

Mollusks from Miocene hydrocarbon-seep deposits in the Ilocos-Central Luzon Basin, Luzon Island, Philippines

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We report 35 molluscan species from Late Miocene cold-seep carbonates from the Amlang Formation in the Ilocos-Central Luzon Basin in Luzon Island, Philippines, collected in a large quarry in the province of Pangasinan. The 19 bivalve species are largely representatives of chemosymbiotic families; the six new species are the nuculid *Acila (Truncacila) interferencia* sp. nov., the mytilid *Bathymodiolus labayugensis* sp. nov., the thyasirid *Conchocele pangasinanensis* sp. nov., the lucinid *Megaxinus gorrospei* sp. nov., the vesicomid *Pliocardia ballesterosi* sp. nov., and *Sisonia frijellanae* gen. et sp. nov., of uncertain taxonomic affinity. The 16 gastropods include one species restricted to seep deposits, the neritid species *Thalassonerita hagai* sp. nov.; the buccinid *Enigmaticolus semisulcata* represents the first fossil record of its genus. Biogeographically, the Pangasinan seep fauna shows several links to Neogene seep faunas in other tropical/subtropical areas, namely the Mediterranean and Caribbean regions. In contrast, shared taxa with nearby but extratropical Japan are few, as are shared taxa with Miocene seep deposits in New Zealand.

Key words: Gastropoda, Bivalvia, chemosynthesis-based ecosystem, deep sea, hydrocarbon seep, Miocene, Philippines.

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Introduction

Methane seeps in the deep sea are inhabited by a distinct fauna dominated by chemosymbiotic animals (Paull et al. 1984; Fisher 1995). The high degree of endemism in these habitats, many families of annelids, crustaceans, and mollusks are known exclusively from methane seeps, hydrothermal vents, and sulfide-rich habitats around sunken whale carcasses and wood, and their specialized physiology spurred the idea that these faunas have a long and distinct evolutionary history (Tunnicliffe 1991; Distel et al. 2000; Vrijenhoek 2013). The fossil record provides the primary evidence for the history of life and indeed has provided unique insights into the questions of antiquity and evolutionary origin of these faunas (Campbell and Bottjer 1995; Little et al. 1997; Kiel and Little 2006; Kiel 2015). Especially the Cenozoic record of methane-seep communities is increasingly well documented (Majima et al. 2005; Campbell 2006; Kiel 2010b; Saether et al. 2010a; Kiel and Hansen

2015; Amano et al. 2019b; Kiel et al. 2020b; Hryniewicz et al. 2021; and references therein); however, the most species-rich area of the world's oceans, the central Indo-Pacific Ocean including the Malayan and Philippine archipelagos, is only beginning to be explored for such faunas (Beets 1953; Majima et al. 2007, 2010; Kase et al. 2019; Kiel et al. 2020a).

The purpose of this study is to document the mollusk fauna of newly discovered Late Miocene methane-seep deposits in the Ilocos-Central Luzon Basin in Luzon Island, Philippines. The Philippine island arc system is an assemblage of allochthonous arcs, ophiolite complexes, continental and oceanic rocks, and lies at the boundary of the Eurasian and the Philippine Sea plates (Karig 1983; David et al. 1997; Hall 2002; Galgana et al. 2007; Yumul et al. 2008; Aurelio et al. 2013). The north-south oriented Ilocos-Central Luzon Basin is one of 16 recognized major sedimentary basins in the Philippines, and stretches from the vicinity of the Manila metropolitan area in the south to Ilocos Norte in the north (Pinet and Stephan 1990a; Peña 2008; MGB

2010). The about 8000 m thick sedimentary sequence filling the basin reflects a wide diversity of depositional environments; source of the clastic sediments are the Luzon Central Cordillera on the eastern side and the Zambales Mountains on the western side of the basin (Saldivar-Sali 1978; Pinet and Stephan 1990a, b).

Both shallow and deep marine deposits of the Ilocos-Central Luzon Basin are exposed in Barangay Labayug in the Municipality of Sison, Pangasinan province, in a large quarry at 16°10'N, 120°34'E (Fig. 1), owned by the Northern Cement Corporation. These deposits include a bedded limestone unit with common reefal fossils, named Labayug Limestone, and alternating sequences of limestone and mudstone beds mapped as part of the Amlang Formation (Lorentz 1984). The seep deposits reported here are from the Amlang Formation, found as floats in the lower part of the quarry, locally known as the “Shale Quarry” (Magtoto and Fernando 2017).

Institutional abbreviations.—NIGSPAL (NIGS-UPGAA Museum) National Institute of Geological Sciences, University of the Philippines, Diliman, Quezon City, Philippines; NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Other abbreviations.—aams, anterior adductor muscle scar; aprs, anterior pedal retractor scar; H, height; L, length; LV, left valve; pams, posterior adductor muscle scar; RV, right valve; W, width. The width of bivalves always refers to specimens with two conjoined valves, measurements on single valves are marked by “(single)”; the plus sign after a measurement indicates that the specimen was incomplete.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:0A7EA08E-1FB4-48D1-833A-A11B3DEE6DC9

Material and methods

The specimens were collected during two field seasons in 2015 and 2019. Four blocks of seep carbonate were sampled in 2015, referred to as blocks A–D; in 2019 we sampled block B again, and we sampled six additional blocks, referred to as blocks E–J. Further specimens were given to us by the staff of the Northern Cement Corporation; they are referred to as coming from the “NCC collection”. Except possibly for block F, all blocks from which we report mollusks were found as floats. The blocks had most likely been left aside or moved away while quarrying the shale. Planktic foraminifera of biostratigraphic relevance extracted from Block B include *Trilobatus sacculifer*, *Trilobatus trilobus*, *Dentoglobigerina altispira altispira*, and *Globorotalia plesiotumida*, among others (Hiroki Hayashi, Shimane University, Japan, personal communication 2020). Based on the occurrence of *G. plesiotumida*, which has its first occurrence at the base of zone N17 (cf., Blow 1969), this block is most likely of Late Miocene

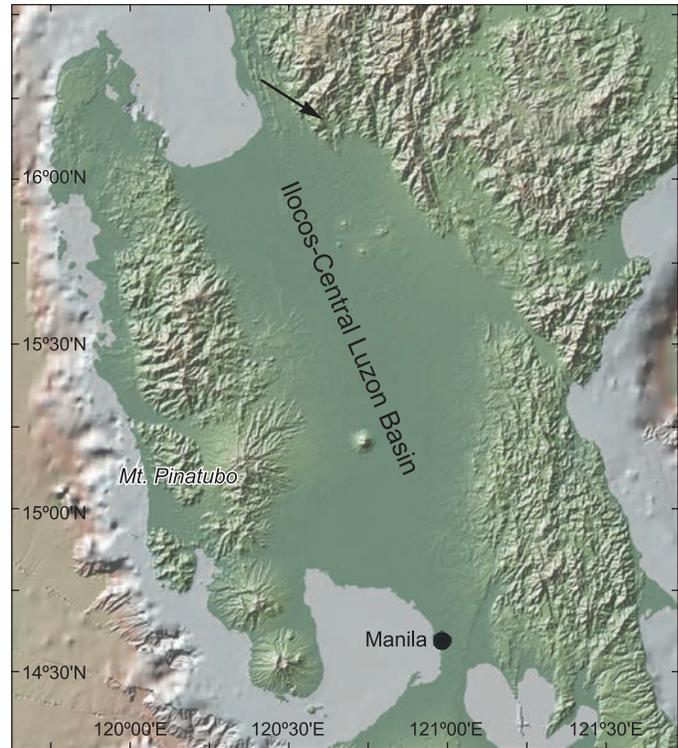


Fig. 1. Map showing the location of the Northern Cement Corporation (NCC) quarry in the province of Pangasinan, Luzon, Philippines (arrow). Modified from www.geomapapp.org (CC-BY) and Ryan et al. (2009).

age. This is consistent with the nannofossil age dating of the Amlang Formation (Lorentz 1984; Magtoto and Fernando 2017). In the lab, specimens were mechanically extracted from the carbonate matrix using pneumatic chisels and needles. All specimens were coated with ammonium chloride prior to photography. Most holotypes and the specimens of the NCC collection are housed at NIGS, the remaining material is housed in the Department of Palaeobiology at NRM.

Discussion

Faunal remarks.—Amano and Ando (2011) noted that the fossil record of very large solemyids in Japan is confined to deep-marine deposits of Early and Middle Miocene age, with specimens of *Acharax yokosukensis* and *A. gigas* reaching almost 300 mm in length. To this we can add the large shells of *Acharax aff. bartschii* reaching 245 mm in length from the Late Miocene-aged deep-marine cold-seep deposits of Luzon, Philippines. But why solemyids reached so much larger sizes in the tropical northwestern Pacific Ocean in (or since) the Miocene, while typically not exceeding 100 mm in length elsewhere, both in the Cenozoic fossil record (Goedert and Squires 1990; Gill et al. 2005; Kiel 2010b; Taviani et al. 2011; Kiel and Hansen 2015; Pérez-Barriá and Nielsen 2020; Kiel et al. 2020b; Hryniewicz et al. 2020) and in the oceans today (Abbott 1974; Coan et al. 2000; Taylor et al. 2008; Kamenev 2009) remains unclear.

The nuculid subgenus *Truncacila* is common at seeps since the Cretaceous (Amano 2003; Amano and Jenkins 2007; Jenkins et al. 2007b; Kiel et al. 2008, 2020b; Amano et al. 2010, Nesbitt et al. 2013; Miyajima et al. 2018) and is most likely a vagrant taking advantage of the abundant organic matter at seeps (Kiel 2010b). Among the bathymodiolins, the genus *Gigantidas* appears to have been established in the western Pacific Ocean by Middle to Late Miocene time (Saether et al. 2010b). The large thyasirid genus *Conchocele* is known from seep deposits since the Late Cretaceous, though mostly from the Pacific Ocean (Hryniewicz et al. 2017). The Miocene records from the Philippines documented here (*Conchocele pangasinanensis* and *Conchocele* aff. *quadrata*) add to the tropical record of the genus (Okutani 2002; Kiel and Hansen 2015; Samadi et al. 2015; Kiel et al. 2020a).

The lucinid *Megaxinus gorrospei* is the first record of this genus from the central Indo-Pacific Ocean and also its easternmost occurrence. Interestingly, no species of *Megaxinus* has been found in the recently described Pliocene and Pleistocene seep deposits in the Philippines, whereas it dominates a Pliocene seep deposit in Italy (Kiel and Taviani 2018). The large *Meganodontia* reached a circum-tropical distribution during the Miocene, reaching from the Tethyan/Mediterranean Sea via Taiwan and the Philippines to the Caribbean Sea (Kiel and Hansen 2015; Kiel and Taviani 2017), with *Meganodontia haunuiensis* from the Early Miocene of New Zealand being the only extra-tropical record (Amano et al. 2018). Also the two species of *Lucinoma* present in the Pangasinan seep deposits show links to extratropical areas: *L. acutilineata* is a widespread North Pacific species (Hirayama 1954; Moore 1963; Majima et al. 2005; Kiel 2010a) and *L. saetheri* occurs in Early to Middle Miocene-aged seep deposits in New Zealand (Amano et al. 2018).

Among the vesicomys, *Pliocardia ballesterosi* is similar to the Japanese *P. crenulomarginata* and *P. kuroshimana*, and hence to the actual genus *Pliocardia* rather than the “*cordata* group” (cf., Johnson et al. 2017). Although not perfectly preserved, the Pangasinan seep deposits produced the as-yet earliest record of *Wareniconcha*, a possible record of *Archivesica*, and two small-sized vesicomys species of uncertain affinity. The enigmatic *Sisonia frijellanae* remains difficult to place among extant and fossil bivalve families, having the shell shape, but definitely not the size, of some Galeommatoidea, and also falls outside the known shell shapes and hinge characteristics of extant and fossil Vesicomysidae. It might have a congener in the Miocene of New Zealand and certainly in the Pleistocene of Taiwan.

Gastropods are neither well preserved nor abundant in the Pangasinan seep deposits. Noteworthy is *Thalassonerita hagai*, representing the first record of this genus from the central Indo-West Pacific Ocean and thus indicating a former widespread occurrence of this genus (Moroni 1966; Taviani 1994; Squires and Goedert 1996; Gill et al. 2005; Hybertsen and Kiel 2018), which is today restricted to a single species, *Thalassonerita naticoides*, in the Gulf of Mexico

and Caribbean Sea (Clarke 1989; Olu et al. 1996; Warén and Bouchet 2001). Another biogeographic link to the Caribbean Sea is a species of the seguenziid *Cataegis*, a genus which has persisted in both the Caribbean Sea and the central Indo-West Pacific at least since the Miocene (McLean and Quinn 1987; Gill et al. 2005; Kiel and Hansen 2015; Vilvens 2016; Kiel et al. 2020a). The buccinid *Enigmaticolus semisulcata* comb. nov. is the first fossil record of this genus, whose extant members live in deep waters of the Indian and West Pacific Oceans. The cephalaspidean *Volvulella* aff. *minoensis*, is one of the few gastropod species showing affinities to the Japanese Miocene deep-water fauna.

Biogeographic remarks.—Although composed of clades typically found at Miocene methane seeps, such as solemyids, bathymodiolins, thyasirids, lucinids, and vesicomysids, the fauna of the Pangasinan seep fauna has a quite distinctive biogeographic character. It shows close links to seep faunas in tropical/subtropical regions, such as *Meganodontia* and *Thalassonerita*, which occur in the Miocene of both the Mediterranean and the Caribbean regions (Taviani 1994; Kiel and Hansen 2015; Kiel and Taviani 2017). Another link to the Caribbean is the gastropod *Cataegis* (Gill et al. 2005; Kiel and Hansen 2015), whereas *Megaxinus* is common in a Pliocene seep deposit in Italy (Kiel and Taviani 2018).

In contrast, the Pangasinan seep fauna shows remarkably few direct links to the well-known Miocene seep faunas of nearby Japan, with which they share only the widespread species *Lucinoma acutilineata* (Majima et al. 2005) and possibly *Conchocele* aff. *quadrata* and *Volvulella* aff. *minoensis*. This is a remarkable difference to the Pliocene to Recent situation, where numerous links between the Philippine and the Japanese seep faunas exist (Kiel et al. 2020a). Other links to extratropical areas are *Gigantidas coseli* and *Lucinoma saetheri*, two species known from Miocene seep deposits in New Zealand (Saether et al. 2010b; Amano et al. 2018).

