

MANGROVE-ASSOCIATED LUCINID BIVALVES OF THE CENTRAL INDO-WEST PACIFIC: REVIEW OF THE “AUSTRIELLA” GROUP WITH A NEW GENUS AND SPECIES (MOLLUSCA: BIVALVIA: LUCINIDAE)

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ABSTRACT. – The mangrove-associated chemosymbiotic lucinid bivalve *Austriella corrugata* (Deshayes, 1843) ranges throughout Southeast Asia where it inhabits mud amongst mangrove trees. Although this species is relatively well-known, our research indicates other quite abundant, related species, also inhabiting mangroves and their margins, which are neglected in the literature. A new genus (*Indoaustriella*) is proposed to include the smaller species that resemble *Austriella* in external characters but possess lateral hinge teeth; these include *Indoaustriella plicifera* (A. Adams, 1855) from Malaysia and India, *I. lamprelli*, new species from Moreton Bay and southern Queensland, Australia, two species with both anterior and posterior lateral teeth, *I. dalli* (Lynge, 1909) from the Gulf of Thailand and *I. scarlatoi* (Zorina, 1978) from southern China and Hong Kong. Species and generic discrimination are corroborated by 18S, 28S rRNA and cytochrome B molecular sequences.

KEYWORDS. – *Austriella*, *Indoaustriella*, *Indoaustriella lamprelli*, morphology, chemosymbiosis, molecular phylogeny.

INTRODUCTION

Bivalves of the family Lucinidae are notable for their symbiosis with sulphide-oxidising bacteria housed in the gills and from which they derive much of their nutrition (Distel, 1998; Taylor & Glover, 2000, 2006). Lucinids occupy a wide range of habitats from the intertidal zone to depths of around 2500 m and they are often associated with reducing, organic-rich habitats such as seagrass beds (Barnes & Hickman, 1999). There are, however, only a few species of Lucinidae commonly associated with organic-rich, suboxic sediments in and around mangroves, one of the limitations to infaunal bivalves being the highly corrosive habitat. Lucinids recorded include the large *Anodontia philippiana* (Reeve, 1850) and *Austriella corrugata* (Deshayes, 1843) in the Indo-West Pacific (Sotto & Cosel, 1982; Leбата & Primavera, 2001; Taylor & Glover, 2005), *Phacoides pectinatus* (Gmelin, 1791) in the western Atlantic (Narchi & Farani Assis, 1980; Frenkiel et al., 1996), and *Keletistes rhizoecus* Oliver, 1986, in West Africa (Oliver, 1986). Both *Austriella corrugata* (often cited under the generic name *Eamesiella*) and *Anodontia philippiana* are common economic species in the central Indo-Pacific, where they are widely eaten in the Philippines (Sotto & Cosel, 1982; Leбата & Primavera, 2001) and also occur in northern Australian aboriginal shell middens (Tenison-Woods, 1881).

Recent systematic studies of tropical Lucinidae have demonstrated the family to be far more diverse than previously thought (Glover & Taylor, 2001, 2007; Taylor & Glover, 2005; Cosel, 2006). For example, it is now apparent that there are several other smaller lucinids, with features resembling the large, better-known *Austriella corrugata*, living in Indo-Pacific mangrove habitats. These have been mistakenly identified as juveniles of *A. corrugata* or are hitherto neglected or unrecognized species. From molecular and morphological evidence, the small species “*Lucina*” *dalli* Lynge, 1909, originally described from near mangroves in southeastern Thailand, and the closely similar, small “*Phacoides*” *scarlatoi* Zorina, 1978, from southern China, are both part of the *Austriella* group. The former species is abundant in inshore waters of the Gulf of Thailand with population densities to 113 m⁻² (see Meyer et al., 2008, this volume).

Mention should also be made of *Bathyaustriella thionipta* Glover, Taylor & Rowden, 2004, a lucinid described from a hydrothermal vent off of northern New Zealand (Glover et al., 2004). This has shell morphology similar to *Austriella corrugata*, with molecular data corroborating a relationship. Living shells of *Bathyaustriella* are highly eroded, indicating a corrosive environment, perhaps with similarities to the acidic mangrove sediments inhabited by *Austriella*.

Table 1. Species sampled, collection locality and GenBank accession numbers for the genes sequenced for each taxon. New sequences in bold.

Species	Locality	Registration No	18S rRNA	28S rRNA	CytB
<i>Austriella corrugata</i>	Dampier, Western Australia	BMNH 20070306	AJ581848	AJ581882	AM774139
"	Sungei Buloh Reserve, Singapore	BMNH 20070290	AM774128	AM774133	AM774140
"	Tanjung Adang, opposite Tanjung Pelepas Port, SW Johor, Malaysia	BMNH 20070307	AM774129	AM774134	AM774141
"	Panglao, Philippines	MNHN BC1625			AM774142
<i>Indoaustriella dalli</i>	Kungkraen Bay, Chantaburi Province, Thailand	BMNH 20070308	AM774130	AM774135	AM774143
<i>Indoaustriella lamprelli</i> , new species	Luggage Point, Moreton Bay, Queensland, Australia	BMNH 20070304	AM774131	AM774136	AM774144
<i>Indoaustriella plicifera</i>	Tanjong Laboh, near Batu Pahat, Johor, Malaysia	BMNH 20070309	AM774132	AM774137	AM774145
<i>Indoaustriella scarlatoi</i>	Tai Tam Bay, Hong Kong	BMNH 20070310	AJ581859	AJ581893	AM774146
<i>Bathyaustriella thionipta</i>	Kermadec Ridge, New Zealand	BMNH 20070337	AJ581858	AJ581892	AM774147
Outgroup					
<i>Lucina pensylvanica</i>	Lower Matecumbe Key, Florida Keys, USA	BMNH 20070311	AM774127	AM774138	AM774148

In this paper, we review the species of the *Austriella* group from the central Indo-West Pacific, and using both morphological and molecular evidence, erect a new genus to include several poorly known species from Southeast Asia and a new species from Queensland.

MATERIALS AND METHODS

Type material of all of the nominal species was examined and imaged and major collections of Lucinidae were studied in London (BMNH), Paris (MNHN), Sydney (AMS), Cardiff (NMGW), Amsterdam (ZMA), Perth (WAM), and Washington (USNM). Additionally, we collected living material of all of the species during fieldwork, notably in Thailand, Malaysia, Singapore, Hong Kong, Dampier, Western Australia, and Moreton Bay, Queensland.

Morphology. – For gill sections and posterior aperture preparations, tissues were dehydrated through ascending concentrations of acetone, critical point dried and examined by scanning electron microscopy (SEM). Other observations were made from serial thin sections of *Indoaustriella dalli* from Kungkraen Bay fixed in Bouin's fluid.

Molecular methods. – Protocols for DNA extraction, amplification of two genes, the nuclear 18S rRNA and 28S rRNA genes, and sequencing followed the methods of Williams & Ozawa (2006). Amplification of the mitochondrial cytochrome B gene (cytB) was performed using the same protocol as for 18S rRNA, but with an annealing temperature of 48°C. New cytB primers for molluscs are: cytbF, GRG GKG CTA CKG TAA TTA CTA A and cytbR_new, AAA TAY CAC TCG GGC TGG ATA TG. These primers work on both bivalves and gastropods.

New DNA sequences for three genes were obtained from four species of *Indoaustriella* and from *Austriella corrugata* collected at three different localities together with an additional cytB sequence for *A. corrugata* from Panglao, the Philippines (Table 1). The lucinid *Lucina pensylvanica* Linnaeus, 1758, was used as outgroup; this had previously been shown (Williams et al., 2004) to be part of the same large clade of Lucinidae as *Austriella*. The hydrothermal vent species *Bathyaustriella thionipta*, morphologically and molecularly similar to *Austriella* (Glover et al., 2004), is also included for comparison. All sequences have been deposited in GenBank. Voucher material is held in the BMNH collections.

Sequences were edited and aligned using Sequencher (v. 4.0, Gene Codes Corporation, Ann Arbor, Michigan). Phylogenies were constructed using the neighbor-joining method as implemented in PAUP* (v. 4.0b10; Swofford, 2002) using Kimura's 2-parameter distance (Kimura, 1980).

Institutional abbreviations. – AMS, Australian Museum, Sydney; BMNH, The Natural History Museum, London; MAGNT, Museum and Art Gallery of the Northern Territory, Darwin; MNHN, Muséum National d'Histoire Naturelle, Paris; NMGW, National Museum and Galleries of Wales, Cardiff; NMV, National Museum of Victoria; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth; ZISP, Zoological Institute, St. Petersburg; ZMA, Zoological Museum, Amsterdam; ZMC, Zoological Museum, Copenhagen.

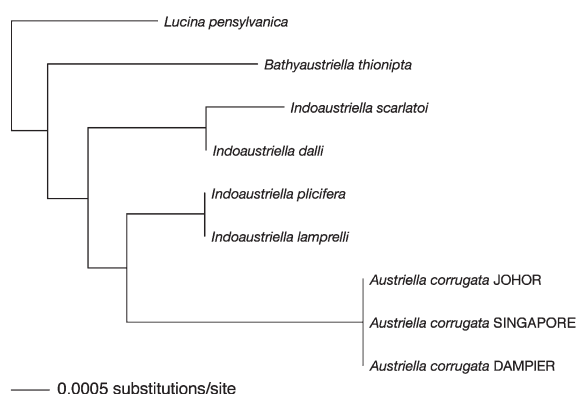
Other abbreviations. – H, shell height; L, shell length; LV, left valve; PI, protoconch I; PII, protoconch II; RV, right valve; T, tumidity of single valve.

