

Mollusks from Pliocene and Pleistocene seep deposits in Leyte, Philippines

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We report 44 mollusk species from four Pliocene to Pleistocene seep deposits in Leyte Island, Philippines. The bivalves are represented by 30 species, of which eleven are new (*Conchocele majimai*, *Conchocele visayaensis*, *Channelaxinus antipoloensis*, *Dulcina liogliogensis*, *Dulcina magoi*, *Elliptiolucina fernandoi*, *Lucinoma canudai*, *Lucinoma velosoi*, *Lucinoma tinagoensis*, *Lucinoma kosatorea*, *Archivesica pastori*), six are extant species known from the Philippines and surrounding waters (*Meganodontia acetabulum*, *Lucinoma dulcinea*, *Lucinoma* aff. *kastoroae*, *Vesicomya margotae*, “*Pliocardia*” *ticaonica*, “*Pliocardia*” *indica*), and five are extant species known from Japanese waters (*Bathymodiolus securiformis*, *Divalucina soyoae*, *Archivesica kawamurai*, *Pliocardia kuroshimana*, *Elliptiolucina ingens*). Remarkable about those latter species is that only a single one of them occurs as fossil in Japan, despite Japan’s rich fossil record of seep communities. This together with the large number of new species with close relatives in Japan suggests that at least part of the modern Japanese vent and seep fauna originated in Philippine waters. More than one third (twelve) of the bivalve species reported here belong to the family Lucinidae, which is also very species-rich in shallow waters around the Philippines. Four new gastropods are described: *Margarites hayashii*, *Vetulonia philippinensis*, *Cataegis ramosi*, and *Provanna azurini*.

Key words: Gastropoda, Bivalvia, chemosymbiosis, Neogene, Quaternary, Indo-Pacific Ocean.

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Introduction

Deep-water methane-seep faunas have a decent Cenozoic fossil record (Majima et al. 2005; Campbell 2006; Kiel 2010b) providing insights into the paleoecology and evolutionary history of these ecosystems (Campbell and Bottjer 1995; Amano and Jenkins 2007; Amano et al. 2010; Kiel 2010a, 2015; Kiel et al. 2016). Seep fossils of Plio-Pleistocene age, however, are relatively rare, probably because there has not been enough time for their uplift (Oppo et al. 2020). A few occurrences of chemosymbiotic bivalves are known from Plio-Pleistocene strata along the American Pacific coast and from Taiwan (Olsson 1942; Squires 1991; Campbell 1992; Wang et al. 2006), the late Pliocene Stirone river seep complex in northern Italy has a diverse fauna of around ten mollusk species (Cau et al. 2015; Kiel and Taviani 2018), and the richest Plio-Pleistocene record is

that of Japan, with around 15 mollusk species (Majima et al. 2005; Amano et al. 2019).

A few Plio-Pleistocene seep deposits are known from the Philippines (Majima et al. 2007, 2010) but their fauna has never been described in detail, save for one large species of the vesicomimid genus *Wareniconcha* (Kase et al. 2019). The Philippines are part of the Indo-Australian Archipelago biodiversity hotspot and hence play an important role in generating biodiversity in the Indo-Pacific region (Ellison et al. 1999; Bellwood and Hughes 2001; Jablonski et al. 2006; Renema et al. 2008). Indeed, the species-rich chemosymbiotic bivalve family Lucinidae appears to have its center of biodiversity in the Philippines (Taylor and Glover 2006; Cosel and Bouchet 2008; Taylor et al. 2014; Glover and Taylor 2016). The Philippines might therefore also be significant for the diversity of deep-water methane-seep faunas. Here we provide a detailed taxonomic account on

the mollusk fauna of these seep deposits, which includes a remarkably high diversity of lucinid bivalves.

Institutional abbreviations.—NMP, National Museum, Manila, Philippines; NMNS PM, National Museum of Nature and Science, Tsukuba, Japan; USNM, Smithsonian Natural History Museum, Washington, DC, USA.

Other abbreviations.—H, height; L, length; RV, right valve; LV, left valve; W, width.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:3B7C70AD-CC73-44D5-921E-B1BA0503FC29

Material and methods

The specimens reported here were collected from four localities on the west coast of the northwestern tip of Leyte Island, Philippines (Fig. 1) (Majima et al. 2007, 2010). Deep-water strata of the Visayan back-arc Basin crop out in this area and are mapped as Bata Shale (Corby et al. 1951) or Bata Formation (Porth et al. 1989). Due to submarine slumping during the deposition and the extensive reworking of the micro- and nannofossils, the beds including the seep fauna described here are difficult to date. Ongoing stratigraphic and micropaleontologic work suggests that of the major four sampled localities, the seep deposits at Liog-Liog Point is of late Pliocene age, while the others are of early Pleistocene age.

Liog-Liog Point.—This site has been described in detail before (Kase et al. 2019). At least four very large calcareous concretionary blocks are scattered in the property of Douglas Pastor at Liog-Liog Point between Tabango and Campopo Bays ($11^{\circ}17'37.7''\text{N}$, $124^{\circ}21'57.5''\text{E}$). The blocks are densely packed with *Archivesica pastori* sp. nov. and *Conchocele majimai* sp. nov., and are most probably derived from the semi-consolidated mudstone horizon well below the Pliocene–Pleistocene boundary, as indicated by microfossil analyses (Kase et al. 2019). One of the very large blocks was extensively sampled and this block is meant when we refer to Liog-Liog Point as type locality; however, a few specimens were also collected from smaller, scattered blocks.

Buhoc Point.—This site is located south of Buhoc Point in Tabango ($11^{\circ}18'49''\text{N}$, $124^{\circ}20'39''\text{E}$; Loc. 2 in Majima et al. 2007). The beds exposed at this site consist of semi-consolidated, tuffaceous, fine-grained sandstone. Huge float concretions derived from the sandstone are scattered on the intertidal platform and are often densely packed with articulated lucinid bivalves. Our microfossil analyses were not successful to date these beds in detail. We consider the beds as being of Pleistocene age because Majima et al. (2007) correlated the beds to the uppermost part of

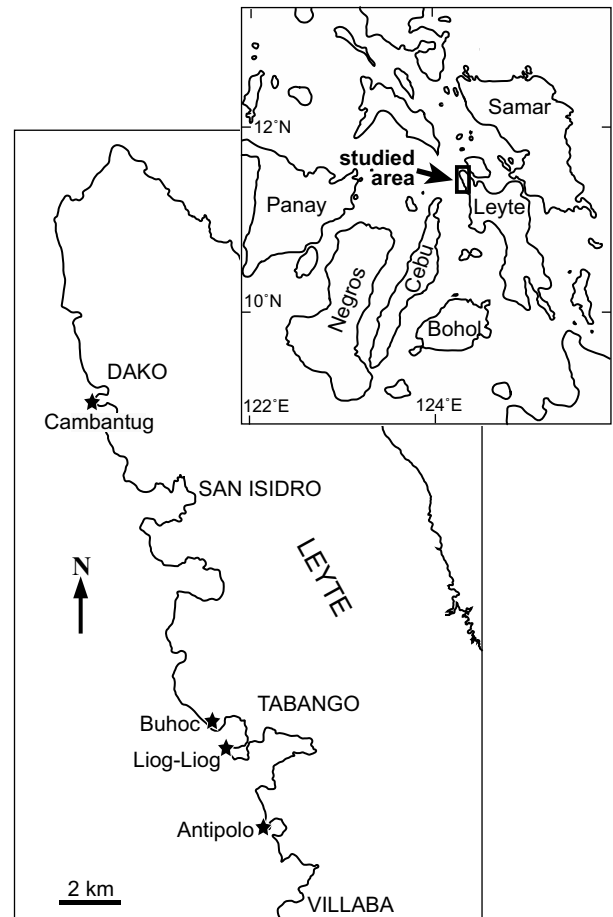


Fig. 1. Maps showing the locations of the four studied localities in the northwestern tip of Leyte Island, Philippines; Liog-Liog Point is of late Pliocene age, Antipolo Point, Buhoc Point, and Cambantug Point are of early Pleistocene age.

the Bata Formation exposed on the intertidal shore at the tip of Liog-Liog Point, which include the planktonic foraminifer *Globorotalia truncatulinoides* diagnostic for the Pleistocene.

Antipolo Point.—This site is Loc. 7 ($11^{\circ}15'28''\text{N}$, $124^{\circ}22'55''\text{E}$) in Majima et al. (2007). Variable-sized and complex concretions resulting from the precipitation of authigenic carbonate around burrows cover the beach and sea cliff at Antipolo Point, and contain a swarm of articulated shells of *Lucinoma* spp. and *Meganodontia acetabulum*. The matrix surrounding these concretions consists of semi-consolidated and unconsolidated muddy sandstone that also yields chemosynthetic bivalves as well as normal deep-water mollusks. The beds in this site have been definitely dated as Pleistocene by planktonic foraminifer and nannofossil analyses.

Cambantug Point.—This site has been described in detail by Majima et al. (2007). It is located at the western corner of Cambantug Point ($11^{\circ}26'55.7''\text{N}$, $124^{\circ}18'18.1''\text{E}$), where massive semi-consolidated mudstone beds are exposed on the beach and in the beach cliff. Abundant bivalves are found in several calcareous concretions of variable size and also in mudstone around the concretions. The bivalves

are mostly articulated and densely packed, keeping their original life orientations. The dating of the mudstone beds remains somewhat questionable: nannofossils provided a middle Pliocene age (NN15), whereas planktonic foraminifers point to an early Pleistocene age. This might indicate reworking of the nannofossils and hence we consider the age of the calcareous concretions as early Pleistocene.

All measurements are given in mm rounded to the nearest first decimal place.

Systematic paleontology

Class Bivalvia Linnaeus, 1758

Family Mytilidae Rafinesque, 1815

Subfamily Bathymodiolinae Kenk and Wilson, 1985

Genus *Bathymodiolus* Kenk and Wilson, 1985

Type species: Bathymodiolus thermophilus Kenk and Wilson, 1985, by original designation; Recent, Galapagos Ridge.

Bathymodiolus securiformis Okutani, Fujikura, and Sasaki, 2004

Fig. 2A, B.

2004 *Bathymodiolus securiformis* sp. nov.; Okutani et al. 2004: 105, figs. 4C, D, 7C, D, 8, 9.

2005 *Bathymodiolus securiformis* Okutani, Fujikura and Sasaki, 2004; Sasaki et al. 2005: 94, fig. 5E.

2019 *Bathymodiolus securiformis* Okutani, Fujikura and Sasaki, 2004; Kuo et al. 2019: 355, fig. 4.

Material.—Liog-Liog Point, Pliocene: five specimens, NMNS PM 28133, 28175, 28203–28205 (L = 118.8 mm, Fig. 2A, B), NMNS PM 28203, and four unnumbered specimens. Antipolo Point, Pleistocene: an isolated right valve, NMNS PM 28169 (L = 129.1 mm).

Remarks.—The Pliocene Philippine specimens reported here differ somewhat from the extant *Bathymodiolus securiformis* from the Okinawa Trough by having a slightly longer anterior portion of the shell. The genetically closest species to *B. securiformis*, *B. tangaroa* Cosel and Marshall, 2003, is less slender, and its subspecies *B. tangaroa tuerkayi* Cosel and Janssen, 2008 is broader on the posterior side (Cosel and Marshall 2003; Okutani et al. 2004; Cosel and Janssen 2008).

Stratigraphic and geographic range.—Pliocene: Leyte, Philippines. Recent: Okinawa Trough.

Unidentified bathymodiolin

Fig. 2C.

Material.—Liog-Liog Point, Pliocene: one right valve, NMNS PM 28170 (L = 25.6 mm).

Description.—Small modioliiform shell, greatest inflation approximately at horizontal midline; low, subterminal umbo, long posterodorsal margin, narrow and almost evenly con-

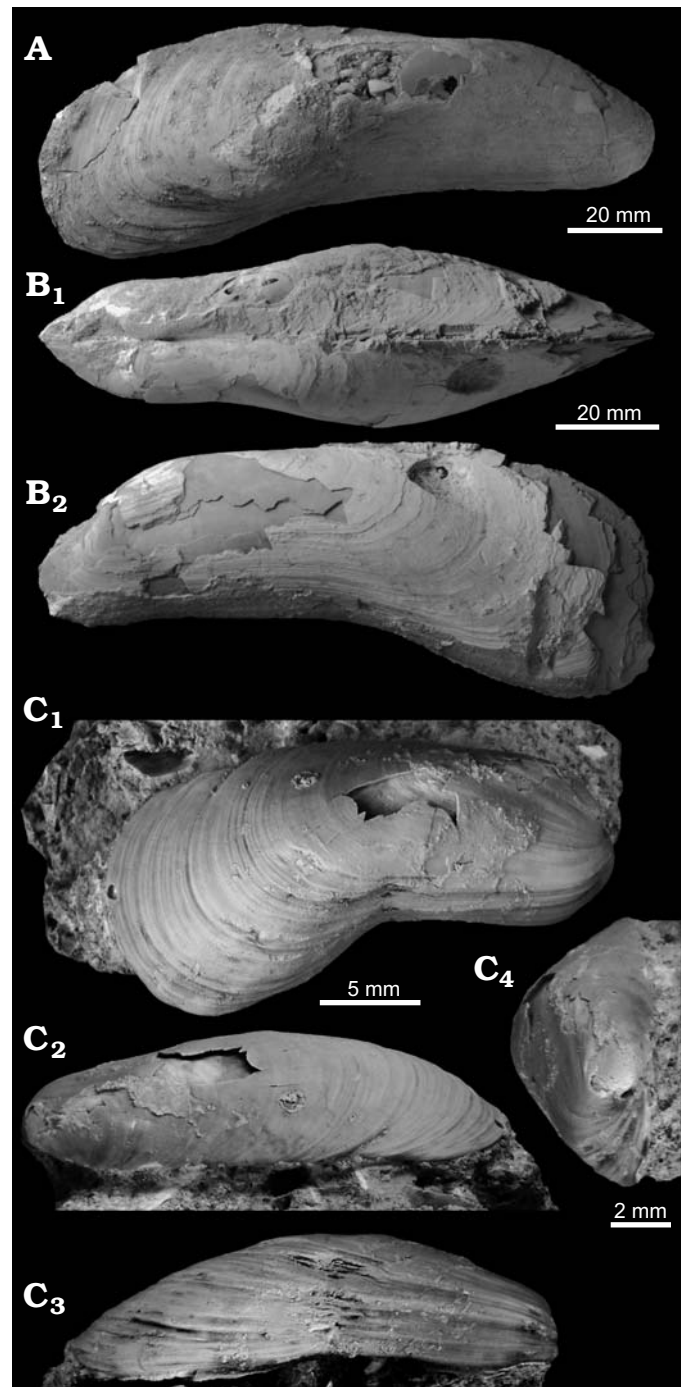


Fig. 2. Bathymodiolin bivalves from Pliocene (B, C, Liog-Liog Point) and Pleistocene (A, Antipolo Point) seep deposits in Leyte, Philippines. A, B. *Bathymodiolus securiformis* Okutani, Fujikura, and Sasaki, 2004. A. NMNS PM 28169, a right valve. B. NMNS PM 28202, an articulated specimen in dorsal view (B₁), exterior of left valve (B₂). C. The unidentified bathymodiolin, NMNS PM 28170, outside of right valve (C₁), specimen in dorsal (C₂), ventral (C₃), and anterior (C₄) views.

vey posterior margin, anterior margin narrowly rounded; shell surface with irregular growth lines.

Remarks.—The single available right valve experienced a shell injury about at its midline, resulting in a deformation that makes the identification of this specimen difficult.

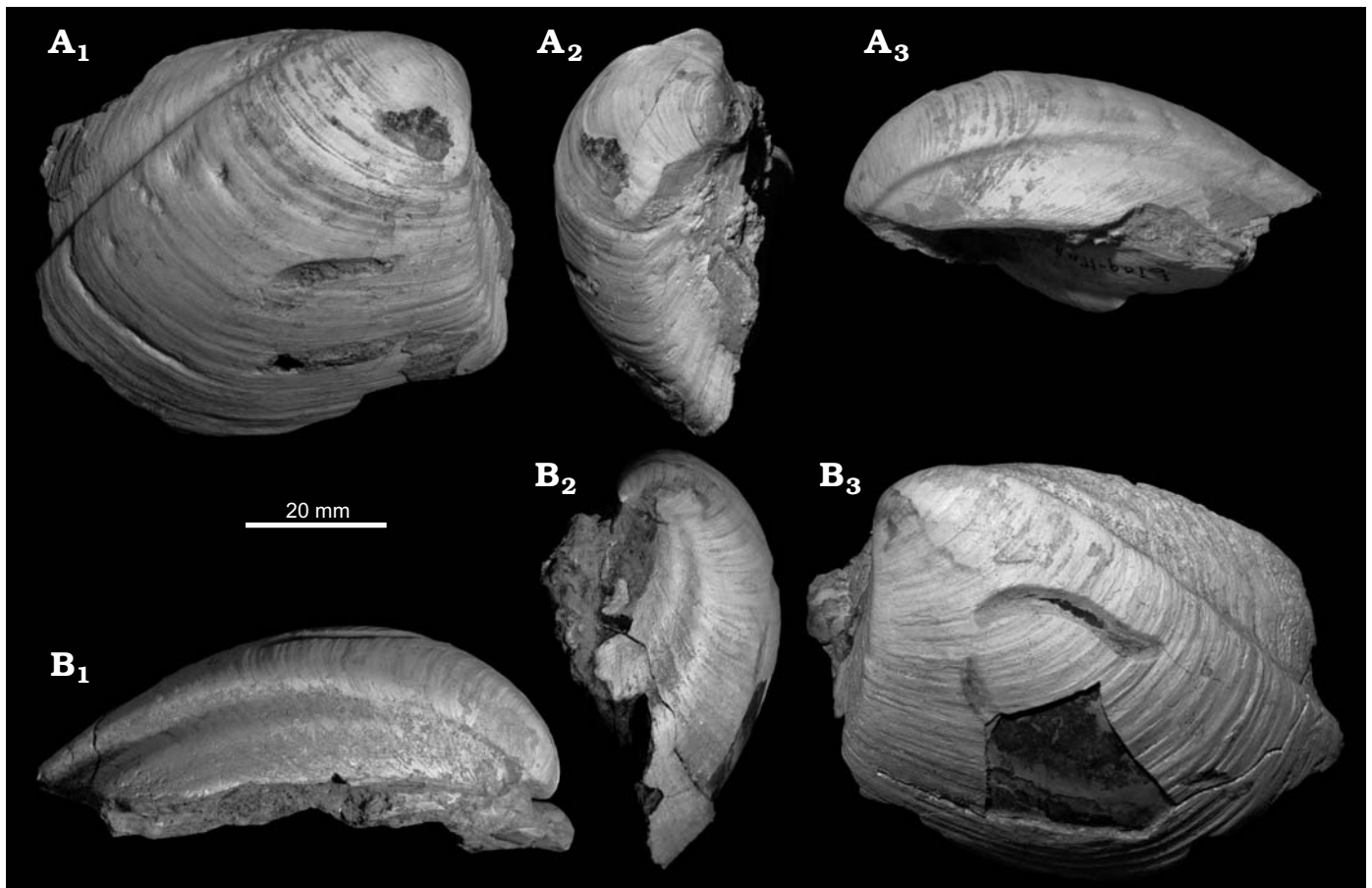


Fig. 3. The thyasirid bivalve *Conchocele majimai* sp. nov. from the Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. **A.** Paratype NMNS PM 28171, an isolated right valve; outer shell surface (A₁), anterior side (A₂), posterodorsal margin (A₃). **B.** Holotype NMP-2159, an isolated left valve; posterodorsal margin (B₁), anterior side (B₂), outer shell surface (B₃).

Bathymodiolus hirtus, *B. japonicus* and *B. platifrons* possess a similar low, subterminal umbo, but those species have a more drawn-out posterior margin that is acutely rounded posteroventrally (Hashimoto and Okutani 1994; Okutani et al. 2004; Sasaki et al. 2005). *Bathymodiolus securiformis* has a similar narrow posterior margin and long posterodorsal margin, but also a much more elongate anterior margin. Two taxa associated with wood and bones in the Westpacific Ocean are also similar: “ESU D” from the Philippines and Japan, and “*Idas* sp. SAL 4” from Vanuatu and Philippines (Lorion et al. 2010).

Family Thyasiridae Dall, 1900

Genus *Conchocele* Gabb, 1866

Type species: *Thyasira bisecta* Conrad, 1849, type by monotypy; Miocene, Astoria Formation, Oregon, USA.

Conchocele majimai sp. nov.

Fig. 3.

Zoobank LSID: urn:lsid:zoobank.org:act:5B70D6CF-1E10-454E-82EE-4E85D1834913

Etymology: In honour of Ryuichi Majima (Yokohama National University), who cooperated field work.

Type material: Holotype NMP-2159, an isolated left valve; paratype NMNS PM 28171, an isolated right valve.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—The type material and two unnumbered specimens from the type locality.

Dimensions (in mm).—NMP-2159, L = 72.0, H = 60.0; NMNS PM 28171, L = 68.0, H = 58.0.

Diagnosis.—Large *Conchocele* with slightly concave anterior margin; broad posterodorsal area with low median ridge, bordered by deep, slightly curved posterior sulcus causing slight indentation of posterior margin; ventral margin straight, broadly curving into posterior margin.

Description.—Large, well-inflated shells, W/H ratio of one valve 0.30–0.33, umbones terminal, blunt, prosogyrate; anterior margin long, slightly concave; anterodorsal area broad with blunt internal ridge starting at umbo, ending at 2/3 of length anterodorsal area; anterior half of ventral margin straight, then turning dorsally in broad curve until reaching posterior end of shell; dorsal margin evenly and slightly convex, transition to posterior margin marked by distinct corner; posterodorsal area broad, bordered by deep, sulcus that is curved on first half of shell, nearly straight on second

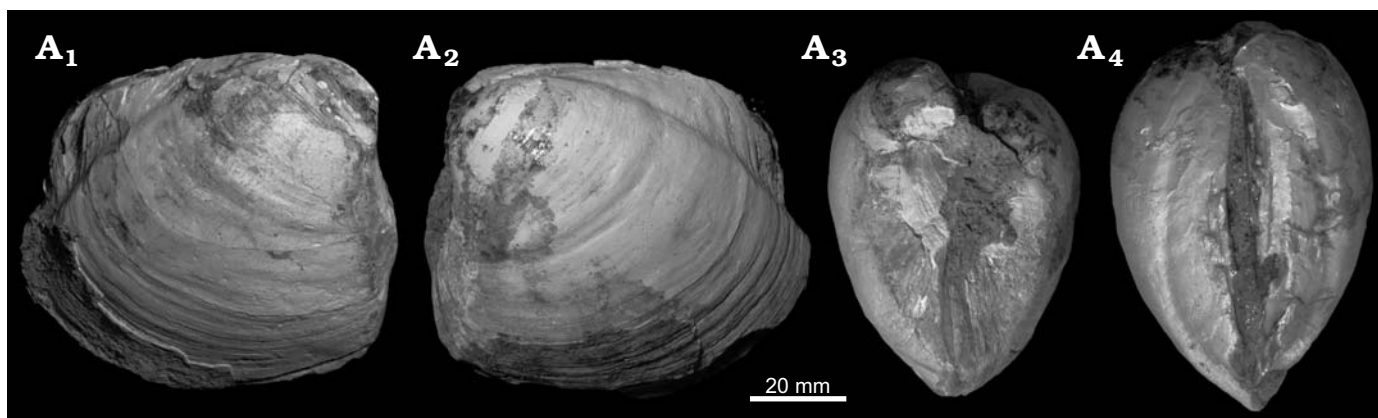


Fig. 4. The thyasirid bivalve *Conchocele visayaensis* sp. nov. from the Pleistocene Cambantug Point seep deposit at Leyte, Philippines, holotype NMP-2160, outer shell surface of right (A₁) and left (A₂) valves; anterior side (A₃), posterodorsal margin (A₄).

half, and causes an indentation on the posterior shell margin; outer surface with fine, irregular growth lines.

Remarks.—*Conchocele majimai* differs from *Conchocele visayaensis* sp. nov. described below by its almost straight posterior sulcus, the broader posterodorsal area, and its straight ventral margin. The extant *Conchocele novaeguineensis* Okutani, 2002 from northern Papua New Guinea differs from *C. majimai* by its strongly coiled umbo (Okutani 2002). The extant *Conchocele ochotica* (Krishtofovich, 1936) (= *Thyasira disjuncta* var. *ochotica* Krishtofovich, 1936) has a more distinctive (= deeper) posterior groove above the posterior ridge, and a narrower posterodorsal area than *Conchocele majimai* (Krishtofovich, 1936). Also extant North Pacific specimens illustrated as *Conchocele bisecta* or *Conchocele disjuncta* (Coan et al. 2000; Kamenev et al. 2001; Kharlamenko et al. 2016) have a narrower posterodorsal area than *Conchocele majimai*. A specimen illustrated as *Conchocele* sp. from Broken Water Bay in Papua New Guinea (Samadi et al. 2015: fig. 2F) has a more rounded ventral margin and a narrower posterodorsal area than *Conchocele majimai*. The Miocene holotype of *Conchocele bisecta* has a much more rounded outlined and a more acutely rounded anterior margin than both *Conchocele majimai* and *Conchocele visayaensis* described below.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Conchocele visayaensis sp. nov.