Conclusions

The mollusks reported here from the Pangasinan seep deposits in Luzon, Philippines, provide new insights into the taxonomic composition and biogeographic relationships of seep faunas from the Neogene central Indo-West Pacific Ocean. The 19 bivalve species are represented largely by chemosymbiotic taxa, many of which are known largely or exclusively from seep and vent environments. The 16 gastropods include only few taxa that are restricted to seep and vent environments; the others are vagrants from the background fauna that took advantage of the abundant organic matter around the seeps. The fauna shows biogeographic links to other tropical seep faunas, especially in Italy and the Caribbean regions. Only few shared species were found with the well-known Miocene seep fauna of Japan, in contrast to the Pliocene–Pleistocene situation, when such links were more common.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Subclass Protobranchia Pelseneer, 1889

Family Solemyidae Gray, 1840

Genus *Acharax* Dall, 1908b

Type species: Solemya johnsoni Dall, 1891, by original designation; Recent, Pacific Ocean.

Acharax aff. *bartschii* (Dall, 1908a)

Fig. 2A–C.

Material.—One specimen from block I (NRM Mo 192667, L = 190.0 mm), two specimens from the NCC collection (NIGSPAL-003, L = 240.0 mm; NIGSPAL-033, L = 160.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—The extant *Acharax bartschii* is a large rare species known from central Philippine waters (Dall 1908a). It agrees well in overall shape with the Miocene specimens reported here, though the radial ribs on the posterior side are directed postero-ventrally in the extant specimens, whereas in the Miocene specimen they are much more ventrally oriented (see Fig. 2A). Hence, we assign the Miocene specimens only hesitantly to *A. bartschii*. The Early to Middle Miocene *Acharax yokosukensis* Kanie and Kuramochi, 1995, from central Honshu, Japan, has a more slender shell, and *Acharax gigas* (Kanno, 1960) from the Miocene Hiranita and Haratajino formations in central Honshu, Japan, has a much shorter posterior side of shell (Kanno 1960; Kanie and Kuramochi 1995, 2002; Amano and Ando 2011: pl. 5: 3).

Acharax sp.

Fig. 2D.

Material.—One specimen from block I (NRM Mo 192660, L = 26.0 mm), one specimen from block J (NRM Mo 192534, L = 20.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—The two small available fragments seem to have parallel dorsal and ventral shell margins, unlike *A. aff. bartschii*, and their radial ribs are broad and flat, unlike the corrugated ribs of *A. aff. bartschii*.

Family Nuculidae Gray, 1824

Genus *Acila* Adams and Adams, 1858

Type species: Nucula divaricata Hinds, 1843, by subsequent designation; Recent, temperate northwestern Pacific Ocean.

Subgenus *Truncacila* Grant and Gale, 1931

Type species: Nucula castrensis Hinds, 1843, by original designation; Pliocene to Recent, northeastern Pacific Ocean.

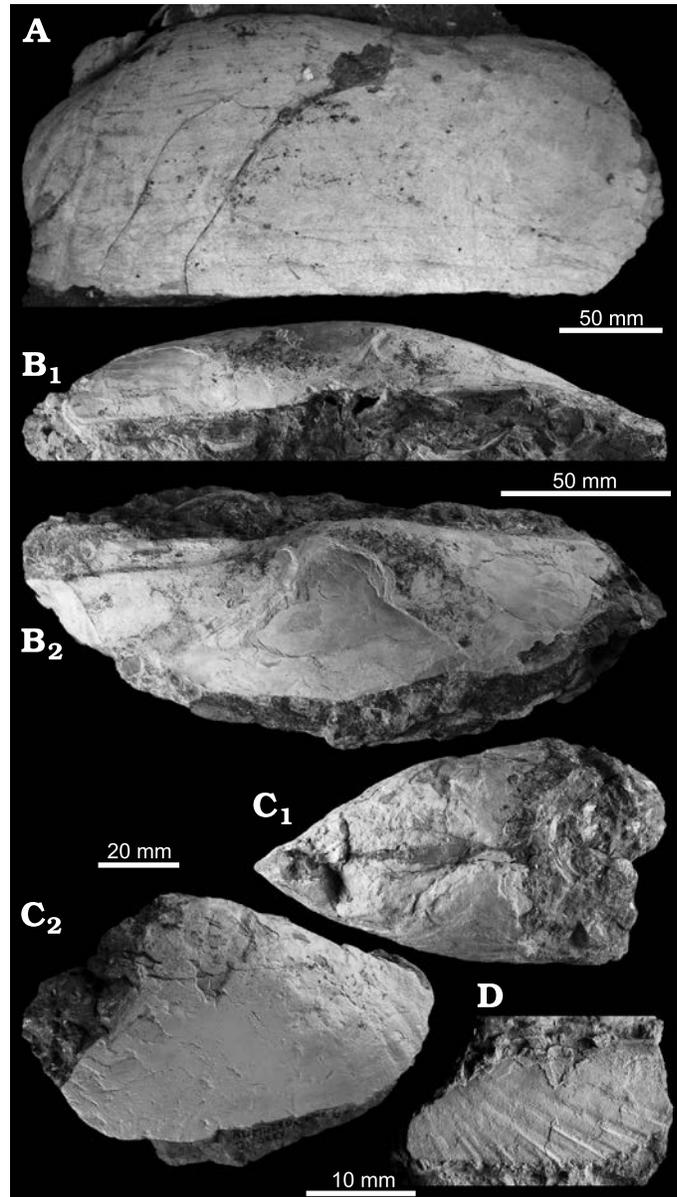


Fig. 2. Solemyid bivalves from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A–C. *Acharax* aff. *bartschii* (Dall, 1908). A. NIGSPAL-003, large RV, view on outer side of shell. B. NRM Mo 192667, large RV in dorsal view (B₁) and view on outer side of LV (B₂). C. NIGSPAL-033, large articulated specimen in dorsal view (C₁) and view on outer side of LV (C₂); note that the specimen is gaping so in dorsal view it appears wider than it is. D. *Acharax* sp. with only the anterior portion preserved (NRM Mo 192660).

Acila (Truncacila) interferencia sp. nov.

Fig. 3.

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Etymology: For the sculpture on the anterior shell portion, where the typical divaricate pattern in *Truncacila* turns into some interference-like pattern.

Type material: Holotype: NIGSPAL-004, articulated specimen with preserved shell material, from block I. Paratype: NRM Mo 192694,

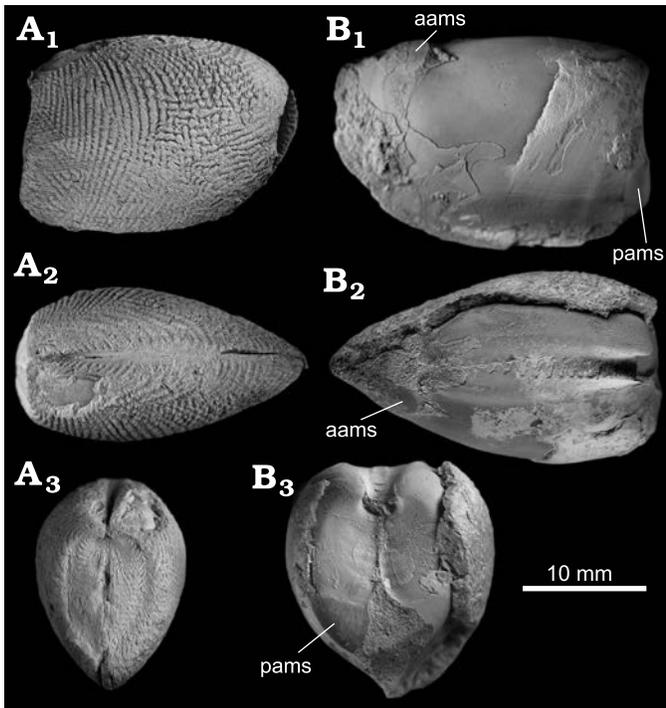


Fig. 3. The nuculid bivalve *Acila (Truncacila) interferencia* sp. nov. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NIGSPAL-004, holotype, an articulated specimen showing external sculpture; view on RV (A₁), dorsal view on anterodorsal margin (A₂) and on posterior margin (A₃). **B.** NRM Mo 192694, paratype, specimen with most of the shell material removed, revealing internal features; view on LV (B₁), dorsal view on anterodorsal margin (B₂) and on posterior margin (B₃). Abbreviations: aams, anterior adductor muscle scar; pams, posterior adductor muscle scar.

articulated specimen with shell partially broken off, from block G from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—Five specimens from block B (NRM Mo 192589–192593), one specimen from block G (paratype NRM Mo 192694), two specimens from block I (holotype NIGSPAL-004, NRM Mo 192659). All from the type locality and horizon.

Dimensions (in mm).—Holotype NIGSPAL-004: L = 23.7, H = 16.0, W = 11.7; NRM Mo 192659: L = 23.4, H = 15.0, W = 12.0; NRM Mo 192592: L = 21.4, H = 13.6; NRM Mo 192694: L = 27.0, H = 15.0, W = 13.0.

Diagnosis.—Average sized shell for the genus; dorsal and ventral margins evenly convex, subparallel; rostral sinus indistinct; escutcheon broad, wide, oval, lunule very narrow; line of primary divarication displaced toward anterodorsal shell margin, divaricate sculpture disintegrates in anteroventral third of shell.

Description.—Shell subquadrate to elliptical; height/length ratio ~0.65, width/height ratio ~0.8. Anterodorsal shell margin evenly convex, anterior margin acutely rounded, ven-

tral margin convex, posterior margin concave; escutcheon broadly oval, with distinct groove and ridge subparallel to margin, ridge with nodular, commarginal ribs, inner part of escutcheon elevated toward ventral side. Line of primary divarication of external sculpture displaced toward anterodorsal shell margin; two secondary lines of bifurcation, one close and subparallel to anterodorsal margin, one posterior at about one third of shell length, divaricate sculpture becomes irregular on anterior third of shell. Anterior adductor muscle scar near anterior end of dorsal margin, nearly round, bounded posteriorly by strong ridge; posterior adductor scar at posterior end of escutcheon, elongate-oval, bounded anteriorly by distinct ridge; pallial line distinct, entire, parallel to ventral shell margin; inner ventral shell margin crenulated. Hinge with up to 20 anterior teeth and nine posterior teeth.

Remarks.—With its elongated shell with nearly parallel dorsal and ventral margins, a very indistinct rostral sinus, and rather unordered sculpture on the anterior half of the shell, this species is quite distinct from other species of *Acila* and *Truncacila*. Similar regarding the elongation is a specimen reported as “*Acila divaricata* (Hinds)” from the Miocene Kabeya Formation in Fukushima prefecture, Japan (Aoki 1954: pl. 1: 17), but that specimen widens anteriorly (rather than narrowing as in *A. [T.] interferencia*) and has a deeper rostral sinus than *A. (T.) interferencia*. The late Oligocene to Early Miocene *Acila vigilia* var. *elongata* Nagao and Huzioka, 1941, from Hokkaido, Japan, has a more distinct and broader escutcheon and a better defined rostrum than *A. (T.) interferencia*, and has finer sculpture without the interference-like pattern (Nagao and Huzioka 1941).

Also similar regarding elongation are several specimens reported as *A. (T.) nehalemensis* Hanna, 1924, from the Eocene Keasey Formation in Oregon (Schenck 1936: pl. 5: 6, 8), and as *A. (T.) conradi* (Meek, 1864) from the Early Miocene Astoria Formation in Oregon and Washington (Schenck 1936: pl. 8: 2, 3, 5–10, 12, 13), but the ribs on the anterior side of these shell radiate in an orderly way toward the shell margin, quite distinct from the granular pattern of *A. (T.) interferencia*. All other species reported by Schenck (1936) are shorter and/or more oval, or have a more distinct posterior projection, and more ordered divaricate sculpture.

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Family Mytilidae Rafinesque, 1815

Genus *Gigantidas* Cosel and Marshall, 2003

Type species: *Gigantidas gladius* Cosel and Marshall, 2003, Recent from the southern Kermadec Ridge in 360–750 m depth.

Gigantidas coseli Saether, Little, Campbell, Marshall, Collins, and Alfaro, 2010b

Fig. 4.

2010 *Gigantidas coseli* sp. nov.; Saether et al. 2010b: 21, figs. 4B, C, 8–10, 17.

2016 *Gigantidas coseli* Saether et al. 2010; Saether et al. 2016: 7, fig. 4.

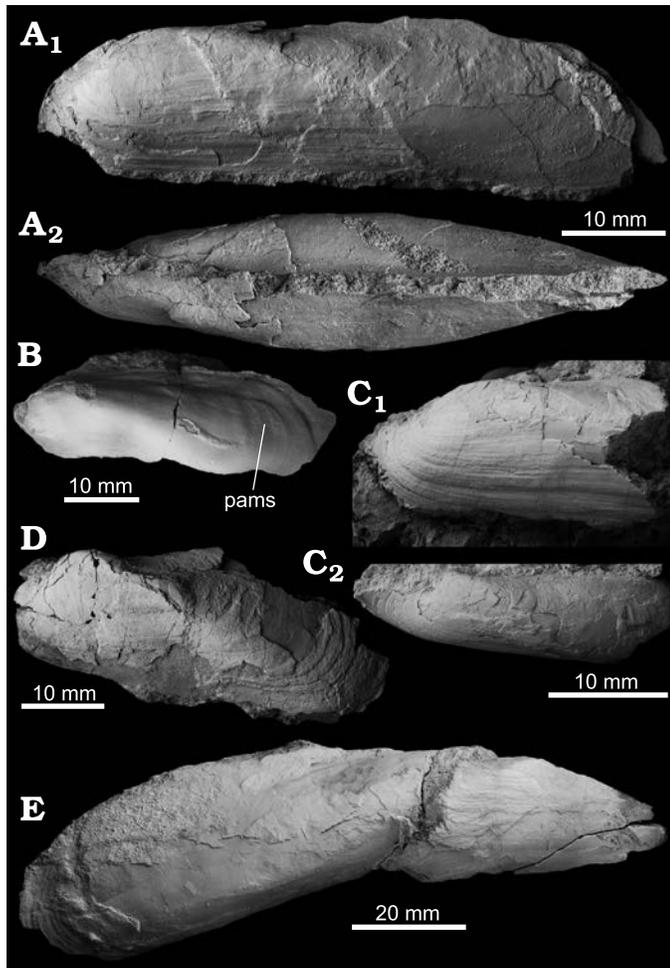


Fig. 4. The bathymodiolin bivalve *Gigantidas coseli* Saether, Little, Campbell, Marshall, Collins, and Alfaro, 2010, from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. NRM Mo 192455, articulated specimen, view on LV (A₁) and dorsal view (A₂). B. NRM Mo 192456, internal mold, view on LV showing posterior adductor muscle scar (pams). C. NRM Mo 192668, isolated LV, view on exterior (C₁) and on dorsal side (C₂). D. NRM Mo 192669, isolated LV, view on exterior. E. NRM Mo 192454, large, articulated, and slightly distorted specimen, view on RV.