MOLECULAR RESULTS

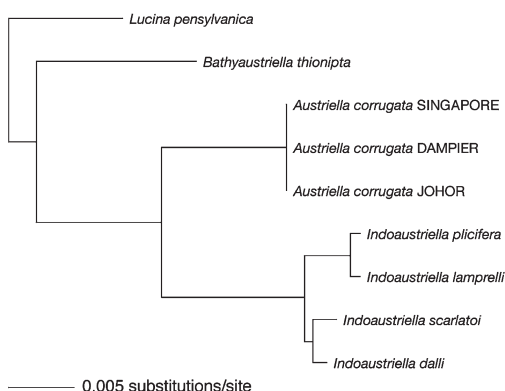
The results of the molecular analyses for species in the “*Austriella*” group are shown in Fig. 1. *Austriella corrugata* specimens from four localities cluster together with no differences for 18S or 28S genes and small differences for the *cytB* (0.3–1.4%, K2P; Kimura, 1980).

In the 28S and *cytB* trees (Fig. 1B–C), the other species (*Indoaustriella*) form a monophyletic group (but not in

A. 18S



B. 28S



C. cytochrome B

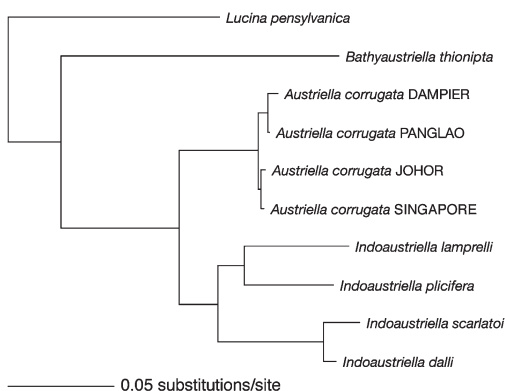


Fig. 1. Neighbour-joining trees for *Austriella* and *Indoaustriella* species based on sequence variation at A, 18S rRNA; B, 28S rRNA; and C, *cytB*. Note that each tree is drawn to a different scale.

the 18S tree) with two subclades comprising *I. plicifera*/*I. lamprelli* and *I. dalli*/*I. scarlatoi*. For the *Indoaustriella* species, *I. scarlatoi* and *I. dalli* differ by one base pair at 18S, whereas 18S sequences from *I. plicifera* and *I. lamprelli* are identical. Sequences from 28S from *I. plicifera* and *I. lamprelli* differ by 0.14% (3 bp) and *I. scarlatoi* and *I. dalli* by 0.27% (4 bp). For *cytB*, the species *I. plicifera* and *I. lamprelli* differ by 9.1% (30 bp) and *I. dalli* and *I. scarlatoi* by 2.3% (8 bp).

Although the species-level systematics below is largely based upon shell characters, the molecular results demonstrate that the toothless *Austriella corrugata* is distinct from the clade of four species possessing lateral hinge teeth. These are separated as a new genus *Indoaustriella*. Molecular results support the species-level distinctions between *I. plicifera* and *I. lamprelli* and between *I. dalli* and *I. scarlatoi*.

TAXONOMY

Lucinidae Fleming, 1828

Austriella Tenison-Woods, 1881

Austriella Tenison-Woods, 1881: 82. Type species: *A. sordida* Tenison-Woods, 1881 (= *Lucina corrugata* Deshayes, 1843). *Pseudolucina* Chavan, 1947: 180. Type species: *Lucina corrugata* Deshayes, 1843.

Eamesiella Chavan, 1951: 211 (new name for *Pseudolucina* Chavan, 1947, non *Pseudolucina* Wilckens, 1909).

Diagnosis. – Large, thick-shelled, subcircular to subtrigonal in outline; posterior dorsal area broad; sculpture of thin, low, commarginal lamellae, with broad interspaces. Ligament external, long, broad. Hinge teeth absent. Anterior adductor muscle scar narrow, detached from pallial line for about four-fifths of length. Inner shell margin smooth.

Remarks. – The genus has several names because Chavan (1947, 1951) was apparently unaware of *Austriella*, or uncertain of its characters, when introducing the name *Pseudolucina* (preoccupied) and subsequently, the replacement name *Eamesiella*. Later, Chavan (1969) placed *Austriella* in “Lucinidae genera dubia” as a possible edentulous unguinid.

Tenison-Woods (1881) mentioned an inconspicuous, arcuate cardinal tooth in the generic diagnosis, but we did not see any trace of cardinal teeth on the syntypes of *Austriella sordida* in AMS or other BMNH specimens from the same locality.

Austriella corrugata (Deshayes, 1843)

(Figs. 2, 3A, 4, 6A, 7A, B)

Lucina corrugata Deshayes, 1843: 1–2, Pl. 82.

Lucina philippinarum Reeve, 1850: Pl. 4, Figs. 18a–b.

Lucina philippinarum Hanley, 1856: 348, Pl. 12, fig. 42.

Austriella sordida Tenison-Woods, 1881: 83, Figs. 10–11.

Lucina (*Anodontia*) *philippinarum* (Hanley) – Martens, 1887: 174.

Pseudomiltha corrugata (Deshayes) – Lamy, 1920: 95.

Pseudomiltha (*Pseudolucina*) *corrugata* (Deshayes) – Chavan, 1947: 180.

Eamesiella corrugata (Deshayes) – Chavan, 1951: 211; Habe, 1981: 34, fig. 1; Sotto & Cosel, 1982: 57, Pl. 12, Figs. 1–2; Robba et al., 2002: 78, Pl. 7, Fig. 8.

Austriella corrugata (Deshayes) – Lamprell & Whitehead, 1992: Pl. 23 Fig. 145.

Type locality. – Although the original label of the *Lucina corrugata* syntypes reads “Philippines,” the locality is given erroneously in the publication as “Habite la mer de Californie.”

Material examined. – Type material: *Lucina corrugata*: 3 syntypes (MNHN), the Philippines; *L. philippinarum* Reeve: probable figured syntype (BMNH 1884.8.26.1); *L. philippinarum* Hanley: 3 syntypes (BMNH 1887.3.10.435–437), Kissaeraing Island, Mergui; *A. sordida*: 1 syntype (NMV F673); 4 syntypes (AMS C171071), Port Denison, Bowen, Queensland.

Other material: MYANMAR: Mergui (BMNH); THAILAND: Praphat Beach, Kampuan, Ranong (BMNH); MALAYSIA: Port Klang, Selangor (USNM); Tg-Adang, southwestern Johor (BMNH); Tuaran, Sabah (ZMA); SINGAPORE: Sungei Buloh (BMNH); INDONESIA: Surabaya (ZMA); Halmahera Island, Moluccas (USNM); Moluccas (ZMA); AUSTRALIA: Cape Condor, Melville Island, Northern Territory (AMS); Port Denison, Northern Territory (BMNH); East Point, Darwin, Northern Territory (BMNH); Camerons Beach, Shoal Bay, Northern Territory (MAGNT); Buccaneer Archipelago, Western Australia (AMS); Exmouth Gulf, Western Australia (WAM); King Bay and Cowrie Cove,

Burrup Peninsula, Dampier, Western Australia (BMNH); Horn Island, Torres Strait (AMS); Cooya Beach, Mossman, Queensland (AMS); Low Isles, Port Douglas, Queensland (AMS); Magnetic Island, Queensland (BMNH); Mackay, Queensland (AMS); Bowen, Queensland (AMS); Gladstone, Queensland (AMS); Eurimbula, Queensland (AMS); Hervey Bay, Queensland (AMS); PHILIPPINES: Bay of Manila (BMNH); Santa Cruz Harbor, Marinduque (USNM); Bais Bay, Negros (BMNH); Maasin, Leyte Island (BMNH); Zamboanga (BMNH); Cebu (AMS); Pangalao (MNHN); Bongao, Borigoo Island, Tawi Tawi (USNM); NEW BRITAIN (AMS); PAPUA NEW GUINEA: Nui Island, Madang (AMS); Kapa Kapa (AMS); Kiriwina Island, Trobriand Islands (AMS).

Description. – Shell large (H to 71 mm, L to 73 mm), thick-shelled, outline subcircular (H/L 0.95, range 0.90–0.98) to quadrate at anterior and posterior, ventral margin rounded, moderately inflated (T/L 0.23–0.29), umbonal area often deeply eroded. Sculpture of numerous prominent, low, irregular, concentric lamellae, occasionally intercalating, with faint radial striations between lamellae. Periostracum thick, olive-green to brown. Lunule broad, heart-shaped, not excavated, symmetrical. Dorsal areas demarcated by ridge running from umbo to bottom edge of posterior adductor muscle scar; anterior area demarcated by two low ridges extending to anterior shell margin. Hinge plate narrow; teeth absent; folds present on anteroventral edge of plate. Ligament external, long, broad, inset deeply into valves at posterior; nymph prominent, plate-like. Posterior termination of nymph

