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Lucinid bivalves of Singapore and their relationships (Bivalvia: Lucinidae)

Emily A. Glover*, Suzanne T. Williams & John D. Taylor

Abstract. A survey of the lucinid bivalves of Singapore recorded 18 species, 12 of these located during the Singapore Strait Biodiversity Workshop, two others previously collected from the Straits of Johor and a further four species identified from museum specimens. These are illustrated and briefly described. In 2013 survey, lucinids were uncommon at most locations but a seagrass bed at the southern end of the artificially constructed beach joining Seringat and Lazarus islands, yielded 9 species of lucinids and numerous other infaunal bivalves. By far the most abundant species was the small *Pillucina profusa*, with fewer numbers of *Euanodontia ovum*, *Cardiolucina macassari*, *Cavatidens bullula*, *Leucosphaera philippinensis* and *Liralucina lyngei*. The associated infaunal bivalves included 36 species from 10 families; the most diverse were Tellinidae with 14 species and these are illustrated to assist local identification. Three lucinids, *Austriella corrugata*, *Indoaustriella dalli*, and *Pegophysema philippiana* occurred amongst mangroves in the Strait of Johor. Species for which only museum records are available, such as *Codakia paytenorum* and *Lepidolucina venusta*, may be locally extinct. Five Singapore lucinid species were included in a new molecular analysis (18S, 28S and cytochrome b genes) to establish their phylogenetic relationships and anatomical details including, in particular, ctenidial structure and morphology of bacterial symbionts for *Eunanodontia ovum* and *Pillucina profusa*.

Key words. Chemosymbiosis, seagrass, molecular phylogeny, taxonomy, Tellinidae

INTRODUCTION

With over 400 living species, the bivalve family Lucinidae is by far the most diverse group of chemosymbiotic bivalves, dependent on sulphide oxidising proteobacteria housed in the ctenidia for most of their nutrition (Taylor & Glover, 2006; 2010). Lucinidae occupy a great range of habitats, from intertidal mangroves, seagrass beds, shallow suboxic sediments to bathyal depths including hydrocarbon seeps, but they are particularly rich in coral reef environments of the Indo-West Pacific and western Atlantic (Glover & Taylor, 2007, in press; Mikkelsen & Bieler, 2008). The discovery of the chemosymbiotic life style of lucinids triggered a surge in taxonomic activity in the previously neglected family and many new species and genera from the Indo-West Pacific have been described over the last 20 years (Glover & Taylor, 2001; Bouchet & Cosel, 2004; Cosel, 2006; Oliver & Holmes, 2006; Glover & Taylor, 2007; Cosel & Bouchet 2008; Okutani, 2011; Taylor & Glover, 2013; Glover & Taylor, 2016). Molecular analyses have concurrently developed a radical new classification and phylogeny of the family and enhanced taxonomic discrimination based on traditional shell characters (Taylor et al., 2011, 2014).

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There has been no comprehensive account of the Lucinidae of Singapore but a few species have figured in taxonomic accounts (Reeve, 1850; Taylor & Glover, 1997; Glover et al., 2008), faunal lists (Tan & Woo, 2010), general books (Chuang, 1973; Ng & Savasothi, 1999; Ng et al., 2008) or mentioned in ecological studies (Vohra, 1971). Curiously, no lucinids were listed by Morris & Purchon (1981) in their account of the bivalves of Singapore and West Malaysia.

During the Singapore Strait Biodiversity Workshop, May–June 2013 we sampled the Lucinidae of southern Singapore by intertidal and shallow subtidal collecting with a few samples obtained from dredge and trawling. Additionally, we document species found elsewhere around Singapore as well as other records obtained from museum collections and also provide a new assessment of prior literature records. We include new molecular data for 18S and 28S rRNA and cytochrome b genes for five Singapore species and incorporate this into to a larger dataset to establish their position and relationships within the Lucinidae.

MATERIAL AND METHODS

Sampling. From the intertidal and shallow subtidal (ca 1 m water depth) sediment was dug to about 15 cm by spade and trowel and sieved through 1 mm and 2 mm mesh. Subsequent to the workshop, 12 core samples, 10 cm diameter × 10 cm deep, were made in seagrass patch at the south end of Seringat Beach (Figs. 1, 2). These were sieved through 2 mm sieve and sorted in the laboratory. Additionally a few

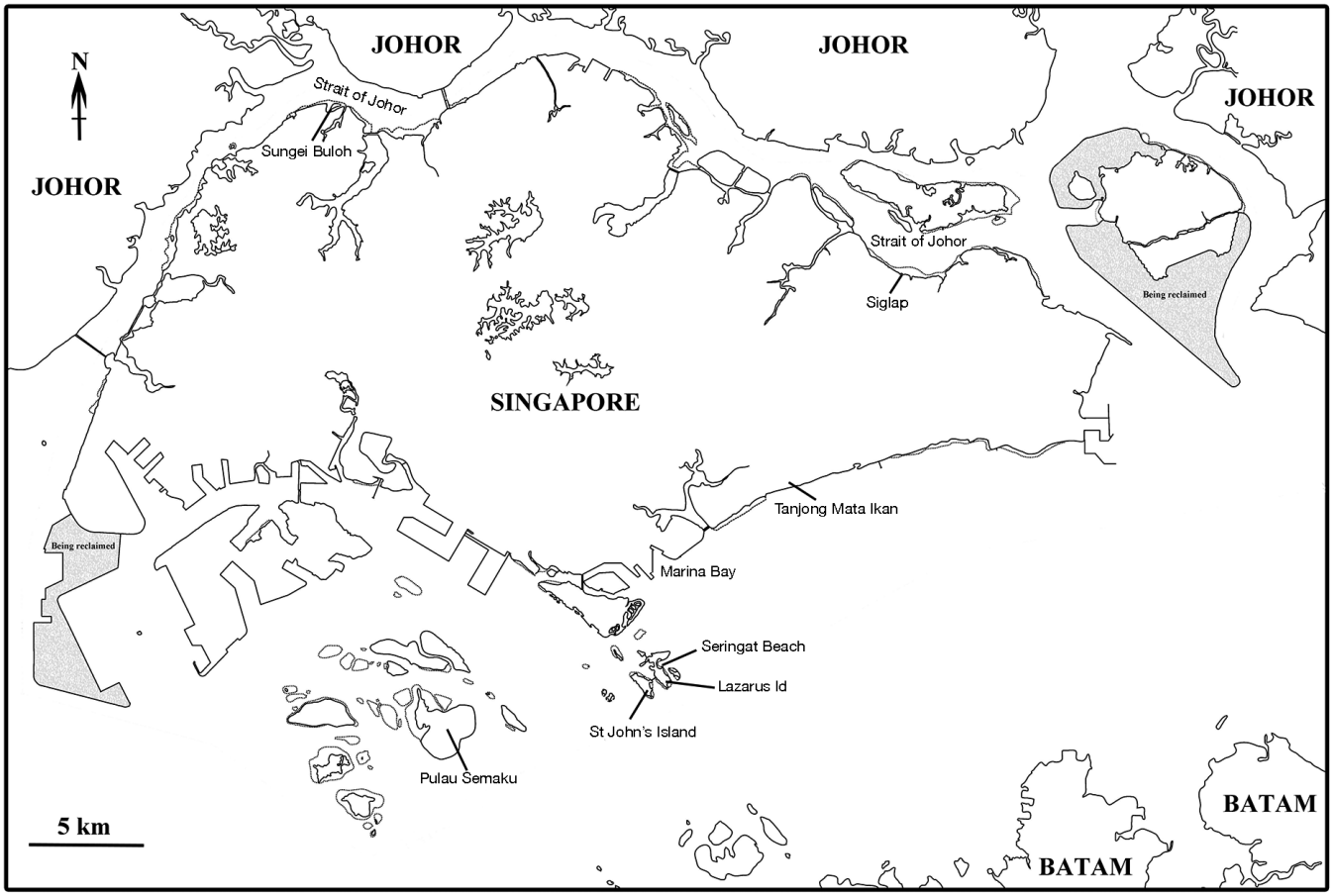

Fig. 1. Outline map of Singapore showing localities mentioned in text.

lucinids were recovered from dredge and trawl samples during the workshop.

Specimen fixation and preparation. Lucinids were preserved either in 95% ethanol or in 5% formaldehyde solution. For anatomical studies preserved lucinids were decalcified in dilute hydrochloric acid, the tissues sliced with a razor blade, dehydrated in ascending acetone solutions and critical point dried. Tissue and dry shell samples were examined with a FEI Quanta scanning electron microscope.

Identification. The bivalve fauna associated with the lucinids was identified using appropriate monographs and comparison with shells from the type collection of bivalves at the NHM, London. Particular attention was directed to Tellinidae as these are abundant and speciose in intertidal habitats and their identification often confused. The revised nomenclature from Huber's (2015) revision of tellinid taxonomy was also employed.

Molecular methods. Four species were newly sequenced for 3 genes 18S, 28S and cytochrome b and data for *Austriella corrugata* was available from previous sampling (see Table 1). The DNA extraction, amplification and sequencing protocols used in Williams & Ozawa (2006) and Taylor et al. (2011, 2014) were used to amplify and sequence portions of the three genes. New sequences were combined with alignments used in Taylor et al. (2014). Sequences for each gene fragment were assembled, edited and all sequences were aligned following the protocol in Taylor et al. (2014), with the exception that the L-INS-i strategy was used in MAFFT (Katoh et al., 2002, 2005). Ambiguously aligned sites were removed using the online Gblock server (Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks_server.html) following Taylor et al. (2014). After removal of ambiguous blocks of data selected by using Gblocks, a total of 924 bp of aligned sequence from 18S rRNA remained to be used in phylogenetic analyses (73% of 1263 bp in the original alignment) and 1355 bp of 28S rRNA (70% of 1937 bp in the original alignment).

Individual gene trees and a concatenated three-gene tree were constructed using MrBayes following the methods of Taylor et al. (2014), with the exception that the GTR+G+I nucleotide model of substitution was chosen as the best model for each gene using jModelTest (v 2.1.5; Darriba et al., 2012) with the number of models limited to those used in MrBayes. The analysis ran for 50,000,000 generations for each dataset, with trees sampled every 5,000 generations. The first 10 percent were discarded as burn in after checking that runs had reached stationarity (following Taylor et al., 2014).

Institutional abbreviations. ANSP, Academy of Natural Sciences at Drexel University, Philadelphia; MHNG, Muséum d'Histoire Naturelle, Geneva; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMUK, The Natural History Museum, London; NMST, National Science Museum, Tokyo; NMW, National Museum of Wales, Cardiff; ZISP,

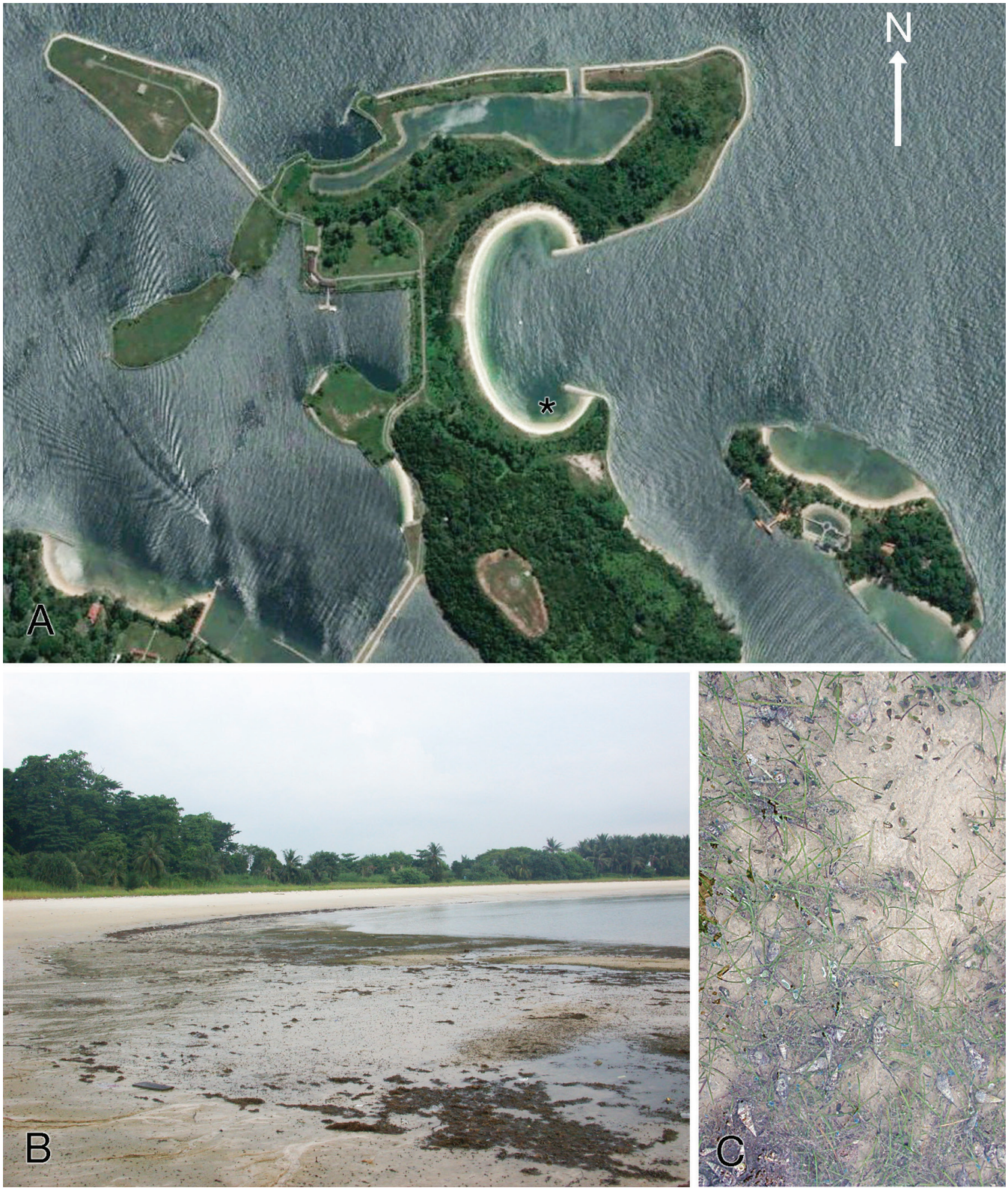

Fig. 2. Lucinid sampling sites. A, Aerial view of Seringat showing arcuate Seringat Beach with main study site marked with asterisk. Google Earth Image taken April 2012; B, Southern end of Seringat Beach at low spring tide showing exposed seagrass the main sampling site; C, Mixed *Halodule* and *Halophila* on sand with abundant grazing gastropods, *Batillaria zonalis*, on surface.