Material.—One specimen from block A (NIGSPAL-039), seven specimens from block E (NRM Mo 192454–192462), two specimens from block I (NRM Mo 192668, 192669). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192454, L = 113.0, H = 28.3, W = 27.3; NRM Mo 192455, L = 60.7, H = 16.2, W = 12.4; NRM Mo 192456, L = 43.0, H = 13.8, W (single) = 0.4; NRM Mo 192668, L = 26.0+, H = 12.8, W (single) = 7.6; NRM Mo 192669, L = 45.8, H = 18.4, W (single) = 7.5.

Remarks.—The New Zealand specimens of *Gigantidas coseli* show some variation regarding the expansion of the posterior shell portion, ranging from being almost straight to bending and expanding ventrally (Saether et al. 2010b),

which is also seen among the specimens from the Northern Cement Corporation quarry.

Stratigraphic and geographic range.—Middle Miocene of New Zealand (North Island) and Upper Miocene of Luzon, Philippines.

Genus *Bathymodiolus* Kenk and Wilson, 1985

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

Bathymodiolus labayugensis sp. nov.

Fig. 5.

Zoobank LCID: urn:lsid:zoobank.org:act:5E3EB20E-A4A9-4E9F-BF8E-0295FF7A96BB

Etymology: For the Barangay Labayug, where the Northern Cement Corporation Quarry is located.

Type material: Holotype NIGSPAL-005, isolated LV with shell partially broken off. Paratypes: NRM Mo 192523–192532, mostly isolated valves embedded in rock matrix; all from block B in the type locality.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—65 specimens from block B (NIGSPAL-005, 006, 007, NRM Mo 192472–192533), one specimen from block D (NIGSPAL-008), one specimen from block F (NRM Mo 192541), six fragmentary specimens from block G, five specimens from block I (NRM Mo 192680–192684). All from the type locality and horizon.

Dimensions (in mm).—Holotype NIGSPAL-005: L = 57.5, H = 27.0, W (single) = 10.0; paratypes: NRM Mo 1922523: L = 41.6, H = 22.5; NRM Mo 1922524: 44.5, H = 24.2; NRM Mo 192525: 41.5+, H = 25.0; NRM Mo 192526: L = 42.5, H = 28.3; NRM Mo 192527: L = 42.5, H = 25.8; NRM Mo 192528: L = 33.0, H = 22.4; NRM Mo 192529: L = 37.1, H = 21.7; NRM Mo 192530: L = 45.4, H = 22.0; NRM Mo 192531: L = 30.3, H = 13.8, W = 9.5; NRM Mo 192532: L = 24.5, H = 13.0.

Diagnosis.—Shell small for genus, widening posteriorly; umbo in subterminal position; anterior side broad, evenly rounded, dorsal margin long, gently convex, ventral margin concave; maximum inflation at center of shell.

Description.—Elongate, arched modioliiform shell of medium size (up to 57.5 mm), height/length ratio about 0.45, width/height ratio ~0.8. Surface smooth except for fine growth lines. Blunt ridge running from beak toward posteroventral area; area before ridge depressed, area dorsal to ridge broad and flat. Beak low, prosogyrate, in subterminal position. Anterior margin rounded; ventral margin concave; posterodorsal margin long, convex, continuing into subtruncated posterior margin. Internal groove running from umbones to dorsal side of large, D-shaped posterior adductor muscle scar.

Remarks.—*Bathymodiolus labayugensis* differs from the Miocene *Bathymodiolus heretaunga* Saether, Little, Camp-

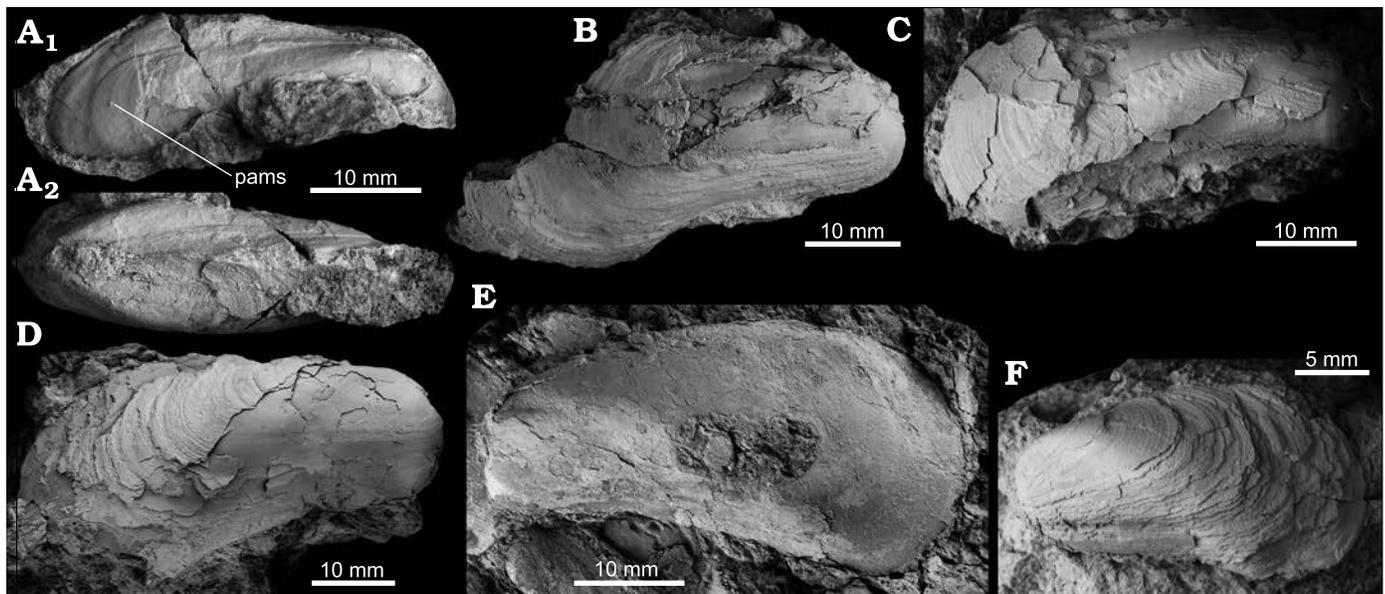


Fig. 5. The bathymodiolin bivalve *Bathymodiolus labayugensis* sp. nov. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. NRM Mo 192681, internal mold showing posterior adductor muscle scar (A₁, pams) and dorsal view showing inflation (A₂). B. NRM Mo 192684, external view of RV. C. NRM Mo 192682, external view of RV. D. NRM Mo 192683, external view of RV. E. NIGSPAL-005, holotype, external view of RV. F. NRM Mo 192532, paratype, external view of RV.

bell, Marshall, Collins, Alfaro, 2010b, from seep deposits in New Zealand by having the umbones in a more anterior position (Saether et al. 2010b). Two fossil *Bathymodiolus* species have been reported from the fossil record of Japan, the Oligocene Japanese “*Bathymodiolus*” *inouei* Amano and Jenkins, 2011 and the Miocene *Bathymodiolus akanudaensis* (Kuroda, 1931); both have a more angular and more anteriorly situated transition from dorsal to posterior margin compared to *B. labayugensis* (Kuroda 1931; Amano et al. 2010; Amano and Jenkins 2011). The Middle to Late Miocene “*Bathymodiolus*” *moroniae* from the “*Calcarei a Lucina*” seep deposits in Italy (Kiel and Taviani 2017) differs from *B. labayugensis* by having a straight dorsal margin, in contrast to the curved one of *B. labayugensis*. The same applies to the Oligocene–Miocene *Bathymodiolus palmarensis* Kiel, Campbell, and Gaillard, 2010, from the Caribbean region (Kiel et al. 2010, Kiel and Hansen 2015).

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Family Thyasiridae Dall, 1901

Genus *Conchocele* Gabb, 1866

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

Conchocele pangasinanensis sp. nov.

Fig. 6A–D.

Zoobank LCID: urn:lsid:zoobank.org:act:157EFA74-F306-45B6-AE7B-CDB71E19469B

Etymology: For the province of Pangasinan, where the Northern Cement Corporation Quarry is located.

Type material: Holotype NIGSPAL-009, isolated RV with preserved hinge; paratype NIGSPAL-011 from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—20 specimens from block B (NIGSPAL-010, 034, NRM Mo 192566–192582, 192588), one specimen from block D (NIGSPAL-035), 2 specimens from block F (NRM Mo 192544–192545), 19 specimens from block G (NIGSPAL-009, NRM Mo 192685–192702), and 4 specimens from the NCC collection (NIGSPAL-036, 037 [3 specimens on one sample]). All from the type locality and horizon.

Dimensions (in mm).—Holotype (NIGSPAL-009): L = 66.0, H = 64.4, W (single) = 22.0; NRM Mo 192544: L = 59.0, H = 59.0, W = 34.4; NRM Mo 192588: L = 61.3, H = 54.5, W = 37.8; paratype (NIGSPAL-011): L = 76.6, H = 63.0, W (single) = 19.7; NIGSPAL-036: L = 77.0+, H = 63.5+, W (single) = 19.7; NIGSPAL-037: L = 68.0, H = 67.2, W (single) = 21.5.

Diagnosis.—Moderate size for genus, well-inflated, outline rounded-quadrate, sharp posterior ridge with wide postero-dorsal area, secondary posterior groove present but indistinct, umbones blunt, strongly prosogyrate.

Description.—Moderately sized, well-inflated shells, W/H ratio 0.58–0.69, rounded-quadrate outline, umbones terminal, blunt, prosogyrate; anterior margin long, concave; anterodorsal area broad, with indistinct internal ridge and groove, bordered by blunt ridge; posterodorsal area wide, bordered by deep sulcus and sharp ridge that form deep indentation at posterior margin, secondary ridge indistinct;

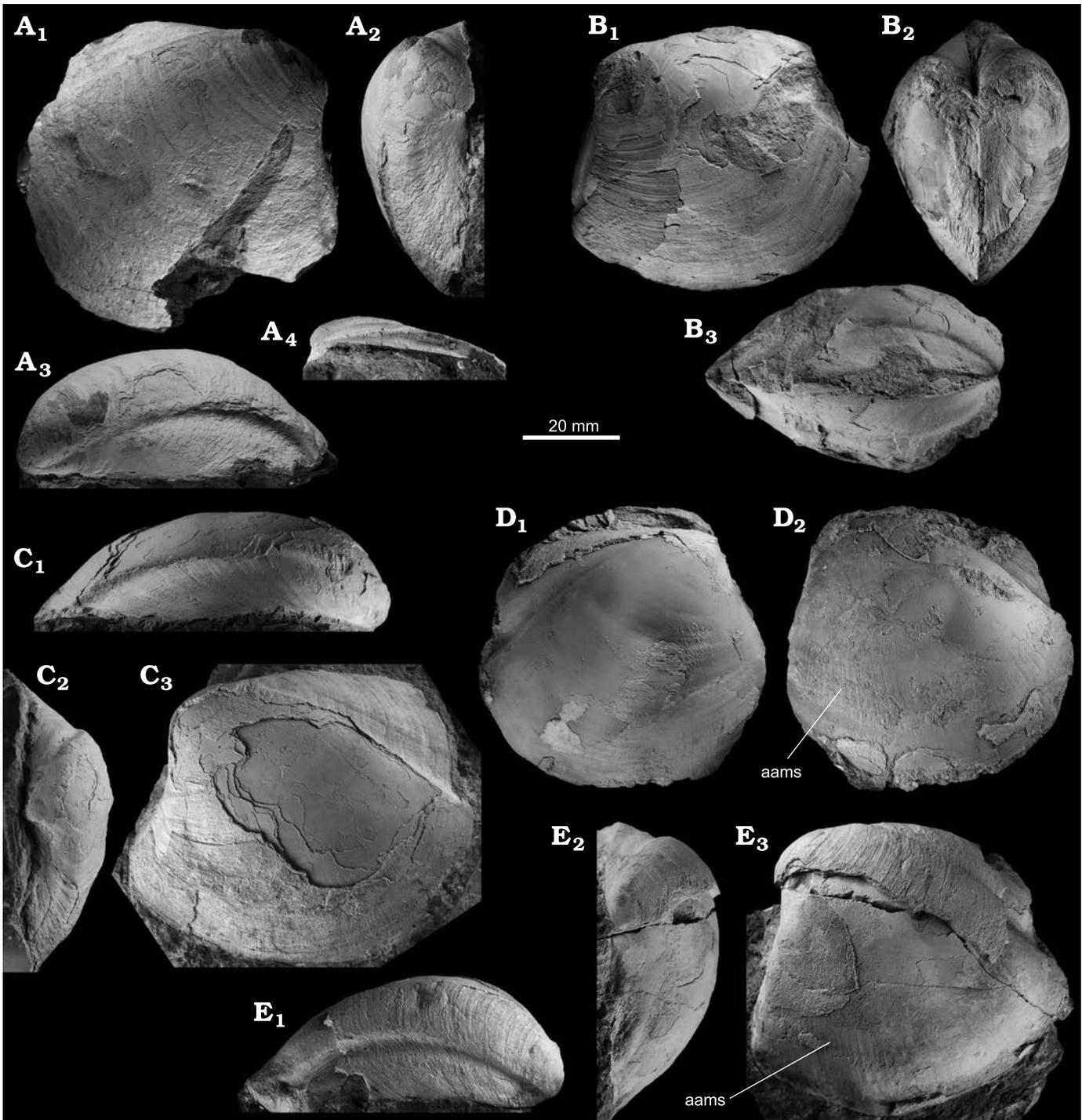


Fig. 6. The thyasirid bivalves *Conchocele* spp. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A–D.** *Conchocele pangasinanensis* sp. nov. **A.** NIGSPAL-009, holotype, isolated RV, view on outer side (A₁), seen from anterior (A₂), dorsal view (A₃) and close-up on hinge and ligament nymph (A₄). **B.** NRM Mo 192588, articulated specimen, view on LV (B₁), seen from anterior (B₂), and dorsal view (B₃). **C.** NIGSPAL-011, paratype, large LV, dorsal view (C₁), seen from anterior (C₂), and lateral view (C₃). **D.** NRM Mo 192544, articulated specimen, view on RV (D₁) and on LV, showing elongated aams (D₂). **E.** *Conchocele* aff. *quadrata* Yabe and Nomura, 1925, NIGSPAL-012, LV, dorsal view (E₁), seen from anterior (E₂), and lateral view showing aams (E₃). Abbreviation: aams, anterior adductor muscle scar.

ventral margin broadly convex, with slight angulation in some specimens, ending posteriorly at posterior sulcus; outer surface with fine, irregular growth lines. Anterior adductor muscle scar narrow, elongate, detached from, and parallel to, pallial line, length about 2/5th of shell length.