Fig. 4.

Zoobank LSID: urn:lsid:zoobank.org:act:B519A43A-40C5-4D98-9DF6-24314E078AC6

Etymology: In reference to the Visaya Basin, the type region.

Type material: Holotype NMP-2160, an articulated specimen.

Type locality: Cambantug Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—The holotype and 11 articulated specimens (in one lot: NMNS PM 28126).

Dimensions (in mm).—NMP-2160, L = 77.6, H = 66.4.

Diagnosis.—Large *Conchocele* with slightly concave anterior margin; posterodorsal area rather narrow, median ridge indistinct to absent, posterior sulcus curved, producing deep indent in posterior shell margin; ventral margin well rounded, transition to posterior margin indistinct.

Description.—Large, well-inflated shells, W/H ratio of single valve ~0.36, umbones terminal, blunt, prosogyrate; anterior margin long, slightly concave; anterodorsal area broad, heart-shaped, bordered by distinct ridge; posterodorsal area narrow, smooth, bordered by blunt sulcus and ridge that form deep indentation at posterior margin; ventral margin gently convex, ending posteriorly at posterior sulcus; outer surface with fine, irregular growth lines.

Remarks.—For differences to *Conchocele majimai* see above. Compared to *Conchocele visayaensis*, *Conchocele* sp. from Papua New Guinea (Samadi et al. 2015: fig. 2F) has a curved rather than angular transition from posterodorsal to posterior margin, and the posterior sulcus in a more dorsal position, resulting in a smaller posterodorsal area and in a broader and more curved posteroventral margin. The same applies to extant North Pacific shells typically identified as *Conchocele bisecta* (Coan et al. 2000; Kamenev et al. 2001; Kharlamenko et al. 2016). Shells identified as “*Conchocele bisecta* Conrad” dredged from Sagami Bay, Japan, in the collection of the National Museum of Nature and Sciences in Tsukuba (T. Haga coll.) are very similar, if not identical, to *Conchocele visayaensis*.

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Genus *Channelaxinus* Valentich-Scott and Coan in Coan and Valentich-Scott, 2012

Type species: *Channelaxinus oliveri* Valentich-Scott and Coan in Coan and Valentich-Scott, 2012, by original designation; Recent, Bahía Santiago, Colima, México.

Remarks.—We follow the revised diagnosis for *Channelaxinus* provided by Oliver and Frey (2014: 466) and the provisional assignment of *Thyasira excavata* Dall, 1901, and

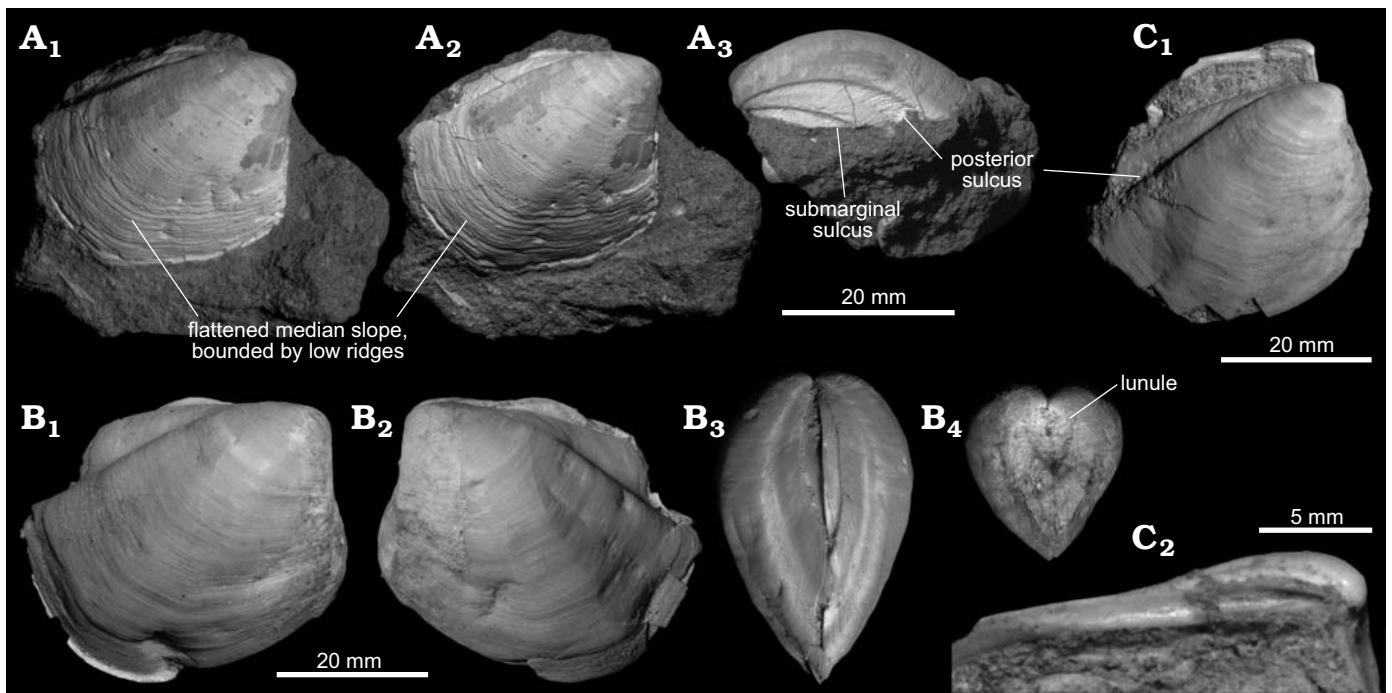


Fig. 5. The thyasirid bivalve *Channelaxinus antipoloensis* sp. nov. from the Pleistocene Antipolo Point seep deposit in Leyte, Philippines. **A.** Paratype NMNS PM 28178, disarticulated right valve embedded in rock matrix; exterior of shell with the light coming from two different angles, emphasizing the posterodorsal sulcus (A₁) and the median angulation (A₂), and view on dorsal margin (A₃). **B.** Holotype NMNS PM 28177, articulated specimen; views on right (B₁) and left (B₂) valves, the dorsal margin (B₃) and the anterior margin showing the lunule (B₄). **C.** Paratype NMNS PM 28179, articulated specimen with displaced valves; view on exterior of right valve (C₁), close-up on edentulous hinge of left valve (C₂). Note the frequent repaired shell injuries on all specimens.

Prothyasira adelaideana Iredale, 1930 to *Channelaxinus* (Oliver and Frey 2014; Oliver 2015).

Channelaxinus antipoloensis sp. nov.

Fig. 5.

Zoobank LSID: urn:lsid:zoobank.org:act:E4A68DB5-CBE8-4083-B52D-3FB54D8B358D

Etymology: In reference to the type locality Antipolo Point.

Type material: Holotype NMNS PM 28177, an articulated specimen; paratypes: NMNS PM 28178, an isolated right valve, NMNS PM 28179, an articulated specimen from the type locality.

Type locality: Antipolo Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—The type material and one lot including eight specimens (NMNS PM 28120) from the type locality.

Dimensions (in mm).—NMNS PM 28177, L = 43.0, H = 38.0, W = 25.3; NMNS PM 28178, L = 30.3, H = 24.0, W (single) = 8.5; NMNS PM 28179, L = 38.0, H = 30.0.

Diagnosis.—Shell of average size for genus; median ridges on shell surface developed as angulations rather than distinct ridges; lunule small for genus, comprising less than half of anterior shell margin; submarginal sulcus distinct but short.

Description.—Shell polygonal, umbones elevated, prosogyrate, rather blunt; short but distinct posterior submarginal sulcus; posterodorsal area of moderate height, rather short, bordered by distinct sulcus and sharp ridge; shell surface

with two low angulations running from umbo to ventral shell margin; anterior margin straight to slightly concave; lunule deep, length slightly less than half of anterior margin; hinge plate narrow, edentulous; ligament nymph short.

Remarks.—*Channelaxinus antipoloensis* sp. nov. is here placed in *Channelaxinus* based on its deeply impressed lunule and flattened median slope that is bounded by low ridges. With these two characters, *C. antipoloensis* clearly differs from members of *Conchocele*, a genus of large thyasirids that is often found at fossil seep deposits (see above). *Ascetoaxinus* Oliver and Frey, 2014, with its type species *Ascetoaxinus quatsinoensis* Oliver and Frey, 2014, has a similar overall shell shape, but *C. antipoloensis* differs from *Ascetoaxinus* by lacking the rounded projections that scallop the lunule edge in *Ascetoaxinus*, and by having a small lunule. *Thyasira* Lamarck, 1818 differs by having shells that are less angular and thinner, and the posterior and submarginal sulci of *C. antipoloensis* are deeper and sharper than in *Thyasira*.

The most similar extant species is *Channelaxinus adelaideanus* (Iredale, 1930); the original illustration is a sketch (Iredale 1930: pl. 63: 6, 7) and photos of the holotype were provided by Oliver (2015: figs. 3E, F). They show a specimen with a more pronounced median ridge compared to the median angulation of *C. antipoloensis*; also the less distinct radial ridge ventral to the median ridge is more pronounced in *C. adelaideanus* than in *C. antipoloensis*. *Channelaxinus excavata* (Dall, 1901) has a larger lunule and a more elongate submarginal sulcus than *C. antipoloensis*.

The only fossil so far assigned to *Channelaxinus* is *Channelaxinus* sp. from the middle Miocene (Langhian) Ca' Cavalmagra seep deposit in northern Italy (Kiel and Taviani 2017: 450, fig. 5); the illustrated specimens differs slightly from *C. antipoloensis* by having a longer postero-dorsal area, which is particularly well-seen in Kiel and Taviani (2017: fig. 5.4). The early Miocene *Thyasira minoensis* Itoigawa, 1960 from the Mizunami Group in central Honshu, Japan is also similar and might belong to *Channelaxinus* but appears to have a more defined median ridge (Itoigawa 1960: pl. 2: 1) compared to the median angulation *C. antipoloensis*. Another potential fossil *Channelaxinus* is the early Miocene (Altonian, ~late Burdigalian) *Thyasira (Prothyasira) bartrumi* Powell, 1935 from a deep-water faunule found near Auckland, New Zealand, which is smaller (L = 15 mm, H = 15 mm), and is more elongate and has a shorter anterior margin than *C. antipoloensis* (Powell 1935: 332, pl. 76: 5, 6).

Three species of similar overall shell shape, especially regarding shell outline, the deep and sharp posterior and submarginal sulci, and the flattened posterior slope, are the extant *Conchocele koyamai* Habe, 1981 from the Pacific shelf of Honshu, Japan, *Conchocele compacta minor* Omori, 1954 from Miocene deposits in Honshu, Japan, and *Thyasira compacta* Ishizaki, 1942 from the late Pleistocene of southern Taiwan (cf. Huang et al. 2006). However, Oliver and Frey (2014) noted that *C. koyamai* bears fine, radiating, punctate sculpture, unknown from *Conchocele* and *Channelaxinus*. Similar granular radial sculpture appears to be present also in *C. c. minor* (Omori 1954: pl. 7: 1–4) and *T. compacta* (Ishizaki 1942: 346, 349, figs. 1a–f, 2).

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Family Lucinidae Fleming, 1828

Genus *Meganodontia* Bouchet and Cosel, 2004

Type species: *Meganodontia acetabulum* Bouchet and Cosel, 2004, by original designation; Recent, Taiwanese waters.

Meganodontia acetabulum Bouchet and Cosel, 2004

Fig. 6.

2004 *Meganodontia acetabulum* sp. nov.; Bouchet and Cosel 2004: 706, figs. 1–3.

Material.—Five specimens from the Pleistocene of Antipolo Point (NMNS PM 28107, 28110, 28112, 28166, 28167).

Dimensions (in mm).—NMNS PM 28167 (largest specimen), L = 132.2, H = 120.6.

Remarks.—There is some variation among the available specimens. Whereas specimens NMNS PM 28166 and 28167 are indistinguishable from the holotype of *Meganodontia acetabulum*, specimens NMNS PM 28110 and 28112 have a slightly more truncate anterodorsal margin, a slightly straighter posterodorsal margin, and a slightly more pointed

beak than the holotype. However, we consider all specimens to belong to the extant *Meganodontia acetabulum*.

Stratigraphic and geographic range.—Early Pleistocene: Leyte, Philippines. Recent: Taiwanese waters.

Genus *Dulcina* Cosel and Bouchet, 2008

Type species: *Dulcina guidoi* Cosel and Bouchet, 2008, by original designation; Recent, central Philippines, 520–550 m.

Remarks.—*Dulcina* and *Elliptiolucina* discussed below differ mainly in two ways: *Dulcina* has a moderately long anterior adductor muscle scar, whereas in *Elliptiolucina* it is quite short; *Dulcina* has its posterior side acutely rounded, in contrast to the rounded and sometimes broad posterior side in *Elliptiolucina*.

Dulcina liogliogensis sp. nov.

Fig. 7.

Zoobank LSID: urn:lsid:zoobank.org:act:4637E9DC-6DE5-43B0-A3D0-4AFC72FAEEC2

Etymology: In reference to the type locality at Liog-Liog Point.

Type material: Holotype NMP-2161, an articulated specimen; paratypes: NMNS PM 28127 (articulated), NMNS PM 28130 (left valve), NMNS PM 28131 (internal mold), NMNS PM 28136 (articulated), 28165 (internal mold).

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—Late Pliocene of Liog-Liog Point: type material and many specimens including (NMNS PM 28127–28130, 28135–28137); early Pleistocene of Buhoc Point: two specimens (NMNS PM 28131, 28165); early Pleistocene of Antipolo Point: four specimens (NMNS PM 28138–28141).

Dimensions (in mm).—NMP-2161, L = 69.5, H = 61.2; NMNS PM 28127, L = 64.4, H = 58.5; NMNS PM 28130, L = 63.7, H = 56.1; NMNS PM 28131, L = 64.3, H = 56.4; NMNS PM 28136, L = 65.6, H = 61.4; NMNS PM 28165, L = 52.0, H = 49.1.

Diagnosis.—Large, little inflated *Dulcina* with broad posterior margin; growth lines irregular, indistinct; hinge plate narrow with remnant of cardinal tooth in left valve.

Description.—Large, rather flat shells with oval outline, W/L ratio c. 0.38; umbones small, prosogyrate, elevated, positioned anteriorly at about 40% of total shell length; anterior margin broad, well-rounded; posterior side tapering on both dorsal and ventral sides, posterior margin truncate; escutcheon lanceolate; lunule small, elongate; anterodorsal area narrow, marked by distinct incision; posterodorsal area narrow, marked by shallow sulcus; external sculpture of irregular commarginal growth increments. Shell interior with faint radial striations; anterior adductor muscle scar elongate, reaching below horizontal midline of shell to ~60% total shell height, detached from pallial line for 3/5 its length; posterior adductor muscle scar pear-shaped, broad groove running from umbo to its anterior margin; hinge plate narrow, left valve with remnant of short cardi-

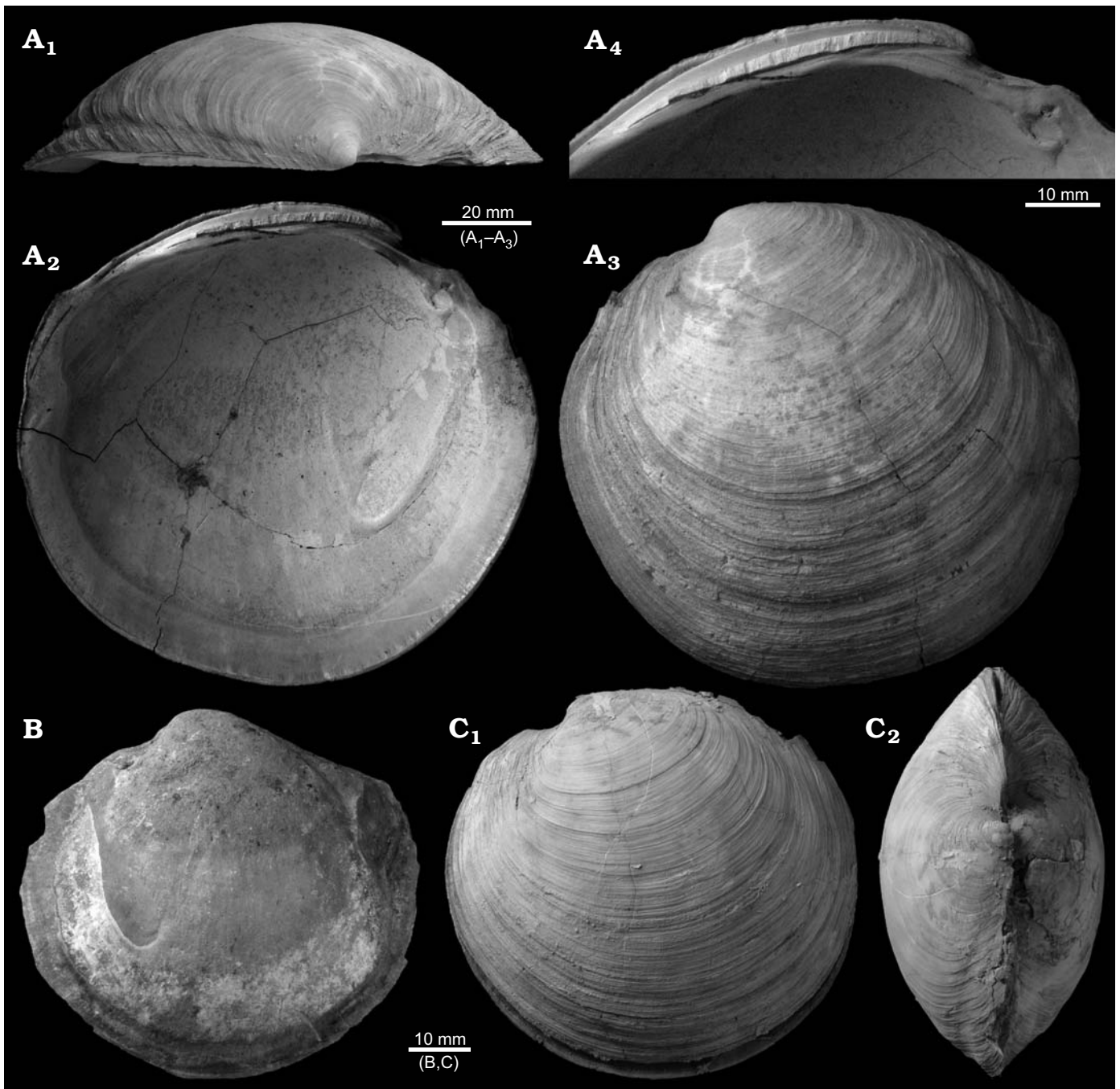


Fig. 6. The lucinid bivalve *Meganodontia acetabulum* Bouchet and Cosel, 2004 from the Pleistocene Antipolo Point seep deposit in Leyte, Philippines. A. NMNS PM 28166, disarticulated left valve; dorsal view (A₁), inner (A₂) and external (A₃) shell surface, close-up on hinge (A₄). B. NMNS PM 28107, internal mold; view on left valve showing the elongate adductor muscle scar. C. NMNS PM 28167, articulated specimen; view on outer shell surface of left valve (C₁), dorsal view (C₂).

nal 4b; length of ligament nymph ~70% of length of posterodorsal margin.

Remarks.—*Dulcina liogliogensis* sp. nov. is somewhat similar to *D. guidoi* but with broader posterior margin (not as acutely rounded as in *guidoi*); furthermore, *Dulcina guidoi* reaches 42 mm, whereas *Dulcina liogliogensis* reaches 60 mm, and the umbones of *D. liogliogensis* are in a more central position compared to *D. guidoi*, where they are displaced toward the anterior.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Dulcina magoi sp. nov.

Fig. 8.

Zoobank LSID: urn:lsid:zoobank.org:act:10726DC8-540E-4521-A334-B1A80540EED4

Etymology. In honour of Wenceslao Mago (Mines and Geoscience Bu-

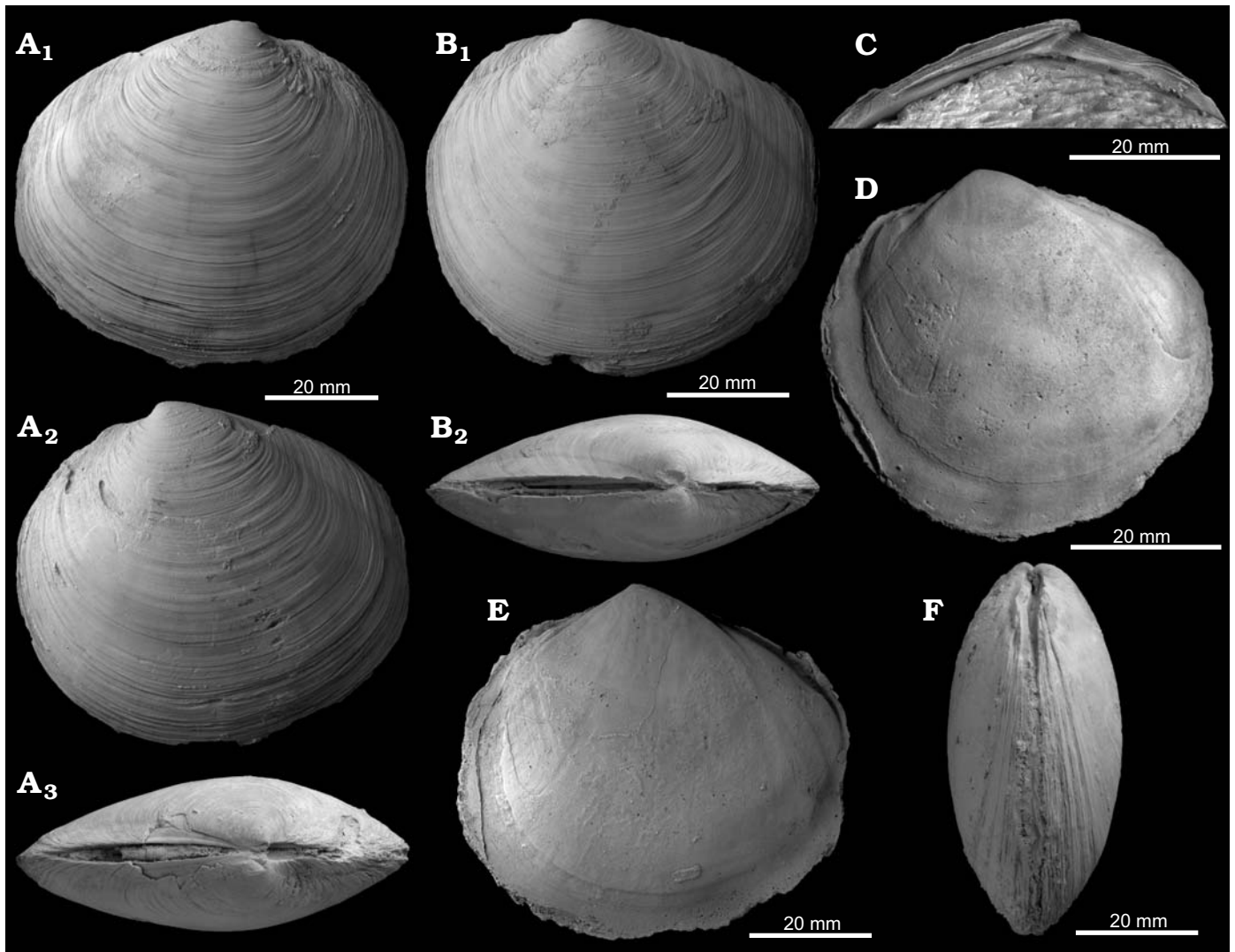


Fig. 7. The lucinid bivalve *Dulcina liogliogensis* sp. nov. from Pliocene (A–D, F, Liog-Liog Point) and Pleistocene (E, Buhoc Point) seep deposits in Leyte, Philippines. **A.** Holotype NMP-2161, articulated specimen; view on outer shell surface of right (A_1) and left (A_2) valves, dorsal view (A_3). **B.** Paratype NMNS PM 28127, articulated specimen; view on outer shell surface of left valve (B_1), dorsal view (B_2). **C.** Paratype NMNS PM 28130, disarticulated left valve, close-up on hinge. **D.** Paratype NMNS PM 28165, internal mold, view on left valve showing anterior adductor muscle scar. **E.** NMNS PM 28131, internal mold of articulated specimen, view on left valve. **F.** NMNS PM 28136, articulated specimen, view on anterior external surface.

reau, Quezon City, Philippines) for his invaluable help with collecting Philippine fossils.

Type material: Holotype NMP-2162, an articulated specimen; paratypes: NMNS PM 28132 (left valve), NMNS PM 28134 (articulated), NMNS PM 28148 (articulated specimen with little shell), and NMNS PM 28409 (internal mold); from type locality. Note that NMNS PM 28132, 28133, and 28148 are from a small (<1 m long) float concretion from the beach; NMNS PM 28134 and 28409 are from the very large block.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—The type material only.