Table 1. Lucinidae from Singapore. Recent collections and museum records. Abbreviations: ANSP – Academy of Natural Sciences, Philadelphia, USA; D – dead; L – live; NHMUK – The Natural History Museum, UK; NMW – National Museum of Wales.

Species	2013 Singapore Strait Workshop Survey (This Study)	Sungei Buloh, West Johor Strait	Museum Records	Molecular Sequence Data Obtained?
Pegophyseminae				
Pegophysema philippiana (Reeve, 1850)	D		NHMUK 1924.1.29.28	No
Eunanodonta ovum (Reeve, 1850)	L		NMW 1955.158.11289 (as *Anodontia ovulum*)	No
Cavatidens bullula (Reeve, 1850)	L			No
Leucosphaerinae				
Leucosphaera cf. *philippinensis* Glover & Taylor, 2016	L		NHMUK 1963548, dredged Siglap (1933)	Yes
Codakiinae				
Ctena bella (Conrad, 1837)	D			No
Codakia paytenorum (Iredale, 1937)			NMW 1955.158.11132, Tanjong Katong	No
Lucininae				
Lepidolucina venusta (Philippi, 1847)			NMW 1955.158.11288, Archer collection	No
Lamellolucina sp.	D			No
Pillucina profusa Glover & Taylor, 2016	L			Yes
Pillucina pusilla Glover & Taylor, 2016			NHMUK 1963485, dredged, Siglap (1933)	No
Pillucina vietnamica Zorina, 1978	D		ANSP 246020, 246036, Mata Ikan	No
Jallenia inanis (Prashad, 1932)	D			No
Liralucina lyngei Huber, 2015	L			No
Austriella corrugata (Deshayes, 1843)		L		Yes
Indoaustriella dalli (Lynge, 1909)		L		No
Scabrilucina vitrea (Deshayes, 1844)	D			
Easmithia desiderata (Smith, 1885)			NHMUK 1963484 dredged St of Johor & Siglap (1933)	No
Cardiolucina macassari (Prashad, 1932)	L		NHMUK 1963552 paralectotypes of *L. pisum*, NHMUK 1953.1.30, dredged St of Johor (1933)	Yes

Table 2. Infaunal bivalves of seagrass at southern end of Seringat Beach. D = dead shell.

Species
Lucinidae
Euanodontia ovum
Cavatidens bullula
Leucosphaera philippinensis
Ctena bella (D)
Pillucina profusa
Pillucina vietnamica (D)
Liralucina lyngei
Scabrilucina vitrea (D)
Cardiolucina macassari
Solenidae
Solen linearis Spengler 1794
Solen soleneae Cosel, 2002
Pharidae
Ensiculus cultellus (Linnaeus, 1758)
Cardiidae
Fulvia undatopicta (Pilsbry, 1904)
Vasticardium pectiniforme (Born, 1780)
Tellinidae
Scutarcopagia pulcherrima (Sowerby, 1825)
Tellinella staurella (Lamarck, 1818)
Tellinella virgata (Linnaeus, 1758)
Arcopaginula inflata (Gmelin, 1791)
Nitidotellina valtonis (Hanley, 1844)
Nitidotellina lux (Hanley, 1844)
'Nitidotellina' sp.
Hanleyanus oblongus (Gmelin, 1791)
Tellinimactra edentula (Spengler, 1798)
Jactellina clathrata (Deshayes, 1835)
Jitlada philippinarum (Hanley, 1884)
Tellinangulus aethiopica (Thiele & Jaeckel, 1931)
Clathrotellina carnicolor (Hanley, 1846)
Pinguitellina pinguis (Hanley, 1844)

Species
Psammobiidae
Soletellina ambigua (Reeve, 1857)
Semelidae
Ervilia bisculpta Gould, 1861
Semele carnicolor (Hanley, 1845)
Semele cf *fragillima* (Issel, 1869)
Semele cordiformis (Holten, 1802
Semele sp. juvenile
Ungulinidae
Felaniella conspicua (Smith, 1885)
Phlyctiderma sp.
Mactridae
Meropesta nicobarica (Gmelin, 1791)
Mactra grandis (Gmelin, 1791)
Mesodesmatidae
Atactodea striata (Gmelin, 1791)
Veneridae
Anomalodiscus squamosus (Linnaeus, 1758)
Gafrarium pectinatum (Linnaeus, 1758)
Circe undatina (Lamarck, 1818)
Dosinia cretacea (Reeve, 1850)
Timoclea lionata (Smith, 1885)
Lioconcha ornata (Dillwyn, 1817)

Zoological Institute, St Petersburg; ZMUC, Zoological Museum, Copenhagen.

Other abbreviations. H, shell height; L, shell length; LV, left valve; RV, right valve.

RESULTS

Southern Singapore. A number of intertidal sedimentary shores (the lagoons) were sampled on the eastern side of St John's Island and the southern end of Lazarus Island but these yielded very few living Lucinidae despite what appeared to be suitable conditions with patches of seagrass. By far the most productive shore for lucinids and other infaunal bivalves was the 'beach' on reclaimed land of Seringat and Lazarus islands, herein referred to as Seringat Beach (Figs. 1, 2) (1°13'32.9"N, 103°51'18.5"E). This artificial, arcuate, east facing bay, 1000 m long (Fig. 2) was constructed when the islands of Seringat and Lazarus were joined during reclamation and remodelling work that began in 2000. The sand for the beach was imported from Indonesia and in place by 2003–2004 protected at the northern and southern ends by rocky seawalls. The highest bivalve numbers and species were found at the southern end of the beach, marked by asterisk on Fig. 1A, where we sampled over five low tides between 29 May and 4 June 2013. The intertidal zone consists of medium quartz sand with a muddy silt overlay, colonised by extensive seagrass, largely *Halophila ovalis* and *Halodule uninervis* either mixed or monospecific stands of *Halodule*. Abundant algae, *Halimeda* and *Padina*, occur amongst the seagrass. Grazing gastropods particularly *Batillaria zonalis* (Bruguière, 1792) and *Clithon oualaniensis* (Lesson, 1831) were very abundant.

We recorded nine species of Lucinidae from Seringat Beach (Table 1, Figs. 3–10), six of them represented by live collected samples and three by dead shells. The small *Pillucina profusa* was by far the most abundant species (120 sampled), with

juvenile *Euanodontia ovum* (13), *Cardiolucina macassari* (4), *Cavatidens bullula* (2), *Leucosphaera philippinensis* (1) and *Liralucina pulchella* (1). Additionally dead shells were recorded of *Ctena bella* and a juvenile *Scabrilucina*.

In addition to the lucinids, we found a remarkable diversity of infaunal bivalves with 46 species from 10 different families (Table 2). The most speciose and abundant family was Tellinidae with 14 species, most frequent were *Pinguitellina pinguis*, *Jactellina clathrata*, and *Tellinides lux*, while Semelidae and Veneridae had six species each. Although tellinids are often abundant on tropical shores their taxonomy has been neglected and species are often confused and misidentified. As an aid for local identification, we illustrate 14 tellinid species (Figs. 11, 12) and have made efforts to check these with available type material and primary literature.

Limited quantitative sampling (12 × 10 cm diameter cores × 10 cm deep, sieved through 1 mm mesh = 942 cm^2) recovered two lucinids: five *Euanodontia ovum*, two *Pillucina profusa* and five other bivalves: eleven *Pinguitellina pinguis*, three *Meropesta nicobarica* and single *Ervilia bisculpta*, *Fulvia undatopictum* and a juvenile *Vasticardium* sp.

Other Singapore lucinid records. In addition to the Seringat Beach samples we recorded dead shells of *Pillucina vietnamica* and *Pegophysema philippiana* and *Euanodontia ovum* at Pulau Semakau (Fig. 1). Live *Cardiolucina macassari* were recorded from stations TR 30 and DR 31 outside of Marina Bay at 19 m depth along with a dead shell of a *Lamellolucina* juvenile. A single valve of *Jallenia inanis* was recovered from station DR 14 in the Eastern Fairway. In the Straits of Johor, for example at Sungei Buloh, *Austriella corrugata* and *Indoaustriella dalli* occur in mangrove muds.

Museum records. From museum collections we have identified the tiny *Pillucina pusilla*, dredged at Siglap in 1933 (NHMUK) and *Easmithia desiderata* (Smith, 1885) from Strait of Johor (NHMUK). A sample of *Cardiolucina macassari*, also dredged from Siglap in 1933 (NHMUK) suggests that the species was once common in the area. Shells from Singapore labelled *Anodontia ovulum* (now identified as *Euanodontia ovum*), *Codakia interrupta*, *C. paytenorum* and *Lepidolucina venusta* are housed in the National Museum of Wales.

Doubtful records from Singapore. Previous records from Singapore of *Cardiolucina* or *Bellucina pisum* (Reeve, 1850), *C. eucosmia* (Dall, 1901) or *C. semperiana* (Issel, 1869) refer to the species now classified as *Cardiolucina macassari* (Prashad, 1932) (see systematic section below for details). Records of *Anodontia edentula* (Linnaeus, 1758) from Singapore could refer to *Pegophysema philippiana*, *Euanodontia ovum* or *Cavatidens bullula* and in the wider context several other Pegophyseminae species; Taylor & Glover (2005) provide reasons to abandon the name *A. edentula*. Vohra (1971) recorded *Wallucina* sp. as an abundant species on a soft substrate transect at Kampong Mata Ikan, eastern Singapore. However, images (provided by Paul Callomon, ANSP) of the specimens sent by R.D. Purchon from Singapore to R.T. Abbott (ANSP) for identification show that they are *Pillucina vietnamica*.

In summary, a total of 18 Lucinidae species are confirmed from Singapore (Table 1), although some with only historical records, such as *Codakia paytenorum* and *Lepidolucina venusta*, may now be extinct in the area. Others such as *Pillucina pusilla* may be too small to have been noticed.

Symbiosis. All Lucinidae studied so far possess symbiotic sulphide oxidising bacteria housed in the gills from which they gain significant part of their nutrition and leading to an assumption that the association is obligate for the family (Taylor & Glover, 2010). Nevertheless, particulate feeding is also recorded in some species (Duplessis et al., 2004). In this study we made anatomical observations of two species, *Pillucina profusa* and *Euanodontia ovum*. In common with other lucinids, the ctenidia of *Pillucina profusa* comprise inner demibranchs, pale pink in colour, with filaments extended abfrontally by a broad bacteriocyte zone (Fig. 7C). Bacteria are potato-shaped, ca 2.5–3 μm long and are abundant within the bacteriocytes (Fig. 7D, E). *Euanodontia ovum* has liver-coloured ctenidia and similar ctenidial filaments (Fig. 4A, B, F) with bacteriocytes (ca 30 μm long) containing bacteria with two morphologies—coccoid forms ca 1.5 μm diameter and rod shapes of around 3 μm long. The rectum contains particulate material with abundant diatom frustules indicating some filter feeding (Fig. 4J). Although not examined in this study *Austriella corrugata* has symbiotic bacteria ca 8–10 μm long and 1.5–1.8 μm wide (Glover et al., 2008) and the bacteria of *Pillucina vietnamica* measure 6–8 μm long and 1.5–2 μm wide (Glover & Taylor, 2001).

Other anatomical features. In *Euanodontia ovum*, the posterior apertures have medium length mantle fusion (fusion index of 0.4, see Taylor & Glover, 2002) involving inner and part of middle folds (Fig. 4C) and the inhalant aperture lacks papillae. A pleated mantle septum extends from the ventral tip of the anterior adductor muscle to the thickened ventral mantle margin (Fig. 4A, B, E). The septum is enlarged near the tip of the adductor muscle and this bilateral structure functions as respiratory mantle gills (Taylor & Glover, 2000, 2006). The small labial palps are typical of most lucinids.

In *Pillucina profusa*, the posterior apertures have a medium length of mantle fusion (fusion index 0.5) involving inner and middle mantle folds with the inhalant aperture edged with a few short papillae, also seen in *Pillucina vietnamica* (Glover & Taylor, 2001). A distinctive feature is the lobate lateral visceral pouch (Fig. 7F) occupied in these specimens by gonadal tissue. Such lateral pouches are seen in a number of other Lucininae including *Parvilucina*, *Bathyaustriella* and *Cardiolucina* (Taylor et al., 2013). Sperm were observed in some preparations with the heads tapering to a sharp point, the acrosome and nucleus 4.2–4.8 μm long and 1.0 μm wide and the midpiece 0.5 μm long (Fig. 7G). These sperm are much shorter than *Ctena orbiculata* (7.5 μm), *Codakia oribicularis* (14 μm) and *Lucina pensylvanica* (15.5 μm) (Biggati et al., 2004).

Molecular results. Sequences for 18S, 28S and cyt b genes of four Singapore lucinid taxa were newly included in molecular analyses together with *Austriella corrugata* (Strait of Johor) from a previous study and the combined tree for three genes is shown in Fig. 13a, b and a subset of cyt b tree results is included as Fig 13a, b. The Singapore species group in three subfamilies of Lucinidae. The Pegophyseminae, characterised by edentulous inflated shells, include most lucine species previously classified as '*Anodontia*' and in molecular analysis form a distinct clade separate from all other lucinids. *Euanodontia ovum* from Singapore groups closely with a similar sample from Queensland (Ball et al., 2009) but distinct from the *E. ovum* identified from Rodrigues. In shell form, tiny *Leucosphaera* species resemble juvenile pegophysemines but the individual sequenced from Seringat Beach groups near to *Leucosphaera philippinensis* from Panglao, Philippines (Glover & Taylor, 2016) re-confirming a position in the subfamily Leucosphaerinae, originally identified from molecular analyses (Taylor et al. 2011, 2014).

The subfamily Lucininae includes many genera from shallow water and three Singapore species are included in this new analysis (Fig. 13A, B). The abundant *Pillucina profusa* from Seringat Beach groups with other Indo-West Pacific *Pillucina* species, *Wallucina* spp and *Chavania* spp in a large subclade that also includes *Loripes* and *Lucinella*, all possessing an internal ligament. Unfortunately, we had no molecular data for *P. profusa* from the Philippines, the type locality, but the Singapore specimen is distinct from *P. pisidium* Dunker from Japan that was previously thought to be widespread across the Indo-West Pacific (Glover & Taylor, 2001) and there is some evidence that there is a complex of *Pillucina* species. The tiny *Pillucina pusilla* from Singapore is known only from a few dead shells but molecular data from the Philippines (Fig 13B) indicates that it is more closely related to *P. vietnamica* than *P. profusa*. Earlier analysis identified the *Cardiolucina* species from Singapore as *C. semperiana* (Issel, 1869), then thought to range from Red Sea to the Philippines (Taylor & Glover, 1997), but more recent research suggests *Cardiolucina macassari* (Prashad, 1932) is a distinct species found in South East Asia (Glover & Taylor, 2016). In the present molecular analysis *Cardiolucina* forms a distinct subclade and within this *C. macassari* aligns most closely with the morphologically similar but genetically distinct *C. semperiana*, from the northwestern Indian Ocean. The mangrove associated *Austriella corrugata* from the Strait of Johor is closely similar to a sample from NW Australia and both group in a subclade with four species of *Indoaustriella* that also live amongst and near mangroves (Glover et al., 2008).