Remarks.—Numerous species- and subspecies-level names exist for large, Neogene thyasirids from the western Pacific region, and many specimens have simply been reported as *Conchocele bisecta* (Conrad, 1849) or *C. disjuncta* Gabb, 1866 (Yabe and Nomura 1925; Krishtofovich 1936, 1964;

Squires and Gring 1996; Majima et al. 2005; Hryniewicz et al. 2017). A revision of these names and taxa is pending. Virtually all of these species, however, differ from *Conchocele pangasinanensis* by being more elongate. Species with more rounded-quadrate shape as *Conchocele pangasinanensis* include *Conchocele majimai* Kiel, Aguilar, and Kase, 2020a, and *Conchocele visayaensis* Kiel, Aguilar, and Kase, 2020a, two Plio-Pleistocene species from seep deposits in Leyte of the Philippine islands (Kiel et al. 2020a). *Conchocele pangasinanensis* differs from those two species by its broader umbonal angle (angle between antero- and posterodorsal margins) and its posterodorsal ridge and sulcus do not slope downward as much as in the two species from Leyte. *Conchocele adoccasa* Van Winkle, 1919, from the Middle Miocene of Trinidad and possibly Oligocene seep deposits of Colombia is flatter and has a narrower posterodorsal area than *Conchocele pangasinanensis* (Van Winkle 1919; Gill et al. 2005; Kiel and Hansen 2015).

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Conchocele aff. *quadrata* (Yabe and Nomura, 1925)

Fig. 6E.

Material.—One specimen from the NCC collection (NIGSPAL-012, L = 66.0 mm, H = 62.7 mm, W [single] = 21.8 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—In overall shape, inflation and especially the narrow posterodorsal area, this specimen resembles *Conchocele quadrata* Yabe and Nomura, 1925, from an unknown locality in Japan (Yabe and Nomura 1925: pl. 1: 1) though it differs from the Japanese specimen by its slightly less truncate posterior margin and the more convex ventral margin. A specimen illustrated as *C. quadrata* from the Upper Miocene of Sakhalin Island in eastern Russia (Krishtovich 1964: pl. 53: 1) is more quadrate and has a wider posterodorsal area than both the Japanese and the Philippine specimens.

Family Lucinidae Fleming, 1828

Genus *Megaxinus* Brugnone, 1880

Type species: *Lucina transversa* Bronn, 1831, subsequent designation by Pallary (1904), see Glover and Taylor (1997) for a detailed discussion; Pliocene, Italy.

Megaxinus gorrospei sp. nov.

Fig. 7.

Zoobank LCID: urn:lsid:zoobank.org:act:768EE30D-DE0E-4B20-B6DF-D90B9B0FCC74

Etymology: For Oliver R. Gorrospe, Vice President and General Manager of the Northern Cement Corporation, who aided collections within the quarry.

Type material: Holotype NIGSPAL-015, articulated specimen with most shell material preserved; paratypes: NIGSPAL-013, 014, 016 (all from block A) and NRM Mo 192433 (from block E), small, isolated LV. All from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—Type material only.

Dimensions (in mm).—Holotype (NIGSPAL-015): L = 31.4, H = 35.1, W = 18.1; paratypes: NIGSPAL-013: L = 31.6, H = 28.2, W = 15.5; NIGSPAL-016: L = 38.3, H = 37.2, W = 22.5; NRM Mo 192433: L = 27.8, H = 25.4.

Diagnosis.—Subquadrate to broadly triangular, moderately inflated shell; anterodorsal shell margin straight; no lunule; hinge plate short, moderately broad, edentulous; blunt posterior ridge close to dorsal shell margin, posterodorsal area narrow; anterior adductor muscle scar narrow, elongate, length 2/5 of shell length, close to pallial line.

Description.—Shell of medium size for genus, ontogenetic change in shell shape from subquadrate in smaller specimens to broadly triangular in adults. Posterior ridge more pronounced in adults, close to dorsal margin, corresponding posterodorsal area narrow; surface sculpture of commarginal growth lines only: umbones elevated above hinge line, pointed, prosogyrate; posterodorsal and ventral shell margins convex, anterodorsal margin nearly straight. Lunule large, elongate. Anterior adductor muscle scar elongate, narrow, close and parallel to ventral shell margin, length about 2/5 of shell length; posterior adductor muscle scar just above mid-height of shell, diamond-shaped; pallial line entire, very close to ventral shell margin. Hinge plate broad, short, edentulous, with weak central undulation.

Remarks.—Species of *Megaxinus* show an ontogenetic change in shell shape, from being circular when small, whereas larger shells are higher with a more quadrate anterior (Glover and Taylor 1997: 8). *Megaxinus gorrospei* sp. nov. resembles those more angular, large species of *Megaxinus*, and is hence placed in this genus. The extant genus *Rasta* Taylor and Glover, 2000, includes shells with very similar shell outline and hinge (Taylor and Glover 1997, 2000; Glover and Taylor 1997; Taylor et al. 2005), but *Rasta* species are much less inflated than *Megaxinus gorrospei* and smaller.

Externally, shells of *Megaxinus gorrospei* are very similar to large specimens of *Megaxinus ellipticus* (Borson, 1825) from the Pliocene of Italy (Kiel and Taviani 2018), and its anterior adductor muscle scar (aams) is very close to the pallial line, as in *Megaxinus ellipticus* as illustrated by Sacco (1901: pl. 17: 13) and *M. stironensis* Kiel and Taviani, 2018. In most extant species of *Megaxinus* illustrated by Glover and Taylor (1997), however, the aams appears to deviate from the pallial line at a somewhat larger angle, especially at its ventral end, than in the Miocene Philippine *Megaxinus gorrospei*. Most extant species of *Megaxinus* have a bulge or convexity in the anterodorsal shell margin (Glover and Taylor 1997), absent in *Megaxinus gorrospei*.

Megaxinus gorrospei differs from *Megaxinus ellipticus* by its longer and more acutely rounded posterior part of the

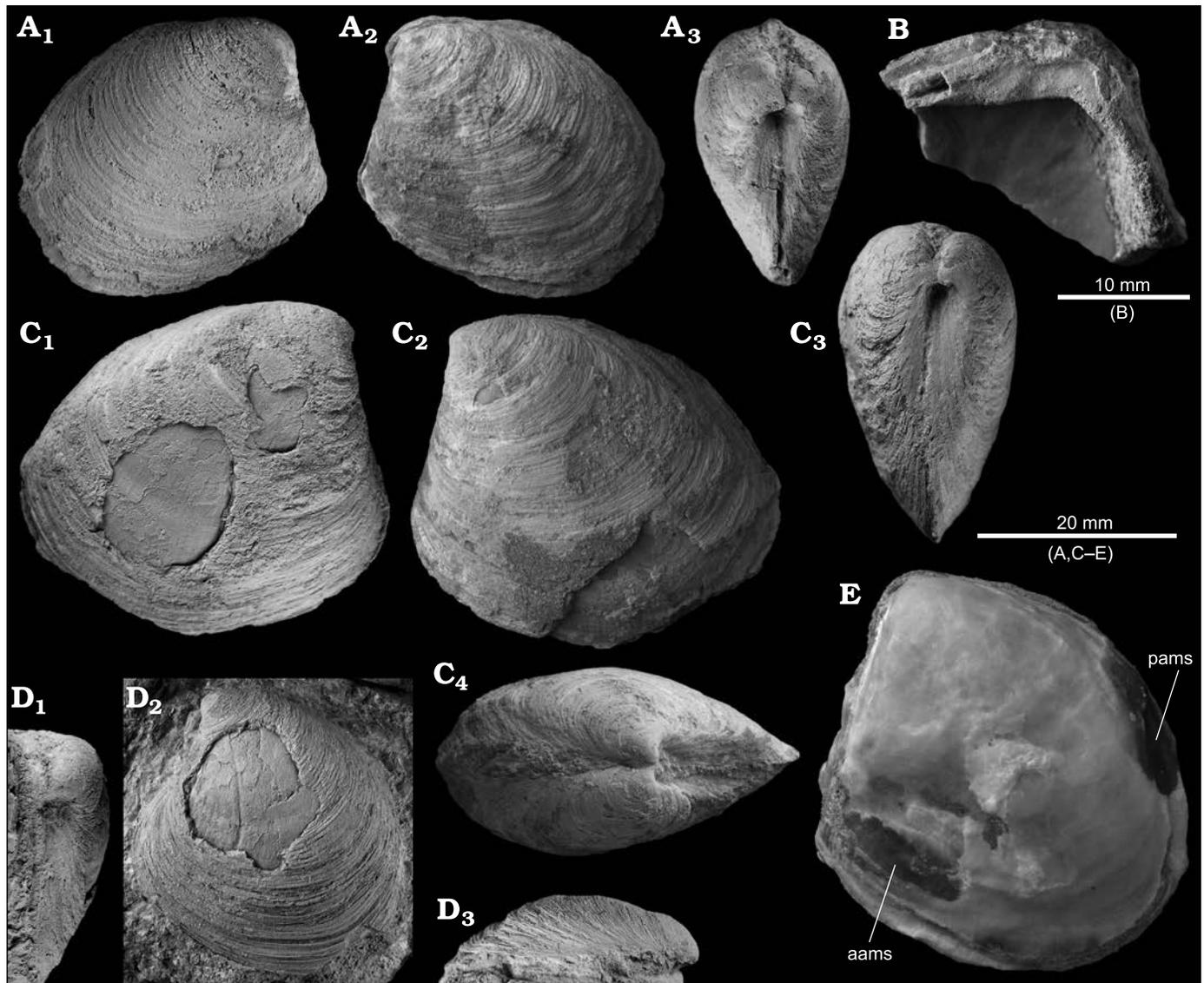


Fig. 7. The lucinid bivalve *Megaxinus gorrospei* sp. nov. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NIGSPAL-013, paratype, articulated, medium-sized specimen, view on RV (A₁), LV (A₂), and anterior margin (A₃). **B.** NIGSPAL-014, paratype, fragment of LV showing the hinge. **C.** NIGSPAL-015, holotype, large, articulated specimen, views on RV (C₁), LV (C₂), anterior margin (C₃), and dorsal margin (C₄). **D.** NRM Mo 192433, paratype, an isolated LV, views on anterior side (D₁), the outer shell (D₂), and the posterodorsal side (D₃). **E.** NIGSPAL-016, paratype, internal mold showing pallial line and adductor muscle scars (aams, anterior adductor muscle scar; pams, posterior adductor muscle scar).

shell, lacking a distinct lunule, and its narrower hinge plate. The Pliocene *Megaxinus stironensis* from Italy has a more roundish outline than *Megaxinus gorrospei*, even at large size, and unlike *Megaxinus gorrospei*, it bears a lunule (Kiel and Taviani 2018).

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Genus *Meganodontia* Bouchet and Cosel, 2004

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

Meganodontia hoernea (Des Moulins, 1868)

Fig. 8.

1868 *Lucina hoernea* sp. nov.; Des Moulins 1898: 368.

2017 *Meganodontia hoernea* (Des Moulins, 1868); Kiel and Taviani 2017: 450, figs. 6, 7.

Material.—Three specimens from block A (NIGSPAL-017–019), 6 specimens from block H (NRM Mo 192403–192409), one from block I (NRM Mo 192661). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192403: L = 87.0, H = 85.0; NRM Mo 192404: L = 80.0, H = 75.5; NRM Mo 192405: L > 100.0; NIGSPAL-017: L = 105.2, H = 103.0, W = 66.6; NIGSPAL-018: L = 90.4, H = 84.4, W = 49.1; NIGSPAL-019: L = 84.1, W = 46.1.

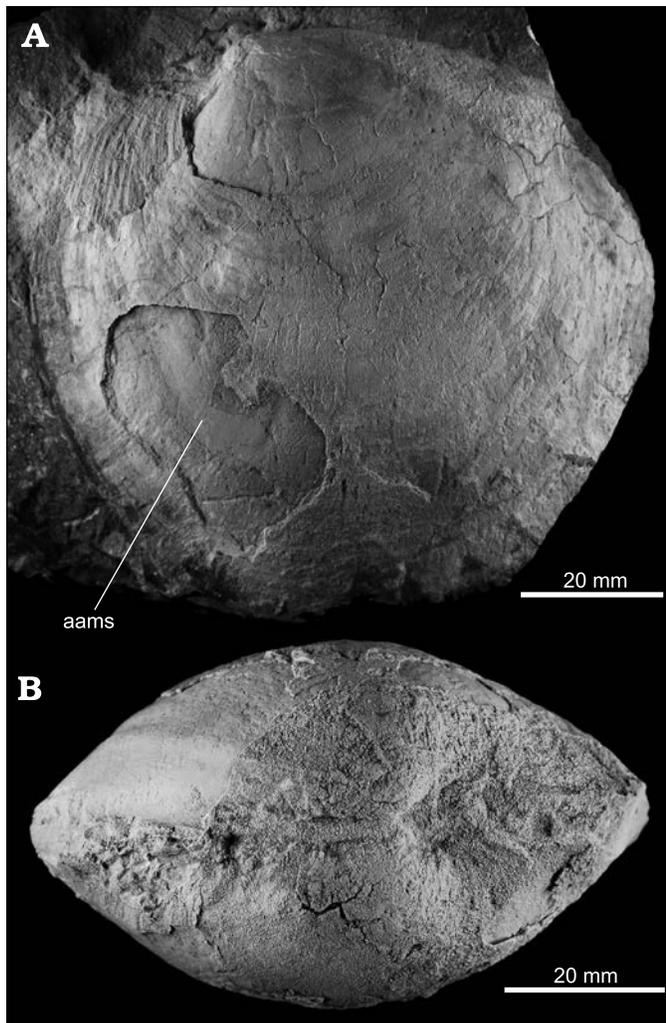


Fig. 8. The lucinid bivalve *Meganodontia hoernea* (Des Moulins, 1868) from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. NRM Mo 192403, isolated LV showing anterior adductor muscle scar (aams). B. NRM Mo 192404, small, articulated specimens in dorsal view.

Remarks.—*Meganodontia hoernea* is widespread and frequent in Middle and Late Miocene-aged seep deposits in northern Italy (Taviani 1994; Kiel and Taviani 2017), and the Late Miocene specimens reported here from the Philippines are virtually identical to well-preserved specimens of *M. hoernea* illustrated in Kiel and Taviani (2017: fig. 7).

The extant and Pleistocene *Meganodontia acetabulum* differs from *M. hoernea* by its more strongly convex posterodorsal margin and narrower posterodorsal area (Bouchet and Cosel 2004; Kiel and Taviani 2017; Kiel et al. 2020a). An Early Miocene *Meganodontia* sp. from Cuba (Kiel and Hansen 2015: fig. 7A–C) is more strongly inflated and has a less distinct posterior sulcus. The medium-sized *M. huanuiensis* Amano, Little, and Campbell, 2018, from Early Miocene seep deposits in New Zealand differs mainly by having a shorter anterior adductor muscle scar (see Amano et al. 2018: fig. 3F₂).

