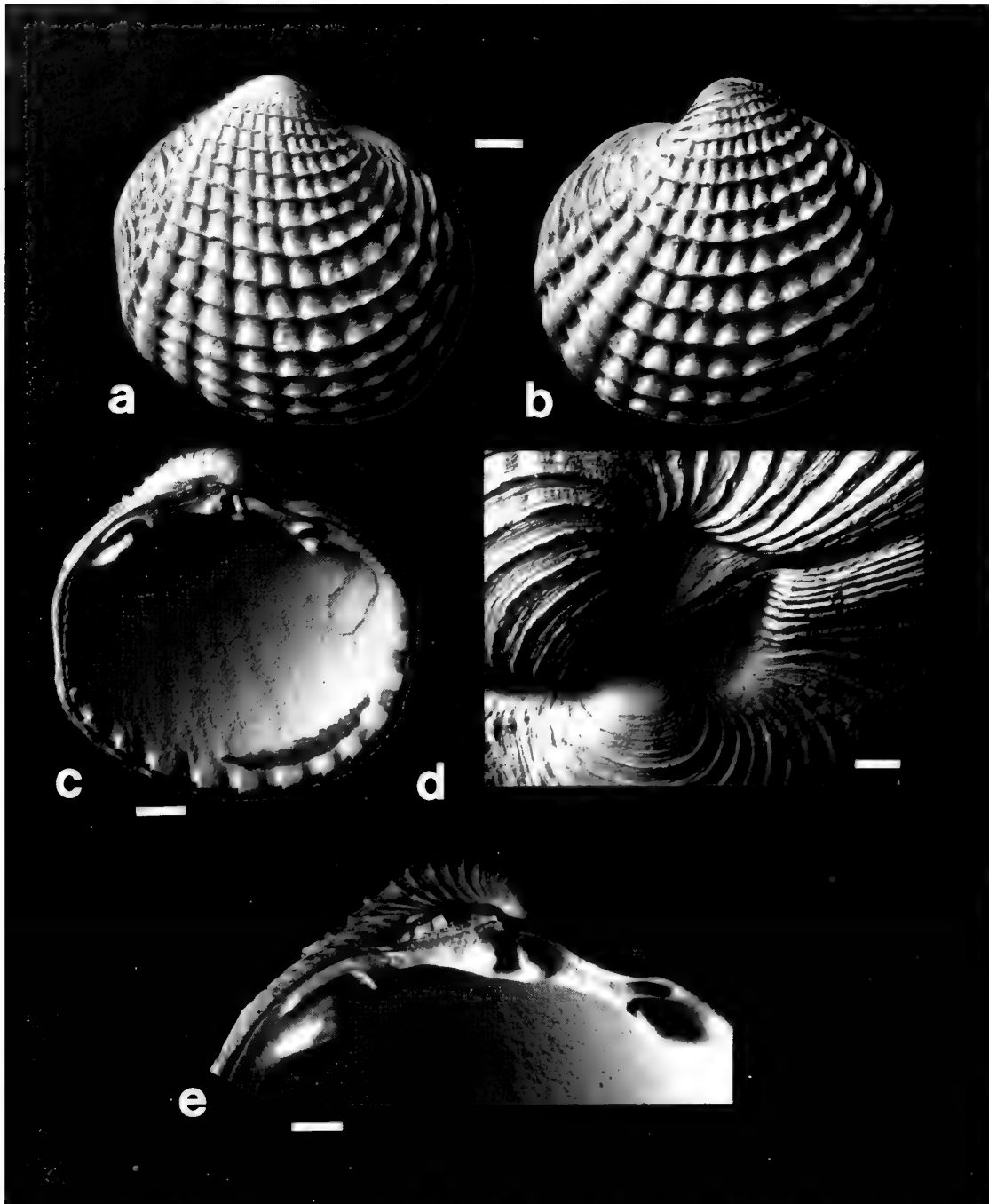


Fig. 24 Geographical distribution of *Cardiolucina semperiana* (Issel).



**Fig. 25** *Cardiolucina siquijorensis* Taylor and Glover new species, Siquijor, Philippines. a, Paratype (USNM 812176), exterior of right valve; b, Holotype (USNM 812176), exterior of left valve; c, Paratype, interior of left valve; d, Holotype, detail of lunule; e, Paratype, hinge of left valve showing posterior lateral tooth with pronounced rim on the socket. Scale bars a–c = 500 $\mu$ m, d = 150 $\mu$ m, e = 250 $\mu$ m.

**DISTRIBUTION.** Northern Red Sea, southern Africa to Philippines (Fig. 24).

**MATERIAL EXAMINED.** **EGYPT:** Gulf of Suez (BMNH 1870.1.19.4); Suez (BMNH 1963492); Nuweiba, Sinai (AM 1954). **YEMEN:** Aden (BMNH 1902.12.30.754–6 & 1963235); Aden (AM C.33727); (USNM 608854). **OMAN:** Qurm, Muscat (NMW Z.1993.061.0434); Masirah (NMW Z.1993.061.0427 & 0433). **ARABIAN GULF:** (USNM 636963); Bahrain (NMW 1993.061.043); Linyah (NMW acc. 55.158); Qatar (BMNH acc.

2258); Abu Dhabi (BMNH). **ZANZIBAR:** Nyange I., 20m (ANSP 251213); 1.5 miles S.W. of Ras Shangani, 18–20m (ANSP 213493); 1 mile N. Bawi I., 22m (ANSP 250912). **KENYA:** Mombasa (BMNH acc. 2223), (NMW 1955.158). **TANZANIA:** Msimbasi Bay, Dar es Salaam 5m (AMC.309448). **MOZAMBIQUE:** Bazaruto I., 8–10 m (NM K5317 & G4458). **SOUTH AFRICA:** Durban Bay, (NM E834 & A2357); Shelly Beach, Izotsha, Natal (NM9898). **MADAGASCAR:** N.W. Madagascar, 30m (AM C.70660); Tuléar (MNHN); 40 miles W.S.W. Tuléar, 33m (USNM 761189); Nossi Bé (USNM 633927); Nossi Bé, shallow water to 35m, (ANSP 261127,



259587, 259028, 260541, 261338, 259901, 261873). **MAURITIUS**: 1.5 m N.W. Black River, 15m (ANSP 273431). **PAKISTAN**: Karachi (BMNH acc. 1831). **INDIA**: 80 miles S.W. Bombay 17° 54'N 72° 27'E, (USNM 716676); Madras (BMNH 1953.1.30.190–4); Madras (BMNH 89.2.17.23–6); Tondi, Madras (NMW acc 55.158); Manapad (BMNH 1953.1.30.26); Mandapam, Gulf of Mannar, 3m (ANSP 302433); Tuticorin (BMNH 1953.1.30.188–89); S. of Krusadai I., Gulf of Mannar, 18m (ANSP 301196); Andaman Islands (AM C.040397, C.040597); Andaman Islands (NMW 55.158). **SRI LANKA**: Colombo (AM); Trincomallee, 29m (AM); E., S., and N. coasts (AM C.309467); BMNH 1963491; Palk Strait, 22m (AM); 9°34.5'N 80°39'E (AM C.309461); northern tip of Eluvativu I., (ANSP 211085). **BURMA**: 57 miles N.W. Tavoy I., Anadamans Sea, 39m (ANSP 293254). **THAILAND**: Koh Kahdat (AM C.031287); Phuket (USNM 661156); south end Light-house I., Phuket, 5m (ANSP 286500); 25 miles N.N.W. Phuket, 42m (ANSP 291734). **MALAYSIA**: Mersing Island, E. Malaya, 3.5m (AM). **SINGAPORE**: BMNH acc. 2172; Singapore (AM C.3437); NMW acc 55.158. **INDONESIA**: Kalimantan (AM C.309470). **PHILIPPINES**: Corregidor, Bay of Manila, intertidal (BMNH); Manila Bay, 18m (ANSP 281443); Manila Bay, 18m (ANSP 328655); off Antonia I., E. Panay, 40m (USNM 293697); N. of Marinduque, 353m (USNM 295197); Lataau I., 33m (USNM 236058); Malampaya Sound, Palawan, 25–35m (USNM 297395); off Tinkata I., Tawi Tawi Islands, 30m (USNM 257677); **VIETNAM**: Vung Tau, Chilins (ANSP 330797). **AUSTRALIA**: **Western Australia**, Shark Bay (AM C.69245); Carnarvon, 7.6m (AM); Carnarvon (AM C.69270); 210 miles N. of Broome, 230m (AM); 110 miles N. of Melville Island, Arafura Sea (AM); 72 miles N.W. of Dampier Island, 110m (AM 2405).

### *Cardiolucina siquijorensis* Taylor and Glover, new species

Fig. 25

**TYPE MATERIAL.** Holotype, articulated specimen (Fig. 25 b) USNM 812176. H=3.4 mm, L=3.5 mm. Paratypes, USNM 812177, 812169.

**TYPE LOCALITY.** Siquijor, Solong-on, Siquijor I., Visayan Islands, Philippines (09° 13'10"N 123° 27'30"E) depth 2–3 m.

**SHELL DESCRIPTION.** Shell very small, to a maximum height of 3.5 mm, outline circular H/L 0.97, inflated, T/L 0.39, tumidity of single valve to 1.3 mm. Shallow posterior sulcus with concentric lamellae. Anterior sulcus absent. Lunule shallow, heart-shaped. Anterodorsal area indistinct, posterodorsal area with concentric lamellae. Exterior sculpture, fenestrate, of 11–12 broad, straight-sided, radial ribs. Interspaces wide, but narrower than the ribs. Ribs are slightly broader towards the anterior. About 14–16 thin, concentric lamellae, project slightly above radial ribs. Hinge plate robust. Left valve with single posterior lateral tooth, the dorsal edge of the socket extended into a sharp rim (Fig. 22 e); two cardinal teeth, triangular in shape and more or less equisized; single anterior lateral tooth. Right valve with single anterior lateral tooth, a single central cardinal tooth and a robust posterior lateral tooth. Ligament extends from beak to the dorsal end of the posterior lateral tooth (Fig. 22 e). Inner margin with 12 coarse crenulations, and fine beading extending to the hinge margins. Anterior adductor muscle scar elongate, not buttressed, with only ventral tip detached from pallial line. Posterior adductor muscle scar rounded. Pallial line continuous. Shell creamy white.

**COMPARISON WITH OTHER SPECIES.** This species is similar in size and ornament to *C. pisiformis* but is distinguished by fewer and broader radial ribs, the shallower lunule, the two equal-sized cardinal teeth in the left valve and the single cardinal in the right valve.

**HABITAT AND DISTRIBUTION.** As for type locality.

**MATERIAL EXAMINED.** **PHILIPPINES**: Siquijor I., collected with type material (USNM 812177, 812176, 812169).

### *Cardiolucina* sp.

Fig. 26

In addition to the species described, we have four lots from the Philippines consisting of rather badly preserved, disarticulated shells and two rather better preserved juvenile shells. These are distinct in a number of shell characters from the other *Cardiolucina* species. Because the adult specimens are badly preserved and because juveniles often differ considerably from adults, we are reluctant to describe a new species based on this material.

The adult shells have maximum height of 10.8mm, with tumidity of a single valve to 2.7mm and H/L 0.98, T/L 0.5. The posterior sulcus is broad and shallow, the anterior sulcus absent. About 17–18 prominently scalloped, concentric lamellae, with more than 20 fine, rounded, radial ribs, which do not cross the concentric lamellae. The interspaces between the ribs are narrow, but relatively deep and the intersection of the concentric and radial ornament produces a deeply-pitted appearance. The lunule is heart shaped and relatively deep. In the left valve, there is a single posterior lateral, two triangular cardinal teeth, and a single posterior lateral. The inner margin of the shell has about 25 crenulations.

This species is similar to *C. semperiana* but can be distinguished by the lack of the anterior sulcus, the shallower posterior sulcus, the pitted appearance of the shell surface and the more rounded anterodorsal area.

**MATERIAL EXAMINED.** **PHILIPPINES**: off Sibugay I., E. of Masbate, 198 m (USNM 292666); Daram Channel, W. Samar, 48 m (USNM 292830); off Matocot Point, W. Luzon, 400 m (USNM 295706); off Corregidor Light, 73 m (USNM 294200).

### ATLANTIC OCEAN SPECIES

#### *Cardiolucina lamothei* (Dautzenberg, 1913)

Figs 27 a & b, 28

*Lucina lamothei* Dautzenberg, 1913: 100–101, pl. 3 figs 50–54.

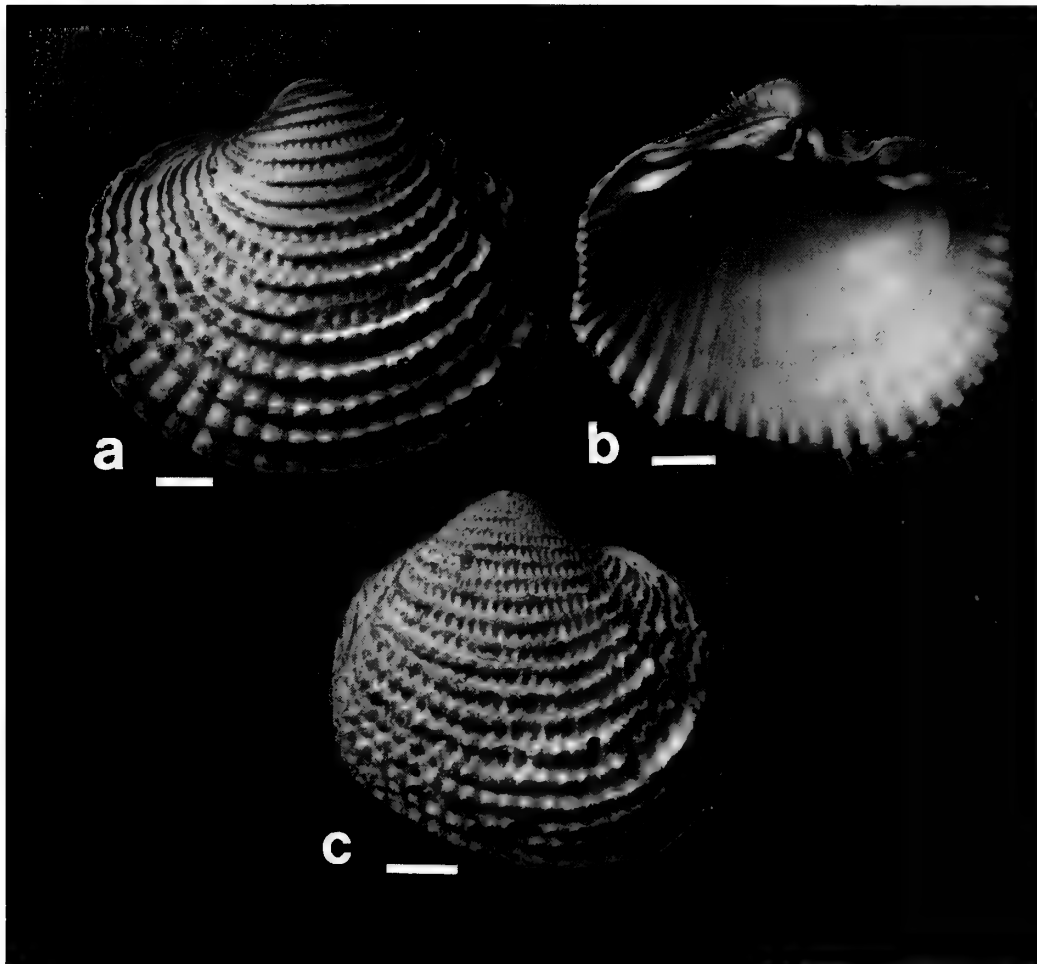
*Phacoides (Parvilucina) congoensis* Thiele & Jaeckel, 1931: 220–221, pl. 4 fig. 91.

*Phacoides (Bellucina) lamothei* (Dautzenberg) – Lamy 1920 : 215.

**TYPE MATERIAL.** Figured specimens of *L. lamothei* – two syntypes from Tamara, Archipel de Los, Guinée, marked TYPE in Dautzenberg's handwriting (MNHN). Numerous other specimens from localities mentioned by Dautzenberg (1913) are housed in the Royal Belgian Institute of Natural Sciences (IRSNB inventory I.G. 10591). Our figured specimen is from a sample sent by Dautzenberg to Tomlin (NMW 1955.158).

**TYPE LOCALITY.** West Africa, Tamara, Archipel de Los, Guinée.

**SHELL DESCRIPTION.** Shell solid, very small, height to maximum of 4.0 mm. Subquadrate, inequilateral, slightly extended anteriorly. Not inflated. Anterior sulcus shallow leading to marginal sinus. Umbones are conspicuous, prosogyrate. Lunule very small, underneath beaks. Anterodorsal area indistinct and slightly convex. Escutcheon with concentric lamellae. Exterior sculpture of 15–18 prominent, narrow concentric lamellae, which are slightly reflexed. About 40 fine, radial ribs in the interspaces between concentric



**Fig. 26** a–b, *Cardiolucina* sp. Corregidor, Philippines (USNM 294200); c, *Cardiolucina* sp Sibugay Island, Masbate, Philippines (USNM 29266). Scale bars a = 400µm, b = 500µm, c=1mm.

lamellae. Hinge plate thick. Left valve with single, hooked anterior lateral tooth, two cardinals and single posterior lateral tooth. Right valve with similar. Indentations on both anterior and posterior margins which correspond to the position of sulci. Inner margin with about 40 crenulations. Anterior adductor muscle scar elongate, not buttressed. Pallial line attached to lower third of anterior adductor muscle scar. Posterior adductor scar reniform in outline. Pallial line continuous. Shell colour grey-white.

**COMPARISON WITH OTHER SPECIES.** This species is similar to *C. rehderi* but has a greater number of fine radial ribs.

**HABITAT.** Fine muddy sand from 4–200 m.

**DISTRIBUTION.** Senegal to Northern Angola (Fig. 28).

**MATERIAL EXAMINED.** **AFRICA:** Guinea, Los Islands (NMW 1955.158).

### *Cardiolucina rehderi* (Britton, 1972)

Fig. 27 c & d

*Parvilucina* (*Bellucina*) *rehderi* Britton, 1972: 7–9, fig. 3.

*Lucina* (*Parvilucina*) *rehderi* (Britton) – Rios, 1994: 252.

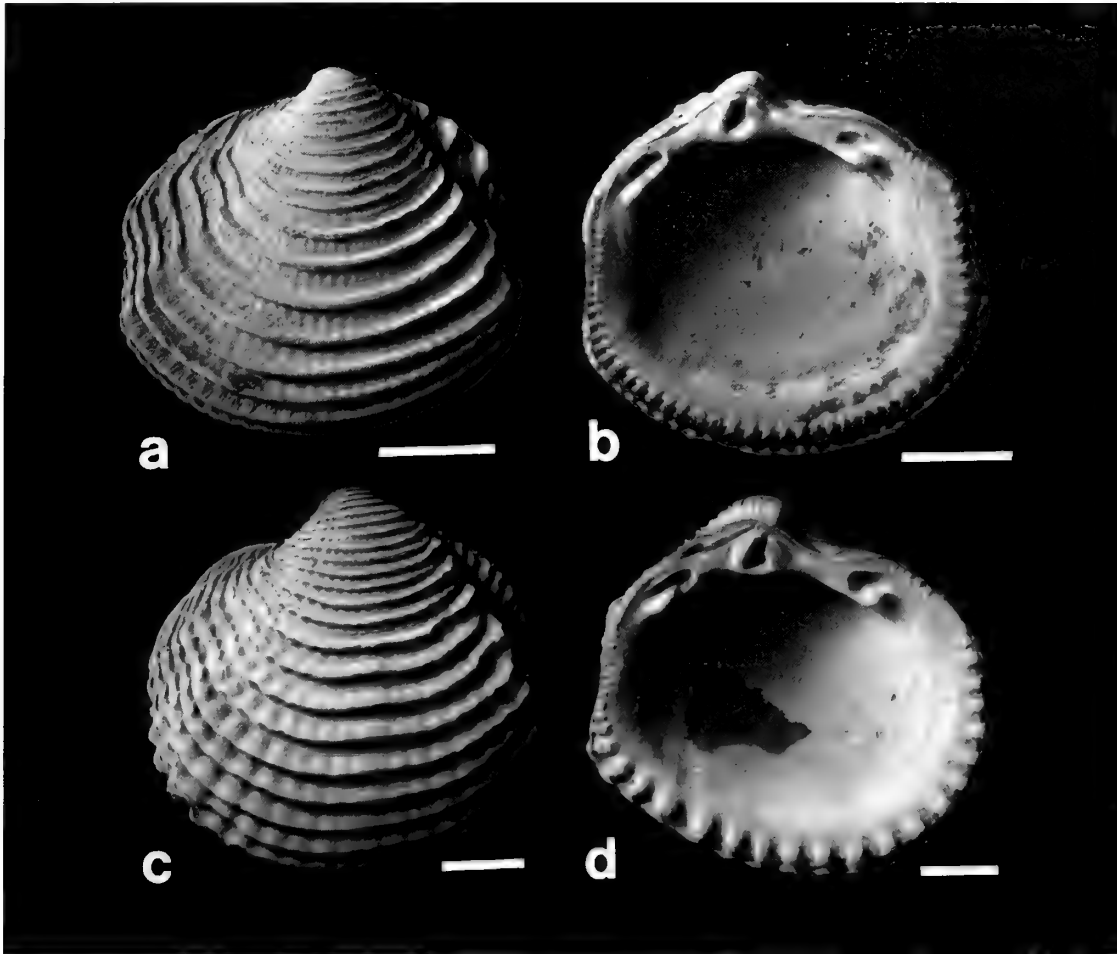
**TYPE MATERIAL.** Holotype, USNM 208255, L = 4.2 mm, H = 4.2 mm, T = 4.1 mm (paired valves), also 9 paratypes.

**TYPE LOCALITY.** Brazil, no further details.

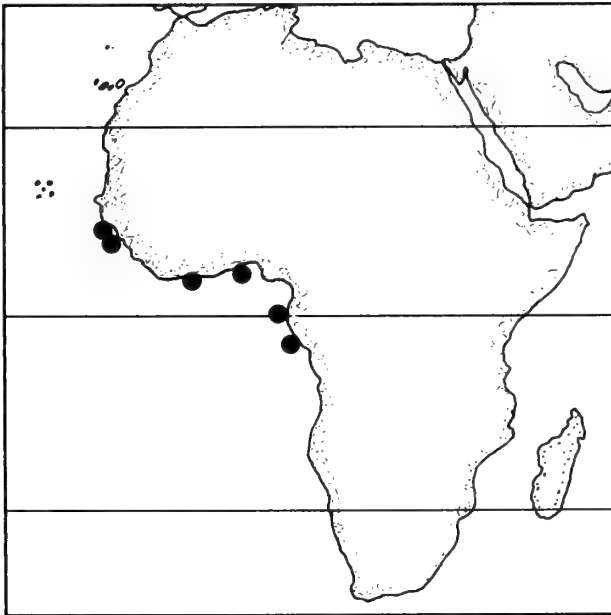
**SHELL DESCRIPTION.** Shell small, height to 4.2 mm. Subcircular; moderately inflated, maximum tumidity on a single valve to 1.9 mm. Inequilateral, slightly extended anteriorly. Broad posterior sulcus. Posterior dorsal area slightly convex, with distinct elevation of concentric lamellae. Shallow anterior sulcus, anterior dorsal area indistinct. Lunule shallow, heart-shaped. Exterior sculpture of about 30 indistinct radial ribs most clearly visible in the interspaces between concentric lamellae, ribs separated by shallow, narrow interspaces. Concentric lamellae, 14–16, prominent, thickened lamellae often appear scalloped at position of intersection with radial ribs. Hinge plate thickened. Left valve with single anterior lateral tooth; two cardinal teeth and single posterior lateral. Right valve with similar. Ligament short, extending about half distance from beak to posterior lateral tooth. Inner margin with about 20 fine crenulations. Anterior adductor muscle scar longer than wide but relatively short with pallial line joining near ventral tip. Posterior adductor muscle scar rounded. Shell colour white. A more extensive description of this species is given by Britton (1972).

**COMPARISON WITH OTHER SPECIES.** This species is closely similar to *C. lamothei*.

**HABITAT.** Unknown.



**Fig. 27** *Cardiolucina lamothei* (Dautzenberg, 1913) and *C. rehderi* (Britton, 1972). a, *C. lamothei* Iles de Los, nr Conakry, Guinea (NMW 1955.158) Left valve. P35.082; b, left valve interior; c, *C. rehderi* Britton, left valve, Paratype NMNH; d, left valve interior. Scale bar a–d = 1.0mm.