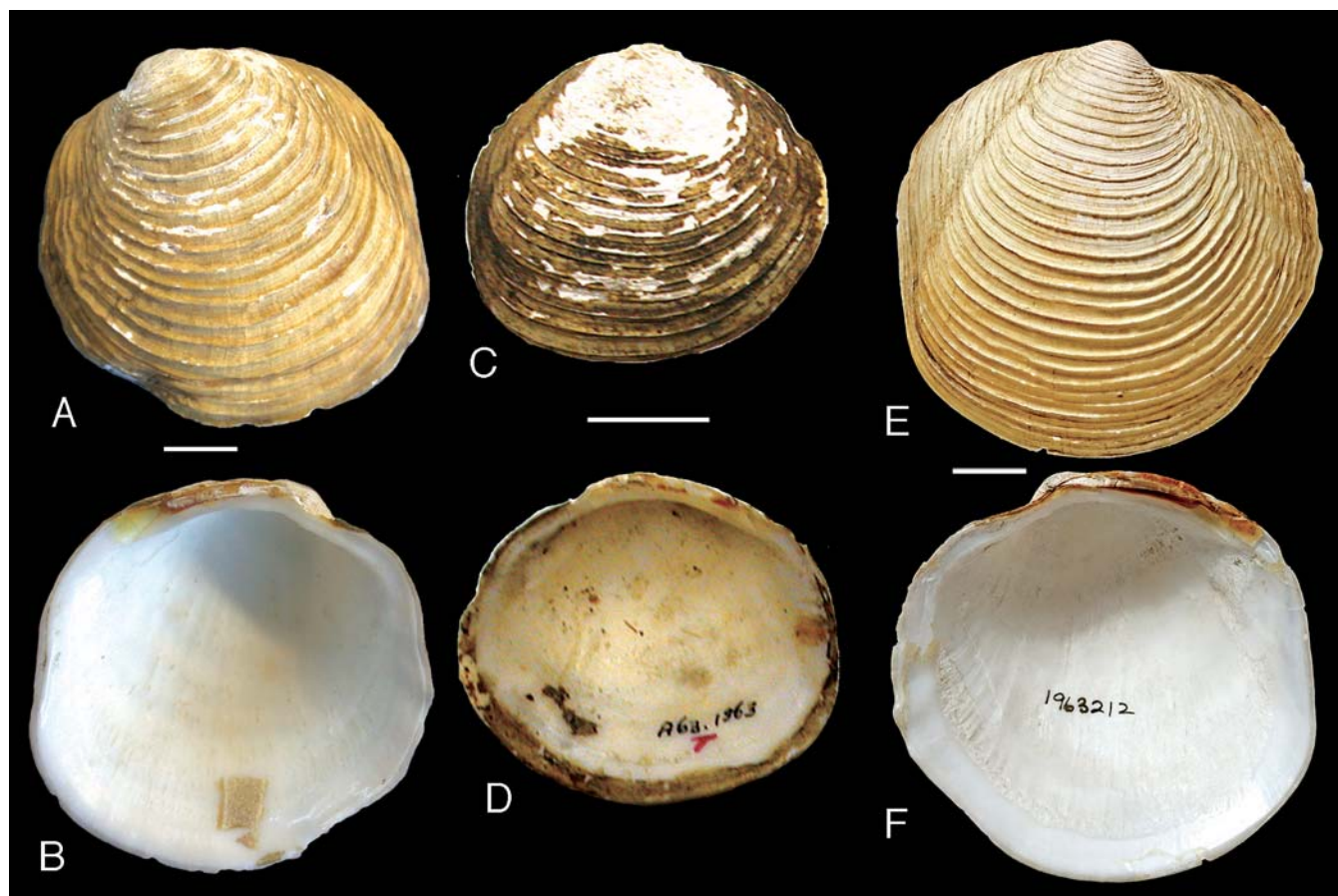


Fig. 2. *Austriella corrugata* (Deshayes, 1843). A–B, syntype of *Lucina corrugata*, the Philippines (MNHN), exterior and interior of LV; C–D, syntype of *Austriella sordida* Tenison-Woods, Port Denison, Bowen, Queensland (AMS C171071), exterior and interior of RV; E–F, *A. corrugata*, Singapore (BMNH 1963212), exterior and interior of RV. Scale bars = 2 mm.

pointed. Ventral margin thick, smooth, glossy. Adductor muscles (Fig. 3A): anterior scar narrow, relatively short, detached from pallial line for four-fifths of length, diverging at angle of about 35°; posterior adductor scar circular. Shell surface dull inside pallial line, with fine radial ridges near line. Shell dirty white, often chalky and heavily-eroded; inner shell margin white, interior cream-coloured.

Anatomy. – Major features of the anatomy, including the symbiotic bacteria, were summarized by Glover et al. (2004: 285, 289, fig. 10).

Distribution. – Central Indo-West Pacific (Fig. 4), western Thailand to New Britain, northern Australia, Vietnam (Lutaenko, 2000), Taiwan (Wu, 1980) and Iriomote Island, Ryukyu Islands (Habe, 1981).

Habitat. – Intertidal, deep burrower in mud amongst mangrove pneumatophores and prop roots.

Remarks. – Compared to species of *Indoaustriella* (below), no hinge teeth are present in *Austriella corrugata*, even in juveniles (smallest seen L 9.7 mm). Reeve's (1850) description of *Lucina philippinarum* predated that of Hanley

(1856) who is frequently taken to be the author of this species. Furthermore, there is often confusion in museum collections between *L. philippinarum* Reeve, 1850, previously the most widely used name for *Austriella corrugata*, and *L. philippiana* Reeve, 1850 (now classified as *Anodontia (Pegophysema) philippiana*, see Taylor & Glover, 2005). This confusion is exacerbated by the lack of hinge teeth in both genera and the association with mangrove habitat.

Indoaustriella, new genus

(Fig. 5)

Type species. – *Lucina (Cryptodon) plicifera* A. Adams, 1855.

Diagnosis. – Shell small, posterior dorsal area broad, with radial ridges at anterior dorsal area; sculpture of thin, closely-spaced commarginal lamellae; ligament long, shallow, external; hinge without cardinal teeth, anterior and posterior lateral teeth present or anterior lateral only; anterior adductor muscle detached for half to two-thirds of length.

Etymology. – “Indo-”, alluding to Southeast Asia, and resemblance to *Austriella*. Gender feminine.

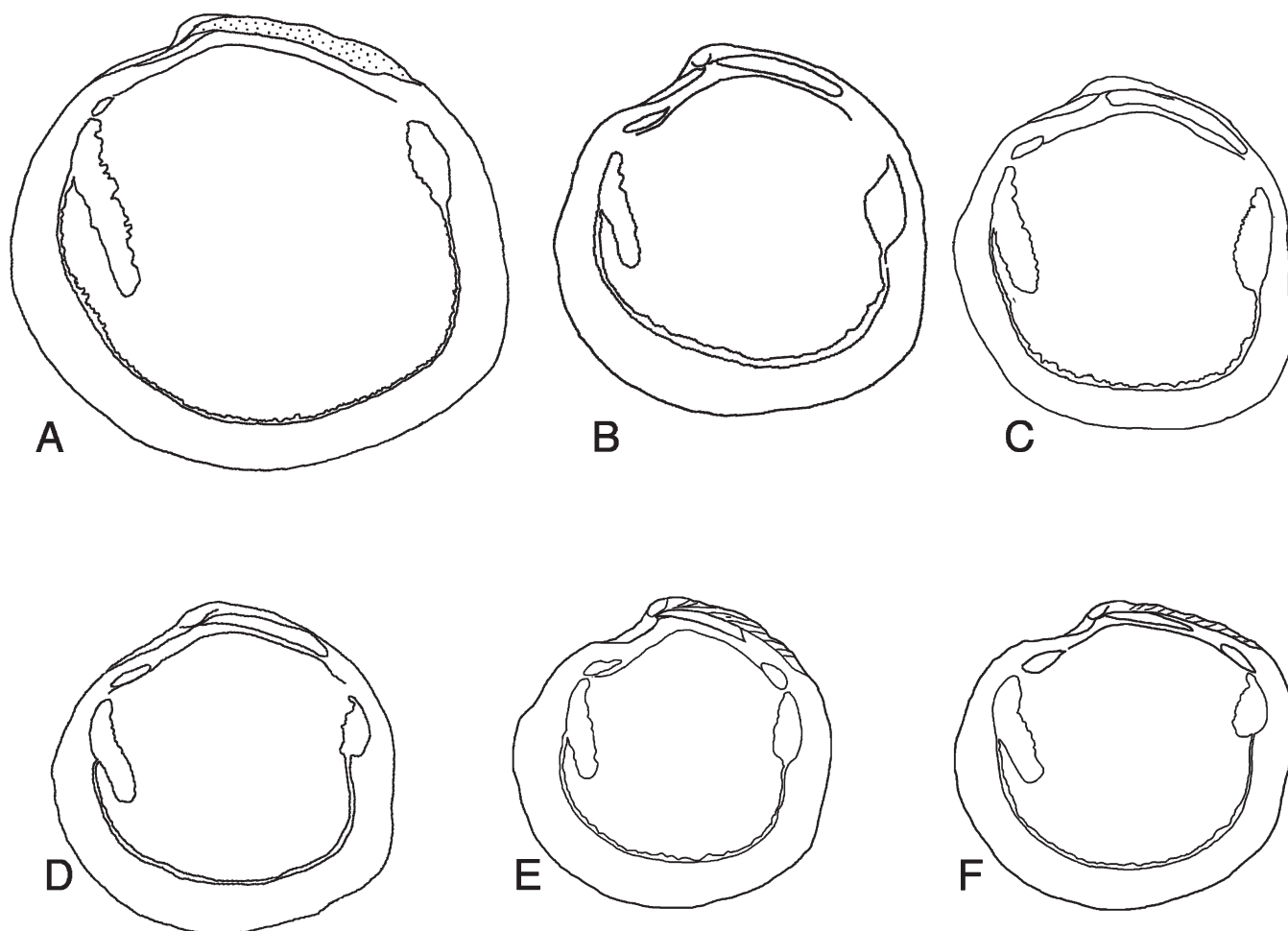


Fig. 3. Drawings of interiors of shells (not to scale): A, *Austriella corrugata*; B, *Indoaustriella plicifera* (syntype); C, *Indoaustriella plicifera* (Malaysia); D, *I. lamprelli*; E, *I. dalli*; F, *I. scarlatoi*.

Remarks. – Although superficially resembling small *Austriella corrugata*, the type species and other species assigned to this genus differ in possessing either only anterior or both anterior and posterior lateral hinge teeth.

Molecular evidence for 28s rRNA and cytB genes (Fig. 1) shows that all of the species with hinge teeth (*Indoaustriella plicifera*, *I. lamprelli*, *I. dalli*, *I. scarlatoi*) group in a clade separate from the edentulous *Austriella corrugata*.