Dimensions (in mm).—NMP-2162 L = 79.3, H = 77.7; NMNS PM 28132, H = 79.0; NMNS PM 28134, L = 70.2, H = 64.6, W = 31.4 (articulated); NMNS PM 28148, L = 80.1, H = 80.0.

Diagnosis.—Large, little inflated, subcircular shell; posterior ridge low; anterodorsal area with shallow, distinct groove; anterior adductor muscle scar elongate, reaching well below midline of shell, detached from pallial line for little more than half its length; hinge plate broad, edentulous.

Description.—Large, subcircular, little inflated shell; umbones small, prosogyrate, elevated, pointed, situated just anterior to vertical midline of shell; lunule narrow, elongate, escutcheon lanceolate; anterodorsal area bordered by low but distinct ridge, shallow but distinct groove in middle; anterior shell margin with distinct angulation at horizontal midline of shell; ventral and posterior margins well rounded; posterodorsal ridge and groove low, close to shell margin; external sculpture of indistinct growth lines. Interior of shell with numerous radial grooves; pallial line

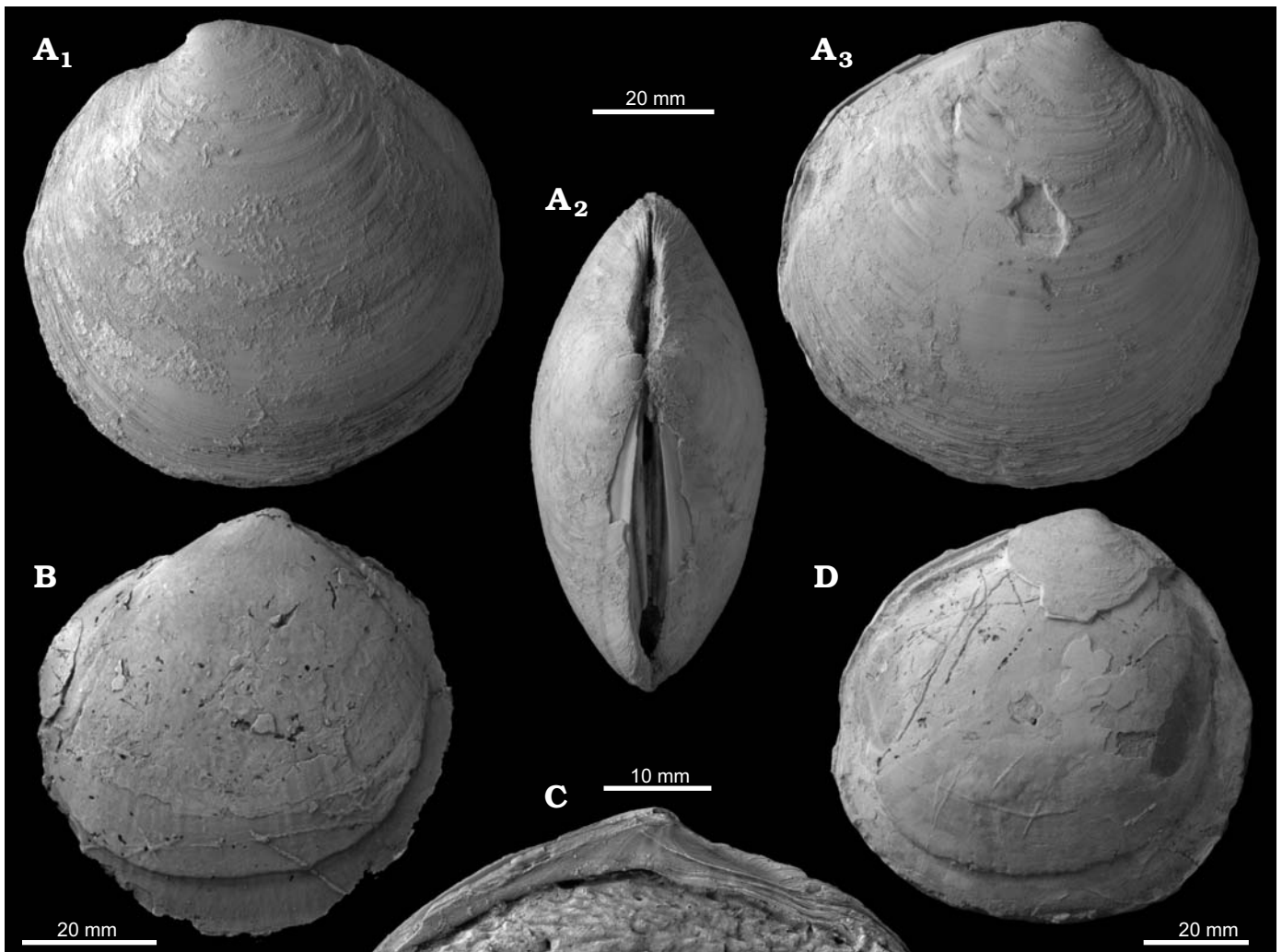


Fig. 8. The lucinid bivalve *Dulcina magoi* sp. nov. from Pliocene (A, C, D from a concretion found float at Liog-Liog Point) and Pleistocene (B, Buhoc Point) seep deposits in Leyte, Philippines. **A**. Holotype NMP-2162, articulated specimen; view on outer shell surface of left (A_1) and right (A_3) valves, dorsal view (A_2). **B**. Paratype NMNS PM 28409, internal mold, view on right valve showing anterior adductor muscle scar. **C**. Paratype NMNS PM 28132, showing hinge area of left valve. **D**. Paratype NMNS PM, view of right valve showing anterior adductor muscle scar.

entire; anterior adductor muscle scar elongate, reaching almost 2/3 of entire shell height, detached from pallial line for just over half its length; posterior adductor muscle scar broad, pear-shaped; hinge plate moderately wide, edentulous, ligament nymph stretching the entire posterodorsal shell margin.

Remarks.—*Dulcina magoi* sp. nov. differs from the five species described by Cosel and Bouchet (2008) (*D. guidoi*, *karubari*, *madagascarensis*, *minor*, and *musorstomi*) by being larger (up to 80 mm length compared to 25–47 mm), and more circular, particular on the anterior side. In addition, *D. minor* and *D. musorstomi* differ by having distinct, sharp commarginal sculpture. From *D. liogliogensis* n. sp. described above it differs by being rounder (=not having an acutely rounded posterior side) and having a longer anterior adductor scar.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Genus *Elliptiolucina* Cosel and Bouchet, 2008

Type species: Elliptiolucina magnifica Cosel and Bouchet, 2008, by original designation; Recent, Philippines, 520–550 m depth.

Elliptiolucina ingens Okutani, 2011

Fig. 9.

2011 *Elliptiolucina ingens* sp. nov.; Okutani 2011: 116, figs. 1A, 2, 3.

Material.—Two specimens from the Pliocene of Liog-Liog Point: NMNS PM 28117, an isolated right valve; NMNS PM 28121, an isolated right valve.

Dimensions (in mm).—NMNS PM 28117, L = 91.0, H = 75.8; NMNS PM 28121, L = 92.4, H = 75.4.

Remarks.—The available specimens from Liog-Liog Point vary regarding the angle at which the anterior adductor muscle scar (aams) deviates from the pallial line. Whereas the aams deviates widely from it in specimen NMNS PM 28121 (Fig. 9C) as in the holotype of *E. ingens*, it is very close to

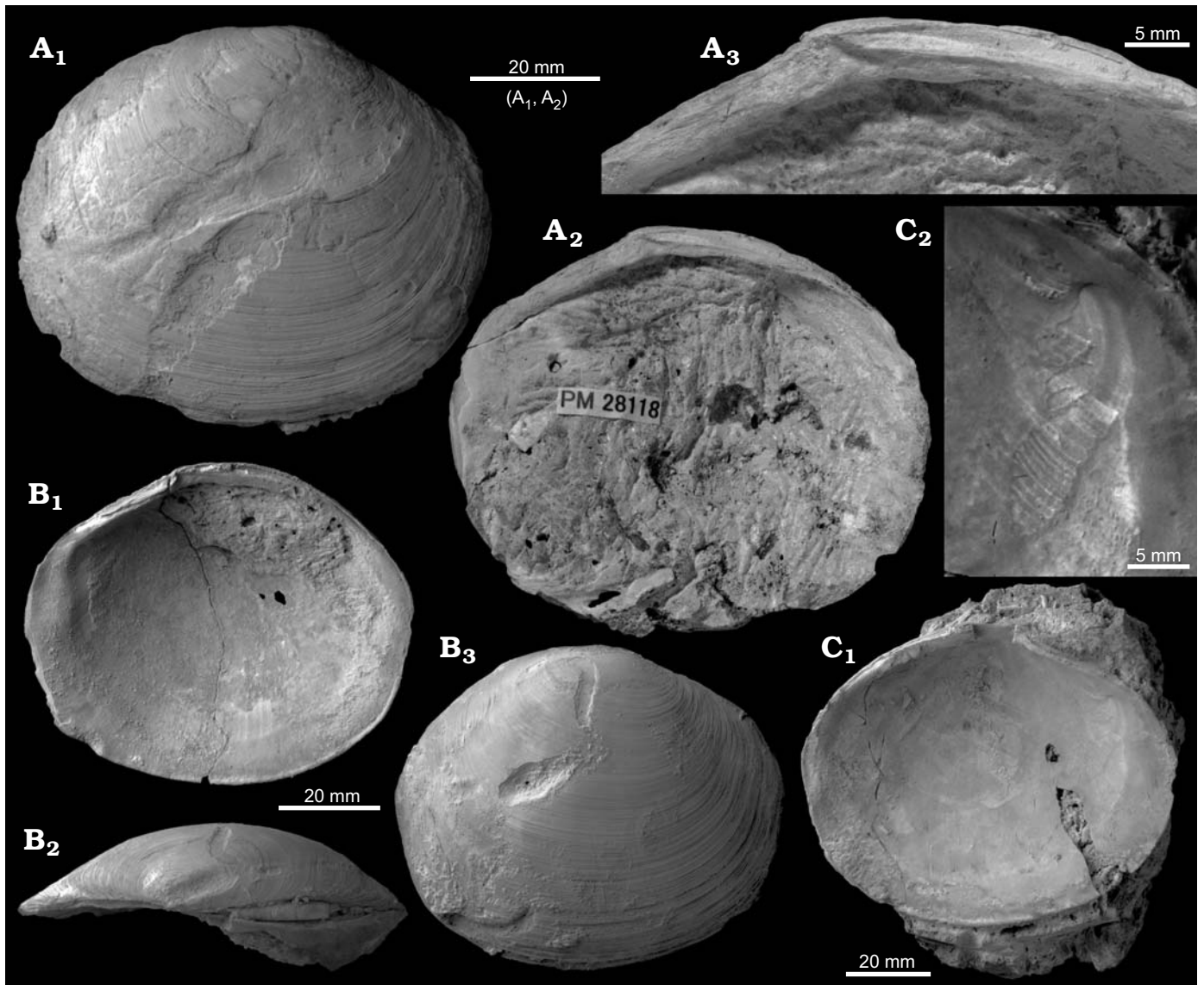


Fig. 9. The lucinid bivalve *Elliptiolumina ingens* Okutani, 2011 from the Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. **A.** NMNS PM 28118, a right valve showing sculpture on outer surface (A₁) and the hinge (A₂, A₃). **B.** NMNS PM 28117, a right valve, interior of right valve showing hinge and adductor muscle scars (B₁), dorsal view showing ligament and inflation (B₂), outer shell surface (B₃). **C.** NMNS PM 28121, left valve showing shell interior (C₁) and anterior adductor muscle scar (C₂).

the pallial line in specimen NMNS PM 28117 (Fig. 9B). Although the extant *E. ingens* is known only from the holotype and intraspecific variability cannot be assessed, for now we consider the observed differences in deviation of the aams as intraspecific variation.

Stratigraphic and geographic range.—Late Pliocene: Leyte, Philippines. Recent: East China Sea.

Elliptiolumina fernandoi sp. nov.

Fig. 10.

Zoobank LSID: urn:lsid:zoobank.org:act:6A60B3D8-F57F-498C-9E7D-895ADB4496FC

Etymology: In honour of Allan Gil S. Fernando (Quezon City, Philippines), for his invaluable help in dating the Bata Formation.

Type material: Holotype NMP-2163, an articulated specimen with the

hinge of the right valve exposed. Paratype NMNS PM 28119, a slightly damaged specimen with the anterior adductor muscle scars exposed from the type locality.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—Three specimens from the Pliocene of Liog-Liog Point: type material and NMNS PM 28149. One specimen from the Pleistocene of Cambantug Point, NMNS PM 28122 and two from the Pleistocene of Buhoc Point, NMNS PM 28123, 28124.

Dimensions (in mm).—NMP-2163, L = 68.0, H = 55.1; NMNS PM 28119, L = 67.5, H = 55.1.

Diagnosis.—Average size for genus, outline oval but not very elongate, moderately inflated; hinge plate broad for

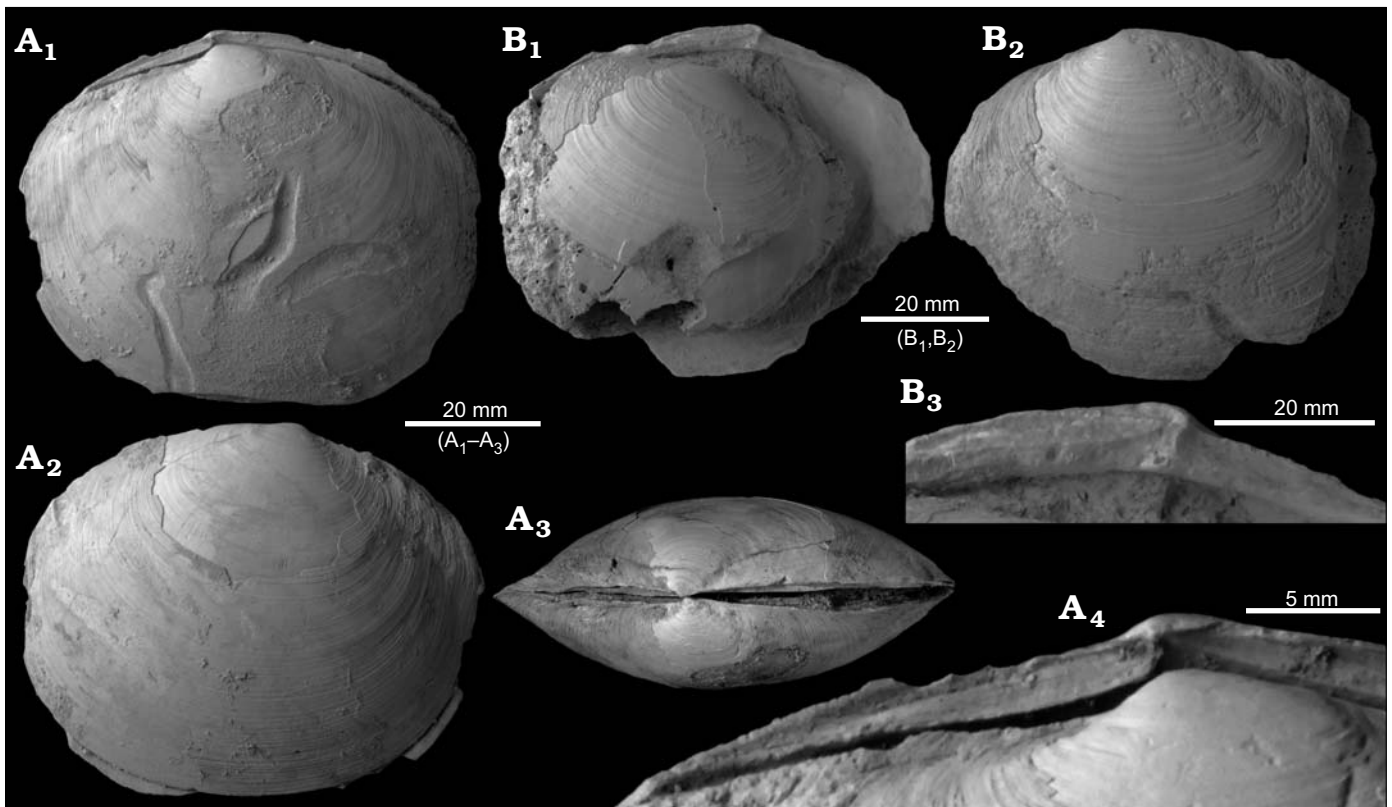


Fig. 10. The lucinid bivalve *Elliptiolucina fernandoi* sp. nov. from the Pliocene Liog-Liog seep deposit in Leyte, Philippines. **A.** Holotype NMP-2163, articulated specimen; view on left (A_1) and right (A_2) valves, view on the dorsal side (A_3), close-up on hinge of right valve (A_4). **B.** Paratype NMNS PM 28119, slightly damaged, articulated specimen; view on exterior of right valve and hinge of left valve (B_1), view on exterior of left valve (B_2), close-up on hinge of left valve (B_3).

genus, with distinct short, thick remnant of a cardinal tooth in left valve; no lateral teeth.

Description.—Shell oval in outline, umbones small, pointed, very little elevated above hinge plate, situated just anterior to vertical midline of shell; anterior margin broadly rounded or slightly oblique below vertical midline; posterior margin broadly rounded; anterodorsal margin straight to slightly convex, posterodorsal margin evenly convex or with slight median angulation; ventral margin evenly convex. Inflation moderate, evenly convex; lunule and escutcheon long, narrow, bordered by sharp ridges. Shell surface covered by fine, commarginal growth increments, most distinct in anterodorsal area; very slight, broad radial depressions marking antero- and posterodorsal areas. Hinge plate strong, right valve with triangular cavity underneath umbo, right valve with short, broad, vertical remnant of cardinal tooth; no lateral teeth. Anterior adductor muscle scar diverging from pallial line by $\sim 40^\circ$, anterior pedal retractor scar round, distinct from adductor muscle scar.

Remarks.—The three extant species described by Cosel and Bouchet (2008) from deep waters of the Philippines and Indonesia (*Elliptiolucina magnifica*, *E. labeyriei*, and *E. virginiae*) differ from *E. fernandoi* by being more elongate and, except for *E. labeyriei*, by having a narrower hinge plate. *E. williamsae* Glover and Taylor, 2016 from 280–679 m

depth in the central Philippines is smaller than *E. fernandoi* (44.1 mm vs. 68.0 mm maximum length) and it possesses a prominent anterior lateral tooth in the right valve that is missing in *E. fernandoi*. The extant *E. ingens* Okutani, 2011 from 576–594 m depth on the slope of the East China Sea (Okutani 2011), growth to bigger size (up to 90.7 mm) and is more inflated than *E. fernandoi*.

Three fossil species of *Elliptiolucina* are described to date. The late Oligocene *E. washingtonia* Kiel, 2013 from western Washington state, USA, is more elongate and has a straighter posterodorsal margin than *E. fernandoi*. The middle Miocene *E. neozelandica* Amano, Little, and Campbell, 2018 from the Moonlight North seep deposit in New Zealand (Amano et al. 2018) is much smaller and has more elevated umbones than *E. cambantugensis*. The late Miocene *Elliptiolucina hetzeli* (Martin, 1933) from asphalt deposit on Buton Island, Indonesia (Martin 1933; Kiel 2013) is more elongate and has more narrowly rounded anterior and posterior margins compared to *E. fernandoi*.

Stratigraphic and geographic range.—Late Pliocene to early Pleistocene: Leyte, Philippines.

Genus *Divalucina* Iredale, 1936

Type species: *Lucina cumingi* Adams and Angus, 1864, by original designation; Recent, Australia and New Zealand.

Divalucina soyoae Habe, 1952

Fig. 11.

1952 *Divaricella soyoae* sp. nov.; Habe 1952: 160.**Material.**—Five specimens from the Pleistocene of Buhoc Point NMNS PM 28142–28146.**Dimensions** (in mm).—NMNS PM 28142, L = 49.0, H = 47.0.**Remarks.**—*Divalucina soyoae* is known from depth of 90 to 200 m in southern Japan (Habe 1952; Dekker and Goud 1994); the genus has not been reported from seep sites before. Extant specimen of *Divalucina soyoae* are said to reach 47 mm in length (Dekker and Goud 1994), which is only marginally smaller than those reported here. See Dekker and Goud (1994) and Amano (2019) for an extensive synonymy and a summary of fossil and recent occurrence of this species.**Stratigraphic and geographic range.**—Late Pliocene: western Honshu, Japan. Pleistocene: eastern Honshu, Japan; Leyte, Philippines. Recent: southern Japan (Amano 2019).Genus *Lucinoma* Dall, 1901**Type species:** *Lucina filosa* Stimpson, 1851, by original designation; Recent, North Atlantic Ocean.*Lucinoma dulcinea* Cosel and Bouchet, 2008

Fig. 12.

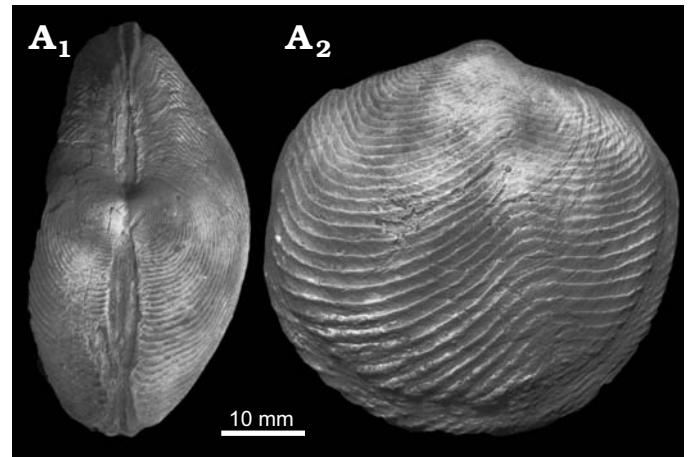
2008 *Lucinoma dulcinea* sp. nov.; Cosel and Bouchet 2008: 165, figs. 37A, B, 41A, 44.2016 *Lucinoma dulcinea* Cosel and Bouchet, 2008; Glover and Taylor 2016: 133, figs. 31A–N; 32A.**Material.**—32 specimens from the Pleistocene of Antipolo Point (*Meganodontia* bed): NMNS PM 28180 (one articulated specimen), NMNS PM 28181 (one articulated specimen), NMNS PM 28182 (one articulated specimen), NMNS PM 28183 (one articulated specimen), NMNS PM 28458 (four articulated specimens), NMNS PM 28459 (four articulated specimens), NMNS PM 28460 (ten articulated specimens), NMNS PM 28461 (three isolated specimens), NMNS PM 28462 (one articulated specimen), NMNS PM 28463 (one articulated specimen), NMNS PM 28464 (one articulated specimen), NMNS PM 28465 (one articulated specimen), NMNS PM 28466 (one articulated specimen), NMNS PM 28467 (one articulated and one isolated specimens). Two worn specimens from the Pleistocene of Cambantug Point: NMNS PM 28160 (two specimens).**Dimensions** (in mm).—NMNS PM 28180, L = 46.1, H = 41.2; NMNS PM 28181, L = 62.0, H = 58.7; NMNS PM 28183, L = 50.0, H = 47.5.**Remarks.**—Extant *Lucinoma dulcinea* occurs in the central Philippines (around Leyte and Panglao islands) at depths of 291–786 m (Cosel and Bouchet 2008; Glover and Taylor 2016).**Stratigraphic and geographic range.**—Early Pleistocene to Recent: central Philippines.

Fig. 11. The lucinid bivalve *Divalucina soyoae* Habe, 1952 from the early Pleistocene Buhoc Point seep deposit (float) in Leyte, Philippines, NMNS PM 28142, dorsal view (A₁), view on right valve (A₂).

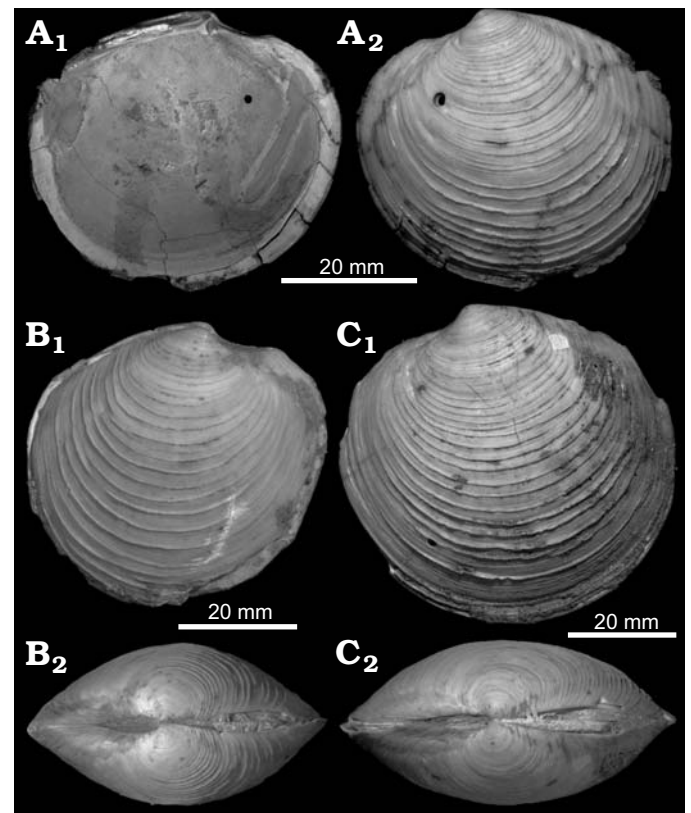


Fig. 12. The lucinid bivalve *Lucinoma dulcinea* Cosel and Bouchet, 2008 from the Pleistocene Antipolo Point seep deposit in Leyte, Philippines. **A.** NMNS PM 28180, left valve, inner shell surface showing the very long anterior adductor muscle scar (A₁), outer shell surface (A₂). **B.** NMNS PM 28183, articulated specimen, outer shell surface of right valve (B₁), dorsal view (B₂). **C.** NMNS PM 28182, articulated specimen, outer shell surface of left valve (C₁), dorsal view (C₂).

