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Deep-sea Protobranchia (Bivalvia) from the SJADES biodiversity cruise, with a description of a new species of *Propeleda* (Nuculanidae)

Tan Koh Siang

Abstract. The diversity of benthic protobranch bivalves collected during the South Java Deep-Sea (SJADES) Biodiversity Expedition 2018 was evaluated. Living and dead material was brought up by dredging and trawling from depths ranging from 100 to 2,000 m across 37 stations off the southeast and southwest coasts of Sumatra and Java respectively in the Sunda Strait and Indian Ocean. A total of 37 species in 17 genera belonging to six families (Nuculidae: *Nucula*, *Acila*, *Ennucula*; Solemyidae: *Acharax*; Nucinellidae: *Huxleyia*, *Nucinella*; Nuculanidae: *Nuculana*, *Propeleda*, *Saccella*, *Yoldia*, *Megayoldia*, *Orthoyoldia*; Malletiidae: *Carinineilo*, *Malletia*, *Katadesmia*; Neilonellidae: *Neilonella*) were identified from some 961 dead valves and 171 intact, living individuals. Of these, 15 are regarded as new records for Indonesia. Amongst nine nuculid species found, the large *Acila fultoni* was surprisingly common and widely distributed in the area and is a new record for Indonesia. Two tiny nucinellids in the genera *Nucinella* and *Huxleyia*, represented only by dead shells, are also new Indonesian records. Not unexpectedly, the suborder Nuculanida comprised the most diverse group, with 11 nuculanids, seven malletiids, and five neilonellids. The most widely distributed, relatively large, deeper-water protobranchs were the nuculids *Nucula donaciformis*, *Acila fultoni*, *Ennucula bengalensis*, the nuculanid *Sacella sibogai*, and the malletiids *Malletia arrouana*, *M. encrypta*, and *Carinineilo* sp. They were all represented by living individuals. In contrast, at least 15 species were relatively rare, mostly represented only by dead shells, with many reported just from a single locality. These included the solemyids, nucinellids, as well as several nuculanids, malletiids, and neilonellids. A new species of *Propeleda* (Nuculanidae) is also described from 1,600 m in the Sunda Strait. Despite the restricted geographical coverage of this study, the diversity of protobranchs observed is comparable to the 35 species documented from the Siboga Expedition in the eastern half of the Indonesian archipelago a century ago.

Key words. checklist, protobranchs, taxonomy, Nuculoida, Nuculanoida

INTRODUCTION

For two weeks in March–April 2018, the South Java Deep-Sea (SJADES) Biodiversity Expedition collected benthic invertebrates and fish from the southern region of the Sunda Strait and along the southwest coastline of Java, from Pelabuhan Ratu to the vicinity of Cilacap at various depths between 100 m and 2,000 m. Many living and dead molluscs were brought up on board R/V *Baruna Jaya VIII* using trawls and dredges, amongst which were a significant number of protobranch bivalves. The presence of this distinctive (but possibly paraphyletic) group (see Combosch et al., 2017) is not unexpected in the area given their widespread benthic distribution in the world's oceans (Allen, 1978; Zardus, 2002), but the deep-water molluscan fauna off the southern coast of Java is poorly documented.

Amongst the early European expeditions (notably on the Challenger, Siboga, Valdivia, Galathea, and Vityaz) to the Indonesian archipelago, only the Danish Galathea and Soviet Vityaz cruises sampled in southwestern Java. However, the sampling stations were located farther offshore at deeper depths in the vicinity of the Sunda and Java Trenches. In the case of Galathea these efforts were mostly unsuccessful (Bruun, 1957; see however Knudsen, 1970), whilst the Russian expedition collected several undetermined protobranchs (*Yoldiella* sp.) from 6,800 m (Beliaev & Vinogradova, 1961; Filatova, 1961). Earlier, Mortensen (1923) surveyed the shallower waters of the Sunda Strait in considerable detail, but the deeper benthos was not sampled. More recently, the German Sonne geological expedition in 1999 collected *Acharax johnsoni* (Solemyidae) from 2,970 m at a methane vent site off southwest Java (Wiedicke et al., 2002; Neulinger et al., 2006). A Japanese expedition on R/V *Yokosuka* to the Java Trench in 2002 did not report on protobranchs, although a new species of the vesicomyid bivalve *Calyptogena garuda* from 2,000 m was described off southwest Java (Okutani & Soh, 2005). The Japan-Indonesia deep sea joint exploration project (2006) examined the demersal fisheries resources off the western and central southern coasts of Sumatra and Java respectively, employing deep-sea trawls. An accompanying illustrated photo guide

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to the larger fishes, shrimps, and cephalopods (Inada & Wudianto, 2006) did not include bivalves.

Farther east, the Challenger and Siboga expeditions collected material east of Java in the Flores and Banda Seas, and many deep-sea bivalves including protobranchs were described by Smith (1885) and Prashad (1932a). To the west of Java, a number of protobranchs from deeper waters off Sumatra (and elsewhere in the Indian Ocean) on the German Valdivia cruise were described by Thiele & Jaeckel (1931). However, since then, only the French–Indonesian CORINDON and KARUBAR expeditions in the early 1980s and 1990s sampled in the vicinity of the Moluccas as well as the Kai, Aru, and Tanimbar Islands of eastern Indonesia (Bouchet et al., 2008), but the protobranchs do not appear to have been examined to date.

Elsewhere in the Indo-Pacific region, deep-sea bivalves, particularly protobranchs, have also been given rather limited attention recently. At the turn of the 20th century, the Investigator expedition collected new species of deep-water protobranchs from the Arabian Sea, Bay of Bengal, and Andaman Sea (see e.g., Smith, 1895, 1906; Alcock, 1902; Annandale & Stewart, 1909; Winckworth, 1940). The John Murray expedition also collected several deep-sea protobranch species from the western half of the Indian Ocean (Knudsen, 1967). The Japanese deep-sea expeditions off the Pacific coast of Japan have resulted in the discovery of a number of protobranch species new to science since the 1950s (e.g., Habe, 1958; Okutani, 1962). In the South China Sea, the diversity of protobranchs from deeper waters has been reported upon by mainland Chinese and Taiwanese workers (e.g., Xu, 1984a, b, 1990, 1999; Lan & Lee, 2001). Protobranch material from the recent joint French–Filipino PANGLAO 2005, AURORA 2007, and LUMIWAN 2008 expeditions to the Philippines (Bouchet et al., 2008) have not been reported upon, apart from *Nucinella giribeti*, a shallow water species (Glover & Taylor, 2013). Two earlier French MUSORSTOM expeditions to the Philippines in 1976 and 1980 reported only two protobranchs: a nuculid *Leionucula niponica* from 750–925 m off Lubang Island (Poutiers, 1981) and a nucinellid *Nucinella boucheti* from 1,580–1,610 m off Mindoro Island (La Perna, 2005) respectively. Likewise, the MUSORSTOM expeditions in and around New Caledonia during the 1990s collected large quantities of crustacean and molluscan material (Bouchet et al., 2008; Richer de Forges et al., 2013), but protobranchs, apart from the nuculids (Bergmans, 1991) are still poorly documented from the region, particularly from deeper waters.

This study provides a first look at protobranch diversity off southwest Java, based on living and dead shells from depths of 100–2,000 m obtained by the SJADES expedition.

MATERIAL AND METHODS

Bivalves were obtained from the following sampling stations and depths: DW01 (Sunda Strait, 100–104 m), CP02 (Sunda Strait, 257–281 m), CP03 (Sunda Strait, 283–398 m), DW06 (Teluk Semangka north of Pulau Tabuan, 266–294 m), CP07 (Teluk Semangka, north of Pulau Tabuan, 379–409 m), CP08 (Teluk Semangka north of Pulau Tabuan, 425–442 m), CP10 (Teluk Semangka north of Pulau Tabuan, 429–446 m), CP13 (Sunda Strait, 1,259–1,268 m), CP14 (Sunda Strait, 1,528–1,539 m), DW17 (Sunda Strait, 448–469 m), CP18 (Sunda Strait, 1,060–1,073 m), DW19 (off Tanjung Layar, SW Java, 172–182 m), CP20 (off Tanjung Layar, SW Java, 325–362 m), CP22 (off Tanjung Layar, SW Java, 864–872 m), CP24 (off Tanjung Layar, SW Java, 1,044–1,068 m), CP25 (off Tanjung Layar, SW Java, 876–937 m), CP26 (off Tanjung Panto, east of Pulau Tinjil, 517–727 m), CP27 (off Tanjung Panto, east of Pulau Tinjil, 481–557 m), CP28 (off Tanjung Panto, east of Pulau Tinjil, 957–1,022 m), CP30 (off Tanjung Panto, east of Pulau Tinjil, 1,270–1,341 m), CP31 (off Tanjung Panto, east of Pulau Tinjil, 1,763–1,796 m), DW32 (off Tanjung Bayongkarenceng, 805–977 m), CP33 (off Tanjung Bayongkarenceng, 312–525 m), CP35 (off Tanjung Gedeh, 603–686 m), CP44 (off Tanjung Simanggu, 970–1,013 m), CP45 (off Tanjung Gedeh, 684–851 m), DW46 (off Tanjung Gedeh, 540–654 m), CP47 (off Tanjung Gedeh, 476–530 m), CP50 (Teluk Pelabuhanratu, 383–425 m), CP51 (Teluk Pelabuhanratu, 569–657 m), CP52 (Teluk Pelabuhanratu, 1,124–1,156 m), CP55 (Teluk Pelabuhanratu, 378–379 m), CP57 (Teluk Pelabuhanratu, 223–269 m), CP58 (Teluk Pelabuhanratu, 505–579 m), CP59 (Teluk Pelabuhanratu, 579–659 m), CP62 (Sunda Strait, 1,623–1,630 m), DW63 (off Krakatau, Sunda Strait, 208–250 m).

Station nos 01 through 25, and 61 to 63 were located in the Sunda Strait. The remaining stations were in the Indian Ocean off the western third of the southern coast of Java (Fig. 1; see also Chim et al., 2021, this volume).

Dredged and trawled samples were sieved in seawater using 5-mm and 1-mm sieves on the vessel deck and both living and dead bivalves were isolated. All living bivalve specimens were preserved in 80% EtOH on the vessel, and further sorted to morphospecies under a stereomicroscope in the laboratory. Dead shells were likewise stored in ethanol and later washed in water and dried for examination. The exterior and interior surfaces of the shells as well as the anatomy of preserved animals were also examined under a stereomicroscope.

Higher taxonomic classification adopted here loosely follows that of Bieler et al. (2010), Carter (2011), Sharma et al. (2013), Cosel & Gofas (2019), and Sato et al. (2020). Descriptive terminology was adapted from Killeen & Turner (2009). The following abbreviations are used in the text: LV: left valve; RV: right valve; SL: shell length; SW: shell width.

RESULTS

Protobranchs were obtained from 37 stations (Fig. 1) and depths ranging between 100 and 1,630 m. From a total of eight successful dredges from depths ranging between 100 and 977 m, five (DW01, 06, 17, 32, 63) contained protobranchs. Of the 45 trawls (CP01 to 62) deployed over depths from 250

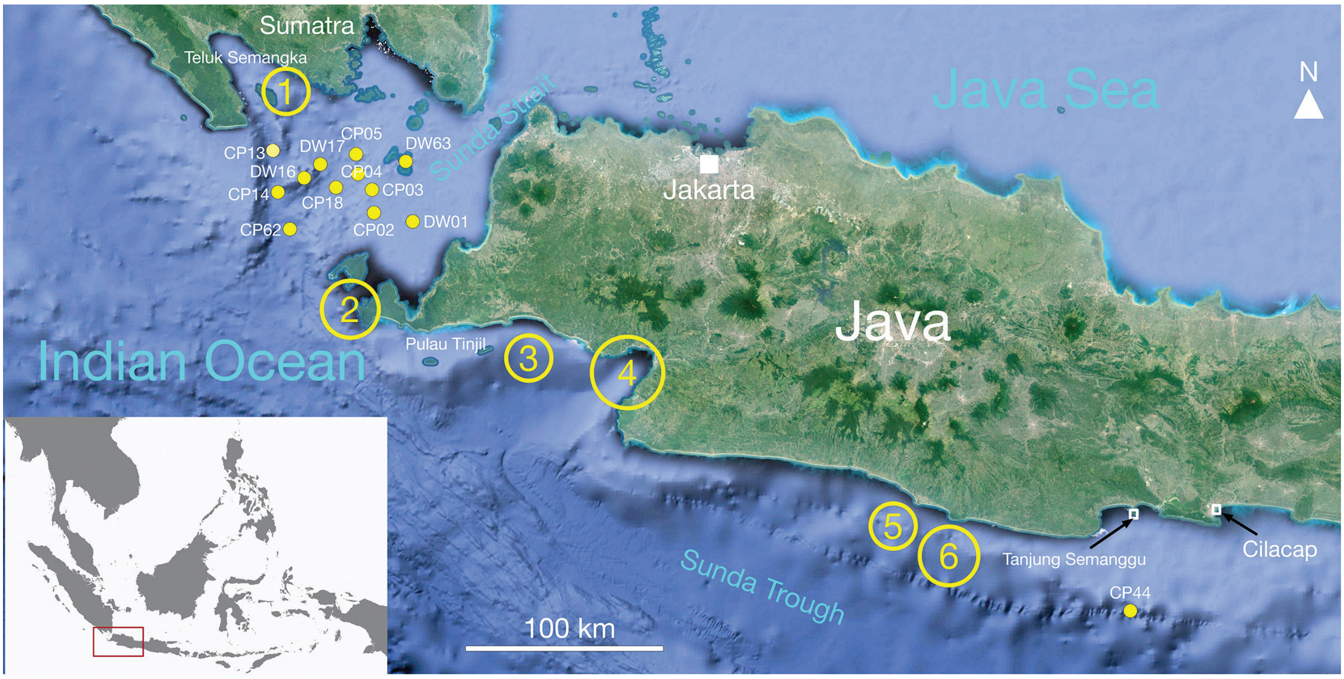

Fig. 1. Approximate positions of sampling stations where protobranchs were collected in the Sunda Strait and off the southwest coastline of Java during the SJADES expedition. Closed circles: individual stations with corresponding station numbers DW01, CP02, CP03, CP13, CP14, DW17, CP18, CP62, DW63 are all in the Sunda Strait except CP44, which is off Tanjung Simanggu; numbered open circles enclose a cluster of sampling stations: 1, Teluk Samangka north of Pulau Tabuan (DW06, CP07, CP08, CP10); 2, off Tanjung Layar, southwest Java (DW19, CP20, CP22, CP24, CP25); 3, off Tanjung Panto, east of Pulau Tinjil (CP26, CP27, CP28, CP30, CP31); 4, Teluk Pelabuhanratu (CP50, CP55, CP57, CP58, CP59); 5, off Tanjung Bayongkarenceng (DW32, CP33); 6, off Tanjung Gedeh (CP35, CP45, DW46, CP47).

to 1,630 m, protobranchs were present in 32 trawls. Living material occurred in 26 trawls and one dredge.

Some 961 dead valves and 171 individuals with intact shells and soft parts were examined. The sample sizes of living and dead representatives indicated against the station numbers for each species below are the number of valves (i.e., right, left, or partially broken but identifiable) found in each sample. Dead but intact specimens are indicated separately.

TAXONOMY

Order Nuculida

Family Nuculidae Gray, 1824

Species obtained were from three genera, namely *Acila*, *Nucula*, and *Ennucula*. An inner nacreous (aragonitic) layer is present in all nuculids. Species of *Acila* and *Nucula* (together with *Deminucula*, *Lamellinucula*, *Pronucula*) possess fine crenulations along the inner ventral margins of both valves. In contrast, members of the genus *Ennucula* (together with *Austronucula*, *Brevinucula*, *Condylonucula*, *Leionucula*, *Nuculoma*, and *Neonucula*) lack these crenulations. The only exception involves *Linucula* spp. which are confined to New Zealand and has crenulations along both inner dorsal and ventral margins.

While this is a convenient and traditional morphological distinction (Schenck, 1934; Gofas & Salas, 1996; Kilburn, 1999; Beu, 2006), Sharma et al. (2013) contended that the loss of crenulations may have occurred in unrelated lineages and has little phylogenetic significance. *Acila* has characteristic divaricate surface sculpture on the external surface of their shells (Adams & Adams, 1858; Schenck, 1936), which is absent in *Nucula* and *Ennucula*. Instead, the shell surface sculpture in *Nucula* is often cancellate in appearance, due to the intersections of fine radial and commarginal lines. In *Ennucula*, the shell surface appears generally smooth without radial lines and only commarginal growth lines observed. Bergmans (1978) pointed out that *Nuculoma* and *Leionucula* are both senior synonyms of *Ennucula*, but there has been a recent shift to limit genera defined by fossil species, such as *Nuculoma* and *Leionucula*, to fossil shells only (Cosel & Gofas, 2019), although concerns for taxonomic stability have been raised (Marshall & Spencer, 2013). For instance, *Tindaria* Bellardi, 1875, is still retained for recent shells, despite its type species being the Pliocene fossil *Tindaria arata* Bellardi, 1875.

Nucula Lamarck, 1799

The genus *Nucula* comprises fossil and extant marine species with small (generally <3 cm), oval shells that possess fine crenulations along the inside ventral margin of both valves. These crenulations are congruent with external radial lines that are often present on the external surface of the shell. Nacre covers the interior surfaces of the valves.

Type species. *Arca nucleus* Linnaeus, 1758.

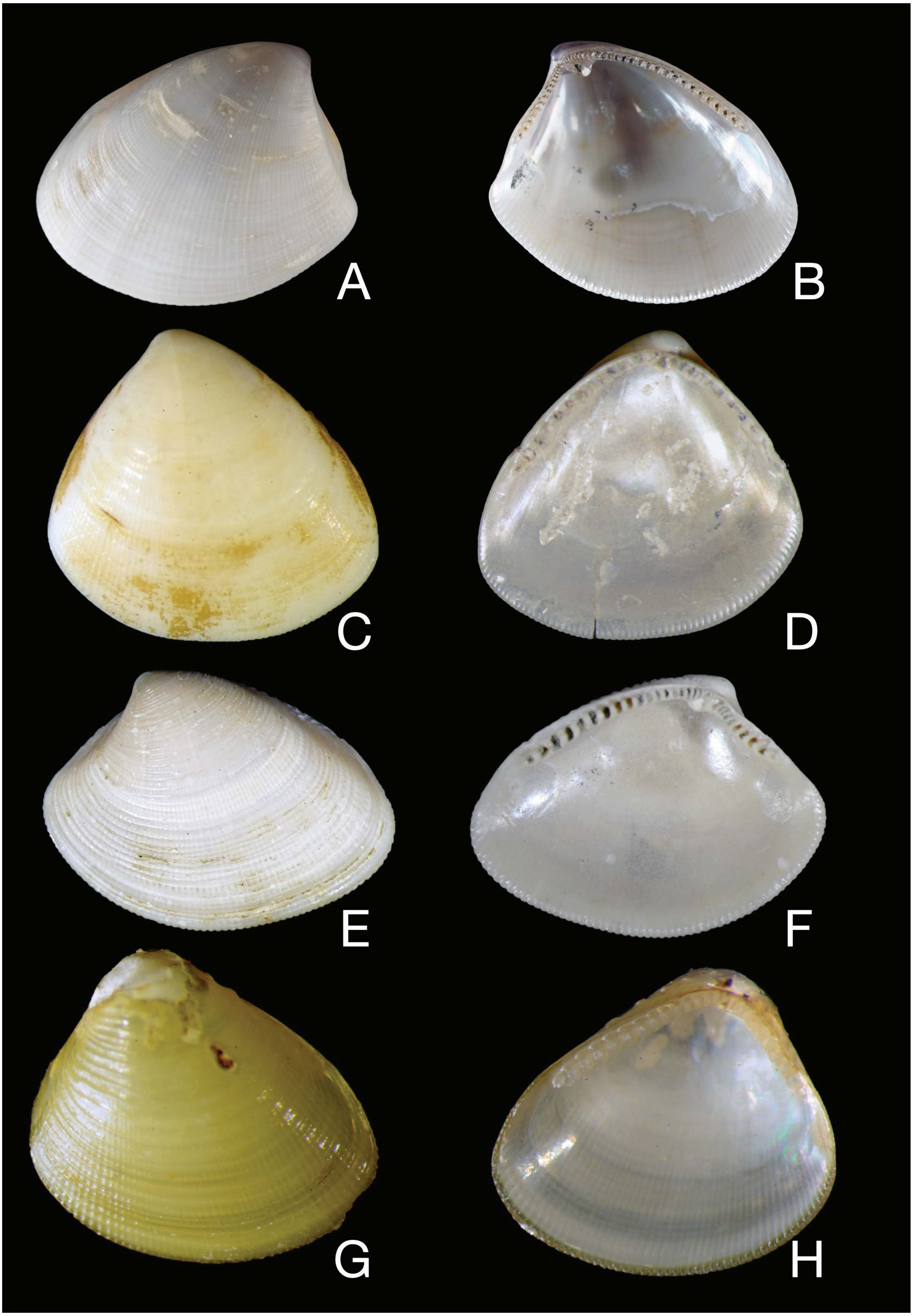

Fig. 2. Nuculidae. A, B, *Nucula donaciformis* Smith, 1895, left valve, station DW32, SL=18.0 mm; C, D, *Nucula* cf. *semen* Thiele, in Thiele & Jaeckel, 1931, right valve, station CP45, SL=6.2 mm; E, F, *Nucula* cf. *sumatrana* Thiele, in Thiele & Jaeckel, 1931, right valve, station DW06, SL=6.2 mm; G, H, *Nucula trigonica* Lan & Lee, 2001, right valve, station CP45, SL=4.4 mm.