TAXONOMY

In this section we provide taxonomic review of the Lucinidae from Singapore; some of the species are relatively well-documented elsewhere and in these cases only basic information is provided but we include more extensive descriptions of the less well known species.

Lucinidae Fleming, 1828

The phylogenetic analyses of the Lucinidae (Taylor et al., 2011, 2014) provided the framework for a new classification of the family into seven subfamilies. The order and grouping of genera into subfamilies used here follows this classification.

Subfamily Pegophyseminae Taylor & Glover, 2011

In molecular analyses, *Anodontia alba* Link, 1807, the type species of *Anodontia*, does not group with the other '*Anodontia*' species. For this reason we combined these into a new subfamily, the Pegophyseminae, and elevated the subgenera of *Anodontia* used in Taylor & Glover (2005) to full generic status (Taylor et al., 2011).

Pegophysema Stewart, 1930

Loripinus (*Pegophysema*) Stewart, 1930:185. Type species: *Lucina schrammi* Crosse, 1876, by original designation. Recent, Western Atlantic.

Diagnosis. Shells large, thin, inflated; outer surface with irregular, rounded, commarginal ridges. Ligament internal, shallowly to deeply inset. Anterior adductor scar short, detached for 70% of length. Pallial line entire, with secondary pallial attachment scars (Taylor & Glover, 2005, Fig. 2) extending posteriorly from below anterior adductor scar.

Pegophysema philippiana (Reeve, 1850)

(Fig. 3A–D)

Lucina philippiana Reeve, 1850: Pl. 5, Figs 23a, b.
Anodontia edentula (Linnaeus, 1758) – Ng & Sivasothi, 1999: 123
Anodontia (*Pegophysema*) *philippiana* (Reeve) – Taylor & Glover, 2005: 303, Fig. 21A, D; Glover & Taylor, 2007: 114, Fig. 2 C, D; Meyer et al., 2008: 45, Fig. 3E.
Anodontia philippiana (Reeve) – Tan & Woo, 2010:10; Tan & Yeo, 2010: 290.
Pegophysema philippiana (Reeve) – Glover & Taylor, in press: XX, Figs XX.

Type material. 3 syntypes, NHMUK 1963122, 1963123/1–2. Type locality not recorded.

Singapore material. One valve, Pulau Semakau, station IT 87, NHMUK20150051; one whole shell NHMUK 1924.1.29.28.

Description. See Taylor & Glover (2005) for details. Shell large, L to 71 mm, inflated, subspherical, thick brown periostracum. Ligament deeply inset laterally.

Remarks. This large, deeply burrowing species typically inhabits the seaward fringes of mangrove stands and is widely recorded from East Africa to New Caledonia but is now uncommon in Singapore.

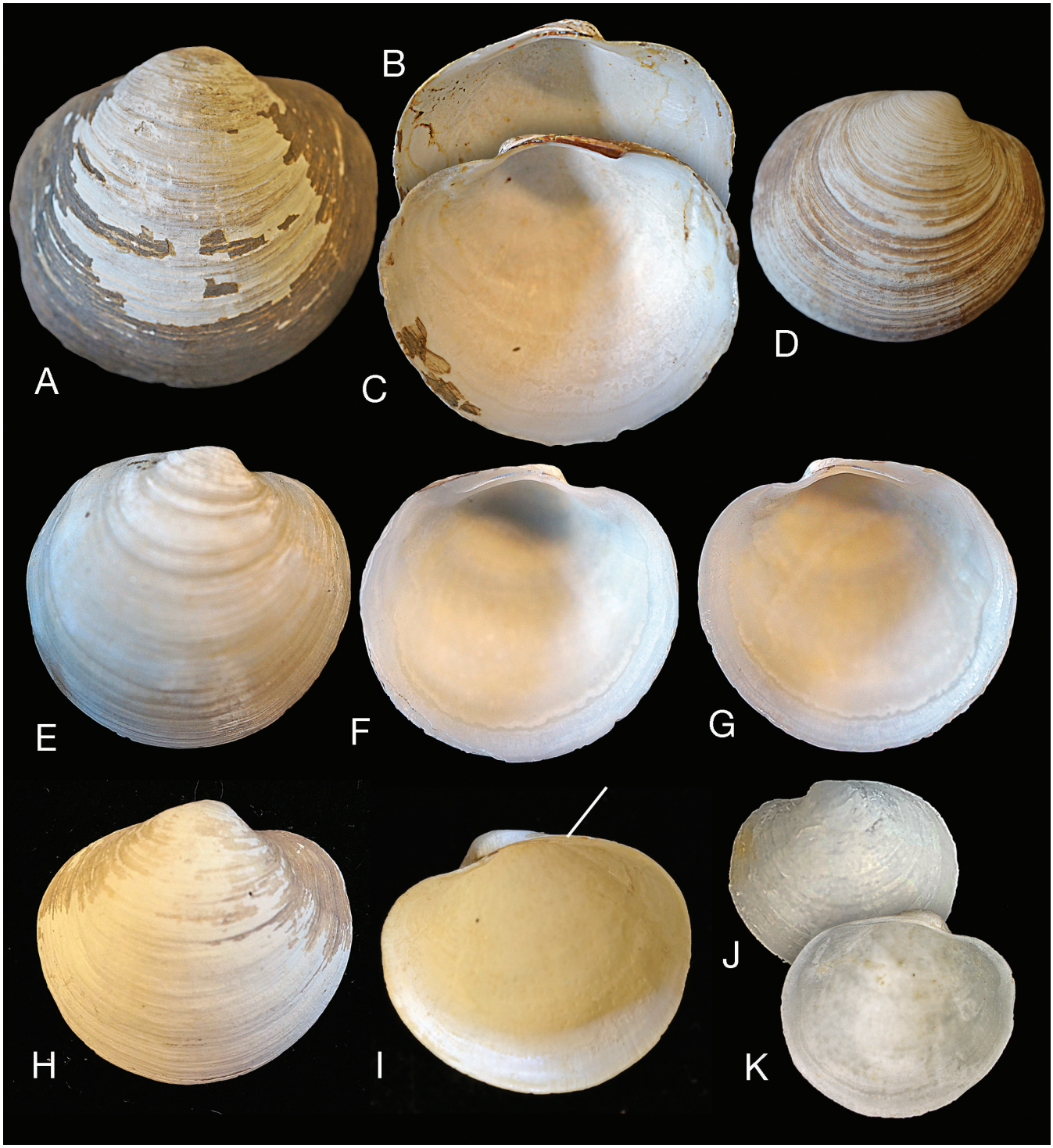

Fig. 3. A–C, *Pegophysema philippiana* (Reeve, 1850) exterior of right valve and interiors of left and right valves. Singapore. Hillier collection NHMUK 1924.1 29.28. L 78.8 mm; D, *P. philippiana* single right valve. Pulau Semakau stn IT87, NHMUK 20150051. L 37.5 mm; E–G, *Euanodontia ovum* (Reeve, 1850) exterior of right valve and interior of left and right valves Pulau Semakau stn IT87. NHMUK 20150052. L 23.0 mm; H–K: *Cavatidens bullula* (Reeve, 1850); H, I, Exterior and interior of right valve, arrow indicates shallowly inset ligament, Sungei Buloh, NHMUK 20150054. L 21.5 mm; J, K, Exterior and interior of left valve, Seringat Beach. NHMUK 20150053. L 8.0 mm.

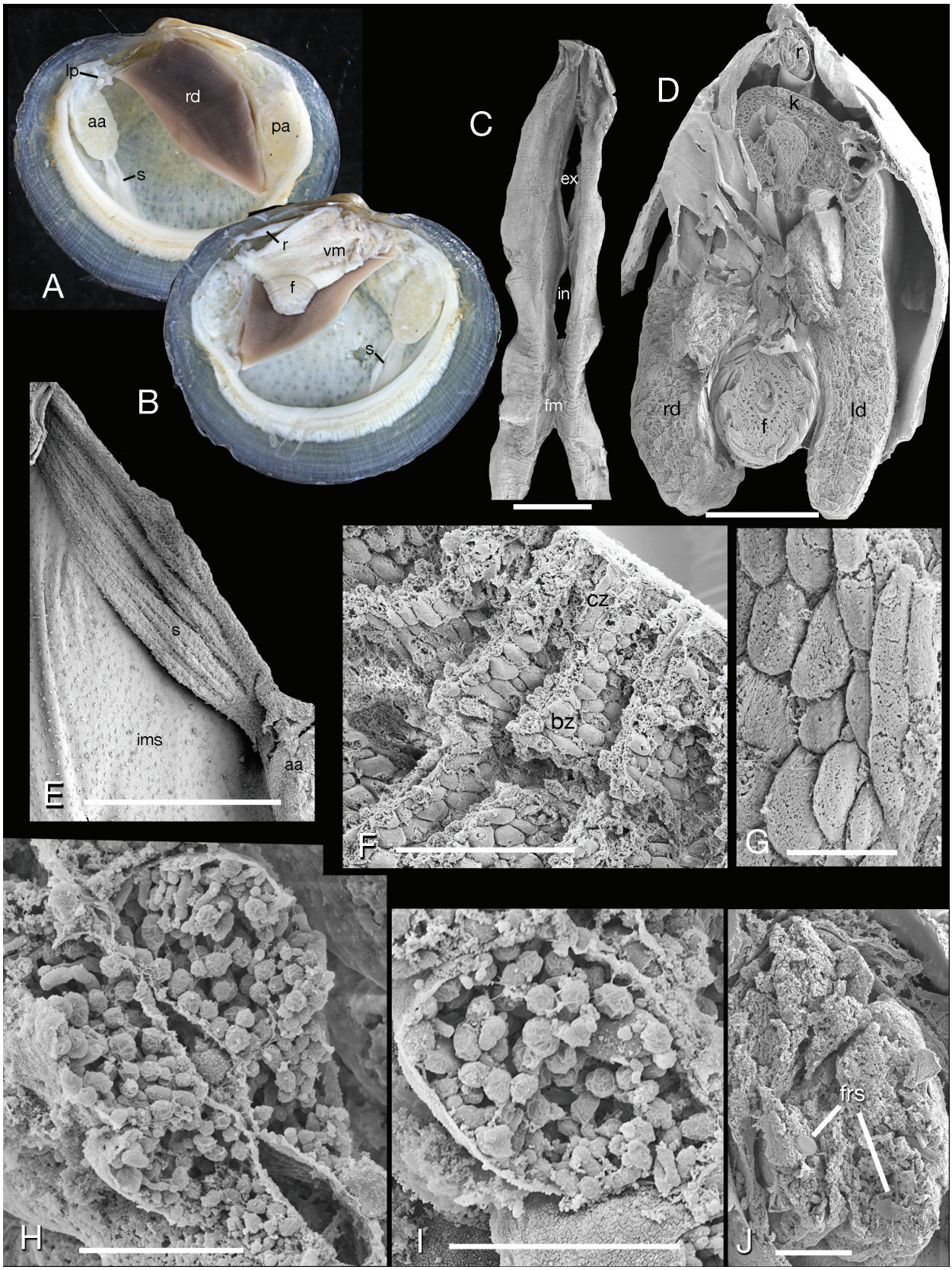

Fig. 4. *Euanodontia ovum* from Seringat Beach, anatomical features. A, B, cut halves of right and left sides of a juvenile specimen to show general features of anatomy, dark liver coloured ctenidia and mantle septum. aa, anterior adductor muscle; lp -labial palps; pa, posterior adductor muscle; s, mantle septum; r, rectum; rd, right demibranch of ctenidia; vm, visceral mass. L = 11.7 mm; C, posterior apertures, ex, exhalant aperture; in, inhalant aperture, fm, fused mantle; D, transverse section of body. f, foot; k kidney; ld, left demibranch; rd right demibranch, r, rectum; E, plicated mantle septum. ims, inner mantle surface; pa, posterior adductor muscle; s, septum; F, ctenidial filaments with ciliated zone and bacteriocyte zone. bz, bacteriocyte zone; cz ciliated zone; G, surface of bacteriocytes; H, section through two bacteriocytes containing bacteria either side of central blood space of ctenidial filament; I, single bacteriocyte with bacteria; J, detail of rectum packed with particulate material and abundant diatom frustules. Scale bars = 500 μm [C–E], 100 μm [F], 30 μm [G] 50 μm [J], 10 μm [H, I].

Euanodontia Taylor & Glover, 2005

Euanodontia Taylor & Glover 2005: 310. Type species: *Lucina ovum* Reeve, 1850, by original designation.

Diagnosis. Small to medium sized shells, near circular in outline. Outer shell smooth except for growth increments, ligament internal, deeply inset laterally. Pallial line entire, anterior adductor scar narrow and relatively short, detached from pallial line for up to 70% of length at an angle of 30–40°.

Euanodontia ovum (Reeve, 1850)
(Figs. 3E–G, 4)

Lucina ovum Reeve, 1850: Pl. 5, species 21.
Anodontia (*Euanodontia*) *ovum* (Reeve) – Taylor & Glover, 2005: 310, Figs 12A, 28A–H.
Anodontia ovum – Tan & Woo, 2010: 10; Tan & Yeo, 2010: 290.
Euanodontia ovum – Glover & Taylor, 2016.

Type material. Two syntypes, NHMUK 1963195/1–2. Type locality: Philippines, Isle of Burias.

Singapore material. 12 juvenile live collected specimens from Seringat Beach and from the lagoons on St John's Island and 8 valves; 1 live collected shell and 25 valves from Pulau Semakau, NHMUK 20150052.

Remarks. Distinguished from *Pegophysema philippiana* by its smaller size, circular shape, often yellowish interior and lack of secondary pallial attachment scars. *Cavatidens bullula* (below) is similar but *E. ovum* has a larger, more robust shell with a more deeply inset ligament.

Cavatidens Iredale, 1930

Cavatidens Iredale, 1930: 391. Type species: *Cavatidens omissa* Iredale, 1930, by original designation.

Diagnosis. Small, thin-shelled, hinge line very narrow, edentulous, ligament narrow, shallowly impressed, anterior adductor scar detached from pallial line for ¾ of length, at a broad angle of 30°. Pallial line thin, entire.

Cavatidens bullula (Reeve, 1850)
(Fig. 3I–K)

Lucina bullula Reeve 1850: Pl. 10, Fig. 35.
Anodontia (*Cavatidens*) *bullula* Taylor & Glover, 2005: 323, Figs 41 G–L.