Lucinoma aff. *kastoroae* Cosel and Bouchet, 2008

Fig. 13.

Material.—Two articulated specimens from the Pliocene of Liog-Liog Point (NMNS PM 28154, 28155).

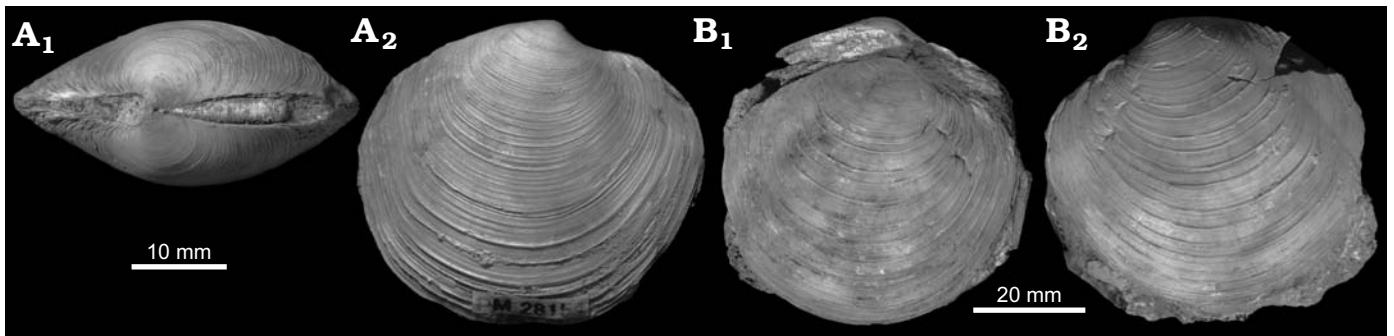


Fig. 13. The lucinid bivalve *Lucinoma* aff. *kastoroae* Cosel and Bouchet, 2008 from the Pliocene Liog-Liog Point seep deposit, Leyte, Philippines. A. NMNS PM 28154, small articulated specimen, dorsal view showing lunule, escutcheon and ligament (A₁), view on right valve (A₂). B. NMNS PM 28155, large articulated specimen, views on right (B₁) and left (B₂) valves.

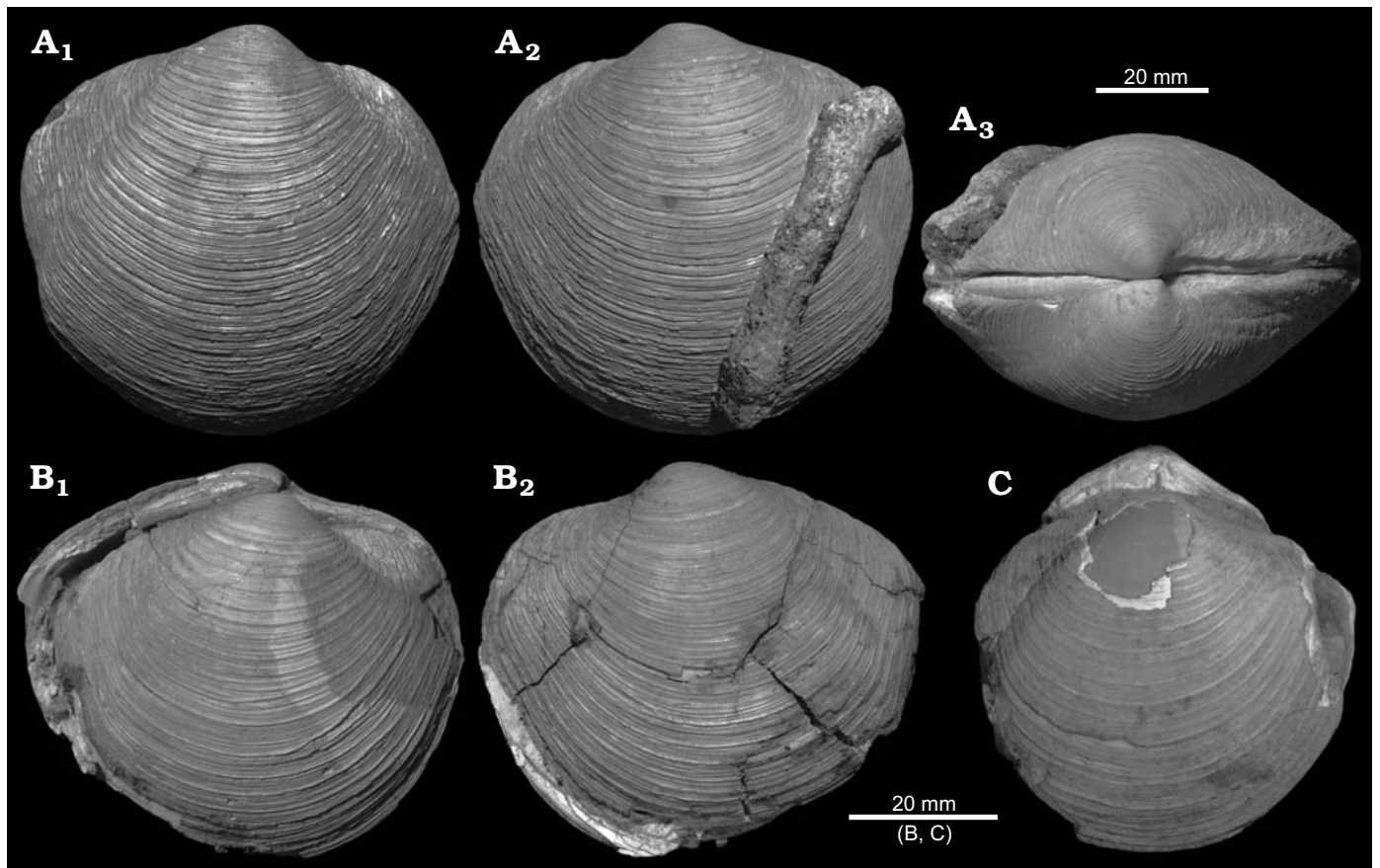


Fig. 14. The lucinid bivalve *Lucinoma canudai* sp. nov. from the Pleistocene Cambantug Point seep deposit, Leyte, Philippines. A. Holotype NMP-2167, large, articulated specimen with attached, filled burrow; outer surfaces of right (A₁) and left (A₂) valves; dorsal side (A₃). B. Paratype NMNS PM 28157, small specimen showing ligament nymph of left valve. C. Paratype NMNS PM 28158, small specimen with remnants of two cardinal teeth in the left valve.

Remarks.—Overall, the specimens from Liog-Liog Point resemble *Lucinoma kastoroae*, but differ slightly in being growing to larger size (up to 55 mm length compared to 34 mm in *L. kastoroae*), by being somewhat taller and by having a slightly less acutely rounded anterior margin. However, we consider these differences too marginal to establish a new species.

Lucinoma canudai sp. nov.

Fig. 14.

Zoobank LSID: urn:lsid:zoobank.org:act:AD227C3A-40D4-45BC-B82A-F075D98C6810

Etymology: In honour of Francisco Canuda (Mines and Geosciences Bureau of the Philippines) for his invaluable assistance with field work.

Type material: Holotype NMP-2167, articulated, inflated specimen with attached burrow. Paratypes: three specimens (NMNS PM 28157–28159) from the type locality.

Type locality: Cambantug Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—The type material only.

Dimensions (in mm).—NMP-2167, L = 77.0, H = 71.3, W = 50.3 (articulated).

Diagnosis.—Large, well-inflated *Lucinoma*, outline angular, umbones blunt, surface sculpture of numerous densely spaced, sharp commarginal ribs, several smaller sharp ridges in interspaces; distinct anterior ridge; posterior sulcus well-developed, lunule long, narrow; ligament long, deeply sunken.

Description.—Large, inflated shell; umbones elevated, blunt; greatest width at middle of shell; anterodorsal margin short, nearly straight, with broad angulation at transition to anterior margin; elevated, blunt ridge running from umbones to anterior end of shell, producing distinct anterodorsal area; posterior area broad, bordered by deep sulcus and distinct ridge running from umbones to posteroventral shell margin; ventral shell margin between ends of those two ridges evenly convex; escutcheon narrow lanceolate, ligament deeply sunken; lunule elongate, deep; surface sculpture of densely spaced, alternating, sharp commarginal ribs.

Remarks.—*Lucinoma canudai* and also *L. velosoi* sp. nov. and *L. tinagoensis* sp. nov., described below), are remarkably more inflated than many species of *Lucinoma*, both extant (*L. yoshidai* Habe, 1958, *L. kastoroae*, and *L. dulcinea*) and fossil (*L. galathea* Marwick, 1953, *L. gracilistriata* Hirayama, 1954, *L. shinokii* Hirayama, 1954) (Marwick 1953; Hirayama 1954; Habe 1958; Okutani and Hashimoto 1997; Cosel and Bouchet 2008; Glover and Taylor 2016). *Lucinoma canudai* differs from the two other strongly inflated *Lucinoma* species reported here (*L. velosoi* and *L. tinagoensis*) by its blunt anterior ridge and correspond-

ing broad anterodorsal area, and its much deeper posterior sulcus. *Lucinoma saetheri* Amano, Little, and Campbell, 2018 from the lower Miocene of New Zealand differs from *L. canudai* by lacking lamellar sculpture and by having smaller umbones (Amano et al. 2018).

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Lucinoma velosoi sp. nov.

Fig. 15.

Zoobank LSID: urn:lsid:zoobank.org:act:7801672C-99B2-48F7-98AB-EB42257D6E9E

Etymology: In honor of Eduardo Veloso, the landowner of the type locality at Antipolo Point, Leyte, Philippines.

Type material: Holotype NMP-2166, disarticulated right and left valves.

Type locality: Antipolo Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—Two specimens from the Pleistocene of Antipolo Point (*Meganodontia* bed): holotype and NMNS PM 28162; two specimens from the Pleistocene of Cambantug Point: NMNS PM 28161, 28163.

Dimensions (in mm).—NMP-2166, L = 70.9, H = 63.8, W = 45.9 (articulated).

Diagnosis.—Well-inflated *Lucinoma*, outline rounded-oval, umbones broad, pointed, surface sculpture of numerous densely spaced, sharp commarginal ribs, few indistinct growth increments in interspaces; posterior sulcus indistinct; lunule broad, short; ligament nymph long.

Description.—Strongly and evenly inflated shell (W/H ratio

Table 1. Overview of the characteristics of *Lucinoma* species discussed here. Abbreviations: H, height; L, length; W, width. Measurements without decimal point were taken from the literature.

Species	L × H × W [mm]	outline	inflation	umbones	lunule	posterior sulcus
<i>Lucinoma anemiophila</i>	61 × 54 × 29	rounded-pentagonal	weak	small, pointed	narrow, long	well developed
<i>Lucinoma annulata</i>	82 [L]	roundish	weak	small, pointed	broad, short	weak
<i>Lucinoma aokii</i>	76 × 69 × 41	roundish-pointed anterior	moderate	pointed, prosogyrate	narrow, long	weak
<i>Lucinoma dulcinea</i>	45 × 41 [L × H]	roundish	moderate	small, pointed	narrow, short	indistinct
<i>Lucinoma galathea</i>	50 × 48 [L × H]	rounded-pentagonal	weak	small, pointed	narrow, long	weak
<i>Lucinoma gracilistriata</i>	62 × 51 × 34	roundish	moderate	pointed, prosogyrate	narrow, long	weak
<i>Lucinoma canudai</i>	77 × 71.3 × 50.3	angular	strong	blunt	narrow, long	well developed
<i>Lucinoma</i> aff. <i>kastoroae</i>	55 × 48.4 [L × H]	roundish to rounded-pentagonal	weak	small, pointed	narrow, long	weak
<i>Lucinoma kastoroae</i>	34.6 × 28.6 [L × H]	pentagonal-pointed anteriorly	weak	small, pointed	narrow, long	weak
<i>Lucinoma kosatorea</i>	52.7 × 46 [L × H]	oval, pointed anteriorly	weak	small, pointed	narrow, long	weak
<i>Lucinoma rhomboidalis</i>	28.0 × 25.2 [L × H]	pentagonal	weak	pointed, elevated	broad, short	weak
<i>Lucinoma saetheri</i>	67.4 × 63.3 × 37.8	roundish	moderate	pointed, prosogyrate	narrow, short	weak
<i>Lucinoma shinokii</i>	60 × 53 × 34	rounded-pentagonal	moderate	blunt, prosogyrate	broad, short	well developed
<i>Lucinoma sibogae</i>	52.2 × 44.0 × 25.5	elongate-pentagonal	weak	small, pointed	narrow, long	weak
<i>Lucinoma taiwanensis</i>	79.6 × 70.5 × 39.1	rounded-pentagonal	strong	blunt, prosogyrate	narrow, long	weak
<i>Lucinoma tinagoensis</i>	57.8 × 57 × 38.9	rounded-pentagonal	strong	pointed, prosogyrate	broad, short	weak
<i>Lucinoma velosoi</i>	70.9 × 63.8 × 45.9	rounded-oval	strong	broad, pointed	broad, short	indistinct
<i>Lucinoma yoshidai</i>	39 × 35 [L × H]	rounded-pentagonal	weak	pointed, prosogyrate	narrow, long	well developed

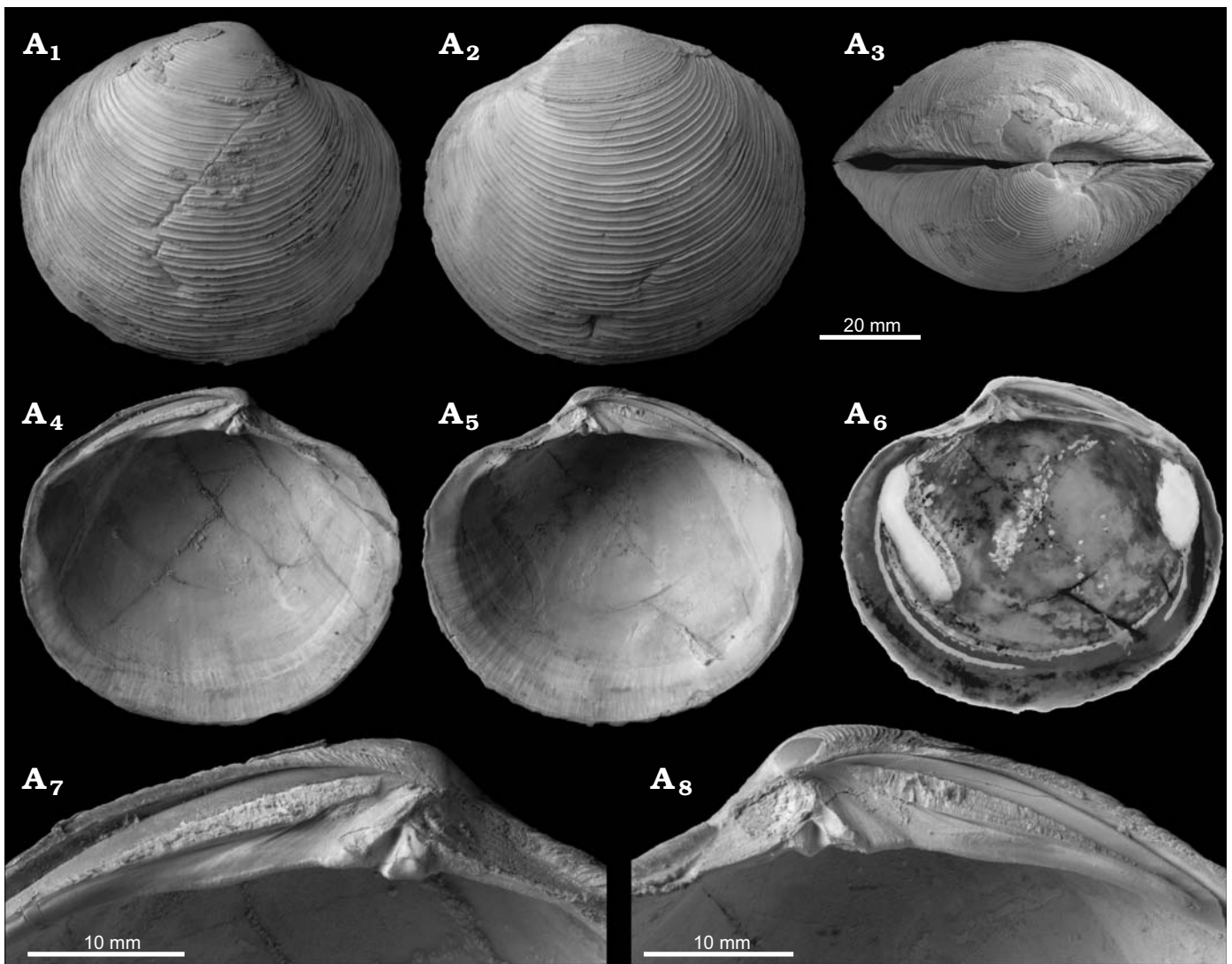


Fig. 15. The lucinid bivalve *Lucinoma velosoi* sp. nov. from the Pleistocene Antipolo Point seep deposits, Leyte, Philippines, holotype NMP-2166, outer surfaces of right (A₁) and left (A₂) valves; dorsal side (A₃); inner surfaces of left (A₄) and right (A₅) valves; UV light image of right valve highlighting muscle scars, blood vessel scar, and pallial line (A₆); close-up on hinges of left (A₇) and right (A₈) valves.

of single valve = 0.37), greatest width at middle of shell; anterodorsal margin slightly concave, with angulation at transition to broadly rounded anterior margin; posterodorsal margin evenly convex, with slight angulation at transition to broadly rounded posterior margin; ventral margin evenly convex, without distinct transitions to anterior and posterior margins; escutcheon lanceolate, greatest width in posterior half; lunule short, broad, deep; hinge plate broad and thick, two thick and short cardinal teeth in each valve, cardinals 1 and 2 pointing downward, cardinals 3 and 4 pointing toward posteroventral margin; ligament nymph lanceolate, about 2/3 of length of posterodorsal shell margin; anterior adductor muscle scar moderately narrow and of moderate length for genus, reaching down to 2/3 of shell height, detached slightly from pallial for ~70% of its length; posterior adductor muscle scar elongate-oval, its lower end situated at about mid-height of shell; shell interior covered by fine striation, most strongly developed at and beyond pallial line.

Remarks.—*Lucinoma velosoi* differs from the similarly inflated *L. tinagoensis* described below by reaching a larger size (Table 1), its more elongated shell (that of *L. tinagoensis* is taller) and its narrower escutcheon. The Pliocene to Recent *Lucinoma galathea* Marwick, 1953 from New Zealand has a more pointed umbo than *L. velosoi*, broader and longer ligament nymph, reaches only about 50 mm in length, whereas *L. velosoi* reaches 70 mm, and is less inflated than *L. velosi* (Marwick 1953; Campbell et al. 2010).

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Lucinoma tinagoensis sp. nov.

Fig. 16.

Zoobank LSID: urn:lsid:zoobank.org:act:77B57F52-B70F-423A-8914-E0C8C7B5EEB4

Etymology: In reference to the Barangay Tinago, in which the type locality is situated.

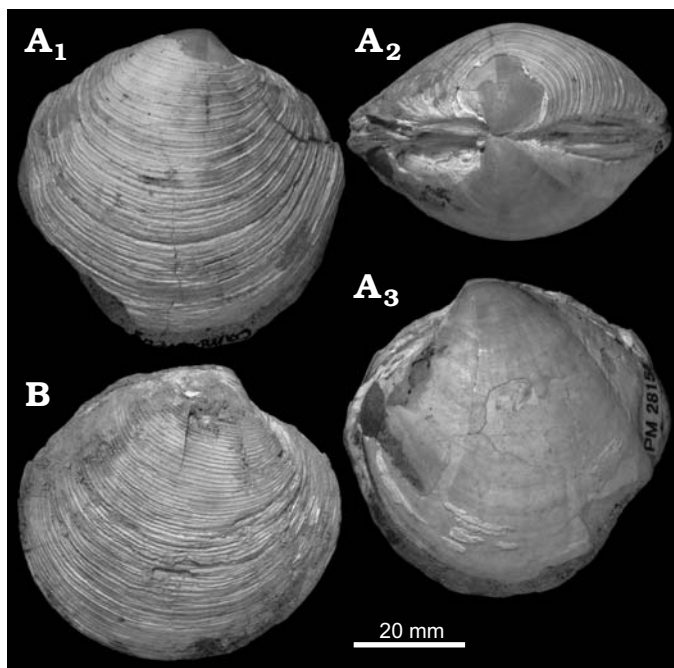


Fig. 16. The lucinid bivalve *Lucinoma tinagoensis* sp. nov. from the Pleistocene Cambantug Point seep deposit, Leyte, Philippines. **A.** Holotype NMP-2164, a large, articulated specimen showing external (A_1) and internal (A_2) features, and its inflation (A_3). **B.** Paratype NMNS PM 28150, showing fine external sculpture on right valve.

Type material: Holotype NMP-2164, an articulated specimen. Paratypes: NMNS PM 28150–28152 (articulated specimens) from the type locality.

Type locality: Cambantug Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—The type material only.

Dimensions (in mm).—NMP-2164, L = 57.8, H = 57.0, W = 38.9 (articulated).

Diagnosis.—Medium-large, well-inflated *Lucinoma*, outline rounded-pentagonal, umbones pointed, markedly prosogyrate for genus; surface sculpture of numerous sharp cord-like commarginal ribs, several fine commarginal cords in interspaces; posterodorsal area narrow, posterior sulcus not well developed; lunule broad, short; escutcheon long, broad.

Description.—Shell medium-large for genus, greatest width at middle of shell (W/H ratio of single valve = 0.37); anterodorsal margin straight to sinuous, with angulation at transition to somewhat acutely rounded anterior margin; posterodorsal margin evenly convex, with slight angulation at transition to broadly rounded posterior margin; ventral margin evenly convex, without distinct transitions to anterior and posterior margins; shell surface covered by densely spaced, sharp to cord-like commarginal ribs; escutcheon elongate, broad, greatest width in middle; lunule elongate, heart-shaped. Anterior adductor muscle scar moderately narrow, of moderate length for genus, reaching down to ~70% of shell height, detached from pallial by ~30° for c. 2/3 its length.

Remarks.—The early Miocene *Lucinoma saetheri* differs by its smaller and more pointed umbones, narrower escutcheon (Amano et al. 2018). *Lucinoma galathea* resembles *Lucinoma tinagoensis* in outline to but is described as “weakly inflated” (Beu and Maxwell 1990: 281) in contrast to the strong inflation of *L. tinagoensis*.

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Lucinoma kosatorea sp. nov.

Fig. 17.

Zoobank LSID: urn:lsid:zoobank.org:act:47983DA6-3C79-49B9-A174-40BE6795CA49

Etymology: By anagram from *kastorae*, a closely related species of *Lucinoma*.

Type material: Holotype NMNS PM 28164, an isolated left valve.

Type locality: Cambantug Point, Leyte, Philippines.

Type horizon: Lower Pleistocene part of the Bata Formation.

Material.—The holotype only.

Dimensions (in mm).—NMNS PM 28164, L = 52.7, H = 46.0.

Diagnosis.—Medium-sized, little-inflated *Lucinoma*, outline oval with acutely rounded anterior margin; rounded-pentagonal, umbones small, pointed, prosogyrate; surface sculpture of numerous densely spaced, sharp commarginal ribs, several smaller sharp ridges in interspaces; posterodorsal sulcus very shallow; lunule long, narrow; ligament nymph long.