**Fig. 28** Geographical distribution of *Cardiolucina lamothei* (Dautzenberg). Data from Dautzenberg (1913).

**DISTRIBUTION.** Known only from type material reported on by Britton (1972).

#### FOSSIL SPECIES OF *CARDIOLUCINA*

Apart from the description of the type species *C. agassizi*, we have not attempted a comprehensive review of the fossil record. However, the species listed below have the characters of *Cardiolucina*. Other fossil species that we do not consider to belong the genus are listed separately.

*Phacoides (Parvilucina) ligatus* Cossmann and Pissarro, 1904. (pages 17–18, pl. 7, figs 1–4).

Described from the Eocene (Lutetian) of Hauteville, Cotentin Peninsula, France. This small species has a thick shell and prominent concentric lamellae with fine radial ribbing similar to that of *Cardiolucina agassizi*. Chavan (1937: 207) first suggested that this species should be classified as a *Bellucina*. On the basis of the published figures, we consider that this is probably the earliest known *Cardiolucina*.

*Lucina nuciformis* Tate, 1887b: 144 (figured in Tate, 1886, p. 158, pl. 12 figs.10a & b).

This Miocene species from Blanche Point, Aldinga Bay, South Australia, is very similar to the Recent *Cardiolucina crassilirata* (Tate).

***Linga (Bellucina) gonzalesi*** Shuto, 1971 (pp. 30–31; Plate 1 figs 8, 11, 13–17; text fig. 6)

Described from the Lower Pliocene Cabatuan Formation of Panay Island, Philippines. This species is well described and illustrated. It has about eight prominent, radial ribs with a fenestrate ornament like the Recent *Cardiolucina eucosmia*, *C. pisiformis* and *C. siquijorensis*. The intersections of the radial ribs and concentric lamellae are 'strongly granulated', a feature found in none of the three Recent species.

***Lucina polli*** Icke & Martin, 1907. (p. 250, plate 18 figs 40, 40a)

Described from the Pliocene of Nias Island, Indonesia. From the illustrations, this is a definite *Cardiolucina* species with fine radial ribbing and prominent concentric lamellae, similar in form to *C. rugosa*.

***Cardiolucina agassizi* var. *regularior*** Sacco, 1904 (p. 90, pl. 20 figs. 40–42) and var. ***constricta*** Sacco, 1904 (p. 90 pl. 20 fig. 43).

Without a morphological analysis of *C. agassizi* populations it is difficult to evaluate these names, but they would seem to be forms of a variable species.

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### **SPECIES EXCLUDED FROM *CARDIOLUCINA*.**

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Listed under original generic assignments as published.

***Phacoides (Bellucina) actinus*** Dall, 1903: 1385, pl. 52 fig. 3. Also Woodring (1925: 126–127; pl. 17 figs 5–8).

Described from the middle Miocene Bowden Formation of Jamaica, this species has 16–22 radial ribs and fine concentric lamellae. However, the lunule is lanceolate and the hinge different from *Cardiolucina* species. We consider that it may belong to the same clade as *Radiolucina amianta* (Dall) (see below).

***Phacoides (Bellucina) amiantus*** Dall, 1901: 826–7, pl. 39 fig. 10.

Although Dall included this Caribbean species in *Bellucina* and Bretsky (1976) used it as the basis of her diagnosis of the genus, it differs in many features from the type species of *Cardiolucina* and *Bellucina*. Britton (1972) discussed this at some length and proposed the new generic name *Radiolucina* with *P. amiantus* as the type species.

***Phacoides (Bellucina) tuomeyi*** Dall, 1903: 1385, pl. 52 fig. 1.

Described from the late Miocene Duplin Marl of North Carolina, this species is similar to the Recent *Radiolucina amianta* (Dall).

***Phacoides (Bellucina) waccamawensis*** Dall, 1903: 1385, pl. 52 fig. 2.

Described from the Pliocene Waccamaw Formation of South Carolina, this species is closely similar to the Recent *Radiolucina ami-*

*anta* (Dall) and was tentatively synonymised by Bretsky (1976).

***Phacoides peritaphros*** Barnard, 1964: 476–477 fig. 22.  
Syntypes: BMNH 1964264

Although Barnard regarded this southern African species as allied to *Cardiolucina lamothei* (Dautzenberg), it lacks radial riblets, has a shallow, open lunule and is more anteriorly extended. This species is similar in many features to *Cavilinga trisulcata* (Conrad, 1841) (see Olsson and Harbison 1953, pl. 7 fig. 4), the type species of the genus *Cavilinga* Chavan, 1937.

***Lucina cancellaris*** Philippi, 1846: 21.

This is a West American twin species to the Caribbean *Radiolucina amianta*. Keen (1971, p. 121) points out that 'Dall unfortunately assigned this species and its Caribbean twin *L. amianta* (Dall, 1901), to the subgenus *Bellucina*, the type of which is an Indian Ocean form only superficially similar, and American authors have been slow to recognise the error.'

***Lucina pulchella*** Lyngø, 1909: 173, pl. 3 figs. 13–15.

Lyngø compared this species with *L. seminula* Gould, *L. pisum* Reeve and *L. semperiana* Issel. We examined the type material (Zoological Museum, Copenhagen) which has a different ribbing pattern from any *Cardiolucina* and lacks posterior and anterior sulci. This species may be an *Epicodakia*.

***Lucina valida*** Smith, 1904: p. 40 pl. 3 fig. 19.

This southern African species is very similar to and a probable senior synonym of *Phacoides peritaphros* Barnard. Syntypes: BMNH 1903.12.19.1270–4.

***Cardiolucina striatula* var. *taurotrigona*** Sacco, 1901: 90, pl. 20 fig. 44–47.

***Cardiolucina striatula* var. *ovatuloides*** Sacco, 1901: 90 pl. 20 fig. 48.

***Cardiolucina taurocrenulata*** Sacco, 1901: 90 pl. 20 fig. 50.

***C. taurocrenulata* var. *aviculina*** Sacco, 1901: 90 pl. 20 figs 51 & 52.

***Cardiolucina oligobliqua*** Sacco, 1901: 91 pl. 20 fig. 53.

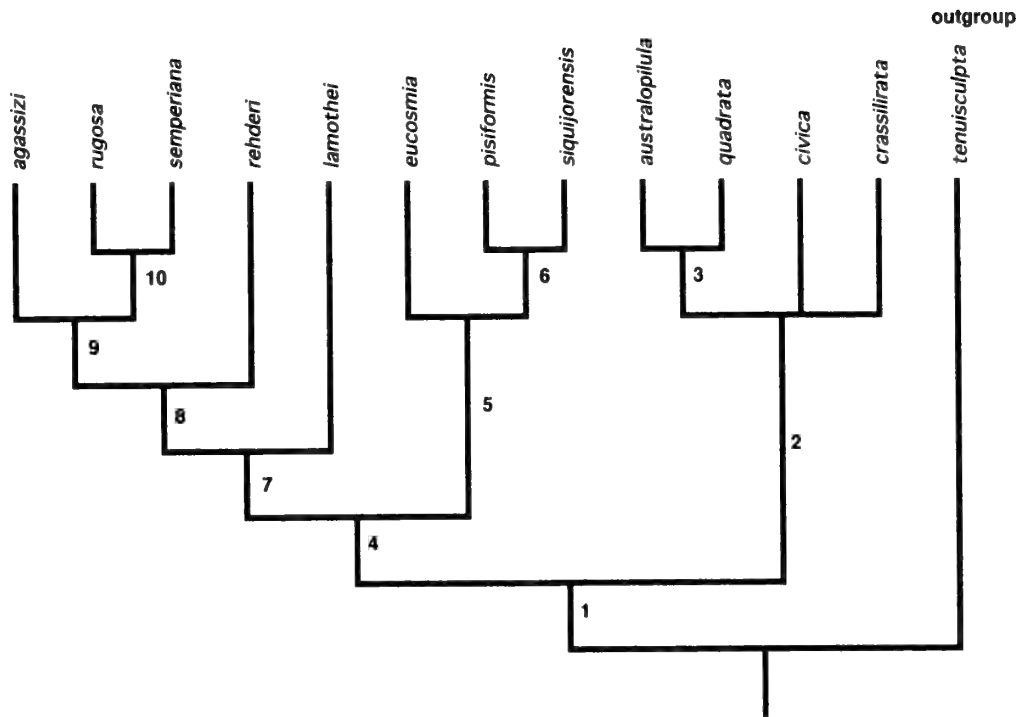
All these taxa were described from the Miocene of Italy. They have concentric ornament only and differ in shape from the type species. In our opinion these taxa should all be excluded from *Cardiolucina*.

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### **RELATIONSHIPS AMONGST THE SPECIES**

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In an attempt to establish relationships amongst the *Cardiolucina* species a preliminary phylogenetic analysis using parsimony was performed using a set of 12 shell characters. We used PAUP version 3.0, with further interpretation of characters with McClade version 3.04. Although it would have been desirable to include anatomical characters these were available for only two species. We selected as an outgroup the northeastern Pacific *Parvilucina tenuisculpta* (Carpenter, 1864), the type species of the genus *Parvilucina*. Since the



**Fig. 29** Strict consensus tree of *Cardiolucina* species derived from two equally parsimonious trees. Outgroup is *Parvilucina tenuisculpta*. Character state changes at numbered internal branches. Branch 1: char. 1, state 2>1; char. 3 state 3>0; char. 6 state 2>1. Branch 2: char. 3 state 0>2; char. 8 state 0>1; char. 11 state 0>1. Branch 3: char. 11 state 1>2. Branch 4: char. 7 state 1>0. Branch 5: char. 4 state 0>1; char. 5 state 0>1; char. 6 state 1>0; char. 12 state 2>0. Branch 6: char. 9 state 0>1. Branch 7: char. 1 state 1>0; char. 2 state 0>2. Branch 8: char. 12 state 2>1. Branch 9: char. 2 state 2>1. Branch 10: char. 10 state 0>1.

**Table 1.** Characters and character state codings used in the phylogenetic analysis.

**1. Posterior sulcus.** This is an indentation in the posterior shell seen on the outer surface extending from the umbo to the shell margin. It is present in all *Cardiolucina* species, deeply incised in some (Fig. 20d), shallow in others (Fig. 2a) and weak and poorly-defined in the outgroup.  
States: 0 - deep prominent; 1 - shallow; 2 - weak

**2. Anterior sulcus.** This is a similar indentation at the anterior end of the shell. This is absent in some species, but where present (Fig. 20) never as prominent as the posterior sulcus.  
States: 0 - absent; 1 - narrow; 2 - broad

**3. Lunule.** Many species have a heart-shaped, shallow lunule (Fig. 20c), but in *C. eucosmia* it is deeply excavated. In other species the lunule is very small and tucked under beak (Fig. 2) and in the outgroup it is lanceolate.  
States: 0 - shallow, heart-shaped; 1 - deeply excavated; 2 - tiny under umbo; 3 - thin lanceolate

**4. Radial ribs - number**  
States: 0 - less than 20; 1 - more than 20

**5. Radial rib - shape**  
Some species have prominent ribs with straight sides and separated by broad interspaces (Figs. 2,3). In others, the ribs are closer together with low rounded profiles and narrow interspaces (Figs. 7,10).  
States: 0 - rounded, narrow interspaces; 1 - straight-sided broad interspaces

**6. Radial rib intersection with concentrics.**  
In some species, ribs appear to cross concentric lamellae without interruption (Fig. 2d) whilst in others the ribs terminate at the intersection with major concentric lamellae (Fig. 7d). In the outgroup the radial ribs are extremely weak.

States: 0 - strong, cross concentrics; 1 - weak, terminate at concentrics; 2 - very weak

**7. Concentric lamellae - number**  
Concentric lamellae are a prominent feature of many *Cardiolucina* species.  
States: 0 - less than 20; 1 - more than 20

**8. Shape of anterior cardinal tooth in left valve**  
The majority of species have a triangular wedge shaped tooth (Fig. 18b) but in some species the anterior cardinal is a hook-shaped projection (Fig. 3c).  
States: 0 - wedge; 1 - hooked

**9. Posterior cardinal of left valve**  
Most species have a relatively thin tooth (Fig. 7c), but in *C. pisiformis*, for example, it is much thicker (Fig. 14c).  
States: 0 - thin; 1 - thick

**10. Denticles on cardinal teeth**  
This refers to small denticles seen at high magnification along the edges of the posterior cardinal (Fig. 12d).  
States: 0 - absent; 1 - present

**11. Hinge buttress**  
The hinge may be projected ventrally below the cardinal teeth to form a rounded buttress (Fig 3c).  
States: 0 - absent; 1 - slight; 2 - prominent

**12. Margin crenulations - number**  
These are seen on the internal ventral margin of shell. These were counted around the shell margin, fine beading not included.  
States: 0 - coarse (n = 10-20); 1 - medium (n = 21-30); 2 - fine (31 +).

**Table 2** Matrix of *Cardiolumina* species and the outgroup *Parvilucina tenuisculpta* and their character states. Character coding as in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>agassizi</i>	0	1	0	1	0	1	1	0	0	0	0	1
<i>australopilula</i>	1	0	2	0	1	0	1	1	0	0	2	1
<i>civica</i>	1	0	2	1	0	1	1	1	0	0	1	2
<i>crassilirata</i>	1	0	2	1	0	1	1	1	0	0	1	2
<i>eucosmia</i>	1	1	1	0	1	0	0	0	0	1	0	0
<i>pisiformis</i>	1	0	0	0	1	0	0	0	1	0	0	0
<i>quadrata</i>	1	0	2	1	0	1	1	1	0	0	2	1
<i>rugosa</i>	0	1	0	1	0	1	0	0	0	1	0	1
<i>semperiana</i>	0	1	0	1	0	1	0	0	0	1	0	1
<i>siqijorensis</i>	1	0	0	0	1	0	0	0	1	?	0	0
<i>lamothei</i>	0	2	0	1	0	1	0	0	0	0	0	2
<i>rehderi</i>	0	2	0	1	0	1	0	0	0	0	0	1
<i>P. tenuisculpta</i>	2	0	3	1	0	2	1	0	0	0	0	2

original designation by Dall (1901), *Cardiolumina* (as *Bellucina*) has been widely listed as a subgenus of *Parvilucina* and the shells have some features in common (descriptions in Hickman 1994). Moreover, there are some similar anatomical features, *P. tenuisculpta* having a visceral lobe resembling that found in *C. semperiana* and *C. australopilula*, as well as the connection of the posterior ctenidia to the mantle and the lack of a fused inhalant aperture (Reid and Brand, 1986). The characters and their states are listed in Table 1.

The distribution of the various character states amongst the *Cardiolumina* species and the outgroup is shown in Table 2. Phylogenetic analysis using this matrix produced 2 equally parsimonious trees of 26 steps with a consistency index of 0.731 and a homoplasy index of 0.269. A strict consensus tree is shown in Fig. 29. The differences in the 2 trees resulted from the grouping of *C. civica* and *C. crassilirata* as a single clade or as a trichotomy with the *C. australopilula*/*C. quadrata* clade.

The analysis suggests that there are three distinct clades of *Cardiolumina* species (Fig. 29). Clade 1 contains *C. australopilula*,

*crassilirata*, *civica* and *quadrata*. Apomorphies which define this clade at Branch 2 are; the tiny lunule, the hooked-shaped, anterior cardinal tooth and the hinge buttress. Clade 2, separated at Branch 4 by a single apomorphy of having less than 20 concentric lamellae, contains two major branches; that comprising the type species *C. agassizi* and the species around *C. semperiana*. (Branch 7) and another branch (Branch 5) containing *C. eucosmia*, *pisiformis* and *siqijorensis*. This latter clade is defined by four apomorphies; having less than 20 radial ribs, which are straight-sided and cross the concentric lamellae and also possess coarse marginal crenulations. The *C. agassizi* – *lamothei* clade is defined at Branch 7 by the prominent posterior sulcus and a broad anterior sulcus.

This hypothesis of relationships should be regarded as tentative because it is based on shell characters alone. Nevertheless, it is open to falsification by additional or alternative character sets.

## GEOGRAPHICAL DISTRIBUTION

Two species, *Cardiolumina lamothei* and *C. rehderi* are found on opposite sides of the Atlantic, whilst the other nine are distributed largely within the tropical Indo-West Pacific Province. One of these, *C. semperiana*, has a wide range from the Gulf of Suez to Philippines whilst the rest have more restricted distributions within the central Indo-Pacific. Four species are endemic to Australia; *C. eucosmia*, *C. pisiformis* and *C. australopilula* to the western and northern coasts and *C. crassilirata* to the temperate southern coast. *Cardiolumina civica* occurs from Japan through Indonesia to the Andaman Islands in the west and Fiji in the east. *C. quadrata* is restricted to deeper water around the Philippines and Indonesia. Apart from *C. rehderi*, which is known from only one vague locality, the species with the most limited range is *C. siqijorensis* from Siquijor Island in the Philippines. All the species are largely tropical in distribution, except for *C. crassilirata* from southern Australia.

**Table 3** Summary of shell characters in *Cardiolumina* species

Species	H	L	T	Radial ribs	Concentric lamellae	Sulcus		Marginal crenulae	Lunule		
						post.	ant.		small, under beak	heart-shaped	
<i>agassizi</i>	7.4	7.1	2.7	c.25	faint, closely spaced	c.20	width of interspaces extremely variable	deep	narrow	28	shallow
<i>australopilula</i>	13.8	12.7	7.5	c.20	interspaces almost as wide as ribs	c.34–36	low, narrow	shallow	none	21	*
<i>civica</i>	10.6	10.4	4.5	>30	fine, closely spaced	>25	conspicuous	shallow	none	>60	*
<i>crassilirata</i>	11.0	11.3	6	>40	fine, closely spaced	>30	fine, clustered in groups of 4–6	shallow	none	31	*
<i>eucosmia</i>	7.8	7.7	3.8	c.12	broad, with wide interspaces	c.13–14	low	v.deep	narrow	12	v. deep
<i>pisiformis</i>	4.4	4.4	2	13–17	low, widely spaced	c.20	narrow	shallow	none	13	deep
<i>quadrata</i>	12.9	13.6	5.3	c.25	fine, closely spaced	25–30	low, broad	shallow	none	25	*
<i>rugosa</i>	3.1	3.2	1.2	>25	faint, closely spaced	c.20	prominent	deep	narrow	20	shallow
<i>semperiana</i>	7.7	7.5	2.7	20–30	low, closely spaced	15–24	interspaces variable in width	deep	narrow, ribbed	20–21	shallow
<i>siqijorensis</i>	3.5	3.5	1.3	12	broad	14–16	thin	shallow	none	12	shallow
<i>lamothei</i>	4	3.9	2	>40	fine, closely spaced	15–18	prominent	deep	broad	40	*
<i>rehderi</i>	4.2	4.2	1.9	>30	fine, faint closely spaced	14–16	prominent	deep	broad	20	*

H=height, max mm, L=length, max mm, T=tumidity, max mm.

The phylogenetic analysis shows that *Cardiolucina lamothei* and *C. rehderi* are closer to the *C. semperiana* clade of species than to the *C. australopilula* or *C. eucosmia* clades. This suggests that the clade containing *C. lamothei-rehderi* and *C. semperiana* had a widespread Tethyan distribution prior to the (late Miocene) closure of the connection between the Indo-Pacific and Atlantic Oceans. This is confirmed by the occurrence of *C. agassizi* in the Middle Miocene of south west Europe. The *C. australopilula* clade is restricted in distribution to the central Indo-Pacific. The Miocene species *C. nuciformis* Tate from South Australia is similar to the Recent *C. crassilirata* from the same area suggesting a long occupancy.

## CONCLUSIONS

In this revision of the systematics of *Cardiolucina* we have redefined the genus and its type species and recognised eleven living species from the tropical Atlantic and Indo-W. Pacific provinces. The previous lumping of many taxa into *C. semperiana* underestimated species diversity. Table 3 provides a summary of the characters of the recognised species as an aid to identification. Anatomical characters are known for only two species, *C. australopilula* and *C. semperiana*. Comparison with other genera is difficult because of the lack of information, but *Parvilucina* has some similar characters, such as the lack of mantle fusion at the posterior inhalant area, the connection of the ctenidia to the posterior mantle and the large visceral lobe (Reid and Brand, 1986). Further work is needed to establish the distribution of these characters in other lucinid taxa.

Although the earliest *Cardiolucina* would seem to be the Eocene species *C. ligata* (Cossmann & Pissarro), the fossil record, apart from *C. agassizi* which is common in the middle Miocene of Europe, is rather scanty. The only species we can confirm are *Cardiolucina nuciformis* (Tate) from the Miocene and, from the Pliocene, *C. gonzalesi* (Shuto) and *C. polli* (Icke & Martin). This paucity of records is unsurprising because, even in Recent faunas, these small lucinids are neglected.

The problems encountered during this systematic revision reflect the current state of systematics within the family Lucinidae. Many genera are defined only by a small number of shell characters, type species of genera are often inadequately described and, moreover, their characters are often ignored by systematists. Species diversity is often greater than realised because taxa have been shoe-horned into a small number of 'well-known' names. Relationships between genera are generally unknown and rigorous phylogenetic analyses are lacking. Bretsky (1970, 1976) produced a phenetic/phylogenetic analysis of lucinid genera, with possible phylogenies for her various lineages. Unfortunately, there are problems with these phylogenies because she lumped together distinct genera and confused type species, for example, using for *Bellucina* characters of *Radiolucina amianta* instead of the type species *B. eucosmia*. Moreover, there is no anatomical or biological information available for the vast majority of species, especially those from the Indo-Pacific province. Recent studies on the chemosymbiosis of lucinids have focused on a small number of species from the Caribbean and temperate north Atlantic and Pacific (reviewed in Fisher, 1990, Le Pennec *et al.*, 1995), but biological information from these studies has yet to be integrated into lucinid systematics. Systematic and phylogenetic studies should be providing the framework to test hypotheses concerning the evolutionary history and radiation of the Lucinidae, but, at present, these are inadequate.

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## REFERENCES

- Allen, J.A. 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philosophical Transactions of the Royal Society of London*, B 241: 421–484.
- Bouchet, P. & Danrigal, F. 1982. Napoleon's Egyptian campaign (1798–1801) and the Savigny collection of shells. *Nautilus*, 96: 9–24.
- Bretsky, S.S. 1970. Phenetic and phylogenetic classifications of the Lucinidae (Mollusca, Bivalvia). *Bulletin of the Geological Institute of the University of Upsala*, new series 2: 5–23.
- 1976. Evolution and classification of the Lucinidae (Mollusca: Bivalvia) *Palaeontographica Americana*, 8(no 50): 219–337.
- Britton, J.G. 1972. Two new species and a new subgenus of Lucinidae (Mollusca: Bivalvia), with notes on certain aspects of lucinid phylogeny. *Smithsonian Contributions to Zoology*, 129: 1–19.
- Cary, S.C., Vetter, R.D. & Felbeck, H. 1989. Habitat characterization and nutritional strategies of the endosymbiont-bearing bivalve *Lucinoma aequizonata*. *Marine Ecology Progress Series*, 55: 31–45.
- Chavan, A. 1937. Essai critique de classification des Lucines. *Journal de Conchyliologie*, 81: 198–216.
- 1969. Family Lucinidae Fleming, 1828. pp. N492–N508. In: Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology*. Part N, Volume 2, Mollusca 6. Bivalvia. University of Kansas Press, Kansas.
- Cossman, M.M. & Peyrot, 1911. Conchologie Néogénique de l'Aquitaine (Pélécytopodes. Clavagellidae à Lucinidae). *Actes de la Société Linnéenne, Bordeaux* 65: 51–333.
- Cossmann, M.M. & Pissarro, G. 1904. Faune Eocénique du Cotentin (Mollusques). *Bulletin de la Société Géologique de Normandie*, 23: 11–29.
- Cotton, B. C. & Godfrey, F.K. 1938. *The molluscs of South Australia. Part I. The Pelecypoda*. 314 p. South Australian Branch of the British Science Guild, Adelaide.
- Dall, W.H. 1901. Synopsis of the Lucinacea and of the American species. *Proceedings of the United States National Museum*, 23: 779–834.
- , 1903. Contributions to the Tertiary fauna of Florida. *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3: 1219–1654.
- Dando, P.R., Southward, A.J. & Southward, E.C. 1986. Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proceedings of the Royal Society of London*, B 227: 227–247.
- , Southward, A.J., Southward, E.C., Terwilliger, N.B. & Terwilliger, R.C. 1985. Sulfur-oxidising bacteria and haemoglobin in gills of the bivalve mollusc *Myrtea spinifera*. *Marine Ecology Progress Series*, 23: 85–98.
- Dautzenberg, P. 1913. Mollusques marins. Mission Gruvel sur la côte occidentale d'Afrique. *Annales de l'Institut Océanographique*, 5: 1–111.
- Deshayes, G.P. 1856–1865. Description des animaux sans vertèbres découverts dans le bassin du Paris pour servir de supplément à la description des coquilles fossiles des environs de Paris comprenant une revue générale de toutes les espèces actuellement connues. Paris, J.B. Baillière et fils, Paris. (*Lucina seminulum* in 1858, volume 1:673).
- Distel, D.L. & Felbeck, H. 1987. Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a reexamination of the functional morphology of the gills as bacteria-bearing organs. *Marine Biology*, 96: 79–86.
- Eichwald, C.E. 1853. *Lethaea Rossica ou paléontologie de la Russie*. Volume 3. 518 p. Stuttgart, E. Schweizerbart.
- Fischer, P. 1871. Sur la Faune conchyliologique marine de la Baie de Suez. *Journal de Conchyliologie*, 19: 209–219.
- Fisher, C.R. 1990. Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Reviews in Aquatic Sciences*, 2: 399–436.
- Fisher, M.R. & Hand, S.C. 1984. Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. *Biological Bulletin*, 167: 445–459.
- Friedberg, W. 1934. *Mieczaki Miocenskie ziem Polskich (Mollusca miocaenica Poloniae)*. Part 2. *Lamellibranchiata Fasc. 1*. 283p. Polskie Towarzystwo Geologiczne, Krakow.