Nucula donaciformis Smith, 1895
(Fig. 2A, B)

Nucula donaciformis Smith, 1895: p. 15, pl. 2 fig. 8 (265–457 m in Bay of Bengal, off Coromandel coast).
Nucula donaciformis—Annandale & Stewart, 1909: pl. 1 fig. 5, 5a–c; Prashad, 1932a: pp. 14, 15; Prashad, 1933: p. 128, pl. 1 fig. 4; Knudsen, 1967: pp. 247, 248, fig. 3 and pl. 1 fig. 2; Huber, 2010: p. 86, fig.; Subba Rao, 2017: pp. 23, 24, pl. 1 fig. 2a–e.

Live collected. CP28 (n=1), CP44 (n=21), CP45 (n=1), CP55 (n=2).

Dead shells. CP26 (n=2), DW32 (n=4), CP33 (n=1), CP44 (n=6), CP45 (n=4, 1 intact indiv.), CP59 (n=2, 1 intact indiv.).

Description. Shell large (to 18 mm), surface with fine radial lines that dominate over commarginal lines; shell grey with or without purplish tinge at the umbonal region; yellowish-brown periostracum; valves distinctive with steep, straight dorso-posterior end; inner ventral margin of valves finely but strongly crenulate. Anterior and posterior hinge plates with 27 and 12 teeth respectively (SL=17 mm). Hinge plates narrow, located close to dorsal margin. Single distinct resilifer present under eight teeth on anterior row of taxodont teeth. Umbones opisthogyrate.

Distribution. Bay of Bengal (Smith, 1895); off south Bali, Straits of Macassar, Ceram Sea (Prashad, 1932a); off southwest Java (this study).

Depth range. 265–457 m (type locality); 210–835 m (Prashad, 1932a); 378–1,022 m (this study).

Remarks. Melvill, in Melvill & Standen (1906: 791 and pl. 54 fig. 7; SL=6.5 mm) described *N. consentanea* from the Gulf of Oman (east of Fujairah) at 285 m depth in a shell-sand substratum. This may prove to be a juvenile shell of *N. donaciformis*, given their similarities in overall shape and hinge morphology, although Prashad (1933) and Subba Rao (2017) both regarded the two species as distinct. Huber (2010: 523) regarded *N. sumatrana* as a synonym of *N. donaciformis*, but the angle of slope of the dorsal anterior margin differs in the two species, with *donaciformis* tracing a steep straight line compared to the more concave outline of *sumatrana*. They are regarded as distinct here.

Nucula cf. *semen* Thiele, in Thiele & Jaeckel, 1931
(Fig. 2C, D)

Nucula semen Thiele, in Thiele & Jaeckel, 1931: p. 200, pl. 7(2) fig. 48, 48a.

Live collected. Nil.

Dead shell. CP45 (1 RV).

Distribution. Off west coast of Sumatra near Siberut Islands (type locality); off southern Java (this study).

Depth range. 750 m (Thiele & Jaeckel, 1931); 684–851 m (this study).

Description. Shell small, SL=6.2 mm, trigonal in shape, external surface dominated by fine radial striae, commarginal lines faint; hinge teeth rather worn in specimen but with small, distinct resilifer oriented more ventrally than anteriorly under 4 teeth on anterior hinge plate, which bears about 16 teeth, whilst the posterior plate has 10 teeth. Umbones opisthogyrate. Ventral margin finely crenulated on inside of shell.

Remarks. The general shape and sculpture (or lack of) of the single, worn specimen collected corresponds closely to the illustration of *Nucula semen* described in Thiele & Jaeckel (1931). This species was described based on a pair of valves collected near the Siberut Islands off Sumatra in 750 m of water as well as on many shells collected by Schöde in the vicinity of Padang, Sumatra (Thiele & Jaeckel, 1931). The hinge plate for a shell of size 2.1 mm (SL) was described as having 10–12 anterior teeth and 5–6 posterior teeth. Huber (2010) considered *N. semen* and *N. nimbosa* Prashad, 1932a (pl. 1, figs. 11, 12; Gulf of Boni, S. Celebes in 1,158 m of water; SL=3.2 mm, with 8 anterior and 5 posterior teeth) to be synonyms, but the mismatch in the hinge teeth count given the difference in shell size may be difficult to reconcile.

Nucula cf. *sumatrana* Thiele, in Thiele & Jaeckel, 1931
(Fig. 2E, F)

Nucula sumatrana Thiele, in Thiele & Jaeckel, 1931: p. 198, 199, pl 7(2) fig. 44, 44a.

Live collected. Nil.

Dead shells. DW06 (n=1), CP27 (n=2); DW32 (n=1), CP62 (n=1).

Distribution. Off west coast of Sumatra near Siberut Islands (*sumatrana*); off southern Java (this study).

Depth range. 750 and 1,280 m (Thiele & Jaeckel, 1931); 266–1,630 m (this study).

Description. Shell medium sized (6–13 mm), commarginal ribs prominent, some of them terminating antero-dorsally as distinct papillae (about 10 can be seen anteriorly along edge of the lunule); commarginal ribs are crossed by fine radial striae; inside edge of valves along ventral margin strongly crenulated; Anterior and posterior hinge plates with 22 and 9 teeth respectively (SL=12mm); prominent resilifer present ventral to opisthogyrate umbo under anterior row of 8 taxodont teeth.

Remarks. The general shell shape, outline, and size of the dead shells closely resemble *N. sumatrana* Thiele, in Thiele & Jaeckel, 1931 (SL=9 mm). However, *Nucula rugulosa* Sowerby, 1833, which is thought to occur in the Persian Gulf also has a similar profile (for *N. rugulosa*, see Sowerby, 1833: 5, fig. 19, SL=11 mm; Hanley, 1843: 171, pl. 20, fig. 10; Prashad, 1933: 131, 132 and pl. 1 fig. 11). In addition, Schenck (1939: 29) contended that *N. rugulosa* may be related to *N. sculpturata* Sowerby, 1904, described from South Africa (from a depth of 62 m; p. 7, pl. 6, fig. 11, SL=9 mm) and *N. papillifera* Thiele, in Thiele & Jaeckel, 1931 (p. 200(42), pl. 7(2) fig. 49, 49a, b; SL=6 mm from unknown depth, Padang, Sumatra).

Nucula trigonica Lan & Lee, 2001
(Fig. 2G, H)

Nucula trigonica Lan & Lee, 2001: p. 3, sp. 2 and p. 6, fig. 2.
Nucula trigonica—Huber, 2010: p. 87.

Live collected. CP44 (n=2), DW46 (n=1), CP51 (n=1).

Dead shells. DW32 (n=6), CP45 (n=3, with 1 intact indiv.).

Description. Shell small (4.5–7.8 mm), trigonal in shape, somewhat flattened laterally, umbones worn, posterior margin nearly straight; shell surface with thin, yellowish-brown periostracum; external surface faintly reticulate, as a result of commarginal lines intersecting fine radial striae; hinge plate with 15 anterior and 9–10 posterior teeth, with distinct small resilifer directed antero-ventrally; inside edge of ventral margin of valves finely crenulated.

Distribution. Pratas Id, South China Sea (type locality); East Indian Ocean (this study).

Depth range. 300 m (type locality); 540–1,013 m (this study).

Remarks. The shells closely resemble *Nucula trigonica* described from Pratas Island in the South China Sea in 300 m of water. The size of the type material ranges between 5.4 to 7.1 mm (Lan & Lee, 2001), which compares well with those obtained in this study. It would seem that the 'horizontal dotted lines of deeper colour' on the escutcheon and lunule referred to by Lan & Lee (2001) are actually the taxodont teeth on the hinge plate visible through the translucent shell. The 24 hinge teeth (13 anterior, 11 posterior) in the type description is comparable with the 23–25 teeth (15 anterior, 9–10 posterior) observed in the Indian Ocean specimens. The northern Australian *Nucula torresi* Smith, 1885 (pl. 18, fig. 9, 9a; SL=2.8 mm; see also Lamprell & Healy, 1998: 32, 33, fig. 3), described from the Cape York in 247 m of water, appears to be closely related, although there are only 14 teeth (6 anterior, 8 posterior) in the holotype that is half the size of *trigonica*. Thiele & Jaeckel (1931) illustrated a shell (p. 200 and pl. 2, fig. 47, 47a, SL=3.8 mm; 17 teeth, 10 anterior, 7 posterior) from 750 m of water off Sumatra (near Siberut Islands) which they alluded to *N. torresi*. Again, the shell outline and shape resemble *N. trigonica*, but the hinge dentition of the two species appears to be different.

Nucula sp.
(Fig. 3A, B)

Live collected. Nil.

Dead shells. DW32 (n=17).

Description. Shell small (6–8 mm), antero-posteriorly elongate with distinctive widely spaced commarginal 'steps' crossed by very fine radial striae; lunule region defined by 6–7 low but distinct ridges. Hinge plates generally broad, located close to dorsal margin. Anterior and posterior plates bear 10 and 21 teeth respectively (SL=7 mm). Resilifer large, elongate, lying below 8 anterior teeth. Inner ventral margin of valves very finely crenulated.

Distribution. Known only from southwest Java.

Depth range. 805–977 m (this study).

Remarks. The illustration provided by Thiele, in Thiele & Jaeckel (1931: pl. 2 fig. 49a) for *Nucula papillifera* shows a shell with somewhat closely set, rounded commarginal ribbing. This does not quite match the widely spaced, flattened ribs of the specimens observed in this study. However, they share the presence of several 'papillae' along the two opposing ridges defining the lunule, and the numerous, very fine crenules along the ventral margin of the inside surface of the valves.

Acila H. Adams & A. Adams, 1858

Members of the distinctive marine genus *Acila* possess divaricating ribs on the external surfaces of their valves and comprise some of the largest species in the Nuculidae, which can exceed 4 cm in shell length (Schenck, 1936). Nacre covers the interior surfaces of the valves, and the inside ventral margins of the shell are crenulate.

Type species. *Nucula divaricata* Hinds, 1843 (by subsequent designation).

Acila fultoni (Smith, 1892)
(Fig. 3C, D)

Nucula (*Acila*) *fultoni* Smith, 1892: p. 111, 112 (Bay of Bengal off the mouth of River Hugli, in deep water; depth unknown).
Nucula (*Acila*) *fultoni*—Annandale & Stewart, 1909: pl. 1 fig. 3, 3a–c; Prashad, 1933: p. 133, 134, pl. 1 fig. 15.
Acila fultoni—Schenck, 1936: p. 102, 103, pl. 16 figs. 1–9; Xu, 1999: p. 49, fig. 29 and p. 51, 52, fig. 31; Subba Rao, 2017: p. 25, pl. 1 fig. 5a, b.

Live collected. CP22 (n=1), CP33 (n=4), CP47 (n=1), CP50 (n=1), CP52 (n=5), CP55 (n=16), CP57 (n=1), CP62 (n=1).

Dead shells. CP03 (n=1), CP07 (n=6), CP08 (n=1), CP20 (n=2), CP26 (n=1), DW32 (n=1), CP33 (n=9), CP45 (n=3, 1 intact indiv.), CP47 (n=4), CP50 (n=1), CP55 (n=5, 2 intact indiv.), CP58 (n=1), CP59 (n=1), CP62 (n=20, 2 intact indiv.).

Description. Shell large (to 47 mm), external surface with distinctive divaricate ribbing covered by a thick, grey-brown periostracum. The ribbing diverges along a radial line that runs from the umbonal region to the ventral margin, dividing almost equally into anterior and posterior halves. Anterior

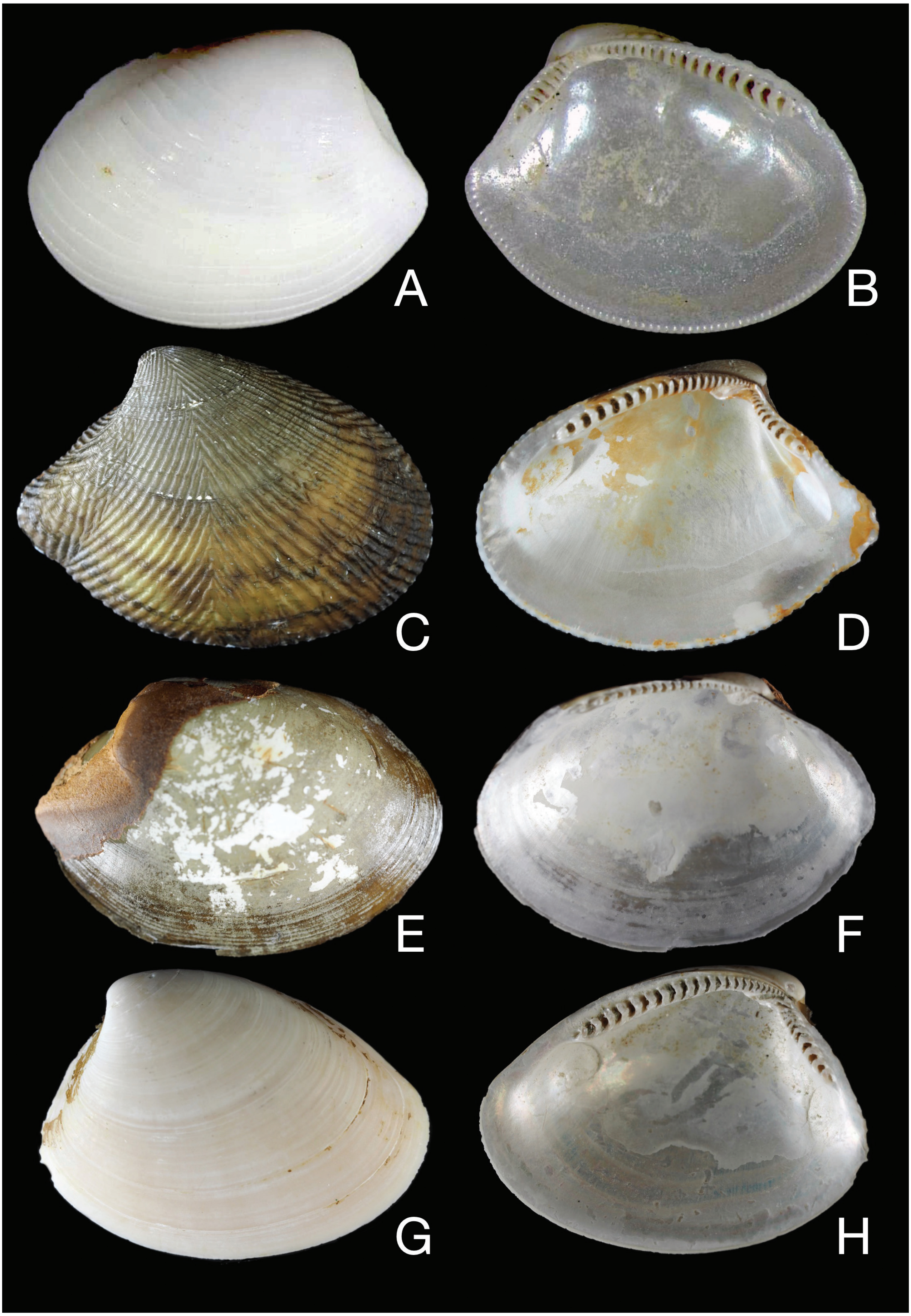

Fig. 3. Nuculidae. A, B, *Nucula* sp., left valve, station DW32, SL=7.0 mm; C, D, *Acila fultoni* (Smith, 1892), left valve, station CP45, SL=24.6 mm; E, F, *Ennucula bengalensis* (Smith, 1895), left valve, station CP44, SL=19.5 mm; G, H, *Ennucula dautzenbergi* (Prashad, 1932a), left valve, station CP02, SL=17.0 mm.

region of shell with distinct, shallow ventrally directed groove from umbonal region to antero-ventral margin. Groove meets ventral margin to form a slight indentation. Umbones opisthogyrate. Straight anterior and slightly arched posterior hinge plates narrow, bearing up to 28 and 13 teeth respectively (SL=46 mm). Resilifer under 8 teeth on anterior plate, directed postero-ventrally; ventral margin inside shell with fine crenulations.

Distribution. Bay of Bengal (type locality); South China Sea (Xu, 1999); Indian Ocean off Java (this study).

Depth range. 1,018 m (Prashad, 1932a); 223–1,630 m (this study).

Remarks. Prashad (1932a; as *Nucula mirabilis* Adams & Reeve, 1850) recorded a single valve (SL=24 mm) from Station 18 located between Bali and Kangeang Id at 1,018 m. Most authors have assumed the synonymy of *A. divaricata* (Hinds, 1843) and *A. mirabilis* (e.g., Schenck, 1936; Knudsen, 1967), but Xu (1984b) observed that the larger *A. mirabilis* possessed a distinct postero-ventral corner that is connected to the umbo by a ridge. Subsequently Zhang et al. (2014) distinguished the smaller-sized *A. divaricata* Hinds from the larger *A. mirabilis* using molecular techniques. They suggested that *A. divaricata*, a smaller species no larger than 15 mm in shell length, has a subtropical distribution, in contrast to *A. mirabilis* (up to 30 mm) which is apparently restricted to the temperate northwestern region of the Pacific Ocean (see also Xu, 1999: 49, fig. 29). However, our results show that large *Acila* are not confined to the temperate Pacific Ocean and support the findings of Smith (1892), who had described a large *Acila*, *A. fultoni* (SL=36.5 mm) from "deep water" in the Bay of Bengal off the mouth of River Hugli. The specimens from Java reach 47 mm in shell length and possess the distinct postero-ventral corner and ridge pointed out by Xu (1984b) to be characteristic of *A. mirabilis*. Given their resemblance in shell form, it remains to be seen if *A. mirabilis* and *A. fultoni* are conspecific despite their disparate geographical distribution and shell size. In his monograph on Chinese protobranchs, Xu (1999) also distinguished *A. fultoni*, as well as *A. schencki* Kira, 1959, from *A. divaricata* and *A. mirabilis*. In contrast, Knudsen (1967) opined that *A. mirabilis* as well as *A. fultoni* are junior synonyms of *A. divaricata.*

Ennucula Iredale, 1931

This speciose genus comprises nuculids whose shells, while possessing taxodont hinges with a distinct resilifer, are externally and internally smooth with little or no sculpture. Bergmans (1991) considered *Leionucula* Quenstedt, 1930, as a senior synonym of *Ennucula* Iredale, 1931, but some recent authors have avoided the use of fossil genera on extant shells. This is a practical approach that is adopted here as far as possible, given the oftentimes poor correlation in shell and anatomical (as well as genetic) characters.

Type species. *Nucula obliqua* Lamarck, 1819 (by original designation).

Ennucula bengalensis (Smith, 1895)
(Fig. 3E, F)

Nucula bengalensis Smith, 1895: p. 15, pl. 2 fig. 9.
Nucula bengalensis—Annandale & Stewart, 1909: pl. 1, figs. 4, 4a–c; Prashad, 1933: p. 126, pl. 1 fig. 1; Winckworth, 1940: p. 25; Knudsen, 1967: pp. 245, 246, fig. 2; pl. 1 fig. 1; Xu, 1999: pp. 42–44, figs. 24, 25.

Live collected. CP20 (n=2), CP23 (n=2), CP28 (n=1), CP31 (n=2), CP45 (n=1), DW46 (n=1), CP62 (n=1).

Dead shells. CP27 (n=1), DW32 (n=3), CP33 (n=2), CP35 (n=6), CP44 (n=1).

Description. Shell large (SL=18–20 mm), greyish-white, slightly inflated, markedly inequilateral; external surface smooth, with very fine commarginal lines that are overlain by a thin, greyish-brown periostracum; inside surface nacreous, inner ventral edge not crenulated; large resilifer present, occupying the length of 4–5 teeth along ventral margin of anterior hinge plate behind the umbo. Anterior and posterior hinge plates both very narrow, lying close to dorsal margin of shell. Hinge teeth number 17 and 7 on anterior and posterior plates respectively. Umbones opisthogyrate.

Distribution. Bay of Bengal (type locality; see also Knudsen, 1967); South China Sea (Xu, 1999); southwest Java (this study).

Depth range. 265–460 m (Smith, 1895); 325–1,630 m (this study).

Remarks. The umbonal and postero-dorsal region of the hinge area in this species is often covered by thin layer of hardened mud. A number of similarly shaped species from the same geographical region makes identification difficult. These include (1) *Ennucula convexa* Sowerby, 1833, described from China (Sowerby, 1833: species 32, fig. 22; see also Xu, 1984b: 181, 182, pl. 1 fig. 3; Petit, 2009); (2) *E. cumingii* (Hinds, 1843) described from 7–42 m depth in the "Indian Archipelago" (see also Hinds, 1844: 62, species 252 and pl. 18 fig. 1; Reeve & Sowerby, 1870: pl. I, fig. 5; Xu, 1984b: 180, pl. 1 fig. 1; Xu, 1999: p. 37, 38 fig. 20 and p. 43 fig. 25); (3) *E. layardi* (A. Adams, 1856) from Ceylon (also Persian Gulf; see also Reeve & Sowerby, 1870: pl. V, fig. 36; Smith, 1906: from 86 m in the Persian Gulf; Oliver, 1995: 203, fig. 899, as *Nuculoma*; Amini et al., 2014: fig. as *Nuculoma*); (4) *E. strangei* (A. Adams, 1856) from New Zealand (see Reeve & Sowerby, 1871: pl. V, fig. 36; Beu, 2006); and (5) *E. semiramiensis* (Preston, 1916) from 4–11 m depth in the Andaman Islands. However, these species were mostly collected from shallower waters not exceeding 100 m depth (although Prashad (1932a: 14) reported *cumingii* from depths of 310–1,301 m) and may not be conspecific with *E. bengalensis*, despite their resemblance in overall shell shape.