Two large Neogene lucinids described from Taiwan most likely also belong to *Meganodontia*. Among them, the Pliocene *Loripes goliath* Yokoyama, 1928, differs from the Philippine specimens of *Meganodontia hoernea* by having stronger, more elevated umbones (Yokoyama 1928: 86, pl. 9: 8, pl. 10: 1). The same applies to *Loripes pregoliath* Hu and Tseng in Hu, 1995, from the Miocene Nanchuang Formation in Taiwan, which is also smaller ($L = 75.0$ mm vs. $L > 100.0$ mm in the Philippine *M. hoernea*) and more inflated than *M. hoernea* from the Northern Cement Corporation quarry (Hu 1995: 1995–1996, pl. 349: 10, 13; pl. 350: 4, 6, 7).

Stratigraphic and geographic range.—Middle and Upper Miocene strata of Italy and the Philippines.

Genus *Lucinoma* Dall, 1901

Type species: *Lucina filosa* Stimpson, 1851, by original designation; Recent, North Atlantic Ocean.

Lucinoma saetheri Amano, Little, and Campbell, 2018

Fig. 9.

Material.—Two specimens from block A (NIGSPAL-020, 021), three specimens from block B (NRM Mo 192623–192625), one specimen from block E (NRM Mo 192434). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NIGSPAL-020: $L = 44.0$, $H = 43.5$; NIGSPAL-021: $L = 52.1$, $H = 45.1$, $W = 29.0$.

Remarks.—A similar species that should be re-assigned to *Lucinoma* is *Lucina* (*Myrtea*) *butonensis* Beets (1942: pl. 30: 143–146); the anterodorsal margin of *Lucinoma saetheri* is more acutely rounded than in *L. butonensis*.

Stratigraphic and geographic range.—Lower and Middle Miocene of New Zealand (North Island), Upper Miocene of Luzon, Philippines.

Lucinoma acutilineata (Conrad, 1849)

Fig. 10.

1849 *Lucina acutilineata* sp. nov; Conrad 1849: 725, pl. 18: 2.

1962 *Lucinoma acutilineatum* (Conrad): Kamada 1962: 95, pl. 9: 10–16, pl. 10: 1–3.

1963 *Lucinoma acutilineata* (Conrad), Moore 1963: 70, pl. 15: 7–10, 12.

Material.—Four specimens from block A (NIGSPAL-022–024), 1 specimen from block B (NRM Mo 192584), 3 specimens from block E (NRM Mo 192428–192430), 2 specimens from block I (NRM Mo 192634, 192635). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NIGSPAL-023: $L = 49.5$, $H = 49.9$, $W = 22.1$; NIGSPAL-024: $L = 36.2$, $H = 33.3$, $W = 13.4$.

Remarks.—The Miocene specimens of *Lucinoma acutilin-*

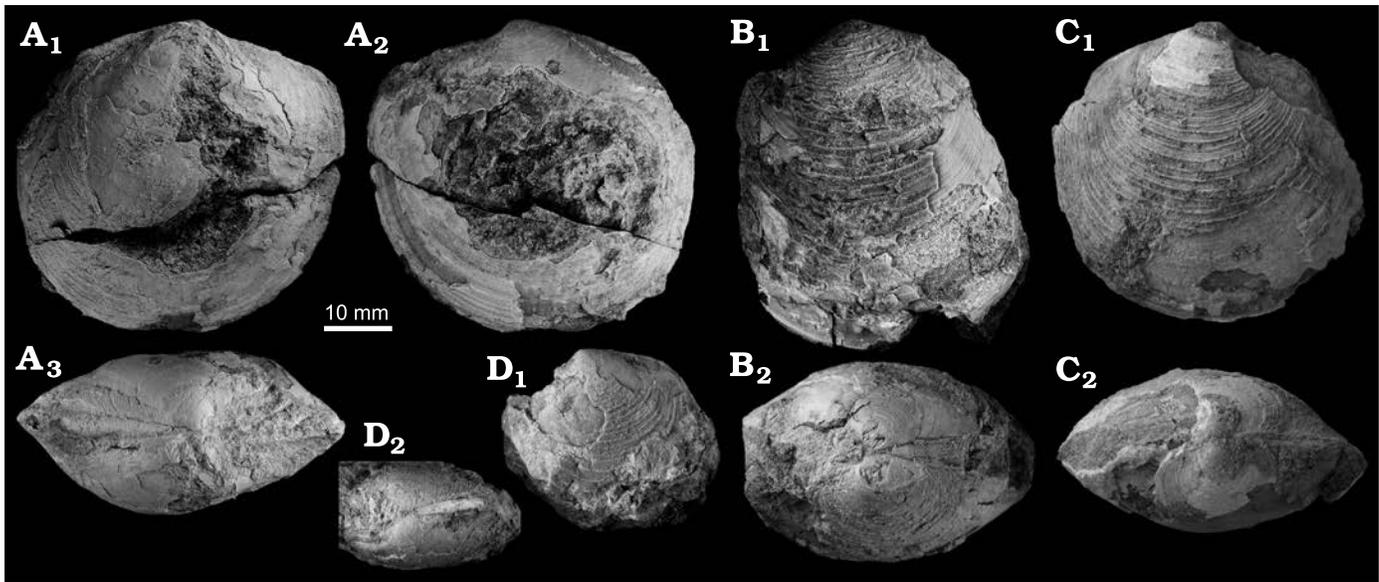


Fig. 9. The lucinid bivalve *Lucinoma saetheri* Amano, Little, and Campbell, 2018, from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NRM Mo 192623, articulated specimen, view RV (A₁), LV (A₂) and on dorsal side (A₃). **B.** NRM Mo 192624, damaged, articulated specimen, view on LV showing fine concentric ribbing (B₁) and on dorsal side showing inflation and ligament (B₂). **C.** NIGSPAL-020, articulated specimen with well-preserved concentric ribs, view on RV (C₁) and on dorsal side (C₂). **D.** NRM Mo 192625, small articulated specimen, view on LV (D₁) and on dorsal side (D₂).

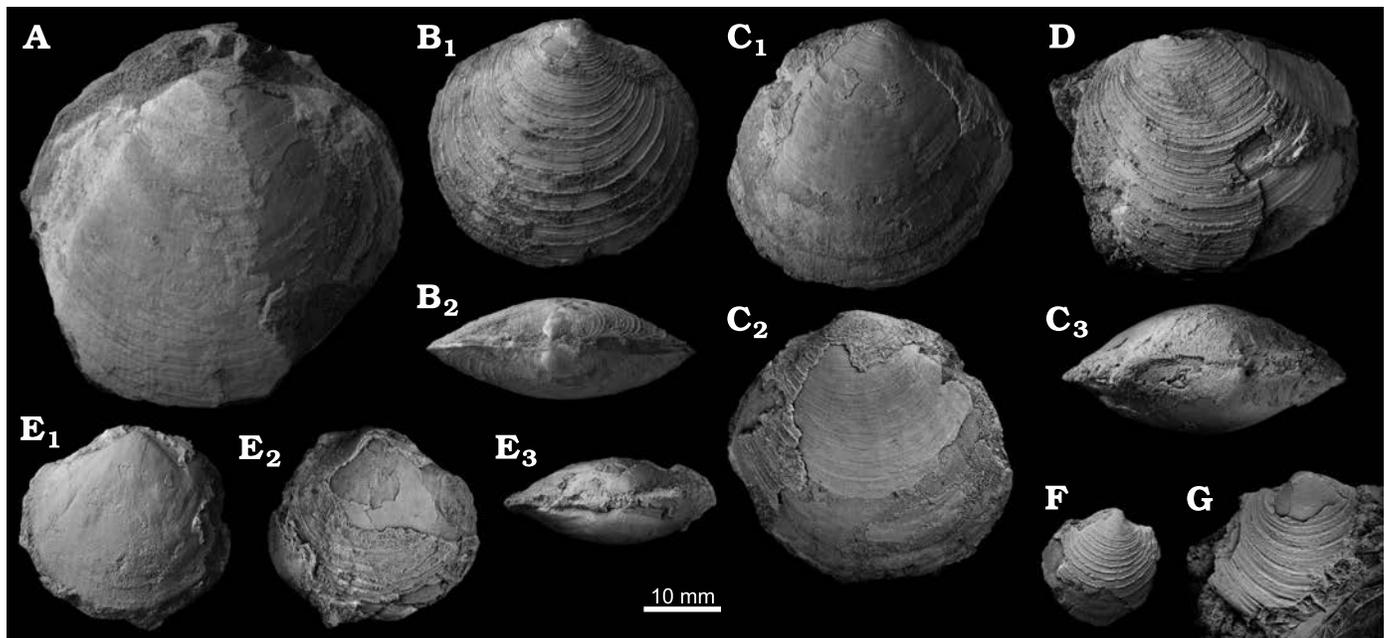


Fig. 10. The lucinid bivalve *Lucinoma acutilineata* (Conrad, 1947) from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NIGSPAL-023, large articulated specimen, view on RV. **B.** NIGAPAL-024, medium-sized, articulated specimen, view on RV showing outline and widely spaced commarginal ribs (B₁), and dorsal view showing inflation, lunule and escutcheon. **C.** NRM Mo 192429, articulated specimen with most shell material detached, showing muscle scars and pallial line, view on RV (C₁), LV (C₂) and on dorsal side (C₃). **D.** NRM Mo 192584, specimen with broken apical portion, view on LV. **E.** NRM Mo 192430, small specimen, RV mostly an internal mold showing muscle scars and pallial line (E₁), LV with preserved shell (E₂), and view on dorsal side showing ligament (E₃). **F.** NRM Mo 192428, small RV showing external sculpture. **G.** NRM Mo 192634, small LV showing external sculpture.

eata from western North America and Japan show a range of outlines from roundish to pentangular shells (Hirayama 1954; Kamada 1962; Moore 1963). The roundish Philippine specimens documented here are quite similar to the holotype, which was re-illustrated in Moore (1963: pl. 15: 9).

Similarly flat *Lucinoma* species from the Neogene of the Philippines include *Lucinoma* aff. *kastoroae* Cosel and Bouchet, 2008, from the Pliocene Liog-Liog Point seep deposit, Leyte, Philippines and *Lucinoma kosatorea* Kiel, Aguilar, and Kase, 2020, from the Pleistocene Cambantug

Point seep deposit, Leyte. Both species have a more acutely rounded anterior shell margin than *L. acutilineata*.

Stratigraphic and geographic range.—Miocene; Philippines, Japan, northwestern North America.

Genus *Elliptiolucina* Cosel and Bouchet, 2008

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

Elliptiolucina sp.

Fig. 11.

Material.—Six specimens from block E (NRM Mo 192466–192471), 2 specimens from block H (NRM Mo 192411–192412), 1 specimen from block I (NRM Mo 192664). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192470: L = 21.0, H = 18.8, W = 9.0; NRM Mo 192469: LV L = 17.2, H = 12.0; NRM Mo

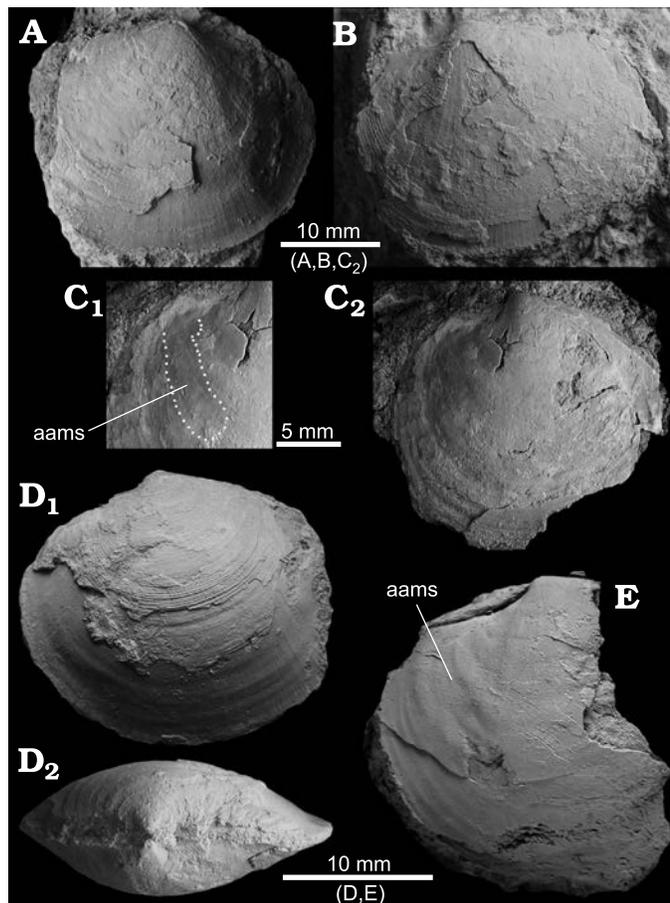


Fig. 11. The lucinid bivalve *Elliptiolucina* sp. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. NRM Mo 192411, small RV. B. NRM Mo 192412, small LV. C. NRM Mo 192412, small LV, showing aams (C₁) and in general view (C₂). D. NRM Mo 192470, larger, articulated specimen, view on LV (D₁) and in dorsal view (D₂). E. NRM Mo 192664, large internal mold of LV. Abbreviation: aams, anterior adductor muscle scar.

192412: LV L = 15.0, H = 14.4; NRM Mo 192411: RV L = 14.3+, H = 11.7; NRM Mo 192664, L = 21.7+, H = 21.8.

Remarks.—Species of *Elliptiolucina* typically have lengths between 70.0 and 140.0 mm (Cosel and Bouchet 2008; Okutani 2011; Kiel 2013; Glover and Taylor 2016; Kiel et al. 2020a). This applies also to the two species of *Elliptiolucina* reported from Pliocene seep deposits in Leyte, Philippines (*E. ingens* Okutani, 2011, and *E. fernandoi* Kiel, Aguilar, and Kase, 2020a), which further differ from the species reported here by having less convex ventral margins (Kiel et al. 2020a). An exception is the Middle Miocene *Elliptiolucina neozelandica* Amano, Little, and Campbell, 2018, which reaches only about 35.0 mm in length, but differs from the species reported here by being more elongated and having a less convex ventral margin (Amano et al. 2018). We consider the small specimens reported here as juveniles and refrain from assigning them to any described or new species.

Family Vesicomidae Dall and Simpson, 1901

Genus *Pliocardia* Woodring, 1925

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

Pliocardia ballesterosi sp. nov.

Fig. 12.

Zoobank LCID: urn:lsid:zoobank.org:act:67677ED9-BF0C-4BD1-B194-A6BFCFC836DF

Etymology: For Alfredo D. Ballesteros, Jr., Sustainable Development and Community Relations Department Head of the Northern Cement Corporation, who aided collecting at the quarry.

Type material: Holotype NIGSPAL-025, isolated RV with preserved shell. Paratypes: NRM Mo 192546–192552, articulated and disarticulated specimens mostly with preserved shell material, from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—Nine specimens from block B (NRM Mo 192613–192618, NIGSPAL-025, 027), 20 specimens from block F (NRM Mo 192546–192565). All from the type locality and horizon.