- Gardner, J.A.** 1926. The molluscan fauna of the Alum Bluff Group of Florida. Part III. Lucinacea, Leptonacea, Cardiacea. *U.S. Geological Survey Professional Paper*, 142-C: 101–149.
- Glover, E.A. & Taylor, J.D.** 1997. Diversity and distribution of subtidal molluscs from the outer continental shelf, Houtman Abrolhos Islands, Western Australia. pp. 281–305. In: *The marine flora and fauna of the Houtman Abrolhos, Western Australia* (Wells, F.E. ed.). Western Australian Museum, Perth.
- Gould, A.** 1862. *Otia Conchologica: Descriptions of Shells and Mollusks*. Gould and Lincoln, Boston.
- Hedley, C.** 1909. Mollusca from the Hope Islands, North Queensland. *Proceedings of the Linnean Society of New South Wales*, 34: 420–466.
- Hickman, C.S.** 1994. The genus *Parvilucina* in the Eastern Pacific: making evolutionary sense of a chemosymbiotic species complex. *Veliger*, 37: 43–61.
- Icke, H. & Martin, K.** 1907. Over Tertiäre en Kwartaire vormingen van het eiland Nias. *Sammlungen des Geologischen Reichsmuseums in Leiden*, ser.1, 8: 204–252.
- Issel, A.** 1869. *Malacologia del Mare Rosso, ricerche zoologiche e paleontologiche*. 387 p. Pisa, Italy.
- Johnson, R.I.** 1964. *The Recent Mollusca of Augustus Addison Gould*. 182 p. Museum of Natural History, Smithsonian Institution, Washington.
- Keen, M.** 1971. *Sea Shells of Tropical West America, Marine mollusks from Baja California to Peru*. 2nd edition. 1064 p. Stanford University Press, California.
- Kuroda, T., Habe, T. & Oyama, K.** 1971. *The Seashells of Sagamai Bay*. 487 p. Maruzen, Tokyo.
- Lamprell, K. & Whitehead, T.** 1992. *Bivalves of Australia*. 182 p. Crawford House Press, Bathurst, Australia.
- Lamy, E.** 1920. Révision des Lucinacea vivants du Muséum d'histoire naturelle de Paris. *Journal de Conchyliologie*, 65: 71–122, 169–222, 233–318, 335–388.
- Le Pennec, M., Beninger, P.G. & Herry, A.** 1995. Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats. *Comparative Biochemistry and Physiology*, 111A: 183–189.
- Lyne, H.** 1909. The Danish Expedition to Siam 1899–1900. IV. Marine Lamellibranchiata. *Kongelige Danske Videnskaberne Selskabs Skrifter*, 5: 101–299.
- Macpherson, J.H. & Gabriel, C.J.** 1962. *Marine molluscs of Victoria*. 475 p. University of Melbourne Press, Melbourne.
- Makiyama, J.** 1959. Matajiro Yokoyama's Tertiary Fossils from various localities in Japan. *Palaeontological Society of Japan Special Papers* 5, part III: 1–4.
- Marshall, B.A.** 1991. Dates of publication and supraspecific taxa of Bellardi and Sacco's (1873–1904) 'I molluschi dei terreni terziari del Piemonte e della Liguria' and Sacco's (1890) 'Catalogo paleontologico del bacino terziario del Piemonte'. *Nautilus*, 105: 104–115.
- Melville, J. C. & Sykes, E.R.** 1898. Notes on a second collection of marine shells from the Andaman Islands, with descriptions of new forms of *Terebra*. *Proceedings of the Malacological Society of London*, 3: 35–48.
- Michelotti, G.** 1839. Brevi cenni di alcuni resti delle Classi Brachiopodi ed Acefali, trovati fossili in Italia. *Annali di Scienze Lombarde veneto*, 9: 1–38.
- Michelotti, G.** 1847. *Description des fossiles des terrains Miocènes*. 408 p. Leiden, Société Hollandaise des Sciences.
- Morton, B.** 1979. The biology and functional morphology of the coral-sand bivalve *Fimbria fimbriata* (Linnaeus, 1758). *Records of the Australian Museum*, 32: 389–420.
- Oliver, P. G.** 1992. *Bivalved Seashells of the Red Sea*. 330 p. Verlag Christa Hemmen & The National Museum of Wales, Cardiff.
- Olsson, A.A. & Harbison, A.** 1953. Pliocene Mollusca of southern Florida. *Mono-graphs of the Academy of Natural Sciences of Philadelphia*, 8: 1–457.
- Philippi, R.A.** 1846. Diagnosen einiger neuen Conchylien-Arten. *Zeitschrift für Malakozoologie*, year 3 part 1 (Feb.): 19–24.
- Ponder, W.F.** 1978. The unfigured Mollusca of J. Thiele, 1930 published in *Die Fauna Südwest-Australiens. Records of the Western Australian Museum*, 6: 423–441.
- Prashad, B.** 1932. The Lamellibranchia of the Siboga Expedition. Systematic Part II Pelecypoda (exclusive of the Pectinidae). *Siboga-Expeditie*, 53c: 1–353.
- Pritchard, G.B. & Gatliff, J.H.** 1903. Catalogue of the marine shells of Victoria. Part VII. *Proceedings of the Royal Society of Victoria*, 16: 96–139.
- Reeve, L. A.** 1850. Monograph of the genus *Lucina* Pls V–XI. *Conchologica Iconica*, Volume 6 Reeve, Benham & Reeve, London.
- Reid, R.G.B.** 1990. Evolutionary implications of sulphide-oxidising symbioses in bivalves. pp. 127–140. In: B. Morton (ed.) *The Bivalvia-Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*. Hong Kong University Press, Hong Kong.
- & **Brand, D.G.** 1986. Sulphide oxidising symbiosis in lucinaceans: implications for bivalve evolution. *Veliger*, 29: 3–24.
- Rios, E.** 1994. *Seashells of Brazil*. 2nd edition, 368 p. Fundacao Universidade do Rio Grande, Rio Grande, Brazil.
- Sacco, F.** 1901. *I molluschi dei terreni terziari del Piemonte e della Liguria. Parte 29*. 216 p. Clausen, Torino.
- 1904. *I molluschi dei terreni terziari del Piemonte e della Liguria. Parte 30*. 203 p. Clausen, Torino.
- Savigny, J.C.** 1817. Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'Expedition de l'armée française, publiée par ordre du gouvernement. Histoire Naturelle. Planches, vol. II. Imprimerie royale, Paris.
- Shuto, T.** 1971. Neogene bivalves from Panay Island, the Philippines. *Memoirs of the Faculty of Science of Kyushu University*, series D. Geology 21: 1–73.
- Slack-Smith, S.M.** 1990. The bivalves of Shark Bay, Western Australia. pp. 129–157. In: Berry, P.F., Bradshaw, S.D. & Wilson, B.R. (eds) *Research in Shark Bay*, Report of the France-Australie Bicentenary Expedition Committee. Western Australian Museum, Perth.
- Smith, E.A.** 1885. Report on the Lamellibranchiata collected by H.M.S. Challenger during the years 1873–76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76*. London. Zoology, 13: 1–341.
- Southward, E.C.** 1986. Gill symbionts in thyasirids and other bivalve molluscs. *Journal of the Marine Biological Association of the U.K.*, 66: 889–914.
- Sowerby, J. de C.** 1836. Descriptive notes respecting the shells figured in Plates XI. to XXIII. In: Fitton, W.H. 1836. Observations on some of the strata between the Chalk and the Oxford Oolite, in the South-east of England. *Transactions of the Geological Society of London*, 4: 103–388.
- Tate, R.** 1886. The lamellibranchs of the older Tertiary of Australia (Part I). *Transactions of the Royal Society of South Australia*, 8: 96–158.
- 1887a. Descriptions of some new species of South Australian marine and freshwater Mollusca. *Transactions of the Royal Society of South Australia*, 8: 62–75.
- 1887b. The lamellibranchs of the older Tertiary of Australia (Part II). *Transactions of the Royal Society of South Australia*, 9: 142–200.
- Taylor, J.D. & Glover, E.A.** 1997. A chemosymbiotic lucinid bivalve (Bivalvia: Lucinoidea) with periostracal pipes: functional morphology and description of a new genus and species. 335–361 pp. In: Wells, F.E. (ed.) *The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*. Western Australian Museum, Perth.
- Thiele, J.** 1930. Gastropoda und Bivalvia. Volume 5, pp. 561–596. In: W. Michaelson & R. Hartmeyer (eds) *Die Fauna Südwest-Australiens*. Gustav Fischer, Jena.
- Thiele, J. & Jaecckel, S.** 1931. Muscheln der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition*, 21: 1–268.
- Woodring, W.P.** 1925. Contributions to the geology and paleontology of the West Indies. Miocene mollusks from Bowden, Jamaica. Pelecypods and scaphopods. *Carnegie Institute of Washington Publication*, 366: 1–222.
- Yokoyama, M.** 1927. Fossil Mollusca from Kaga. *Journal of the Faculty of Science Imperial University of Tokyo*. Section II (Geology), 2 (part 4): 165–182.



# A new species of water mouse, of the genus *Chibchanomys* (Rodentia, Muridae, Sigmodontinae) from Ecuador

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**SYNOPSIS.** A new species of the rodent genus *Chibchanomys* is described from Ecuador on the basis of external and cranial morphology. A phylogenetic analysis is used to assess the relationship of the new species to other ichthyomyine taxa.

## INTRODUCTION

The New World rodents currently placed in the large and complex subfamily Sigmodontinae (*sensu* Carleton & Musser, 1984) include a morphologically and ecologically distinctive group of semi-aquatic South American genera (Voss, 1988), for which it is convenient here to use the name ichthyomyines. In a monograph of ichthyomyine rodents, Voss (1988) included five genera: *Ichthyomys* Thomas, 1893 (four species), *Anotomys* Thomas, 1906a (monotypic), *Rheomys* Thomas, 1906b (four species), *Neusticomys* Anthony, 1921 (four species) and a new genus, *Chibchanomys* Voss, 1988 for an enigmatic species of uncertain generic affinity. *Chibchanomys trichotis* (Thomas, 1897) was originally placed in *Ichthyomys* but was subsequently assigned to *Rheomys* (see Tate, 1932; Cabrera, 1961), then to *Anotomys* (see Handley, 1976). Subsequent to the revision by Voss, an additional ichthyomyine species, *Neusticomys mussoi* Ochoa & Soriano, 1991, has been described.

During the course of several zoological surveys of Las Cajas Plateau, Ecuador from 1981 to 1987, five specimens of an undescribed species of ichthyomyine rodent were captured. Observations were made on two of these animals, which subsequently escaped, while three specimens were donated to The Natural History Museum. Another specimen was filmed for the 1992 BBC National Geographic wildlife film 'Avenue of the Volcanoes' (Jim and Theresa Clare, personal communication). On the basis of external and craniodental characters the study specimens agree most closely with the generic diagnosis of *Chibchanomys* but are also sufficiently similar in some features to *Neusticomys* to warrant a phylogenetic analysis.

## MATERIALS AND METHODS

The description of the new species is based on conventional morphological characteristics and the terminology used follows Voss (1988). Specimens were measured using dial calipers, with all measurements provided in millimetres. The skeletal elements remaining in the skins were observed by means of X-rays.

A parsimony analysis (PAUP Version 3.0) was carried out to determine the position of the new species relative to other ichthyomyines. Details of the eighteen characters used, listed below, are given more fully in Voss (1988 pages 440–442); the

hypothesised primitive state, using the criteria defined by Voss, is scored as '0'.

1. Pelage: glossy (0); dull (1).
2. Ventral pelage countershaded: absent (0); present (1).
3. Tail: unicolored (0); bicolored (1).
4. Philtrum: present (0); absent (1).
5. Pinnae: large, visible above fur (0); small, concealed in fur (1).
6. Superciliary vibrissae: present (0); absent (1).
7. Plantar pads of manus: hypothenar pad separate, not fused with third interdigital pad (0); hypothenar and third interdigital pads fused (1); hypothenar and thenar pads fused respectively with adjacent third and first interdigital pads (2).
8. Fringing hairs on pes: weakly developed (0); well developed (1).
9. Lower third molar: entoconid-hypoconid cusp pair distinct (0): m3 peglike, entoconid-hypoconid cusp pair absent or reduced to a small conule (1).
10. Nasal bones: long, produced anteriorly beyond premaxillae (0); short, truncated behind premaxillae (1).
11. Supraorbital foramina: on the lateral surface of the frontals, within orbital fossae (0); on the dorsal surface of the frontals between the orbital fossae (1).
12. Carotid arterial supply (see Voss, 1988 page 296): pattern 1 (0); pattern 2 (1); pattern 3 (2).
13. Orbicular apophysis of maleus: present (0); absent (1).
14. Metatarsal configuration:  $III \geq IV > II \gg V > 1$  (0);  $IV > III > II, V > I$  (1).
15. Omohyoid muscle: present (0); absent (1).
16. Gastric glandular epithelium: present (0); restricted (1).
17. Gall bladder: present (0); absent (1).
18. Bacular cartilage: tridigitate, medial digit lacking a calcified centre (0); single digit (1); tridigitate, medial digit grossly swollen with calcified core (2).

The character states for the new species were assessed by PJ but the character state assessments for the other taxa were taken directly from Voss (1988 Table 45, page 441). Characters of the visceral and reproductive systems (characters 15–18 above) were unobservable in the new taxon because of the lack of whole bodies. In an initial analysis, all character states were unordered; in a second analysis, multistate characters were ordered (as by Voss):  $0 \rightarrow 1 \rightarrow 2$  for characters 7, 12 but also for character 18. For character 18, the order recommended by Voss (1988) was  $0 \rightarrow 1; 0 \rightarrow 2$ , a sequence not readily handled by the analysis and affecting only one generic group

(*Rheomys*); Voss (personal communication) recommended an alternative ordering of this character (1 → 0 → 2) so in a third analysis, characters 7 and 12 were ordered as above and character 18 by this alternative.

## ABBREVIATIONS USED IN THE TEXT

BMNH – The Natural History Museum [formerly British Museum (Natural History)]

M1, M2, M3 respectively first, second and third upper molars  
m1, m2, m3 respectively first, second and third lower molars

## ABBREVIATIONS USED FOR TAXA IN THE PAUP ANALYSIS:

Ale	<i>Anotomys leander</i> Thomas, 1906a
Ctr	<i>Chibchanomys trichotis</i> (Thomas, 1897)
Cor	<i>Chibchanomys</i> undescribed species
Ihy	<i>Ichthyomys hydrobates</i> (Winge, 1891)
Ipi	<i>Ichthyomys pittieri</i> (Handley & Mondolfi, 1963)
Itw	<i>Ichthyomys tweedii</i> Anthony, 1921
Nmo	<i>Neusticomys monticolus</i> Anthony, 1921
Nve	<i>Neusticomys venezuelae</i> (Anthony, 1929)
Rme	<i>Rheomys mexicanus</i> Goodwin, 1959
Rha	<i>Rheomys raptor</i> Goldman, 1912
Rtt	<i>Rheomys thomasi</i> Dickey, 1928
Run	<i>Rheomys underwoodi</i> Thomas, 1906b

## RESULTS

### *Chibchanomys orcesi*, sp. nov.

**HOLOTYPE.** BMNH 82.816, adult male, skin and skull; collectors' number 148; collected 22 August 1981 by members of the Oxford Expedition to Las Cajas from Lake Luspa, Las Cajas, Provincia Azuay, Ecuador, 02°50'S 79°30'W, altitude 3700m.

**PARATYPES.** BMNH 82.815, adult male, skin and skull; collectors' number 146, other details as for the holotype. BMNH 84.349, adult male, skin and skull; collectors' number 78; collected 7 August 1983 by members of the Combined Universities Expedition to Ecuador 1983, from Lake Llaviucu, Zorracucho Valley, Las Cajas, Provincia Azuay, Ecuador, 02°51'S 79°01'W, altitude 3100m.

### DIAGNOSIS

An ichthyomyine species belonging to the genus *Chibchanomys* in the following combination of features. Dorsal pelage dull; small pinnae concealed in pelage of head; tail longer than head and body; manus with five separate plantar pads; hindfoot broad with well developed fringing hairs; supraorbital foramina open laterally within orbits; carotid circulation pattern 1.

Differing from *Chibchanomys trichotis* in the following characters. Rhinarium light brown; philtrum present; nasals medium in length, barely projecting anterior to premaxillae; orbicular apophysis of maleus present; upper incisors slightly inclined medially; M3 and m3 reduced in size; anteromedian flexid absent or barely indicated on anteroconid of m1; metatarsals III ≥ IV > II >> V > I.

### DESCRIPTION

Tail subequal to or slightly longer than head and body (see Table 1

**Table 1** External and cranial measurements of *Chibchanomys trichotis* and *C. orcesi*. Dimensions given as mean, plus or minus standard deviation, followed by range, with sample size in parentheses.

	<i>C. trichotis</i> Venezuela	<i>C. trichotis</i> Colombia	<i>C. trichotis</i> Peru	<i>C. orcesi</i> Ecuador
Head and body length	113.5 ± 5.50 105–120 (4)	125 (1)	102 (1)	105 ± 1.63 103–107 (3)
Tail length	126.8 ± 7.36 115–133 (4)	131 (1)	123 (1)	113.3 ± 6.18 108–122 (3)
Hindfoot length	31.8 ± 1.09 30–33 (4)	30, 33 (2)	31 (1)	22 ± 2.16 19–24 (3)
Ear length	7.5 ± 1.5 6–10 (4)	8 (1)	6 (1)	11.5 ± 1.87 9.5–14 (3)
Weight (in grams)	–	–	–	37 ± 2.83 35–41 (3)
Ratio of tail length to head and body length	1.12 ± 0.02 1.10–1.15 (4)	1.05 (1)	1.21 (1)	1.08 ± 0.06 1.02–1.16(3)
Ratio of tail length to condylo-incisive length	4.9 ± 0.12 4.7–5.0 (4)	5.1 (1)	5.2 (1)	4.3, 4.7 (2)
Ratio of hindfoot length to head and body length	0.28 ± 0.00 0.28–0.29 (4)	0.26 (1)	0.30 (1)	0.21 ± 0.02 0.18–0.23 (3)
Condyloincisive length	25.7 ± 1.01 24.3–26.9 (4)	25.9 (1)	23.8 (1)	23.0, 24.6 (2)
Diastema Length	6.3 ± 0.54 5.7–7.0 (3)	–	5.7 (1)	5.3 ± 0.29 5.0–5.7 (3)
Length of upper molars	4.4 ± 0.08 4.3–4.5 (3)	4.4 (1)	4.2 (1)	4.2 ± 0.05 4.1–4.2 (3)
Incisive foramina length	5.0 ± 0.27 4.6–5.3 (4)	5.1 (1)	4.5 (1)	4.5 ± 0.09 4.4–4.6 (3)
Breadth of incisor tips	1.2 ± 0.11 1.0–1.3 (4)	c1.2, 1.3 (2)	1.0 (1)	1.4 ± 0.05 1.4–1.5 (3)
Breadth of incisive foramina	1.9 ± 0.15 1.7–2.1 (4)	2.4 (1)	1.9 (1)	2.1 ± 0.09 2.0–2.2 (3)
Breadth of palatal bridge	3.1 ± 0.29 2.7–3.4 (3)	–	2.6 (1)	2.2 ± 0.08 2.1–2.3 (3)
Nasal length	9.0 ± 0.41 8.5–9.5 (3)	8.1 (1)	8.5 (1)	9.3 ± 0.29 8.9–9.6 (3)
Nasal breadth	3.0 ± 0.05 2.9–3.0 (4)	3.0 (1)	2.8 (1)	3.2 ± 0.05 3.1–3.2 (3)
Interorbital breadth	4.7 ± 0.13 4.5–4.8 (4)	4.9 (1)	4.3 (1)	4.6 ± 0.08 4.5–4.7 (3)
Zygomatic breadth	13.4 ± 0.66 12.3–14.1 (4)	c13.9 (1)	11.7 (1)	c12.8 (1)
Braincase breadth	13.4 ± 0.27 13.0–13.7 (4)	13.8 (1)	12.4 (1)	1.9, 12.0 (2)
Ratio of inter-orbital breadth to braincase breadth	0.35 ± 0.02 0.33–0.37 (4)	0.36 (1)	0.35 (1)	0.38, 0.39 (2)
Breadth of zygomatic plate	1.1 ± 0.05 1.0–1.1 (4)	1.0, 1.2 (2)	1.0 (1)	1.1 ± 0 1.1 (3)
Breadth of first upper molar	1.6 ± 0.05 1.5–1.6 (3)	1.5 (1)	1.4 (1)	1.3 ± 0.05 1.3–1.4 (3)
Height of upper incisor	4.6 ± 0.33 4.1–5.0 (4)	5.3 (1)	3.9 (1)	4.3–4.5 (3) 4.4 ± 0.08
Depth of upper incisor	1.3 ± 0.12 1.1–1.4 (4)	1.2 (1)	1.0 (1)	1.2–1.3 (3) 1.3 ± 0.05
Breadth across occipital condyles	7.4 ± 0.18 7.2–7.6 (4)	7.6 (1)	7.8 (1)	6.6, 6.7 (2)



Fig. 1 Live specimen of *Chibchanomys orcesi*.

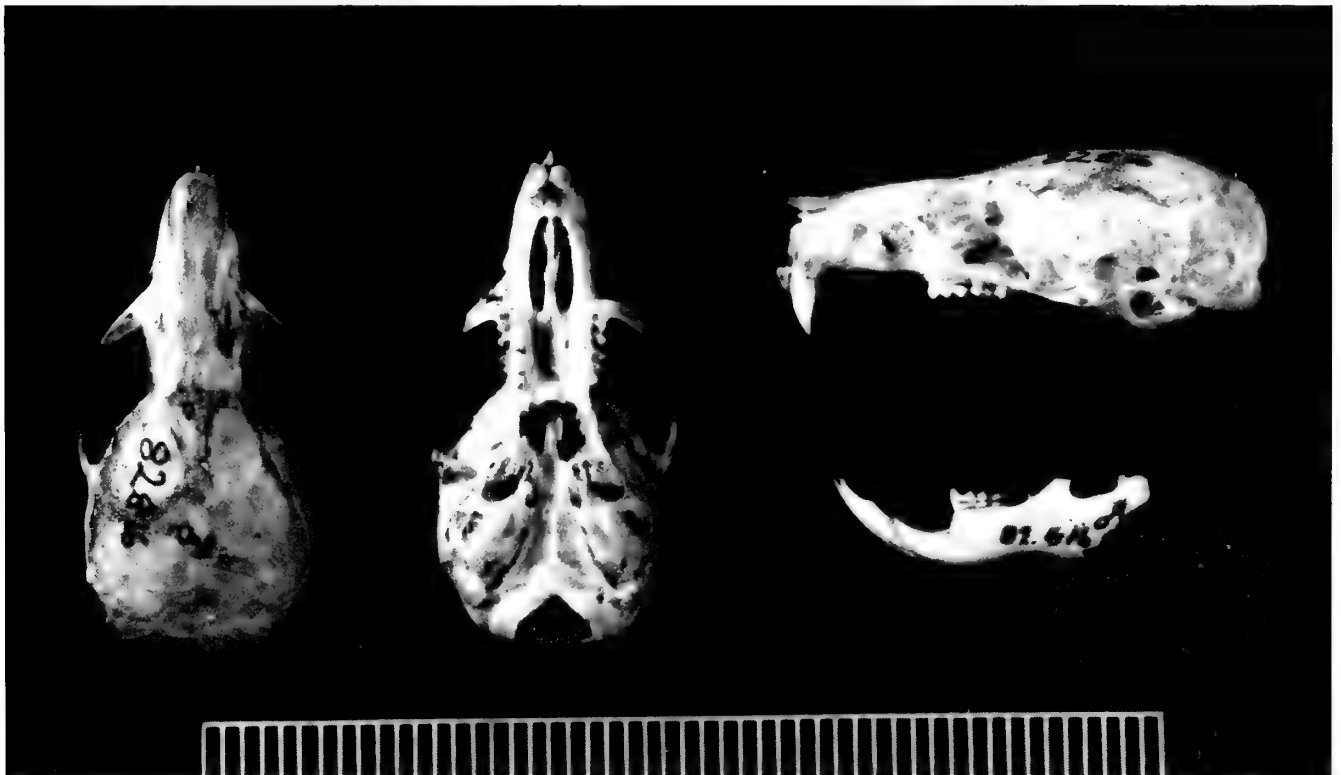


Fig. 2 Skull of *Chibchanomys orcesi* (BMNH 1982.816) from left to right in dorsal, ventral and lateral view.

for measurements). Pelage soft, dense and woolly, dark brownish grey dorsally, light grey ventrally; tail greyish brown, densely haired, grey brown and brown hairs predominate proximally, with a proportional increase of buff and cream hairs distally, extending beyond tip in a short pencil. Distal portion of muzzle light grey in young adults, cream in older individuals (age based on degree of dental wear); rhinarium light brown in dry specimens; philtrum present; conspicuous silvery-grey mystacial vibrissae present. Pinnae small, concealed by pelage; region of more-or-less conspicuous light grey hairs ventro-lateral to pinnae. Manus with three interdigital and two carpal pads. Well developed fringe of stiff hairs on margin of metatarsus and digits of pes; claw of fifth digit extends beyond first interphalangeal joint of fourth digit; claw of first digit reaches midway along first phalange of second digit. See Fig. 1 for external features visible in a photograph of a live specimen.