A feature of *Indoaustriella* species is the extensive posterior mantle fusion ventral to the posterior apertures (Fig. 6). The mantle fusion index (see Taylor & Glover, 2002) ranges between 0.81 and 0.82, standing as the highest degree of mantle fusion recorded within the Lucinidae; other relatively highly fused species include *Austriella corrugata* (0.67), *Bathyaustriella thionipta* (0.60) (Glover et al., 2004), *Phacoides pectinatus* (0.76) and *Anodontia* spp. (0.67–0.69) (Taylor & Glover, 2005). These contrast with other lucinids such as *Codakia* (0.2) and *Lamellolucina* (0.4) (Taylor & Glover, 2002) where mantle fusion is slight. Most species with extensive fusion are deeply burrowing in suboxic environments such as mangrove sediments or black muds. Species with shorter mantle fusion tend to inhabit better oxygenated habitats. No papillae occur around the inhalant or exhalant apertures of *Austriella* or *Indoaustriella* spp. but, in contrast, are present around inhalant aperture of

Bathyaustriella thionipta (see Glover et al., 2004: Figs. 6E–F) and in many other lucinids (Taylor & Glover, 2006). *Bathyaustriella* lives shallowly burrowed in sediments around hydrothermal vents and the papillae might help to keep the inhalant aperture free of sediment particles.

Another remarkable feature of *Indoaustriella* species (not confirmed in *I. scarlatoi*) is the presence of densely-packed, large, spherical (8–9 µm diameter) granules throughout the abfrontal bacteriocyte zone of the gill filaments (Fig. 7C–F). Similar granules have been recorded from a few other lucinids, including *Codakia*, *Ctena*, and *Lucinoma* (Frenkiel & Mouëza, 1995; Oliver & Holmes, 2006; Taylor & Glover, 2006; Meyer et al., 2008, this volume) and although their function is uncertain, they are known to be cystine-rich. Like all studied lucinids, *Indoaustriella* species possess symbiotic bacteria, held in bacteriocytes. These generally are rod-shaped and 4–8 µm long (Fig. 7C–F).

Included species: *Indoaustriella plicifera* (A. Adams, 1855), *I. dalli* (Lyngø, 1909), *I. lamprelli* new species, *I. scarlatoi* (Zorina, 1978).

***Indoaustriella plicifera* (A. Adams, 1855)**
(Figs. 3B, 5, 6B, 7D)

Lucina (*Cryptodon*) *plicifera* A. Adams, 1855: 225.

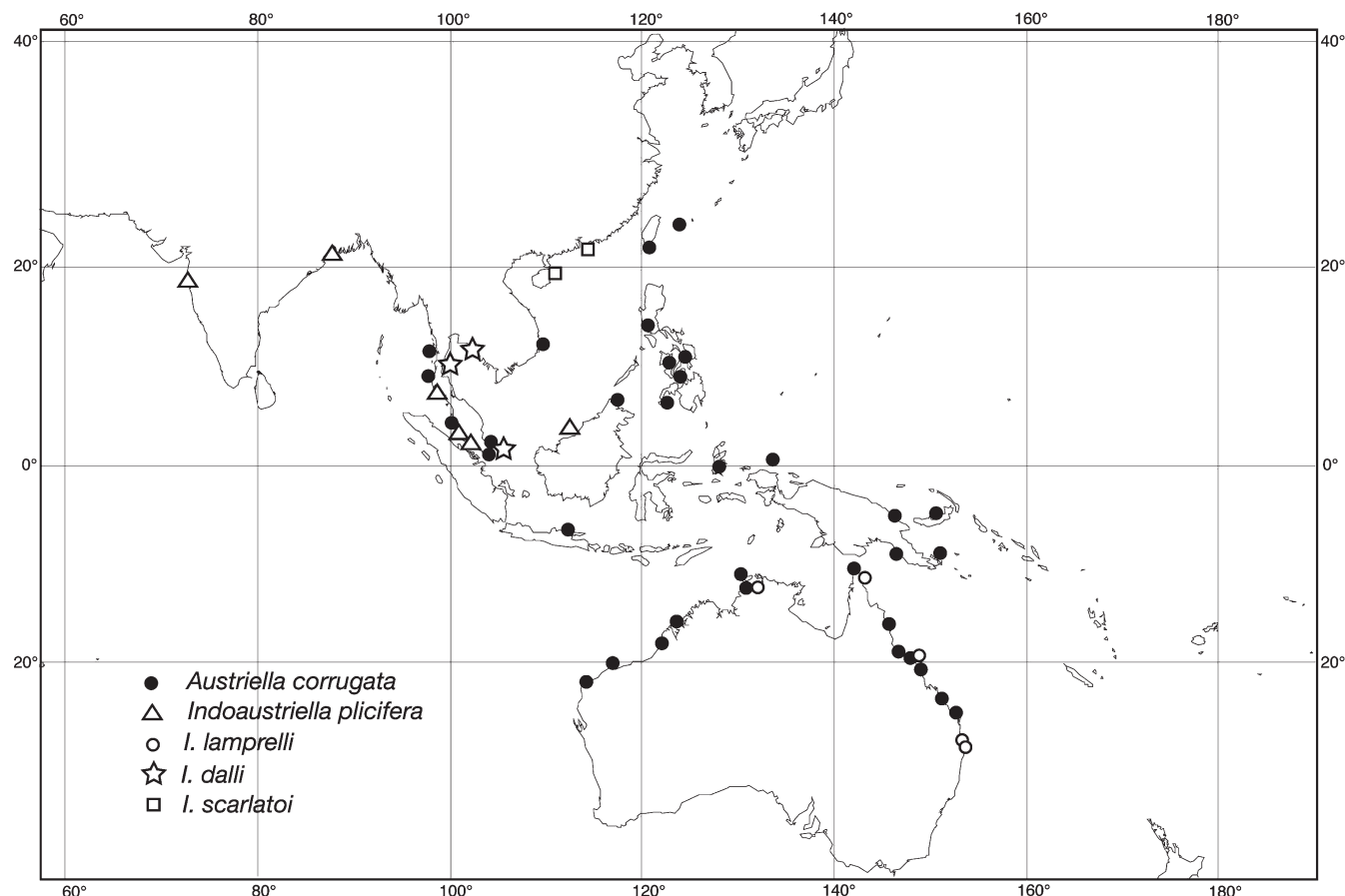


Fig. 4. Map showing distribution of *Austriella corrugata* and *Indoaustriella* species.

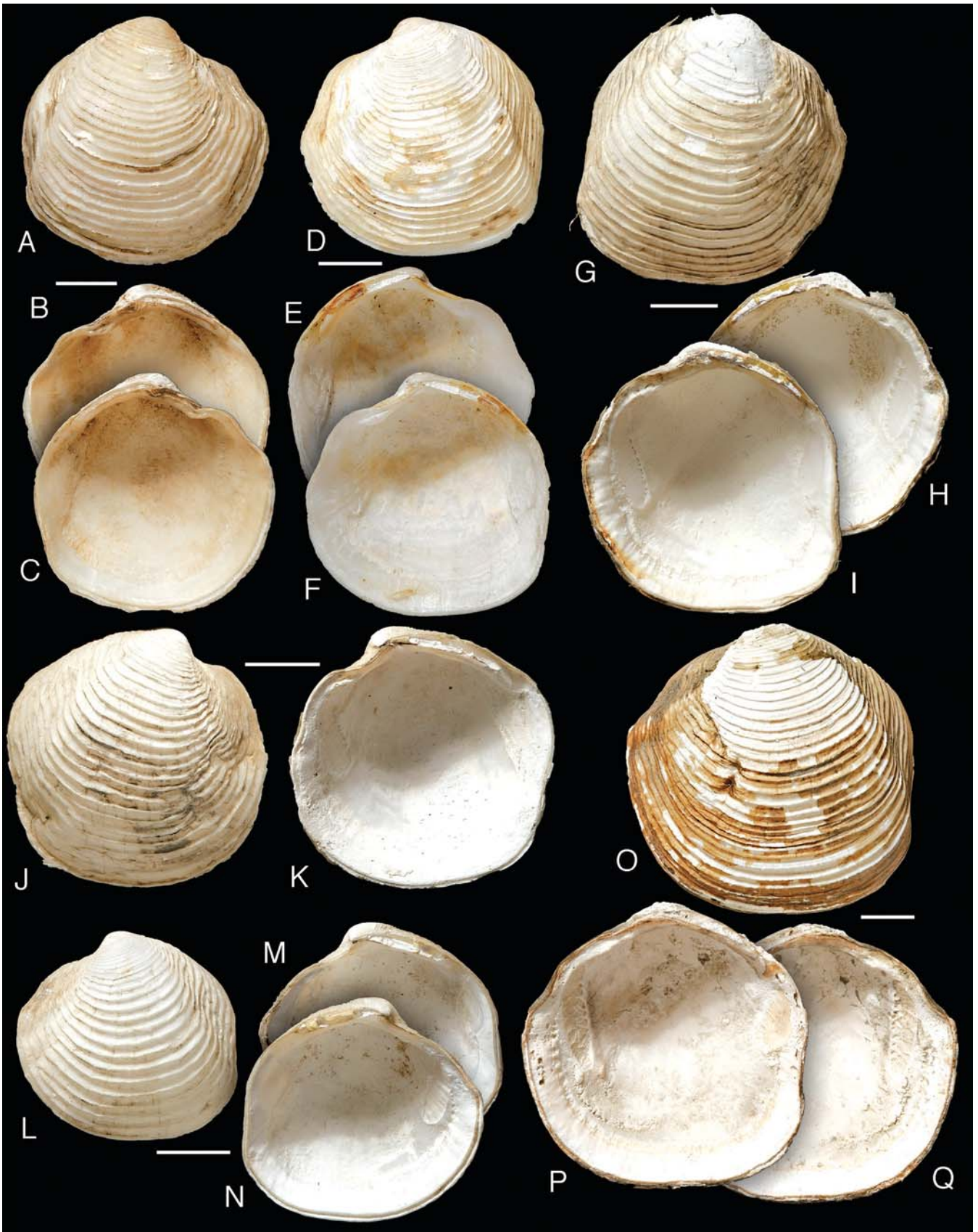


Fig. 5. *Indoaustriella plicifera* (A. Adams, 1855): A–F, Exterior and interior of two syntypes, Borneo (BMNH 1963558); G–N, exterior and interiors of three shells from Tanjong Laboh, south of Batu Pahat, Johore, Malaysia (BMNH); O–Q, exterior of LV and interiors of both valves, Mutlah River, Port Canning, India (BMNH). Scale bars = 5 mm.