Type material. Lectotype NHMUK 1963184. Type locality: unknown.

Singapore material. Two valves Sungei Buloh, 1999 dead collected, NHMUK 20150054; 2 live collected and 5 valves from Seringat Beach, NHMUK 20150053.

Remarks. The shells of this small thin-shelled species are characterised by the shallowly impressed ligament. From molecular results elsewhere (Fig. 12A, B) we suspect that specimens classified as *C. bullula* (or *A. bullula*) may be an amalgam of several morphologically similar species but more samples and data are needed to confirm this.

Subfamily Leucosphaerinae Taylor & Glover, 2011

The subfamily Leucosphaerinae, with 15 genera, mostly recorded from deeper water to 1000 m, was introduced for a well-supported clade in molecular analyses (Taylor et al., 2011). A single species is recorded from Singapore.

Leucosphaera Taylor & Glover, 2005

Leucosphaera Taylor & Glover, 2005: 331. Type species: *Lucina* (*Loripinus*) *salamensis* Thiele & Jaeckel, 1931 by original designation. Western Indian Ocean.

Diagnosis. Shells small (L <12 mm), inflated, thin-shelled, white to translucent. Outline ovate. Sculpture of regularly spaced, fine commarginal lamellae. Hinge teeth absent, small knob lies below the umbones of both valves contiguous with thin flange on the anterior part of the hinge. Ligament narrow, short, set in shallow groove. Anterior adductor muscle scar short, Pallial line entire, sometimes with dorsal extensions. Shell margin with thin groove.

Remarks. *Leucosphaera* species are widely distributed in subtidal muddy habitats in the IWP to depths of around 160 m. The small, diaphanous, fragile shells have been little studied and usually confounded with juvenile Pegophyseminae. Molecular analyses place *Leucosphaera* (as *L.* cf *diaphana* from the Philippines) as a sister taxon to all other genera and species classified in the Leucosphaerinae (Taylor et al., 2011).

Leucosphaera cf *philippinensis* Glover & Taylor, 2016
(Fig. 5A–C)

Singapore material. Single live collected shell L 6.3 mm from Seringat Beach, NHMUK 20150055. Single valve, dredged Siglap in 1933, NHMUK 1963548, Winckworth collection.

Remarks. Shells of the Singapore specimens are similar to *Leucosphaera philippinensis* (Glover & Taylor, 2016) from the Philippines (figured as *Leucosphaera* cf *diaphana* in Taylor et al. 2011: fig. 7a) but molecular distance (cytochrome b) suggests they are different species, as is another *Leucosphaera diaphana* from Vanuatu. However, there is insufficient material from Singapore to describe this as a new species.

Subfamily Codakiinae Iredale, 1937

Molecular analyses recognise this as a distinct clade that includes the genera *Codakia*, *Ctena*, *Epicodakia*, and *Lucinoma* (Taylor et al., 2011, 2014).

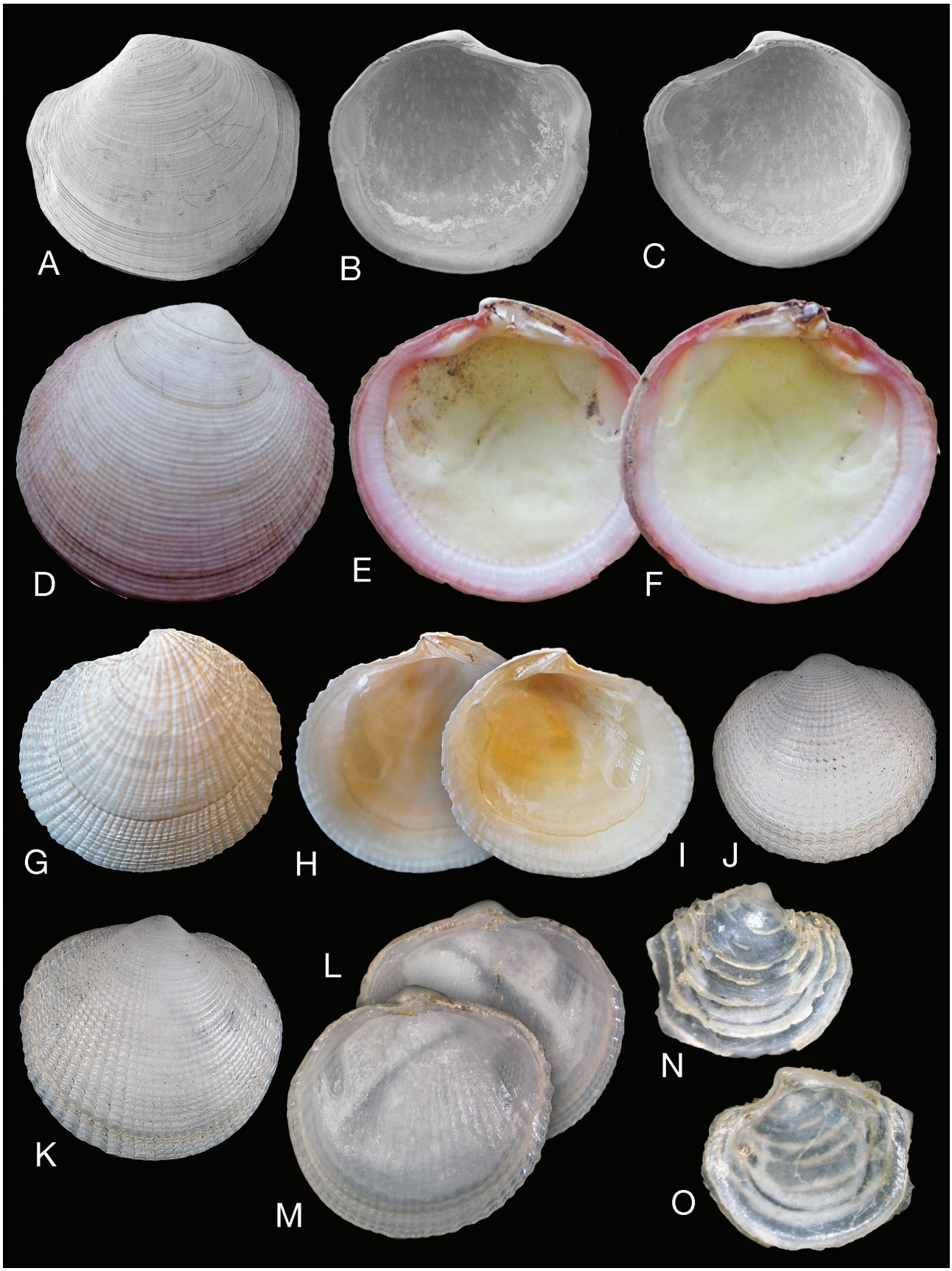

Fig. 5. A–C, *Leucosphaera* cf *philippinensis* Glover & Taylor, 2016. Exterior of left and interior of left and right valves. Seringat Beach intertidal. NHMUK 20150055. L 6.3 mm; D–F, *Codakia paytenorum* (Iredale, 1937) exterior of right and interiors of right and left valves. Tanjong Katong, NMW 1955.158.11132. L 33.5 mm; G–I, *Ctena bella* (Conrad, 1837), exterior of left valve and interiors of right and left valves. Seringat Beach. NHMUK 20150056. L 10.8 mm; J–M, *Lepidolucina venusta* (Philippi, 1847), Singapore, NMW 1955. 11288; J, exterior of left valve. L 5.6 mm; K–M, exterior of right valve and interiors of right and left valves. L 7.3 mm; N–O, *Lamellolucina* sp. juvenile, exterior and interior of right valve. stn TR30. L 2.9 mm.

Codakia Scopoli, 1777

Codakia Scopoli, 1777: 398. Type species: *Chama* '*codak*' Adanson, 1757 non-bionomial =*Venus orbicularis* Linnaeus, 1758, by monotypy. Western Atlantic.

Diagnosis. Shells medium to large, L to 150 mm, robust, discoidal. Sculpture of numerous, fine to broad, low radial ribs crossed by fine commarginal lamellae. Lunule short, triangular to ovate, deeply incised. Right valve with two cardinal teeth and a large anterior lateral set close to cardinals, posterior lateral teeth indistinct or absent. Left valve with two cardinal teeth and an anterior lateral. Anterior adductor scar long detached for about ½ of length, pallial line entire, shell margin smooth. Shells white often yellow internally with margins white, rose-pink or yellow.

Codakia paytenorum (Iredale, 1937)
(Fig. 5D–F)

Lentillaria paytenorum Iredale, 1937: 240, Pl. 16, Figs. 2, 3.
See Glover & Taylor, 2007 for details.

Singapore material. Two whole shells, NMW 1955.158.11132, Tanjong Katong.

Remarks. Externally this species is similar to *Codakia interrupta* (Lamarck, 1818); both have radial sculpture that is subdued in the central part of the shell and the two species have often been synonymized or confused, although molecular evidence indicates that they are distinct (Taylor et al., 2011). The shell interiors differ; in *C. paytenorum* the inner shell margin and hinge area is coloured intensely rose-pink and the shell inside the pallial line lemon-yellow while *C. interrupta* (syntype MHNG INVE 50347) has a pale yellow shell margin and interior. We regard the records of *C. interrupta* (e.g., Chuang, 1973) from Singapore as *C. paytenorum*.

Ctena Mörch, 1861

Ctena Mörch 1861: 201. Type species: *Lucina pectinata* Carpenter, 1857 non C. B. Adams, 1852 = *Codakia* (*Jagonia*) *mexicana* Dall, 1901, by subsequent designation, Dall et al., 1938).

Diagnosis. Shell small to medium sized, sub-circular. Sculpture of prominent radial ribs that bifurcate and intercalate and crossed by fine commarginal lamellae forming scales along the ribs. Hinge with two cardinal teeth and posterior and anterior lateral teeth in both valves. Ligament short, set in deep, oblique resilifer.

Ctena bella (Conrad, 1837)
(Fig. 5G–I)

Lucina bella Conrad, 1837: 254, Pl. 19, Fig. 11.
See Glover & Taylor, 2007: 134 for full synonymy.

Type material. Not located. Type locality: Hawaii (see Dall, Bartsch & Rehder 1938).

Remarks. We found only a single dead shell from Seringat Beach, NHMUK20150056. *Ctena* has not been previously recorded from Singapore although widely distributed across the Indo-West Pacific. The Singapore specimen resembles shells identified as *Ctena bella* from the western Pacific (Glover & Taylor, 2007) and is distinct from *Ctena delicatula* (Pilsbry, 1904) that ranges from eastern Thailand to Japan.

Subfamily Lucininae Fleming, 1828

This is the largest and most diverse of the lucinid subfamilies and recently redefined from the classification of Chavan (1969) by molecular analyses (Taylor et al., 2011). It includes over 42 morphologically disparate, living genera, the majority of these from tropical, shallow water habitats but with some from deeper water (Taylor et al., 2014).

Lepidolucina Taylor & Glover, 2007

Lepidolucina Taylor & Glover, 2007: 142. Type species: *Lucina venusta* Philippi, 1847, by original designation. Indo-West Pacific.

Remarks. This genus was introduced for a group of Indo-West Pacific species that are characterised by many narrow ribs bearing fine dorsally inclined, arcuate scales and previously often assigned to *Lucinisca* (from the western Atlantic and Eastern Pacific).

Lepidolucina venusta (Philippi, 1847)
(Fig. 5J–M)

Lucina venusta Philippi, 1847: 206, Pl. 1, Fig. 2.
Lepidolucina venusta (Philippi) – see Glover & Taylor, 2007: 142 for full synonomy

Type material. Not located and type locality unknown.

Singapore material. Five whole shells L 5.6–7.3 mm NMW 1955.11288, no precise locality in Singapore.

Description. Shells up to 34 mm length, sub-circular, inflated, with fine radial ribs bearing closely spaced arcuate scales. Ribs broader and more widely spaced at anterior and posterior.

Remarks. The shells from Singapore are likely juveniles with the largest only 7.3 mm. *Lepidolucina venusta* ranges from Sri Lanka, Thailand, Philippines to northern Australia.

Lamellolucina Taylor & Glover, 2002

Lamellolucina Taylor & Glover, 2002: 319. Type species: *Lamellolucina pilbara* Taylor & Glover, 2002, by original designation. Northwestern Australia.

Remarks. This genus was introduced for six species from the Indo-West Pacific (Taylor & Glover, 2002) characterised by prominent, thin, sometimes serrated, regularly spaced commarginal lamellae that are often highly elevated dorsally; shell with deeply incised posterior and anterior sulci.

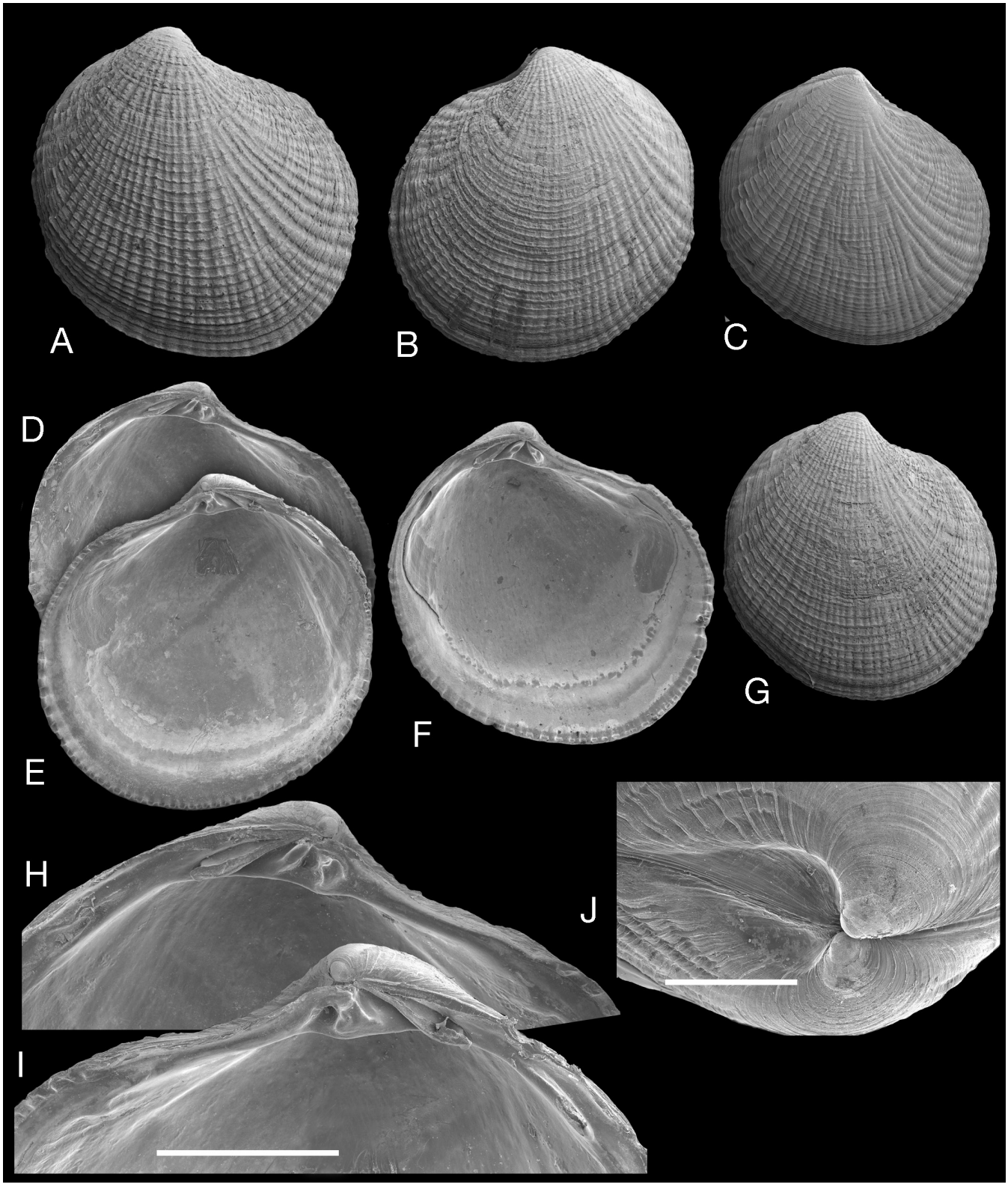

Fig. 6. *Pillucina profusa* Glover & Taylor, 2016, Seringat Beach NHMUK 20150058. A, exterior of right valve. L = 3.7 mm; B, exterior of left valve. L = 4,7 mm; C, exterior of right valve, L 3.3 mm; D, E, interior of left and right valves, L = 4.4 mm; F, interior of left valve, L 3.5 mm; G, exterior of right valve. L 4.9 mm; H, I, detail of hinge teeth of left and right valves; J, dorsal view showing asymmetrical lunule. Scale bars =1.0 mm [H, I] 500 μm [J].