Dimensions (in mm).—NIGSPAL-025: L = 31.0, H = 24.0, W (single) = 11.0; NRM Mo 192552: L = 32.4, H = 24.7, W = 20.0; NRM Mo 192550: L = 29.7, H = 22.3, W = 16.8; NRM Mo 192546: L = 30.0, H = 2.1, W (single) = 8.0; NRM Mo 192551: L = 35.0, H = 25.7, W (single) = 10.0; NRM Mo 192547: L = 30.6, H = 25.2, W (single) = 7.8; NIGSPAL-026: L = 26.1, H = 20.1, W = 16.0.

Diagnosis.—Large, well inflated, oval to subquadrate shell, posterodorsal sulcus poorly developed; blunt, elevated, prosogyrate umbones in very anterior position; lunular incision well-defined; small, shallow pallial sinus.

Description.—Shell large compared to the type species of *Pliocardia*, but small compared to members of the “*cordata*

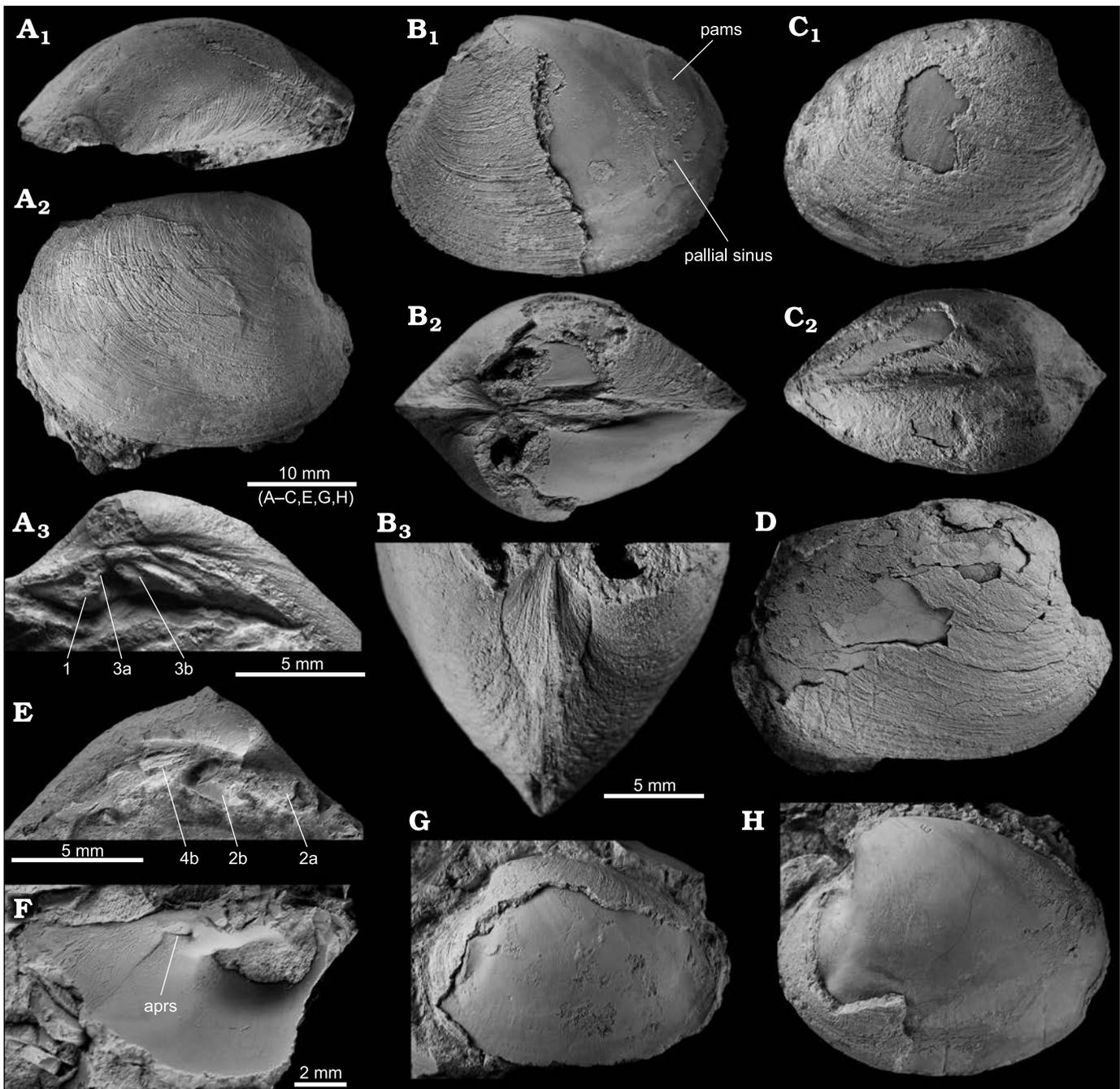


Fig. 12. The vesicomyid bivalve *Pliocardia ballesterosi* sp. nov. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NIGSPAL-025, holotype, an isolated RV with preserved hinge, in apical view showing lunular incision (A₁), view on outer shell showing sculpture and outline (A₂), and close-up on hinge with cardinal teeth numbers indicated (A₃). **B.** NRM Mo 192552, paratype, articulated specimen with partially removed shell, view on LV showing pallial sinus and pams (B₁), in apical view showing strong inflation (B₂), close-up on anterior side showing lunular incision (B₃). **C.** NRM Mo 192550, paratype, articulated shell with only moderate inflation, view on RV (C₁) and apical view (C₂). **D.** NRM Mo 192549, paratype, outer side of large RV. **E.** NRM Mo 192546, paratype, hinge of LV with cardinal teeth numbers indicated. **F.** NRM Mo 192548, paratype, fragment of interior of RV showing anterior muscle scars. **G.** NRM Mo 192551, paratype, isolated LV showing pallial line. **H.** NRM Mo 192547, paratype, large, isolated LV showing pallial line. Abbreviations: aprs, anterior pedal retractor scar; pams, posterior adductor muscle scar.

group”, reaching 32.4 mm in length; outline oval to subquadrate, posterior margin subtruncated to acutely rounded, ventral and posterodorsal margin convex, anterior margin narrow, more-or-less acutely rounded; posterior ridge and groove poorly developed on most specimens; lunular incision deep, outline broadly lenticular; escutcheon narrow,

poorly defined; no external sculpture except for numerous fine growth increments. Hinge plate moderately broad, rather short, three cardinal teeth in each valve; in RV, cardinal strong, pointing anteroventrally, cardinal 3a short, parallel to shell margin, 3b elongate, bifurcated, raised edges, subparallel to shell margin, posterior edge about three time

the length as anterior edge; in LV, cardinal 2a strong, pointing anteriorly, cardinal 2b blunt, broadly trapezoid, with two short raised edges, cardinal 4b moderately long, parallel to shell margin. Anterior adductor muscle scar oval, with narrow connection to small pedal retractor scar; posterior adductor muscle scar round to slightly oval, distinct but not deep; pallial line entire, with shallow pallial sinus.

Remarks.—Most similar to *P. ballesterosi* in overall shell shape is the extant *Pliocardia kuroshimana* Okutani, Fujikura, and Kojima, 2000, which occurs also in a Pleistocene seep deposit in the central Philippines (Kiel et al. 2000). *Pliocardia ballesterosi* differs from *P. kuroshimana* mainly by its smaller and less elevated umbones, with *P. kuroshimana* having the point of maximum inflation in the shell's center whereas it is displaced toward the anterior in *P. ballesterosi*, and by having a narrower but longer ligament nymph. Another similar species is "*Pliocardia*" *ticaonica* Dall, 1908a, extant off Ticao island (central Philippines) and also found in the early Pleistocene Cambantug Point seep deposit in Leyte, Philippines (Kiel et al. 2020a). *Pliocardia ballesterosi* differs from "*P.*" *ticaonica* by having distinct lunular incision, which is only very indistinct in "*P.*" *ticaonica*, by its slightly less prosogyrate and prominent umbones, and by having a less distinct posterodorsal ridge than "*P.*" *ticaonica*.

The Early to Middle Miocene *Pliocardia kawadai* (Aoki, 1954) from Japan has a deeper posterior groove and associated wider posterodorsal area, and its pallial sinus reaches up to the anterior margin of the posterior adductor muscle scar (see Amano and Kiel 2012: figs. 7 and 12), whereas in *Pliocardia ballesterosi* the pallial sinus is entirely below the posterior muscle scar, and the pallial line reaches the scar on its ventral side. The Middle Miocene *Pliocardia?* *tanakai* Miyajima, Nobuhara, and Koike, 2017, from Japan differs from *P. ballesterosi* by its more elongate-oval shell outline, smaller and more pointed umbones. *Pliocardia?* *tanakai* is also less inflated and thus has a narrower and more elongate lunular area, and lacks a pallial sinus (Miyajima et al. 2017).

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Genus *Archivesica* Dall, 1908

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

Remarks.—*Archivesica* is used here in the sense of Amano and Kiel (2010) and Amano et al. (2019a); in molecular studies, this genus is often referred to as "*gigas/kilmeri* complex" or "*gigas* group" (Audzijonyte et al. 2012; Valdés et al. 2013; Johnson et al. 2017).

Archivesica? sp. 1

Fig. 13.

Material.—One specimen from block B (NIGSPAL-029), 17 specimens from block C (NIGSPAL-028), 3 specimens from block E (NRM Mo 192418–192420), 3 specimens from block I (NRM Mo 192670–192672). Upper Miocene of the

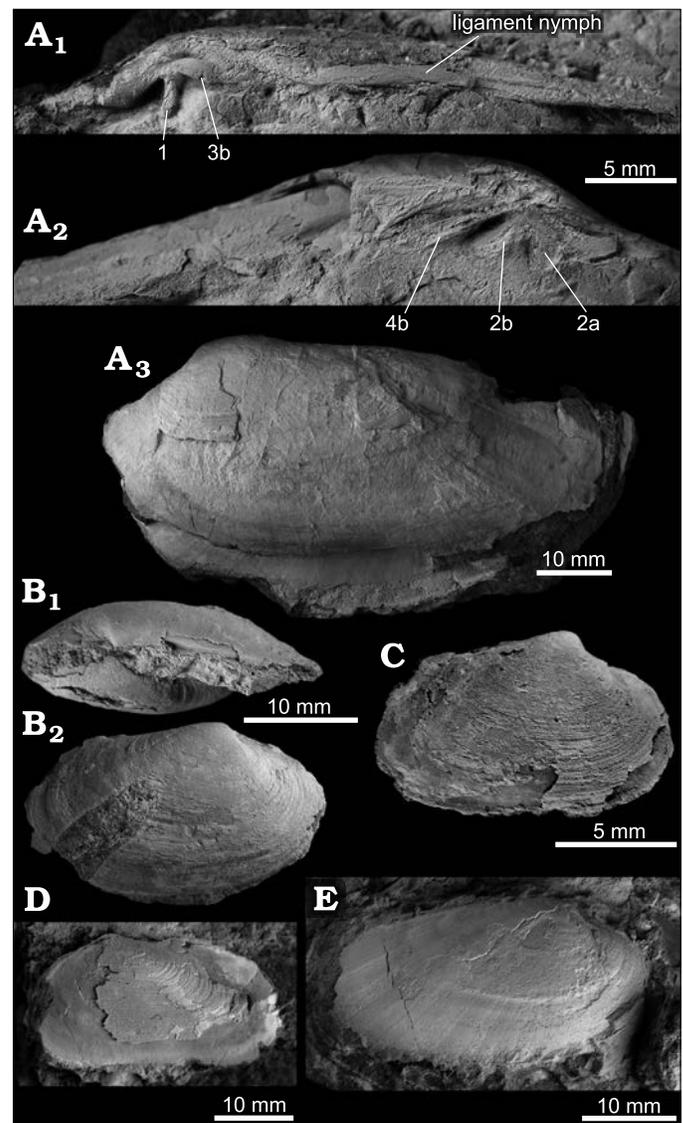


Fig. 13. The vesicomyid bivalve *Archivesica?* sp. 1 from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NRM Mo 192671, views on hinges of RV (**A₁**) and LV (**A₂**), cardinal teeth numbers indicated; and view on outer side of LV showing interior radial striations (**A₃**). **B.** NRM Mo 192418, small, articulated specimen, in dorsal view showing absence of lunule or lunular incision (**B₁**), and view on RV (**B₂**). **C.** NRM Mo 192419, very small specimen showing pallial line and posterior adductor muscle scar. **D.** NRM Mo 192672, small, isolated LV. **E.** NRM Mo 192670, medium-sized, isolated RV showing internal radial striation.

"shale quarry" within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192670: L = 34.5, H = 18.7; NRM Mo 192671: L = 68.3, H = 38.4; NRM Mo 192672: L = 16.5, H = 9.3.

Description.—Elongate, oval shell, umbones positioned at anterior 20% of shell; external surface smooth, internal surface with radial striation; hinge plate short, moderately broad; RV hinge with two radiating, strong cardinal teeth, cardinal 1 pointing downward, cardinal 3b pointing poster-

orly; LV hinge with three radiating, strong cardinals, 2a and 2b at almost right angles to each other, 4b short, subparallel to dorsal margin.

Remarks.—These specimens have the general outline of other elongate, fossil *Archivesica*, and also the hinge dentition resembles that of other *Archivesica* species. However, they are only hesitantly assigned to *Archivesica* because the available material does not show the taxonomically important pallial sinus. The internal radial striation seen on some of the specimens is uncommon among vesicomysids, but has for example been documented from the elongate, extant West African vesicomysid *Christineconcha regab* (Cosel and Olu, 2009) (Krylova and Cosel 2011).

Archivesica? sp. 2

Fig. 14.

Material.—Four specimens from block I (NRM Mo 192676–192679). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192676: L = 51.8, H = 43.2, W = 23.0; NRM Mo 192677: L = 50.6, H = 41.0, W = 24.1; NRM Mo 192678: L = 38.2, H = 31.4, W = 13.7; NRM Mo 192679: L = 17.2, H = 12.3, W = 7.2.

Description.—Short, oval shell, umbones elevated, proogyrate, positioned at anterior 27–31% of total shell length; anterior margin acutely rounded, posterior margin wide, broadly rounded. External surface with fine growth increments, internal surface with radial striation; no lunular incision; hinge plate narrow, RV with three thick, short cardinal teeth: cardinal 1 displaced anteriorly, 3a just anterior to beak, pointing anteriorly, 3b just posterior to beak, pointing posteriorly; no subumbonal pit.