Material examined. – Type material: 3 syntypes (3 pairs: H 20.4 mm, L 20.6 mm; H 18.7 mm, L 18.6 mm; H 20.8 mm, L 21.1 mm) (BMNH 1963558), H. Cuming Collection.

Other material: INDIA: Kon Kan, Mumbai (BMNH, NMGW); Port Canning, Bengal (BMNH); Port Canning (BMNH); THAILAND: Ban Sapam, Phuket (BMNH); Had Nop Parat Thara, 08°02.44'N 98°48.17'E, eastern Krabi Province (ZMA); MALAYSIA: mangrove mud, Kamung Lua Linggi, Strait of Malacca (BMNH); mangrove mud, Tanjung Laboh, S of Batu Prahat, Johore (BMNH).

Type locality. – Borneo.

Description. – Small to medium-sized (H to 29 mm, L to 28 mm), moderately inflated (T/L 0.28–0.34). Subtrigonal in shape (H/L 0.98, range 0.91–1.03); umbones prominent, often eroded; posterior lateral margin truncate; anterior margin sinuously rounded. Periostracum straw-coloured. Anterior dorsal area with two shallow sulci and low radial ridges. Posterior dorsal area broad, conspicuous. Sculpture of regularly spaced, thin, commarginal lamellae with radial striations in interspaces; shells often with crumpled appearance. Lunule inconspicuous, short, lanceolate. Ligament relatively long, set in shallow groove. Posterior termination of nymph bluntly rounded. Hinge: RV with

single anterior lateral tooth, no cardinal or posterior lateral teeth; LV with two small anterior laterals (Fig. 5B–C), no cardinal or posterior laterals. Anterior adductor scar elongate, ventrally detached from pallial line for about two-thirds of length, diverging at angle of about 25°. Posterior scar ovoid/reniform. Pallial line entire. Ventral shell margin smooth. Shells often thickened and considerably eroded in umbonal area so that features are poorly preserved.

Distribution. – Mumbai, India, to Southeast Asia (Fig. 4).

Habitat. – Intertidal mud, amongst mangrove prop roots.

Remarks. – Strangely, this name appears to have been unused, except for a brief mention by Smith (1885: 191) and Lamy (1920: 119), since the original description in 1855 and the syntypes are illustrated here for the first time. We have seen the name “*Lucina induta* Stoliczka” attached to museum specimens of this species (see also Lamy, 1920: 97), but we have been unable to trace any original publication. *Indoaustriella plicifera* is probably widespread in Southeast Asia, although often identified as juveniles of *Austriella corrugata*, from which it can be easily distinguished by the presence of anterior lateral teeth. Specimens from India

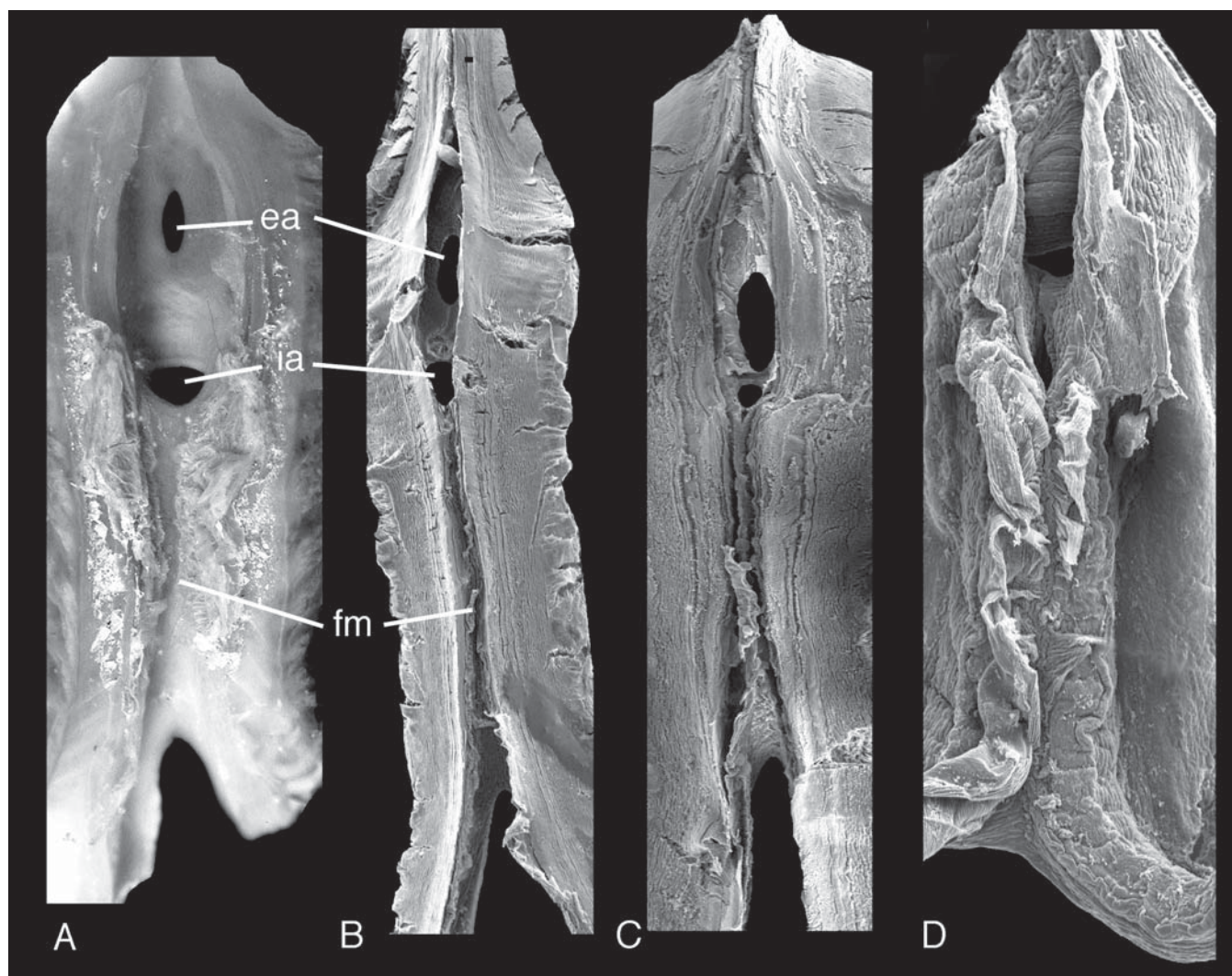


Fig. 6. SEM images of posterior apertures of *Austriella* and *Indoaustriella*: A, *Austriella corrugata*, B, *Indoaustriella plicifera*, C, *I. lamprelli*, D, *I. dalli* (not to scale). ea, exhalant aperture; ia, inhalant aperture; fm, ventral fusion of mantle.

(BMNH) are larger (H 25–28 mm) compared with Malaysian samples (H 18–20 mm) and the syntypes from Borneo (H 18–21 mm) and, with study of more material, might be recognized as a separate species.

IndoaustrIELla lamprelli, new species

(Figs. 3C, 6C, 7E, F, 8)

Type material. – Holotype (H 12.9 mm, L 12.6 mm, T 3.8 mm) (QM-MO78588), mangrove mud, Luggage Point (27°23'N 153°10'E),