Knudsen (1967) synonymised the northern Pacific species *Nucula mirifica* Dall, 1907 (collected off the south coast of Hokkaido at 484 m and illustrated in Dall [1926: pl. 29 figs. 4, 10]) with *E. bengalensis*, but the shell of *mirifica* is significantly larger (to 36 mm, as compared to 17 mm in *bengalensis*) and its antero-ventral shell outline appears more rounded than that of *E. bengalensis*. A more similar shell to *E. bengalensis* is that of *E. niponica* (Smith, 1885) collected off southern Japan at 630 m depth with a shell length of 22 mm (see Smith, 1885: 226 and pl. 18, figs. 8, 8a; Okutani, 1962: pl. 1, fig. 7). *Ennucula niponica* was also reported from the Yellow Sea as a first record in China by Xu (1984b: 181, pl. 1 fig. 2 as *Nucula* [*Leionucula*] *nipponica*) from 44–80 m depth; SL range: 9.5–12.2 mm) and the Philippines by Poutiers (1981, as *Leionucula*) from 750–925 m. However, *E. bengalensis* appears to possess a stronger antero-dorsal ridge than *E. niponica*. On the other hand, Okutani et al. (2009, also as *Leionucula*) considered *E. mirifica* to be either an adult form or cold water morphotype of *E. niponica*.

Ennucula dautzenbergi (Prashad, 1932a)
(Fig. 3G, H)

Nucula dautzenbergi Prashad, 1932a: p. 17, pl. 1 figs. 13–16.

Live collected. DW32 (n=6), DW46 (n=1).

Dead shells. CP02 (n=1), DW32 (n=3).

Description. Shell large (SL=11–17 mm), external surface with thin periostracum, generally smooth, interrupted by faint, irregularly but widely spaced commarginal lines. Anterior and posterior hinge plates relatively broad, set some distance away from dorsal margins. There are 15 and 7 teeth on the anterior and posterior plates, respectively (SL=13 mm), with a narrow resilifer below 8 teeth along the anterior plate. Inside surface nacreous, inner ventral margin of valves not crenulated. Umbones opisthogyrate.

Distribution. Samau Strait, SW Timor (type locality; Prashad, 1932a); between Flores and Sumba Ids (Prashad, 1932a); Sunda Strait and southwest Java (this study).

Depth range. 390 and 959 m (Prashad, 1932a); 257–977 m (this study).

Remarks. The several intact (living) and dead shells obtained in this study have a close resemblance to *Nucula dautzenbergi* Prashad, 1932a (pl. 1, figs. 13–16) in terms of overall shape and size. The anterior and posterior plates in the holotype (SL=10.4 mm) was described by Prashad as "…moderately strong, anterior series with 14, posterior with 7 teeth, both series slightly arched". Although 'anterior' and 'posterior' are reversed in his description, and the condition of the ventral shell margin (i.e., whether crenulations occur on the inside margin) could not be ascertained, Prashad's description and illustration of the holotype are also consistent with the characters observed in the shells collected in this study.

Ennucula siberutensis (Thiele, in Thiele & Jaeckel, 1931)
(Fig. 4A, B)

Nucula siberutensis Thiele, in Thiele & Jaeckel, 1931: p. 199 and pl. 4, fig. 45 off Pulau Siberut, 750 m (SL=7 mm).

Live collected. CP24 (n=1), CP51 (n=1), CP62 (n=2).

Dead shells. CP24 (n=2; 1 intact indiv.), DW32 (n=14), CP45 (n=2; 1 intact indiv.), CP57 (n=2; 1 intact indiv.).

Description. Shell small (5–7 mm), external surface generally smooth with widely spaced commarginal growth lines, covered with thin yellow-green periostracum; antero-dorsal region traces an angled margin along hinge line. Inner ventral edge not crenulated, smooth. Inside the shell, a small but distinct resilifer is present between anterior and posterior taxodont teeth rows. 17 anterior and 9 posterior teeth are present on the anterior and posterior hinge plates respectively (SL=6 mm). Umbones nearly orthogyrate.

Distribution. Siberut Islands off Sumatra, Indian Ocean (Thiele & Jaeckel, 1931); off southwest Java (this study).

Depth range. 750 m (Thiele & Jaeckel, 1931); 223–1,630 m (this study).

Remarks. Thiele & Jaeckel (1931) described the hinge of *Nucula siberutensis* (SL=7 mm) as having 14 and 8 teeth on the anterior and posterior plates respectively, which are slightly lower in number than in material collected in this study. Another similarly shaped shell, *N. bathybia* Prashad, 1932a (p. 16 and pl. 1, figs. 7, 8), collected from 1,886 m depth off the southern tip of Muna Island in southern Sulawesi, has 12 anterior and 6 posterior teeth (SL=8 mm).

Order Solemyida

Family Solemyidae Gray, 1840

The solemyids are a distinctive group of elongate bivalves having a thick, glossy periostracum that extends beyond the margins of the thin, calcified valves whose hinges are edentate (Pojeta, 1988; Taylor et al., 2008; Sato et al., 2013a, b; Walton, 2015). They are often associated with anoxic sulphide-rich sediment and are partially or entirely dependent on chemosymbiotic bacteria found in their enlarged ctenidia. In some species, the alimentary canal is absent altogether (Kuznetzov & Schileyko, 1984).

Acharax Dall, 1908a

Some nine species of this genus are currently recognised but the few which are known from the Indian and western Pacific Oceans are poorly defined (see below; also Huber, 2010: 527).

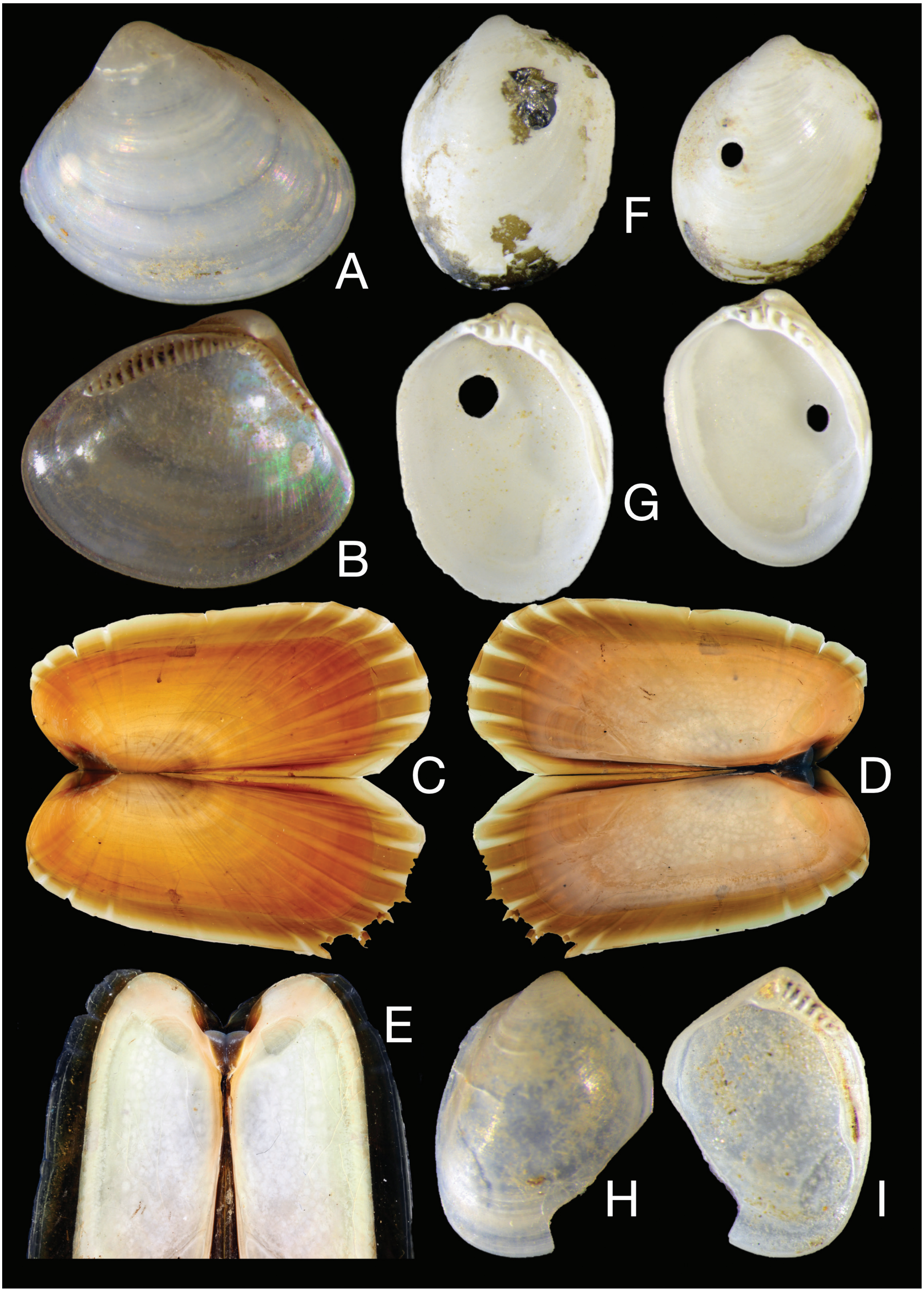

Fig. 4. Nuculidae, Solemyidae, and Nucinellidae. A, B, *Ennucula* cf. *siberutensis* (Thiele, in Thiele & Jaeckel, 1931), right valve, station DW32, SL=7.0 mm; C–E, *Acharax* cf. *johnsoni* (Dall, 1891), dead intact specimen, station CP25, SL=20.0 mm (excluding periostracal extension); C: external view; D: internal view; E: internal view, detail of hinge and posterior adductor muscle scar; F, G, *Nucinella maxima* (Thiele, in Thiele & Jaeckel, 1931), left valves, station DW32, larger SL (umbo to farthest margin)=4.1 mm, smaller SL=4.0 mm; H, I, *Huxleyia sulcata* A. Adams, 1860, left valve, station DW32, SL (umbo to farthest margin)=3.5 mm.

Type species. *Solemya johnsoni* Dall, 1891 (by original designation).

Acharax cf. *johnsoni* (Dall, 1891)

(Fig. 4C–E)

Solemya johnsoni Dall, 1891: p. 189.
Solemya johnsoni—Dall, 1895: p. 712, 713, pl. 25 fig. 1.
Acharax johnsoni—Knudsen, 1970: p. 70–72 and pl. 7 figs. 1–3; Kafanov & Lutaenko, 1997: p. 157, fig. 1; Xu, 1999: p. 22, 23, figs. 8, 13; Coan et al., 2000: p. 66, pl. 1; Kamenev, 2009: p. 256–258, figs. 101–108; Huber, 2010: p. 91, fig. and p. 527–528; Coan & Valentich-Scott, 2012: p. 52 and pl. 16; Kolpakov et al., 2019: p. fig. 1A, B.

Live collected. Nil.

Dead shells. CP25 (n=14).

Description. SL to 34.7 mm (shell only; to 41 mm if periostracum is included), external surface of shell covered with shiny, dark brown to yellow-brown periostracum which extends beyond the shell margins. A series of narrow radial rays are conspicuous over the shell surface, numbering about eight over the anterior region, and about four over the narrower posterior area. Faint commarginal lines are also present. Shell thin, fragile, compressed, inequilateral, rectangular, umbones located about ¾ way behind the anterior edge. Antero-ventral and antero-dorsal margins of the shell are almost parallel to each other, whilst the postero-dorsal margin is angled ventrally. The anterior end of the shell is nearly truncate, whilst the posterior end is comparatively narrow and rounded. SL/SH ratio 2.71±0.11, range 2.5–2.9, n=14; shell only). Interior of shell smooth. Anterior adductor muscle scar about three times the size of posterior scar. Ligament external, arched dorsally, opisthodetic; chondrophore narrow.

Distribution. Off southwest Java (this study); South China Sea (Xu, 1999); otherwise known from the eastern Pacific Ocean across the north and north-west Pacific Ocean (Kamenev, 2009).

Depth range. 876–937 m (this study); 100–5,000 m (Kamenev, 2009).

Remarks. The material obtained here are only tentatively assigned to *johnsoni*, in view of the difficulties in delineating *Acharax* species due to their very similar morphologies and lack of robust conchological characters. While Prashad (1932a) did not document any solemyid protobranchs from the Siboga Expedition in eastern Indonesia, Wiedicke et al. (2002) observed living *Acharax* sp. (which Neulinger et al., 2006 attributed to *johnsoni*) from methane venting areas in the Sunda Trough at a depth of 2,900 m. It is possible that they are conspecific with those obtained in the current study, given the collection sites are located nearby (even though differing by some 2,000 m in depth). However, all of the SJADES material were relatively small in size (40 mm, in contrast to typical *johnsoni* which can grow to 150 mm; the shell size of material analysed by Neulinger et al. was not stated) and there are no radial ribs visible on the inside surface of the shells of SJADES material, unlike those from the northwest Pacific Ocean observed by Kamenev (2009). *Acharax johnsoni* was first described by Dall (1891) from 1,834 m off the coast of Lower (Baja) California in the eastern Pacific Ocean. The specimen was described to be 115 mm in length (Dall, 1891). Its current geographical range extends from Peru northwards to Alaska and Japan (Coan et al., 2000; Kamenev, 2009) but Xu (1999) also obtained a single living specimen (SL=38 mm) off Nansha Islands in the South China Sea from 2,626–2,830 m depth. Together with the present record, the geographical range of this species could be extended southwards substantially in the Pacific Ocean. This appears to be in agreement with the suggestion of Neulinger et al. (2006) who suggested the existence of two *Acharax* species with similarly wide distributions across the Pacific and Indian Oceans (distinguished as Makran-Oregon-Peru or MOP-*Acharax* and Java-Aleutian Trench-Costa Rica or JAC-*Acharax*) based on 18S rRNA sequence analysis. However, Neulinger et al. did not attempt to distinguish the two clades and it is still unclear which clade is actually *A. johnsoni*. Further, it is also still uncertain if *Acharax patagonica* (Smith, 1885), first described from southwest Atlantic Ocean, actually occurs in the Indian Ocean as well, as reported by Smith (1895: 11, 12; 1906: 253). Although Prashad (1932b) later distinguished one of the specimens to be *Solemya* (*Acharax*) *grandis* (later *prashadi* Vokes, 1955, due to homonymy), the illustration and brief description given by Prashad are insufficient to distinguish it from *johnsoni* and *patagonica*. Similarly, *Solemya* (*Acharax*) *bartschii* Dall, 1908b, collected from 1,097 m in the Philippines, *A. eremita* Kuznetzov & Schileyko, 1984, from 900 m in the Gulf of Aden (which incidentally is rather similar to the SJADES material in terms of their size and shell shape), and *Acharax alinae* Métivier & von Cosel, 1993, from 1,890 m in the Lau Basin off Fiji, are all difficult to differentiate based on their original descriptions and/or figures provided. Clearly the genus *Acharax* is in need of taxonomic revision to delineate the nine or more species currently assigned to it.

Family Nucinellidae Vokes, 1956

Members of the family Nucinellidae (frequently as Manzanellidae Chronic, 1952, but see Oliver & Taylor, 2012) anatomically resemble solemyids (Allen & Sanders, 1969) and form a distinct protobranch clade (Sharma et al., 2013) that may be basal to the Solemyoidea (Sato et al., 2020) but at the same time is basal to the Autobranchia (Combosch et al., 2017), comprising species in two genera, *Nucinella* Wood, 1851, and *Huxleyia* A. Adams, 1860. All 22 extant species have a single (anterior) adductor with no posterior adductor muscle. The two genera are distinguished based on the position of the ligament, which is located either externally or in a sunken resilifer in the case of *Nucinella*, whereas the ligament is wholly internal in *Huxleyia*. In addition, there are no hinge teeth posterior to the umbo in *Huxleyia*, unlike in *Nucinella* where a small number of taxodont teeth extend both anterior and posterior to the umbo. Some 15 extant shallow and deep-water species of

Nucinella worldwide are currently recognised, whilst seven species of *Huxleyia* are known only from the Indo-Pacific region. Limited anatomical studies have revealed that they have large ctenidia, but some species lack labial palps and a digestive system (Kuznetzov & Schileyko, 1984; Taylor & Glover, 2010), and derive their food from chemosymbiosis with endosymbiotic bacteria resident in the ctenidia (Oliver & Taylor, 2012).

Nucinella Wood, 1851

Type species. *Pleurodon ovalis* Wood, 1840 (by original designation).

Nucinella maxima (Thiele, in Thiele & Jaeckel, 1931)
(Fig. 4F, G)

Pleurodon maximus Thiele, in Thiele & Jaeckel, 1931: p. 188, pl. 1(6), fig. 28, a, b.
Nucinella maxima—Vokes, 1956: p. 665; Kuznetzov & Schileyko, 1984: p. 45, 46 and p. 44 fig. 4A, B, D, E.

Live collected. Nil.

Dead shells. DW32 (n=2 LV).

Description. SL=4 mm, external surface with thin periostracum and fine commarginal striae; has single anterior adductor muscle scar, pallial line entire; hinge with 7 cardinal teeth (4 anterior to umbo, 3 posterior to umbo) in addition to lateral teeth; ligament external.

Distribution. Zanzibar Canal (type locality); south Java (this study).

Depth range. 463 m (Thiele & Jaeckel, 1931); 805–977 m (this study).

Remarks. Thiele & Jaeckel (1931) described this species based on a single left valve (SL=12.5 mm). Kuznetzov & Schileyko (1984) reported upon a specimen (SL=4.2 mm) from 393 m in the Gulf of Aden. See Oliver & Taylor (2012); Taylor & Glover (2010); also Glover & Taylor (2013).

Huxleyia A. Adams, 1860

Type species. *Huxleyia sulcata* A. Adams, 1860 (by monotypy).

Huxleyia sulcata A. Adams, 1860
(Fig. 4H, I)

Huxleyia sulcata A. Adams, 1860: p. 303.
Cyrilla sulcata—A. Adams, 1868: p. 42 and pl. 4, fig. 2 (external and internal views of shell).
Nucinella (*Huxleyia*) *sulcata*—Vokes, 1956: p. 666, 667.
Huxleya sulcata—Habe, 1977: p. 13, pl. 1, figs. 6, 7; Sasaki, 2008: p. 195 and p. 196 fig. 16B, C.

Live collected. Nil.

Dead shells. DW32 (n=1 LV).

Description. Shell (maximum dimension 3.5 mm) thin, translucent; external surface with fine commarginal striae; single adductor muscle scar, pallial line entire; hinge with 7 teeth which are all anterior to umbo; a deep resilifer is present posterior to the umbo, ligament wholly internal.

Distribution. Indonesia (this study) to Korea (Adams, 1860) and Japan (Sasaki, 2008).

Depth range. 100–200 m (Habe, 1977); 805–977 m (this study).

Remarks. See Oliver & Taylor (2012); *H. sulcata* was first described from off "Mino-Sima, Straits of Korea" (now Mishima, Japan) from 112 m depth. This is the type species of the genus.

Order Nuculanida

Family Nuculanidae H. Adams & A. Adams, 1858

The exact limits of this speciose family are still unclear (see e.g., Sharma et al., 2013) but it is generally accepted that nuculanids are protobranchs that possess moderately to markedly inequilateral valves bearing commarginal ribs or lines with a resilifer located between the anterior and posterior taxodont hinge plates bearing numerous teeth. Umbones are opisthogyrate. Nuculanids bear siphons which are held posteriorly and the recurved, elongate shape of the posterior region of the shell reflect this, as does the inscribed pallial sinus within. The hind gut comprises a single anterior loop on the right side of the animal (Allen & Sanders, 1996a). Nuculanid genera include *Nuculana* (=*Jupiteria*, according to Sharma et al., 2013), *Ledella* (=*Bathyspinula*, according to Sharma et al., 2013), *Propeleda*, and *Parayoldiella*.

Nuculana Link, 1807

Type species. *Arca rostrata* Bruguière, 1789 (by original designation).

Nuculana cf. _corbuloides_ (Smith, 1885)
(Fig. 5A, B)

Leda corbuloides Smith, 1885: p. 239, 240 pl. 20 fig. 1, 1a.
Nuculana (*Nuculana*) *corbuloides*—Lamprell & Healy, 1998: sp. 23, p. 36, 37.

Live collected. Nil.

Dead shells. DW32 (n=1 RV).