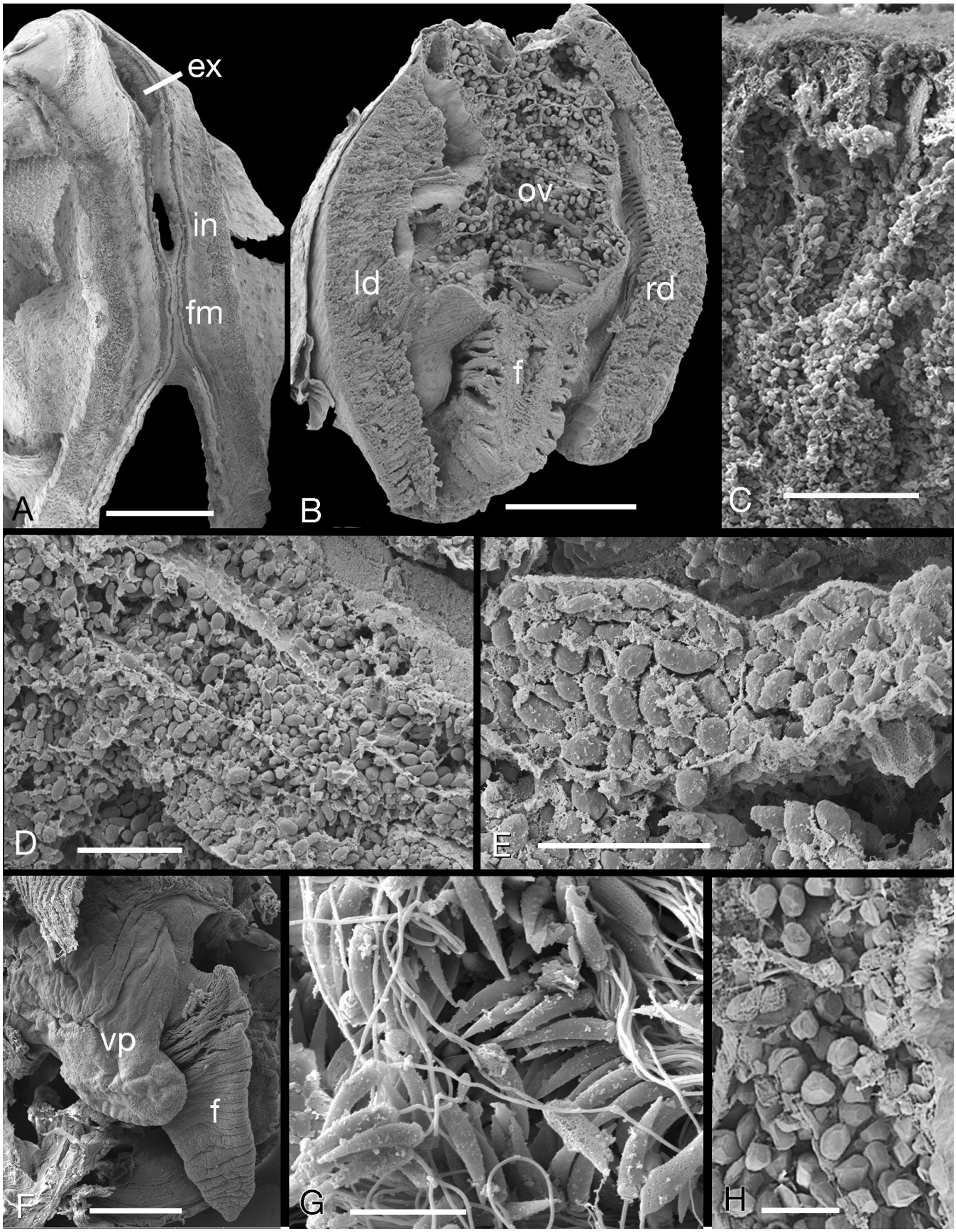

Fig. 7, *Pillucina profusa* Seringat Beach, anatomical features. A, posterior apertures, ex, exhalant aperture; fm, fused mantle; in, inhalant aperture; B, transverse section through body, ovary with abundant oocytes. f, foot; ld left demibranch; ov, ovary; rd, right demibranch; C, ctenidial filaments with broad bacterial zone and abundant bacteria; D, several closely packed ctenidal filaments with bacteriocytes packed with bacteria; E, section of two bacteriocytes with abundant bacteria; F, Curved visceral pouch and foot. F, foot; vp visceral pouch; G, Sperm; H, Part of ovary with oocytes. Scale bars = 500 μm [A, B, F] 50 μm [C, H], 20 μm [D], 10 μm [E] 5 μm [G].

Lamellolucina sp.
(Fig. 5N, O)

Singapore material. Single juvenile shell, L 2.9 mm from TR 30 outside of Marina Bay at 19 m.

Remarks. Although clearly a *Lamellolucina* species and possibly close to *L. pilbara* from NW Australia, we cannot positively identify this juvenile shell.

Pillucina Pilsbry, 1921

Pillucina Pilsbry, 1921: 382. Type species: *Pillucina spaldingi* Pilsbry, 1921, by original designation (junior subjective synonym of *Lucina hawaiiensis* Smith, 1885).
Sydlorina Iredale, 1930: 390.

Diagnosis. Shells small, H to 14 mm, inflated, sculpture of fine to broad radial ribs that often bifurcate, crossed by fine, low, commarginal lamellae; radial ribs usually more prominent on anterior and posterior shell. Hinge with two cardinal teeth in left valve and a single cardinal tooth in right valve. Posterior lateral tooth present in both valves (digitiform in two species), anterior lateral tooth present or absent. Ligament internal, located on short to elongate resilifer that widens to the posterior. Anterior adductor muscle scar short and detached from pallial line for about 1/4–1/2 of length, pallial line often discontinuous. Inner shell margin finely to coarsely crenulate. See Glover & Taylor 2001; 2007 for further details.

Remarks. In molecular analyses (Taylor et al., 2011; 2014) species of *Pillucina*, *Wallucina* and *Chavania* form a well-supported clade, sister to *Loripes* and are also united by the presence of a internally inset ligament.

Pillucina profusa Glover & Taylor, 2016
(Figs. 6, 7)

Pillucina profusa Glover & Taylor, 2016.

Type material. Holotype MNHN 26589. Type locality: Philippines, Panglao Island, Tagbilaran Channel, 9°38'N 123°51.4'E, 2–3 m sand.

Singapore material. Seringat Beach (stn IT115), 120 live collected shells; St John's Island: North lagoon (stn SW12) one live shell; Public jetty lagoon (SW 61) three live collected shells; Eastern Fairway (DR 14) whole live shell.

Description. Small, L to 6.1 mm, white, ovoid, higher than long, umbones prominent. Sculpture of 60–70 bifurcating radial ribs, broader at anterior and posterior, narrower and finer in central parts of shell. Radial ribs crossed by fine, thin, commarginal lamellae, central shell finely reticulate. Lunule heart-shaped, asymmetrical, larger in LV. Ligament short, internal. Hinge: RV with a single cardinal tooth, a small posterior lateral and a poorly defined anterior lateral; LV with two small cardinals, a small posterior lateral and no anterior lateral. Anterior adductor scar short, detached for 1/2 of length at angle of 50°. Pallial line irregularly discontinuous. Inner shell margin finely denticulate.

Remarks. The Singapore samples are closely similar to an abundant shallow water species newly recognised from the southern Philippines and we consider them conspecific. *Pillucina profusa* differs from *P. pusilla* (see below) in the finer external sculpture and lacks the distinctive dentate lateral teeth.

Pillucina pusilla Glover & Taylor, 2016
(Fig. 8A–G)

Pillucina pusilla Glover & Taylor, 2016.

Type material. Holotype MNHN 26591 and paratypes MNHN 26592. Type locality Philippines, Bohol Island, Manga, 9°41.1'N, 123°51.4'E, 3–4 m, mud.

Singapore material. Three valves, L 1.2 mm, dredged Siglap 18.05.1933. NHMUK 1963485, Winckworth colln.

Description. Very small, L to 1.8 mm, glossy, higher than long, umbones prominent. Sculpture of thin commarginal lamellae elevated to anterior and posterior. 17–25 low rounded radial ribs, divaricate in anterior part of shell. Juvenile shell with elevated commarginal lamellae but no radial ribs. Hinge: RV with single cardinal tooth, large anterior lateral tooth and complex posterior lateral tooth consisting of four to five digitate folds on dorsal surface of narrow flange, LV with two cardinal teeth, the anterior larger, anterior lateral socket, posterior lateral with sockets for digitiform projections of the right valve. Anterior adductor scar very short, inner shell margin coarsely crenulate.

Remarks. *Pillucina pusilla* is so far the smallest known lucinid and is easily distinguished by the dentate lateral teeth. The tiny specimen (ca L 1.5 mm) from the Gulf of Thailand identified as *Pillucina pisidium* (Robba et al., 2002: 78, pl. 7 fig 6), also has the distinctive lateral teeth. *Pillucina denticula* Glover & Taylor, 2001 from Natal, South Africa is similar but differs in dentition.

Pillucina vietnamica Zorina, 1978
(Fig. 8H–M)

Pillucina vietnamica Zorina, 1978: 195, Figs. 3, 6; Glover & Taylor, 2001: 273, Figs. 9A–F, 10.

Type material. 13 syntypes, (ZISP). Type locality: Hainan

Singapore material. Single whole shell from Seringat Beach and six valves from Pulau Semakau NHMUK 20150057.

Description. Shell small, L to 15 mm, sculpture of fine commarginal lamellae and radial ribs that are more prominent and curve dorsally towards anterior and posterior. Lunule lanceolate. Ligament short, internal in broadly triangular resilifer. Right valve with single cardinal and short anterior and posterior lateral, left valve with two narrow cardinal teeth

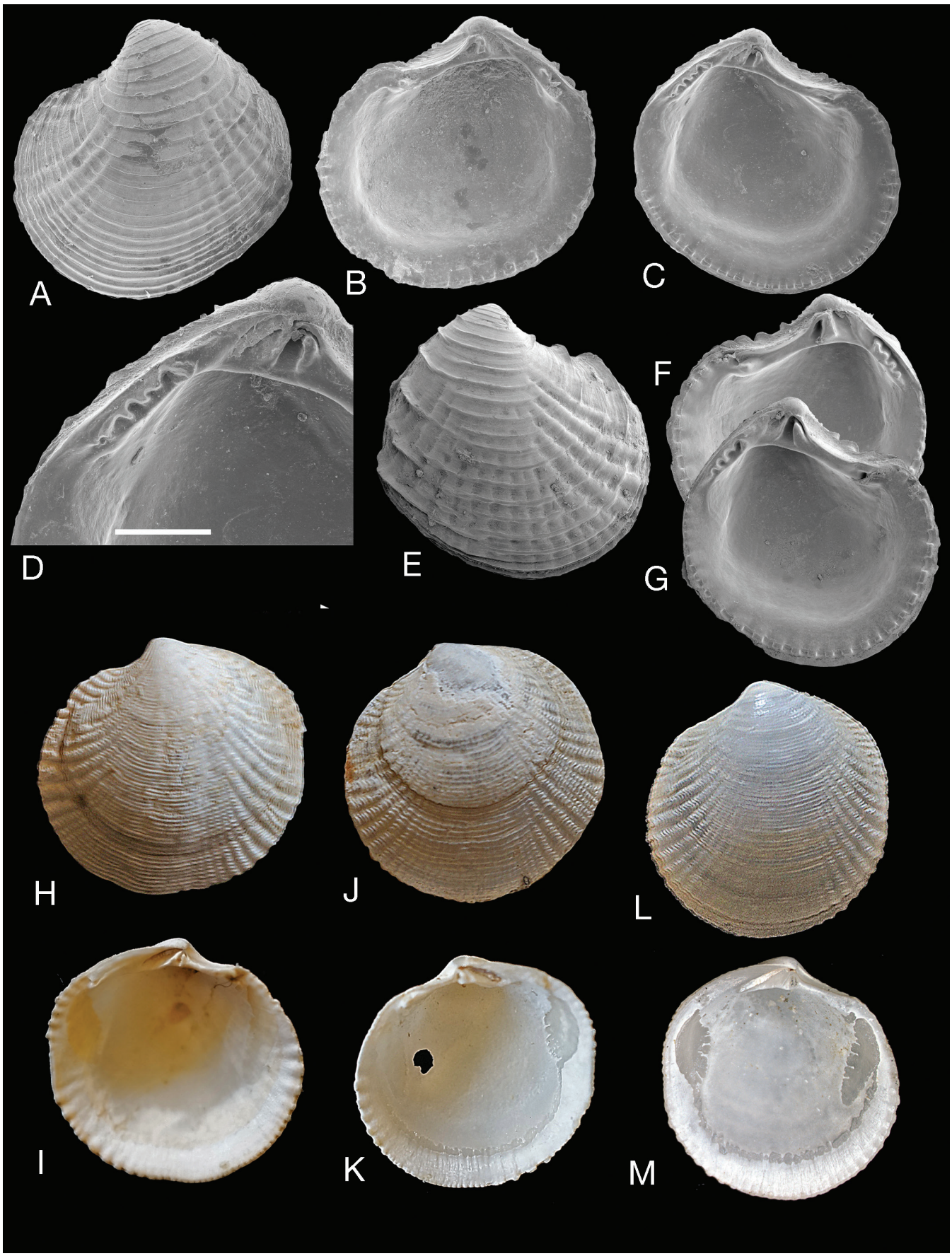

Fig. 8, A–C, *Pillucina pusilla* Glover & Taylor, 2016, exterior of left valve and interiors of right and left valves. Dredged Siglap, 1933, Winckworth collection NHMUK 1963485. L 1.2 mm; D, *P. pusilla* detail of hinge of Fig. 7C; E–G, *Pillucina pusilla* from Manga, Isle of Bohol, Philippines, exterior of right valve (Holotype MNHN 26591) L 1.2 mm and paratype (MNHN 26592) interior of right and left valves. L 1.05 mm; H–M, *Pillucina vietnamica* Zorina, 1978, Pulau Semakau, intertidal, dead collected 2013. NHMUK 20150057. H–I, exterior and interior of left valve. L 8.5 mm; J, exterior of right valve. L 8.7 mm; K, interior of right valve. L 9.5mm; L–M, exterior and interior of left valve. L 6.9 mm. Scale bar = 200 μm [D]

and small anterior and posterior laterals. Anterior adductor scar detached for ½ of length. Inner shell surface fluted and shell margin crenulated. Colour yellowish white.