Description.—Weakly, evenly inflated shell with small, pointed umbones, greatest width at middle of shell; anterodorsal margin undulating, slightly concave, with distinct angulation at transition to acutely rounded anterior margin; posterodorsal margin convex, posterodorsal area broad, bordered by indistinct, low ridge at which commarginal ribs are deflected; ventral margin almost evenly convex, without distinct transitions to anterior margin, and weak angula-

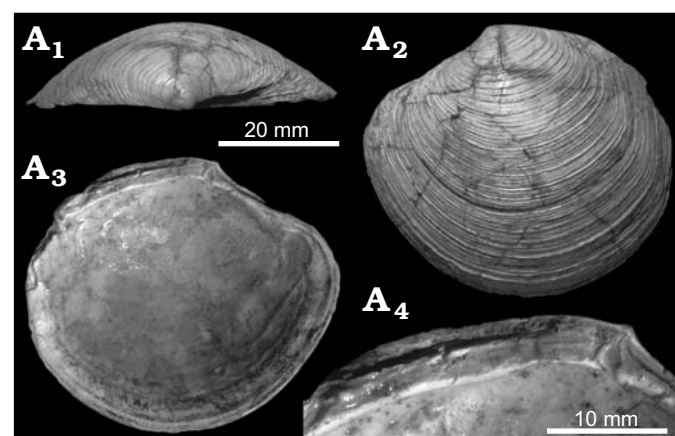


Fig. 17. The lucinid bivalve *Lucinoma kosatorea* sp. nov. from the Pleistocene Cambantug Point seep deposit, Leyte, Philippines, holotype NMNS PM 28164, an isolated left valve; dorsal side (A_1), exterior surface showing sculpture (A_2), interior surface showing muscle scars and pallial line (A_3), close-up on hinge (A_4).

tion at transition to posterior margin; escutcheon lanceolate; lunule long, moderately deep; hinge plate narrow and thick, two thin cardinals in left valve, both pointing downward; thin, elongate anterior lateral tooth in left valve; ligament nymph long, narrow; anterior adductor muscle scar long and narrow, reaching down to 70% of shell height, detached slightly from pallial for c. 70% of its length; posterior adductor muscle scar rounded-oval, its lower end situated at about mid-height of shell; interior of ventral margin marked by two thin ridges with groove in between.

Remarks.—Very similar in shell shape is the Pleistocene Japanese species *Lucinoma aokii* Hirayama, 1958, but it is larger than *L. kosatorea* (L = 76.0 mm vs. L = 52.7 mm in *L. kosatorea*), has a broader lunule with a clearly delimited margin, the hinge plate has an excavated area posterior to the umbo, and the ligament nymph is much narrower than in *L. kosatorea* (Hirayama 1958). A specimen reported as *L. aokii* from a Pleistocene seep deposit on the Boso Peninsula in Japan (Shibasaki and Majima 1997: 1068, fig. 4.12): differs from the holotype of *L. kosatorea* by having a shorter but broader hinge plate, a straighter anteroventral margin, and a distinct external ridge running from the umbo to the anterior shell margin.

Lucinoma canudai, *L. velosoi*, and *L. tinagoensis* are much more inflated than *Lucinoma kosatorea*. A similarly acutely

rounded anterior margin is seen in the extant *Lucinoma anemiophila* Holmes, Oliver, and Sellanes, 2005 from methane seeps off of central Chile. But *L. anemiophila* has a truncated, angular posterior margin and a more distinctive posterior ridge than *Lucinoma kosatorea* (Holmes et al. 2005).

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines.

Family Vesicomidae Dall and Simpson, 1901

Genus *Vesicomya* Dall, 1886

Type species: *Callocardia atlantica* Smith, 1885, by original designation; Recent, Azores to Cape Verde Basin.

Vesicomya margotae Beets, 1953

Fig. 18.

1953 *Vesicomya (Waisiuconcha) margotae* sp. nov.; Beets 1953: 255, pl. 1: 11–15.

Material.—Seven specimens from the Pliocene of Liog-Liog Point: NMNS PM 28410, 28411, 28412 (five individuals).

Dimensions (in mm).—NMNS PM 28410, L = 8.3, H = 6.9; NMNS PM 28411, L = 12.5, H = 10.0.

Remarks.—*Vesicomya margotae* has a hinge dentition like *Vesicomya* (Beets 1953: pl. 1: 11, 15) and should therefore not be associated with *Waisiuconcha*. A very similar extant

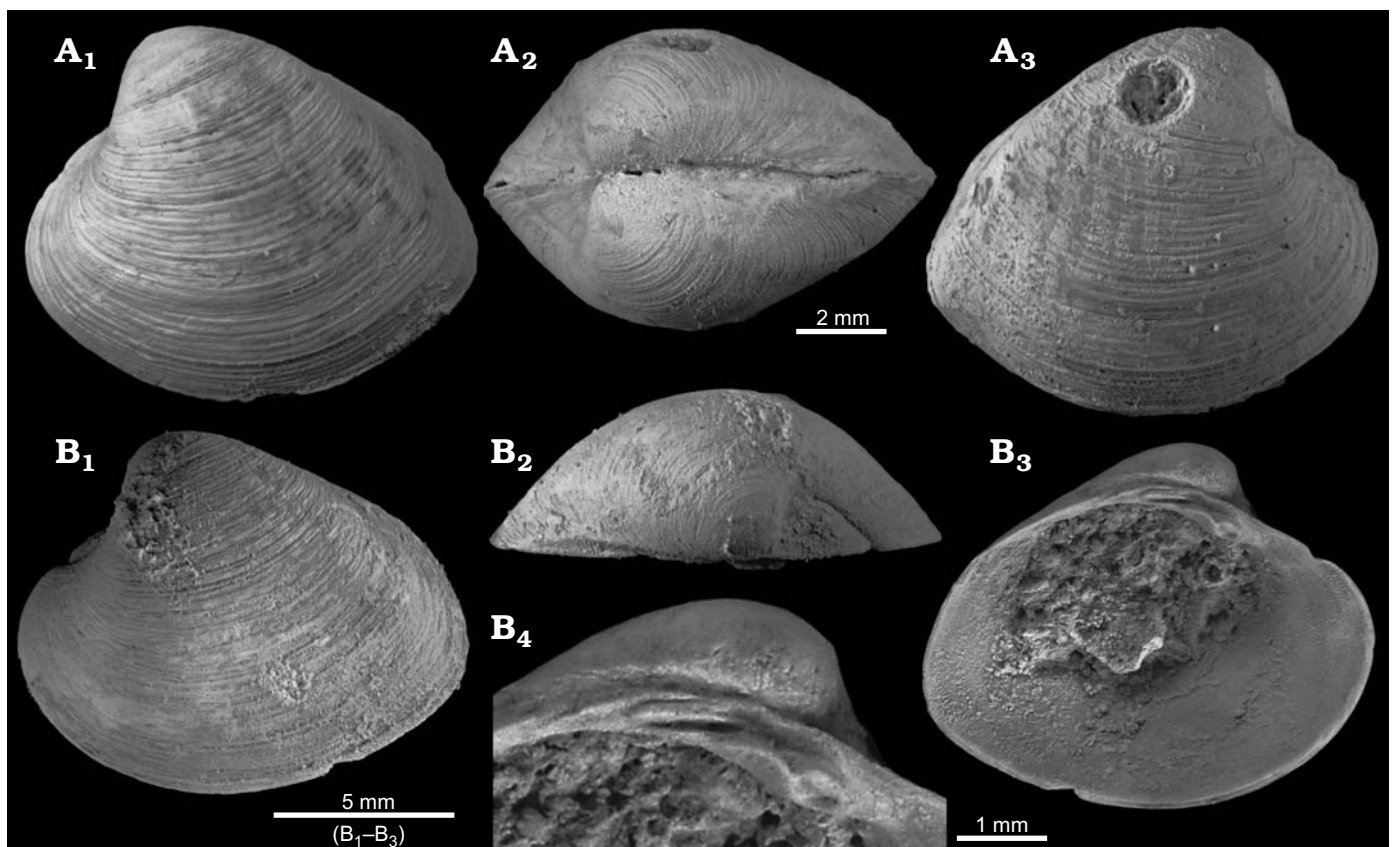


Fig. 18. The vesicomid bivalve *Vesicomya margotae* Beets, 1953 from the late Pliocene seep deposit at Liog-Liog Point, Leyte, Philippines. A. NMNS PM 28410, articulated specimen, view on left valve (A₁), dorsal view (A₂), view on right valve (A₃), note drill hole. B. NMNS PM 28411, isolated left valve, view on exterior (B₁), dorsal view showing lunular incision, (B₂), view on inner side (B₃), and close-up on hinge dentition (B₄).

species is *Vesicomya katsuae* Kuroda, 1952 from 200–400 m depth in Sagami and Tosa Bays, Japan. That species has a *Vesicomya*-like hinge (Kuroda 1952: figs. 7–9) and a lunular incision (Kuroda 1952: fig. 5), which identifies it as a member of *Vesicomya* and not of *Waisiuconcha* (cf., Habe 1976b; Cosel and Salas 2001). *Vesicomya margotae* differs from *V. katsuae* by being less elongate and having larger and more elevated umbones. The extant Japanese species *Vesicomya nakaii* Okutani, 1962, reported here from the late Pliocene of Cambantug Point (below), differs from both *V. margotae* and *V. katsuae* by being shorter and higher, and by having more prominent and elevated umbones.

Stratigraphic and geographic range.—Late Miocene: southern Sulawesi, Indonesia. Late Pliocene: Leyte, Philippines.

Vesicomya nakaii Okutani, 1962

Fig. 19A.

1962 *Vesicomya nakaii* sp. nov.; Okutani 1962: 22, pl. 4: 1a.

2000 *Vesicomya nakaii* Okutani, 1962; Okutani 2000: 997, pl. 496: 1.

Material.—One left valve on small block from the Pleistocene of Cambantug Point: NMNS PM 28413 (L = 8.0 mm, H = 7.3 mm).

Remarks.—Cosel and Salas (2001) considered *V. nakaii* as belonging to *Isorropodon*, but the species has a distinct lunular incision and hence belongs to *Vesicomya*. The specimen illustrated here from Cambantug Point has the posterior ridge and truncate posterior margin of *V. nakaii*, whereas *V. margotae* from Liog-Liog Point is posteriorly more elongated. The specimen clearly shows a lunular incision. Unfortunately, the hinge of our specimen is concealed in rock matrix.

Stratigraphic and geographic range.—Early Pleistocene: Leyte, Philippines. Recent: west coast of Kyushu, Japan.

Genus *Isorropodon* Sturany, 1896

Type species: *Isorropodon perplexum* Sturany, 1896, by monotypy; Recent, eastern Mediterranean Sea.

Remarks.—The differences between *Isorropodon* and *Vesicomya* were defined as follows: “*Isorropodon* is distinguished from *Vesicomya* by the much larger and more oval to oval-oblong shell, the poorly developed to missing lunular incision and the smooth valve margins without an incision. *Vesicomya* is smaller, the shells are very tumid to nearly spherical, the general hinge teeth configuration however is the same in both” (Cosel and Salas 2001).

Isorropodon cf. *perplexum* Sturany, 1896

Fig. 19B–E.

Material.—Six specimens from the Pliocene of Liog-Liog Point (NMNS PM 28414–28416, and NMNS PM 28418, representing three specimens); one specimen from the Pleistocene of Cambantug Point (NMNS PM 28417).

Dimensions (in mm).—NMNS PM 28415, L = 10.0, H = 7.8; NMNS PM 28416: L = 11.0, H = 8.5.

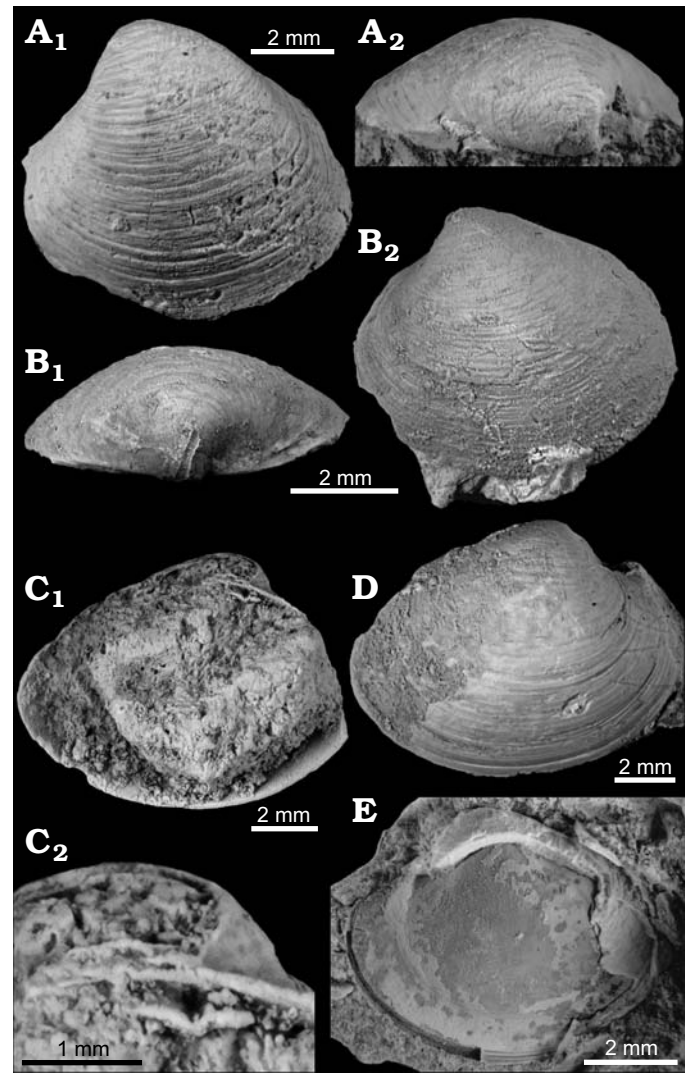


Fig. 19. Small vesicomyid bivalves from late Pliocene (B–D, Liog-Liog Point) and early Pleistocene (A, E, Cambantug Point) seep deposits in Leyte, Philippines. A. *Vesicomya nakaii* Okutani, 1961, NMNS PM 28413, isolated left valve, view on outer side. B–D. *Isorropodon* cf. *perplexum* Sturany, 1896. B. NMNS PM 28414, small left valve, outside view (B₁) and dorsal view (B₂). C. NMNS PM 28415, isolated left valve, insight view (C₁); close-up on hinge (C₂). D. NMNS PM 28416, isolated right valve, view on outer shell surface. E. *Isorropodon* cf. *perplexum* Sturany, 1896, NMNS PM 28417, left valve with shell broken off, showing anterior adductor muscle scar.

Remarks.—The available specimens are virtually indistinguishable from the syntypes of *I. perplexum* as illustrated by Cosel and Salas (2001: figs. 33–35), but with the hinge dentition of the Philippine specimens unknown, we only hesitantly assign them to the extant Mediterranean species *I. perplexum*.

Genus *Archivesica* Dall, 1908b

Type species: *Callocardia gigas* Dall, 1896, by original designation; Recent, Gulf of California.

Archivesica kawamurai (Kuroda, 1943)

Fig. 20.

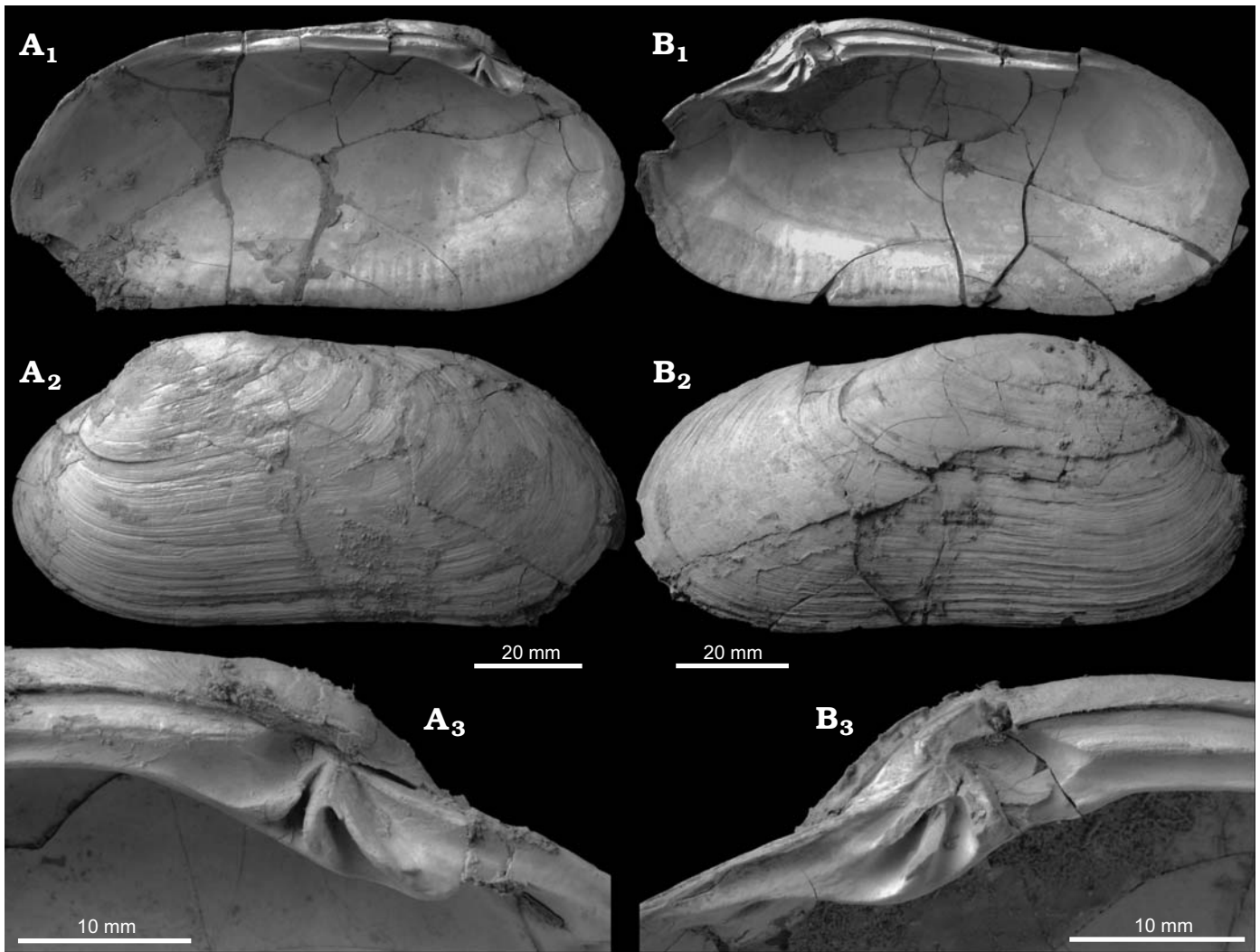


Fig. 20. The vesicomyid bivalve *Archivesica kawamurai* (Kuroda, 1943) from the Pleistocene Cambantug Point seep deposit in Leyte, Philippines. **A.** NMNS PM 28174, left valve, inside (A₁), outside (A₂), close-up on hinge (A₃). **B.** NMNS PM 28173, right valve, inside (B₁), outside (B₂), close-up on hinge (B₃).

1943 *Akebiconcha kawamurai* sp. nov.; Kuroda 1943: 14–18, text-figs. 1–3, pl. 13.

Material.—14 specimens from the Pleistocene of Cambantug Point: NMNS PM 28173, 28174, 28223–2830, 28305–28308. Two specimens from the Pliocene of Liog-Liog Point: NMNS PM 28192, 28193.

Dimensions (in mm).—NMNS PM 28173, L = 109.1, H = 53.3; NMNS PM 28174, L = 109.1, H = 52.9.

Remarks.—See Amano and Kiel (2010) for an extensive synonymy.

Stratigraphic and geographic range.—Pliocene–Pleistocene: Pacific side of central Japan to Leyte, Philippines. Recent:

Pacific side of central to southern Japan (Amano and Jenkins 2011; Amano et al. 2019).

Archivesica pastori sp. nov.

Fig. 21.

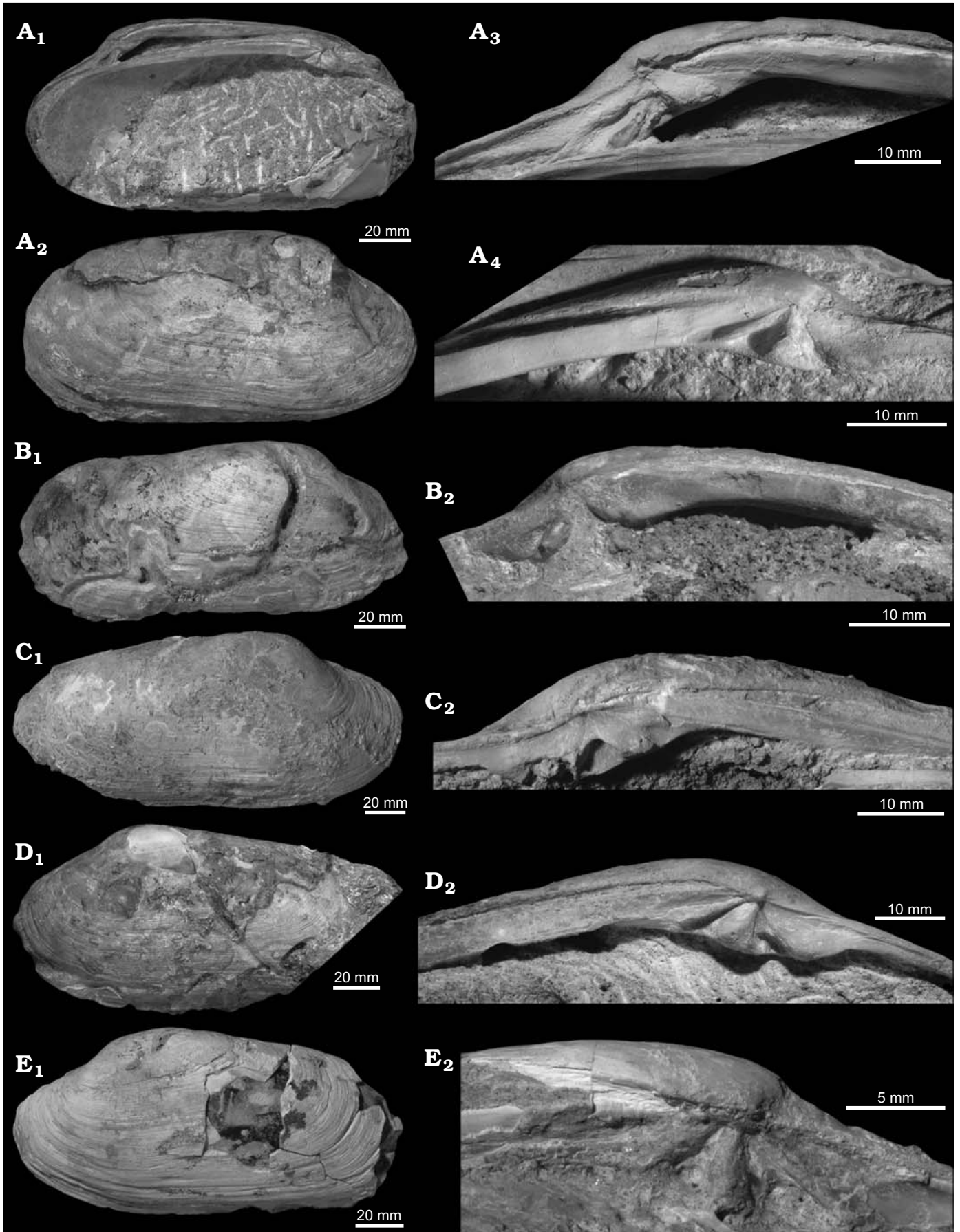
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Etymology: In honour of Douglas Pastor, owner of the property of the type locality at Liog-Liog Point, Leyte, Philippines.

Type material: Holotype NMP-2165a, a disarticulated right valve. Paratypes: NMNS PM 28194–28196 (a right valve and two left valves), NMP-2165b (left valve), NMNS PM 28206 (right valve) from the type locality.

Type locality: Liog-Liog Point, Leyte, Philippines.

Fig. 21. The vesicomyid bivalve *Archivesica pastori* sp. nov. from the late Pliocene Liog-liog Point seep deposit. **A.** Left valve (paratype NMP-2165b) → and right valve (holotype NMP-2165a) nested into one another; inside view of the two shells (A₁), outside view on RW (A₂), close-up on hinge of RV (A₃); close-up on hinge of LV (A₄). **B.** Paratype NMNS PM 28206, large isolated right valve with broad posterodorsal area, outside view (B₁), close-up on hinge (B₂). **C.** Paratype NMNS PM 28194, large isolated right valve with gently sloping posterodorsal margin; outside view (C₁), close-up on hinge (C₂). **D.** Paratype NMNS PM 28195, isolated left valve, posteriorly damaged, outside view (D₁), close-up on hinge (D₂). **E.** Paratype NMNS PM 28196, disarticulated left valve, outside view (E₁) and close-up on hinge (E₂).



Type horizon: Lower Pliocene part of the Bata Formation.

Material.—22 specimens from the type locality: type material and NMP-2165a (representing 16 specimens) and 21 paratypes, NMP-2165b, NMNS PM 28194–28196, 28206–28222.

Dimensions (in mm).—NMP-2165a, L = 143.2, H = 69.0.

Diagnosis.—Large, elongate *Archivesica* with three radiating teeth in each valve, cardinal 2b very thick, cardinal 3a occasionally reduced, cardinals 3b and 4b short; ligament nymph about half of total shell length.

Description.—Large elongate-oval shell, umbones blunt, elevated, slightly prosogyrate, situated anterior at c. 26–31% of total shell length; anterodorsal margin straight; anterior margin acutely rounded, anterior-most point somewhat above midline of shell; ventral margin straight or slightly concave; posterior margin broadly rounded; posterodorsal margin gently sloping. Hinge plate strong, broad, with three relatively thick cardinals in each valve, radiating outward from underneath umbo; right valve: cardinal 1 elongate, protruding, pointing anteroventrally, 3a elongate, subparallel to shell margin, reduced, 3b elongate-triangular, pointing posterodorsally; left valve: cardinal 2a moderately thin and of same length or longer as 2b, pointing anteroventrally, 2b triangular, thick, occasionally bifid, pointing to center of ventral margin, cardinal 4 short, narrow, pointing posterior, with shallow, elongate posterior depression; nymph plate elongate, about ½ of total shell length, starts tapering posteriorly after about half its length. Outer shell surface with faint, irregular growth increments.