Skull (see Fig. 2) with moderately long nasals, overlapping nasal orifice to conceal incisors in dorsal view but barely projecting beyond premaxillae; rostrum short and narrow, naso-lacrymal capsules evident in dorsal view; interorbital region moderately narrow relative to braincase breadth (0.38, 0.39 ( $n = 2$ ); frontals slightly inflated, braincase moderately broad and long; posterior border of incisive foramina between anterior roots of M1s, palatal foramina lie between posterior roots of M1s; bullae slightly inflated; orbicular apophysis of maleus present. Carotid circulation pattern 1, based on osteological features (see Voss, 1988: 298).

Upper incisors moderately narrow, anterior enamel surface pale buff, slightly inclined medially. No anteroloph on M1; small posteroloph on M2; M3 small, protocone and paracone evident in unworn dentition, posterior conule absent. Anteroconid of m1 simple or with slight indication of anteromedian flexid; no anterolophid on m2; small posterolophids on m1 and m2, small mesolophids present or absent; m3 small, with small posterior basally positioned conulid.

Metatarsal proportions: third metatarsal slightly longer than fourth, fourth longer than second; all three far longer than first and fifth; fifth longer than first. Configuration:  $III \geq IV > II \gg V > I$ .

#### ETYMOLOGY

This species is named in honour of Professor Gustavo Orcés, a pioneer of Ecuadorian mammalogy. He was of great help to AB with fieldwork organisation in Ecuador, and his kindness and knowledge were a source of inspiration.

#### DISTRIBUTION AND ECOLOGY

Known only from Las Cajas Plateau, Ecuador, where specimens have been recorded from three localities: Lake Luspa, Lake Llaviucu, Zorracucho Valley and Lake Torreadora. All specimens were trapped in close proximity to fast-flowing streams at altitudes ranging from 3100m to 4000m, in high-altitude moorland vegetation (paramo) (see Barnett, 1992). For more precise details of the habitat at each site and notes on diet see Barnett (1997).

#### COMPARISON WITH *C. TRICHOTIS*

The new species is similar in external appearance to *C. trichotis*, except that the pelage is paler and slightly harsher, and the rhinarium is light brown in dry specimens of *C. orcesi*, black in *C. trichotis*. A philtrum is present in *C. orcesi* but absent in *C. trichotis*. *Chibchanomys orcesi* is smaller in external size and averages smaller in cranial size than all known specimens of *C. trichotis*, with the exception of the single specimen from Peru (see below for comments on the status of this specimen). Both species of *Chibchanomys* are similar in external proportions, except that the hindfoot is proportionately shorter in *C. orcesi* (see Table 1). The metatarsal

configuration differs in the two species:  $IV > III > II = V > I$  in *C. trichotis*;  $III \geq IV > II \gg V > I$  in *C. orcesi*. The two species differ in the following cranial features: while the nasals of both species are of comparable length, those of *C. orcesi* are slightly broader and barely project anterior to the premaxillae, unlike those of *C. trichotis*, which project anteriorly and conceal the incisors and nasal orifice in dorsal view. In lateral view, the globose braincase of *C. trichotis* rises abruptly in the frontal region, unlike the narrower and less inflated braincase of *C. orcesi*; the braincase is slightly broader and the breadth across occipital condyles is greater in *C. trichotis* (see Table 1). The orbicular apophysis of the maleus is present in *C. orcesi* but absent in *C. trichotis*. The upper incisors of *C. orcesi* are less delicate and slightly broader than those of *C. trichotis* (see Table 1), the anterior enamel surface of *C. trichotis* is cream coloured and not medially inclined unlike *C. orcesi*. The third upper molar is smaller relative to M1 and M2, and m3 is smaller relative to m1 and m2 in *C. orcesi* than in *C. trichotis*. The anteromedian flexid is absent or barely indicated on the anteroconid of m1 in *C. orcesi* but present in *C. trichotis*, dividing the anteroconid into small but distinct lingual and labial conulids. The posterior conulid of m3 is positioned more basally in *C. orcesi* than in *C. trichotis* (when present).

According to Voss (1988) the young specimen that he identified as *C. trichotis* from Peru differs from the northern specimens of *C. trichotis* in several features: the braincase is much less inflated, the occipital condyles are slightly broader, the bullae are somewhat smaller and an indistinct philtrum is indicated; features that resemble those of the new species. Voss mentioned that these differences might indicate that southern populations of *Chibchanomys* are phenotypically distinctive from their northern counterparts. Unfortunately it has not proved possible to examine the Peruvian specimen, although information on it was kindly provided by Mark Hafner (personal communication). It is possible that the Ecuadorian and Peruvian specimens are conspecific but additional material and more extensive comparisons are required to elucidate the status of the latter specimen.

#### COMPARISON WITH OTHER ICHTHYOMINE GENERA

*Chibchanomys* is readily distinguished from *Anotomys*, *Ichthyomys* and *Rheomys* (see Voss, 1988). *Chibchanomys* and *Neusticomys* differ from other ichthyomyines in showing carotid arterial circulation pattern 1 and in the distribution of the glandular epithelium around the stomach. *Chibchanomys* differs from *Neusticomys* in having small pinnae concealed in the pelage (pinnae obvious in *Neusticomys*); ventral countershading present (absent in *Neusticomys*); tail longer than head and body (tail shorter than head and body in *Neusticomys*); the hindfoot is broader with longer digits and the fringing hairs are well developed (narrower with shorter digits and less developed fringing hairs in *Neusticomys*). The new species does however share several features with *Neusticomys* which are not exhibited by *C. trichotis*, such as the similar metatarsal configuration and presence of a philtrum, while the orbicular apophysis of the malleus is also present in some species of *Neusticomys*.

#### RESULTS OF THE PHYLOGENETIC ANALYSIS

There is evidence in support of the ichthyomyines as a monophyletic group of the subfamily Sigmodontinae (*sensu* Carleton & Musser, 1984) (see Voss, 1988). In contrast, evidence in support of the monophyly of the Sigmodontinae is lacking and a tribal level classification of this subfamily, while convenient in many respects, is unsatisfactory from a phylogenetic point of view, making difficult the choice of satisfactory outgroups for phylogenetic analyses (see Voss, 1988: 436–438, 1991: 33–37; Carleton & Musser, 1989: 53–55; Voss & Carleton, 1993: 21–22). The necessity of making such a

Table 2. Matrix showing character state distributions among 12 ichthyomyine species (for details see text and Voss, 1988). The character state assessments for all taxa other than *C. orcesi* were taken directly from Voss (1988 Table 45, page 441). Character states for the new species were assessed by PJ except for those of the visceral and reproductive systems (characters 15–18) which were unobservable in the new taxon, so scored as ‘?’.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ale	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	1
Ctr	1	1	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0
Cor	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	?	?	?
Ihy	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Ipi	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Itw	0	1	0	0	0	1	0	1	0	1	1	2	0	1	0	1	1	0
Nmo	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Nve	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
Rme	0	1	1	1	1	1	2	1	1	0	0	2	0	1	1	1	0	2
Rha	0	1	0	0	0	1	1	1	0	0	0	2	0	1	0	1	0	2
Rtt	0	1	0	0	0	1	1	1	0	0	0	2	0	1	0	1	0	2
Run	0	1	1	1	1	1	2	1	0	0	0	2	0	1	0	1	0	2

choice has been avoided in the current study, since it is aimed at determining the level of affinity of the new taxon to other ichthyomyines, rather than seeking to add any new dimension to the phylogenetic status of the ichthyomyines as a group. Instead an hypothetical outgroup was constructed in which all character states were assessed as primitive, which was used to root the trees.

Using branch and bound algorithms, a search was made of the character data summarised in Table 2. In the analysis in which all character states were unordered, the length of the shortest tree was equal to 32 character state transformations and six trees were retained. In each of the other analyses (with the multistate characters 7 and 12 ordered, and character 18 varyingly ordered) the length of the shortest tree was equal to 33 character state transformations but

only three trees were retained. The variation in treatment of character 18, was not considered to be particularly important in this study, since character state 2 is exhibited only by taxa of the genus *Rheomys*. In both of the latter analyses *C. orcesi* and *C. trichotis* are non-monophyletic in all three trees and also in the semistrict consensus of these trees (see Fig. 3). The only evidence of a monophyletic generic grouping shown in the semistrict consensus tree is for *Ichthyomys*, and this tree is similar in most respects to the most parsimonious hypothesis of ichthyomyine relationships shown by Voss (1988: Fig.88).

### DISCUSSION

There is obvious conflict in that the results of the phylogenetic analysis do not support the generic classification currently in use. The morphological data is sufficiently persuasive to conclude that, on the available material, the new taxon is correctly attributed to the genus *Chibchanomys* as currently construed.

**ACKNOWLEDGEMENTS.** We are grateful to Jim and Theresa Clare for unpublished information on *Chibchanomys* and to the late Professor Gustavo Orcés for support and encouragement during fieldwork. We are indebted to Robert Voss (American Museum of Natural History) who initially recognised the uniqueness of the new species and who provided much helpful advice when commenting on drafts of the manuscript. Particular gratitude is owed to Darrell Siebert (Natural History Museum) for guidance with the phylogenetic analysis, and for constructive comments and criticism of the manuscript. Mark Hafner (Museum of Zoology of Louisiana State University) kindly provided photographs and measurements of the specimen of *C. trichotis* from Peru. As always the staff of the Natural History Museum freely provided support; in particular we thank Richard Sabin (Mammal Group) and Deryck Jones (Electronics) for the X-rays, Phil Hurst (Photographic Unit) for the photographs, while Clive Moncrieff (Biometrics) patiently assisted with the PAUP analysis.

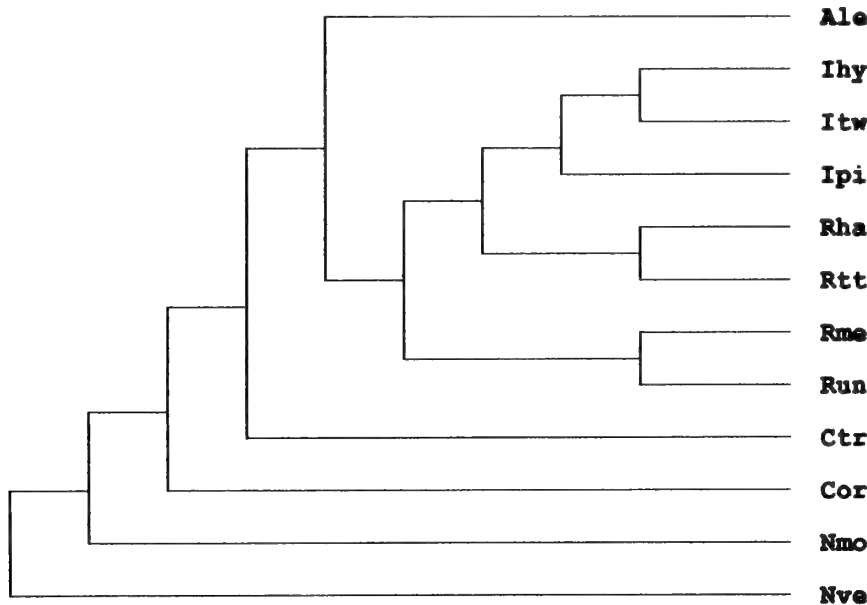


Fig. 3 Semistrict consensus tree showing hypothetical phylogenetic relationship of *Chibchanomys orcesi* to other taxa of ichthyomyine rodents. Consistency Index 0.636, Retention Index 0.786.

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**REFERENCES**


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- Anthony, H.E.** 1921. Preliminary report on Ecuadorean mammals No.1. *American Museum Novitates* (20): 1–6.
- 1929. Two genera of rodents from South America. *American Museum Novitates* (383): 1–6
- Barnett, A.** 1992. Notes on the ecology of *Cryptotis montivaga* Anthony, 1921 (Insectivora, Soricidae), a high-altitude shrew from Ecuador. *Mammalia* **56** (4): 587–592.
- 1997. The ecology and natural history of a fishing mouse *Chibchanomys* spec. nov. (Ichthyomyini: Muridae) from the Andes of southern Ecuador. *Zeitschrift für Säugetierkunde* **62**: 43–52.
- BBC–National Geographic** wildlife film ‘Avenue of the Volcanoes’
- Cabrera, A.** 1961. Catálogo de los mamíferos de América del Sur. *Rev Mus Argentina Cienc Nat ‘Bernadino Rivadavia’* **4** (2): 309–732.
- Carleton, M.D. & Musser, G.G.** 1984. Muroid rodents pp. 289–379. In Anderson, S and Knox-Jones, J (eds.) *Orders and families of Recent mammals of the world*. New York, Wiley.
- & — 1989. Systematic studies of Oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microrozomys*. *Bulletin of the American Museum of Natural History* (191): 1–83.
- Dickey, D.R.** 1928. Five new mammals of the rodent genera *Sciurus*, *Orthogeomys*, *Heteromys* and *Rheomys* from El Salvador. *Proceedings of the Biological Society of Washington* **41**: 7–14.
- Goldman, E.A.** 1912. New mammals from eastern Panama. *Smithsonian Miscellaneous Collections* **60** (2): 1–18.
- Goodwin, G.G.** 1959. Descriptions of some new mammals. *American Museum Novitates* (1967): 1–8.
- Handley, C.O.** 1976. Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin Biological Series*. **20** (5): 1–89, fig.1.
- & **Mondolfi, E.** 1963. A new species of fish-eating rat, *Ichthyomys*, from Venezuela (Rodentia, Cricetidae). *Acta Biologica Venezuelica* **3**: 417–419.
- Ochoa, J.G. & Soriano, P.** 1991. A new species of water rat, genus *Neusticomys* Anthony, from the Andes of Venezuela. *Journal of Mammalogy* **72** (1): 97–103.
- Tate, G.H.H.** 1932. The taxonomic history of certain South and Central American cricetid Rodentia: *Neotoma* with remarks upon its relationships; the cotton rats (*Sigmodon* and *Sigmomys*); and the ‘fish-eating’ rats (*Ichthyomys*, *Anotomys*, *Rheomys*, *Neusticomys* and *Daptomys*). *American Museum Novitates* (583): 1–10.
- Thomas, [M.R.] O.** 1893. On some mammals from central Peru. *Proceedings of the Zoological Society of London* **23**: 333–341.
- 1897. Descriptions of four new South American mammals. *Annals and Magazine of Natural History* (6) **20**: 218–221.
- 1906a. A new aquatic genus of Muridae discovered by consul L. Soderström in Ecuador. *Annals and Magazine of natural History* (7) **17**: 86–88.
- 1906b. A third genus of the *Ichthyomys* group. *Annals and Magazine of natural History* (7) **17**: 421–423.
- Voss, R.S.** 1988. Systematics and ecology of ichthyomine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History*. **188** (2): 259–493.
- 1991. An introduction to the Neotropical muroid genus *Zygodontomys*. *Bulletin of the American Museum of Natural History* (210): 1–113.
- & **Carleton, M.D.** 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. *American Museum Novitates* (3085): 1–17.
- Winge, H.** 1891. *Habrothrix hydrobates* n. sp. en Vandrotte fra Venezuela. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* **5** (3): 20–27.

# A new species in the asterinid genus *Patiriella* (Echinodermata, Asteroidea) from Dhofar, southern Oman: a temperate taxon in a tropical locality

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**SYNOPSIS.** The status of the hitherto temperate-water asterinid genus *Patiriella* is briefly discussed, including in its diagnosis details of actinal plate and ventral/lateral plate arrangement. A new species, *P. paradoxa*, is described from shallow water on the Dhofar coast of Oman. The distribution of *Patiriella* on the Dhofar coast is discussed in relation to the peculiar oceanographic conditions and vicariant events in the region.

## INTRODUCTION

Although one of us (ACC) made extensive collections along the coasts of the Sultanate of Oman between 1983 and 1990 (Campbell and Morrison, 1988 and Marsh and Campbell, 1991), the echinoderm fauna of southern Arabia remains incompletely known. However, those echinoderms which have been recorded are tropical species or endemic species with tropical affinities (Clark and Rowe, 1971; Price, 1982; Campbell and Morrison, 1988; Marsh and Campbell, 1991). The discovery (by FWER) of three specimens of a new species of the predominantly temperate-water, asterinid starfish genus *Patiriella* Verrill (1913) among the Omani shallow water (less than 10m) collections from two sites in Dhofar therefore poses a paradox.

Here we briefly discuss the status of the genus *Patiriella* and describe fully the new species. This work attempts to explain the presence of an otherwise temperate-water echinoderm genus in this tropical location, given the peculiar local oceanic conditions which include upwelling (see summary by Campbell and Morrison, 1988), and past vicariant events.

The type specimens have been deposited in the Natural History Museum, London U.K.

## SYSTEMATIC DESCRIPTION

### *PATIRIELLA* Verrill

*Patiriella* Verrill, 1913: 483; 1914: 263; Fisher, 1919: 410; H.L. Clark, 1946: 134; Dartnall, 1971: 39; A.M. Clark and Courtman-Stock, 1976: 80; A.M. Clark, 1983: 365; A.M. Clark and Downey, 1992: 192.

**TYPE SPECIES.** *Asterina (Asteriscus) regularis* Verrill, 1870 (1867); by original designation.

### DIAGNOSIS

After A.M. Clark in A.M. Clark and Downey (1992), amended.

A genus of Asterinidae with five to about eleven short rays (R up to c. 60mm); pentagonal to stellate in outline; aborally arched; primary abactinal plates in two 'fields', a slightly irregular radial (usually the midradial and first dorsal-lateral series on either side) 'field' and a regular lateral 'field' on either side; mid-radial abactinal plates with proximal edge trilobed or simply crescentic; the proximal concave sides of abactinal plates subtend spaces with usually one to several papular pores, separated by one to several small secondary plates; abactinal armament comprising relatively few (< 40 per plate) very coarse, almost granuliform, multipillared

spinelets; actinal plates distinctly aligned in oblique series between the second or third, and subsequent adambulacral plates and the inferomarginal plates and delimiting a membranous, proximal, triangular area which is usually filled by several plates; ventral-lateral angle of rays supported internally by abactinal plates which meet the actinal plates by virtue of the oblique alignment of both; towards the ray base as the ventral-lateral angle becomes less acute with ray depth, totally internalised plates, spanning between the abactinal and actinal plates, can be found; actinal armament coarse, short spines, mostly single, not more than two per plate; furrow spines usually two (sometimes one) per plate; subambulacral spines one (rarely two); suboral spines one to four or none; no pedicellariae.

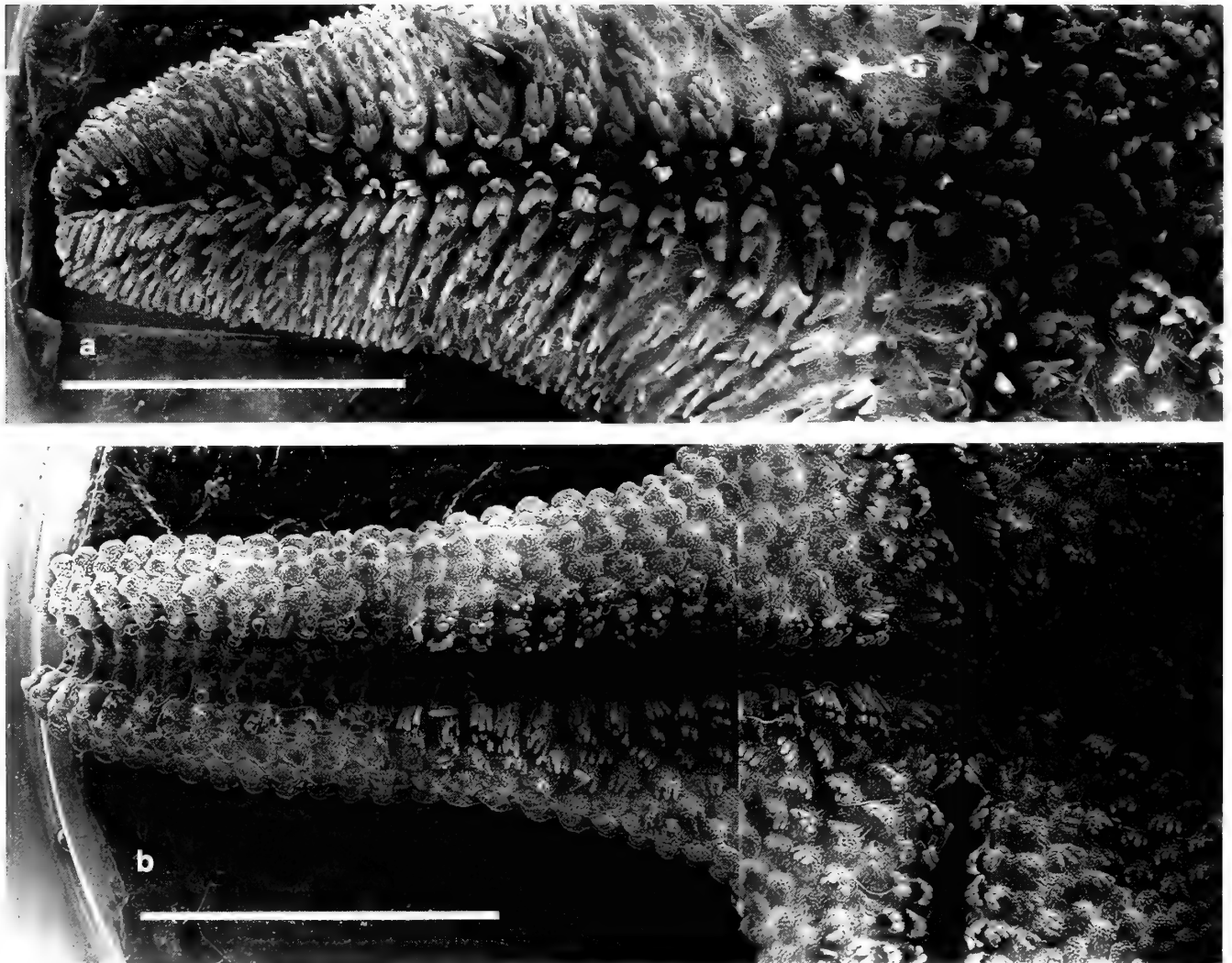
Species included: *Patiriella brevispina* H.L. Clark, 1938; *Asterias calcar* Lamarck, 1816; *Asteriscus calcarata* Perrier, 1869; *Asteriscus chilensis* Lutken, 1859; *Asterina dyscrita* H.L. Clark, 1923; *Asterias exigua* Lamarck, 1816; *Asterina fimbriata* Perrier, 1875; *Asterina gunni* Gray, 1840; *Patiriella inornata* Livingstone, 1933; *Asterina oliveri* Benham, 1911; *Patiriella parvivipara* Keough and Darnall, 1978; *Patiriella pseudoexigua* Darnall, 1971 (with subspecies *pacifica* (Hayashi, 1977, as *Asterina*); *Asterina* (*Asteriscus*) *regularis* Verrill, 1870 (1867); *Patiriella vivipara*

Darnall, 1969b; *Patiriella paradoxa* sp. nov.

Other species *Patiriella nigra* H.L. Clark, 1938 and *Patiriella obscura* Darnall, 1971 are considered to be conspecific with *P. oliveri* (Benham) and *P. pseudoexigua* Darnall respectively by Rowe (in Rowe and Gates, 1995); *Patiriella tangribensis* Domantay and Acosta, 1970, is inadequately described and cannot confidently be assigned to this genus.