Remarks. *Pillucina vietnamica* is widely distributed across the northern Indo-West Pacific on continental margins, although preliminary molecular results suggest that there may be more than a single widespread species. *Pillucina vietnamica* was reported as *Wallucina* sp. by Vohra (1971) and probably as *Divaricella* sp. by Tan & Woo (2010).

Austriella Tenison-Woods, 1881

Austriella Tenison-Woods 1881: 82. Type species: *Austriella sordida* Tenison-Woods (= *Lucina corrugata* Deshayes, 1843), by original designation.

Diagnosis. Shell large, H to 75.0 mm, thick-shelled, subcircular with defined posterior dorsal area, sculpture of thin low commarginal lamellae with broad interspaces, hinge teeth absent, anterior adductor scar long and detached for 4/5 of length, inner margin smooth. Periostracum thick, brown.

Remarks. This is a monospecific genus (see Glover, Taylor & Williams, 2008 for details of nomenclature), and although the name *Eamesiella* Chavan, 1951 has been used this is a junior synonym. *Austriella corrugata* is closely associated with mangrove habitats in the central IWP (Glover et al., 2008).

Austriella corrugata (Deshayes, 1843)
(Fig. 9A, B)

Lucina corrugata Deshayes, 1843: 1–2, Pl. 82.
Lucina philippinarum Reeve, 1850, Pl. 4, figs 18 a, b.
Austriella sordida Tenison-Woods, 1881: 83, Figs 210–211.
Eamesiella corrugata (Deshayes) – Sotto & Cosel, 1982: 57, Pl. 12, figs. 1, 2. Robba et al., 2002: 123, Pl. 7, fig. 8.
Austriella corrugata (Deshayes) – Glover et al., 2008: 27, figs 2, 3A; Tan & Woo, 2010: 10; Tan & Yeo, 2010: 290.

Type material. Three syntypes MNHN 20019. Type locality: given as Philippines on syntype label but in publication erroneously as 'Habite de la mer de Californie'.

Singapore material. Sungei Buloh, two live collected shells (NHMUK); NHMUK 1963212, one whole shell; NHMUK1963150, two whole shells, Cuming colln.

Indoaustriella Glover, Taylor & Williams, 2008

Indoaustriella Glover et al. 2008: 29. Type species: *Lucina* (*Cryptodon*) *plicifera* A. Adams, 1855, by original designation. Central Indo-West Pacific.

Diagnosis. Shell small, sculpture of thin, closely spaced commarginal lamellae with radial folds in anterior dorsal area; hinge without cardinal teeth, anterior and posterior teeth present or anterior lateral only. Anterior adductor muscle scar detached for half to 2/3 of length.

Remarks. Four species have been described from peri-mangrove muddy habitats in the central IWP (see Glover et al. 2008); *I. plicifera*, *I. dalli* (Lynge, 1909), *I. scarlatoi* (Zorina, 1978) and *I. lamprelli* Glover, Taylor & Williams, 2008. *Indoaustriella plicifera* has been confused with juvenile *Austriella corrugata* but the latter lacks lateral teeth, even in the juveniles, although it occupies similar habitats.

Indoaustriella cf *dalli* (Lynge, 1909)
(Fig. 9C–G)

Indoaustriella dalli – Glover et al., 2008: 35, figs 3D, 6D, 7C, 9.

Type material. Syntypes ZMC BIV-449: Type locality: Koh Chang, Gulf of Thailand.

Singapore material. Two whole juvenile shells from Sungei Buloh, NHMUK 20150059.

Remarks. These are tentatively identified as *I. dalli* that has both anterior and posterior lateral teeth. *Indoaustriella plicifera* is similar but lacks posterior lateral teeth (see Glover et al., 2008).

Easmithia Glover & Taylor, 2016

Easmithia Glover & Taylor, 2016. Type species: *Easmithia brevis* Glover & Taylor, 2016, by original designation. Central Indo-West Pacific.

Diagnosis. Shells small, semi-translucent, sub-ovate, usually higher than long, with fine, sharp commarginal lamellae and thin radial folds in the interspaces, anterior and posterior dorsal areas with elevated scaley lamellae. Hinge with two cardinal teeth and small to obscure anterior and posterior lateral teeth in the RV, LV without lateral teeth. Lunule lanceolate, asymmetric, greater part in RV. Anterior adductor scar usually short. Pallial line entire, sometimes lobate. Shell margin smooth.

Easmithia desiderata Smith 1885
(Fig. 9A, B)

Lucina (*Loripes*) *desiderata* Smith 1885: 185, pl. 13, fig. 10a.

Type material. Holotype (NHMUK 1887.2.9.2783) disintegrated. Type locality: off southern New Guinea.

Singapore material. One whole shell, L 4 mm and one valve, dredged Siglap and Johor Strait, 1933 Winckworth colln, NHMUK 20150060.

Remarks. *E. desiderata* can be distinguished from the similar *E. brevis* Glover and Taylor (2016) from Philippines by the much higher shell and stronger hinge with more prominent cardinal and lateral teeth. *Easmithia* species are recorded from shallow to offshore muddy habitats around S.E. Asia.

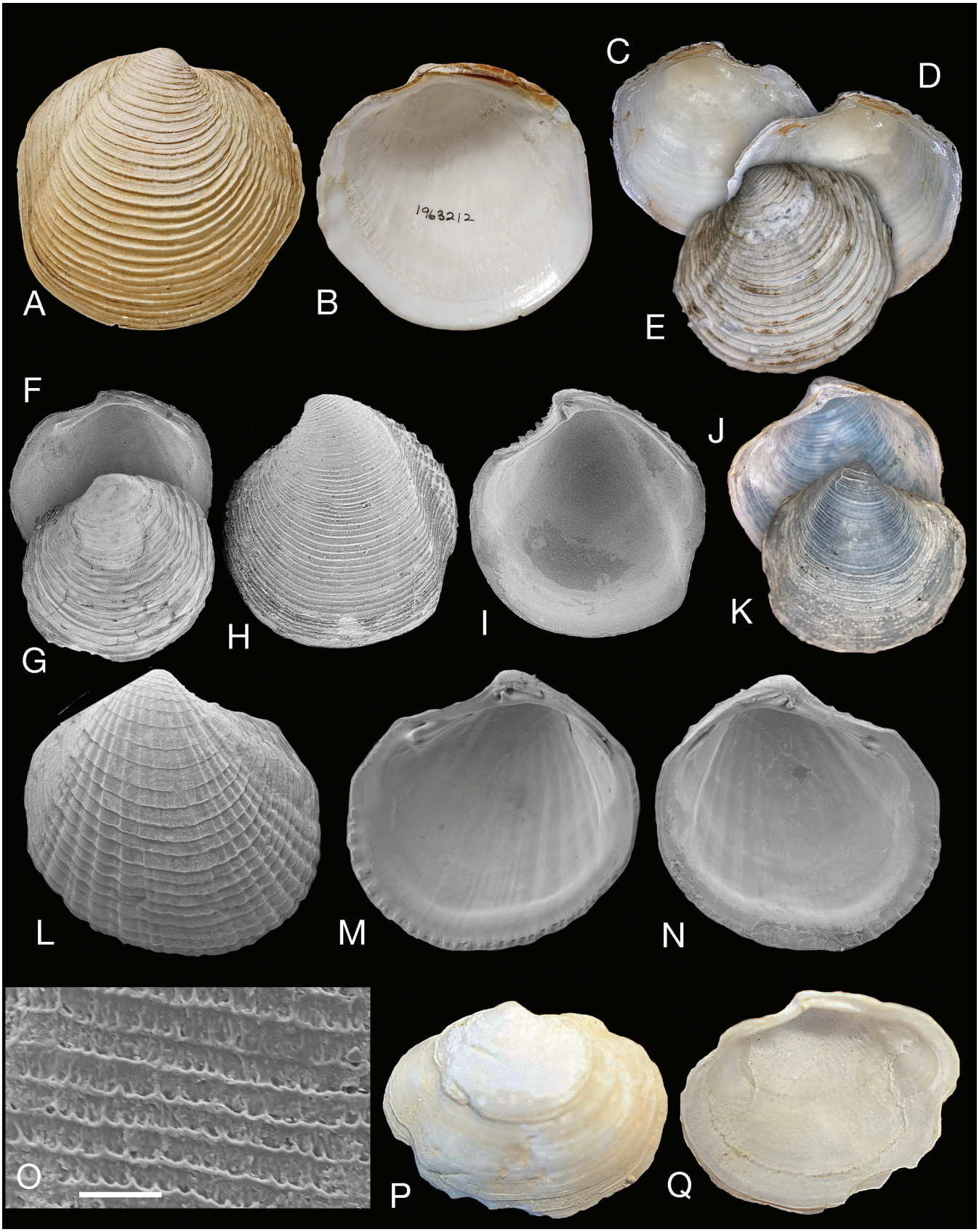

Fig. 9. A, B, *Austriella corrugata* (Deshayes, 1843) exterior and interior of right valve NHMUK 1963212, Singapore. L 59.3 mm; C–E, *Indoaustriella dalli* (Lynge, 1909) interior of left and right valves and exterior of left valve. Sungei Buloh. L = 5.8 mm; F, G, *Indoaustriella dalli* (Lynge, 1909) Interior of right valve and exterior of left valve, Sungei Buloh. NHMUK 20150059. L 5.7 mm; H, I, *Easmithia desiderata* (Smith, 1885) exterior of left valve and interior of right valve. Dredged Strait of Johor, 1933 Winckworth collection NHMUK 20150060 L 4.0 mm; J, K, *Scabrilucina vitrea* (Deshayes, 1844) juvenile, exterior and interior of right valve. Seringat Beach. NHMUK 20150061, L 4.4 mm; L–N, *Liralucina lyngei* Huber, 2015 exterior of right valve and interior of right and left valves. Seringat Beach. NHMUK 20150062. L 3.4 mm; O, *Liralucina lyngei* Huber, 2015 as Fig 8E, detail of microsculpture; P – Q, *Jallenia inanis* (Prashad, 1932), exterior and interior of right valve. Dredged stn DR14. NHMUK 20150063. L 11.9 mm. Scale bar = 10 μm [O]

Scabrilucina Taylor & Glover, 2013

Type species. *Cryptodon victorialis* Melvill, 1899, by original designation. Indian Ocean.

Diagnosis. Small to medium size, thin, ovoid to subtrigonal, strong posterior sulcus with broad sinus at posterior margin. Sculpture of sharp, fine, commarginal lamellae. Hinge with small to vestigial cardinal teeth in both valves, lateral teeth usually absent Anterior adductor muscle scar long, thin, ventrally detached from pallial line for ½–3/4 of length. Interior shell with translucent spots.

Scabrilucina vitrea (Deshayes, 1844)
(Fig. 9C, D)

Lucina vitrea Deshayes 1844: Pl.106.
Scabrilucina vitrea – Taylor & Glover 2013 p 75, figs 3B, 5 for full description.

Type material. Not located; type locality: Sumatra.

Singapore material. Juvenile single valve (L 4.4 mm), Seringat Beach, NHMUK 20150061.

Remarks. We tentatively assign this minute shell to *S. vitrea* that was first described from off Sumatra and now recorded from Andaman Sea, Malacca and the Gulf of Thailand (Taylor & Glover, 2013).

Liralucina Glover & Taylor, 2007

Liralucina Glover & Taylor 2007: 147.

Type species. *Phacoides sperabilis* Hedley, 1909, by original designation. Indo-West Pacific.

Diagnosis. Shells small (<10 mm), subcircular, inflated, with prominent radial ribs (up to 35) crossed by regularly spaced, very thin, commarginal lamellae. Hinge teeth small, LV with anterior lateral, two cardinal teeth and posterior lateral; RV with anterior lateral, a single cardinal and posterior lateral. Anterior adductor muscle scar short, slightly detached from pallial line. Inner shell margin crenulate.

Remarks. Glover & Taylor (2007) introduced the genus *Liralucina to* include four species from the Indo-West Pacific with strong radial ribs compared to *Parvilucina tenuisculpta* (Carpenter, 1864), the type species of *Parvilucina* from the temperate NE Pacific. Although poorly represented in museum collections and little researched, *Liralucina* species are probably widespread and sometimes abundant from the shallow subtidal to 300 m.

Liralucina lyngei Huber, 2015
(Fig. 9E–H)

Lucina (*Phacoides*) *pulchella* Lynge, 1909: 173, Pl. 3, Figs 13-15 (non *Lucina pulchella* C.B. Adams, 1845, a tellinid)
Parvilucina (*Parvilucina*) *pulchella* (Lynge) – Robba et al. 2002: 78, Pl. 7, Fig. 5.
Liralucina lyngei Huber, 2015: 426. (replacement name for *Lucina pulchella* Lynge, 1909).

Type material. Syntypes ZMUC-BIV-479, ZMUC-BIV-480, ZMUC-BIV-481. Type locality: Gulf of Thailand, several locations.