Description. Shell (SL=4.7 mm) solid, inequilateral, posterior region with distinct rostrum that terminates sharply; external surface with about 12 raised concentric commarginal riblets; riblets strongest in the central region but become flattened towards the anterior and posterior regions of the shell,

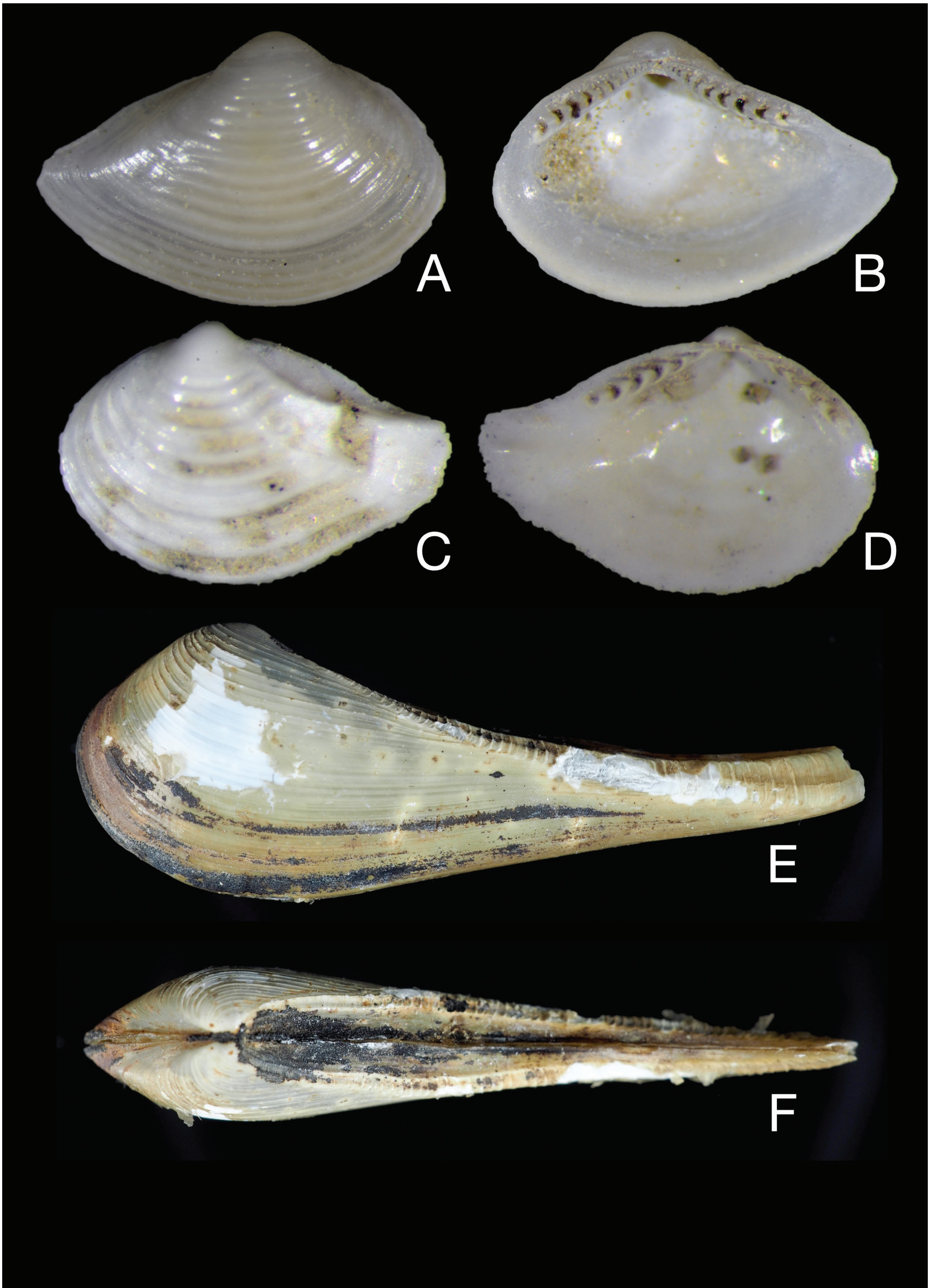

Fig. 5. Nuculanidae. A, B, *Nuculana* cf. *corbuloides* (Smith, 1885), right valve, station CP59, SL=11.8 mm; C, D, *Nuculana* (*Thestyleda*) *jovis* (Thiele, in Thiele & Jaeckel, 1931), left valve, station DW06, SL=2.9 mm; E, F, *Nuculana scalata* Prashad, 1932a, intact individual, station CP44, SL=27.1 mm; E: view of left valve; F: dorsal view showing wide escutcheon.

although at the postero-dorsal rostral region, 5–6 distinct riblets occur; small triangular resilifer recessed under opisthogyrate umbones; anterior and posterior hinge plates robust, broad with 12 and 11 teeth respectively; pallial sinus indistinct.

Distribution. Southern New Guinea (Smith, 1885); Northern Queensland to Northern Territory, Australia (Lamprell & Healy, 1998); off southwest Java (this study).

Depth range. 51 m (Smith, 1885); 15.3 m (Lamprell & Healy, 1998); 805–977 m (this study; 1 dead valve).

Remarks. A single right valve was collected, which resembles the syntype of *Leda corbuloides* Smith figured and described by Smith (1885). Subsequently a photograph of the type was provided in Lamprell & Healy (1998). The shell may also be mistaken for *Nuculana husamaru* Nomura, 1940, which was described from Japan and selected by Habe (1951) as the type species of the genus *Costanuculana*. However, in the substantially larger *N. husamaru* (to 16 mm, occurring at depths between 50–200 m; Kurozumi et al., 2017), the anterior region of the shell is ribbed (see e.g., Kurozumi et al., 2017: pl. 462, fig. 6), in contrast to the smooth surface observed in the single specimen observed here.

Nuculana (*Thestyleda*) *jovis* (Thiele, in Thiele & Jaeckel, 1931)
(Fig. 5C, D)

Leda jovis Thiele, in Thiele & Jaeckel, 1931: p. pl. 7(3) fig. 55.
Leda sp. juv. Thiele & Jaeckel, 1931: pl. 7(3) figs. 56, 56a.
Nuculana (*Thestyleda*) *forticostata* Xu, 1991: p. 83, fig. 2.
Nuculana (*Thestyleda*) *forticostata*—Xu, 1999: p. 71, fig. 46 and p. 72, 73, fig. 48; Lutaenko & Xu, 2008: p. 44 and p. 60, fig. 8C.

Live collected. Nil.

Dead shells. DW06 (n=9), DW32 (n=1, RV).

Description. Shell small (2–5 mm), white, inequilateral, anterior margin rounded, without keel; posterior region truncate, with double keel; external surface with about 16 strong commarginal ribs which are absent in the prodissoconch; width of groove between adjacent ribs about width of ribs; small triangular resilifer present between anterior and posterior hinge plates bearing 12 and 12 teeth respectively; pallial sinus not traceable. Short longitudinal siphonal ridge present on inside edge of truncate posterior margin.

Distribution. Off Siberut Islands, Sumatra (type locality); off Pulau Nias, Sumatra (juvenile; Thiele & Jaeckel, 1931); Nansha Islands, South China Sea (*forticostata*; Xu, 1991, 1999); East Indian Ocean off southwest Java (this study).

Depth range. 470 m (sp. juv.) and 750 m (*jovis*; Thiele & Jaeckel, 1931); 102–200 m (Xu, 1999); 266–977 m (this study).

Remarks. Thiele & Jaeckel (1931: 204 and pl. 7(3) fig. 55) described this small species based on a single left valve (SL=5 mm) from 750 m depth off Siberut Islands, Sumatra. Hinge teeth number 10 and 14 on the anterior and posterior plates, respectively. Another even smaller specimen (SL=2.3 mm; right valve with about five hinge teeth each on anterior and posterior plates, based on pl. 7(3) fig. 56) was considered to be possibly a juvenile of *jovis* collected in 470 m of water off Pulau Nias. However, Thiele & Jaeckel (1931: 204) was unsure if this was indeed the case due to its being less elongate and having stronger commarginal ribs (pl.7(3) fig. 56a) and did not name the smaller shell. Here it is proposed that both represent the same species. It is further proposed that *Nuculana forticostata* Xu, 1991, is a junior synonym. This species was described from three intact but dead shells from Nansha (Spratly) Islands (Xu, 1991, 1999) in 108–200 m of water and assigned to the subgenus *Thestyleda* Iredale, 1929, in view of its strong commarginal ribs. Habe (1958) described a subspecies "*arai*" of *Nuculana* (*Thestyleda*) *yokoyamai* (Kuroda) from southern Japan in 84–112 m of water with a shell length of 7.5 mm and 15 concentric ribs that resembles *jovis*.

Nuculana scalata Prashad, 1932a
(Fig. 5E, F)

Nuculana (*Thestyleda*) *scalata* Prashad, 1932a: p. 22 pl. 1 figs. 30, 31.
Nuculana (*Thestyleda*) *scalata*—Habe, 1958: p. 246, 247; p. 280 pl. 11, figs. 34, 35; Xu, 1999: p. 70–72 figs. 46 (map), 47 (shells).

Live collected. CP44 (n=1).

Dead shells. Nil.

Description. Shell markedly inequilateral, somewhat inflated (SL=27.1 mm), posterior region drawn out into a long, gently upturned and tapering, flattened tube. External surface covered with thin, yellow-brown periostracum, overlying numerous commarginal striae that are strongest over the dorsal half of the shell, and becoming obsolete towards the ventral edge. These striae are contiguous with strong ridges over the rostrum that define the escutcheon, and these ridges dominate the spout region. The escutcheon itself is relatively wide with discontinuous longitudinal lines over the uneven surface. Lunule shallow, short. Umbones opisthogyrate. About 20 anterior and 53 posterior fine chevron-shaped teeth are present along the hinge. A prominent L-shaped resilium is inserted between the anterior and posterior hinge plates just ventral to the umbo. Anterior adductor muscle scar with rounded oval outline, located ventral to far end of anterior hinge plate, whilst the posterior adductor muscule scar is markedly elongate, occupying the last third of the length of the posterior hinge plate. A longitudinal ridge is present on the inside edge of the posterior end of the shell.

Anatomy. Foot large, muscular, folded forwards; sole divided into two narrow halves lengthwise, bluntly frilled along their edges; ctenidia long, narrow, tapering towards posterior. Palps proboscoides long, tape-like. The intestine makes a large loop on the right side of the animal.

Table 1. Comparison of conchological features and depth ranges of *Nuculana scalata* Prashad, 1932a (holotype), *N. subscalata* Okutani, 1962, *N. tanseimaruae* Tsuchida & Okutani, 1985, and the specimen obtained in this study from station CP44.

	SJADES specimen	*scalata*	*subscalata*	*tanseimaruae*
shell length (mm)	27.1	13	11.2	17.2
shell height (mm)	9.2	5	4.7	6.1
number of commarginal striae on rostrum	40	?30	?>50	80–100
distance between adjacent major commarginal striae on valve surface	wide	wide	narrow	narrow
number of anterior/posterior hinge teeth	20/53	?	8/22	18/50
depth range (m)	970–1,013	918	740–1,680	353–550

Distribution. Timor (Prashad, 1932a); Japan (Habe, 1958); Nansha (Paracel) Islands (Xu, 1999); southwest Java (this study).

Depth range. 918 m (type locality); 96 m (Xu, 1999); 274 m (Habe, 1958); 970–1,013 m (this study).

Remarks. The shell fits the description and illustration of *Nuculana scalata* provided by Prashad (1932a), although the intact specimen from the SJADES material is more than twice the size of the type. Prashad's specimen (SL=13 mm) was collected off the south coast of Pulau Rote, SW of Timor from a depth of 918 m. Habe (1958) provided the first record of this species off the south coast of Shikoku, Japan (SL=11.3 mm, depth: 274 m). Okutani (1962) subsequently described a similar shell (SL=11.2 mm) specimen off Oshima Island, Japan from 1,560–1,640 m (and some 80 other specimens off Miyake Island and Sagami Bay between 550 m and 1,350 m) as *N. subscalata* (see also Matsukuma, 2003: pl. 4 fig. 1; SL=10.5 mm). Another closely related species, *N. tanseimaruae* was described by Tsuchida & Okutani (1985) from material collected off the Kii peninsula in Japan in 300–500 m of water.

It was noted that *N. scalata* possessed "…more distantly spaced and highly raised concentric rugae…" compared to *N. tanseimaruae*, while *N. subsulcata* has "…a less rugous shell, duller exterior coloration, more protruded anterior portion, much dense scales on the rostrum, and less number of hinge teeth (8+22 in the holotype [of *subsulcata*])" (Tsuchida & Okutani, 1985). Although the specimen from Java is the largest amongst the three species, the number of commarginal striae appears to be small (about 40) compared to *N. subsulcata* or *N. tansemaruae*. In addition, while the hinge teeth count in *N. tanseimaruae* is comparable to that in the Java specimen, it is difficult to reconcile these numbers in relation to their substantial discrepancy in shell size (17 vs. 27 mm). It was further observed that *N. tanseimaruae* occurred in shallower waters (353–550 m) compared to *subsulcata* (740–1,680 m) (Tsuchida & Okutani, 1985) or the Java specimen (970–1,013 m). Taken together, the data (see Table 1 for summary) suggest that the living specimen from station CP44 is likely to be *N. scalata*.

Xu (1999) reported a small (SL=6 mm) specimen based on a single LV from a depth of 96 m off Vietnam in the Nansha (Paracel) Islands.

Saccella Woodring, 1925

Species in this genus are characterised by having a well-defined, often curved posterior rostral keel and the external surface of the valves bearing prominent commarginal ribs which are extensive and closely set (La Perna, 2007a). The presence of an anterior keel in *Saccella* is sometimes used to differentiate this genus from the closely related *Jupiteria* that has less prominent and more closely set commarginal riblets.

Type species. *Nucula commutata* Philippi, 1844.

Saccella discrepans (Prashad, 1932a)
(Fig. 6A, B)

Nuculana (?*Ledella*) *discrepans* Prashad, 1932a: p. 23, 24, pl. 1 figs. 38, 39.

Live collected. Nil.

Dead shells. CP03 (n=2), DW32 (n=22).

Description. Shell small (SL= 4.4–7.5 mm), inequilateral, posterior region with distinct keel forming broad escutcheon, with a rostrum on either side of the valves that terminates sharply. The dorso-anterior region has a low, indistinct keel. External surface with about 23–24 high, raised concentric lamellate commarginal riblets; small triangular resilifer recessed under opisthogyrate umbones; anterior and posterior hinge plates with 13–19 and 12–17 teeth respectively; pallial sinus very shallow.

Distribution. Madura Bay (Prashad, 1932a); southwest Java (this study).

Depth range. 69–91 m (Prashad, 1932a); 283–977 m (this study).

Remarks. Shell resembles *Saccella brookei* (Hanley, 1860) from Borneo, but the anterior shell margin is decidedly

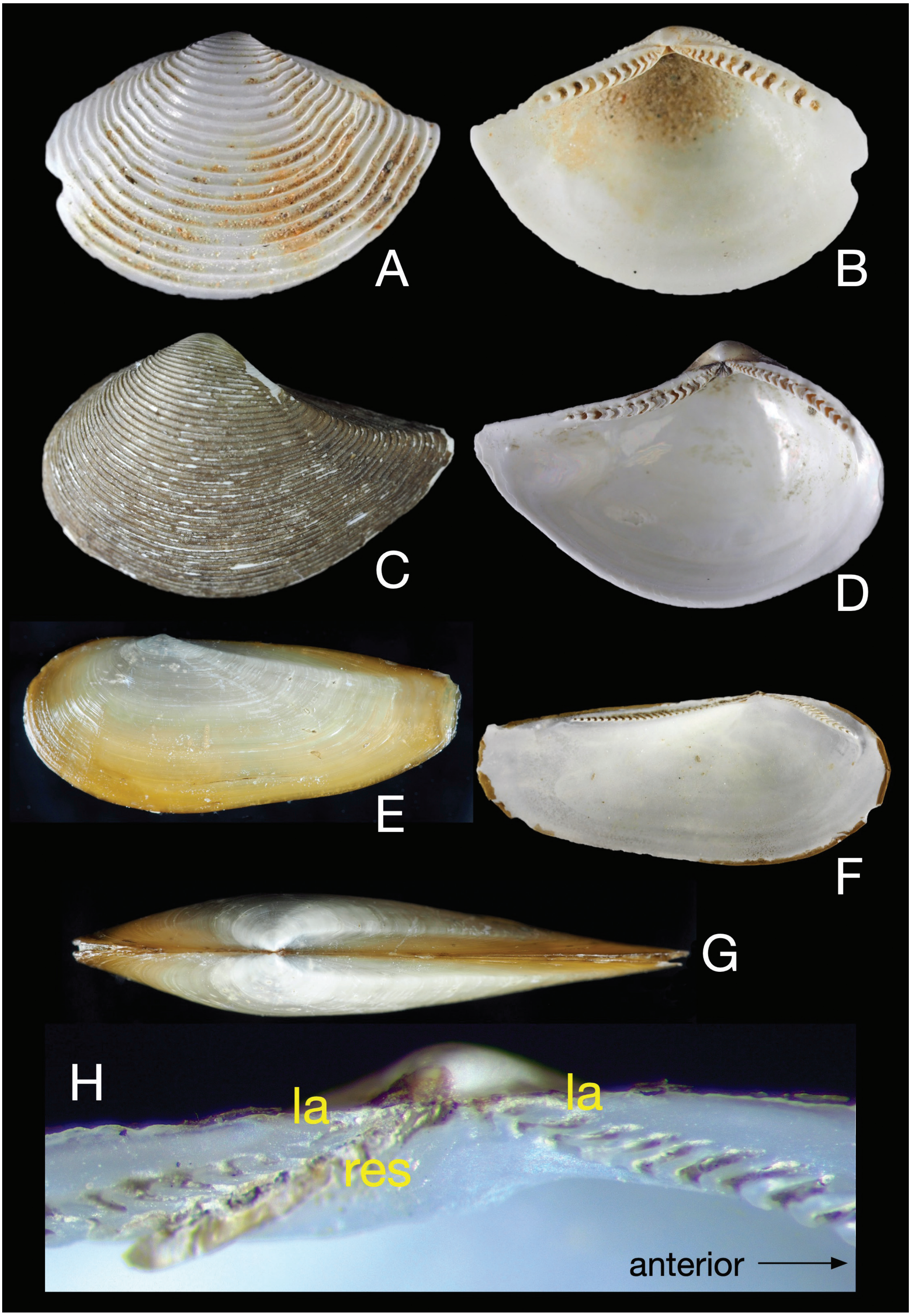

Fig. 6. Nuculanidae. A, B, *Saccella discrepans* (Prashad, 1932a), left valve, station DW32, SL=4.4 mm; C, D, *Saccella sibogai* (Prashad, 1932a), left valve, station CP07, SL=12.8 mm; E–H, *Propeleda dirham*, new species, station CP62, Sunda Strait. E, G: holotype, SL=23.1 mm; E: view of left valve; G: dorsal view; F: paratype, SL=19.3 mm, internal view; H: paratype, SL=21.5 mm, detail of hinge at umbonal region showing resilifer (res) and lamellate teeth (la) along anterior and posterior hinge plates nearest the umbo.

angulate in *discrepans*, in contrast to the rounded outline in *brookei*. *Saccella confusa* (Hanley, 1860) (see e.g., Hanley, 1860: pl. III (228), fig. 85; Xu, 1999: 76, fig. 51; Kurozumi et al., 2017: pl. 462 fig. 3) also has a similar appearance but the ventral margin of *discrepans* is more convex than *confusa*. The commarginal riblets of *discrepans* are also more pronounced (raised higher above the shell surface) and spaced wider apart than those of *confusa*.

***Saccella sibogai* (Prashad, 1932a)**
(Fig. 6C, D)

Nuculana (*Nuculana*) *sibogai* Prashad, 1932a: p. 19, pl. 1 figs. 17, 18.

Live collected. CP07 (n=8), CP08 (n=1), CP18 (n=4), CP22 (n=1), CP24 (n=1), CP25 (n=1), CP44 (n=4).

Dead shells. CP07 (n=46), CP24 (n=2), DW32 (n=8), CP44 (n=4; 1 intact indiv.).

Description. Shell relatively large (largest SL=17.0 mm), inequilateral, somewhat inflated; periostracum yellow-brown, thin; anterior margin steeply rounded, with indistinct keel dorsally; posterior region concave, strongly keeled, drawn out into an acute angle; dorso-posterior margin sharply indented; external surface with numerous (>50) strong, rounded closely set commarginal concentric riblets (rugae); width of groove between adjacent ribs about width of ribs; small triangular resilifer recessed under opisthogyrate umbones; escutcheon a flat and wide valley relative to lunule, well-defined by left and right posterior ridges with a slightly raised region where the left and right valves meet. Pallial sinus shallow.

Distribution. Between Flores and Sumba, off SW Waigeu, Halmahera Sea, off N Ceram, SW tip of Timor (Prashad, 1932a).

Depth range. 469–959 m (Prashad, 1932a); 379–1,073 m (this study).

Remarks. Externally this species resembles *Saccella mauritiana* (Sowerby, 1833) (see e.g., Hanley, 1860: species 38, pl. 4, fig. 99; Reeve & Sowerby, 1871: pl. 6, fig. 33 as *Leda*) as well as *Saccella kirai* (Habe, 1953) (see Matsukuma, 2003: 10, 11, pl. 3 fig. 4). However, the rounded, steep anterior margin of *sibogai* is sufficiently distinct to separate it from the two former species, which were first reported from Mauritius and Tosa Bay, Shikoku, Japan, respectively. *Saccella mauritiana* and *S. kirai* have since been collected from the South China Sea (Scott, 2003: pl. 1 fig. B; Xu, 1999) in depths less than 100 m. *Saccella cuspidata* (Gould, 1861) (see e.g., Johnson, 1964: pl. 23 fig. 4; Xu, 1999: 77, fig. 52) described from Hong Kong is probably a junior synonym of *S. mauritiana*. Some 49 strikingly similar species of *Saccella* are listed in WoRMS (accessed 6 July 2020) from various regions, and apart from *S. sibogai*, three other species, namely *S. approximans* (Prashad, 1932a), *S. bathybia* (Prashad, 1932a), and *S. cygnea* (Thiele, in Thiele & Jaeckel, 1931), were also described previously from Indonesia.

***Propeleda* Iredale, 1924**

Type species. *Leda ensicula* Angas, 1877.

***Propeleda dirham*, new species**
(Fig. 6E–H)

Live collected. CP62 (4 intact specimens).

Dead shells. CP 62 (9 valves, 4 RV, 5 LV).

Types. Holotype–MZB.Pel.2197 Sunda Strait, Indonesia; SL=23.1 mm (Fig. 6E, G). 2 Paratypes–MZB Cibinong (SL=19.3 mm, Fig. 6F); ZRC (LKCNHM), Singapore (SL=21.5 mm, Fig. 6H).