#### REMARKS

The genus *Patiriella* Verrill, 1913, has had a rather chequered history. It has been considered a valid taxon by most recent authors (e.g. Fisher, 1919; H.L. Clark, 1928; 1938; 1946; Livingstone, 1933; Madsen, 1956; Darnall, 1971; A.M. Clark and Rowe, 1971; A.M. Clark and Courtman-Stock, 1976; A.M. Clark, 1983; A.M. Clark and Downey, 1992) or a synonym of *Asterina* Nardo, 1834 (e.g. H.L. Clark, 1916; 1923; Hayashi, 1940; 1977; Mortensen, 1933 (as a subgenus of *Asterina*)). The history and current status of *Patiriella* has been most recently discussed by A.M. Clark (1983; 1992 (in Clark and Downey)) who commented (1992:178) that 'The very coarse and abbreviated, almost granuliform, armament of the upper side may warrant a supra-specific distinction from *A. gibbosa* of *P.*



**Fig. 1** a, Scanning electron micrograph of the actinal surface of *Asterina gibbosa* from Plymouth U.K. Scale bar = 5mm . G = gonopore; b, Scanning electron micrograph of the actinal surface of *Asterina cepheus* from Wadi Haart, Sakh. Dhofar, Southern Oman. Scale bar = 5mm



*regularis* together with *P. gunni* (Gray) and *P. calcar* (Lamarck) from Australia, also *P. exigua* (Lamarck) which extends from the Indo-West Pacific into the S.E. Atlantic'. She thought reassessment of the rank of *Patiriella* was best left to 'one of several Australasian specialists to determine . . .', retaining the species *exigua* as a member of the genus *Patiriella*. A new review of the family Asterinidae, including a reappraisal of the status of *Patiriella* is being undertaken by F.W.E.R. elsewhere. However, whilst in the present paper we acknowledge that a very close relationship exists between the genera *Asterina*, *Patiriella* and *Patiria* (Gray, 1840) (*Patiria* is considered a synonym of *Asterina* by Hayashi (1940) and A.M. Clark (1983 (in Clark and Downey, 1992)); we accept their separate generic status, until the matter is more clearly resolved, such a resolution being outside the scope of this paper<sup>1</sup>. In taking this stance, we have amended A.M. Clark's in Clark and Downey, 1992) diagnosis of *Patiriella* to include a description of the alignment of actinal plates (included by Verrill (1913) in his diagnosis of the genus) and the internal alignment of actinal/abactinal plates at the ventral/lateral angle (described by Verrill (1913) as a feature of the family Asterinidae). As a taxonomic character, actinal plate alignment has been largely ignored. The exception was Fisher (1917; 1919) who thought this a useful character when distinguishing his new genus *Paranepanthia* (type-species *Nepanthia platydisca* Fisher, 1913) in which the plates are aligned obliquely across the actinal surface, from *Asterina* in which he saw the actinal plates forming chevrons across each interradial area, the plates being aligned only parallel to the furrows along each ray. Fisher (1919) was, however, comparing *Paranepanthia platydisca* with the species '*Asterina*' *cepheus* (Müller & Troschel), and '*A.*' *coronata* (von Martens) and not the type species *A. gibbosa*. In accepting *Asterina* in this sense, Fisher was clearly not familiar with the fact that in the type-species, *A. gibbosa*, the actinal plates, as in *Patiriella* and *Paranepanthia*, are clearly aligned obliquely between furrow and margin Fig 1a & b (there is no question, however, that *Paranepanthia* is a valid genus (F.W.E.R.). A.M. Clark (1971, in A.M. Clark and Rowe) noted Fisher's work when identifying two specimens of an undetermined species of what she considered a *Paranepanthia* from Zanzibar. She considered (1971:71) the importance of actinal plate arrangement, as a functional and taxonomic character, required investigation. However, A.M. Clark (1983) did not expand further on this matter in her more recent revision of the family Asterinidae. Although a recent survey of the family by one of us (F.W.E.R.) does show actinal plate arrangement to be a useful character in distinguishing some of the genera, actinal plate arrangement undoubtedly has a functional role which is probably micro-habitat related. We include description of the internal structure of the ventral/lateral angle in our diagnosis following A.M. Clark (1983) who concluded that differences in arrangement of these internal plates were important in indicating taxonomic affinities, a conclusion supported herein, though on the basis also, that it may relate to ray shape within the family.

### *Patiriella paradoxa* sp. nov.

**DIAGNOSIS.** Stellate species of *Patiriella* with five rays; abactinal plates of aboral, radial 'field' tri-quadrilobed, forming a delicate reticulum; papular areas each with three to six papulae and one to two secondary plates; no suboral spines; proximal actinal plates each with a single spine.

<sup>1</sup> Species attributed to *Asterina* s.s. from outside the Atlantic region are **NOT** congeneric with the type-species, *A. gibbosa* (Pennant), and require reallocation to other existing or new asterinid genera according to Rowe (in Rowe and Gates, 1995); the suggested recognition of *Asterinides* Verrill (1913) (type-species *A. folium* (Lütken)) as a valid subgenus of *Asterina*, by A.M. Clark (1983; 1992 (in Clark and Downey)) is supported, but at generic level, by Rowe (in Rowe and Gates, 1995).

**HOLOTYPE.** BMNH (dry) BMNH 1997.1016

**TYPE LOCALITY.** 0.5 km southeast of Wadi Haart and about 4 km north east of Sath village, Sultanate of Oman (17° 04'N, 55° 06'E), intertidal, just below level of the conspicuous barnacle *Tetraclita squamosa rufotincta*, collected together with '*Asterina*' *cepheus* (Müller & Troschel, 1842), A.C. Campbell 4 May 1987 (210050201) (fig.2).

**MATERIAL.** In addition to the holotype, two paratypes (dry). Paratype 1 BMNH 1997.1017, collected at the same locality with the holotype. Paratype 2 BMNH 1997.1018, Raaha, 2.5 km west of Wadi Ayn, Sultanate of Oman (16° 58'N, 54° 50'E), c. 8 m depth, on rocks amongst corals, coll. A.C. Campbell, 5 Dec., 1986 (210050202) (fig.2).

**EYMOLOGY.** The species name (Lat. paradoxum) refers to the unexpected occurrence of this predominantly temperate-water genus along an otherwise tropical coastline.

**DESCRIPTION OF HOLOTYPE.** (Figs 3 a & b; 4 a & b). Specimen stellate in outline, R=17.8 mm, r=9.0 mm, R/r=1.98; br=10.3 mm (across base of ray between first superomarginal on each side), R/br=1.73. Orally flat, aborally arched. Rays more or less elongate triangular, tapering from a relatively wide base to a rounded tip. Centre of disc delimited by a complete ring of prominent, spinelet-bearing plates, outside of which a second, more or less complete ring of less prominent plates evident. The prominent, ovate madreporite occurs in interradius CD.

Beyond the central disc, the imbricating primary abactinal plates form two 'fields' along the rays. Radial 'field' comprising an irregular, zig-zag series of mid-radial (carinal) plates and the first dorsal-lateral row on each side. Shape of this 'field' elongate-leaf-shaped along the ray, tapering proximally and distally and widest at about ½R. Denuded plates deeply notched, mostly quadrilobed (X-shaped), but, at least between ½–¾R, some mid-radial plates tri-lobed (Y-shaped), the plates together forming a relatively delicate reticulum. Papular areas, between the plates, are relatively large, up to 0.8 mm diameter, each subtending 3–6 papulae between which 1 or 2 minute, spinelet-bearing secondary plates usually occur. Primary plates with crystal bodies, except on their proximal, crescentic ridge which carries 5–7 granuliform spinelets in a single series; spinelets range from c. 0.30 mm long × 0.12 mm wide (straight sided) to about 0.37 mm long × 0.14 mm wide (these larger spinelets becoming club-shaped (0.18 mm wide) towards their tip). Lateral 'field' comprising about 10 regularly arranged rows of plates at the base of the rays, closely imbricate with a deep proximal notch subtending 1–3 papulae occurring in the proximal half of the first 5 rows of plates, the papulae not extending to the superomarginal line. Lateral 'field' plates with crystal bodies and from 2–7 spinelets.

Ventral-lateral margin sharply delimited, however neither inferomarginals nor superomarginals significantly larger than immediately adjacent actinal or abactinal plates respectively. Inferomarginal plates aligned in the same plane as the actinal surface, slightly protrude laterally and bear a group of 2–3 minute spinelets. Superomarginal plates aligned vertically, correspond with the inferomarginals below them and bear 1–2 spinelets.

About 10 rows of actinal plates counted; the first two extending to the tip of the ray; plates are aligned both parallel to the furrow but also distinctly obliquely across the actinal surface between the adambulacral plates and inferomarginal plates. Oblique alignment accentuated both by the actinal spination and narrow, shallow

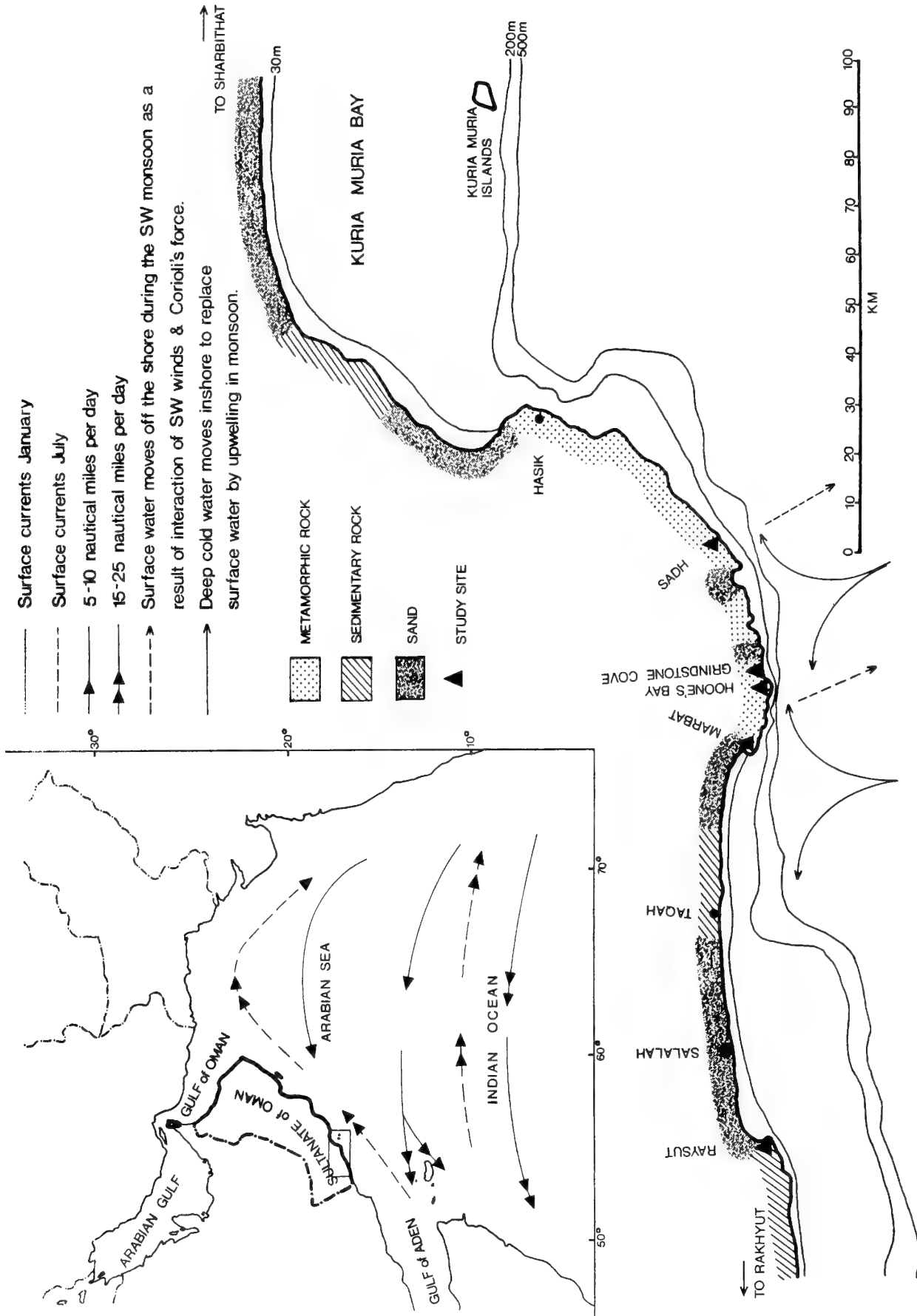
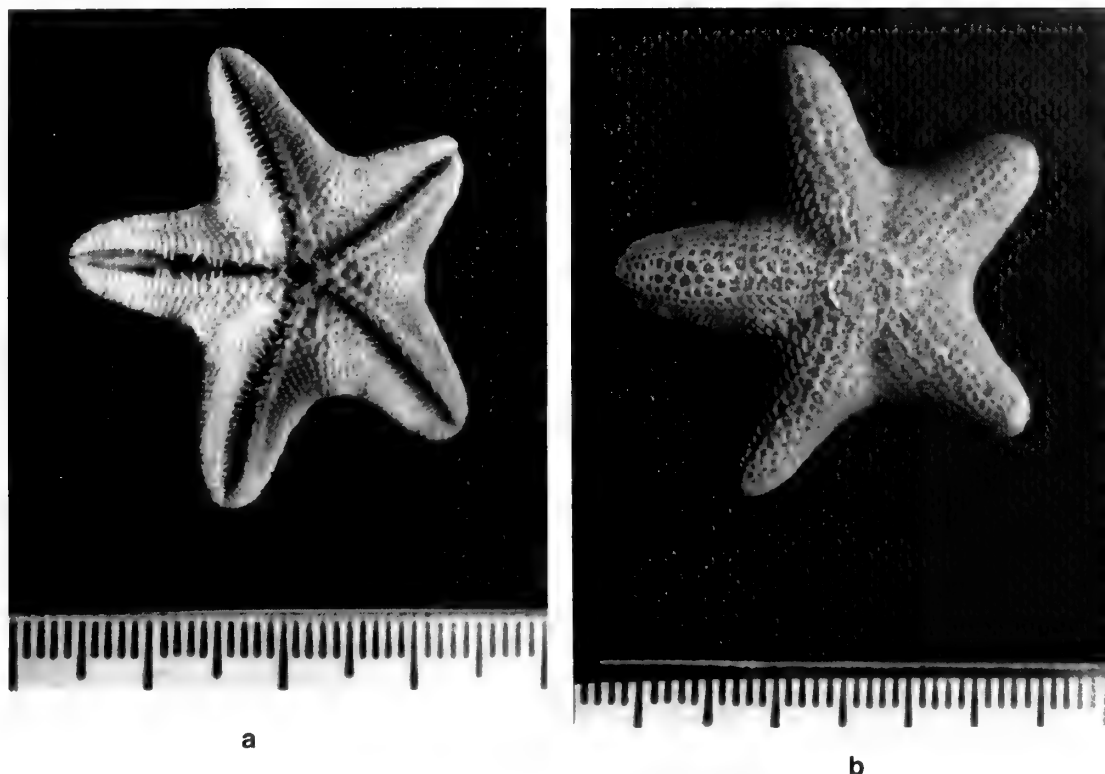


Fig. 2 Map of Dhofar, Southern Oman, showing submarine contours and monsoon events. Reproduced by kind permission from *Echinoderm Biology* (eds. R.D. Burke *et al*) 1988, published by A.A. Balkema, Rotterdam and Brookfield.



**Fig. 3** a, Photograph of *Patriella paradoxa*, Holotype, from Wadi Haart, Sadh, Dhofar, Southern Oman. Abactinial view. Scale in mm; b, Photograph of *Patriella paradoxa*, Holotype, from Wadi Haart, Sadh, Dhofar, Southern Oman. Actinial view. Scale in mm.

furrows occurring between the oblique lines of plates. First complete oblique line of plates arises opposite the second adambulacral plate in each furrow, creating a triangular area bounded by the first adambulacral plates, distal edge of the oral plates and first oblique series in each actinal intermediate area. This proximal area occupied by 2 (interradii BC, DE and EA), 3 (interradius AB) or 4 (interradius CD) plates. A small circular patch of non-calcified skin (up to 0.6mm diameter) occurring adjacent to the distal edge of the oral plates in interradii AB, CD and EA. Actinal plates each bear a single, tapering spinelet (up to 0.64mm long  $\times$  0.30mm at base) on the proximal 80% of the actinal surface, the remaining distal plates with 2 small spinelets.

There are 28–29 pairs of adambulacral plates to each furrow. These are twice as wide as long. First 12–14 plates bear 2 tapering furrow spines, proximalmost more slender and shorter than distalmost spine (on adambulacral 3: distalmost spine measures 1.0mm long  $\times$  0.35mm wide, at base tapering 0.20mm wide near tip; proximalmost spine measures 0.78mm long  $\times$  0.23mm wide at base, tapering to 0.14mm wide near tip). Proximalmost spine becomes rapidly smaller and peg-like towards the 12th–14th plate, beyond which the adambulacral plates each bear a single furrow spine. A single, stouter, subambulacral spine (on adambulacral 3: 0.87mm long  $\times$  0.29mm wide, more or less cylindrical) occurs on each adambulacral plate. The oral plates each with 4 oral (furrow) spines of which the apicalmost is longest. No suboral spines.

Gonopores not occurring on the oral surface and cannot be distinguished aborally.

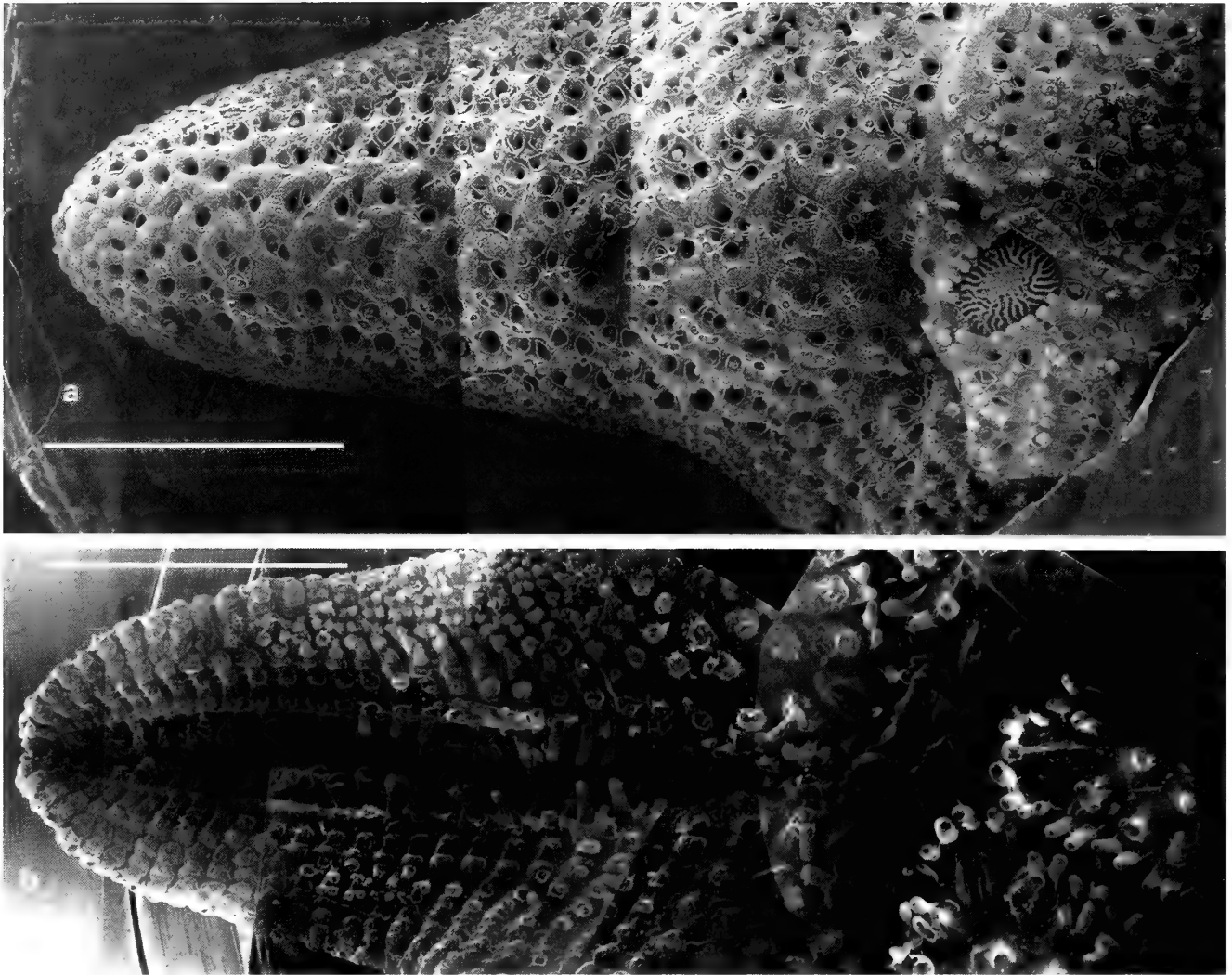
**COLOUR.** Dried holotype is a uniform, pale 'museum' buff colour. Colour in life is not recorded.

**PARATYPE 1.** BMNH 1997.1017 has  $R=19.0$ mm,  $r=7.9$ mm.

$R/r=2.4$ ;  $br=9.4$ mm,  $R/br=c.2$ . Generally very similar in appearance to the holotype, differing only in minor detail. Two furrow spines occurring only on the 1st–4th adambulacral plates, thereafter the plates with a single furrow spine. Small patch of non-calcified skin occurs adjacent to the distal edge of the oral plates in each interradius, this proximal actinal triangle being filled by 1 (interradii CD, DE) or 2 (interradii EA, AB, BC) plates.

**PARATYPE 2.** BMNH 1997.1018 has  $R=19.0$ mm,  $r=10.00$ mm,  $R/r=1.9$ ;  $br=11.2$  mm,  $R/br=1.7$ . The dry specimen is contorted. It differs from the holotype and paratype 1 in the following features. Rays are slightly broader at their bases relative to their lengths. Aborally, centre of disc not delimited by a prominent ring or rings of plates. Radial 'field' of abactinal plates is compact, plates closely imbricating with only the ridge evident and bearing 5–7 spinelets. Papular areas contain 1–4 papulae and occasionally a single secondary plate. Actinal spinulation coarser, otherwise the plate arrangement closely similar to the other type specimens. Actinal proximal triangle filled by 1 or 2 plates, no patches of non-calcified skin evident. Some 36 pairs of adambulacral plates along each furrow; each bearing a single furrow and single subambulacral spine, with the exception of the first plate with a second, smaller proximal furrow spine. Furrow and subambulacral spines flattened along their length with a squared-off tip. Several furrow spines spaced along length of the furrow, with bifid tip. Oral plates and spines are similar to those of both the holotype and paratype 1. The paratype 2 is uniformly light grey in colour.

**HABITAT.** The holotype and paratype 1 were collected on 4.5.87, 0.5km. south east of Wadi Haart and about 4 km. north east of Sadh village. These were collected, together with '*Asterina cepheus*' intertidally on a gently shelving exposed rocky shore with tide pools just below the level of the conspicuous barnacle *Tetraclita squamosa*



**Fig. 4** a. Scanning electron micrograph of the abactinal surface of *Patiriella paradoxa* from Wadi Haart, Sadh, Dhofar, Southern Oman. Scale bar: 5mm; b. Scanning electron micrograph of the actinal surface of *Patiriella paradoxa* from Wadi Haart, Sadh, Dhofar, Southern Oman. Scale bar: 5mm.

*rufotincta*. During the monsoon period, July–September, the middle shore is richly cloaked with the green alga *Ulva* sp. and brown algae develop on the lower shore. These growths are burnt off by December, and then the intertidal remains almost alga free until the next south west monsoon. It is worth noting that perennial beds of the kelp *Ecklonia radiata* have been recorded off Sadh head (Barratt *et al.*, 1986) approximately 5 km. to the south west of this site. *Ecklonia* may actually occur much closer as fragments were found washed up on the beach.

Paratype 2 was collected on 5.12.86 at Raaha 2.5 km. west of Wadi Ayn at 8 m depth on rocks amongst corals. This site faced south south east and comprised a sandy cove bordered to the east by a ridge of metamorphic rock sloping down to sand at 10 m. The rock ridge was well covered with many scleractinian colonies, especially *Acropora* sp. During the south west monsoon period this 'coral garden' became completely overgrown with the brown alga *Sargassopsis zanardini*. At the time of the collection the *S. zanardini* growths had broken up and dispersed. No *Ecklonia radiata* was seen growing in the immediate vicinity.