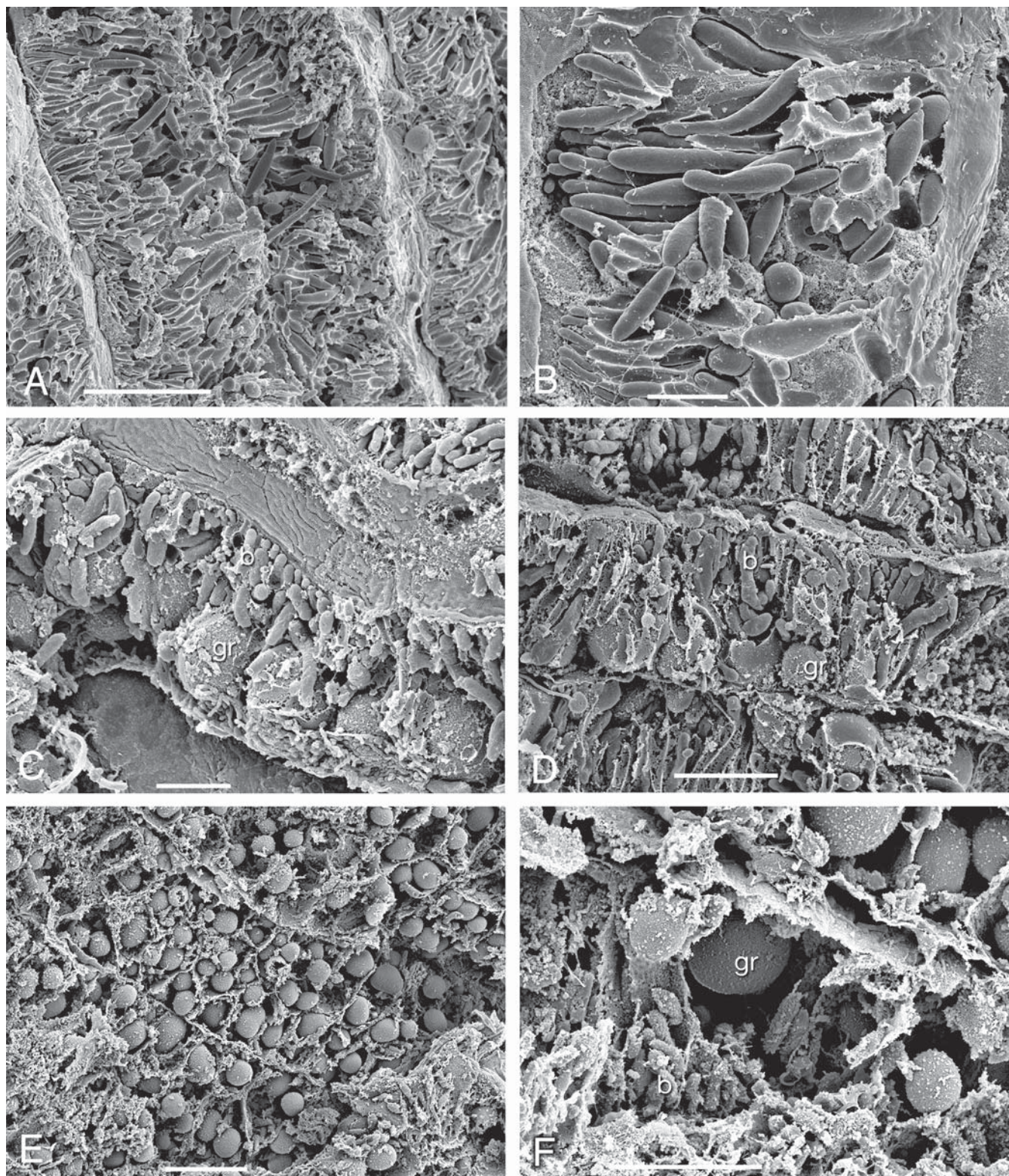


Fig. 7. Sections of gill filaments of *Austriella* and *IndoaustrIELla* showing bacterial symbionts and granules: A, Gill filament of *A. corrugata* showing rod-shaped bacteria; B, *A. corrugata*, detail of bacteriocyte with bacteria; C, *IndoaustrIELla dalli*, section of gill filament with bacteria and large spherical granules; D, *I. plicifera*, section through gill filament with bacteria and large granules; E, *I. lamprelli*, section through gill filaments with abundant spherical granules; F, *I. lamprelli*, bacteriocyte with rod-shaped bacteria and granule (cell contents not well fixed in 100% ethanol). Scale bars = A, E, 20 µm; B, C, 5 µm; D, F, 10 µm. b, bacteria; gr, granules.

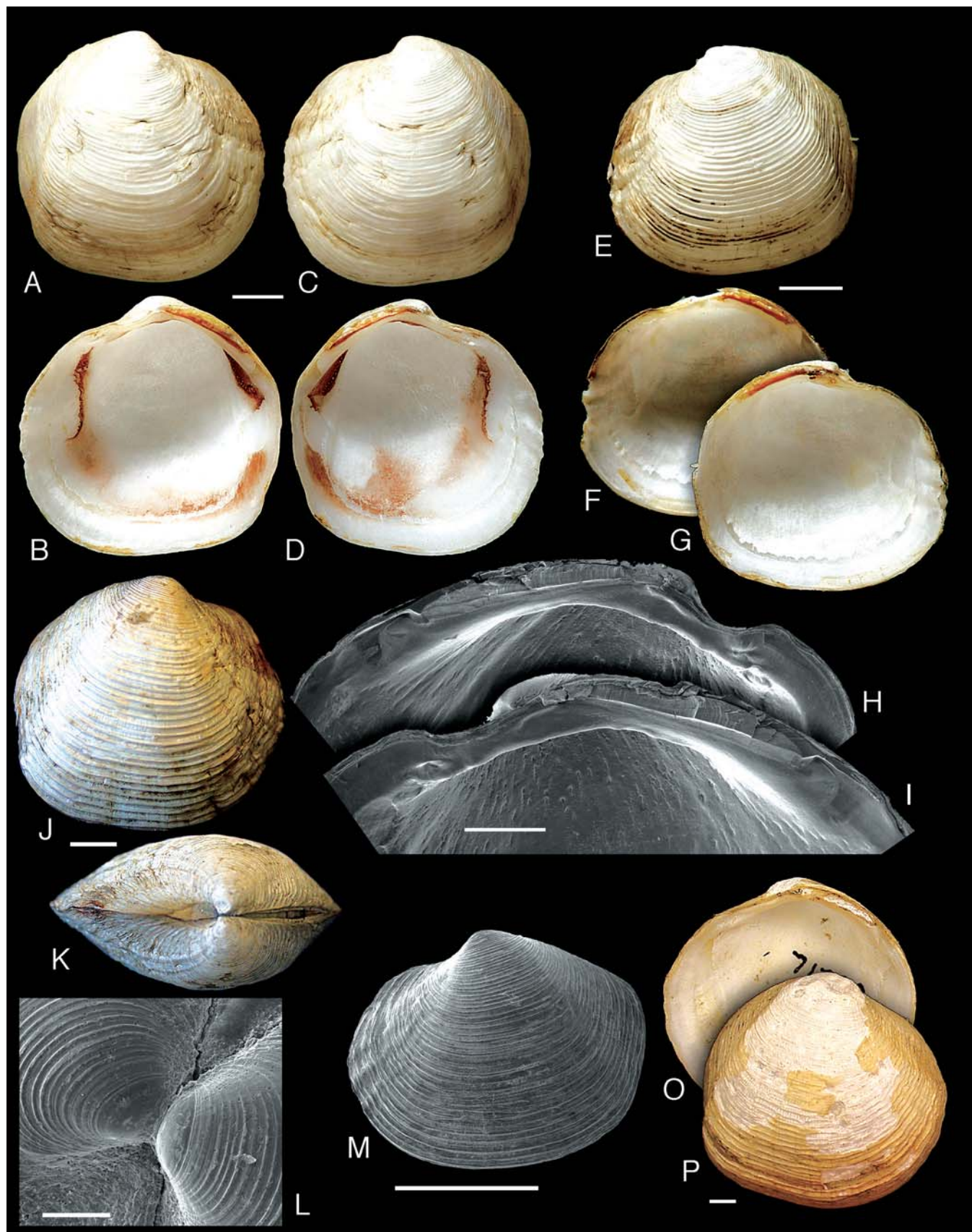


Fig. 8. *Indoaustriella lamprelli*, new species: A–D, Holotype, Luggage Point, Brisbane River, Moreton Bay, Queensland (QM-MO78588); E–G, paratype exterior of LV and interior of both valves, same locality as A–D (BMNH 20070303); H–I, paratype, details of hinge (SEM) of LV (H) and RV (I), same locality as A–D (BMNH 20070303); J–K, paratype, exterior of RV and dorsal view, Deception Bay, Queensland (MAGNT P035719); L, umbo and protoconch (MAGNT P035719); M, juvenile shell (MAGNT P035719); O–P, paratype, exterior of RV and interior of LV from North Stradbroke Island, Moreton Bay, Queensland (AMS C71792). Scale bars = 2 mm, except H–I, 1 mm and L, 100 μ m.

off mouth of Brisbane River, Moreton Bay, Queensland, Australia. Paratypes: 2 whole shells (H 9.8 mm, L 10.4 mm, T 3.2 mm; H 7.6 mm, L 8.1 mm, T 2.4 mm; Fig. 4E–G) (BMNH 20070303), same locality as holotype; 10 whole shells (in alcohol) (BMNH 20070304), same locality as holotype; 100 live-collected specimens (MAGNT P035719), mud in seagrass, outside Queensland State Fisheries Laboratory, Deception Bay, Moreton Bay, Queensland, 27°2'S 153°3'E; 4 shells (AMS C71792), mud in mangroves, between Dunwich and Myorah, North Stradbroke Island, Moreton Bay, Queensland.

Other material: AUSTRALIA: Redland, Moreton Bay, Queensland, intertidal seagrass (BMNH); Hinchinbroke Channel, Moreton Bay, Queensland (BMNH); Woody Point, Clontarf, Moreton Bay, Queensland (AMS); Cockle Bay, Magnetic Island, Queensland (BMNH); Noosa River, Queensland (AMS C61559); Cape York, Queensland (AMS C15750); mangroves, East Point, Darwin, Northern Territory (BMNH, MAGNT).

Etymology. – Named for the late Kevin Lamprell in recognition of his contribution to the systematics of Australian bivalves.

Description. – Small (H to 19 mm, L to 20 mm), thin-shelled, subtrigonal (H/L 0.94, range 0.91–0.99), inflated (T/L 0.30, range 0.24–0.33); posterior margin truncate; anterior margin rounded. Umbones and shell often highly eroded. Periostracum light brown, relatively thick. Posterior dorsal area slightly demarcated; anterior dorsal area with two radial ridges divided by shallow sulcus. Protoconch 150 µm long; PI large, PII narrow. Sculpture of fine, low, commarginal lamellae, somewhat irregularly spaced, occasionally anastomosing. Lunule lanceolate, asymmetrical, with greater part in RV. Hinge: RV with anterior lateral tooth, no cardinal teeth, posterior lateral absent; LV with small anterior lateral tooth. Ligament curving, slightly inset; posterior termination of nymph bluntly rounded. Anterior adductor muscle scar detached for about half of length, diverging from pallial line at angle of around 20°; posterior adductor scar oval. Pallial line entire but with irregular dorsal extensions. Inner shell margin smooth. Colour grey-white.

Distribution. – Queensland to Northern Territory, Australia (Fig. 4) with most records from the Moreton Bay area.

Remarks. – *Indoaustriella lamprelli* is most similar in size and shape to *I. plicifera* from Southeast Asia, but the latter is much more coarsely ribbed (Fig. 5). Molecular sequences from cytB gene (Fig. 1C) for the two species (*I. plicifera* from Malaysia) differ by 9.1% K2P.

Although most records of *Indoaustriella lamprelli* are from Moreton Bay in southern Queensland, we have four shells from Darwin and a few scattered records from elsewhere in Queensland suggesting that the species is widely distributed in northern Australia.