Remarks.—Very similar regarding hinge dentition are the extant Japanese species *Archivesica similaris* (Okutani et al. 1997) and *Archivesica tsubasa* (Okutani et al. 2000), but both are more elongate than *Archivesica pastori*. As a result of being more elongate, their dorsal and ventral margins are more parallel than in *A. pastori*. However, this feature shows some variability in *A. pastori*, for example the specimen shown on Fig. 21B₁ has rather parallel dorsal and ventral margins, but is not as elongate as *A. similaris* and *A. tsubasa*. Another extant species with similar hinge dentition is *Archivesica ochotica* Scarlato, 1981, which is less elongate compared to *A. pastori* and has a proportionally shorter ligament nymph (Scarlato 1981). The early Miocene Japanese *Archivesica sakoi* Amano, Jenkins, Ohara, and Kiel, 2014 also shows a similar hinge dentition and overall shape, but its cardinal 3b in the right valve is more elongate and subparallel the shell margin unlike the shorter and oblique tooth of *A. pastori*, and *A. sakoi* also has more prominent and more prosogyrate umbones (Amano et al. 2014), and is much smaller (L = 80 mm in *A. sakoi* compared to L = 143 mm in *A. pastori*).

The hinge dentition of *A. pastori* is also somewhat similar to that of *Archivesica magnocultellus* (Okutani et al. 2002) except that *A. pastori* lacks the large pit posterior to the cardinals seen in *A. magnocultellus*. *Archivesica pastori*

differs from the type species of *Archivesica*, *A. gigas* (Dall 1896), by having a short cardinal 2a and a strong, thick cardinal 2b in the left valve, whereas *A. gigas* has a very elongate 2a and a narrow 2b. Furthermore, *A. pastori* has a long ligament nymph (c. ½ of shell length), whereas the ligament nymph is short in *A. gigas*.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Genus *Pliocardia* Woodring, 1925

Type species: *Anomalocardia bowdeniana* Dall, 1903, by original designation; Pliocene, Bowden Formation, Jamaica.

Remarks.—Molecular data indicate that species currently assigned to *Pliocardia* (cf., Krylova and Sahling 2010) belong to two distinct clades (Audzijonyte et al. 2012; Valdés et al. 2013; Johnson et al. 2017). The first clade includes “*Pliocardia*” *cordata* and “*Pliocardia*” *ponderosa* and is referred to as “*Pliocardia* 1” by Valdés et al. (2013) and as “*cordata* group” by Johnson et al. (2017). The second clade includes *P. kuroshimana* and *P. crenulomarginata* and was called “*Pliocardia* 2” by Valdés et al. (2013) and “*Pliocardia*” by Johnson et al. (2017). It remains unclear, however, to which, if any, of these two clades the fossil type species belongs. Hence, we use *Pliocardia* here in inverted commas only.

Pliocardia kuroshimana (Okutani, Fujikura, and Kojima, 2000)

Fig. 22.

2000 *Vesicomya kuroshimana* sp. nov.; Okutani et al.: 83–84, figs. 2, 6.
2000 *Vesicomya kuroshimana* Okutani, Fujikura, and Kojima, 2000; Okutani 2000: 996–997, pl. 496.

Material.—Eight specimens from early Pleistocene non-seep sediments at the tip of Liog-Liog Point (NMNS PM 28189–28191 and five unnumbered specimens).

Dimensions (in mm).—NMNS PM 28189, L = 48.0, H = 36.6; NMNS PM 28190, L = 48.0, H = 36.3; NMNS PM 28191, L = 48.0, H = 36.6.

Remarks.—The largest extant specimen is 58.9 mm long (Okutani et al. 2000) whereas the largest early Pleistocene specimen from Liog-Liog Point is only 48.0 mm long. But morphologically we see no difference between the extant and the Pliocene specimens. This is the first fossil record of “*Pliocardia*” *kuroshimana*; despite Japan’s a rich Plio-Pleistocene fossil of chemosymbiotic bivalves, no *Pliocardia* has been reported from sediments of Plio-Pleistocene age yet (Amano and Jenkins 2011; Amano et al. 2019). *Pliocardia kawadai* (Aoki, 1954) is known from the early to middle Miocene, and *Pliocardia? tanakai* Miyajima, Nobuhara, and Koike, 2017 is known from the middle Miocene (Aoki 1954; Miyajima et al. 2017; Amano et al. 2019).

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines. Recent: Okinawa Trough.

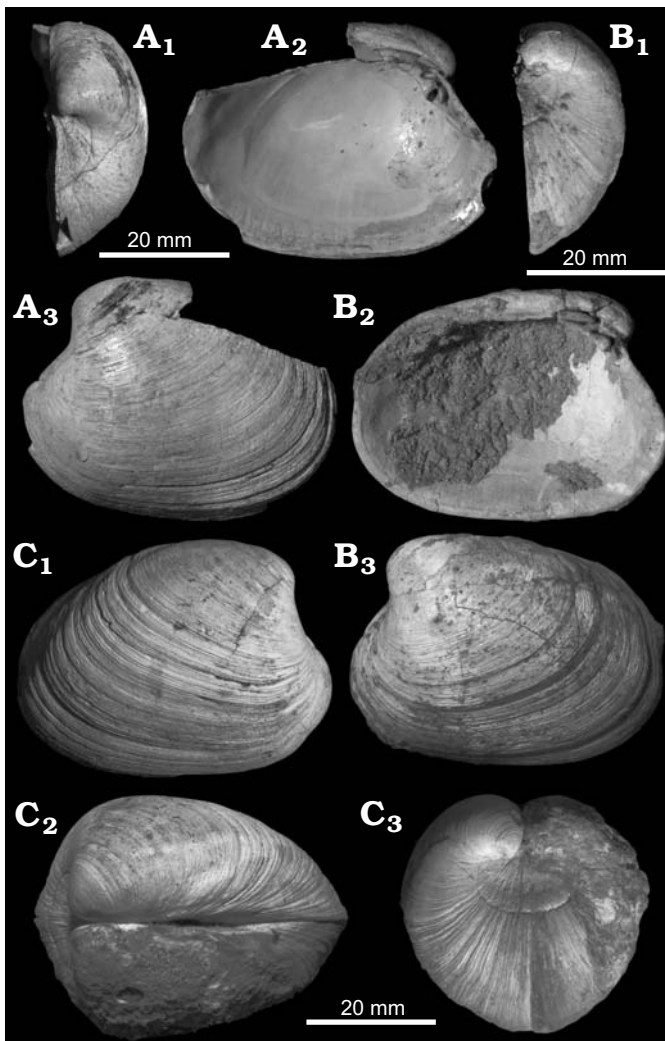


Fig. 22. The vesicomyid bivalve “*Pliocardia*” *kuroshimana* (Okutani, Fujikura and Kojima, 2000) from early Pleistocene non-seep deposits at the tip of Liog-Liog Point in Leyte, Philippines. **A.** NMNS PM 28190, partially broken left valve, anterior side showing lunular incision (A₁), inner shell surface and hinge (A₂), outer shell surface (A₃). **B.** NMNS PM 28191, left valve, anterior side showing lunular incision (B₁), inner shell surface (B₂), outer shell surface (B₃). **C.** NMNS PM 28189, articulated specimen, outer shell surface of right valve (C₁), dorsal view showing the strong inflation (C₂), anterior side showing lunular incision (C₃).

Clade *Pliocardia* “*cordata* group”

Remarks.—“*Pliocardia*” *ticaonica* reported below was considered very closely related to “*Pliocardia*” *cordata* (cf., Boss 1968) and hence most likely belong to the “*cordata* group” sensu Johnson et al. (2017).

“*Pliocardia*” *ticaonica* Dall, 1908a

Fig. 23.

1908 *Vesicomys ticaonica* sp. nov.; Dall 1908a: 63.

Material.—Three disarticulated specimens from the Pleistocene of Cambantug Point (NMNS PM 28184–28186).

Dimensions (in mm).—NMNS PM 28185, L = 68.2, H = 52.5.

Remarks.—Huber (2010) considered “*Pliocardia*” *tica-*

nica as a synonym of “*Pliocardia*” *indica* (Smith, 1904). However, “*Pliocardia*” *ticaonica* is more elongate than “*P.*” *indica*, and “*P.*” *indica* has a more distinctive lunular incision than “*P.*” *ticaonica*. Hence, we prefer to retain the name “*P.*” *ticaonica*. The original description of *Vesicomys ticaonica* did not include a figure (Dall 1908a). Although we have not seen the holotype of *P. ticaonica*, the Philippine Pliocene specimens are indistinguishable from two specimens labeled “*Vesicomys ticaonica*”, housed in the USNM (USNM 248063 from the Philippines, station 5446 and USNM 229320 from Sibuko Bay, Borneo, Indonesia, station 5592).

When Boss (1968) described “*Pliocardia*” *cordata*, he considered it “remarkably similar, and probably most closely related, to *V. ticaonica* Dall” (Boss 1968: 735). The two shells are indeed very similar, and we concur with this view. Boss (1968) also considered the late Miocene

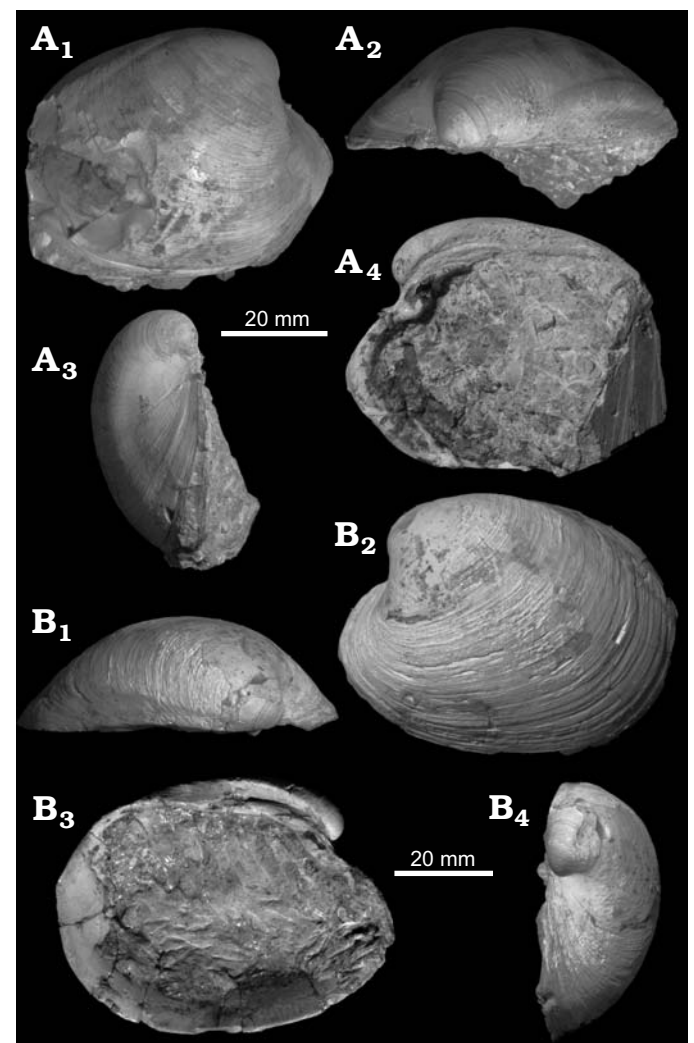


Fig. 23. The vesicomyid bivalve “*Pliocardia*” *ticaonica* Dall, 1908 from the early Pleistocene Cambantug Point seep deposit in Leyte, Philippines. **A.** NMNS PM 28186, right valve, outer shell surface (A₁), dorsal side (A₂), anterior side (A₃), inner side showing hinge (A₄). **B.** NMNS PM 28185, left valve, dorsal side (B₁), outer shell surface (B₂), inner side showing hinge (B₃), anterior side (B₄).

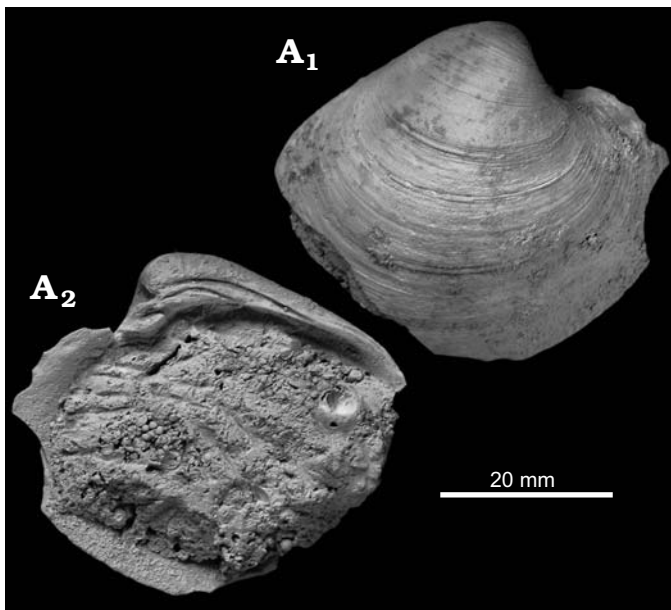


Fig. 24. The vesicomid bivalve “*Pliocardia*” *indica* (Smith, 1904) from the early Pleistocene seep deposit at Cambantug Point, Leyte, Philippines, NMNS PM 28419, an isolated right valve, seen from the outside (A₁) and inside (A₂).

Waisiuconcha alberdinae Beets, 1942 from Buton Island, Sulawesi, Indonesia, as a precursor or possibly even as a synonym of *V. ticaonica*. However, whether the much smaller (23 mm) and thin-shelled *W. alberdinae* is indeed closely related to the thick-shelled “*P.*” *ticaonica* and “*P.*” *cordata* remains to be tested.

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines. Recent: Philippines and Indonesia.

“*Pliocardia*” *indica* (Smith, 1904)

Fig. 24.

1904 *Vesicomya indica* sp. nov.; Smith 1904: 9.

Material.—One right valve from the Pleistocene of Cambantug Point NMNS PM 28419 (L = 45.9 mm, H = 38.8 mm).

Remarks.—For comments on the synonymy of “*P.*” *indica* and “*P.*” *ticaonica* see above.

Stratigraphic and geographic range.—Early Pleistocene, Leyte, Philippines. Recent: Bay of Bengal.

Genus *Wareniconcha* Cosel and Olu, 2009

Type species: *Vesicomya guineensis* Thiele and Jaekel, 1931, by original designation; Recent, from ca. 2500 to 4000 m depth on the West African continental margin (Cosel and Olu 2009).

Wareniconcha guineensis (Thiele and Jaekel, 1931)

Fig. 25.

1931 *Vesicomya guineensis* sp. nov.; Thiele and Jaekel 1931: 229, pl. 9: 102.

1970 *Vesicomya (Vesicomya) guineensis* Thiele and Jaekel, 1931; Boss 1970: 71–72, figs. 5–6, 18–19.

2009 *Wareniconcha guineensis* (Thiele and Jaekel, 1931); Cosel and Olu 2009: 2362, figs. 11–14, 29G–H.

Material.—Five specimens from the Pliocene of Liog-Liog Point (NMNS PM 28197–28201). NMNS PM 28197: L = 46.9 mm, H = 35.5 mm; NMNS PM 28199: L = 37.0 mm, H = 30.4 mm.

Remarks.—Cosel and Olu (2009) documented shell shape and hinge variability for *Wareniconcha guineensis* and the specimens from Liog-Liog Point fall well within this variability. In particular, specimen NMNS PM 28199 has a very similar outline as the *Wareniconcha guineensis* syntype stored at the Museum für Naturkunde, Berlin (Moll.101.600).

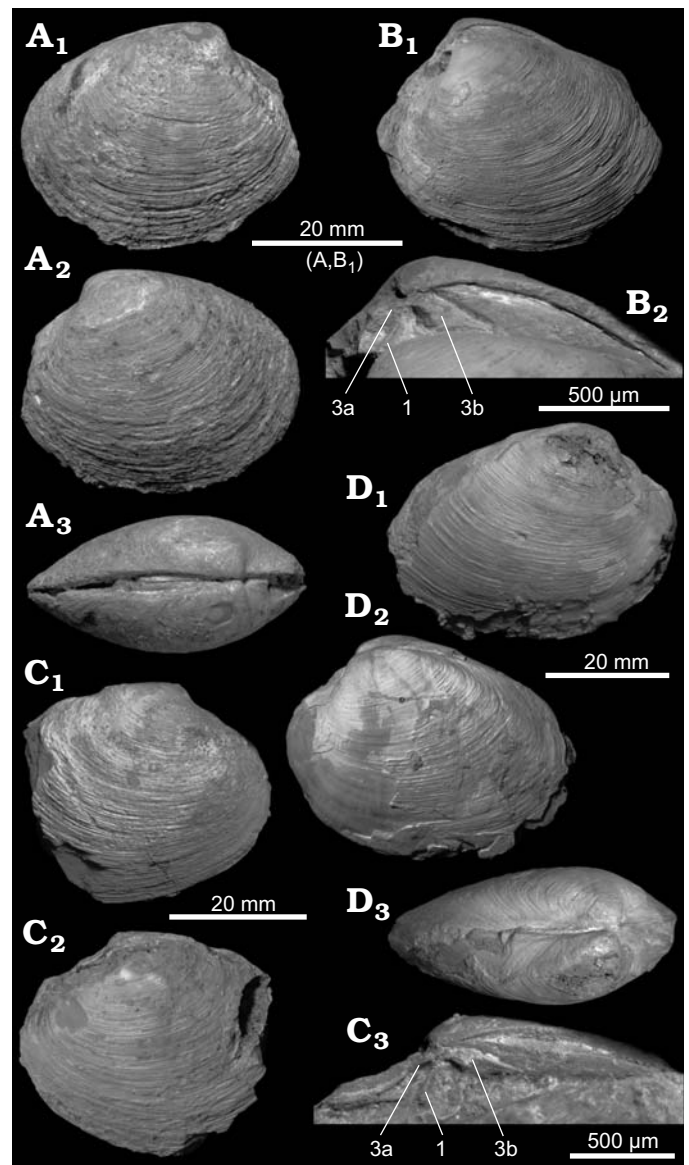


Fig. 25. The vesicomid bivalve *Wareniconcha guineensis* (Thiele and Jaekel 1931) from the late Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. **A.** NMNS PM 28199, oval-round articulated specimen, right valve (A₁), left valve (A₂), dorsal view (A₃). **B.** NMNS PM 28200, oval-round articulated specimen, left valve (B₁), close-up on hinge of right valve (B₂). **C.** NMNS PM 28201, articulated specimen, right (C₁) and left (C₂) valve; close-up on RV hinge (C₃). **D.** NMNS PM 28197, articulated elongate-oval specimen, right (D₁) and left (D₂) valves; dorsal view (D₃). Numbers indicate cardinal teeth.

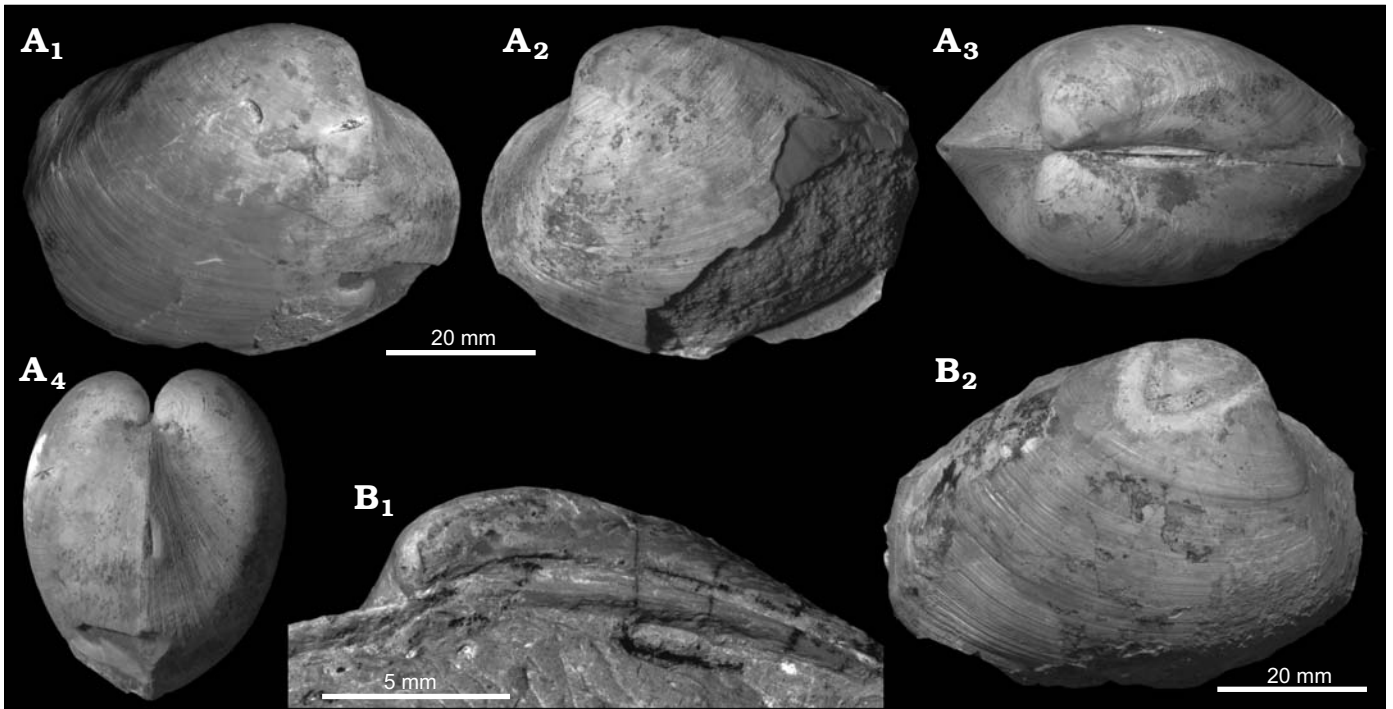


Fig. 26. The vesicomyid bivalve *Wareniconcha* aff. *winckworthi* (Prashad, 1932) from the Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. A. NMNS PM 28188, articulated specimen, with views on right (A₁) and left (A₂) valves, dorsal (A₃) and anterior (A₄) sides. B. NMNS PM 28187, right valve with hinge partly exposed, close-up on hinge (B₁), view on outer shell surface (B₂).

Stratigraphic and geographic range.—Late Pliocene: Leyte, Philippines. Recent: west coast of tropical Africa.

Wareniconcha aff. *winckworthi* (Prashad, 1932)

Fig. 26.

Material.—Two specimens from the Pliocene of Liog-Liog Point: NMNS PM 28187, a right valve with partly exposed hinge and NMNS PM 28188, an articulated specimen.

Dimensions (in mm).—NMNS PM 28187, L = 64.0, H = 56.6; NMNS PM 28188, L = 58.0, H = 44.1.

Remarks.—*Wareniconcha* aff. *winckworthi* is slightly more inflated and has broader umbones than the extant *Wareniconcha winckworthi* from Indonesia (Prashad 1932). Furthermore, it has a truncate posterior margin (see Fig. 26B₂) whereas it is more obliquely truncated in *Wareniconcha winckworthi*; however, this difference might not be a distinguishing character but instead a case of intraspecific dimorphism, as reported for example for the vesicomyid genus *Calyptogena* (see Krylova and Sahling 2006). The recently described *Wareniconcha mercenarioides* Kase, Isaji, Aguilar, and Kiel, 2019 from the same seep deposit is much larger (up to 120 mm) and has a roundish-triangular outline, whereas *W.* aff. *winckworthi* has an oval outline.

Genus *Waisiuconcha* Beets, 1942

Type species: *Waisiuconcha alberdinae* Beets, 1942, by original designation; Buton Island, Indonesia, late Miocene (Janssen 1999).

Remarks.—According to Cosel and Salas (2001: 339) there

are “two Recent species described from Japan: *Waisiuconcha katsuae* (Kuroda 1952), and *W. surugensis* Habe, 1976 (Habe 1976a: fig. 81) (see also Higo et al. 1999); a third Japanese species cited by these authors in the genus *Waisiuconcha*, *W. nakaii* (Okutani 1962) may be, according to the original drawing (Okutani 1962: pl. 4: 1a), a species of *Isorropodon*”. “*Waisiuconcha*” *margotae* Beets, 1953 from the late Miocene asphalt beds of Buton Island, Indonesia, looks quite like *Vesicomya katsuae* and might be the same as the *Vesicomya* from Liog-Liog. *Vesicomya katsuae* and *Vesicomya nakaii* were assigned to *Waisiuconcha* by Habe (1976a).

Waisiuconcha sp. 1

Fig. 27A–C.

Material.—Three specimens from the Pliocene of Liog-Liog Point (NMNS PM 28420–28422).

Dimensions (in mm).—NMNS PM 28420, L = 4.5, H = 3.5.