**DISTRIBUTION.** Known only from the type localities on the coast

of Dhofar, southern Oman.

**REMARKS.** Based on arrangement and shape of skeletal plates and their armament, *paradoxa* is without doubt congeneric with *Patiriella regularis*, the type species of *Patiriella*. It differs from that species, as with the majority of its congeners in the form of the radial 'field' of abactinal plates, the high number of papulae per papular area and absence of suboral spines. The absence of suboral spines is shared with four species from the southern Australian coast. Of these *P. parvivipara* is a small, precociously viviparous, pentagonal, cushion-shaped star; *P. brevispina* and *gunni* have six, non-projecting rays, and are more or less cushion-shaped and hexagonal in outline. Additionally, these species differ from *P. paradoxa* in the increased frequency of two spines on each of the proximal actinal intermediate plates, and *gunni* possesses two subambulacral spines per adambulacral plate. *P. paradoxa* may appear to be most closely related to *P. calcar*, differing most obviously in having a more delicate abactinal plating and armament and having 5 instead of 7–11 short rays. Clearly the geographical isolation of *paradoxa* from its congeners has resulted in the evolution of a combination of characters which isolates it within the genus.

## ZOOGEOGRAPHICAL CONSIDERATIONS.

The genus *Patiriella*, as accepted herein, is distributed predominantly in temperate seas. No fewer than 10 of the 15 species included occur in Australian waters (Rowe & Gates, 1995). Six of the species (*brevispina*, *calcar*, *gunni*, *inornata*, *parvivipara* and *vivipara*) are endemic to Southern Australia. Two species range across the Tasman Sea between southeastern Australia and New Zealand (*regularis*) or Lord Howe Island and Kermadec Islands (*oliveri*). One species (*pseudoexigua*) is essentially tropical, ranging from northeastern Australia north to Japan. The somewhat ubiquitous *P. exigua* ranges from southern Australia, westward across the southern Indian Ocean to St. Helena Island off southwestern South Africa in the southern Atlantic. Of the other species, *dyscrita* is endemic to South Africa; *calcarata* is endemic to Juan Fernandez Islands; *chilensis* occurs between Chile and Peru and, *fimbriata* is distributed from southern Chile to the Falkland-Magellan area and southern Argentina (A.M. Clark, 1993). With the exception of *fimbriata* which has a known depth range from intertidal to c. 300m, species of *Patiriella* are essentially intertidal, occurring at most to about 30m depth (A.M. Clark, 1993).

The occurrence of a species of *Patiriella* isolated on the Dhofar coast of Oman, in the tropical, northwestern Indian Ocean, is difficult to explain; whether as the result of distributive, accidental or vicariant events.

To seek explanation by a distributive means requires knowledge of reproductive strategies within the genus. Unfortunately, we have been unable to determine reproductive strategy in *P. paradoxa* through examination of the gonads, since the three specimens collected to date were preserved and dried. Since gonopores do not occur on the oral surface (see p. 133), and it is clearly not viviparous, then we assume aboral gonopores occur in *P. paradoxa* and the strategy involves either planktotrophic or lecithotrophic larvae. However, life histories of at least seven species of *Patiriella* occurring in Australia, including *P. regularis* which also occurs in New Zealand have been determined (Byrne, 1991; 1992; Byrne and Barker, 1991). Of these, *regularis* exhibits an indirect/planktotrophic developmental pattern with feeding bipinnaria and brachiolaria larvae; *gunni*, *calcar*, *pseudoexigua* exhibit a direct/lecithotrophic developmental pattern with planktonic non-feeding brachiolaria larvae; *exigua* exhibits direct/lecithotrophic developmental pattern with a benthic non-feeding brachiolaria larva; *vivipara* and *parvivipara* exhibit a direct/viviparous pattern of development as intra-ovarian brooders, without larvae. The occurrence on the the Dhofar coast of Oman of *Patiriella* originating via larval distribution from either southern Africa or the Australasian region, even though the nearest congeners are *P. dyscrita* (S. Africa) and *P. pseudoexigua* (recorded as *P. exigua* by Koehler, 1910), from the northeastern Indian Ocean, is difficult to envisage. The present-day water currents of the Indian Ocean must have been established for at least the last 15–10my, following separation of the Indian Ocean (see Adams, 1981; van Andel, 1981). The isolation of *P. paradoxa*, on the Dhofar coast suggests a genetic isolation which is not receiving input from other parts of the generic range.

An explanation of the origin of the temperate-water genus *Patiriella* on the tropical Omani coast in association with a secondary agent is, however, not at first sight, unreasonable to propose. For instance, Dartnall (1969a) considered the New Zealand species *P. regularis* had been introduced into Tasmanian waters amongst oyster spat. The distribution of *P. exigua* from southern African to St. Helena Island, in the south Atlantic, has been attributed, by Mortensen (1933) to probable transport on the holdfasts of the kelp *Ecklonia*, which

though not established itself on St. Helena was washed ashore there. A.M. Clark (1992, in A.M. Clark and Downey) considered this a reasonable supposition since *exigua* is not recorded from Ascension Island, to the north of St. Helena where the current is from the east. The occurrence of *Ecklonia radiata*, otherwise known only from around the coasts of South Africa, Australia and New Zealand, which has been recruited to the southeastern coast of Arabia via the deep Antarctic current from the south (Sheppard, 1992, in Sheppard, Price and Roberts) might have provided a 'raft' for *Patiriella* to reach the Dhofar coast, originating either from South Africa or the *Patiriella*-species-rich southern coast of Australia. However, such 'rafting' or 'accidental' introductions tend only to extend species range, as it has done with *Ecklonia*. To seek a solution here for *Patiriella* requires invocation of the **subsequent** evolution of the species *P. paradoxa* and extinction of its ancestor on the coast of Dhofar. Once again, the genetic and geographic isolation of *P. paradoxa* would not appear to support such an argument of its origin on the Dhofar coast, even from its geographically nearest congeners (see above).

The lack of fossil history of the family Asterinidae does not preclude ancient history. It may be more productive, therefore to seek a linkage between the distribution of *Patiriella* (particularly considering its very close relationship with *Asterina* s.s., from the Atlantic, and *Patiria*, from the North Pacific) and vicariant events in the Indian Ocean. The oceanographic and geological configurations of the area appears to have been relatively stable for at least the last 15–10 my (Powell *et al.*, 1981; Adams 1981).

Coincident with this time the complete opening of Drake's Passage (25–15 mya) established the circum-Antarctic current and a sharp drop occurred in surface and bottom sea-water temperatures (van Andel, 1981). It can be concurred that the present-day areas of upwelling, including those within the Indian Ocean were also established at that time. This is of interest for two reasons. Firstly, a major area of upwelling is known off the coast of Dhofar (fig. 2). This produces turbulent, nutrient-rich surface waters and almost temperate conditions (minimum recorded water temperature of 15.9°C near Sadh; Savidge, *et al.*, 1986) which prevail in the coastal region of Dhofar for at least 4 months of the year (June–mid September) (see Currie *et al.*, 1973; Campbell and Morrison, 1988; Miller and Morris, 1988 for details) and this is coincident with the known distribution of *P. paradoxa*. Secondly, the general temperate-water distribution of species of *Patiriella* (as included herein), *Asterina* s.s. (including only species *gibbosa*, *phylactica*, *stellifera* and possibly *pancera*; according to FWER, unpublished) and *Patiria* (including species *miniata*, *pectinifera* and possibly *minor*; according to FWER, unpublished), which appear (with the exceptions of *Patiriella pseudoexigua* and *Asterina stellifera* along the tropical west coast of Africa, part of its range) not to extend into locations much, if at all, above the 20°C isotherm (distribution data taken from A.M. Clark, 1993). The implication of the present-day distribution pattern of these three genera is that their ancestor was more widespread in cooler parts of the Tethyan system (possibly during the later part of the Oligocene epoch (c. 40–25 mya) (see van Andel, 1981)) and before its closure, following which event the structural differences recognised in separating the three genera would appear to have evolved in the fairly discrete geographical isolation which occurred between them. Although the distribution of its congener *pseudoexigua* across the tropics from northeastern Australia to southern Japan is somewhat confounding, the isolated, endemic occurrence of *P. paradoxa* on the southern Arabian coast might be explained in terms of its being a relic. This is all the more likely due to the influence of local seasonal upwelling, providing more temperate conditions, suitable for the genus, at least for part of the year, the

species clearly having evolved to survive year-round conditions on the coast in this tropical part of the world. Upwelling along the west coast of Africa may well account for the extension of *Asterina stellifera* into more tropical regions in the western Atlantic part of its distribution. It will be of interest now to investigate whether other shallow temperate-water echinoderms (other than the globally ubiquitous ophiuroid, *Amphipholis squamata*) (see Price, 1982) or other invertebrate taxa (see Barratt et al, 1984) might be found to occur in the Dhofar region, which might support this thesis, particularly since no other temperate-water distributed taxa appear to have been recorded from the area.

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## REFERENCES

- Andel, J.H. van. 1981. *Science at sea. Tales of an old ocean*. W.H. Freeman and Co. : San Francisco.
- Adams, C.G. 1981. An outline of Tertiary Palaeogeography. In Cocks, L.R.M. (ed.) *The evolving earth*. pp. 221–235. British Museum (Natural History). Cambridge University Press.
- Barratt, L., Ormond, R.F.G. and Wrathall, T.J. 1986. *Ecological Studies of Southern Oman Kelp Communities* Part I. Tropical Marine Research Unit, Biology Department, University of York, U.K. Report to the Council for Conservation of the Environment and Water Resources, Muscat, Sultanate of Oman, and Regional Organisation for the Protection of the Marine Environment, Kuwait.
- Benham, W.B. 1911. Stellerids and echinids from the Kermadec Islands. *Transactions of the New Zealand Institute*. **43**: 140–163. 23 Figs.
- Byrne, M. 1991. Developmental diversity in the starfish genus *Patriella*. In: Yanagisawa, T., Yasumasu, I. Oguro, C., Suzuki, N. and Motokawa, T (eds) *Biology of Echinodermata*. Balkema. Rotterdam pp. 499–508.
- Byrne, M. 1992. Reproduction of sympatric populations of *Patriella gunnii*, *P. calcar* and *P. exigua* in New South Wales, asterinid seastars with direct development. *Marine Biology* **114**: 297–316.
- Byrne, M. & Barker, M.F. 1991. Embryogenesis and larval development of the asteroid *Patriella regularis* viewed by light and scanning microscopy. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole* **180**: 332–345.
- Campbell, A.C. and Morrison, M. 1988. The echinoderm fauna of Dhofar (southern Oman) excluding holothurids. In Burke, R.D., Mladenov, P.V., Lambert, P. and Parsley, R.L. (eds). *Echinoderm Biology*: 369–378 A.A. Balkema, Rotterdam.
- Clark, A.M. 1983. Notes on Atlantic Asteroidea. 3. Families Ganeriidae and Asterinidae. *Bulletin of the British Museum (Natural History) (Zoology)* **45**: 369–380.
- Clark, A.M. 1993. An index of names of recent Asteroidea. Part 2. Valvatida. *Echinoderm Studies*, **4**: 187–366.
- Clark, A.M. & Courtman-Stock, J. 1976. *The echinoderms of southern Africa*. British Museum (Nat. Hist.) London. Publ. no 766.
- Clark, A.M. & Downey, M.E. 1992. *Starfishes of the Atlantic*. Chapman & Hall: London (Natural History Museum Publications).
- Clark, A.M. & Rowe, F.W.E. 1971. *Monograph of shallow-water Indo-West Pacific echinoderms*. British Museum (Natural History) London. Publ. No. 690.
- Clark, H.L. 1916. Report on the sea-lilies, starfishes, brittlestars and sea-urchins obtained by the F.I.S. 'Endeavour' on the coasts of Queensland, New South Wales, Tasmania, Victoria, South Australia and Western Australia. *Endeavour Research*. **4**: 1–123.
- Clark, H.L. 1923. The echinoderm fauna of South Africa. *Annals of the South African Museum* **13**: 221–435.
- Clark, H.L. 1928. The sea lilies, sea-stars, brittle-stars and sea-urchins of the South Australian Museum. *Records of the South Australian Museum*, **3**: 361–482.
- Clark, H.L. 1938. Echinoderms from Australia. *Memoirs of the Museum of Comparative Zoology, Harvard*. **55**: 1–596.
- Clark, H.L. 1946. The Echinoderm fauna of Australia. Its composition and its origin. *Publications of the Carnegie Institution, Washington*, (566):1–567.
- Currie, R.I., Fisher, A.E. and Hargreaves, P.M. 1973. Arabian Sea upwelling. In Zeitzschel, B (Ed.) *The Biology of the Indian Ocean*. Springer-Verlag, pp 37–52.
- Dartnall, A.J. 1969a. New Zealand sea stars in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, **103**: 53–55.
- Dartnall, A.J. 1969b. A viviparous species of *Patriella* (Asteroidea: Asterinidae) from Tasmania. *Proceedings of the Linnean Society of New South Wales*, **93**: 294–296.
- Dartnall, A.J. 1971. Australian sea stars of the genus *Patriella* (Asteroidea: Asterinidae). *Proceedings of the Linnean Society of New South Wales*, **96**: 39–49.
- Domantay, J.S. & Acosta, T.E. 1970. The littoral echinoderm fauna of Ilocos Sur between Candon and Vigan. *Acta Manila (A)* **5** (10): 49–103.
- Fisher, W.K. 1913. New Starfishes from the Philippine Islands, Celebes and the Moluccas. *Proceedings of the United States National Museum* **46**: 201–224.
- Fisher, W.K. 1917. A new genus and subgenus of East-Indian sea-stars. *Annals and Magazine of Natural History*, **20**: 172–173.
- Fisher, W.K. 1919. Starfishes of the Philippine seas and adjacent waters. *Bulletin of the United States National Museum (100)* **3**: 1–547.
- Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma (Asterias Linnaeus). *Annals and Magazine of Natural History*, **6**: 275–290.
- Hayashi, R. 1940. Contributions to the classification of the sea-stars of Japan. I. Spinulosa. *Journal of the Faculty of Science of Hokkaido Imperial University, Zoology* **7**: 107–204.
- Hayashi, R. 1977. A new sea star of *Asterina* from Japan, *Asterina pseudoexigua pacifica* n. ssp. *Proceedings of the Japanese Society for Systematic Zoology*, **13**: 88–91.
- Keough, M.J. & Dartnall, A.J. 1978. A new species of viviparous asterinid asteroid from Eyre Peninsula, South Australia. *Records of the South Australian Museum*, **17**(28): 407–416.
- Koehler, R. 1910. *Shallow-water Asteroidea*. Echinoderms of the Indian Museum. Calcutta.
- Lamarck, J.B.P.A. De. 1816. *Stellerides. Histoire naturelle des animaux sans vertébré Ed. 1. 2*: 522–568. Paris.
- Livingstone, A.A. 1933. Some genera and species of Asterinidae. *Records of the Australian Museum*, **19**: 1–22.
- Lütken, C. 1859. Bidrag til Kundskab om de ved Kysterne af Mellem-og syg-America levende arter af Sostjerner. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*. **1859**: 25–96.
- Madsen, F.J. 1956. Reports of the Lund University Chile Expedition 1948–1949. 24. Asteroidea, with a survey of the Asteroidea of the Chilean Shelf. *Acta Universitatis Lundensis (n.s.)* **52** (2): 1–53 6 pls.
- Marsh, L.M. and Campbell, A.C. 1991. A new species of *Ferdina* (Echinodermata: Asteroidea) from the Sultanate of Oman with discussion of the relationships of the genus within the family Ophidiasteridae. *Bulletin British Museum, Natural History (Zoology)* **57**: 213–219.
- Miller, A.G. and Morris, M. 1988. *Plants of Dhofar the Southern Region of Oman Traditional, Economic and Medicinal Uses*. The Office of the Advisor for Conservation of the Environment, Diwan of Royal Court Sultanate of Oman.
- Mortensen, T. 1933. The echinoderms of St. Helena (other than crinoids). *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*. **93**: 401–472.
- Nardo, J.D. 1834. *De Asteriis. Isis, Jena*. Encyclopaedische Zeitung 716–717pp
- Perrier, J.O.E. 1869. Resches sur les Pedicellaires et les Ambulacres des Asteries et des Ourisins. Paris.
- Perrier, J.O.E. 1875. *Revision de la collection de Stellerides du Museum d'Histoire Naturelle de Paris* 1–384 pp.
- Powell, C. McA., Johnson, B.D. and Veevers, J.J. 1981. The early Cretaceous breakup of Eastern Gondwanaland, the separation of Australia and India and their interaction with southeast Asia. pp. 17–29. In Keast, A. (ed.) *Ecological biogeography of Australia*. Junk: Hague.
- Price, A.R.G. 1982. Echinoderms of Saudi Arabia. Comparison between Echinoderm Faunas of Arabian Gulf, S.E. Arabia, Red Sea and gulfs of Aqaba and Suez. *Fauna of Saudi Arabia*, **4**: 3–21.
- Rowe, F.W.E., and Gates, J., 1995. Echinodermata. In Wells, A (ed.) *Zoological Catalogue of Australia Vol. 33*. Canberra: ABRIS.
- Savidge, G., Lennon, H.J. and Matthews, A.D. 1986. Ecological studies of southern Oman kelp communities. Part II. A shore based survey of oceanographic variables in the Dhofar region of southern Oman August–October 1985. Queens University of Belfast, Marine Biol. Sci. Report to the Council for the Conservation of the Environment and Water Resources, Muscat, Oman and Regional Organisation for the Protection of the Marine Environment, Kuwait.
- Sheppard, C., Price, A. & Roberts, C. 1992. *Marine Ecology of the Arabian Region. Patterns and Processes in the extreme tropical environments*. Academic Press. London.
- Verrill, A.E. 1867, 1870. Notes on the Radiata in the Museum of Yale College. 1. Descriptions of new starfishes from New Zealand. *Transactions Connecticut Academy Arts and Science* (1867) **1**(2): 247–251.
- Verrill, A.E. 1913. Revision of the genera of starfishes of the subfamily Asterininae. *American Journal of Science* **4**(35): 477–485.
- Verrill, A.E. 1914. Monograph of the shallow-water starfishes of the North Pacific coast from the Arctic Ocean to California. *Harriman Alaska Series, Smithsonian Institution*. **14**: 1–408.

# Morphological observations on *Oncaea mediterranea* (Claus, 1863) (Copepoda, Poecilostomatoida) with a comparison of Red Sea and eastern Mediterranean populations

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**SYNOPSIS.** The taxonomic status of the allegedly cosmopolitan *Oncaea mediterranea* (Claus, 1863) is reviewed. Comparison of Claus' fragmentary original description and the subsequent redescription by Giesbrecht in 1892 revealed significant differences which might lead to taxonomic confusion. Most authors have adopted Giesbrecht's identification, but it is clear that several, as yet unnamed, species have been recorded in the literature under the wrong name *O. mediterranea*. The species is redescribed in detail on the basis of material from the Red Sea and eastern Mediterranean. The occurrence of two size morphs in the eastern Mediterranean populations is briefly discussed. *O. mediterranea sensu Bourne* (1889) is regarded as *species inquirenda* in the genus.

## INTRODUCTION

*Oncaea mediterranea* (Claus, 1863) is one of the most widely distributed oncaeids (Copepoda: Poecilostomatoida) and according to the literature assumes a cosmopolitan distribution. It has been recorded in epi- and mesopelagic layers of all three main oceans between approximately 60° N and 60° S (Malt, 1983a: Fig. 14; Heron and Bradford-Grieve, 1995). In some areas such as the offshore waters of the Lebanon (Malt *et al.*, 1989) it represents the most common oncaeid.

*O. mediterranea* is a well studied species. The naupliar development has been documented by Hanaoka (1952), and Malt (1983c) discussed the polymorphism and pore signature pattern of the species. Paffenhöfer (1993) obtained quantitative information on reproduction rates and longevity of adult females. It was found that early copepodids of *O. mediterranea* ingested about 100% of their body weight daily when feeding at relatively high food levels. Average reproduction rates of field-collected females ranged from 5.3 to 13.3 nauplii day<sup>-1</sup>. According to Paffenhöfer (1993) neither nauplii, nor copepodids or adults of *O. mediterranea* create a feeding current, and because of their limited swimming performance the encounter with food has to be created either by motile food particles or by the copepod jumping repeatedly to locate a food-rich environment. *O. mediterranea* has been observed on discarded appendicularian houses (e.g. Alldredge, 1972) which probably serve as a major constituent of detritus and a food source for copepods in the epi- and mesopelagic zones (Ohtsuka *et al.*, 1996).

Like in many other so-called cosmopolitan planktonic species the taxonomy of *O. mediterranea* is potentially confusing. Most identifications of this species are based on the redescription of Giesbrecht (1892) from the Gulf of Naples, which was excellent by contemporary standards, and do not consider the type description of Claus (1863, as *Antaria mediterranea*) from Messina. Comparison of Claus' and Giesbrecht's text and illustrations casts certain doubts, as to whether both descriptions are based on the same species. As part

of an ongoing study on Red Sea oncaeids the taxonomic history of *O. mediterranea* is reviewed and the species is redescribed herein on the basis of material from the eastern Mediterranean and various regions in the Red Sea.

## METHODS

Oncaeids were collected using a multiple opening-closing net with a mesh size of 0.05 mm during cruise 5/5 of R/V *Meteor* in the Southern and Central Red Sea and in the Eastern Mediterranean Sea. A station list and sampling data are given in Table 1. The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with hexamethylene tetramine and transferred after ca 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976). Specimens were dissected in lactic acid, and mounted on slides in lactophenol. All figures have been prepared using a camera lucida on a Leitz Dialux differential interference contrast microscope.

Total body length and the ratio of prosome to urosome (excluding caudal rami) were calculated as the sum of the middorsal lengths

**Table 1** Station data of sampling with 0.05 mm mesh multiple opening closing net during R/V *Meteor* Cruise 5.

Stn. No.	Haul No.	Date (1987)	Time	Latitude (°N)	Longitude (°E)	Depth of Haul (m)	Total water depth (m)
<i>Red Sea</i>							
663	17/4	20.07	Day	22°58.4'	37°19.4'	50–100	1200
703	39/5	03.08	Day	15°34.8'	41°54.9'	0–50	970
	39/4					50–100	
<i>Eastern Mediterranean</i>							
44	31/5	24.01	Day	34°07.1'	31°54.7'	0–50	2530

of individual somites measured in lateral view. In the case of telescoping somites these lengths are measured from the anterior to the posterior margin. This approach differs from that traditionally used in oncaeid taxonomy, where the telescoping of somites is not considered in length measurements. Thus, sizes of the species in this paper are not directly comparable to those of previous descriptions (e.g. Heron, 1977; Heron and Bradford-Grieve, 1995) or earlier studies in the Red Sea (Böttger-Schnack *et al.*, 1989). Length data given by the latter authors are only about 70% of the length presented in this paper, due to the excessive telescoping of somites in the sorting medium.

Descriptive terminology for body and appendages follows that of Huys and Boxshall (1991). Abbreviations used in the text are: ae = aesthetasc; CR = caudal rami.

## SYSTEMATICS

Order **POECILOSTOMATOIDA** Thorell, 1859

Family **ONCAEIDAE** Giesbrecht, 1892

Genus **ONCAEA** Philippi, 1843

*Oncaea mediterranea* (Claus, 1863)

(Figs 1–5)

SYNONYMS. *Antaria mediterranea* Claus, 1863; *Oncaea mediterranea* (Claus, 1863); *Oncäa mediterranea* (Claus, 1863).

ORIGINAL DESCRIPTION. Claus (1863): 159–160, Tafel XXX, Fig. 1–6 (♀), 7 (♂).

OTHER DESCRIPTIONS. Giesbrecht (1892) [as *Oncäa mediterranea*]; Heron (1977) and Heron & Bradford-Grieve (1995) [as *Oncaea mediterranea*].

TYPE LOCALITY. Tyrrhenian Sea; Messina.

MATERIAL EXAMINED. (see Table I for locality data)

- (1) The Natural History Museum, London: Southern Red Sea: Stn 703; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 39/4); depth 50–100 m: 10 ♀ and 10 ♂ in alcohol (reg. nos 1996.1095–1114); leg. R. Böttger-Schnack;
- (2) Dr Böttger-Schnack (personal collection):
  - (a) Southern Red Sea: Stn 703; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 39/4); depth 50–100 m; leg. R. Böttger-Schnack: several ♀ and ♂ in alcohol;
  - (b) Central-Northern Red Sea: Stn 663; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 17/4); depth 50–100 m; leg. R. Böttger-Schnack: several ♀ and ♂ in alcohol;
  - (c) Eastern Mediterranean: Stn 44; R/V *Meteor* leg 5/1; collected with MSN 0.05 mm net (Haul 31/5); depth 50–100 m; leg. R. Böttger-Schnack: (i) small form: 1 ♀ and 1 ♂ dissected on slides, 1 ♀ in alcohol; (ii) broad form: 2 ♀ dissected on slides, 1 ♂ in alcohol.