Etymology. The species is named after Dr Dirhamsyah, former Director of the Research Center for Oceanography, Indonesian Institute of Sciences, who was instrumental in the realisation of the SJADES biodiversity cruise. The epithet is used as a noun in apposition.

Diagnosis. Valves thin, laterally compressed, with rounded anterior margin and squarely blunt, tapering posterior end, slightly gaping on both ends; dorsal posterior margin of each valve with distinct keel defining a narrow escutcheon. Anterior and posterior dorsal margins directly adjacent to the umbones are almost level with each other. Shell surface yellowish-brown with barely visible commarginal growth lines. Umbones opisthogyrate. Hinge comprises of lamellate and chevron-shaped teeth on both anterior and posterior plates. Pallial sinus deep. Internal longitudinal ridge absent inside posterior margin of shell.

Description. Shell of moderate size (dead shells: SL range 19.3–22.7 mm; SW range 8–9 mm, n=9; intact shells: SL range 15.6–24.6 mm, SW range 6.6–10.2 mm, n=4) elongate, thin, laterally compressed, slightly gaping, covered with thin yellowish-brown periostracum; valves highly inequilateral with rounded anterior margin and oblong posterior region (Fig. 6E). Anterior and posterior dorsal margins directly adjacent to the umbones are almost level with each other. Posterior dorsal margin continues as a nearly straight line or bulging slightly outwards with a keel defining a narrow escutcheon (Fig. 6G). Lunule absent. External surface with barely visible commarginal growth lines, appearing smooth under worn periostracum; umbones opisthogyrate, thin, external amphidetic ligament visible between umbones. Inside the shell, a narrow, slanting, trigonal posteriorly broadening resilifer is present between anterior and posterior rows of mostly chevron-shaped teeth on hinge plates that are set apart from the dorsal margins (Fig. 6F, H). The anterior and posterior hinge plates bear 19–24 and 28–34 teeth, respectively. Of these, on the anterior plate, 4–6 teeth nearest the umbones are lamellate, whilst on the posterior hinge plate, 8–10 teeth nearest the umbones are lamellate (Fig. 6H). Interior surface white, porcelaneous, with moderately deep pallial sinus. The inside of the posterior end of the shell is smooth, with no longitudinal ridge.

Anatomy. Anterior adductor muscle mass ventrally elongate, about twice the size of the antero-posteriorly elongate posterior adductor muscle mass. Three small bundles of foot retractor muscles are also attached to the inside of the shell just under the anterior hinge plate on each side of the animal. Foot large, muscular, folded forwards; sole divided into two narrow halves lengthwise, bluntly frilled along their edges; ctenidia long, narrow and tapering. Its posterior tips touch the base of Type A siphons which are tubular and containing the siphonal pallial septum. The siphon is held together by cellular junctions and the left and right halves readily separated lengthwise when dissected and are about half the length of the ctenidium in preserved specimens. The intestine makes a large loop on the right side of the animal before passing through the heart towards the rectum.

Distribution. Known only from the type locality (Sunda Strait).

Depth range. 1,623–1,630 m.

Remarks. The general shape of the valves of the new species resembles nuculanids in the genera *Lamellileda*, *Poroleda*, *Propeleda*, *Silicula*, and *Tenuileda*. However, members of *Lamellileda* and *Silicula* only have lamellate hinge teeth, whilst *Poroleda* and *Propeleda* (and probably *Tenuileda*) possess V-shaped hinge teeth, with *Poroleda* having such V-shaped teeth only on the anterior hinge plate (Kamenev, 2014). The valves of the new species possess mostly chevron-shaped teeth on both its anterior and posterior hinge plates, with several lamellate teeth nearest the umbo on the anterior and posterior plates. This condition closely resembles the hinge condition in *Propeleda ensicula* (Angas, 1877), the type species of *Propeleda* (Iredale, 1924) (see Iredale, 1924: 181, 186; Heinberg, 1989; Kamenev, 2014). The genus purportedly contains the following nine species (WoRMS, accessed 20 May 2020): *carpenteri* Dall, 1881, from Gulf of Mexico and Southern Atlantic Ocean (200–2,323 m; Allen & Sanders, 1996a); *conceptionis* Dall, 1896, from California; *ensicula* Angas, 1877, from SE Australia (20–128 m; Iredale, 1924); *fortiana* Esteves, 1984, from Brazil; *longicaudata* Thiele, 1912, from Antarctica (to 23.8 mm; Güller & Zelaya, 2015); *louiseae* Clarke, 1961, from southern Atlantic Ocean (3,815–5,223 m; Allen & Sanders, 1996a); *paucistriata* Allen & Sanders, 1996a, from Angola Basin (527–542 m; Allen & Sanders, 1996a); *platessa* Dall, 1890, from Brazil (107 m; Dall, 1890: 256; 27–89 m; Nijssen-Meyer, 1972a, b); and *rhytida* Dall, 1908a, from southern Chile to Beagle Channel (to 13.2 mm, depth 120–460 m; Güller & Zelaya, 2015). This study augments this list with the tenth species of this genus. Based on the revised definition of *Propeleda* by Kamenev (2014), the majority of species in this genus are in the Atlantic Ocean, with a few from southern Australia, and one in Antarctica. Most species in the Pacific Ocean appear to belong to *Lamellileda*. *Propeleda dirham* is the first tropical Indo-west Pacific species to be described from Indonesia.

Similar species. Prashad (1932a: 23) described *Nuculana* (*Poroleda*) *sibogaensis* from off the north coast of Ceram, 835 m depth. Its size (SL=18.8 mm; SW=6 mm) and external shell features (Prashad, 1932a: pl. 1 fig. 37) are comparable to (albeit narrower than) the new species. However, the considerably fewer hinge teeth (12 and 6 on its anterior and posterior hinge plates respectively) in *sibogaensis* suggest that these teeth are probably lamellate, unlike those in the new species where there are both lamellate and chevron-shaped teeth. Hence Prashad's assertion that *sibogaensis* is closely allied to the smaller (SL=13.3mm, SW=5.4mm) *Nuculana* (*Poroleda*) *parallelodonta* which is also described as a new species from a depth of 1,595 m in the Banda Sea in the same publication (Prashad, 1932a: 23 and pl. 1 figs. 35, 36), is likely to be correct. Prashad (1932a: pl. 8 figs. 1, 2) illustrated the hinge teeth of *parallelodonta*, which are clearly lamellate, having 7 anterior and 4 posterior elongate teeth. Both *sibogaensis* and *parallelodonta* are currently placed in the genus *Lamellileda* in WoRMS (accessed 3 July 2020), in view of their possession of only lamellate hinge teeth.

Externally, members of *Silicula* also resemble the new species in overall shape (see Kamenev, 2014) but in general *Silicula* species are smaller in size (to 15 mm) and distinguished by having only lamellar hinge teeth (Kamenev, 2014), unlike *Propeleda* where the hinge teeth are mostly chevron-shaped and lamellar teeth are restricted to several teeth close to the umbones. The larger (to 30 mm) eastern Pacific *Nuculana* (*Tenuileda*) *conceptionalis* (Dall, 1896) (see Coan & Valentich-Scott, 2012: pl. 22 figured syntype) bears a strong resemblance to the new species with chevron-shaped teeth along the hinge, but lamellate teeth appear to be absent. The dorsal and ventral margins are also drawn to a narrow, obliquely truncate posterior region in *conceptionalis*, while the posterior margin traces a more rounded outline in the new species. The smaller northwestern Pacific species *Propeleda* (*Tenuileda*) *ikebei* Suzuki & Kanehara, 1936 (originally described as a subspecies of *conceptionalis* Dall; see Matsukuma, 2003: pl. 4 fig. 2; Kurozumi et al., 2017: 1161 and pl. 462 fig. 1) is also very similar to the new species but the posterior region is arched dorsally in *ikebei*, whereas it is straight in the new species. Suzuki & Kanehara (1936: 183) described the Pliocene fossil as having small, hooked teeth that number 11 on the anterior (SL=14 mm). As the smallest *P. dirham* (SL=19.3 mm) already has 19 teeth on its anterior plate, it would appear that *P. dirham* is unlikely to be *P. ikebei*. *Propeleda ikebei* is the type species of the (sub)genus *Tenuileda* Habe, 1977, and was given a more detailed diagnosis by Kafanov & Savizky (1995) as "shell sharply inequilateral, with posterior part oblong and somewhat curved upward. Posterior end of valve sharpened. Prominently outlined keel stretching between minutely sharpened umbo and posterior end of valve. Resilifer pit vague, but anterior and posterior branches of hinge evidently cut beneath umbo; the anterior branch 1.5–2 times shorter than posterior one. External surface of valve smooth".

A northern Japanese species, *Robaia robai* (Kuroda, 1929) (see Amano & Narita, 1992; Kamenev, 2013) has some resemblance to the new species in overall shape and in the absence of a siphonal ridge on the inside surface of the shell. However, the slope angles of the dorsal anterior and posterior margins from the umbones are considerably steeper than those of *P. dirham*.

Ledella Verrill & Bush, 1897

Type species. *Ledella bushae* Warén, 1978 (by subsequent designation; see Warén, 1981 and ICZN Opinion 1306).

Ledella cf. *ultima* (Smith, 1885)
(Fig. 11C, D)

Leda ultima Smith, 1885: p. 324, fig.
Ledella ultima—Knudsen, 1970: p. 34–37 figs. 17, 18A and pl. 2, fig. 15; pl. 3, fig. 4.

Live collected. Nil.

Dead shells. DW32 (n=1).

Description. Right valve small (4.2 mm), thick, inequilateral, with slight but distinct keel; external surface with fine commarginal riblets, no resilifer, 9 taxodont teeth on both anterior and posterior rows of hinge plate. Umbones located well above and dorsal to hinge plate.

Distribution. Atlantic and Indian Oceans (see Knudsen, 1970).

Depth range. 2,278–5,130 m (Knudsen, 1970); 283–977 m (this study).

Remarks. The single right valve obtained in this study closely resembles *Ledella ultima*. However, it was obtained from a relatively shallow depth of less than 1,000 m, which throws this finding into doubt. This is because the species is generally considered to be an abyssal species, living at depths in excess of 2,000 m. In addition, *L. ultima* (and *L. crassa*) is most commonly found in the Atlantic Ocean (Smith, 1885; Thiele & Jaeckel, 1931; Knudsen, 1970), with reduced genetic diversity over long distances (Etter et al., 2011). Nevertheless, the presence of Atlantic abyssal deep-sea species in the Indian Ocean (Arabian Sea) was noted by Oliver (2015, 2019). In addition, Filatova & Schileyko (1984: fig. 25) in their treatment of *Ledella* species, indicated the presence of *L. ultima* off southern Java although the locality was not documented in their formal description of the species in the same paper. Two *Ledella* species are known from Indonesia: *L. aequatorialis* (Thiele, in Thiele & Jaeckel, 1931) and *Ledella procumbens* (Prashad, 1932a) (see Table 2). The former species was collected by the Valdivia expedition off the Siberut Islands, Sumatra in 750 m of water but the overall shape of the shell and disposition of the posterior keel do not fit those of the shell collected in this study. The latter species was obtained during the Siboga expedition (type locality: off northeast tip of Pulau Selayar in the Gulf of Boni, Macassar) and is also known from the Bay of Bengal (Filatova & Schileyko, 1984). However, it has strong commarginal ribs that are widely spaced apart and a distinct ventrally directed spine, which are quite unlike the closely spaced, fine commarginal riblets and blunt posterior of *L. ultima*. The shell of *Ledellina convexirostra* Filatova & Schileyko, 1984, from the abyssal depths of the northwestern Pacific Ocean (4,820–6,608 m) bears some resemblance to *Ledella ultima* in terms of shape, size, sculpture, and number of hinge teeth. However, *L. convexirostra* has a thin, fragile shell (which is diagnostic for the genus *Ledellina*) and its umbonal region appears to be considerably smaller and less inflated (Filatova & Schileyko, 1984: fig. 6I, III) than in *L. ultima*.

Yoldia Möller, 1842

The genus *Yoldia* encompasses medium-sized to large nuculanid species with valves having a decidedly elongate but rounded or truncated posterior region enclosing a pair of siphons and no distinct surface sculpture apart from commarginal lines. The hinge has a distinct and large resilifer between the anterior and posterior hinge plates. Together with a number of other genera including *Megayoldia*, *Orthoyoldia*, and *Yoldiella*, they have sometimes been grouped together as the family Yoldiidae Dall, 1908a (see e.g., Bieler et al., 2010; Huber, 2010; Coan & Valentich-Scott, 2012) but others have retained them in the Nuculanidae (e.g., Ockelmann & Warén, 1998; Xu, 1999; Killeen & Turner, 2009). Molecular evidence (see Sharma et al., 2013) does not appear to support its family status.

Type species. *Yoldia hyperborea* Torell, 1859 (by subsequent designation).

Yoldia cf. *serotina* (Hinds, 1843)
(Fig. 7A, B)

Nucula serotina Hinds, 1843: p. 99.
Leda serotina—Hanley, 1860: species 54, p. 136, 137, pl. 226, figs. 19–21.
Yoldia serotina—Reeve & Sowerby, 1871: pl. 2, species 5, fig. 5; Xu, 1999: p. 86, 87, figs. 60, 65 (map).

Live collected. Nil.

Dead shells. DW01 (n=22, 4 intact indiv.), DW06 (n=54, 11 intact indiv.), DW19 (n=9, 2 intact indiv.), DW32 (n=64), CP52 (n=1), DW63 (n=2).

Description. Shell medium sized (SL to 15 mm), elongate, slightly inequilateral, posterior half elongated, with a distinct, gently curved keel; shell not gaping; external surface with very thin yellow-brown periostracum and fine commarginal growth lines that are widely spaced regularly apart (about 250 μm); these lines continue into the escutcheon as crowded lines after making an acute angle along the keel; small resilifer; anterior and posterior hinge plates broad, with 23–25 and 22–24 teeth respectively; the hinge plates are set slightly off the dorsal margin; deep and broad pallial sinus.

Distribution. Singapore (type locality); Gulf of Tonkin (Xu, 1999); Sunda Strait and southwest Java (this study).

Depth range. 100–1,156 m (this study).

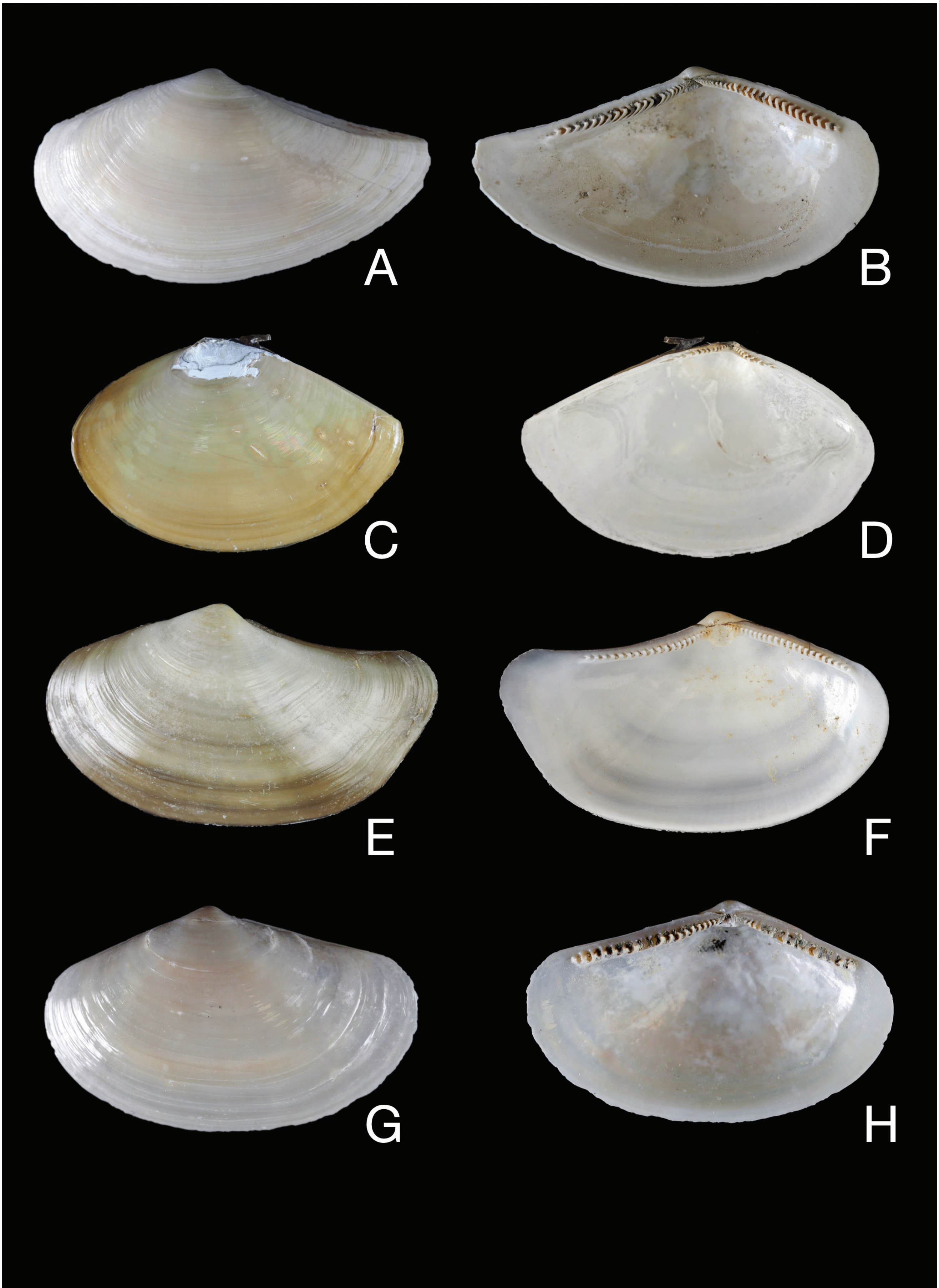

Fig. 7. Nuculanidae. A, B, *Yoldia* cf. *serotina* (Hinds, 1843), left valve, station DW06, SL=16.9 mm; C, D, *Yoldia* sp. 1, left valve, station CP30, SL=26.9 mm; E, F, *Megayoldia lischkei* (Smith, 1885), left valve, station CP57, SL=21.9 mm; G, H, *Orthoyoldia* cf. *lepidula* A. Adams, 1856, left valve, station CP59, SL=11.8 mm.

Remarks. Specimens bear some resemblance to *Yoldia serotina* described from Singapore, as figured in Hanley (1860). From the relatively large number of valves collected, they appear to be quite common in the Sunda Strait and off southern Java.

Yoldia sp.
(Fig. 7C, D)

Live collected. Nil.

Dead shells. CP30 (n=2, damaged), CP62 (n=1).

Description. Shell large (to 27 mm), laterally flattened, external surface generally smooth, marked faintly with commarginal growth lines that are covered with thin, shiny yellow-green periostracum. Antero-dorsal margin slightly convex, whilst the posterior dorsal margin is nearly straight, meeting the ventral margin at a sharp angle. Lunule absent; escutcheon flat, narrow, lanceolate, defined on either valve by a sharp ridge. Umbonal and hinge regions small and narrow. Hinge plate is broadest at the umbonal region, where a shallow, oval resilifer is present. Anterior and posterior hinge plates with 10 and 11 hinge teeth. About 4 teeth on posterior hinge plate nearest the umbo positioned dorsal to resilifer. Internal surface with broad pallial sinus.

Distribution. Sunda Strait and southwest Java.

Depth range. 1,270–1,630 m (this study).

Remarks. This is a large *Yoldia* species that appears to be undescribed.

Megayoldia Verrill & Bush, 1897

The genus *Megayoldia* was proposed by Verrill & Bush (1897) for large, compressed, gaping shells with a very short, blunt, indefinite, postero-dorsal rostrum as well as having a large chondrophore. The type species is a well-known northwestern Atlantic species.

Type species. *Nucula thraciaeformis* Storer, 1838.

Megayoldia lischkei (Smith, 1885)
(Fig. 7E, F)

Yoldia lischkei Smith, 1885: p. 242, pl. 20 fig. 4, 4a, 4b.
Portlandia (*Portlandella*) *lischkei*—Okutani, 1962: p. 12, pl. I, fig. 16; Kuroda et al., 1971: p. 323, 512, pl. 66 figs. 8, 9, 11.
Megayoldia lischkei—Huber, 2010: p. 101, fig.

Live collected. CP57 (n=5).

Dead shells. DW32 (n=7), CP45 (n=1), CP47 (n=1), CP57 (n=21, 2 intact indiv.).

Description. Shell large (SL to 24 mm), elongate, slightly inflated, with upturned truncated posterior end; keel absent, but posterior half of shell compressed. External surface with thin but intact grey-brown periostracum, with characteristic 2–3 commarginal light and dark coloured bands; commarginal growth lines visible but faint; distinct keel at dorsal edge of each valve forming a narrow escutcheon. Anterior taxodont hinge plate about same length as posterior plate, bearing about 25 teeth each (SL=22.4 mm). A large resilifer is present between the hinge plates, with numerous (>50) fine, irregular, ventrally directed lines on internal surface. Shell has deep and broad pallial sinus.

Distribution. NW Pacific Ocean, and Indian Ocean.

Depth range. 631 m (Smith, 1885); 223–977 m (this study).

Remarks. *Megayoldia lischkei* (Smith) was collected in 345 fathoms (631 m) off Inoshima (=off Enoshima Island in Sagami Bay), central Japan during the Challenger Expedition. Smith (1885) compared it with *Yoldia japonica* Adams & Reeve, 1850, which is superficially similar but is recognised to be a separate species found in shallower waters between 10–250 m (as *Portlandia*; Kuroda et al., 1971; Qi, 2004). Okutani (1962) reported *M. lischkei* in Sagami Bay, Japan from depths ranging between 650 and 1,400 m. This is the first record of this species from Indonesia.