***Indoaustriella dalli* (Lynge, 1909)**

(Figs. 3D, 6D, 7C, 9)

Lucina (*Phacoides*) *dalli* Lynge, 1909: 75–76, Pl. 3 Figs. 9–12.
“*Lucina*” sp. – Swennen et al., 2001: 77, Fig. 084.

Material examined. – Type material: Syntypes, 12 whole shells and 26 single valves (ZMC BIV-449). Syntypes, 7 whole shells and 5 single valves (H of complete shells 7.5, 6.7, 5.0, 4.9, 4.8, 4.7, 4.1, 3.5, 2.9 mm) (NMGW 1955.158.02031), coll. T. Mortensen, identified by H. Lynge.

Other material: SINGAPORE: Sungei Buloh Reserve, mangrove mud (BMNH); THAILAND: Kungkrabaen Bay, Chantaburi Province, intertidal mud flats (BMNH); Pattani, Etang near Marnat, C. Swennen coll. sta. 9710.1997.04.00 (BMNH donated by ZMA).

Type locality. – “The strand off the mangrove at Koh Chang”, Gulf of Thailand.

Description. – Shells small (H to 9.2 mm, L to 9.1 mm), moderately inflated (T/L 0.28–0.32), subcircular; umbones prominent; anterior margin rounded, slightly sinuate; posterior lateral margin quadrate; ventral margin rounded. Protoconch 130 µm long. Periostracum straw-coloured. Sculpture of low but sharp, regularly spaced, commarginal lamellae. Interspaces with growth increments only, with occasional discontinuous radial threads crossing the lamellae. Anterior part of shell with ill-defined, low ridges; posterior dorsal area marked by shallow sulcus, with commarginal lamellae slightly more elevated along dorsal margin. Lunule heart-shaped, slightly impressed, slightly asymmetrical, with larger part in RV. Hinge: RV with prominent, short anterior lateral tooth, no cardinals, and posterior lateral ridge; LV with prominent anterior lateral socket, no cardinal tooth, and posterior groove for lateral tooth. Ligament inset, straight, short. Anterior adductor scar elongate, detached from pallial line for about half of length, diverging at angle of ca. 20°; posterior scar ovoid to comma-shaped, pallial line entire. Shell interior glossy; shell margin smooth. Within pallial line, low radial grooves and dots of mantle attachment. Pallial blood vessel scar visible. Shell exterior light-brown; interior yellow.

Habitat. – Abundant in intertidal, muddy sand near mangroves (see Meyer et al., 2008, this volume).

Distribution. – Southeast Asia; Singapore to eastern Thailand (Fig. 4).

Remarks. – It is surprising that this abundant species has never been recognised or its name used in recent literature from Southeast Asia. The closely similar species from Hong Kong has been described as *Phacoides scarlatoi* Zorina (see below) where it is common in intertidal, muddy sand near mangroves.

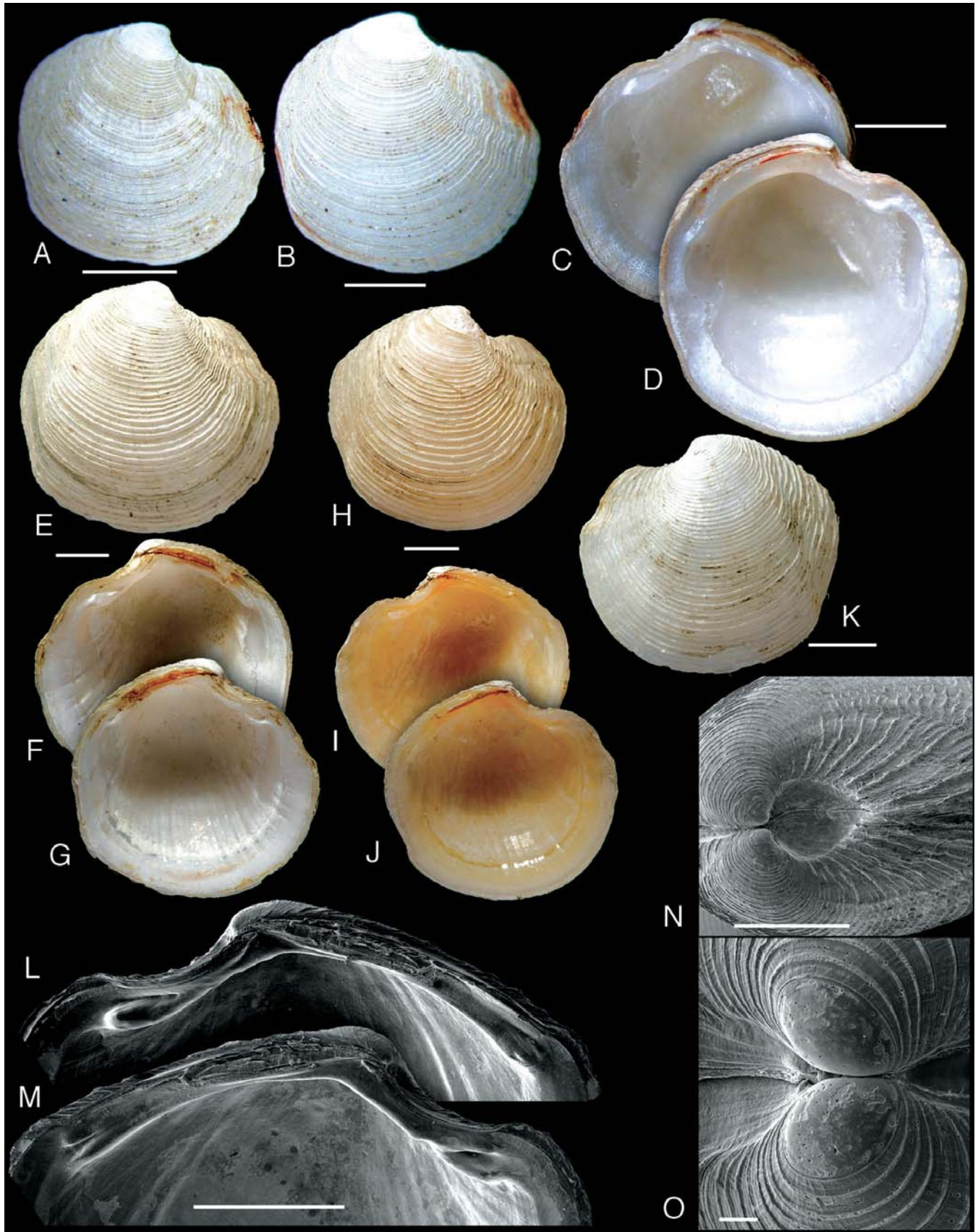


Fig. 9. *Indoaustraliella dalli* (Lyngé, 1909): A–D, Syntypes *Lucina dalli* (NMGW); A–B, exterior of RVs; C–D, interior of both valves of syntype B; E–O, shells from Kungkrabaen Bay, Thailand (BMNH); E–G, exterior RV and interiors of both valves; H–J, exterior of RV and interiors of both valves; K, exterior of left valve; L–M, detail (SEM) of hinge; N, umbonal area showing heart-shaped lunule; O, protoconchs. Scale bars = A–M, 2 mm; N, 1 mm; O, 50 μ m.

Indoaustriella scarlatoi (Zorina, 1978)
(Figs. 3E, 10)

Phacoides scarlatoi Zorina, 1978: 193–194, Figs. 1–2; Lutaenko, 2000: Pl. 1, figs. 4–5, Pl. 3, fig. 3.
Lucina scarlatoi Zorina. – Bernard et al., 1993: 58.

Type locality. – Southern coast of Hainan Island, China Sea, intertidal muddy sand in mangroves.

Material examined. – Type material: Syntypes (H 6.9 mm, L 7.3 mm; see illustration of one syntype by Lutaenko, 2000) (ZISP Cat. No. 2).

Other material: CHINA: Tai Tam Bay, Hong Kong (BMNH); Daya Bay, Guangdong Province (BMNH).

Description. – In most characters this species is similar to *Indoaustriella dalli*, but it has a relatively longer ligament, a curved hinge line and escutcheon, and a shallower lunule.

Distribution. – Southern China (Fig. 4).

Remarks. – *Indoaustriella dalli* and *I. scarlatoi* are closely similar in shell form; Zorina (1978) distinguished *I. scarlatoi* from *I. dalli* on the basis of the length to height ratio, but