Singapore material. One whole shell from Seringat Beach, NHMUK 20150062.

Remarks. This small shell (L 3.4 mm) can be confused with *Pillucina* cf *profusa* but is distinguished by its more elongate shape, an external rather than internal ligament and prominent radial ribbing. *Liralucina lyngei* is similar to *Liralucina sperabilis* (Hedley, 1909) from the western Pacific (Glover & Taylor, 2007, fig. 25) but has both dividing and intercalating radial ribs. *Liralucina yamakawi* (Yokoyama, 1920) from Japan is similar but classified as *Pillucina* (*Sydlorina*) *yamakawi* by Matsukuma (2000). The relationships and status of these poorly documented species are uncertain.

Jallenia Glover & Taylor, 2016

Type species. *Dentilucina* (*Dentilucina*) *inanis* Prashad, 1932 by original designation. Indo-West Pacific.

Diagnosis. Shell L to 20 mm, sub-rectangular, with an irregular shell surface. Sculpture of fine lamellae. Lunule long, sunken. Hinge with two obscure cardinal teeth in LV and one in RV, lateral teeth absent. Anterior adductor short detached for ½ length. Pallial line sometimes divided, shell margin smooth, shell interior surface often with point scars of mantle attachment.

Jallenia inanis (Prashad, 1932)
(Fig. 9I, J)

Dentilucina (*Dentilucina*) *inanis* Prashad, 1932: pl. 5, figs 9–10.
Tinalucina inanis (Prashad) – Cosel & Bouchet, 2008: 191, figs 55 G–I, J–M, 56 G–I.
Cavatidens imajimai Habe, 1981: 90, pl. 2, fig. 4.
Jallenia inanis (Prashad) – Glover & Taylor, in press: XX , figs XXX

Type material. Holotype ZMA 135310, NCB, Naturalis, Leiden. L 6.7 mm, H 6. 0 mm. Type locality: Indonesia, north coast of Sumbawa, Saleh Bay 8°19'S, 117°41'N, 274 m (Siboga Expedition stn 312).

Singapore material. One valve (L 11.9 mm) from Eastern Fairway, stn DR14, 18m, NHMUK 20150063.

Remarks. Although known from Indonesia and Philippines *Jallenia inanis* is probably more widespread in the central IWP. Figures of the holotype of *Cavatidens imajimai* (NSMT-MO 56857) from southern Japan at 80–120 m (Higo et al., 2001: 160, fig. B 614) indicate that it is very similar to *J. inanis*. Little is known of the biology and relationships of this species but it resembles and maybe related to *Bretskya* Glover & Taylor, 2007. It likely also shares a similar unusual habitat of decaying wood and other plant debris.

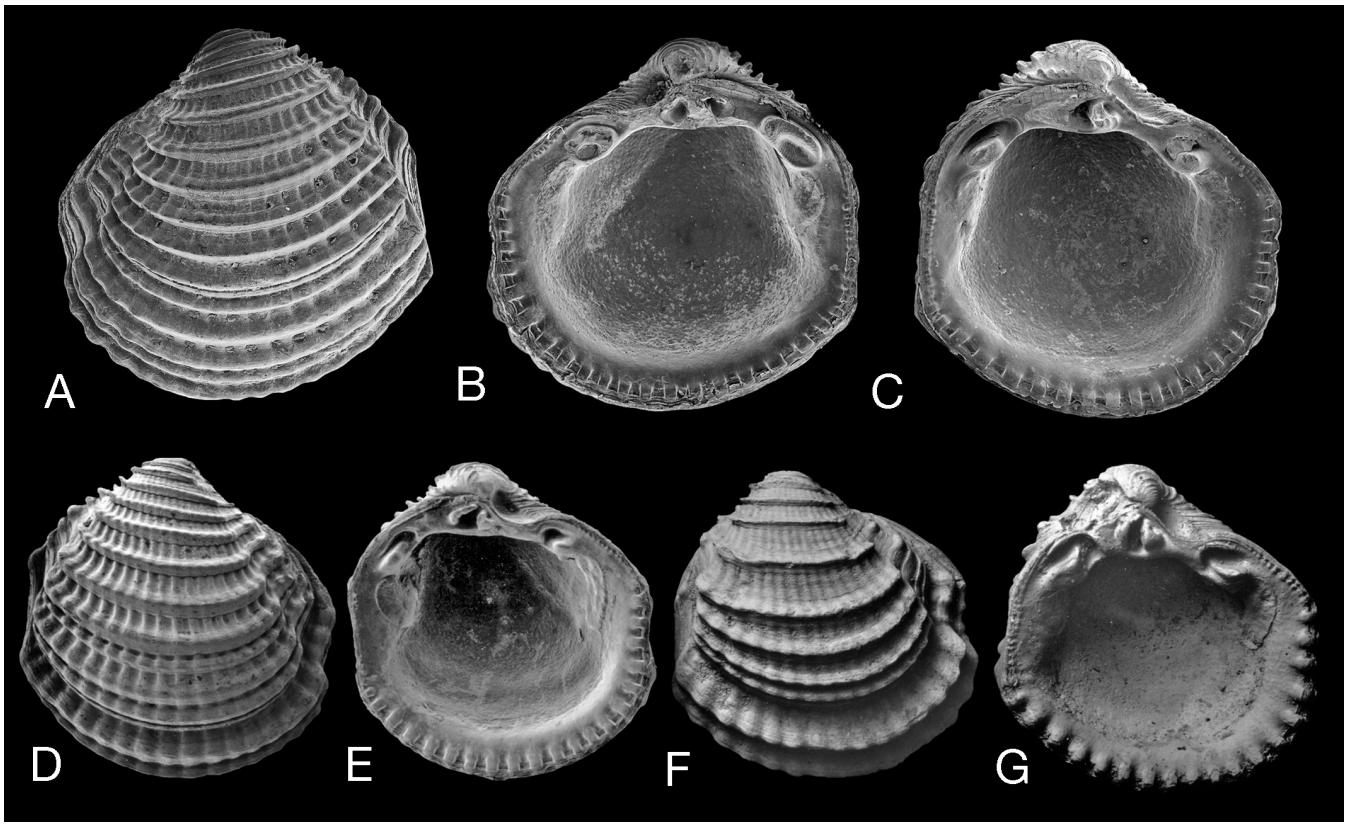

Fig. 10. *Cardiolucina macassari* (Prashad, 1932). A–C, Exterior of left valve and interior of right and left valves. Seringat Beach. NHMUK 20150064. L 4.0 mm; D, E, *Lucina pisum* Reeve (1850) paralectotype NHMUK 1963552. Exterior of right and interior of left valves. L 3.9 mm; F, G, *Dentilucina* (*Bellucina*) *macassari* Holotype ZMA Moll. 135275, NCB Naturalis, Leiden, exterior of right and interior of left valves. L 5.1 mm.

Cardiolucina Sacco, 1901

Cardiolucina Sacco, 1901 (June): 89.
Bellucina Dall 1901 (August): 806.

Type species. *Lucina agassizi* Michelotti, 1839, by original designation.

Diagnosis. Small (<14 mm) subcircular, inflated to subspherical. Sculpture of radial ribs crossed by commarginal lamellae that are often fluted. Lunule can be deeply impressed. Hinge plate thick, teeth prominent, two cardinal teeth and anterior and posterior lateral teeth in both valves. Anterior adductor scar short, slightly detached from pallial line. Inner shell margin denticulate. See Taylor & Glover (1997), Glover & Taylor (2007) and Cosel & Bouchet (2008) for further details.

Remarks. *Cardiolucina* is one of the most speciose of the Lucinidae genera, often abundant from the shallow intertidal to bathyal depths. In molecular analysis they form a distinct subgroup within the Lucininae that diversified within the Miocene (Taylor et al., 2011). Fourteen species are now recognised: 12 from the IWP, one from southern Australia and two from the southern Atlantic. They were reviewed by Taylor & Glover (1997) but since then *C. undula* has been described from New Caledonia (Glover & Taylor, 2007) and we now regard *C. macassari* (Prashad, 1932) as a distinct species rather than as a form of *C. semperiana* (see below).

Cardiolucina macassari (Prashad, 1932)
(Fig. 10A–G)

Lucina pisum Reeve, 1850 (part) pl. 11, fig. 66b (non *Lucina pisum* Sowerby, 1836 – a Cretaceous fossil species).
Dentilucina (Bellucina) macassari Prashad, 1932: 163, pl. 5, figs 13–16.
Cardiolucina semperiana (Issel) – Taylor & Glover, 1997: 107, fig. 21. Non *C. semperiana* Issel 1869, Singapore specimen is C. *macassari.*
Cardiolucina macassari (Prashad) – Glover & Taylor, 2016.

Type material. *D.* (*B.*) *macassari*, holotype ZMA Moll. 135275, NCB Naturalis, Leiden. Indonesia, Sulawesi, Makassar, 5°06”S, 119°22”E, 32 m (Siboga Expedition stn 71) (Fig 9F, G). *Lucina pisum* (part) four paralectotypes NHMUK 1963552, Singapore, 6 fathoms, sandy mud, Cuming collection (Fig. 9D, E).

Singapore material. Four whole shells Seringat Beach, NHMUK 20150064; five live collected shells, outside Marina Bay, stn DR 31, 19 m and TR 30, 19 m; 28 whole shells dredged Strait of Johor, Winckworth coll. 06/1933, NHMUK 1953.1.30.

Description. Shell white, very small L 4.8 mm, highly inflated, sculpture of prominent coarse, irregularly spaced commarginal lamellae that are more elevated near the umbones, crossed by rounded radial ribs giving fluted appearance to commarginals. Prominent posterior sulcus

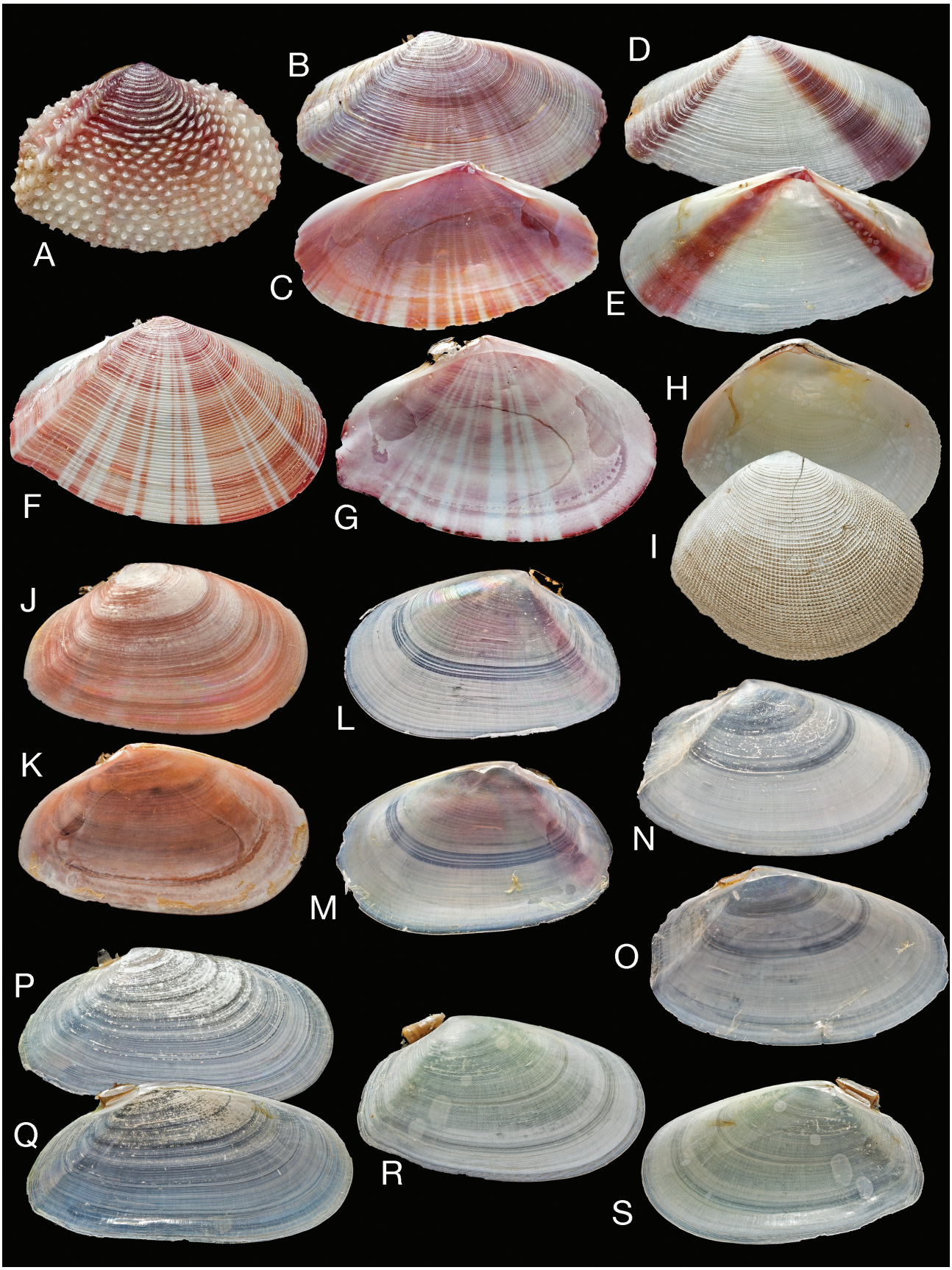

Fig. 11. Tellinidae from Seringat Beach. A, *Scutarcopagia pulcherimma* (Sowerby, 1825) right valve. L 9.2 mm; B, C, *Tellinella staurella* (Lamarck, 1818) exterior and interior of right valve. L 16.1 mm; D, E, *Tellinella staurella* colour variant. L 12.7 mm; F, G, *Tellinella virgata* (Linnaeus, 1758) exterior of right and interior of left valves. L 33.4 mm; H, I, *Clathrotellina carnicolor* (Hanley, 1846) interior of left and exterior of right valves. L 20.5 mm; J, K, *Nitidotellina valtonis* (Hanley, 1844) exterior of right valve and interior of left valve. L 11.9 mm; L, M, *Nitidotellina lux* (Hanley, 1844) exterior of left and interior of right valves. L 13.8 mm; N, O, *Hanleyanus oblongus* (Gmelin, 1791) exterior of right and interior of left valves. L 14.8 mm; P, Q, '*Nitidotellina'* sp. exterior of right and interior of left valve. L 11.1 mm; R, S, *Jactellina clathrata* (Deshayes 1835) exterior and interior of right valve. Note oblique scissulate sculpture. L 14.6 mm.