Orthoyoldia Verrill & Bush, 1897

The genus was named by Verrill & Bush (1897) for medium-sized (18 mm) oblong, gaping shells that are blunt or rounded at both ends, with neither a distinct rostrum nor carina (Verrill & Bush, 1897, 1898). *Yoldia scapania* Dall, 1890, collected off Brazil in 108 m of water, was designated as the type species, for which Dall (1890) remarked upon its "soleniform" shape and indistinct umbones.

Type species. *Yoldia scapania* Dall, 1890 (by original designation).

Orthoyoldia cf. *lepidula* A. Adams, 1856
(Fig. 7G, H)

Yoldia lepidula A. Adams, 1856: species 19, p. 50, 51.
Leda lepidula—Hanley, 1860: species 55, p. 137, pl. 226, fig. 6.
Yoldia lepidula—Reeve & Sowerby, 1871: pl. 2, species 7, fig. 4; Prashad, 1932a: p. 24; Xu, 1984a: p. 174, fig. 13.
Portlandia lepidula—Xu, 1999: p. 88–90, fig. 63.
Orthoyoldia lepidula—Huber, 2010: p. 101, fig.

Live collected. Nil.

Dead shells. DW06 (n=129), CP07 (n=1), DW19 (n=21), DW32 (n=7), CP59 (n=1).

Description. Shell medium-sized (to 13 mm), elongate, inequilateral, shiny white and yellow surface smooth, dorsal anterior and posterior margins straight, with a small umbonal hump; anterior and posterior ends bluntly rounded. The dorsal posterior region bears a very narrow escutcheon defined by a strong keel along each valve. The shell external surface comprises fine, regularly spaced commarginal lines (about 10–22; SL range 7.5–17 mm) each formed by a slight difference between the heights of stepped surfaces. These lines are between 250–300 µm apart. Umbones opisthogyrate. Chondrophore recessed under junction of anterior and posterior hinge plates bearing 19–22 and 22–23 teeth, respectively; deep pallial sinus.

Distribution. Borneo (type locality), Java Sea (Prashad, 1932a), China (Ong Che & Morton, 1991; Xu, 1999; Scott, 2003), Sunda Strait and off southwest Java (this study).

Depth range. 9–82 m (Prashad, 1932a); 12.5–65.5 m (Xu, 1999); 805–977 m (this study).

Remarks. The shape of the shells obtained in this study does not entirely agree with Hanley's (1866) illustration (presumably of the type specimen) in that the ventral margin traces a gentle arc in the Indonesian specimens, in contrast to the somewhat angular ventral outline with a straight edge along the central region of the shell shown by Hanley's figure (see also Huber, 2010). Nearly all records to date have shown that *Orthoyoldia lepidula* occurs in the shallow subtidal. If the SJADES material proves to be indeed this species, it has a wider depth range than previously thought.

Family Malletiidae H. Adams & A. Adams, 1858

Members of this family are distinguished from the externally similar nuculanids in having somewhat thin, elongate shells lacking in strong concentric sculpture, by an edentulous region between the anterior and posterior hinge plates, and having an external, amphidetic or opisthodetic ligament. A resilifer, if present, is very small and located below the umbones, which are prosogyrate. Members have large labial palps with narrow palp proboscoides, as in yoldiids; the hind gut comprises a single anterior loop on the right side of the animal (Sanders & Allen, 1985). Genera currently included in this family are *Carinineilo*, *Katadesmia*, *Malletia*, and *Pseudomalletia*. Malletiids share many similarities with nuculanids (Yonge, 1939; Knudsen, 1970). Apart from the overall likeness in their general shell shape and sculpture, members of both families possess an anterior adductor muscle that is larger than the posterior one, a sense organ along its anterior mantle edges, and a single posterior siphonal tentacle emanating from the posterior mantle edge at the base of the siphon on either the left or right side of the animal.

***Malletia* Des Moulins, 1832**

Type species. *Malletia chilensis* Des Moulins, 1832 (by monotypy).

***Malletia arrouana* Smith, 1885**
(Fig. 8A, B)

Malletia arrouana Smith, 1885: pp. 244, 245, pl. 20, figs. 7, 7a, b off Arrou Islands, depth 1,463 m.

Live collected. CP13 (n=1), CP14 (n=2), CP18 (n=1), CP24 (n=5), CP28 (n=11), CP44 (n=2), CP62 (n=1).

Dead shells. DW01 (n=1), CP22 (n=1), CP28 (n=2, 1 intact indiv.), CP29 (n=4, 2 intact indiv.), CP44 (n=5).

Description. Shell relatively large (to 29.4 mm), inequilateral, escutcheon narrow, no distinct keel, thin, porcelaneous; ligament external, opisthodetic, short, about ⅓ to ¼ length of posterior dorsal margin; posterior margin of shell abuts dorsal margin at almost right angles; external surface with thin greenish- or yellow-brown periostracum over fine, more or less equally spaced commarginal lines that become obsolete over the dorso-posterior shell surface. Commarginal lines are continuous from the anterior to the last quarter region towards the posterior where these lines become obsolete and replaced by much narrower commarginal striae which cross the commarginal lines at an obtuse angle. Internally there is no distinct resilifer; anterior and posterior rows of taxodont teeth separated by a narrow groove; posterior hinge teeth plate about twice length of anterior plate, with 20 teeth on anterior plate and 38 on posterior plate. Siphon present, unpaired posterior tentacle present on right side at base of siphon.

Distribution. Timor Sea (type locality); East China Sea(?) Indian Ocean; Arabian Sea(?).

Depth range. 300 m (Taiwan) to 2,000 m (Ceylon); 100–1,630 m (this study).

Remarks. Smith (1895: 17 and pl. 2, fig. 12) in describing *Malletia conspicua* from 1,165 m in the Arabian Sea off the west coast of India (SL=21.5 mm; see also Annandale & Stewart, 1909: pl. 2, figs. 7, 7a, 7b; Subba Rao, 2017: figured a possible paratype, SL=17 mm with 14 teeth on either side of umbo but this does not agree with Smith's description of the larger holotype with 18 anterior and 30 posterior teeth), noted its close relationship to this species; it may eventually prove to be synonymous with *M. arrouana*. In a subsequent paper, Smith (1906) described *M. brevis* based on a single specimen collected off the west coast of Ceylon in 2,000 m of water, noting that it "Differs from *M. conspicua* Smith, in form and sculpture, being more rounded in front, shorter, and squarer posteriorly" but *M. brevis* was never illustrated (see Winckworth, 1940). The holotype is in the Zoological Survey of India (ZSI M3780/1; Subba Rao, 2017). Knudsen (1967: 254, 255, fig. 7B, C) described *M. conspicua* (SL=24 mm) from the "Bali Sea" from 1,165–1,135 m which appears to be *M. arrouana*, whilst Xu (1990, 1999) reported *M. conspicua* off northern Taiwan from 550 m based on a single right valve (Xu, 1999: fig. 33, SL=19.4 mm).

Another similarly shaped species is *M. humilior* Prashad, 1932a. A small species at 6.4 mm (holotype), it was described from 1,301 m in the Strait of Macassar. This may turn out to be a juvenile of *M. arrouana* that is "slightly rostrate" and has "two radial ridges…on posterior slope" as described by Prashad (1932a: 26). Sato & Sasaki (2015) illustrated a specimen (p. 54, fig. 22; SL=13 mm) identified as *M. humilior*

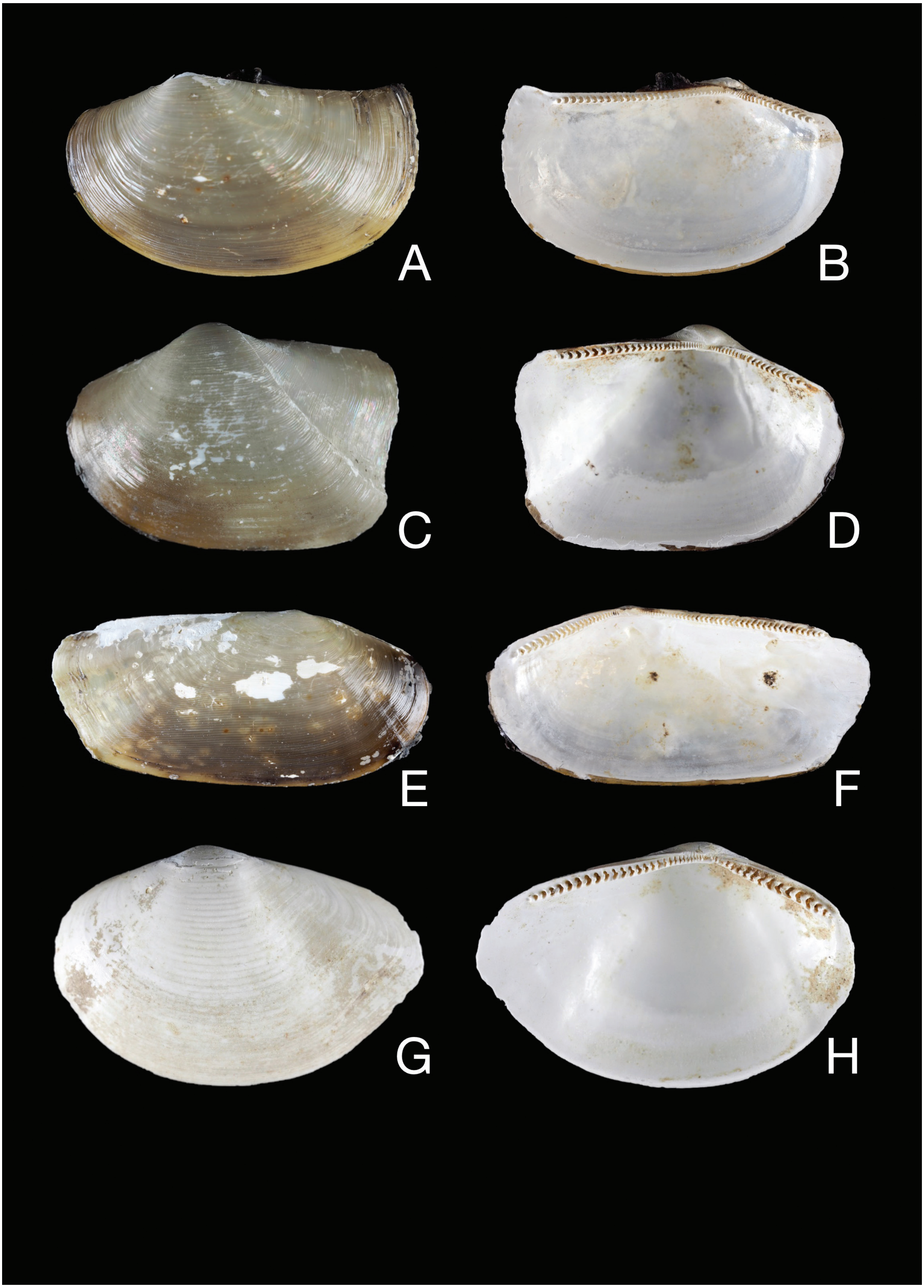

Fig. 8. Malletiidae. A, B, *Malletia arrouana* Smith, 1885, left valve, station CP28, SL=24.8 mm; C, D, *Malletia encrypta* Prashad, 1932a, left valve, station CP22, SL=15.8 mm; E, F, *Malletia neptuni* Thiele, in Thiele & Jaeckel, 1931, right valve, station CP28, SL=26.3 mm; G, H, *Katadesmia sansibarica* (Thiele, in Thiele & Jaeckel, 1931), left valve, station DW32, SL=11.0 mm.

collected from 600 m off the Amami-Oshima Islands, Japan in the East China Sea. However, the Japanese specimen is more similar to the SJADES specimens of *arrouana* in which neither a rostrum nor radial ridges are present. At the other end of the size range is the large *Portlandia* (*Taiwannuculana*) *exotica* Okutani & Lan, 1999. The holotype is 39.6 mm in length, described from 300–500 m of water off northern Taiwan. The posterior region appears to be more drawn out than the SJADES specimens, but otherwise the general attributes of the Taiwanese species agree with those of *M. arrouana*.

Malletia encrypta Prashad, 1932a
(Fig. 8C, D)

Malletia encrypta Prashad, 1932a: p. 26, pl. 1, figs. 44, 45.
Malletia inaequilateralis—Xu, 1999: p. 54, 55, fig. 32 (non *inaequilateralis* Habe, 1951); Huber, 2010: p. 103 (non *inaequilateralis* Habe, 1951).
Pseudomalletia taliensis Lan & Lee, 2001: pp. 3, 4, fig. 3.

Live collected. CP24 (n=1), CP25 (n=4), CP59 (n=1).

Dead shells. CP22 (n=8, 1 intact indiv.), DW32 (n=7), CP35 (n=1), CP47 (n=1), CP58 (n=1), CP59 (n=7), CP62 (n=2, damaged).

Description. Shell relatively large (to 20 mm; holotype SL=13 mm), straight posterior and dorsal margins meet at right angle; shell moderately inflated with distinct keel that extends 45 degrees from umbonal region to meet the lower end of the shell's posterior margin; shell thin, porcelaneous; external surface with fine, closely-set commarginal lines with thin, light brown periostracum; umbones orthogyrate; opisthodetic external ligament; no resilifer, 22 anterior and 28 posterior rows of taxodont teeth (SL=15.6 mm) separated by small gap; narrow but deep pallial sinus present to accommodate a siphon as observed in preserved specimens. Single posterior tentacle present at base of siphon on right side of animal.

Distribution. Off Ceram Island (type locality); southwest Java and Sunda Strait (this study).

Depth range. 835 m (Prashad, 1932a); 476–1,630 m (this study).

Remarks. *Malletia encrypta* described by Prashad (1932a) somewhat resembles *M. taliensis* (Lan & Lee, 2001) in general shape and size, but the two species are considered to be distinct here. The latter species, described from 300 m off northeast Taiwan near Kue-shan, is slightly smaller (12–13 mm) and has a deep pallial sinus; the holotype is described to have 12 anterior and 16 posterior teeth (SL=12 mm), which appears to be rather small in number compared with the holotype of *M. encrypta*, which has 14 anterior and 22 posterior teeth (SL=13 mm; Prashad, 1932a).

Xu (1999) described and illustrated *M. encrypta* (SL=17.0 mm) based on a single valve from 671 m depth off Nansha (Paracel) Islands which was erroneously identified as *M. inaequilateralis* Habe, 1951. Although the general shape of the shell of *M. inaequilateralis* Habe, 1951 (p. 21 figs. 14, 15; SL=11.5 mm holotype; see also Habe, 1968: pl. 48 fig. 8) resembles that of *M. encrypta*, they are regarded as separate species here, as the anterior region of *M. inaequilateralis* is drawn to a sharper point (Habe, 1951) than in *M. encrypta*, i.e., the anterior ventral margin of *M. inaequilateralis* traces a more gradual upward curve in comparison to that of *M. encrypta*, in which the straight ventral margin steeply curves towards the anterior tip of the valves. Habe (1951: 22) further described *M. inaequilateralis* to possess a "deep but wide pallial sinus", whereas *M. encrypta* has a deep and narrow pallial sinus. The holotype of *M. inaequilateralis* possesses 16 and 29 anterior and posterior hinge teeth respectively (SL=11.5 mm), in comparison with the larger sized holotype of *M. encrypta* (SL=13 mm) which has fewer anterior (14) and posterior (22) taxodont teeth. Apart from Xu (1999), Huber (2010) also appears to have mistaken *M. encrypta* for *M. inaequilateralis*. Habe (1968) later suggested that *M. dunkeri* Smith, 1885, which was described from a small shell (5 mm length) taken from station 237 off the SE coast of Japan in 3,429 m of water, may be a juvenile shell of *M. inaequilateralis*. If this proves correct, *M. dunkeri* takes precedence over *M. inaequilateralis*. Prashad (1932a) regarded the *M. dunkeri* and *M. encrypta* as distinct species.

Malletia neptuni Thiele, in Thiele & Jaeckel, 1931
(Fig. 8E, F)

Malletia neptuni Thiele, 1931, in Thiele & Jaeckel, 1931: pp. 49, 50, pl. 8, fig. 67 (Zanzibar Canal, 463 m).
Malletia erronea Prashad, 1932a: p. pl. 1, figs. 40–43 (off SW Timor Id, 918 m).

Live collected. CP24 (n=2), CP28 (n=12).

Dead shells. CP28 (n=8), CP52 (n=1).

Description. Shell elongate, relatively large (26 mm); posterior end distinctly obliquely truncate, with the posterior margin approximating a ship's bow in outline. Shell surface over the posterior half of the valves bears two or three barely visible radiating lines. Fine, equally spaced commarginal lines under thin olive brown periostracum present on shell surface from the anterior to posterior region; these lines terminate at the posterior end of the shell, rather than tracing the outline of the ventral edge towards the dorso-posterior region. Lunule distinctly depressed, narrow; escutcheon longer and narrower than lunule. Umbones orthogyrate; ligament amphidetic but more prominent externally posterior to beak; resilifer absent; pallial sinus deep.

Distribution. Indian Ocean: Zanzibar (type locality), SW Java (this study), Timor Sea (Prashad, 1932a).

Depth range. 463 m (Thiele & Jaeckel, 1931); 918 m (Prashad, 1932a); 957–1,156 m (this study).

Remarks. This species is distinguished by its elongate shell that is obliquely truncate posteriorly and having 2–3 feeble, low radiating ridges that enclose flattened surfaces on the posterior half of the valves. This is only the third record of the species in the literature and appears to have a wide distribution across the Indian Ocean.

Katadesmia Dall, 1908a

Type species. *Yoldia vincula* Dall, 1908a (by original designation).

Katadesmia sansibarica (Thiele, in Thiele & Jaeckel, 1931)

(Fig. 8G, H)

Malletia sansibarica Thiele, in Thiele & Jaeckel, 1931: p. 206, 207, pl. 3, fig. 68.

Live collected. Nil.

Dead shells. DW32 (n=1).

Description. Valve (SL=11.0 mm) inequilateral, shell antero-posteriorly elongate, commarginal lines formed as stepped surface present over central region of valve but are obsolete towards the anterior and posterior; an indistinct keel is present over the dorso-posterior region. Resilifer absent, anterior hinge plate offset from dorsal margin; anterior and posterior hinge plates with 17 and 26 teeth respectively; ligament external, opisthodetic; pallial sinus deep.

Distribution. Dar-es-Salaam and Zanzibar Canal (Thiele & Jaeckel, 1931); off southwest Java (this study).

Depth range. 404–463 m (Thiele & Jaeckel, 1931); 805–977 m (this study).

Remarks. This species has been placed in the genus *Katadesmia* Dall, 1908a, in view of its external resemblance to its type species *K. vincula* (Dall, 1908a) from the East Pacific (see Coan & Valentich-Scott, 2012). The single valve collected agrees well with the shape and size of *sansibarica* provided by Thiele & Jaeckel (1931) based on shells collected in East Africa. In their description, the shell was 9.5 mm in length, with 13 anterior and 22 posterior teeth on the hinge plates.

Carinineilo Kuroda & Habe, 1971

Type species. *Malletia carinifera* Habe, 1951 (by original designation).

Carinineilo carinifera (Habe, 1951)

(Fig. 9A, B)

Malletia (*Neilo*) *carinifera* Habe, 1951: p. 22, figs. 16, 17.
Carinineilo carinifera—Kuroda et al., 1971: p. 505, 506 and 318, 319, pl. 66 fig. 2; Huber, 2010: p. 104 fig. (RV); Kurozumi & Tsuchida, 2017: p. 1163, pl. 464 fig. 6.

Live collected. CP14 (n=2), CP24 (n=3), CP31 (n=1).

Dead shells. Nil.

Description. Shell large (to 20 mm), inequilateral, laterally compressed, dorso-ventrally wide; periostracum thin, olive-yellow to brown; anterior end somewhat pointed, with indistinct keel dorsally; posterior region slightly drawn out, no distinct keel. Escutcheon very narrow, defined by sharp ridge on either side of raised posterior suture. External surface nearly smooth, with barely visible concentric lines. Umbones prosogyrate, umbonal region broad, inflated. External ligament opisthodetic. Very narrow, straight posterior hinge plate about three times as long as the curved, anterior plate. Resilifer absent. Broad, shallow pallial sinus. A single posterior siphonal tentacle emanating from the posterior mantle edge at the base of the siphon is present on right side of the animal.

Distribution. Southern Japan (Habe, 1951; Kuroda et al., 1971); southwest Java (this study).

Depth range. 1,044–1,796 m (this study).

Remarks. This species can be distinguished from *Carinineilo* species 1 and 2 as listed below by its inflated, subequilateral valves.

Carinineilo sp. 1

(Fig. 9C, D)

Live collected. CP10 (n=1), CP25 (n=3), CP49 (n=1), DW46 (n=1).

Dead shells. CP07 (n=1), CP20 (n=3), CP22 (n=2), CP26 (n=1), CP27 (n=4), DW32 (n=35), CP33 (n=3), CP35 (n=1), CP45 (n=20), CP47 (n=1), CP50 (n=1), CP57 (n=22), CP59 (n=2), CP62 (n=2).

Description. Shell relatively large (largest SL=22.0 mm), inequilateral, laterally compressed, gaping at anterior and posterior ends; periostracum thin, olive-yellow to brown; anterior end somewhat pointed, with slight keel; posterior region slightly drawn out, with distinct keel that defines the ventral limits of a dorso-posterior 'wing'. External surface nearly smooth, with barely visible concentric lines. Resilifer absent. External ligament amphidetic. Very narrow, straight posterior hinge plate about three times as long as the curved, anterior plate, bearing 15–16 and 34–43 teeth respectively. Umbones prosogyrate. Escutcheon very narrow, defined by sharp ridge on either side of raised posterior suture. Broad, moderately deep pallial sinus. Anterior adductor muscle scar larger than posterior scar.