Remarks.—These specimens show an unusual combination of shell characters. The overall shape (short, oval, little inflation) resembles that of species of *Wareniconcha* or *Calyptogena* (see Krylova and Sahling 2006; Cosel and Olu 2009). But the hinge with its strong, thick, radiating teeth is very similar to those of *Archivesica nankaiensis* (Okutani, Kojima, and Ashi, 1996), *A. soyoae* (Okutani, 1957), *A. solidissima* (Okutani, Hashimoto, and Fujikura, 1992a) and *A. okutanii* (Kojima and Ohta, 1997), all of which, however, are much more elongated and inflated (Okutani 1957; Okutani et al. 1992a; Kojima and Ohta 1997; Okutani et al. 1997; Sasaki et al. 2005). Furthermore, species of *Archivesica* possess a subumbonal pit, lacking in the present specimens. Therefore, we only hesitantly assign this species to *Archivesica*.

Genus *Wareniconcha* Cosel and Olu, 2009

Type species: *Vesicomys guineensis* Thiele in Thiele and Jaekel, 1931, by original designation; Recent, central eastern Atlantic Ocean.

Wareniconcha sp.

Fig. 15.

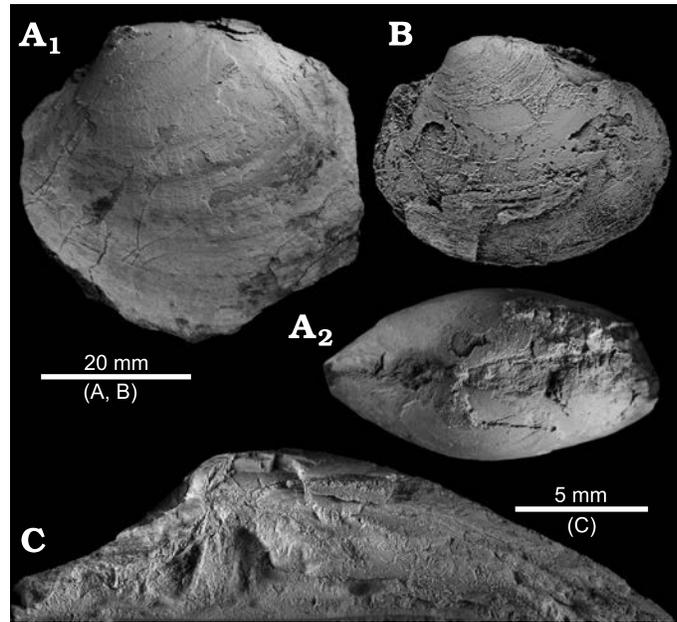


Fig. 14. The vesicomysid bivalve *Archivesica?* sp. 2 from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NRM Mo 192676, large articulated specimen, view on LV showing interior posterior ridge (A₁), dorsal view showing moderate inflation and lunule (A₂). **B.** NRM Mo 192678, articulated specimen, view on LV showing general outline. **C.** NRM Mo 192677, isolated RV, view on hinge.

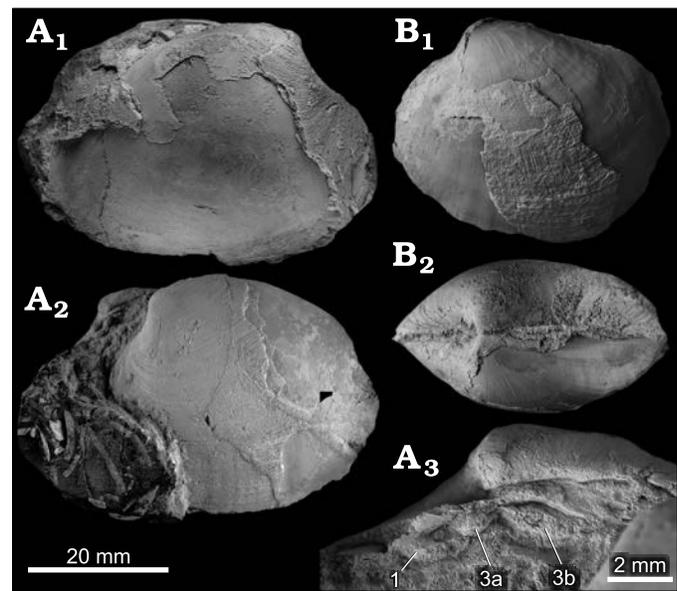


Fig. 15. The vesicomysid bivalve *Wareniconcha* sp. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** NRM Mo 192537, large, slightly disarticulated specimen, view on RV (A₁), view on LV and RV hinge plate (A₂), and close-up on RV hinge with cardinal teeth numbers indicated (A₃). **B.** NRM Mo 192538, articulated, medium-sized specimen, view on LV (B₁) and on dorsal side showing inflation and lack of lunular incision (B₂).

Material.—Three specimens from block F (NRM Mo 192537–192539). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192539: L = 49.0, H = 34.0, W (single) = 13.0; NRM Mo 192538: L = 40.0, H = 33.0, W = 22.0; NRM Mo 192537: L = 44.0+, H = 41.0, W (single) = 15.0.

Description.—Medium-sized, moderately inflated, oval shell; umbones elevated, prosogyrate; blunt posterior ridge creating broad posterodorsal area, no escutcheon and lunule; hinge plate narrow, RV with three thick cardinal teeth arranged more-or-less parallel to dorsal shell margin.

Remarks.—The available specimens are too poorly preserved for species-level identification.

Vesicomysidae gen. et sp. indet. 1

Fig. 16A.

Material.—15 specimens from block E (NRM Mo 192438–192453), many specimens on a rock sample from the NCC collection. Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192439: L = 15.6, H = 13.0, W = 8.9; NRM Mo 192440: L = 20.8, H = 15.7; NRM Mo 192442: L = 23.2, H = 19.4; NRM Mo 192444: L = 22.3, H = 17.3, W = 12.4; NRM Mo 192446: L = 20.0, H = 14.6, W = 11.3.

Remarks.—This locally very abundant, small-sized vesicomysid defies a more precise classification because the available material does not show internal characters such as hinge, muscle scars and pallial line. It is smaller and more elongate than *Pliocardia ballesterosi*. Its overall shell outline is similar to that of *Isorropodon* cf. *perplexum* Sturany, 1896, from Pliocene seep deposits in Leyte Island, Philippines (Kiel et al. 2020a), but that species lacks a lunular incision, clearly visible in vesicomysid sp. 1 reported here.

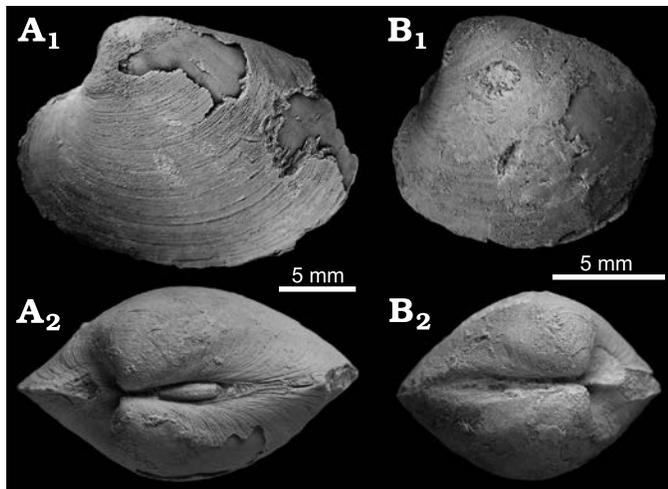


Fig. 16. Small vesicomysid bivalves from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. Vesicomysidae gen. et sp. indet. 1, NRM Mo 192444, articulated specimen, view on LV (A₁) and view on dorsal side showing lunular incision and ligament (A₂). B. Vesicomysidae gen. et sp. indet. 2, NRM Mo 192426, articulated specimen, view on LV (B₁) and view on dorsal side showing lunular incision and escutcheon (B₂).

Vesicomysidae gen. et sp. indet. 2

Fig. 16B.

Material.—Seven specimens from block E (NRM Mo 192422–192427, 192435). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192424: L = 11.7, H = 9.5; NRM Mo 192425: L = 14.7, H = 12.0; NRM Mo 192426: L = 10.8, H = 9.8, W = 7.0; NRM Mo 192427: L = 11.8, H = 10.8, W = 8.3; NRM Mo 192435: L = 10.2, H = 8.4.

Remarks.—This small species is shorter and more inflated than vesicomysid sp. 1 reported above. It resembles the smaller of the specimens reported as *Vesicomysa margotae* Beets, 1953, from the Pliocene of Leyte Island, Philippines (Kiel et al. 2020a: fig. 18A), and is also similar to *Vesicomysa nakaii* Okutani, 1962, for example as illustrated from the Pliocene of Leyte Island, Philippines (Kiel et al. 2020a: fig. 19A). But as internal characters cannot be assessed, we prefer to keep these specimens in open nomenclature.

Family uncertain

Genus *Sisonia* nov.

Type species: *Sisonia frijellanae* sp. nov., see below.

Species included: Possibly belonging to *Sisonia* are three specimens identified as “Solemyidae gen. indet.” from the Miocene Moonlight North seep deposit in New Zealand (Saether et al. 2016: fig. 3B). The figured specimen shows a similar overall outline and muscle scar pattern, though it is much less inflated than *Sisonia frijellanae*. Further specimens most likely belonging to *Sisonia* have been found in a Pleistocene seep deposit in Taiwan (SK unpublished data).

Etymology: For the Municipality of Sison, where the type locality is located in Pangasinan province.

Diagnosis.—As for the type species.

Remarks.—This genus is difficult to place among the heterodont bivalves. Its overall outline and hinge resembles some vesicomysids, though the strong posterior inflation is uncommon in that family. The most distinctive difference of *Sisonia frijellanae* from vesicomysids is the rather indistinct and elongate, pear-shaped anterior adductor muscle scar. Vesicomysids of this size typically have a distinct, deeply impressed anterior adductor muscle scar bound by a strong ridge on the posterior side. Trapeziidae have a somewhat similar outline and also lack a pallial sinus, but their umbones is more prosogyrate, and they possess posterior lateral teeth, absent in *Sisonia frijellanae*. Remarkably similar shell shapes, both internally and externally, can be found among the galeommatoids (Morton and Scott 1989), for example the lasaeid *Neaeromya rugifera* (Carpenter, 1864) or *Bornia sebetia* (Costa, 1830). However, galeommatoids rarely reach sizes beyond 10.0 mm and are thus much smaller than the almost 70.0 mm long *Sisonia frijellanae*. Interestingly, at least one galeommatoid species, the saxicavellin *Atopomya dolobrata* Oliver, 2013, harbors symbiotic bacteria in its gills (Oliver 2013).

Sisonia frijellanae sp. nov.

Fig. 17.

Zoobank LCID: urn:lsid:zoobank.org:act:08086988-4440-4724-B293-0C12A48F2B82

Etymology: For Myra Vanessa A. Frijellana, Environmental Health and Safety Staff of the Northern Cement Corporation, who aided collecting at the quarry.

Type material: Holotype NIGSPAL-030, articulated specimen with exposed RV hinge. Paratypes: NRM Mo 192594–192596, 192598 (block B), NRM Mo 192707 (block G), NRM Mo 192673, 192674 (block I), articulated specimen with partially preserved shell, from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—25 specimens from block B (NIGSPAL-031 [for a lot of 8 specimens]; NRM Mo 192594–192599, 192601–192611), 14 specimens from block G (NRM Mo 192703–192714), 3 specimens from block I (NRM Mo 192673–192675), one specimen from block J (NRM Mo 192536). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NIGSPAL-030: L = 39.6, H = 25.6, W = 20.7; NRM Mo 192595: L = 37.4, H = 24.7, W = 19.0; NRM Mo 192707: L = 32.4, H = 22.4, W = 13.5; NRM Mo 192674: L = 68.7, H = 40.0, W = 31.8; NRM Mo 192673: L = 48.5, H = 31.3, W (single) = 10.5.

Diagnosis.—Shell trapezoid to short modioliform in outline, strongly inflated, umbones in anterior third of shell, slightly elevated above hinge line, nearly orthogyrate; blunt ridges running from umbo to antero- and posterodorsal margins, area in between depressed; no lunule or escutcheon, ligament external; sculpture of fine growth increments only, internally with radiating striations; adductor muscle scars indistinct, pallial line entire, apparently no sinus; hinge with two strong, radiating cardinals in each valve.

Description.—Shell reaching 68.7 mm in length, strongly inflated, widest in posterior third of shell, outline short modioliform, dorsal and ventral margins subparallel, posterior margin truncate, anterior margin rounded to acutely rounded; ventral margin concave. Umbones broad, slightly elevated above hinge line, in anterior third of shell; ridge from umbo to posteroventral corner broad but distinct, ridge from umbo to anteroventral corner broad, indistinct; area between ridges deeply depressed, causing concavity of ventral margin; no sculpture except fine growth increments. Ligament short, resting on deeply incised nymphs; no lunule and escutcheon. Anterior adductor muscle scar indistinct, elongated pear-shaped, broadening ventrally, situated about midline of shell; pallial line starting just posterior of its ventral base; pallial line faintly impressed, moderately distant from shell margin, undulating, entire, apparently no sinus; anterior pedal retractor scar elongate, connected to adductor scar; poste-

rior adductor muscle scar indistinct, shaped like an inverted comma, situated dorsally to groove running from umbo to posterior side of shell. Hinge plate narrow, subumbonal pit and two strong, short, radiating cardinals in each valve, RV with cardinal 1 and 3b, 3a apparently reduced, LV with cardinal 2a and 2b, cardinal 4 may be reduced.

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Class Gastropoda Cuvier, 1795

Unidentified limpet gastropod

Fig. 18A, B.

Material.—One poorly preserved specimen from block B (NRM Mo 192585), 1 specimen from block F (NRM Mo 192421), 1 specimen from block G (NRM Mo 192715), 1 large specimen from block I (NRM Mo 192656). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192421: L = 9.0, W = 7.5, H = 4.6; NRM Mo 192715: L = 6.2, W = 4.5, H = 2.5; NRM Mo 192656: L = 15.2, W = 11.8, H = 7.5.

Remarks.—Shape and the cancellate ornament of these specimens are very similar to species typically assigned to *Bathyaemaea* (Okutani et al. 1992b; Jenkins et al. 2007a; Chen et al. 2019).

Order Neomphalina McLean, 1981

Family Neomphalidae McLean, 1981

Genus *Retiskenea* Warén and Bouchet, 2001

Type species: *Retiskenea diploura* Warén and Bouchet, 2001, by original designation; Recent, North Pacific Ocean.

Retiskenea sp.

Fig. 18C.

Material.—One specimen from block F (NRM Mo 192540, W = 1.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—The single small specimen is embedded in matrix, blocking the view on the aperture and hence not allowing an identification to species level.

Order Seguenziida Haszprunar, 1986

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 sp.

Fig. 18D, E.

Material.—One specimen from block F (NRM Mo 192543), 2 specimens from block I (NRM Mo 192665, 192666).