Remarks.—Compared to the holotype of *Waisiuconcha alberdinae* Beets, 1942 (Beets 1942: figs. 147–151), *Waisiuconcha* sp. 1 from Liog-Liog Point has a more acutely rounded posterior margin, the anterior adductor muscle scar is more elongate than the diamond to drop-shaped scar of *W. alberdinae*, the pallial line starts at the base of the anterior adductor scar rather than on its posteroventral side, and the pallial line is closer to the shell margin as in *W. alberdinae*. The two extant species *W. surugensis* Habe, 1976a and *W. haekeli* Cosel and Salas, 2001 have shorter shells than *Waisiuconcha* sp. 1 from Liog-Liog Point (Habe 1976a; Cosel and Salas 2001; Hoffman et al. 2019).

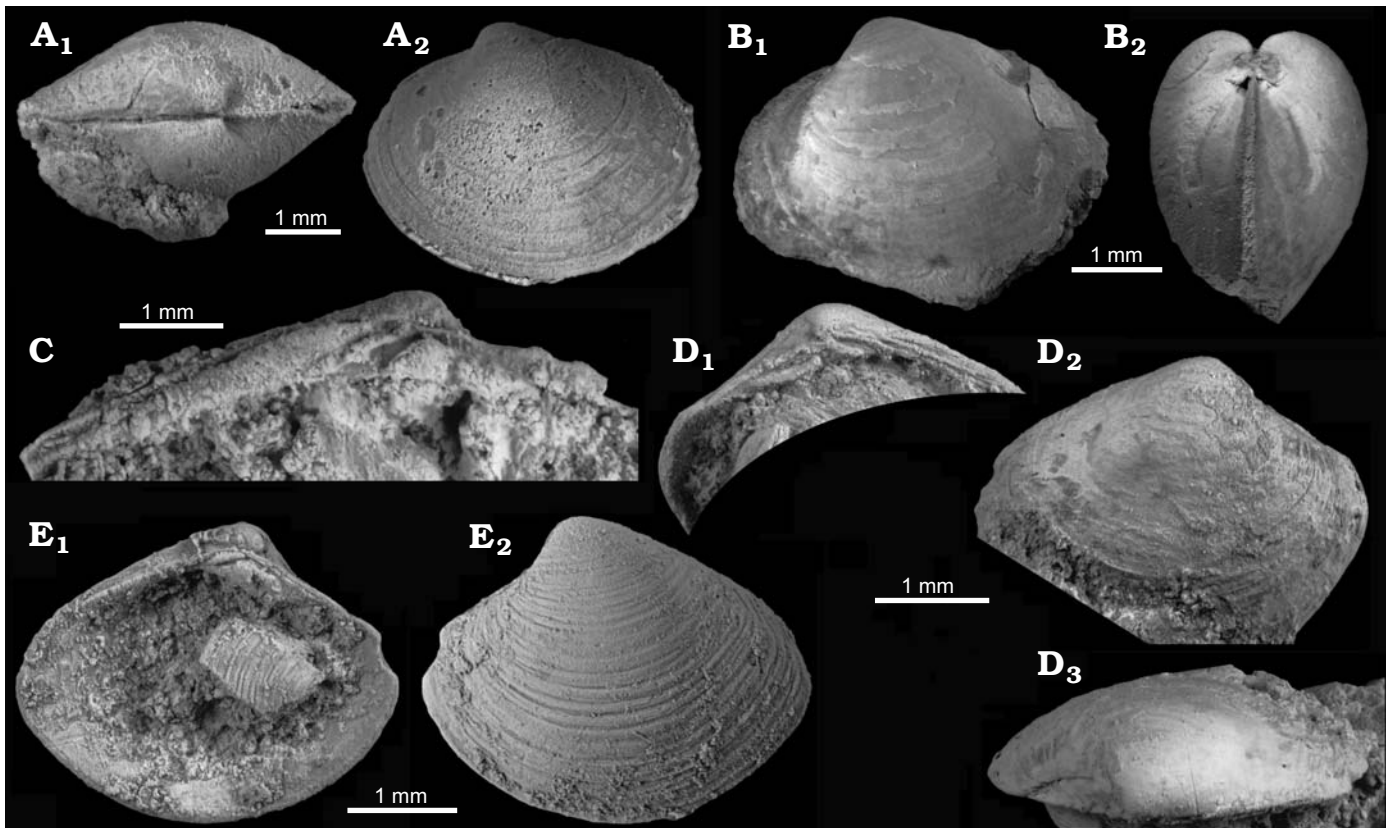


Fig. 27. Two species of the vesicomyid bivalve genus *Waisiuconcha* Beets, 1942, from the late Pliocene (A–C, Liog-Liog Point) and early Pleistocene (D, E, Cambantug Point) seep deposits in Leyte, Philippines. A–C. *Waisiuconcha* sp. 1. A. NMNS PM 28420, articulated specimen, dorsal view showing lunular incision (A₁), view on outer side of left valve (A₂). B. NMNS PM 28421, articulated specimen with partially removed shell, view on outer side of left valve (B₁), anterior view showing anterior adductor muscle scars (B₂). C. NMNS PM 28422, isolated left valve, showing hinge dentition. D, E. *Waisiuconcha* sp. 2. D. NMNS PM 28423, an isolated right valve partially embedded in rock matrix, showing hinge dentition (D₁), view on outer side (D₂), in dorsal view showing lunular incision (D₃). E. NMNS PM 28424, an isolated left valve, showing hinge dentition (E₁) and irregular outer surface sculpture (E₂).

Waisiuconcha sp. 2

Fig. 27D, E.

Material.—Two specimens from the Pleistocene of Cambantug Point (NMNS PM 28423, 28424).

Dimensions (in mm).—NMNS PM 28423, L = 3.5, H = 2.5; NMNS PM 28424, L = 3.5, H = 2.8.

Remarks.—The early Pleistocene *Waisiuconcha* sp. 2 has a more distinctive lunular incision and more elevated umbones than the late Pliocene *Waisiuconcha* sp. 1 reported above from Liog-Liog Point.

Class Gastropoda Cuvier, 1795

Limpets of uncertain affinities

Remarks.—In the absence of data on shell microstructure and protoconch, the four species reported below are difficult to place. *Serradonta* Okutani, Tsuchida, and Fujikura, 1992 and *Bathyacmaea* Okutani, Tsuchida, and Fujikura, 1992 (Pectinodontidae) have been shown to vary greatly in outline (from oval to pointed egg-shaped), in the position of the apex (subcentrally to displaced anteriorly) and surface sculpture (from nearly smooth to having strong beaded ra-

dial ribs), both within genera as well as within species (Chen et al. 2019). Very similar external morphologies are for example also found among member of the paralepetopsids and neolepetopsids (McLean 1990, 2008, Warén and Bouchet 2009).

Limpet gastropod sp. 1

Fig. 28A–D.

Material.—Eight specimens from the Pliocene of Liog-Liog Point: NMNS PM 28427–28430; NMNS PM 28431 (attached to the same block as *Archivesica kawamurai* NMNS PM 28192), and three unnumbered specimens; one specimen from the Pleistocene of Antipolo Point (unnumbered).

Dimensions (in mm).—NMNS PM 28429, L = 11.0, W = 9.3.

Description.—Moderately elevated limpet (H/L ratio ~0.46), apex displaced slightly toward the anterior, outline oval with anterior side slightly narrower than posterior side, flanks more-or-less straight; external surface with concentric growth rings only, or with numerous narrowly spaced, tuberculate radial ribs; base straight or slightly convex.

Remarks.—Similar species can be found among the pectinodont patellogastropod genus *Serradonta* Okutani, Tsuchida,

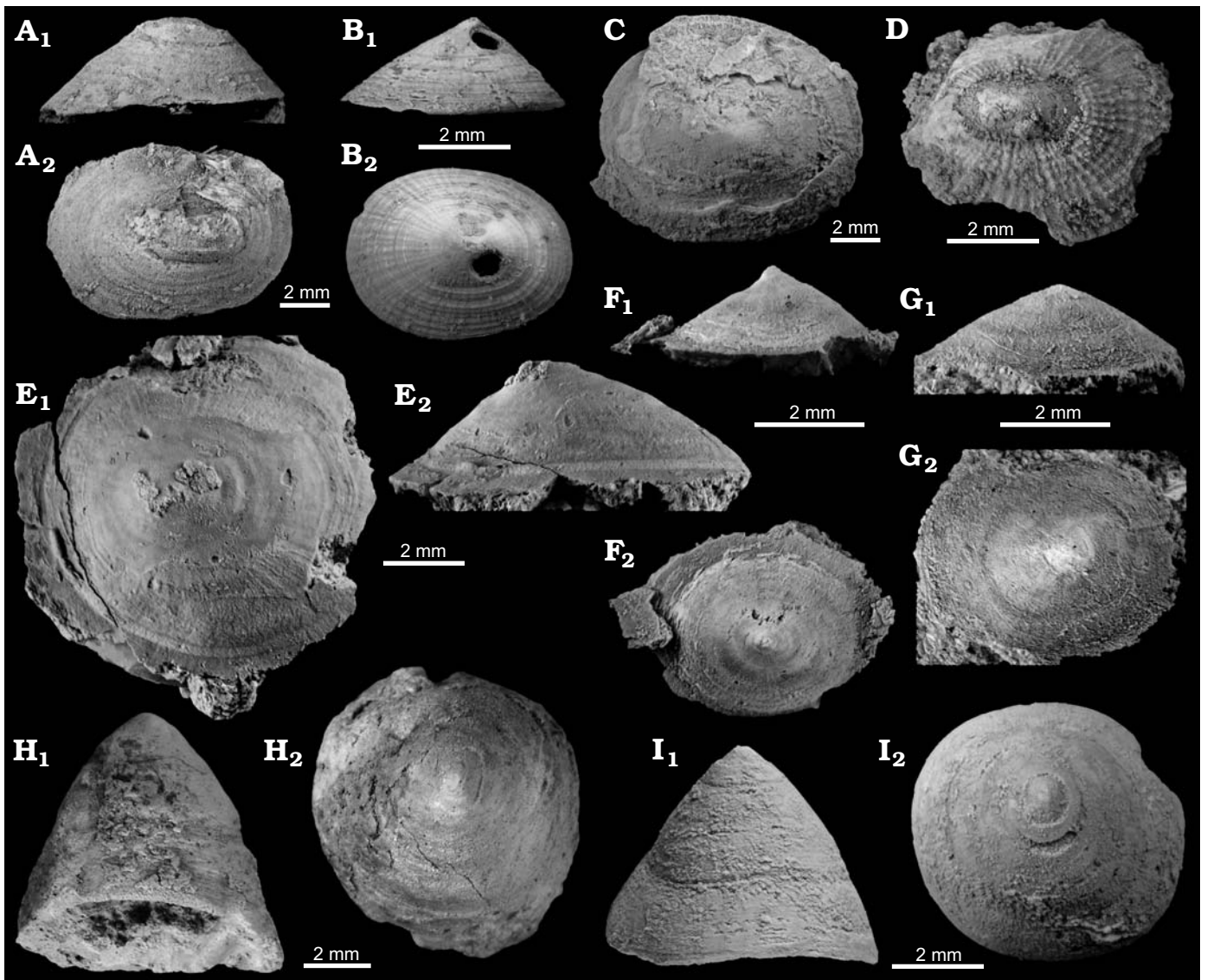


Fig. 28. Limpet gastropods from late Pliocene (A–D, E, H, I, Liog-Liog Point) and Pleistocene (F, G, Antipolo Point) seep deposit in Leyte, Philippines. A–D. Limpet gastropod sp. 1. A. NMNS PM 28427, specimen with only concentric growth increments, in lateral (A₁) and apical (A₂) views. B. NMNS PM 28428, specimen with fine radial ribs and a drill hole, in lateral (B₁) and apical (B₂) views. C. NMNS PM 28429, corroded specimen showing outline, in apical view. D. NMNS PM 28430, corroded specimen with tuberculate radial sculpture, in apical view. E. NMNS PM 28432, limpet gastropod sp. 2, in apical (E₁) and lateral (E₂) views, note subparallel muscle attachment scars. F, G. Limpet gastropod sp. 3, both specimens in lateral (F₁, G₁) and apical (F₂, G₂) views. F. PNMNS PM 28433, small specimen with pointed apex. G. NMNS PM 28434, corroded specimen with convex base. H, I. Limpet gastropod sp. 4, two specimens, in lateral (H₁, I₁) and apical (H₂, I₂) views. H. NMNS PM. I. NMNS PM 28426.

and Fujikura, 1992, which is a morphologically variable genus that includes axially ribbed as well as smooth species, with a fossil record ranging back into the Cretaceous (Okutani et al. 1992; Jenkins et al. 2007; Chen et al. 2019). Neolepetopsids such as *Neolepetopsis* McLean, 1990 and *Paralepetopsis* McLean, 1990 are another group of patellogastropods with similar shells (McLean 1990, 2008). Cocculiniform limpets with oval, radially ribbed shells with subcentral apex are known from the genera *Coccoliter* Haszprunar, 1987 and *Coccoligya* Marshall, 1986 (Marshall 1986; Haszprunar 1987; McLean and Harasewych 1995); the latter has a fossil record ranging back to the early Oligocene (Kiel et al. 2020).

Limpet gastropod sp. 2

Fig. 28E.

Material.—One specimen from the Pleistocene of Antipolo Point: NMNS PM 28432 (L = 8.5 mm, W = 9.5 mm, H = 3.4 mm).

Description.—Low to moderately elevated limpet (H/L ratio ~0.4), outline irregularly-round, apex displaced anteriorly; anterior slope straight, posterior slope slightly convex; pallial attachment line close to base; two elongate, slightly curved muscle scars at about 1/3 of shell height, one on each lateral side of shell, tapering slightly anteriorly, posterior end broadened.

Remarks.—The two subparallel muscle attachment scars combined with the almost circular base of the shell are unusual among limpet gastropods, and we have not found a suitable taxonomic place for it.

Limpet gastropod sp. 3

Fig. 28F, G.

Material.—Two specimens from the Pleistocene of Antipolo Point (NMNS PM 28433, 28434).

Dimensions (in mm).—NMNS PM 28433, L = 4.9, W = 3.6, H = 1.7; NMNS PM 28434, L = 5.0, W = 3.5, H = 1.8.

Description.—Moderately elevated limpet (H/L ratio ~0.34), outline evenly oval, apex central, base slightly convex; inner surface with fine radial striations; flanks very slightly convex.

Remarks.—The outer shell surface is missing in both specimens; hence the external sculpture is unknown. Compared to limpet sp. 1, these specimens are generally smaller, have a lower elevation and the apex in a more central position. Such shells are often found among the cocculiniforms, such as *Cococrater portoricensis* (Dall and Simpson 1901) from the western Atlantic Ocean (McLean and Harasewych 1995), or *Cocculina tenuitesta* Hasegawa, 1997, a species associated with sunken wood in Suruga Bay, Japan (Hasegawa 1997).

Limpet gastropod sp. 4

Fig. 28H, I.

Material.—Two specimens from the Pliocene of Liog-Liog Point (NMNS PM 28425, 28426).

Dimensions (in mm).—NMNS PM 28425, L = 8.8, W = 8.0, H = 8.0; NMNS PM 28426, L = 5.7, W = 6.0, H = 6.0.

Description.—Tall, medium-sized limpets, apex subcentral, outline irregular-round, base concave, flanks irregularly convex; surface with fine growth increments only.

Remarks.—Tall, roundish limpets of the size of these two specimens are common among the genus *Pectinodonta*; however, all *Pectinodonta* species show distinct axial ribbing (Marshall 1985, 1998; Marshall et al. 2016; Zhang and Zhang 2018), which is lacking in the two Philippine specimens reported here.

Subclass Neomphaliones Bouchet, Rocroi, Hausdorf, Kaim, Kano, Nützel, Parkhaev, Schrödl, and Strong, 2017

Family Neomphalidae McLean, 1981

Genus *Retiskenea* Warén and Bouchet, 2001

Type species: *Retiskenea diploura* Warén and Bouchet, 2001, by original designation; Recent, off Oregon.

Retiskenea? sp.

Fig. 29A–C.

Material.—Three specimens from the Pliocene of Liog-Liog Point (NMNS PM 28435–28437).

Dimensions (in mm).—NMNS PM 28435, W = 4.8, H = 3.9.

Remarks.—The specimens from Liog-Liog Point have a lower spire than the extant *R. diploura*, than the Eocene–Oligocene *R. statura* (Goedert and Benham, 1999) from Washington state (Goedert and Benham 1999), and also than the early Oligocene *Retiskenea?* sp. from northern Peru (Kiel et al. 2020). Most similar is the Cretaceous *R.? tuberculata* Campbell, Peterson, Alfaro, 2008 from California (Campbell et al. 2008).

Genus *Planorbidella* Warén and Bouchet, 1993

Type species: *Depressigyra planispira* Warén and Bouchet, 1989, by original designation; Recent, hydrothermal vents on the East Pacific Rise.

Planorbidella? sp.

Fig. 29D.

Material.—Three specimens from the Pliocene of Liog-Liog Point (NMNS PM 28438–28440) and one specimen (NMNS PM 28117) from the Pleistocene of Cambantug Point.

Dimensions (in mm).—NMNS PM 28438, W = 2.9, H = 1.3.

Remarks.—Shells of the heterobranch genera *Hyalogyra* and *Hyalogyrina* are quite similar, but the “archaegastropod”-type protoconch (Fig. 29D₃) makes affinities with the neomphaline *Planorbidella* more likely. However, the protoconch lacks the irregular net sculpture typical for *Planorbidella*, but this might be an artefact of preservation.

Subclass Vetigastropoda Salwini-Plawen, 1980

Superfamily Trochoidea Rafinesque, 1815

Family Skeneidae Clark, 1851

Genus *Dillwynella* Dall, 1889

Type species: *Teinostoma modesta* Dall, 1889, by monotypy; Recent, Gulf of Mexico.

Dillwynella sp.

Fig. 29F.

Material.—One specimen from the Pliocene of Liog-Liog Point: NMNS PM 28441, W = 4.5 mm, H = 4.0 mm.

Remarks.—Species of *Dillwynella* can be variable in the height of the spire, as shown for *Dillwynella vitrea* Hasegawa, 1997 from wood-falls in Japanese waters (Hasegawa 1997). Two species with a similar spire and a similarly narrow umbilicus as the specimen reported here are *D. haptricola* Marshall, 1988 living on algal holdfasts, and *D. ingens* Marshall, 1988 living on wood falls in New Zealand waters (Marshall 1988).

Genus *Lopheliella* Hoffman, Van Heugten, and Lavaleye, 2008

Type species: *Lopheliella rockallensis* Hoffman, Van Heugten, and Lavaleye, 2008, by original designation; Recent, Rockall Trough, NE Atlantic Ocean.

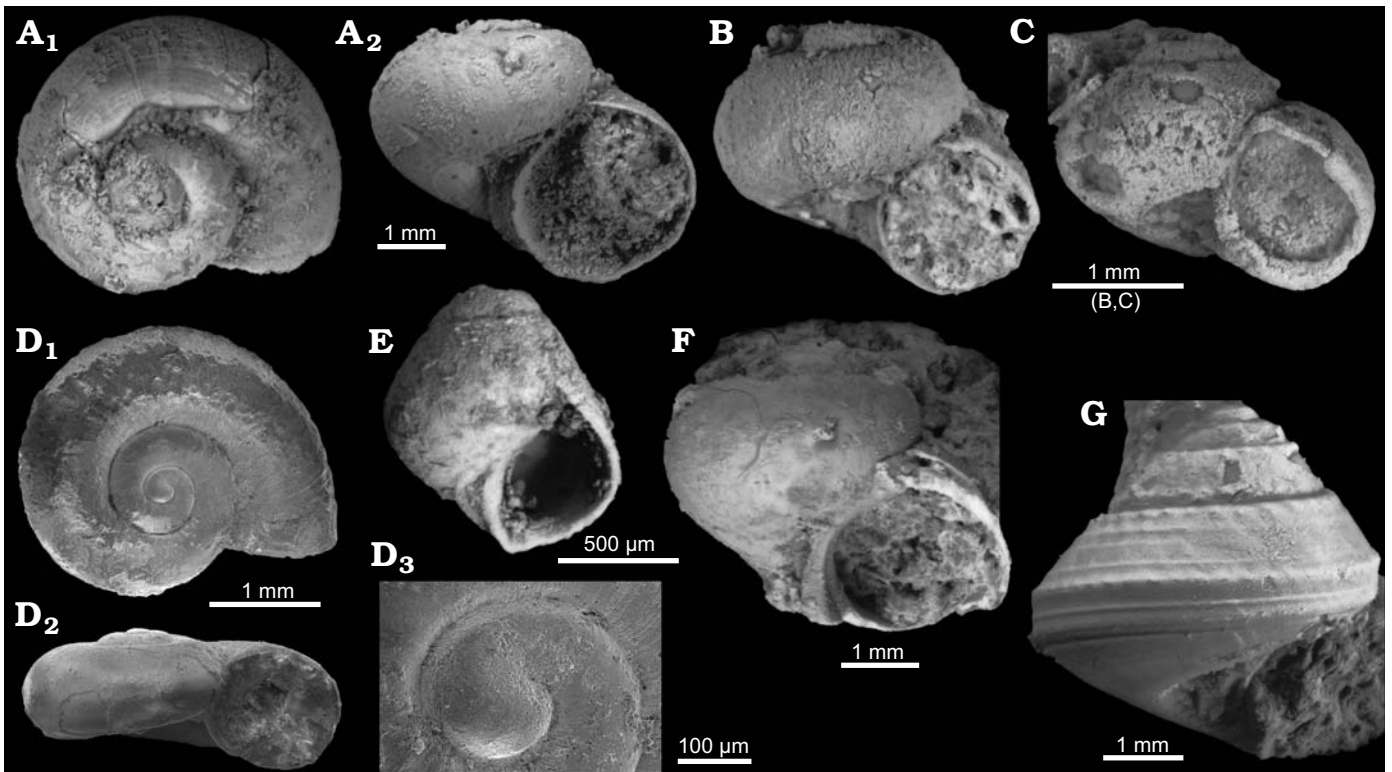


Fig. 29. Neomphalinae and Vetigastropoda from late Pliocene (A–F, Liog-Liog Point) and Pleistocene (G, Antipolo Point) seep deposit in Leyte, Philippines. A–C. The neomphalid *Retiskenea* sp. A. NMNS PM 28435, in apical (A₁) and apertural (A₂) views. B. NMNS PM 28436, apertural view. C. NMNS PM 28437, apertural view. D. The neomphalid *Planorbidella* sp., NMNS PM 28438, in apical (D₁) and apertural (D₂) views, and close-up on protoconch (D₃). E. *Lopheliella?* sp., NMNS PM 28442, apertural view, note umbilical slit bordered by distinct ridge. F. The skeneid vetigastropod *Dillwynella* sp., NMNS PM 28441, apical view. G. The trochoid vetigastropod *Solariella* sp., NMNS PM 28443, apical view.

Lopheliella? sp.

Fig. 29E.

Material.—One specimen from the Pliocene of Liog-Liog Point: NMNS PM 28442 (W = 1.0 mm, H = 1.1 mm).

Remarks.—This tiny specimen resembles *Lopheliella rockallensis* in its overall egg-shape with rather straight-sided whorls. However, it bears a distinct ridge along the umbilical chink, which is more pronounced than in any known species of *Lopheliella* (Hoffman et al. 2008, 2018).

Family Solariellidae Powell, 1951

Genus *Solariella* Wood, 1842

Type species: *Solariella maculata* Wood, 1842, by monotypy; Pliocene, England.

Solariella sp.

Fig. 29G.

2005 *Solariella tobaruensis* Noda, 1988; Hasegawa 2005: fig. 4E.
2017 *Solariella tabaruensis* [sic!] Noda; Sasaki 2017: 754, pl. 26: 12.

Material.—One specimen from the Pleistocene of Antipolo Point: NMNS PM 28443 (W = 4.5 mm, H = 4.5 mm).

Remarks.—This specimen is identical to an extant shell identified as *Solariella tobaruensis* Noda, 1988, collected in c. 520 m depth off Omami-oshima island (Ryukyu Islands,

southern Japan) and illustrated in Hasegawa (2005) and Sasaki (2017). However, the name *Solariella tobaruensis* is based on a Plio-Pleistocene fossil from Okinawa, Japan (Noda 1988: 33, pl. 5: 5, 6), which has a more distinct shoulder and a deeper suture than both the extant specimen just mentioned and the Philippine specimen reported here.

Family Margaritidae Thiele, 1924

Genus *Margarites* Gray, 1847

Type species: *Turbo helycinus* Phipps, 1774, by original designation; Recent, North Atlantic Ocean.

Margarites hayashii sp. nov.

Fig. 30.

Zoobank LSID: urn:lsid:zoobank.org:act:24D9CA99-1B02-434F-B900-EFEC6D8BFC

Etymology: For Hiroki Hayashi (Shimane University, Japan) who provided preliminary results of planktonic foraminifer analyses for biostratigraphy.

Type material: Holotype: NMNS PM 28444. Paratypes: NMNS PM 28445, 28446 from the type locality; all specimens with defoliated shells.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Lower Pliocene part of the Bata Formation.