### ADULT FEMALE

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1400 µm

Exoskeleton well chitinized. Prosome 2.2 times length of urosome, excluding caudal rami, 1.9 times urosome length including caudal

rami. Leg 2-bearing somite without conspicuous dorso-posterior projection (Fig. 1B). Leg 3-bearing somite with conspicuous raised pore protruding laterally (Fig. 1a). Other integumental pores on prosome as indicated in Fig. 1A–B. Pleural areas of leg 4-bearing somite with constricted posterolateral corners.

Proportional lengths (%) of urosomites are 9.7 : 60.7 : 8.2 : 8.8 : 12.6. Proportional lengths (%) of urosomites and caudal rami are 8.1 : 50.7 : 6.8 : 7.3 : 10.5 : 16.5.

Genital double-somite nearly twice as long as maximum width (measured in dorsal aspect) and twice as long as postgenital somites combined; largest width measured at anterior third, posterior part tapering gradually. Paired genital apertures located at about halfway the distance from anterior margin of genital double-somite; armature represented by 1 spine and 1 diminutive spinule (Fig. 1H). Pore pattern on dorsal surface as indicated in Fig. 1C.

Anal somite 1.3 times wider than long; about 2/3 the length of caudal rami (Fig. 1C). Secretory pore discernible on either side of anal opening. Anterior margin of anal opening (vestigial anal operculum) with transverse row of minute denticles. Posterior margin of somite finely serrate ventrally and laterally (Fig. 1D).

Caudal ramus (Fig. 1F) about 3.0 times as long as wide. Armature consisting of 6 elements: antero- and posterolateral setae long, spiniform and unipinnate along medial margin; outer terminal seta long and plumose; inner terminal seta longest and plumose; terminal accessory seta more than 2/3 the length of outer terminal seta and more than twice the length of caudal ramus; dorsal seta about half the length of terminal accessory seta, plumose and bi-articulate at base. Inner margin of somite with fringe of long, setules. Dorsal anterior surface (Fig. 1F) with secretory pore near insertion of seta II. Dorsal surface covered with numerous small scales (Fig. 1F).

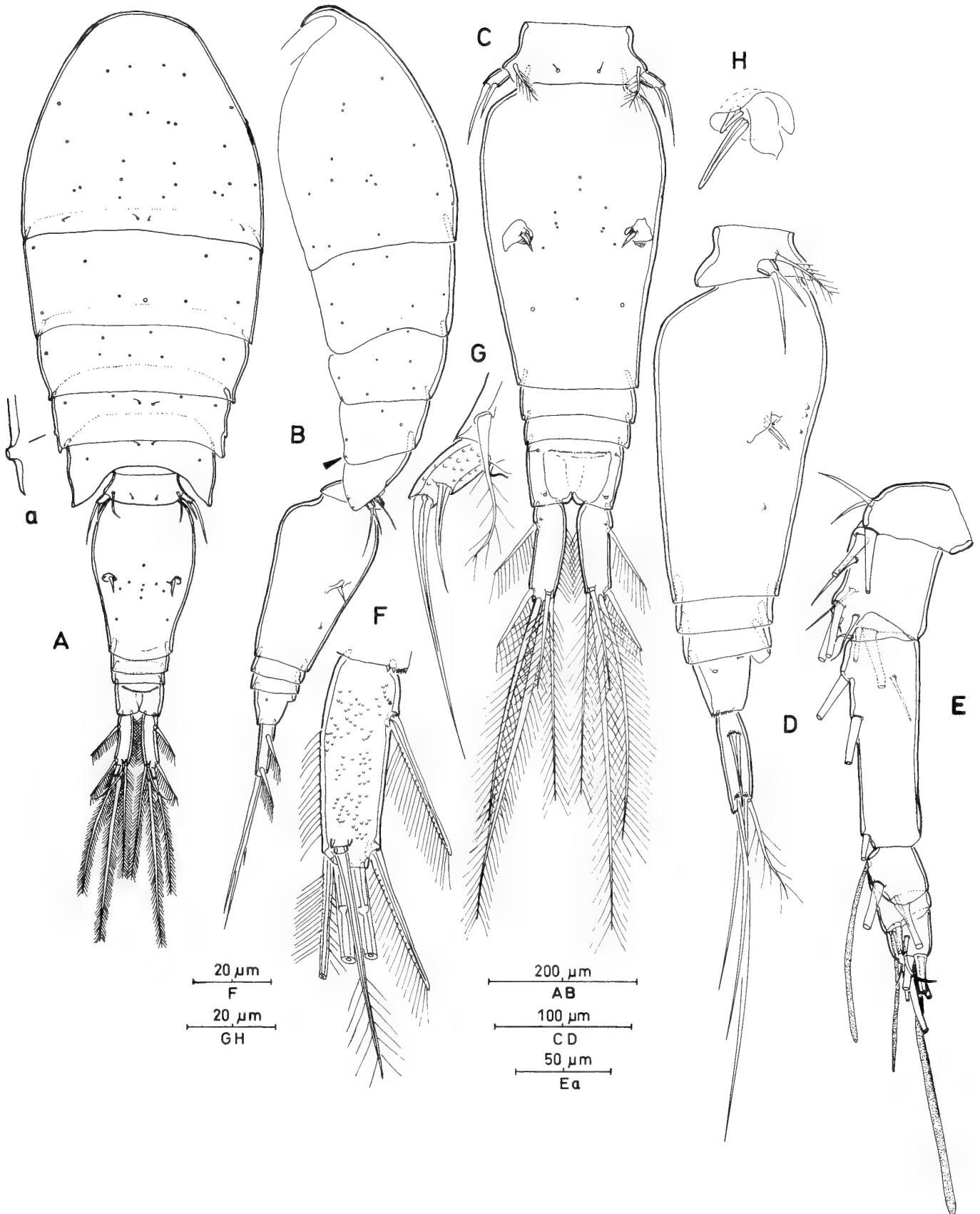
Antennule 6-segmented (Fig. 1E), relative lengths (%) of segments measured along posterior non-setiferous margin 6.2 : 20.6 : 46.4 : 10.3 : 6.2 : 10.3. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)].

Antenna 3-segmented, distinctly reflexed (Fig. 2A). Coxobasis with row of long, fine spinules or setules along outer and inner margins and with few additional spinules on proximal and distal part of outer (exopodal) margin; with bipinnate seta at inner distal corner. Endopod segments unequal in length; proximal endopod segment subtriangular forming outer lobate outgrowth bearing spinular patch, with row of denticles along posterior inner margin. Distal endopod segment slightly shorter than proximal exopod segment, with narrow cylindrical base articulating; with two patches of short spinules along outer margin; lateral armature consisting of 1 unipinnate spiniform seta and 3 curved setae, one of them sparsely pinnate, all armature elements similar in length; distal armature consisting of 5 long unipinnate setae and 2 short naked setae; none of armature elements spiniform or geniculate.

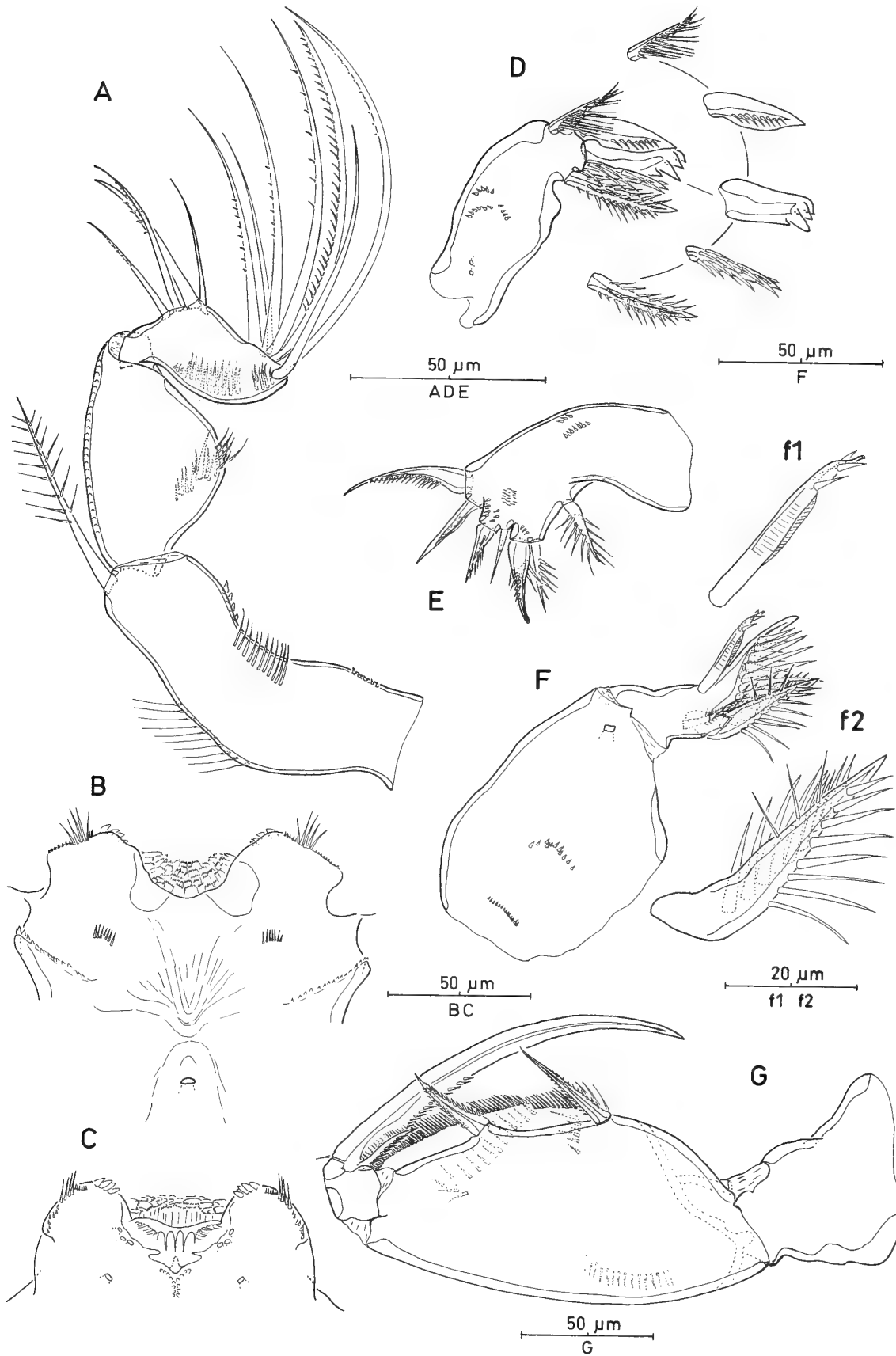
Labrum (Fig. 2B–C) distinctly bilobed. Distal margin of each lobe with 4 strong dentiform processes medially, short row of long fine setules latero-distally and row of minute spinules laterally. Lobes separated by semicircular vertex covered anteriorly by overlapping rows of hyaline petaloid flaps. Posterior part of medial incision with four rounded integumental thickenings. Anterior surface (Fig. 2B) with short row of spinules either side of median swelling, raised row of small strong denticles latero-posteriorly; median swelling with large secretory pore posteriorly. Posterior surface (Fig. 2C) with group of 3 secretory pores located on proximal part of each lobe and an additional one basally.

Mandible (Fig. 2D) with minute spinules on surface of coxa; gnathobase with 5 elements: 1 at subdistal ventral corner, 2 along distal margin and 2 along subdistal dorsal margin; ventral element shorter than ventral blade, with long, fine setules along dorsal

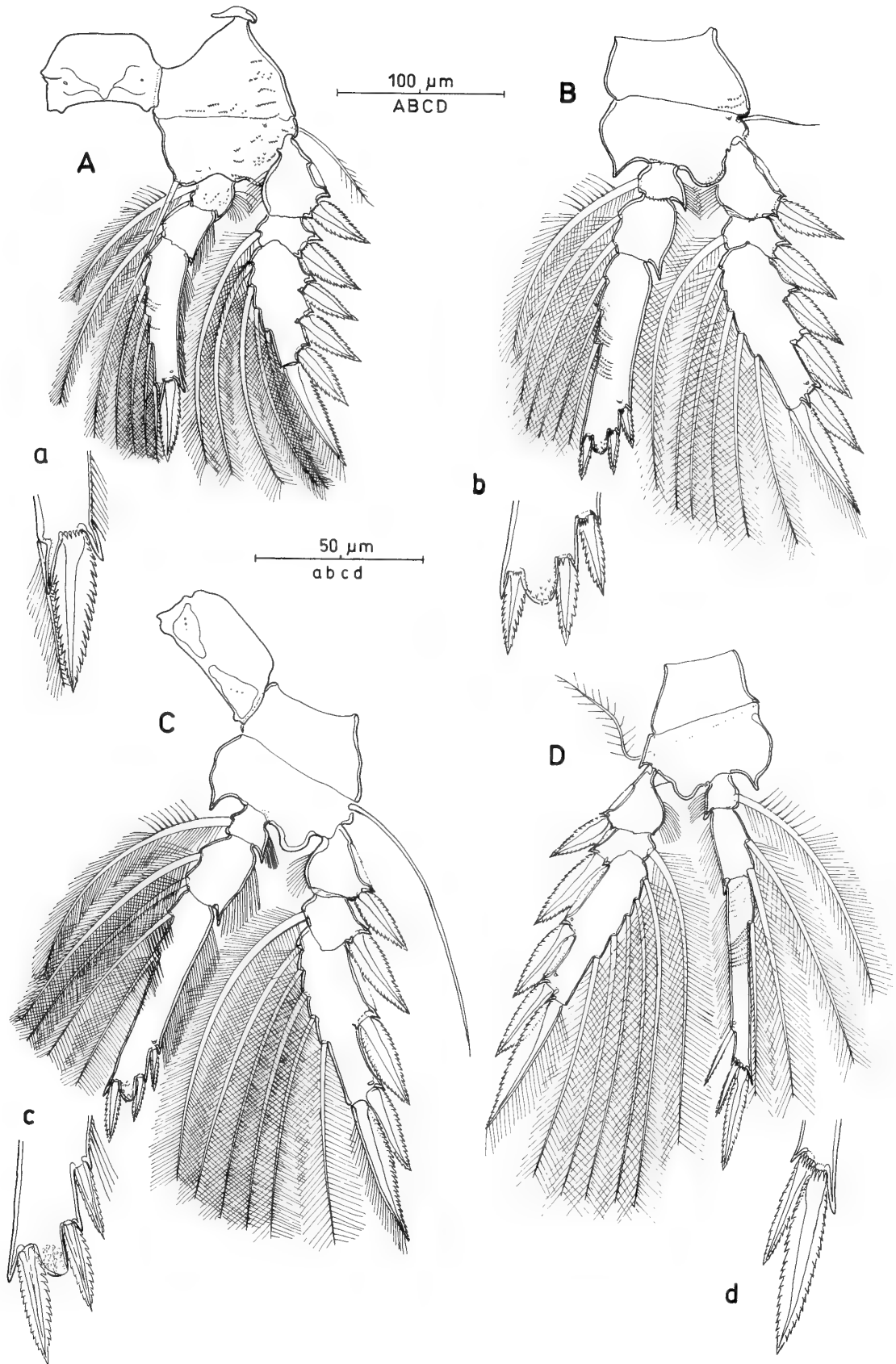




**Fig. 1** *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, habitus, dorsal [a: lateral raised pore, enlarged]; B, same, lateral (appendages omitted), arrow indicating position of lateral raised pore; C, urosome, dorsal; D, urosome, lateral; E, antennule; F, caudal ramus, dorsal; G, leg 5, dorsal; H, leg 6.



**Fig. 2** *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, antenna; B, labrum, anterior; C, same, posterior; D, mandible, showing individual elements; E, maxillule; F, maxilla, [f1, distal seta; f2, proximal seta]; G, maxilliped.



**Fig. 3** *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, leg 1, anterior [a, terminal part of endopod]; B, leg 2, anterior [b, terminal part of endopod]; C, leg 3, posterior [c, terminal part of endopod]; D, leg 4, anterior [d, terminal part of endopod].

margin; ventral blade strong and spiniform, with row of setules on posterior surface; dorsal blade strong and broad, with four dentiform processes around distal margin; dorsal elements setiform, the shorter hyaline, flat and densely setose, the longer multiipinnate.

Maxillule (Fig. 2E) indistinctly bilobed, with numerous spinules on anterior and posterior surfaces. Inner lobe subcylindrical, with 3 elements: outermost one spiniform, swollen at base, fringed with coarse spinules, others setiform and bipinnate; innermost one located along concave inner margin at some distance from other elements. Outer lobe with 4 elements; outermost element spiniform, curved and unipinnate, longer than the following; other elements with sparse spinules, innermost one shortest.

Maxilla (Fig. 2F) 2-segmented, comprising syncoxa and allobasis. Syncoxa unarmed, surface ornamented with 2 spinular rows and 1 large secretory pore. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta almost extending to tip of allobasal claw, ornamented with few strong spinules distally and a thin hyaline lamella bilaterally, tip of seta with tubular extension (Fig. 2f1); inner margin with slender pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and single row of shorter spinules along outer margin (Fig. 2f2).

Maxilliped (Fig. 2G) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, without surface ornamentation. Basis robust, inner margin with 2 spiniform bipinnate elements nearly equal in length; fringe of long pinnules between proximal seta and articulation with endopod; two rows of long setules on anterior surface as illustrated in Fig. 2G. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along proximal half of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1–4 biramous (Fig. 3A–D), with 3-segmented rami. Spine and setal formulae as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0-0	1-1	0-1; 0-1; 0,I,5	I-0; I-1; III,I,4
Leg 2	0-0	1-0	0-1; 0-2; I,II,3	I-0; I-1; III,I,5
Leg 3	0-0	1-0	0-1; 0-2; I,II,2	I-0; I-1; II,I,5
Leg 4	0-0	1-0	0-1; 0-2; I,II,1	I-0; I-1; II,I,5

Intercostal sclerites well developed, without ornamentation. Coxae and bases of legs 1–3 with surface ornamentation as shown in Fig. 3A–C. Bases with plumose (legs 1, 4), short naked (leg 2) or very long naked, outer seta (leg 3); with anterior secretory pore near outer proximal corner; inner portion slightly produced adaxially in legs 2–4 (Fig. 3B–D). Inner basal seta on leg 1 long, spiniform and naked. Respective legs without distinct length differences between rami with endopod slightly longer than exopod. Bases of spines on exopodal and endopodal segments surrounded by small spinules which are most obvious around terminal endopod spines of legs 2 and 4 (Fig. 3b,d). Surface ornamentation of all segments with small scales, similar to those on caudal ramus (Fig. 1F).

Exopods. Outer margin of exopod segments with well developed serrated hyaline lamella; inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments. Hyaline lamellae on outer exopodal spines well developed. Terminal spine of leg 1 equal in length to (leg 1) or shorter than (legs 2–4) distal exopod segment.

Endopods. Outer margin of endopod segments with fringe of long setules. Inner seta of proximal endopod segment slightly swollen. Distal endopod segments with single secretory pore on posterior surface; distal margin of legs 2 and 3 produced into conical projection ornamented with minute spinules anteriorly (Fig. 3B,C,b,c). Outer subdistal spine equal in length to distal spine in legs 2–4. Outer margin of distal segment of leg 1 terminating in a long process obscuring insertion of distalmost inner seta (Fig. 3a). Inner setae of distal endopod segments of legs 2–4 with spinule comb along proximal inner margin; this comb less obvious in leg 1; also present on distal inner seta of middle endopod segment in leg 4.

Leg 5 (Fig. 1G) comprising small plumose seta arising from lateral surface of somite, and small free segment representing exopod. Exopod slightly longer than wide, bearing stout curved seta apically and smaller slender seta inserted subdistally; surface covered with minute denticles

Leg 6 (Fig. 1C, H) represented by operculum closing off each genital aperture; armed with a spine and a short spinule.

Egg-sacs paired, oval-shaped; each sac containing approximately 40 eggs (diameter 50–65  $\mu\text{m}$ ).

#### ADULT MALE

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 960  $\mu\text{m}$ . Sexual dimorphism in antennule, antenna, maxilliped, legs 5–6, caudal ramus and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.4 : 70.0 : 3.4 : 3.8 : 3.0 : 10.5 ; proportional lengths (%) of urosomites (caudal rami included) 8.4 : 62.1 : 3.0 : 3.3 : 2.7 : 8.1 : 11.6. Leg 5-bearing somite with transverse row of denticles dorsally (Fig. 4D). Caudal rami 1.8 times longer than wide, markedly shorter than in female. Caudal setae with proportional lengths as in female. Dorsal surface of genital somite covered with scale-like structures in anterior half, arranged in a specific pattern (not figured). Surface of genital flaps and ventral surface of anal segment ornamented with several rows of small spinules (Fig. 4E). Dorsal surface of caudal ramus covered with minute scales as in female.

Antennule (Fig. 4B) 4-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 14.5 : 19.7 : 42.1 : 23.7. Armature formula: 1-[3], 2-[8], 3-[4], 4-[1+2ae+(1+ae)].

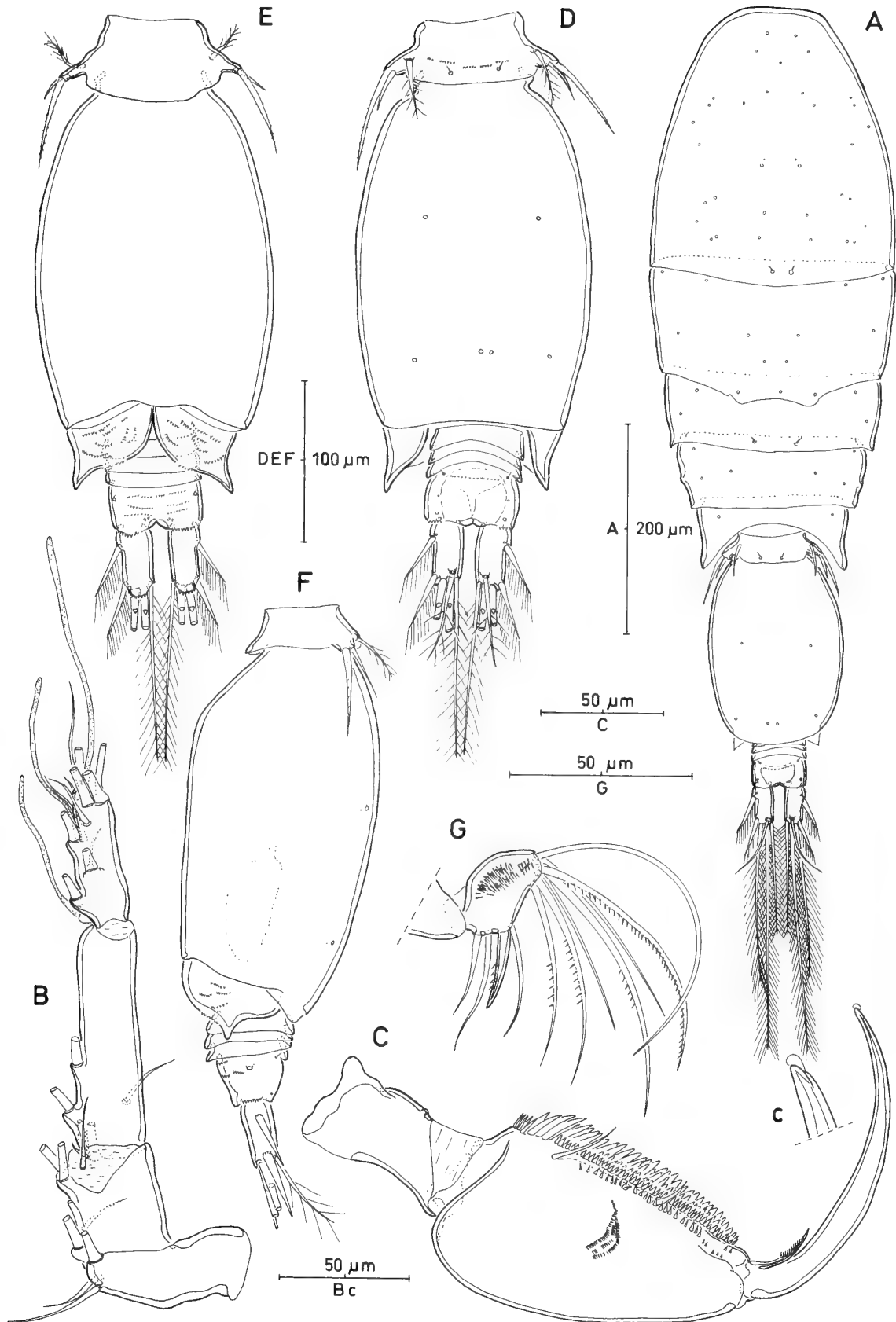
Antenna as in female, except for lateral armature on distal endopod segment (Fig. 4G), with third spiniform element being much stouter than in female and shorter than the 2 adjacent setae.