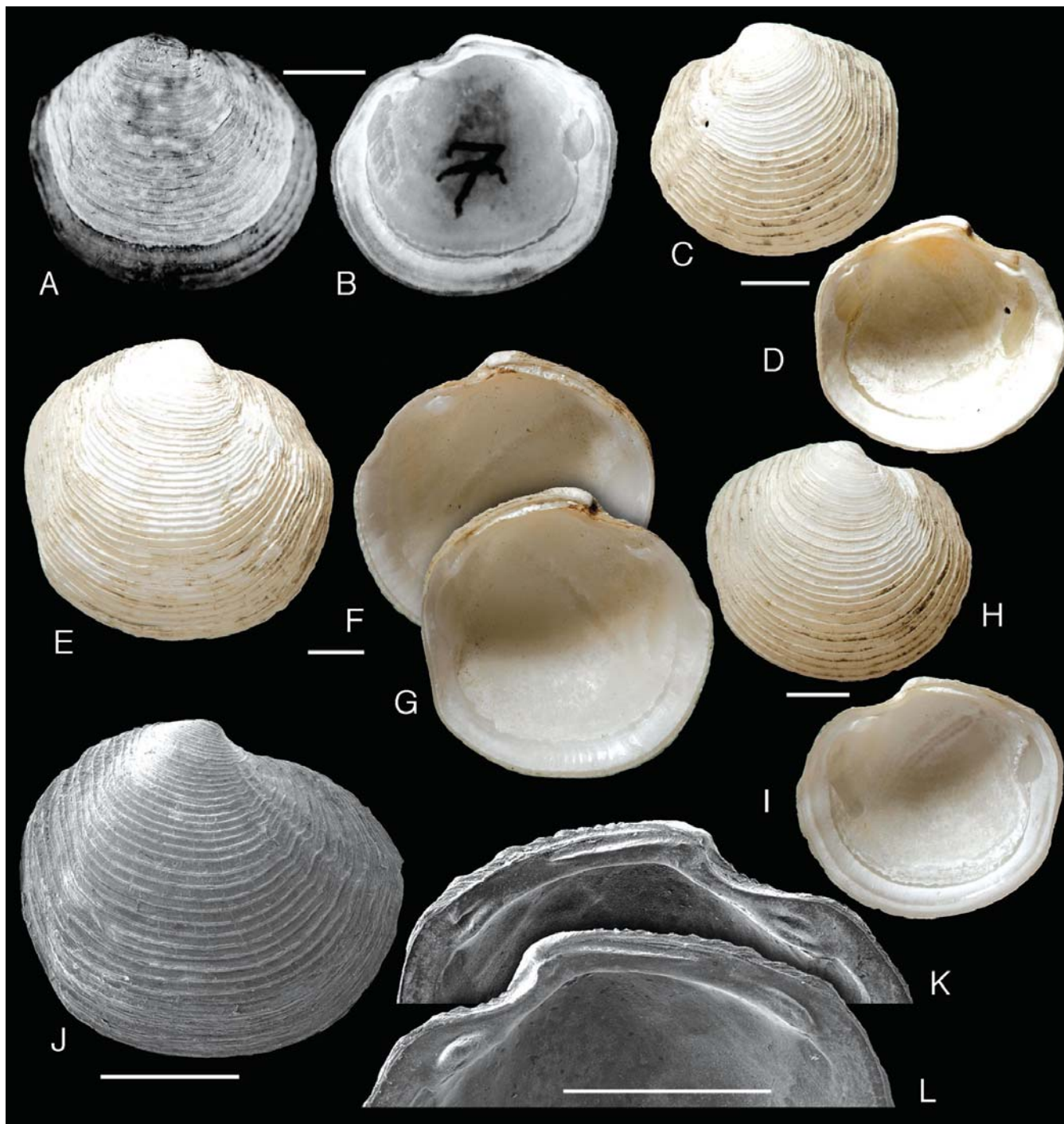


Fig. 10. *Indoaustriella scarlatoi* (Zorina, 1978): A–B, Syntype (ZISP), Hainan, South China Sea, exterior of RV and interior of LV; C–L, Tai Tam Bay, Hong Kong (BMNH), C–D, exterior of LV and interior of RV; E–G, exterior RV and interior of both valves; H–I, exterior and interior of right valve; J, exterior of juvenile shell; K–L, detail (SEM) of hinge. Scale bars = 2 mm.

using a larger sample of both species, we found no significant difference. Molecular sequences of three genes, however, show some differences (Fig. 1) in 18S rRNA (1 bp), 28S rRNA (4 bp) and cytochrome B (8 bp), which indicate a likely species-level separation.

Indoaustriella species A

(Fig. 11)

Material examined. – 1 whole shell (BMNH 20070305), Auki, Malaita, Solomon Islands, from saltmarsh, coll. Royal Society BSIP, 1965.

Brief description. – Shell small (H 12.8 mm, L 13.6 mm, T 3.6 mm), with fine concentric sculpture; hinge with small anterior tooth, no cardinal teeth; anterior dorsal area marked by three narrow sulci.

Remarks. – We have only a single specimen of this species that differs from *Indoaustriella lamprelli* in having finer, sharp commarginal lamellae.

DISCUSSION

Although lucinid bivalves are often associated with organic rich and dysaerobic habitats, relatively few species are known to be closely associated with mangroves. The large *Austriella corrugata* (also known as *Eamesiella corrugata*) is one of the few, large lucinids that are common in mangrove and peri-mangrove habitats of the central Indo-West Pacific. This species is commercially fished in the Philippines but, remarkably, there have been no studies of its biology or ecology. The *Indoaustriella* species have been either hardly mentioned since their original descriptions or remain undescribed and furthermore, are very poorly represented in museum collections. Nevertheless, *I. plicifera*, *I. dalli*, and *I. lamprelli* are often locally abundant in and near mangroves in Malaysia, Thailand and northeastern Australia.

The bivalves described here are another example where diversity of shallow-water Lucinidae has been underestimated

because species have been loosely lumped together without critical assessment (Taylor & Glover, 2002, 2005). Our morphological and molecular evidence demonstrates that the smaller species with lateral teeth, now classified as *Indoaustriella*, are not juveniles of *Austriella corrugata* that lose their teeth when they become adults, but form a distinct, separate clade. This is reminiscent of the eastern Pacific lucinid, *Neophysema aphanes* (Taylor & Glover, 2005), until recently regarded as juveniles with cardinal teeth of the larger, edentulous *Anodontia edentuloides* (Verrill, 1870) but separated as distinct taxa by Taylor & Glover (2005).

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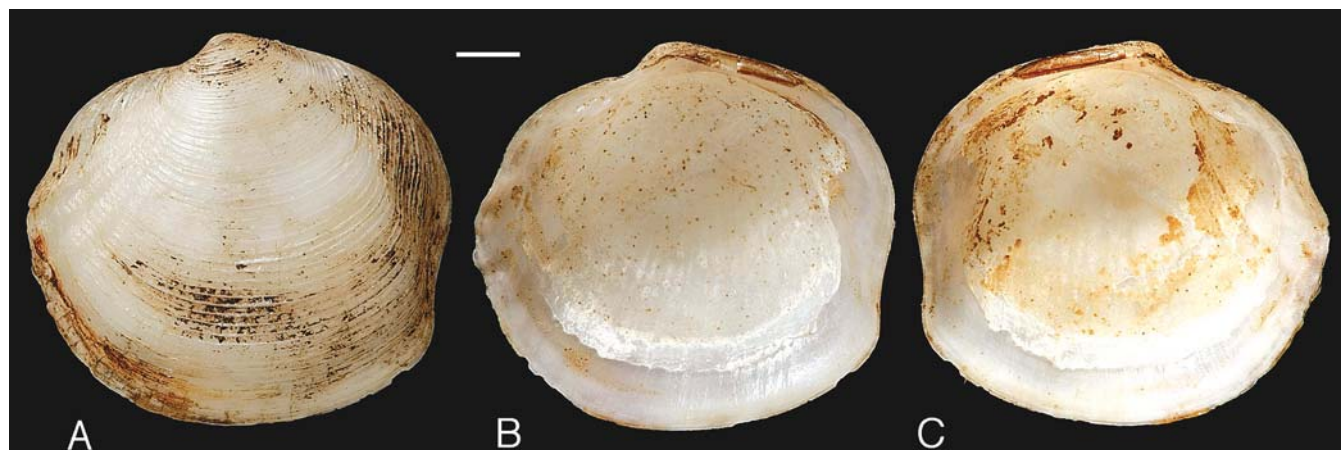


Fig. 11. *Indoaustriella* species A: A–C, Auki, Malaita, Solomon Islands (BMNH 20070305), exterior of LV and interiors of both valves. Scale bar = 2 mm.

(BMNH), and Konstantin Lutaenko (Institute of Marine Biology, Vladivostok) for macrophotography. Lisa Smith and Pat Dyal (BMNH) carried out some molecular sequencing. Additional funding for this work was provided by the BMNH Zoological Research Fund and NERC Small Grant NER/B/S/2003/00759. We are grateful for continuing support from The Natural History Museum, London.

THAI ABSTRACT

หอยสองฝาเคมีซิมไบโอติก (chemosymbiotic) ในวงศ์ลูซิเนียดีซึ่ชื่อ *Austriella corrugata* (Deshayes, 1843) มีการแพร่กระจายทั่วภูมิภาคเอเชียตะวันออกเฉียงใต้ โดยอาศัยอยู่ในโคลนตมระหว่างคันไม้ในป่าชายเลน ถึงแม้ว่าหอยสองฝาชนิดนี้จะมีผู้ทำการศึกษาค้นคว้าและวิจัยไว้บ้างพอสมควรแต่งานวิจัยฉบับนี้กล่าวถึงรายละเอียดเกี่ยวกับหอยสองฝาชนิดที่มีความสัมพันธ์ใกล้ชิดกันทางอนุกรมวิธาน แต่มีรายละเอียดรายงานไว้น้อย ซึ่งอาศัยอยู่ในสิ่งแวดล้อมเดียวกันคือภายในและบริเวณโดยรอบพื้นที่ป่าชายเลน ผู้วิจัยขอนำเสนอชื่อสกุลใหม่ (*Indoaustriella*) เพื่อใช้เรียกชื่อหอยสองฝาที่มีลักษณะภายนอกคล้าย *Austriella* แต่มีขนาดเล็กกว่า และมีฟันบานพับเปลือกชนิด lateral teeth โดยให้รายละเอียดเกี่ยวกับหอยสองฝา *Indoaustriella plicifera* (A. Adams, 1855) จากประเทศมาเลเซียและอินเดีย รวมทั้ง *I. lamprelli* ที่เป็นหอยค้นพบใหม่จาก อ่าว Moreton Bay และบริเวณรัฐ Queensland ตอนใต้ ในประเทศออสเตรเลีย และหอยสองฝาอีกสองชนิดที่มีทั้ง anterior และ posterior lateral teeth คือ *I. dalli* (Lyngé, 1909) จากอ่าวไทย และ *I. scarlatoi* (Zorina, 1978) จากประเทศสาธารณรัฐประชาชนจีนตอนใต้ และฮ่องกง ความใกล้เคียงหรือแตกต่างทางพันธุกรรมที่นำเสนอในที่นี้อยู่บนพื้นฐานของรายละเอียดการเรียงตัวของโมเลกุลพันธุกรรมบน 18S, 28S rRNA และ cytochrome B

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