Anatomy. Unpaired posterior tentacle emanating from left posterior mantle edge.

Distribution. Off southwest Java (this study).

Depth range. 223–1,630 m (this study).

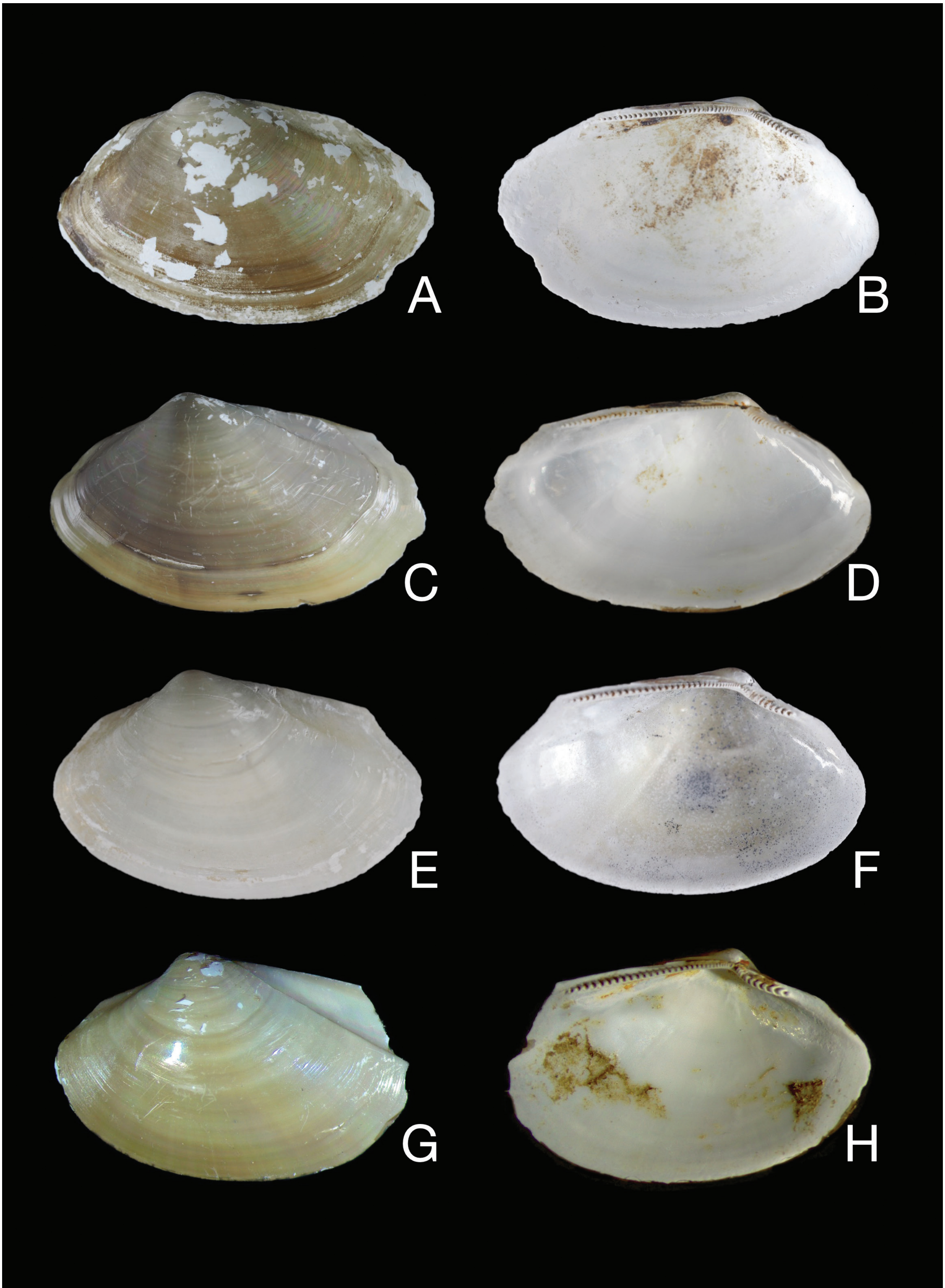

Fig. 9. Malletiidae. A, B, *Carinineilo carinifera* Habe, 1951, left valve, station CP22, SL=19.0 mm; C, D, *Carinineilo* sp. 1, left valve, station CP20, SL=20.1 mm; E–H, *Carinineilo* sp. 2, left valves; E, F: station CP03, SL=13.6 mm; G, H: station CP57, SL=6.8 mm.

Remarks. Two species are currently assigned to the genus *Carinineilo* Kuroda & Habe, 1971, by Huber (2010). The shell of the type species *C. carinifera* (Habe, 1951) collected off Tosa, Shikoku, Japan (no depth provided) is about the same size (SL=17.5 mm; Habe, 1951: p. 21, figs. 16, 17 and p. 22) and subequilateral (see above; also Kuroda et al., 1971: pl. 66 fig. 5). The holotype has 14 teeth on the anterior hinge plate and 36 on the posterior plate (Habe, 1951). The larger *C. angulata* (Sowerby, 1888: pl. 11, fig. 15; SL=26 mm) from a depth of 365 m in the Bay of Bengal has a decidedly angular posterior end. The species observed from SJADES shares the following characters with the type species: (a) the presence of anterior and posterior carinae; (b) anterior hinge teeth larger and smaller in number than those on the posterior hinge. The SJADES specimens clearly belong to *Carinineilo*, but it is neither *carinifera* nor *angulata*, as it is distinctly inequilateral with an elongated posterior region, and the dorsal margin is not angulate.

***Carinineilo* sp. 2**
(Fig. 9E–H)

Live collected. Nil.

Dead shells. CP03 (n=1), CP57 (n=2).

Description. Shell medium sized (11 mm), inequilateral, with distinct oblique carina on dorso-posterior region of shell at an acute angle; shell surface with thin, yellow-green periostracum over fine commarginal growth lines; pallial sinus not visible; resilifer absent; short anterior row of taxodont teeth is curved, but posterior row is straight and about thrice length of anterior row.

Distribution. Sunda Strait and Teluk Pelabuhanratu, Java (this study).

Depth range. 223–398 m.

Remarks. This species has a decidedly angulate posterior dorsal margin resembling *C. angulata* (Sowerby, 1888) from the Bay of Bengal. Their overall shell outlines are also comparable, and it may turn out that *Carinineilo* sp. 2 is a juvenile of *C. angulata*. However, *Bathymalletia takii* (Okutani, 1968) illustrated in Tsuchida (1994, in part: pl. 1 fig. 6; SL=8.4 mm) also has some resemblance to the shells from Java. Further studies are warranted.

Family Neilonellidae Schileyko, 1989

The family Neilonellidae contains species with robust inequilateral or equilateral valves that usually have fine commarginal sculpture, prosogyrate umbones, and an external, amphidetic ligament. There is no resilifer present between the anterior and posterior hinge plates. The posterior region of the shell can be truncated or drawn out posteriorly, in contrast to the rounded outline of the anterior region. The animal has siphons and a deep pallial sinus is present. The family was first mentioned in passing by Allen (1978: 390) but the name is generally attributed to Schileyko (1989) as Allen (1978) did not provide a formal description. *Neilonella* Dall, 1881, is currently the sole genus contained in the family, although *Pseudoneilonella*, *Pseudotindaria*, *Neilo*, and *Protonucula* have also been placed within (Allen & Sanders, 1996a; La Perna, 2007b). Its phylogenetic relationship with the Nuculanidae and Malletiidae is still unclear.

***Neilonella* Dall, 1881**

Type species. *Leda corpulenta* Dall, 1881 (by original designation).

***Neilonella coix* Habe, 1951**
(Fig. 10A, B)

Neilonella coix Habe, 1951: p. 21 figs. 12, 13 and p. 23 (description).
Neilonella dubia coix—Habe, 1968: p. 160 and pl. 48 fig. 10 (non Prashad, 1932a).
Neilonella dubia Prashad, 1932a—Kurozumi & Tsuchida, 2000: p. 837, 838, pl. 416 fig. 2 (non Prashad, 1932a).
Neilonella coix—Okutani et al., 2009: p. 201 and fig. 2K (?); Kurozumi et al., 2017: p. 1163 and pl. 464 fig. 7.

Live collected. Nil.

Dead shells. CP03 (n=2), DW06 (n=7), DW17 (n=9), DW32 (n>80).

Description. Shell small (SL to 10 mm; holotype 8.2 mm in Habe, 1951), inequilateral, posterior region decidedly drawn out; external surface with numerous (28–38; SL range 5.5–10 mm) commarginal riblets that are spaced regularly apart and are clearly demarcated across most of the shell surface except at the indistinct lunule and escutcheon. Prosogyrate umbones are raised high dorsally, with a corresponding excavated internal space under hinge. Internally, a deep pallial sinus can be seen; anterior and posterior hinge plates continuous with 13 and 19 teeth respectively with no resilifer between the two plates. A distinct strut between front end of anterior taxodont teeth row and internal surface is visible. This is absent in the back end of posterior row of teeth.

Distribution. Tosa, Japan (type locality); Sagami Bay to Kyushu (Habe, 1968); Sunda Strait and off southwest Java (this study).

Depth range. 266–977 m.

Remarks. This species has been confused with *Neilonella dubia* Prashad, 1932a, but can be distinguished based on differences in surface sculpture (see under *N. dubia*, this study). *Neilonella coix* is in general a smaller species (largest shell length observed in this study is 10 mm) compared to *N. dubia* which can reach 16 mm in shell length. Okutani et al. (2009: 201 and fig. 2K) illustrated a specimen (SL=9.4 mm) from 246 m depth in waters off NE Honshu, Japan that was identified as *Neilonella coix*, but the commarginal riblets are obsolete over the posterior and dorsal halves of the shell. This does not entirely seem to agree with the original description and illustration provided by Habe (1951).

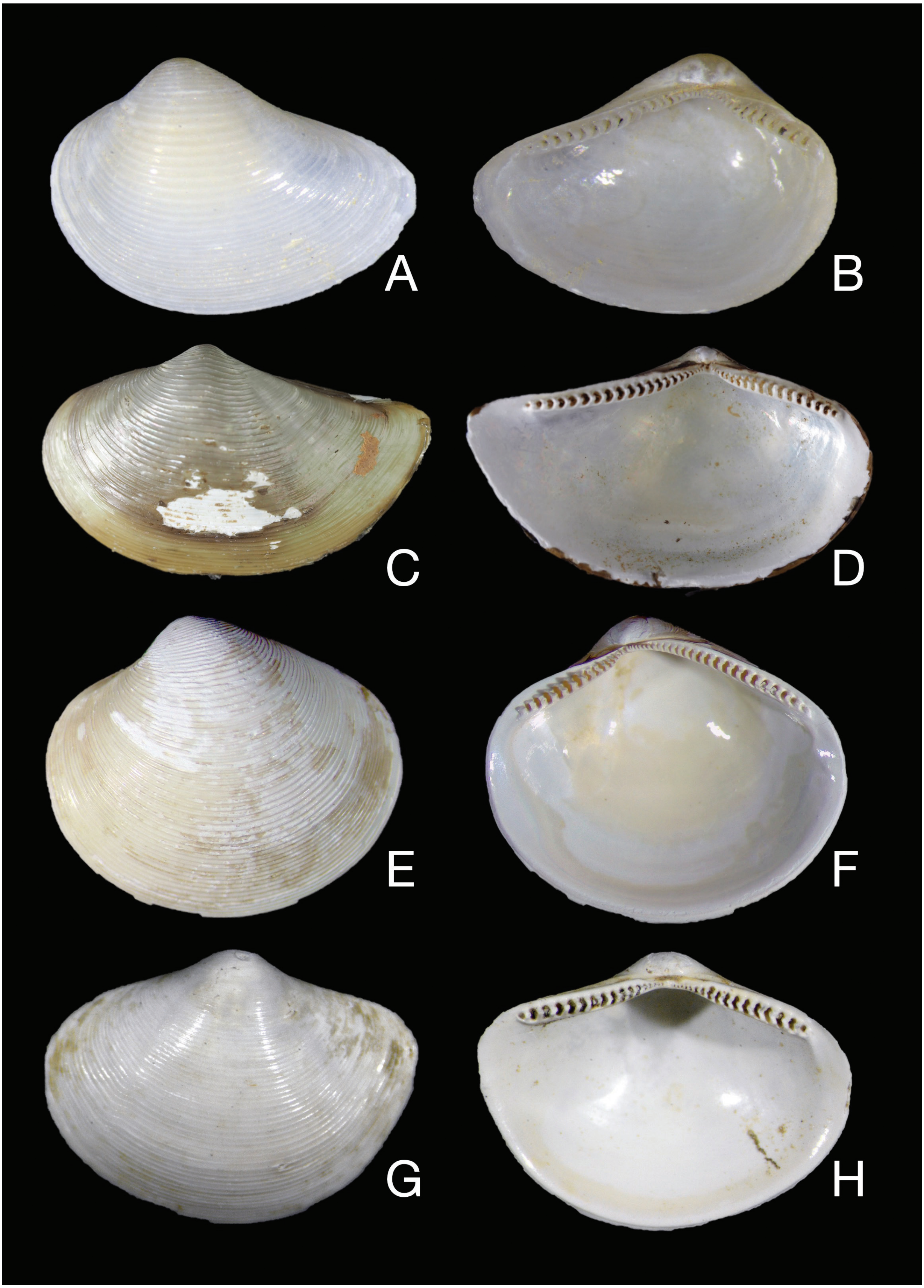

Fig. 10. Neilonellidae. A, B, *Neilonella coix* Habe, 1951, left valve, station DW32, SL=6.5 mm; C, D, *Neilonella dubia* Prashad, 1932a, left valve, station CP24, SL=13.5 mm; E, F, *Neilonella* (*Tindaria*) *siberutensis* (Thiele, in Thiele & Jaeckel, 1931), left valve, station CP27, SL=9.7 mm; G, H, *Neilonella* (*Tindaria*) sp. 1, left valve, station CP35, SL=8.3 mm.

Neilonella dubia Prashad, 1932a
(Fig. 10C, D)

Neilonella dubia Prashad, 1932a: p. 27 and pl. 1, figs. 48, 49.
Neilonella dubia—Bernard et al., 1993: p. 20 (list); Xu, 2008: p. 549 (list); Huber, 2010: p. 104 fig.

Live collected. CP14 (n=1), DW32 (n=1), CP52 (n=5).

Dead shells. CP03 (n=1), DW06 (n=4, 2 intact indiv.), CP24 (n=11, 4 intact indiv.), CP26 (n=4), CP27 (n=2), DW32 (n=24), CP45 (n=20, 3 intact indiv.), CP52 (n=4, 1 intact indiv.), CP59 (n=1), CP62 (n=1).

Description. Shell relatively large (largest SL=15.6 mm), inequilateral, somewhat inflated; periostracum olive green, thin; anterior margin rounded, without keel; posterior region drawn out into an acute angle, dorso-posterior margin almost straight; external surface with numerous (>40) weak, low, rounded but fine, widely spaced commarginal concentric lines which become obsolete over the posterior third of the shell surface. The width of the grooves between adjacent ribs may be up to twice those of the ribs. The concentric lines over the dorso-central region of the valves trace a slight 'hump' directed dorsally and characteristically converge toward the umbones. Escutcheon a narrow, shallow valley relative to lunule, defined by low left and right posterior ridges enclosing a slightly raised sutural region where the left and right valves meet. Internally a very small triangular depressed region between the anterior and posterior hinge plates is recessed under orthogyrate umbones; pallial sinus deep. Ligament external, amphidetic. Resilifer is absent.

Distribution. Channel between Flores and Sumba (type locality); South China Sea (Xu, 2008); Sunda Strait and off southwest Java (this study).

Depth range. 959 m (Prashad, 1932a); 266–1,630 m (this study).

Remarks. *Neilonella coix* (Habe, 1951) described from Shikoku, Japan (see preceding species, this study) is a similar species and sometimes synonymised with *N. dubia*. However, the commarginal lines over the central region of the shell of *N. coix* do not trace a "hump" (Habe, 1951: 21, fig. 12) that is characteristic of *N. dubia*. Externally this species also resembles *Nuculana* (*Sacella*) *sibogai* Prashad, 1932a (see also above) but *N. dubia* is distinguished by not having a well-defined rostrum along the dorsal posterior region, unlike those of *N. sibogai* which delineates a wide, broad, clearly defined escutcheon. In addition, the obsolete commarginal concentric sculpture over the posterior region of the valves of *N. dubia* is in contrast to the strong, ribbed surface present on the entire external surface of the shell in *N. sibogai*.

The obsolete concentric sculpture appears to be also a characteristic of *Neilonella indica* (Smith, 1895) from the Bay of Bengal off the Coromandel coast in 265–457 m of water (SL=12 mm), which may prove to be the same species as *N. dubia*. Smith (1895) however referred to the "transverse plicae on the central part of the valves, which become obsolete on each side...". The anterior region of the valves of *N. dubia* has well-defined ribs and cannot be considered to have obsolete plicae.

Neilonella lediformis (Thiele, in Thiele & Jaeckel, 1931: 51, pl. 3 figs. 73, 73a; SL=12 mm) from East Africa in 400–463 m of water also appears closely related to *N. dubia*, but again the surface sculpture of *lediformis* does not show the characteristic "hump" of *dubia*, nor do the commarginal lines become obsolete in the posterior region as in *dubia*.

Neilonella (_Tindaria_) _siberutensis_ (Thiele, in Thiele & Jaeckel, 1931)
(Fig. 10E, F)

Tindaria siberutensis Thiele, in Thiele & Jaeckel, 1931: p. 210 and pl. 3 (8), fig. 75, 75a (SL=10 mm; from 750 m depth off Siberut Islands, Sumatra.
Neilonella weberi Prashad, 1932a: p. 28 and pl. 8 figs. 5–8 (SL=4.3 mm; from 1,788 m depth off east of Aru Ids, Arafura Sea).
Tindaria jinxingae Xu, 1990: p. 186.
Tindaria jinxingae—Xu, 1999: p. 62, fig. 40 (map); p. 64, fig. 41 (shell); Lutaenko & Xu, 2008: p. 44 and p. 46, fig. 2C.
Tindaria weberi—Okutani, 2006: p. 144 and p. 147, fig. 2A; Kurozumi et al., 2017: p. 1164, 1165 and pl. 464 fig. 21.

Live collected. Nil.

Dead shells. CP27 (n=3).

Description. Shell small (7.7–9.7 mm), shell nearly equilateral, globose, external surface with strong commarginal ribs separated by equally deep grooves; umbones prosogyrate. Anterior hinge plate wide with 14–15 teeth, posterior hinge plate with 25 teeth; resilifer absent. Anterior adductor muscle scar about twice as large as posterior adductor muscle scar. Pallial sinus shallow.

Distribution. Arafura Sea (Prashad, 1932a), East China Sea (Xu, 1990, 1999), Nansei Islands (Japan; Okutani, 2006; Kurozumi et al., 2017), and eastern Indian Ocean (Thiele & Jaeckel, 1931, and this study).

Depth range. 750 m (Thiele & Jaeckel, 1931); 1,788 m (*T. weberi*; Prashad, 1932a); 550 m (*T. jinxingae*; Xu, 1990); 481–557 m (this study).

Remarks. The (sub)genus *Tindaria* Bellardi, 1875, contains species with inflated, subequilateral shells bearing commarginal lirae or riblets, prosogyrate umbones, and having a hinge with no resilifer. They also lack a pallial sinus. The type species of *Tindaria* is based on a Mediterranean Pliocene fossil *T. arata* Bellardi, 1875. Verrill & Bush (1897) recognised the group as a subfamily soon after, and recent authors have since accepted its status as a family (e.g., Ockelmann & Warén, 1998; Huber, 2010; Coan & Valentich-Scott, 2012). However, the limits remain unclear as to whether they are malletiids or neilonellids lacking a siphon (e.g., Habe, 1953; Knudsen, 1970; Allen, 1978). Based on molecular analyses, *Tindaria* appears to be more closely related to *Neilonella* than to *Malletia* (Sharma et al., 2013; Combosch et al., 2017), but the conchological differences between *Neilonella* and *Tindaria* are not entirely distinct, and hence the two "*Tindaria*-like" species are provisionally assigned to *Neilonella* in this study.

The three dead shells obtained bear a very close resemblance to *Tindaria siberutensis* (Thiele, in Thiele & Jaeckel), *T. weberi* (Prashad), and *T. jinxingae* (Xu) in having a deep, ventrally expanded, nearly equilateral shell that has well-rounded anterior, ventral, and posterior margins. The commarginal ribs on the external shell surface are closely set, such that the widths of ribs and grooves were equal. Inside the shell, the anterior hinge plate is widest midway along its short length, while the posterior plate is narrow throughout its length. However, the number of teeth borne on the anterior and posterior plates are 10 and 16 respectively in both *weberi* (SL=4.3 mm) and *jinxingae* (SL=4.5 mm), whilst the smallest shell (SL=7.7 mm) from off Java bore 14 and 25 teeth, respectively. This is more similar to *T. siberutensis*, with 15 and 26 teeth on its anterior and posterior hinge plates (SL=10 mm; Thiele & Jaeckel, 1931). The sizes of adductor muscle scars in *T. siberutensis* and *T. weberi* were neither described nor clearly indicated in the original descriptions, but Xu (1999) remarked that *T. jinxingae* possessed a much larger anterior scar relative to the posterior scar. This size difference was also observed in the two RVs and one LV obtained in this study. In addition, *T. siberutensis* and *T. jingxingae* also clearly share prosogyrate umbones, whereas the illustration of the holotype of *T. weberi* appears to indicate orthogyrate umbones (Prashad, 1932a: pl. 8, figs. 7, 8). Without examining a larger range of specimens, it is difficult to delineate species boundaries but in view of their overall similarities the three taxa are regarded as synonyms here.