Maxilliped (Fig. 4C) 3-segmented, comprising syncoxa, basis and 1-segmented endopod. Syncoxa without surface ornamentation, unarmed. Basis robust, particularly inflated in proximal half forming bulbous swelling; anterior surface with 2–3 transverse spinular rows in addition to row of short flat spinules along inner margin (Fig. 4C); posterior surface with 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 4C); with 2 small naked setae inserted within the longitudinal cleft, the proximal one being slightly longer than the distal one. Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of short, unipectinate spine basally fused to inner proximal corner of claw; claw with minute hyaline apex (Fig. 4c).

Legs 1–4 with armature as in female; variable number of spinules on conical projection of endopods of legs 2 and 3.

Leg 5 (Fig. 4D, F) exopod not delimited from somite, general shape and armature as in female; small plumose seta arising from lateral surface of somite as in female.

Leg 6 (Fig. 4E) represented by posterolateral flap closing off



**Fig. 4** *Oncaea mediterranea* (Claus, 1863), ♂ (Red Sea). A, habitus, dorsal; B, antennule; C, maxilliped, anterior [c, tip of claw, showing hyaline lamella]; D, urosome, dorsal; E, urosome, ventral; F, same, lateral (spermatophores immature); G, antenna, distal endopod segment.

genital aperture on either side; covered by pattern of denticles as shown in Fig. 4E; posterolateral corners protruding laterally so that they are discernible in dorsal aspect (Fig. 4D).

Spermatophore oval, of variable size according to state of maturity (Fig. 4F); swelling of spermatophore during development not affecting shape or relative size of genital somite.

## TAXONOMIC HISTORY

Claus (1863:159) presented a concise original description of *Antaria mediterranea* with some illustrations of both sexes. Later Claus (1866) identified two size groups upon re-examination of original material from Messina: the large one [1.3 mm excluding CR setae] being the one that was mentioned in the original description; the small one [0.8–0.9 mm] which he also recorded from Nice; no overlap was found between both size morphs from Messina.

Lilljeborg (1875) recorded a single specimen from Mosselbay (Spitsbergen), and Car (1884) found it in plankton samples taken off Trieste in the Adriatic Sea. Both authors, however, gave no descriptions or figures and their records therefore remain unconfirmed.

Bourne (1889) [as *Oncaea mediterranea*] found 2 females in surface waters off Plymouth. Giesbrecht (1892) regarded this record doubtful and pointed out the discrepancy between the text and figures with regard to the CR/anal somite length ratio. Careful comparison of this character is hampered by the fact that Claus (1863) only figured the female in lateral aspect and by the possibility that the urosome is considerably telescoped in the specimen illustrated by Bourne. Giesbrecht's statement that Bourne's and Claus' specimens differ fundamentally in maxilliped structure is equivocal since he compared the former with what he had identified as *O. mediterranea* rather than with the original type material. On the basis of Brady's (1883) illustrations [Challenger Expedition], Bourne (1889) also tentatively regarded *Oncaea obtusa* (Dana) as a possible synonym of *O. mediterranea*, however, as Giesbrecht (1892) and subsequent authors suspected, the latter could as well be conspecific with *O. venusta* Philippi.

Giesbrecht (1892) reviewed the earlier literature on *Antaria* and *Oncaea*, and summarized the synonymies of the respective species known at that time. Dana's (1849) species *Antaria obtusa* and *A. crassimana* were included under the synonymy of both *O. venusta* and *O. mediterranea*, reflecting the author's undecisiveness on this matter. Giesbrecht redescribed *O. mediterranea* on the basis of material from Naples and distinguished two colour varieties *flava* and *rubra*.

Comparison of Giesbrecht's illustrations with Claus' original description, however, raises some doubts as to the conspecificity of the Messina and Naples specimens. The major obstacle in this comparison lies in the form, position and size of the setae on the maxillipedal basis which is usually considered as an important discriminant in oncaeid systematics. The issue is even more complicated by the discrepancy between text and figures in Claus' original description. Claus (1863) stated that there are two ornated setae on the palmar margin of the basis, yet in his figure (Tafel XXX, Fig. 6) only one naked seta is illustrated. From the position of this seta, being located halfway the inner margin, it is conceivable that Claus has overlooked the proximal seta. This hints at the possibility that Claus' *O. mediterranea* is related to the 'englishi species-group' which includes *O. ornata* Giesbrecht, 1891, *O. shmelevi* Gordejeva, 1972, *O. englishi* Heron, 1977 and *O. alboranica* Shmeleva, 1979. In these species the distal element is long, slender and minutely pinnate, whereas the proximal one is spiniform and because of its

small size easily overlooked or misinterpreted as a spinule. In Giesbrecht's *O. mediterranea*, however, both elements are (1) of about the same size and only half the length of the proximal seta in the Messina material, and (2) positioned differently, i.e. the proximal one at 1/3 distance from the syncoxa-basis joint, the distal one at 2/3 distance. A second possibility is that the long palmar seta in Claus' original illustration is in fact a maxillary element superimposed on the maxilliped since Claus believed that both appendages represented the rami of a single limb, i.e. the maxilliped.

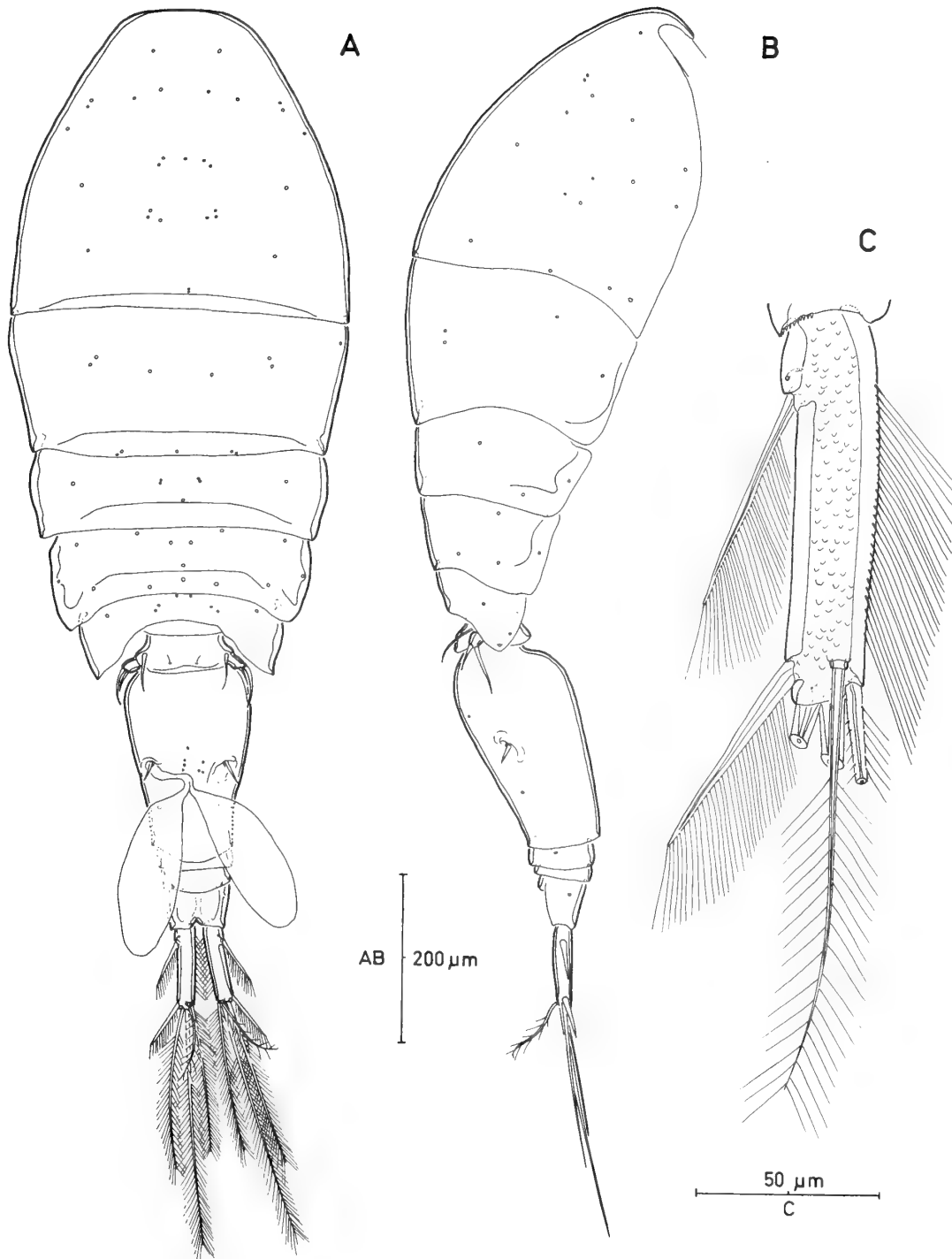
Other differences are found in the female leg 5 which is longer in the original description and the shape of the genital double-somite in lateral aspect which does not have the pronounced swelling antero-ventrally as shown in Giesbrecht's illustration (Taf. 4, Fig. 16). The male of Claus' *O. mediterranea* shows an exceptionally long leg 5 exopod (his Taf. XXX Fig. 7) which might or might not be free. This character has thus far been found in only a small number of *Oncaea* species belonging to the *notopus* group, such as *O. damkaeri* Heron, 1977 and *O. parila* Heron, 1977 (Heron, 1977; Heron *et al.*, 1984) which also display a very long leg 5 exopod in the females. Species of the *notopus* group have a setation pattern on the female maxilliped which is significantly different from that displayed in the *englishi* group which raises the suspicion that Claus (1863) might well have based males and females on different species.

As a result of this comparison it is clear that Claus' original text and drawings contain several internal inconsistencies and lack the detail that is necessary to allow unequivocal identification. The setation of the maxilliped is a potentially critical character in this process as confirmation or refutation of Giesbrecht's identification depends on whether more weight is given to the text statement or to the illustration. Given the fact that Claus' figures of the other cephalic appendages are similarly poor (setation elements are missing from every limb) it is preferred here to give more weight to the text as this will lead to nomenclatural stability. Pending the rediscovery of Claus' types (which are in all probability lost) this admittedly subjective decision is the best course of action. In view of the grossly fragmentary original description in which the sexes were based on two different – but unidentifiable – species and in the absence of formal holotype designation the taxonomic problem is in our opinion unsolvable. Moreover, it is considered highly unlikely that collection of topotype material from Messina would be informative as 130 years have lapsed since Claus' discovery of the species in an open pelagic environment that might have been subjected to major changes since, such as the opening of the Suez Canal in 1869.

*O. mediterranea* (Claus, 1863) *sensu* Bourne (1889) is clearly different from the Mediterranean material and is regarded here as *species inquirenda* in the genus.

## Other records of *O. mediterranea*.

*O. mediterranea* has been recorded from a wide range of localities such as the Antarctic (Heron, 1977) and the Red Sea (Böttger-Schnack, 1988). Many of its records, however, remain unconfirmed such as the Red Sea records of Cleve (1900, 1903) and Thompson and Scott (1903) [compiled by Halim (1969)]. Since most authors have followed Giesbrecht's identification and ignored Claus' original description it is likely that at least one, as yet unnamed, species became established in the literature under the wrong name *O. mediterranea*. For example, re-examination of material collected during the *Terra Nova* and *Challenger* expeditions (deposited in The Natural History Museum) proved to belong to at least two distinct species differing in several aspects from *O. mediterranea*. Scott (1894) recorded this species ('1 or 2 females') from the Gulf of Guinea, but re-examination of his illustrations leave little doubt that



**Fig. 5** *Oncaea mediterranea* (Claus, 1863), ♀, broad form (eastern Mediterranean). A, habitus, dorsal; B, same, lateral; C, caudal ramus.

he was dealing with a species of the *englishi* group. Supporting evidence for this is found in the morphology of the antenna, maxilliped and leg 4. Dakin and Colefax (1940) recorded the species from New South Wales from a depth of 0–200 m where it was 'rare' but it is doubtful whether they were dealing with *O. mediterranea* since material collected from the Great Barrier Reef and identified with Claus' species proved upon re-examination to belong to a closely related undescribed species. Razouls (1974) described *O. mediterranea* from the region of Banyuls-sur-mer (Golfe du Lion) and summarized previous records from the Mediterranean Sea. His

drawing (Fig. 4G) of the male shows a terminal conical projection on the endopod of swimming leg 4 which disproves his identification as this is a character exclusively found in representatives of the *coniferasimilis* complex. Ferrari (1973, 1975) recorded the species from the Gulf of Mexico and the northern Caribbean Sea and distinguished three size variants, the status of which will be discussed below under 'form variants' of *O. mediterranea*. Boxshall (1977a) recorded *O. mediterranea* from the Northeastern Atlantic near the Cape Verde Islands and in another report (Boxshall, 1977b) gave detailed information on their vertical distribution and diurnal vertical migration.

Many more records of *O. mediterranea* from different localities in the world ocean are known [see Malt (1983a) for a review], but are not considered here, because they did not include figures or a description that positively identified the species.

## FORM VARIANTS

In the eastern Mediterranean, *O. mediterranea* exhibits two forms in both sexes: a smaller and more slender form and a larger, more robust form. These forms differ only in the general appearance and in the length : width ratio of the caudal ramus in the females. The difference in general habitus between the two is caused by the greater width of the leg 2-bearing and leg 3-bearing somites in the larger form (Fig. 5A). In the females, the length to width ratio of the caudal rami is larger in the broad form (4:1) (Fig. 5C) as compared to the small form (3:1, cf. Fig. 1F), whereas in the males no corresponding difference could be found. No other morphological differences were discernible between the two morphs. The small form of *O. mediterranea* corresponds to the small variant described by Malt (1983a), while the large form seems to be similar to her 'typical' *mediterranea* form. Only one size morph of *O. mediterranea* was found in the Red Sea, which can be identified as the small form found in the eastern Mediterranean and on the basis of the length to width ratio of caudal rami seems to resemble the small form of *O. mediterranea* recognized by Malt (1983b). A small colourless form of *O. mediterranea* (in addition to the larger 'orange-golden' form) was found south of New Zealand by Farran (1929) but no further description was provided.

Ferrari (1975) reported the existence of three distinct size groups in *O. mediterranea* of the Gulf of Mexico. The two larger forms differed only in size, but had a similar length to width ratio of the caudal ramus of 4:1. On the basis of their morphometry they might be assigned to the typical form of *O. mediterranea* (*sensu* Malt). The smaller size group had a length to width ratio of the caudal ramus of 3.0–3.5:1 and might thus be similar to the small form *sensu* Malt and to that found in the Red Sea. The smaller morph was initially regarded as a potential new species (Ferrari, 1973) since it differed both in the proportional lengths of body somites as well as in total body size. Subsequently, Ferrari (1974), quoting *O. conifera* Giesbrecht, 1891 as an exemplar of gross relative size variation in oncaeids, considered it as merely another size group of *O. mediterranea* since not structural differences could be detected in the appendages. The recent outstanding work on the *conifera*-complex by Heron and Bradford-Grieve (1995) has amply demonstrated that much of the 'variation' in *O. conifera* can be explained by the fact that morphologically similar species can co-exist and that this morphological similarity can even cause anomalies in the mate guarding configurations of certain species. It is conceivable that many of the form variants represent genuine species which can no longer be discriminated using traditional  $\alpha$ -taxonomical methods. For example, Malt (1983c) mapped the pore signature pattern of the two female forms of *O. mediterranea* from the North Atlantic but failed to reveal any significant difference between them. It seems therefore that the question whether the large morph found in the Eastern Mediterranean represents a sibling species of *O. mediterranea* can perhaps only be resolved by breeding experiments or alternative methods using molecular data such as enzyme electrophoresis, immunological distance methods or ribosomal RNA sequencing.

## ECOLOGICAL NOTES

### Geographical distribution.

*O. mediterranea* is distributed throughout the Red Sea (see review in Halim (1969); Böttger-Schnack, 1990b, 1995). It was also found in small mesh net samples from the northernmost part of the Gulf of Aqaba (Böttger-Schnack, unpubl.).

### Vertical distribution and vertical migration.

During summer and autumn, when a strong seasonal thermocline is developed, the core of the *O. mediterranea* population during the day is situated in the zone below the thermocline, at 50–150 m (Böttger-Schnack, 1990a, unpubl.). Parts of the population migrate into the upper 50 m during the night, with males showing a greater proportion of migrating individuals than females. For females, a bimodal vertical distribution can be found during these seasons, with the lower part of the population dwelling in the 250–400 m layer, in the core of the oxygen minimum zone. In the northern Red Sea the mesopelagic populations of females are found at greater depths than in the central area, corresponding to the regional differences in the depth of minimal oxygen concentrations (Böttger-Schnack, 1990b). These deep dwelling populations are not found during winter (Böttger-Schnack, 1990b).

### Seasonal variation in abundance (central Red Sea).

No consistent seasonal variation in abundance was found for *O. mediterranea* in the central Red Sea, indicating that the populations are not substantially recruited by those from the south (Böttger-Schnack, 1995).

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## REFERENCES

- Allredge, A.L. 1972. Abandoned larvacean houses: Unique food source in the pelagic environment. *Science*, **177**: 885–887.
- Böttger-Schnack, R. 1988. Observations on the taxonomic composition and vertical distribution of cyclopoid copepods in the central Red Sea. *Hydrobiologia*, **167/168**: 311–318.
- 1990a. Community structure and vertical distribution of cyclopoid copepods in the Red Sea. I. Central Red Sea, autumn 1980. *Marine Biology*, **106**: 473–485.
- 1990b. Community structure and vertical distribution of cyclopoid copepods in the Red Sea. II. Aspects of seasonal and regional differences. *Marine Biology*, **106**: 487–501.
- 1992. Community structure and vertical distribution of cyclopoid and poecilostomatoid copepods in the Red Sea. III. Re-evaluation for separating a new species of *Oncaea*. *Marine Ecology Progress Series*, **80**: 301–304.
- 1995. Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods. *Marine Ecology Progress Series*, **118**: 81–102.
- 1997. Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep Eastern Mediterranean (Levantine Sea). *Oceanologica Acta*, **20**: 399–419.
- Schnack, D. & Weikert, H. 1989. Biological observations on small cyclopoid copepods in the Red Sea. *Journal of Plankton Research*, **11**: 1089–1101.
- Bourne, G.C. 1889. Report on the pelagic Copepoda collected at Plymouth in 1888–89. *Journal of the Marine Biological Association of the United Kingdom, new series*, **1**: 144–151.
- Boxshall, G.A. 1977a. The planktonic copepods of the northeastern Atlantic Ocean:



- Some taxonomic observations on the Oncaeidae (Cyclopoida). *Bulletin of the British Museum (Natural History), Zoology*, **31**: 103–155.
- **1977b**. The depth distributions and community organization of the planktonic cyclopoids (Crustacea : Copepoda) of the Cape Verde Islands region. *Journal of the Marine Biological Association of the United Kingdom*, **57**: 543–568.
- Brady, G.S. 1883**. Report on the Copepoda collected by H.M.S. Challenger during the years 1873–76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger, Zoology*, **8**(23): 1–142.
- Car, L. 1884**. Ein Beitrag zur Copepoden-Fauna des adriatischen Meeres. *Archiv für Naturgeschichte*, **50**: 236–256.
- Claus, C. 1863**. Die freilebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. 230 pp. Wilhelm Engelmann, Leipzig.
- **1866**. Die Copepoden-Fauna von Nizza. Ein Beitrag zur Charakteristik der Formen und deren Abänderungen 'im Sinne Darwin's'. *Schriften der Gesellschaft zur Beförderung der Gesamten Naturwissenschaften zu Marburg, Supplement 1*: 1–34.
- Cleve, P.T. 1900**. Plankton from the Red Sea. *Öfversigt af Konglige Vetenskaps-Akademiens Förhandlingar, Stockholm*, **57**: 1025–1038.
- **1904**. Report on plankton collected by Mr. Thorild Wulff during a voyage to and from Bombay. *Arkiv för Zoologi*, **1**: 329–381.
- Dakin, W.J. & Colefax, A.N. 1940**. The plankton of the Australian coastal waters off New South Wales. Part I. *Publications of the University of Sydney, Department of Zoology, Monogr.* **1**: 1–215.
- Dana, J.D. 1849**. Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicæ Fœderatæ Duce, lexit et descripsit Jacobus D. Dana. Pars II. *Proceedings of the American Academy of Arts and Sciences*, **2**: 9–61.
- Farran, G.P. 1929**. Crustacea. Part X.—Copepoda. *Natural History Reports, British Antarctic ("Terra Nova") Expedition, 1910, Zoology*, **8**: 203–306.
- Ferrari, F.D. 1973**. Some Corycaeidae and Oncaeidae (Copepoda: Cyclopoida) from the epipelagic waters of the Gulf of Mexico. Ph.D. Dissertation, Texas A&M University, 214 pp.
- **1975**. Taxonomic notes of the genus *Oncaea* (Copepoda: Cyclopoida) from the Gulf of Mexico and Northern Caribbean Sea. *Proceedings of the Biological Society of Washington*, **88**: 217–232.
- Giesbrecht, W. 1892**. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. *Fauna und Flora des Golfes von Neapel*, **XIX**: 1–831.
- Halim, Y. 1969**. Plankton of the Red Sea. *Oceanography and Marine Biology, Annual Review*, **7**: 231–275.
- Hanaoka, T. 1952**. On nauplius of *Oncaea mediterranea* and *Corycaeus* sp. *Bulletin of the Naikai regional Fisheries Research Laboratory*, **1**: 37–41.
- Heron, G.A. 1977**. Twenty-six species of Oncaeidae (Copepoda : Cyclopoida) from the Southwest Pacific-Antarctic area. In: D. L. Pawson (ed.). *Biology of the Antarctic Seas, VI, Antarctic Research Series*, **26**: 37–96.
- & **Bradford-Grieve, J.M. 1995**. The marine fauna of New Zealand: Pelagic Copepoda: Poecilostomatoidea: Oncaeidae. *New Zealand Oceanographic Institute Memoir*, **104**: 1–57.
- **English, T.S. & Damkaer, D.M. 1984**. Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea* and *Epicalymma* (Poecilostomatoidea: Oncaeidae), with remarks on distributions. *Journal of Crustacean Biology*, **4**: 448–490.
- Huys, R. & Boxshall, G.A. 1991**. *Copepod Evolution*. 468 pp. The Ray Society, London.
- Lilljeborg, A.W. 1875**. De under Svenska vetenskapliga expeditionen till Spetsbergen 1872–1873 derstädes samlade Hafs-Entomostraceer. *Öfversigt af Konglige Vetenskaps-Akademiens Förhandlingar, Stockholm*, **32**(4): 3–12.
- Malt, S.J. 1983a**. Studies on the taxonomy and ecology of the marine copepod genus *Oncaea* Philippi. Ph.D. Dissertation, University of London, 500 pp.
- **1983b**. Crustacea, order: Copepoda, suborder: Cyclopoida, family: Oncaeidae, genus: *Oncaea*. *Fiches D'Identification du Zooplancton*, **169/170/171**: 1–11.
- **1983c**. Polymorphism and pore signature patterns in the copepod genus *Oncaea* (Cyclopoida). *Journal of the Marine Biological Association of the United Kingdom*, **63**: 449–466.
- **Lakkis, S. & Ziedane, R. 1989**. The copepod genus *Oncaea* (Poecilostomatoidea) from the Lebanon: taxonomic and ecological observations. *Journal of Plankton Research*, **11**: 949–969.
- Ohtsuka, S., Böttger-Schnack, R., Okada, M. & Onbé, T. 1996**. In situ feeding habits of *Oncaea* (Copepoda: Poecilostomatoidea) from the upper 250 m of the central Red Sea, with special reference to consumption of appendicularian houses. *Bulletin of Plankton Society of Japan*, **43**: 89–105.
- Paffenhöfer, G.-A. 1993**. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *Journal of Plankton Research*, **15**: 37–55.
- Razouls, C. 1974**. Les Oncaeidae (Copepoda, Cyclopoida) de la région de Banyuls (Golfe du Lion). *Vie et Milieu, (A)* **24**(2): 235–264.
- Scott, T. 1894**. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray. B.Sc. *Transactions of the Linnean Society of London, Zoology*, (2) **6**: 1–161.
- Steedman, H.F. 1976**. Examination, sorting and observation fluids. In H. F. Steedman (ed.), *Zooplankton fixation and preservation, Monographs on Oceanographic Methodology*, **4**, (Paris: Unesco Press), pp. 182–183.
- Thompson, I.C. & Scott, A. 1903**. Report on the Copepoda collected by Professor Herdman, at Ceylon, in 1902. In: W. A. Herdman (ed.), *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, **1**, (Supplement 7): 227–30.



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