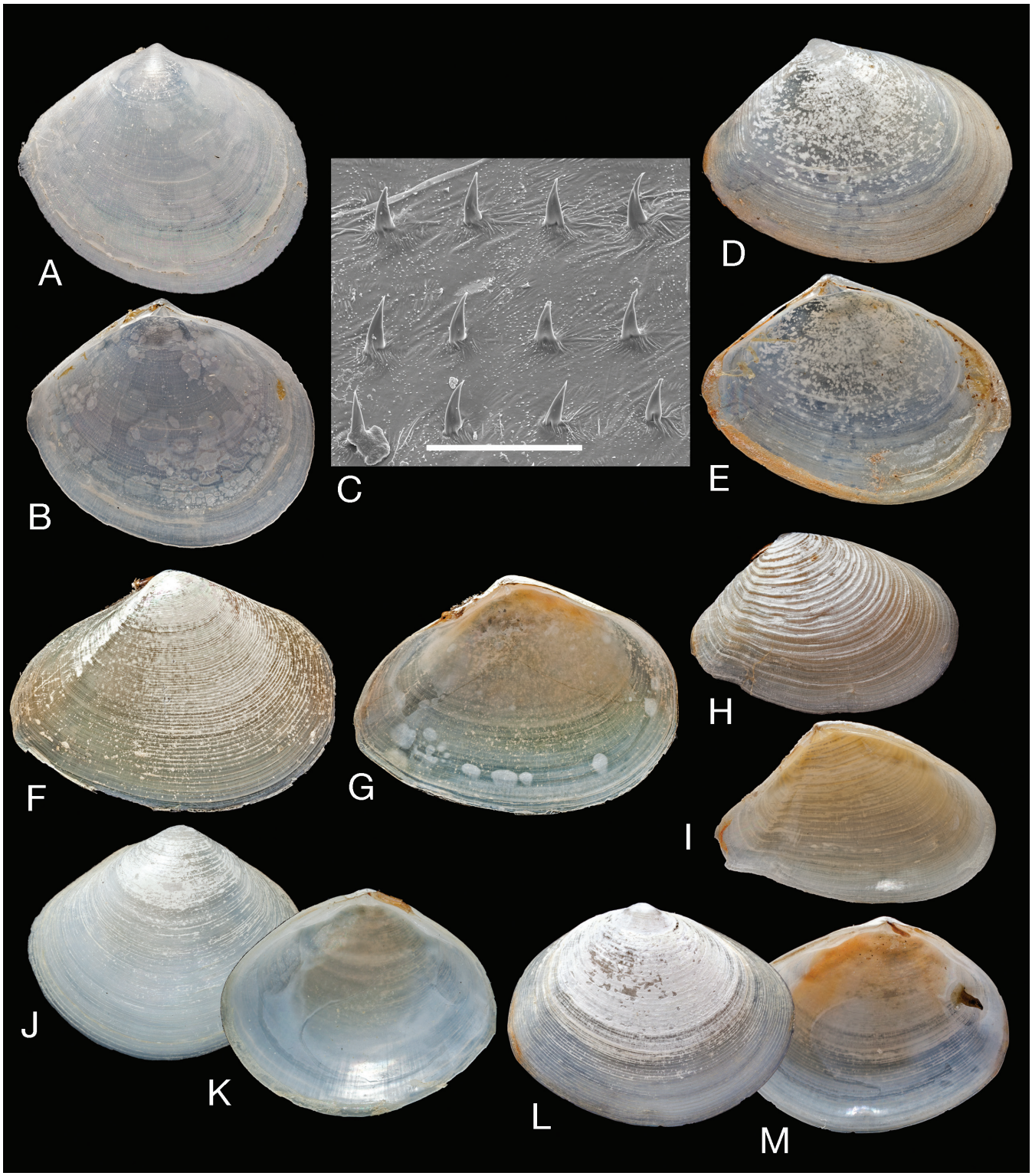

Fig. 12. Tellinidae and a Semelidae from Seringat Beach. A, B, *Arcopaginula inflata* (Gmelin, 1791) exterior of right and interior of left valve. L 13.8 mm; C, *A. inflata* detail of periostracal spikes; D, E, *Tellinimactra edentula* (Spengler, 1798) exterior of right valve and interior of left valve. L 7.9 mm; F, G, *Jitlada philippinarum* (Hanley, 1844), exterior of right and interior of left valves. L 17.7 mm; H, I, *Tellinangulus aethiopica* (Thiele & Jaeckel, 1931) exterior of left and interior of right valves. L 6.2 mm; J, K, *Pinguitellina pinguis* (Hanley, 1844) exterior of left and interior of right valves. L 10.3 mm; L, M, *Semele* cf *fragillima* (Issel 1869) similar in shape to and easily confused with *Pinguitellina pinguis* but has an internal ligament typical of Semelidae. L 8.3 mm. Scale bar = 100 μm [C]

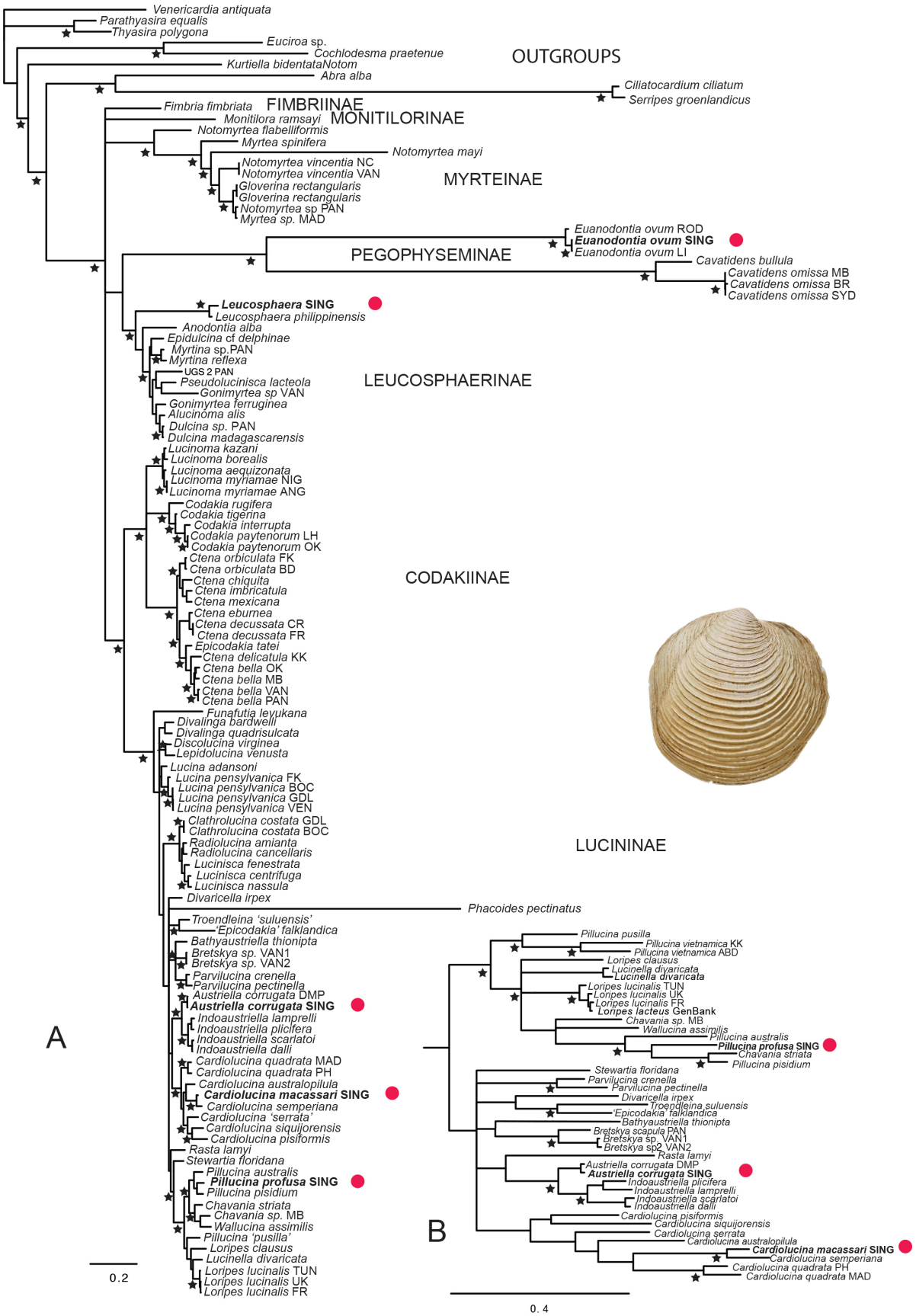

Fig. 13. A, combined gene tree for Lucinidae based on three genes (18S, 28S and cytochrome b) based on Bayesian inference using MrBayes. Support values of 95% and above are indicated by a star. Singapore species are indicated in bold and a red spot; B, portion of cytochrome b tree with details of *Pillucina* and *Cardiolucina* clades. Details of other lucinids and outgroups are fully documented in Taylor et al. (2014). GenBank numbers and NHMUK voucher registration numbers for new sequences of Singapore species are as follows: *Euanodontia ovum* (NHMUK 20150048) – 18S KP980695, 28S KP980699, cyt b KP980705; *Leucosphaera cf philippinensis* (NHMUK 20150047) – 18S KP980696, 28S KP980700, cyt b KP980704; *Pillucina profusa* (NHMUK 20150049) – 18S KP980697, 28S KP980701, cyt b KP980702; *Cardiolucina macassari* (NHMUK 20150050) – 18S KP980694, 28S KP980698, cyt b KP980703.

with commarginal lamellae only. Lunule short, heart-shaped, deep. Hinge robust with strong cardinal teeth in both valves, large anterior and posterior laterals in both valves. Anterior adductor scar short, barely detached from the pallial line. Pallial line entire, shell margin coarsely dentate.

Distribution. Singapore, Thailand, Indonesia, Philippines, intertidal and shallow water.

Remarks. In a previous paper, we (Taylor & Glover, 1997) considered *C. macassari* as an eastern form of *C. semperiana*. Since then study of more samples from the type locality of *C. macassari* shows that it is a distinct species living in Southeast Asia. The syntypes of *Lucina pisum* Reeve included two species, one from Singapore and the other Port Essington, Northern Territory, Australia and the selected lectotype (see Taylor & Glover, 1997: 103, NHMUK 1963194/1) from Port Essington has the distinctive, deeply excavated lunule mentioned by Reeve (1850) in the original description. As the name *L. pisum* Reeve was preoccupied by *L. pisum* Sowerby, 1836 the replacement name *Lucina eucosmia* Dall, 1901 is used for the northern Australian species. *Dentilucina* (*Bellucina*) *macassari* Prashad is the next available name for Reeves's *Lucina pisum* from Singapore.

DISCUSSION

The island of Singapore is situated within the globally richest area of marine bivalve diversity but its marine habitats have been extensively altered by much development including land reclamation, harbour construction and channel dredging over the last 50 years. Nonetheless, pockets of diversity remain (see http://www.wildsingapore.com/) and surprisingly, the 10-year old artificial Seringat Beach supported high numbers of infaunal bivalves with 46 species in 11 families.

Our study has identified 18 species of chemosymbiotic Lucinidae from Singapore, with 12 species (six live, six dead) recovered during the 2013 workshop and two species from previous collections at Sungei Buloh with a further four species recorded from museum collections. It is likely that some species known only from museum records may now be locally extinct, including *Codakia paytenorum* and *Lepidolucina venusta*. Very small species such as *Pillucina pusilla* and *Easmithia desiderata* may still be extant but unlikely to be recognised without microsampling. By comparison the highest diversity of Lucinidae yet recorded resulted from intensive sampling in the central Philippines with 48 species from less than 200 m and a total of 78 species including all taxa down to 1000 m (Glover & Taylor, 2016). Further afield, 34 species were recorded from New Caledonia from shallow water (Glover & Taylor, 2007). By contrast, in the Caribbean we record 21 species from intensive sampling around the island of Guadeloupe, while more broadly in the tropical West Atlantic around 46 species are known from less than 200 m depth (Taylor & Glover, work in progress).

The most abundant species in Seringat Beach was *Pillucina profusa* and this was also the most common shallow water seagrass associated species in the central Philippines from where it was first described (Glover & Taylor, 2016). Other *Pillucina* species are also well known in similar environments, for example *P. vietnamica* from Gulf of Thailand (Meyer et al., 2008) and Nakaoka et al. (2002) record high densities of *Pillucina* sp from southwestern coast of Thailand. In southern Japan *Pillucina pisidium* is abundant in *Zostera* beds (Uede & Takahashi, 2008). Interestingly, no living *Pillucina vietnamica* were found during our survey in 2013 but Vohra (1971) recorded it (as *Wallucina* sp) abundantly on a transect in shallow water seagrass in eastern Singapore. In phylogenetic analyses *Pillucina* species group in a subclade with other small lucinids such as *Wallucina assimilis*, *W. fijiensis* and *Chavania striata* that are also often abundant in shallow seagrass communities in Australia (Barnes & Hickman, 1999; EG & JT unpublished observations). Another related species and one of the most intensively studied is *Loripes lucinalis* that reaches very high densities in the Mediterranean (Johnson et al., 2002; Rossi et al., 2013) and Mauritania (van der Heide et al., 2012). Some lucinids are closely associated with mangrove habitats and these have been recorded from the Strait of Johor particularly from Sungei Buloh Wetland Reserve. These include *Austriella corrugata*, *Indoaustriella dalli*, *Cavatidens bullula* and *Pegophysema philippiana* although the latter species is rarely found at present.

As well as Lucinidae, other small infaunal bivalves were abundant at Seringat Beach, particularly species of Tellinoidea, including *Pinguitellina*, *Nitidotellina*, *Jactellina* and *Tellinella*. Amongst these we recovered two live shells of the rarely recorded species *Tellinangulus aethiopicus*, and also some living *Arcopaginula inflata* that is widely known from the Indo-West Pacific but we show here that it possesses unusual, previously unrecognised periostracal spines (Fig. 12C). Tellinoidea are ecologically important in tropical shallow water communities but their systematics is in need of major revision with much confusion of generic concepts and species identifications. Huber (2015) has made a major contribution with a new classification and many nomenclatural changes. The next step would be the development of a comprehensives molecular framework to establish the phylogenetic relationships of this major group of bivalves.

Lately, there has been a newly revived interest in the functional ecology of tropical seagrass beds, including the interaction of seagrass and chemosymbiotic bivalves, especially Lucinidae (van der Heide et al., 2012; Rossi et al., 2013; van der Geest et al., 2014). Although Seringat Beach is an artificial and recent construction, it would provide a convenient and local habitat for study, with the possibilities of better understanding of chemosymbiotic bivalves, particularly the abundant *Pillucina profusa*, and their ecological relationship with seagrass communities. More widely, it might be a suitable research location for the study of colonisation of artificial soft substrate habitats.

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