Although *Tindaria sundaensis* Knudsen, 1970, was described from 2,780 m depth off southern Java in the Sunda Trench, its expanded posterior half of the shell distinguishes it from *T. siberutensis*, whose shell is nearly symmetrical along its dorso-ventral line. *Tindaria aequatorialis* Thiele, in Thiele & Jaeckel, 1931 (p. 210) from Siberut Islands (750 m) and East Africa (693 m), *T. bengalensis* Knudsen, 1970 (pp. 56, 57) from 2,820 m depth in the Bay of Bengal, and *Tindaria soyoae* Habe, 1953 (p. 135, figs. 1, 2; Kurozumi & Tsuchida, 2000: pl. 417, fig. 1) from southwest Kyushu in 241 m of water all possess expanded posterior shell regions unlike *T. siberutensis*.

***Neilonella* (*Tindaria*) sp. 1**
(Fig. 10G, H)

Live collected. CP24 (n=1), CP27 (n=1), CP33 (n=1), DW46 (n=3).

Dead shells. CP03 (n=5, 2 intact indiv.), CP24 (n=2), CP35 (n=4).

Description. Shell small, SL range 5–10 mm, valves nearly equilateral, globose; anterior margin rounded in comparison with more acute posterior margin. External surface thin yellow periostracum covering low, narrow commarginal lines, numbering about 40, regularly but widely separated; shell thick, no resilifer, external ligament amphidetic; internally, pallial sinus not visible. About equal number of teeth (12–18 teeth for shells 5–10 mm in size) on either side of opisthogyrate umbones, anterior and posterior hinge plates of about the same length, continuous.

Distribution. Sunda Strait and southwest Java (this study).

Depth range. 312–1,068 m (this study).

Remarks. The nearly equilateral shells with gently sloping anterior and dorsal margins distinguish this species.

***Neilonella* sp. 2**
(Fig. 11A, B)

Live collected. Nil.

Dead shells. DW32 (n=1).

Description. Shell small (3.1 mm), equilateral, external surface with fine commarginal lines that are spaced apart; no resilifer. There are about 7 hinge teeth on either side of the umbones.

Distribution. Off southwest Java (this study).

Depth range. 805–977 m (this study).

Remarks. The single, possibly right valve bears some resemblance to the preceding species described above (*Neilonella* sp. 1) but is distinguished by having a small umbonal hump flanked by almost straight anterior and posterior dorsal margins.

DISCUSSION

The deeper waters off the southwest coast of Java is populated by a diverse protobranch fauna. A total of 37 species in five (of 13 worldwide) families was collected across some 2,000 km from depths ranging between 100 to 2,000 m in less than two weeks. The number of species enumerated is surprisingly comparable to the 35 species evaluated by Prashad (1932a) from the Siboga Expedition (see Table 2), which spent a year sampling 323 stations over a much wider area, covering a distance of some 22,000 km in the Indonesian archipelago east of Surabaya. On the other hand, Thiele & Jaeckel (1931) recognised some 16 protobranch species from just three stations off Sumatra sampled during the Valdivia expedition (Table 2). There is also not a great deal of overlap in the protobranch species collected by the Valdivia, Siboga, and SJADES expeditions, possibly reflecting the inherent high diversity and patchy distribution of protobranchs in Indonesian waters. About half of the

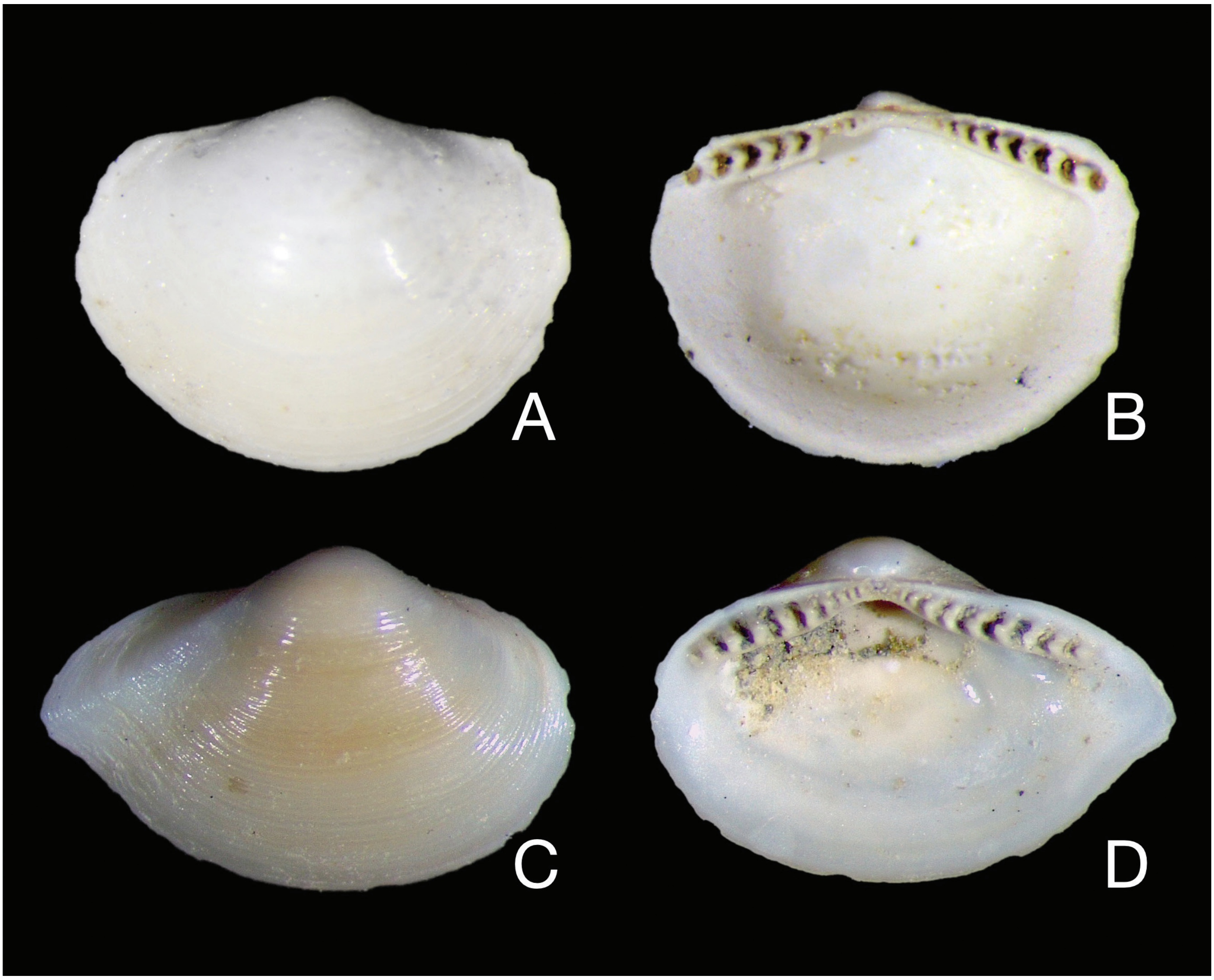

Fig. 11. Neilonellidae and Nuculanidae. A, B, *Neilonella* sp. 2 (Neilonellidae), right valve, station DW32, SL=3.1 mm; C, D, *Ledella* cf. *ultima* (Smith, 1885) (Nuculanidae), right valve, station DW32, SL=4.2 mm.

number of species collected during the SJADES cruise were recorded previously from Indonesia, with the remaining comprising a new species of *Propeleda* (Nuculanidae) and 15 new records (Table 2). Hence the total number of distinct species of protobranchs in Indonesia would appear to be in the region of 70 species (Table 2), after taking into account those collected by other expeditions to the region. Though not entirely unexpected, this compares favourably with other regions in the vicinity where the protobranchs are better known, e.g., China with 65 species (Xu, 2008), Japan with 93 species (Okutani, 2017), and Australia with 52 species (Lamprell & Healy, 1998). Protobranch diversity in the Atlantic Ocean is estimated to be in the region of 100 species (Allen & Sanders, 1996b). However, perhaps because the samples obtained were limited to depths less than 2,000 m, members of several other protobranch families were conspicuously absent from the SJADES material. These included the Sareptidae, Bathyspinulidae, Phaseolidae, and Siliculidae. At the same time, the presence of a recognisable single valve of *Ledella* cf. *ultima*, which normally inhabits the abyssal depths of the Atlantic Ocean, is difficult to explain.

The haphazard nature of sampling the benthos using the trawl and dredge precluded any meaningful quantitative analyses of species abundance. Nevertheless, based on the numbers of specimens collected for each species from the 37 stations, *Carinineilo* sp. 1 and *Acila fultoni* appeared to be the most widespread and common species off southwest Java. They were recorded from 19 and 17 stations respectively, totalling six living individuals and 98 dead valves for *Carinineilo*, and more than 40 living individuals and 40 dead valves for *Acila*. Many valves and living individuals of *Ennucula bengalensis* and *Neilonella dubia* were also collected from 12 and 11 stations, respectively. *Nucula donaciformis*, *Saccella sibogai*, and *Malletia encrypta* were each observed from eight stations. At the other end of the spectrum, some 12 species (including the new species *Propeleda dirham*) were recorded only from a single station, and of these, seven species were represented by only 1–2 valves. These included the tiny nucinellids *Huxleyia* and *Nucinella*, but also the relatively large *Nuculana scalata*, of which only a single living individual was collected during the expedition.

The taxonomic composition of the deep-sea protobranchs collected by the SJADES expedition contains both Indian

Table 2. List of protobranch bivalve species reported from the Indonesian Archipelago. An asterisk against the species name denotes a junior synonym of another listed name. Of the 37 species identified from the SJADES material, 15 species were previously reported upon from Indonesia. NR: new record for Indonesia, *: junior synonym.

	Species (genus names assigned are based on current WoRMS listings)	Challenger Expedition (Smith, 1885)	Valdivia Expedition (Thiele & Jaeckel, 1931)	Siboga Expedition (Prashad, 1932a) total 323 stations	SJADES (this study), and other recent findings
1	*Nucula aequalis* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=2.8 mm		
2	*Nucula donaciformis* Smith, 1895			Stns 27, 87, 178, 210–835 m; SL to 18 mm (sp. no 3)	378–1022 m; SL to 18 mm
3	*Nucula exodonta* Prashad			Stn 300, 918 m; SL=4.7 mm (sp. no 6)	
4	*Nucula rugifera** Prashad (=*Nucula papillifera* Thiele, in Thiele & Jaeckel, 1931)		Padang, Sumatra SL=3 mm	Stn 173, 567 m; SL=5 mm (sp. no 4)	
5	*Nucula semen* Thiele, in Thiele & Jaeckel, 1931 (?=*Nucula nimbosa* Prashad)		Padang, Sumatra SL=2.1 mm	Stn 211, 1158 m; SL=3.2 mm (sp. no 9)	684–851 m; SL=6.2 mm
6	*Nucula sumatrana* Thiele, in Thiele & Jaeckel, 1931		Stns 190, 191, 750–1280 m; SL=9 mm		266–1630 m; SL to 13 mm
7 NR	*Nucula trigonica* Lan & Lee, 2001				540–851 m; SL to 7.8 mm
8 NR	*Nucula* sp. 1				805–977 m; SL to 8 mm
9 NR	*Acila fultoni* (Smith, 1892)				223–1630 m; SL to 47 mm
10	*Acila mirabilis* (Adams & Reeve, 1850)			Stn 18, 1018 m; SL=24.2 mm (sp. no 11)	
11	*Ennucula bathybia* (Prashad)			Stn 208, 1886 m; SL=8 mm (sp. no 7)	
12 NR	*Ennucula bengalensis* (Smith, 1895)				325–1630 m; SL to 20 mm
13	*Ennucula cumingii* Hinds, 1843		Padang, Sumatra	Stns 87, 88, 254, 300, 163, 169, 310–1301 m; SL=? (sp. no 2)	
14	*Ennucula dautzenbergi* (Prashad)			Stns 52, 59, 390–959 m; SL=10.4 mm (sp. no 10)	257–977 m; SL to 17 mm
15	*Ennucula obliqua* (Lamarck, 1819)	Arafura Sea, Stn 188, 51 m; SL=28 mm			
16	*Ennucula pachydonta* (Prashad)			Stn 178, 835 m; SL=5.4 mm (sp. no 8)	
17	*Ennucula siberutensis* (Thiele, in Thiele & Jaeckel, 1931)		Stn 191, 750 m; SL=7 mm		223–1630 m; SL=7 mm

	Species (genus names assigned are based on current WoRMS listings)	Challenger Expedition (Smith, 1885)	Valdivia Expedition (Thiele & Jaeckel, 1931)	Siboga Expedition (Prashad, 1932a) total 323 stations	SJADES (this study), and other recent findings
18	*Nucula diaphana* Prashad (=*Ennucula similis* Rhind & Allen, 1992)			Stn 52, 959 m; SL to 8 mm (sp. no 5)	
19	*Ennucula superba* (Hedley, 1902)			Stn 163, 29 m; SL=20.5 mm (sp. no 1)	
20 NR	*Nucinella maxima* Thiele, in Thiele & Jaeckel, 1931				805–977 m; SL=4 mm
21 NR	*Huxleyia sulcata* A. Adams, 1860				805–977 m; SL=3.5 mm
22	*Acharax* cf. *johnsoni* (Dall, 1891)				876–937 m; SL to 34 mm; see also Wiedicke et al., 2002; Neulinger et al., 2006
23	*Nuculana corbuloides* (Smith, 1885)	Stn 188, 51 m; SL=6.5mm			805–977 m; SL=4.7 mm
24	*Nuculana elaborata* Prashad			Stn 52, 959 m; SL=7.5 mm (sp. no 21)	
25	*Nuculana jovis* (Thiele, in Thiele & Jaeckel, 1931)		Stn 191, 750 m; SL=5mm		266–977 m; SL to 5 mm
26	*Nuculana modica* Prashad			Stn 52, 178, 212, 462–959 m; SL=11.2 mm (sp. no 19)	
27	*Nuculana scalata* Prashad			Stn 300, 918 m; SL=13 mm (sp. no 20)	970–1013 m; SL=27.1 mm
28	*Sacella approximans* (Prashad)			Stn 59, 159, 390–411 m; SL=16.5 mm (sp. no 17)	
29	*Sacella bathybia* (Prashad)			Stn 178, 835 m; SL=6.4 mm (sp. no 16)	
30	*Nuculana discrepans* Prashad (?=*Saccella brookei* (Hanley, 1860))		Padang, Sumatra	Stn 51, 69–91 m; SL=6.1 mm (sp. no 24)	805–977 m; SL to 7.5 mm
31	*Saccella confusa* (Hanley)			Stn 53, 64, 71, 36 m; SL=? (sp. no 12)	
32	*Saccella cygnea* (Thiele, in Thiele & Jaeckel, 1931)		Padang, Sumatra SL=20 mm		
33	*Saccella mauritiana* (Sowerby, 1833)		Padang, Sumatra SL=?		
34	*Saccella novaeguineesis* (Smith, 1885)	Stn 188, 51 m; SL=7 mm			
35	*Saccella robsoni* (Prashad)			Stn 4, 9 m; SL=? (sp. no 14)	

	Species (genus names assigned are based on current WoRMS listings)	Challenger Expedition (Smith, 1885)	Valdivia Expedition (Thiele & Jaeckel, 1931)	Siboga Expedition (Prashad, 1932a) total 323 stations	SJADES (this study), and other recent findings
36	*Saccella sibogai* (Prashad)			Stns 52, 156, 178, 300, 469–959 m; SL=14.5 mm (sp. no 13)	379–1073 m; SL=17 mm
37	*Ledella aequatorialis* (Thiele, in Thiele & Jaeckel, 1931)		Pulau Siberut 750 m; SL=3 mm		
38	*Ledella inopinata* (Smith, 1885)			Stns 88, 211, 221, 1158–2798 m; SL=? (sp. no 18)	
39	*Ledella procumbens* (Prashad)			Stn 211, 1158 m; SL=5.8 mm (sp. no 15)	
40 NR	*Ledella* cf. *ultima* (Smith, 1885)				283–977 m; SL=4.2 mm
41	*Propeleda dirham*, new species				1623–1630 m; SL=23.1 mm
42	*Lamellileda parallelodonta* (Prashad)			Stn 226, 1595 m; SL=13.3 mm (sp. no 22)	
43	*Lamellileda sibogaensis* (Prashad)			Stn 178, 835 m; SL=18.8 mm (sp. no 23)	
44	*Yoldia* sp.			Stn 18, 1018 m; SL=? (sp. no 26)	
45	*Yoldia nanula* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=3.75 mm		
46	*Yoldia serotina* Hinds, 1843				100–1156 m; SL=15 mm
47	*Yoldia siberutensis* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=7 mm		
48	*Yoldia sundaica* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=5.5 mm		
49 NR	*Yoldia* sp. 1				1270–1630 m; SL=27 mm
50 NR	*Megayoldia lischkei* (Smith, 1885)				223–977 m; SL to 24 mm
51	*Orthoyoldia lepidula* (A. Adams, 1856)			Stn 2, 4, 319, 9–82 m; SL=? (sp. no 25)	805–977 m; SL to 13 mm
52	*Malletia arrouana* Smith, 1885	Stn 191, 1463 m; SL=20.5 mm			100–1630 m; to 29.4 mm
53	*Malletia conspicua* Smith, 1895 (?=*arrouana* Smith)			Stn 18, 48, 52, 300, 314, 694–2060 m; SL=? (sp. no 27)	
54	*Malletia encrypta* Prashad			Stn 178, 835 m; SL=13 mm (sp. no 29)	476–1630 m; to 20 mm

	Species (genus names assigned are based on current WoRMS listings)	Challenger Expedition (Smith, 1885)	Valdivia Expedition (Thiele & Jaeckel, 1931)	Siboga Expedition (Prashad, 1932a) total 323 stations	SJADES (this study), and other recent findings
55	*Malletia erronea** Prashad (=*neptuni* Thiele, 1931)			Stn 300, 918 m; SL=18.6 mm (sp. no 28)	957–1068 m; to 26 mm
56	*Malletia humilior* Prashad (?=*arrouana* Smith)			Stn 88, 1301 m; SL=6.4 mm (sp. no 30)	
57	*Malletia sumatrensis* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=5.75 mm		
58	*Malletia tripartita* Prashad			Stn 211, 1158 m; SL=7.4 mm (sp. no 31)	
59 NR	*Carinineilo carinifera* Habe, 1951				1044–1796 m; SL to 20 mm
60 NR	*Carinineilo* sp. 1				223–1630 m; SL to 22 mm
61 NR	*Carinineilo* sp. 2				223–269 m; SL=11 mm
62 NR	*Katadesmia sansibarica* (Thiele, in Thiele & Jaeckel, 1931)				805–977 m; SL=11 mm
63	*Neilonella coix* Habe, 1951				266–977 m; SL to 10 mm
64	*Neilonella delicatula* Prashad			Stn 211, 1158 m; SL=4 mm (sp. no 35)	
65	*Neilonella dubia* Prashad			Stn 52, 959 m; SL=12 mm (sp. no 32)	266–1068 m; SL to 15.6 mm
66	*Neilonella schepmani* Prashad			Stn 221, 2798 m; SL=6.5 mm (sp. no 33)	
67 NR	*Neilonella* sp. 1				312–1068 m; SL to 10 mm
68 NR	*Neilonella* sp. 2				807–977 m; SL=3.1 mm
69	*Tindaria aequatorialis* Thiele, in Thiele & Jaeckel, 1931		Stn 191, 750 m; SL=3.4 mm		
70	*Tindaria siberutensis* Thiele, in Thiele & Jaeckel, 1931 (=*weberi* Prashad)		Stn 191, 750 m; SL=10 mm		481–557 m; SL to 9.7 mm
71	*Tindaria sundaensis* Knudsen, 1970				Sunda Trench, 2780 m; SL=9.1 mm (Knudsen, 1970)
72	*Tindaria weberi** (Prashad) (=*siberutensis* Thiele, in Thiele & Jaeckel, 1931)			Stn 271, 1788 m; SL=4.3 mm (sp. no 34)	

Ocean and Pacific Ocean elements, which may be part of the explanation for the high species diversity observed in southwest Java and the Sunda Strait. Many of the nuculids collected were first described from the Bay of Bengal or from off the west coast of Sumatra, and they have so far not been subsequently reported from elsewhere in the South China Sea or Pacific Ocean. These species include *Acila fultoni*, *Nucula donaciformis*, and *Ennucula bengalensis*, which were fairly common in the samples obtained in this study and represented by living individuals. Similarly, *Nucula trigonica* seems to be a widespread species, but in contrast to the other nuculids, it appears to be distributed from Taiwan to the Sunda Strait. The presence of both the Pacific *Huxleyia sulcata* and the Indian Ocean *Nucinella maxima* (though only represented by a few dead shells) at one locality perhaps provide support to this hypothesis. Amongst the nuculanoids, the Pacific Ocean *Megayoldia lischkei* and *Carinineilo carinifera* occur together with the Indian Ocean *Malletia neptuni*. Admittedly our understanding of the geographical distributions and taxonomic limits of most species is generally poor, but the busy shipping gateway between the Indian and Pacific Oceans does appear to have a diverse protobranch fauna that is worth further investigation. On the other hand, it is also well known that protobranchs can be highly endemic (Zardus, 2002), and it remains to be seen if the Sunda Trough along Sumatra and Java has elements of protobranch endemism.

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