Material.—Six specimens from the Pliocene of Liog-Liog

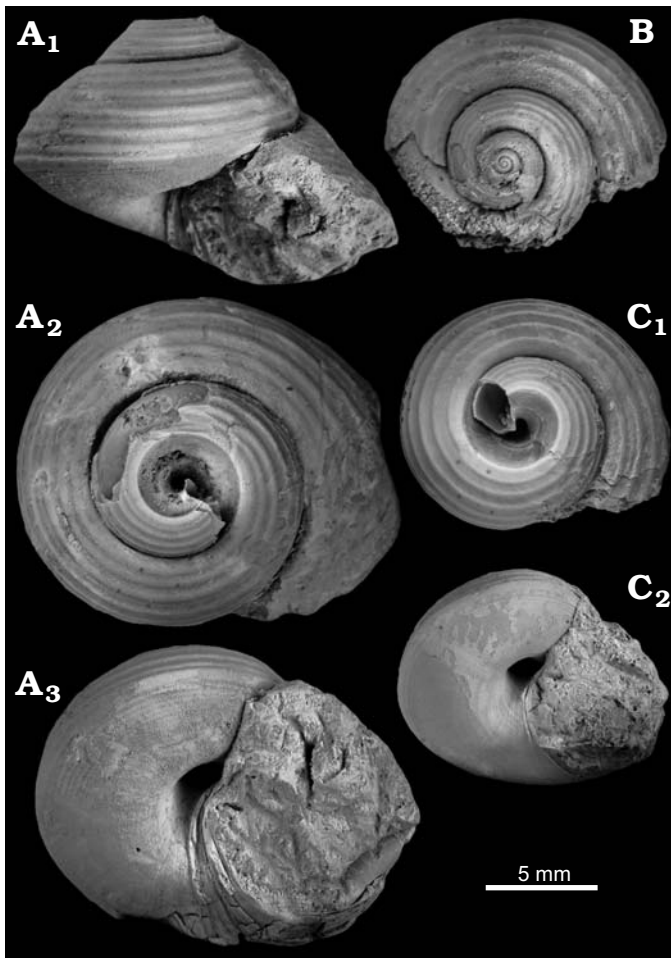


Fig. 30. The trochoid gastropod *Margarites hayashii* sp. nov. from the late Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. A. Holotype NMNS PM 28444, in apertural (A₁), apical (A₂), and basal (A₃) views. B. Paratype NMNS PM 28445 in apical view. C. Paratype NMNS PM 28446, in apical (C₁) and basal (C₂) views.

Point: the type material and NMNS PM 28451 (three individuals).

Dimensions (in mm).—NMNS PM 28444, W = 17.0, H = 16.0; NMNS PM 28445, W = 12.5, H = 8.0 (specimen with most complete spire); NMNS PM 28446, W = 12.0.

Diagnosis.—Trochiform *Margarites* with weakly convex whorls, sculptured by six spiral cords and a finer spiral between cords; umbilicus narrow, base with fine spiral lines.

Description.—Shell trochiform, at least five whorls with convex profile, sculpture of up to six low, widely spaced cords crossed by strongly prosocline growth lines, some interspaces with fine cord; basal margin marked by another cord; base sculptured by finer and more densely spaced spiral lines than whorl flanks; umbilicus conical, width about 1/3 of shell diameter; aperture circular, strongly inclined.

Remarks.—Two similar species are *Margarites shinkai* Okutani, Tsuchida, and Fujikura, 1992 living around seep sites in Sagami Bay, Japan (Okutani et al. 1992; Sasaki et

al. 2010) and *M. similis* Zhang and Zhang, 2017 from the Okinawa Trough (Zhang and Zhang 2017). The former differs from *Margarites hayashii* by having a more angular whorl profile, more numerous spiral cords on the whorls and narrower umbilicus. *M. similis* has a lower spire and more conical base than *Margarites hayashii*, and more densely spaced spiral cords.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Superfamily Seguenzoidea Verrill, 1884

Family Seguenziidae Verrill, 1884

Genus *Vetulonia* Dall, 1913

Type species: *Vetulonia galapagana* Dall, 1913, by original designation; near Galapagos in deep water.

Vetulonia philippinensis sp. nov.

Fig. 31.

Zoobank LSID: urn:lsid:zoobank.org:act:D0C715F7-098E-412C-81CF-6AD3831BC53C

Etymology: In reference to its origin, the Philippines.

Holotype: NMNS PM 28447, specimen with the apertural area concealed by sediment.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—The holotype only.

Dimensions (in mm).—NMNS PM 28447, W = 2.5, H = 2.0.

Diagnosis.—Small turbiniform shell, 3¼ evenly convex whorls, sculpture of strongly sinuous axial ribs crossed by very fine spiral striae, umbilicus narrow.

Description.—Minute, turbiniform shell, protoconch about 0.4 mm across, teleoconch of 3¼ whorls, last whorl very large; whorls strongly convex, sculptured by ~20 very distinct, oblique axial ribs reaching into umbilical area, their interspaces about twice of rib width; ribs and interspaces crossed by ~10 very fine spiral threads.

Remarks.—*Vetulonia philippinensis* sp. nov. differs from the known species of *Vetulonia* as follows: *Vetulonia galapagana* is the most similar species but has fewer axial ribs

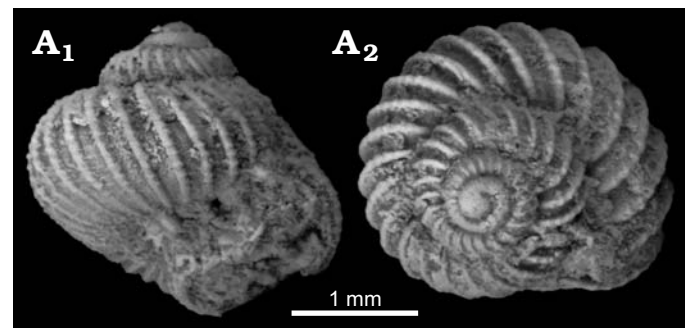


Fig. 31. The seguenzoid gastropod *Vetulonia philippinensis* sp. nov. from the late Pliocene seep deposit at Liog-Liog Point, Leyte, Philippines, NMNS PM 28447, apertural (A₁) and apical (A₂) views.

per whorl (Dall 1913); *Vetulonia densilirata* Dall, 1927 has a flat spire according to Dall (1927: 120) in contrast to the trochiform shell of *Vetulonia philippinensis*; *Vetulonia giacobbei* Renda and Micali, 2016 has much stronger spiral ornament, giving the whorls an angular appearance; *Vetulonia parajeffreysi* Absalão and Pimenta, 2005 has a lower spire, and fewer and more oblique axial ribs; and *Vetulonia phalcatata* Warén and Bouchet, 1993 has finer and more numerous axial ribs (Dautzenberg 1889; Dall 1927; Warén and Bouchet 1993, Absalão and Pimenta 2005; Renda and Micali 2016).

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Family Cataegidae McLean and Quinn, 1987

Genus *Cataegis* McLean and Quinn, 1987

Type species: *Cataegis toreuta* McLean and Quinn, 1987, by original designation; Recent, Gulf of Mexico and Caribbean Sea.

Cataegis ramosi sp. nov.

Fig. 32.

Zoobank LSID: urn:lsid:zoobank.org:act:429B5F94-C73C-4BEA-85A2-19EB3E311F7A

Etymology: In honour of Foracio Ramos (former director of the Philippine Mining and Geoscience Bureau Central Office) for supporting field work in the Philippines.

Type material: Holotype: NMNS PM 28448. Paratype: NMNS PM 28449 from the type locality; two complete specimens.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—Three specimens from the Pliocene of Liog-Liog: the type material and NMNS PM 28450 (two individuals).

Dimensions (in mm).—NMNS PM 28448, W = 18.0, H = 17.0; NMNS PM 28449, W = 18.0; H = 16.0.

Diagnosis.—Average-sized *Cataegis* with four distinct spiral cords per whorl, third spiral forming distinct shoulder; base with two strong spiral cords, one of them forming basal margin, and seven finer, equally strong spiral lines; aperture with apical notch, inner lip callused.

Description.—Trochiform shell with up to five whorls, suture deeply incised; whorls sculptured by four spiral cords, first two thin, closely spaced and close to upper suture, third cord strong, marking whorl's shoulder, fourth of same strength as third, situated vertically below third close to lower suture; entire whorl surface covered by finely spaced, distinct, oblique growth increments; basal margin marked by two cords of equal strength; base rather straight with seven densely spaced, beaded spiral cords; umbilical slit covered by callus; aperture circular inclined backwards, inner lip callused with groove between umbilical and lip callus.

Remarks.—*Kanoia* Warén and Rouse, 2016 was separated from *Cataegis* based on radula characters (Warén and Rouse 2016), which are typically not preserved in fossils. Based on a comparison of the known species of *Kanoia* and *Cataegis*,

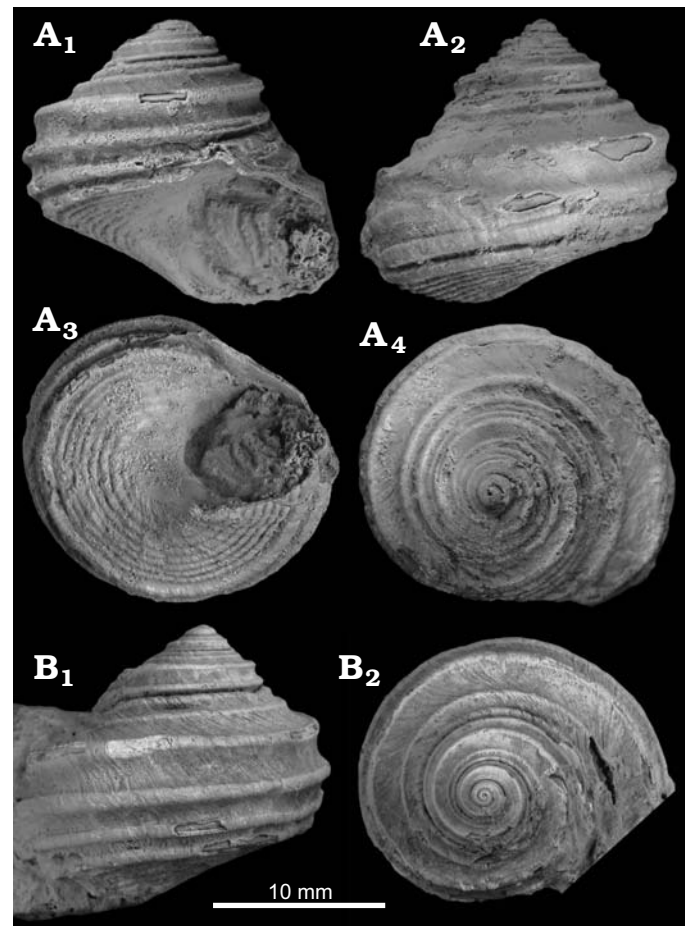


Fig. 32. The seguenzoid gastropod *Cataegis ramosi* sp. nov. from the late Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. **A.** Holotype NMNS PM 28448, in apertural (A₁), abapertural (A₂), basal (A₃), and apical (A₄) views. **B.** Paratype NMNS PM 28449, in abapertural (B₁) and apical (B₂) views.

the latter appears to have a higher, more conical spire whereas the spire of *Kanoia* appears somewhat dome-shaped (see McLean and Quinn 1987; Fu and Sun 2006, Warén and Rouse 2016; Vilvens 2016). Based on these shell characters we place *C. ramosi* in *Cataegis* rather than *Kanoia*.

The type species *C. toreuta* differs from *C. ramosi* by having fewer and stronger spiral cords on the base and a less distinct whorl's shoulder (McLean and Quinn 1987). Also *C. celebesensis* McLean and Quinn, 1987 has fewer spiral cords on the base than *C. ramosi*. *Cataegis leucogranulatus* (Fu and Sun 2006) from the South China Sea has more granular sculpture than *C. ramosi* and it also has secondary, fine spiral lines between the main spiral cords, a feature not seen in *C. ramosi*. Among the three species of *Cataegis* described by Vilvens (2016) from the deep waters around the Solomon Islands, *C. stroggile* Vilvens, 2016 is most similar to *C. ramosi* but differs from it by having a more convex whorl profile with three main spiral cords instead of two, and by having fewer spiral lines on the base.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

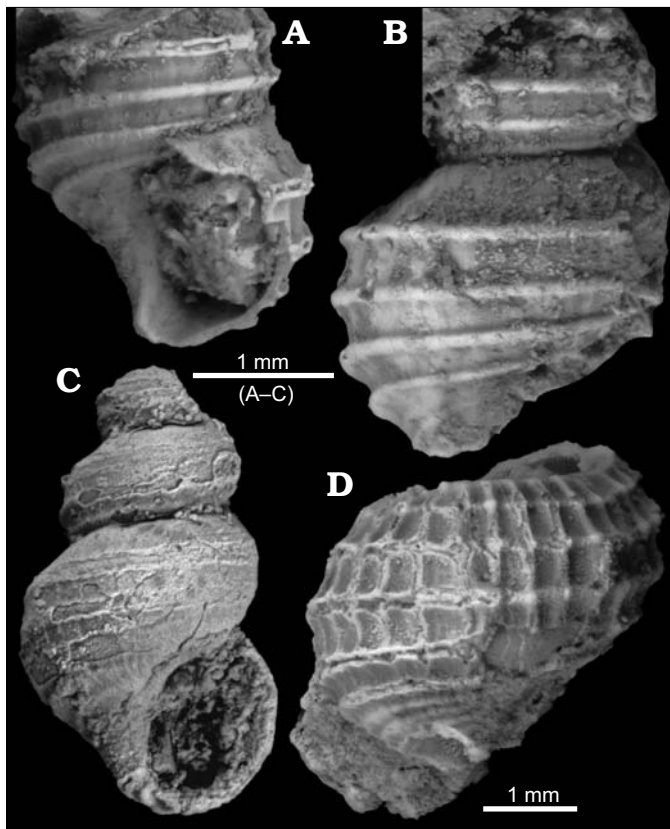


Fig. 33. Provannid gastropods from the late Pliocene Liog-Liog Point seep deposit in Leyte, Philippines. A–C. *Provanna azurini* sp. nov. A. Paratype NMNS PM 28453 in apertural view. B. Paratype NMNS PM 28454 in abapertural view. C. Holotype NMNS PM 28452, specimen in apertural view with three preserved whorls but poorly preserved sculpture. D. *Desbruyeresia?* sp., NMNS PM 28457 in abapertural view.

Subclass Caenogastropoda Cox, 1960

Family Provannidae Warén and Ponder, 1991

Genus *Provanna* Dall, 1918

Type species: Trichotropis lomana Dall, 1918, by monotypy; Recent, off California, USA.

Provanna azurini sp. nov.

Fig. 33A–C.

Zoobank LSID: urn:lsid:zoobank.org:act:F26418F1-EC73-4512-A485-35241B398A0D

Etymology: In honour of Emolyn Azurin (Philippine Mining and Geoscience Bureau, Quezon City, Philippines) for safely driving us during the field work in Leyte.

Type material: Holotype NMNS PM 28452, shell with three whorls and spiral sculpture. Paratypes: NMNS PM 28453, 28454, shells preserving few whorls and different sculptural styles from the type locality.

Type locality: Liog-Liog Point, Leyte, Philippines.

Type horizon: Upper Pliocene part of the Bata Formation.

Material.—Four specimens from the Pliocene of Liog-Liog Point: the type material and NMNS PM 28456 (six individuals, some of them fragmentary).

Dimensions (in mm).—NMNS PM 28452, H = 3.2 (at three

whorls), W = 1.8. Widest available whorl fragment (unnumbered): W = 3.0.

Diagnosis.—Small for genus; tall, slender shell, whorls angular, with two equally strong spiral cords per whorl, no axial sculpture; three spiral cords of decreasing strength on base, upper one marking basal margin; aperture slightly oval.

Description.—Tall, slender shell composed of at least 3 whorls, reaching at least 4 mm in height; whorls profile angular, shoulder nearly straight and smooth, two distinct spiral cords per whorl, with broad, smooth interspace; base with three further spiral cords of decreasing strength and beaded appearance, the uppermost marks the basal margin; aperture slightly oval with small, short siphonal notch, columellar and parietal lip callused.

Remarks.—*Provanna* species having exclusively spiral ornament are rare. The most similar extant species are *Provanna macleani* Warén and Bouchet, 1989 from seeps off of Oregon, USA (Warén and Bouchet 1989), and *Provanna cingulata* Chen, Watanabe, and Ohara, 2018, from the Shinkai seep field in the southern Mariana Trench (Chen et al. 2018). *Provanna macleani* differs from *Provanna azurini* by having four to five spiral cords per whorl, whereas *Provanna azurini* has only two. *Provanna cingulata* has an increasing number of spiral cords per whorl, starting with two spiral cords on very early whorls. However, the whorls of *Provanna cingulata* are more angular and the species is overall less slender than *Provanna azurini*. Among fossil species, *Provanna antiqua* Squires, 1995 from Oligocene seeps in Washington state, USA, and northern Peru (Squires 1995; Kiel et al. 2019), has very variable sculpture including specimens with almost exclusively spiral ornament. But as in the extant *P. macleani*, these are more numerous (3–4) than in *Provanna azurini*.

Stratigraphic and geographic range.—Late Pliocene, Leyte, Philippines.

Genus *Desbruyeresia* Warén and Bouchet, 1993

Type species: Desbruyeresia spinosa Warén and Bouchet, 1993, by original designation; Recent, North Fiji Basin.

Desbruyeresia? sp.

Fig. 33D.

Material.—One fragment from Liog-Liog Point (NMNS PM 28457, H = 3.8 mm, W = 3.9 mm). It consists of about one convex whorl sculptured by four equally spaced spiral cords, crossed by equally strong axial ribs; the lowermost spiral cord forms the basal margin, and the base bears about five smaller cords.

Remarks.—A similar species is *D. chamorroensis* from South Chamorro Seamount on the southeastern Mariana Forearc (Chen et al. 2016). But with only a fragment consisting of one whorl with concealed aperture available, and similar shells known from deep-water rissoids (Warén 1996; Okutani 2000), this specimen is only hesitantly placed in *Desbruyeresia*.

Discussion

The Pliocene and Pleistocene seep faunas reported here are from four different localities, and contain a total of 30 species of chemosymbiotic bivalves and 14 species of gastropods (Table 2). 27 of these species are from the late

Pliocene Liog-Liog Point site, which is a remarkably high diversity compared to other Pliocene seep faunas around the world. For comparison, there are only cursory mentions of some chemosymbiotic bivalves in Plio-Pleistocene strata the eastern Pacific region (Olsson 1942; Squires 1991; Campbell 1992), a few lucinids have been reported from

Table 2. The species reported here and their occurrences. * from early Pleistocene non-seep sediments at the tip of Liog-Liog Point.

Taxon	Liog-Liog Point (Pliocene)	Antipolo Point (Pleistocene)	Buhoc Point (Pleistocene)	Cambantug Point (Pleistocene)
Bivalvia				
<i>Bathymodiolus securiformis</i> Okutani, Fujikura, and Sasaki, 2004	×	×		
Unidentified bathymodiolin	×			
<i>Conchocele majimai</i> sp. nov.	×			
<i>Conchocele visayaensis</i> sp. nov.				×
<i>Channelaxinus antipoloensis</i> sp. nov.		×		
<i>Meganodontia acetabulum</i> Bouchet and Cosel, 2004		×		
<i>Dulcina liogliogensis</i> sp. nov.		×	×	
<i>Dulcina magoi</i> sp. nov.	×		×	
<i>Elliptiolumina ingens</i> Okutani, 2011	×			
<i>Elliptiolumina fernandoi</i> sp. nov.	×		×	×
<i>Divalucina soyoae</i> (Habe, 1952)			×	
<i>Lucinoma dulcinea</i> Cosel and Bouchet, 2008	×	×		
<i>Lucinoma</i> aff. <i>kastoroae</i> Cosel and Bouchet, 2008	×			
<i>Lucinoma canudai</i> sp. nov.				×
<i>Lucinoma velosoi</i> sp. nov.		×		×
<i>Lucinoma tinagoensis</i> sp. nov.				×
<i>Lucinoma kosatorea</i> sp. nov.				×
<i>Vesicomya margotae</i> Beets, 1953 Pliocene	×			
<i>Vesicomya nakaii</i> Okutani, 1962				×
<i>Isorropodon</i> cf. <i>perplexum</i> Sturany, 1896	×			×
<i>Archivesica kawamurai</i> (Kuroda, 1943)				×
<i>Archivesica pastori</i> sp. nov.	×			
<i>Pliocardia kuroshimana</i> (Okutani, Fujikura, and Kojima, 2000)	×*			
“ <i>Pliocardia</i> ” <i>ticaonica</i> Dall, 1908				×
“ <i>Pliocardia</i> ” <i>indica</i> (Prasad, 1932)				×
<i>Wareniconcha guineensis</i> (Thiele and Jaeckel, 1931)	×			
<i>Wareniconcha</i> aff. <i>winckworthi</i> (Prasad, 1932)	×			
<i>Wareniconcha mercenarioides</i> Kase, Isaji, Aguilar, and Kiel, 2019	×			
<i>Waisiuconcha</i> sp. 1	×			
<i>Waisiuconcha</i> sp. 2				×
Gastropoda				
Limpet gastropod sp. 1	×	×		
Limpet gastropod sp. 2		×		
Limpet gastropod sp. 3		×		
Limpet gastropod sp. 4	×			
<i>Retiskenea?</i> sp.	×			
<i>Planorbidella?</i> sp.	×			×
<i>Dillwynella</i> sp.	×			
<i>Lopheliella?</i> sp.	×			
<i>Solariella</i> sp.				×
<i>Margarites hayashii</i> sp. nov.	×			
<i>Vetulonia philippinensis</i> sp. nov.	×			
<i>Cataegis ramosi</i> sp. nov.	×			
<i>Provanna azurini</i> sp. nov.	×			
<i>Desbruyeresia?</i> sp.	×			

Pliocene seep sites in Taiwan (Wang et al. 2006), and seven species of chemosymbiotic bivalves are known from the late Pliocene Stirone river seep complex in northern Italy (Kiel and Taviani 2018). From the well-sampled Plio-Pleistocene seep deposits around Japan, eight named vesicomys and a few in open nomenclature are known (Amano et al. 2019), and only a few taxa of the other families of chemosymbiotic bivalves have been reported, including two solemyids (*Acharax johnsoni* and “*Solemya* sp.”), the thyasirid *Conchcele bisecta*, the lucinid *Lucinoma acutilineata*, and the mytilid *Bathymodiolus* sp. (Majima et al. 2005).

A comparison of the Leyte seep faunas to Plio-Pleistocene to Recent Japanese seep faunas is interesting. Of the five extant species from Japanese waters reported here from the late Pliocene and early Pleistocene of the Philippines (*Bathymodiolus securiformis*, *Elliptiolucina ingens*, *Vesicomys nakaii*, *Pliocardia kuroshimana*, *Archivesica kawamurai*), only the widespread *Archivesica kawamurai* has a fossil record in Japan (Amano et al. 2019). Thus it appears that a remarkable portion of the extant Japanese seep mollusks originated around the Philippines and spread to Japanese waters only recently. Furthermore, Amano et al. (2019) pointed out that the present-day distribution of vesicomysid bivalves in Japan is probably related to temperature. Whereas *Calyptogena* originated in colder waters and today inhabits the colder North Pacific waters of Japan, *Archivesica* has a warmer-water origin and today inhabits the warmer waters of southern and southeastern Japan (Amano et al. 2019). This argument could possibly be extended to a wider range of the seep fauna because all five extant Japanese taxa with a Philippine origin mentioned above presently live in areas of southern Japan influenced by the warm-water Kuroshio Current that originates around the Philippines and flows toward Japan (Saito 2019).

Another remarkable feature of the Philippine Plio-Pleistocene seep mollusks reported here is the high number of lucinids. More than one third (12 out of 30) of all bivalve species are lucinids, and nearly two thirds of the new bivalve species (7 out of 11) are lucinids. Such a large proportion of lucinids is unusual for extant seep faunas (Sibuet and Olu 1998; Sasaki et al. 2005; Olu-Le Roy et al. 2007; Cordes et al. 2010) but is more commonly seen in the fossil record. For example, in the Pliocene Stirone river seep complex, five out of seven chemosymbiotic bivalve species are lucinids (Kiel and Taviani 2018). This discrepancy might relate to the infaunal mode of life of the lucinids, due to which they are rarely found on video observations or in surface collections at modern seeps (Glover et al. 2004; Taylor and Glover 2010; Kiel 2010b).

Conclusions

We report the most diverse Plio-Pleistocene seep faunas to date; the late Pliocene Liog-Liog Point deposit alone

yielded 27 species, followed by the Pleistocene Cambantug Point site (14 species) and the Antipolo Point site (9 species). Most species either belong to extant species living in the western Pacific Ocean, or are closely related to them. Remarkable is that several species occur in Japanese waters today, especially the Okinawa Trough, but those species are absent from the well-studied fossil record of seeps in Japan. The only exception is the widespread species *Archivesica kawamurai*, for which a warm-water origin has been suspected (Amano et al. 2019).

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