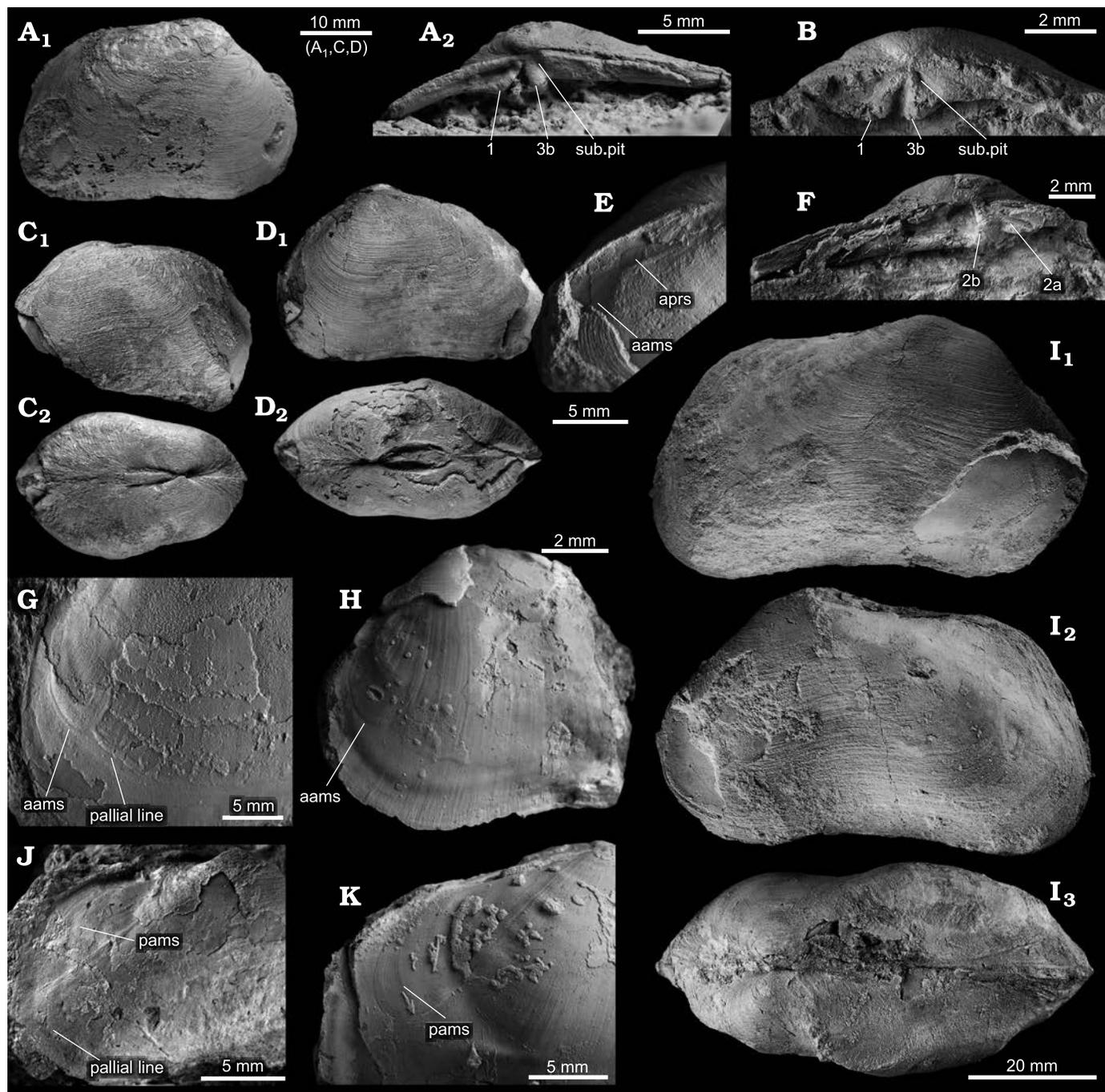


Fig. 17. The bivalve *Sisonia frijellanae* gen. et sp. nov. from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. A. NIGSPAL-030, holotype, articulated specimen with exposed RV hinge; view on exterior of RV (A₁), close-up on hinge of RV (A₂). B. NRM Mo 192594, hinge of isolated right valve. C. NRM Mo 192707, articulated specimen with ventral side missing, view on left valve (C₁) and dorsal view showing inflation and short ligament (C₂). D. NRM Mo 192595, paratype, articulated specimen, view on left valve (D₁) and dorsal view (D₂). E. NRM Mo 192596, paratype, close-up on anterior side of left valve of an articulated specimen, showing aams and aprs. F. NRM Mo 192598, paratype, hinge of isolated left valve. G. NRM Mo 192673, close-up on anterior side of isolated internal mold of left valve, showing aams and pallial line. H. NRM Mo 192596, paratype, close-up on anterior side of isolated internal mold of left valve, showing aams and internal, radial striation. I. NRM Mo 192674, paratype, very large specimen with mostly intact shell, views on right valve (I₁), left valve (I₂) and on dorsal side showing median sulcus and posterior ridge (I₃). J. NRM Mo 192703, close-up on posterior side of RV showing pams and pallial line. K. NRM Mo 192704, close-up on posterior side of RV showing pams. Abbreviations: aams, anterior adductor muscle scar; aprs, anterior pedal retractor scar; pams, posterior adductor muscle scar; sub.pit, subumbonal pit; cardinal teeth numbers indicated in images A₂, B and F.

Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192543: H = 11.5, W = 10.0; NRM Mo 192665: W = 13.0, H = 11.6; NRM Mo 192666: W = 10.7, H = 9.5.

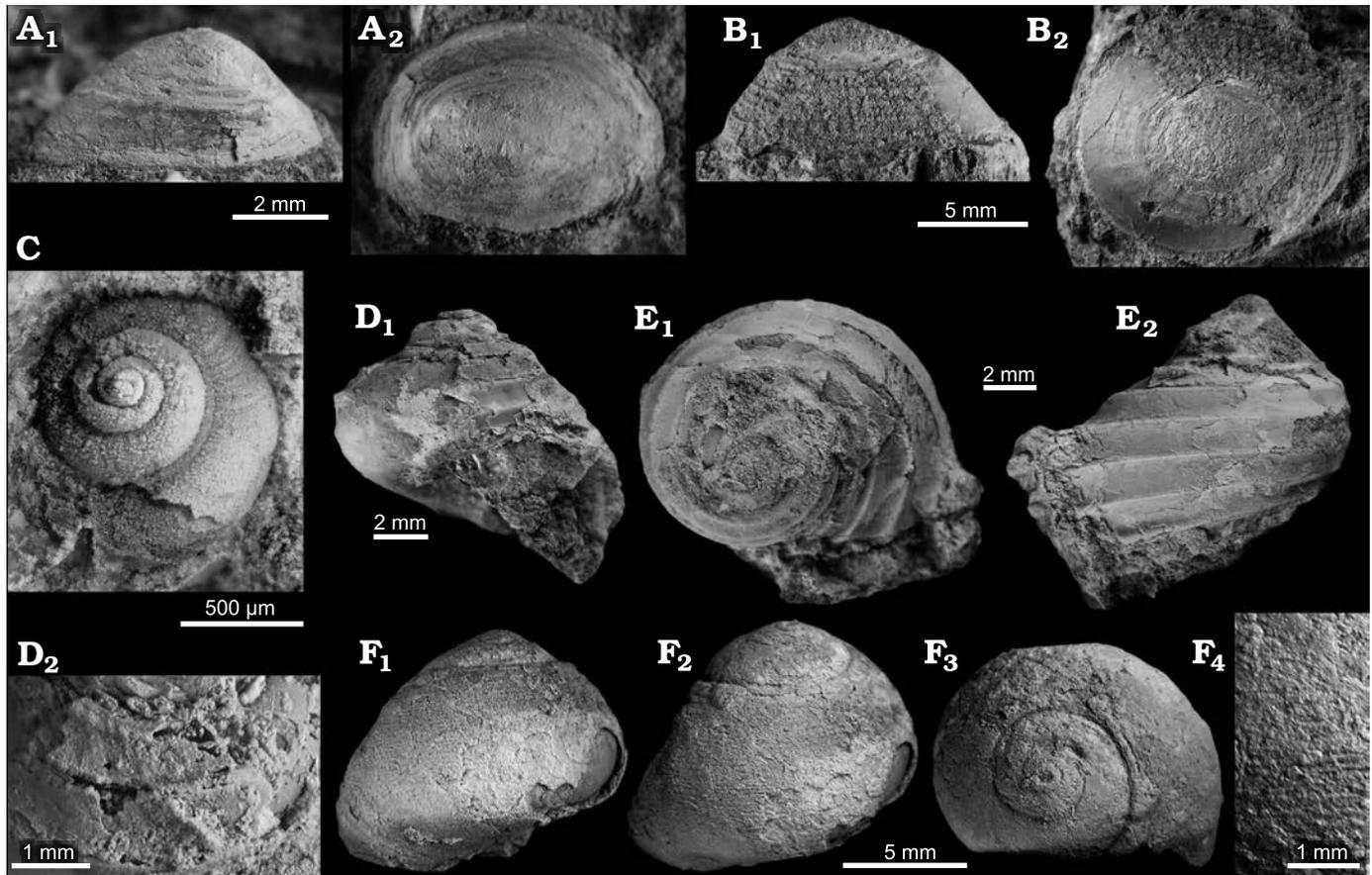


Fig. 18. Limpets, neomphalids, and vetigastropods from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A, B.** Unidentified limpet gastropod. **A.** NRM Mo 192715, small specimen, mostly an internal mold. **B.** NRM Mo 192656, large specimen with sculpture. **C.** The neomphalin *Retiskenea* sp., NRM Mo 192540, apical view on specimen embedded in rock matrix. **D, E.** The seguenzoid *Cataegis* sp. **D.** NRM Mo 192666; note sculpture on D_2 . **E.** NRM Mo 192665, specimen showing the strong spiral ribs, in apical (E_1) and abapertural (E_2) views. **F.** The colloniid *Homalopoma* sp., NRM Mo 192583, views on entire shell (F_1 – F_3) and close-up on spiral sculpture (F_4).

Description.—Low turbiniform shell, ca. 3.5 evenly convex whorls bearing four strong, equally spaced spiral keels, lowest ridge forming basal margin, surface of keels with fine nodular ornament; growth increments fine, strongly opisthocline; base with three further keels.

Remarks.—Due to the poor preservation of the available specimens, we are unable to assign *Cataegis* sp. to any existing or new species. Apart from being slightly lower spired, *Cataegis* sp. is similar to the extant *Cataegis celebesensis* McLean and Quinn, 1987, from Indonesia, which also has nearly evenly spaced spiral ribs; other species of *Cataegis* tend to have the keels more closely spaced on the whorl's shoulder and more widely spaced on the flanks (McLean and Quinn 1987; Vilvens 2016). This applies also to *Cataegis ramosi* Kiel, Aguilar, and Kase, 2020a, from late Pliocene-aged Liog-Liog Point seep deposit in Leyte, Philippines, which has a more distinctive shoulder than *Cataegis* sp. reported here. The Late Miocene *Cataegis godineauensis* (Van Winkle, 1919) from seep deposits in Trinidad (see Kiel and Hansen 2015: fig. 14E) has very similar sculpture but a lower spire than *Cataegis* sp.

The related cataegid *Kanoia myronfeinbergi* Warén and

Rouse, 2016, has a much more angular whorl profile than the specimens reported here (Warén and Rouse 2016). Members of the genus *Carinotrochus* Zhang, Zhang, and Zhang, 2020a, from seamounts in the tropical western Pacific (Zhang et al. 2020a) are superficially similar to *Cataegis* sp. but have nearly smooth spiral ridges lacking the nodular sculpture of *Cataegis*.

Order Trochida

Family Colloniidae Cossmann in Cossmann and Peyrot, 1917

Genus *Homalopoma* Carpenter, 1864

Type species: *Turbo sanguineus* Linnaeus, 1758, by monotypy; Recent, Mediterranean Sea.

Homalopoma? sp.

Fig. 18F.

Material.—One specimen from block B (NRM Mo 192583: W = 11.8 mm, H = 9.6 mm).

Remarks.—*Homalopoma* has been reported from fossil seeps of Cretaceous age onwards. The specimen reported here has

much finer and more numerous spiral cords compared to both *Homalopoma abeshinaiensis* Kaim, Jenkins, and Hikida, 2009, from the Upper Cretaceous of Hokkaido, Japan (Hikida et al. 2003; Kaim et al. 2009), and *Homalopoma domeniconii* Moroni, 1966, from Middle–Late Miocene seep deposits in Italy (Moroni 1966). Species with similar spiral ornament but taller shells and a more convex whorl profile include the middle to late Eocene *Homalopoma?* sp. from the Humptulips seep deposit in Washington state, USA (Goedert and Squires 1990), *Homalopoma watsi* (Dickerson, 1916) from a middle Eocene wood fall in Washington (Kiel 2008), *Homalopoma* sp. from fossil seeps of somewhat uncertain Cenozoic age in Barbados (Gill et al. 2005), and the extant *Homalopoma bicolor* Okutani, 2001, from the northern Mariana Ridge (Okutani 2001). *Homalopoma tosaense* Habe, 1953, reported from the Plio-Pleistocene of Luzon Island, Philippines (Helwerda et al. 2014), is smaller, taller, and has very distinct spiral keels rather than fine spiral cords has the specimen reported here from the Northern Cement quarry.

Of very similar overall shape are species of *Phanerolepida*, including *Phanerolepida rehderi* MacNeil, 1960, from the Plio-Pleistocene of Okinawa, southern Japan (Noda 1988: pl. 5: 3) but the Philippine specimen illustrated here clearly has spiral sculpture instead of the net-like rhombohedral pattern of *Phanerolepida* (Hickman 1972).

Subclass Neritimorpha Golikov and Starobogatov, 1975

Family Phenacolepadidae Pilsbry, 1895

Genus *Thalassonerita* Moroni, 1966

Type species: Nerita (Thalassonerita) megastoma Moroni, 1966, by original designation; Miocene, Italy.

Thalassonerita hagai sp. nov.

Fig. 19.

Zoobank LCID: urn:lsid:zoobank.org:act: 5A82FE2C-D3D5-41FD-B011-9AD5924DE4B9

Etymology: For Takuma Haga (Tsukuba, Japan), who collected the specimens.

Type material: Holotype: NIGSPAL-032, specimen with some shell, aperture obscured by rock matrix. Paratypes: NRM Mo 192657, 192658, partially preserved specimens from the type locality and horizon.

Type locality: The “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Type horizon: Seep carbonate blocks enclosed in the Amlang Formation (Upper Miocene).

Material.—Type material only.

Dimensions (in mm).—NIGSPAL-032: W = 25.0, H = 17.3.

Diagnosis.—Shell large for genus, two whorls, sculpture of 13 widely spaced axial ribs on last whorl.

Description.—Large neritiform shell, up to 25.0 mm wide, at least two whorls, spire apparently flat; sculpture of 13 oblique axial ribs, interspaces between ribs 2–3 times the width of ribs, both ribs and interspaces covered by fine axial lirae.

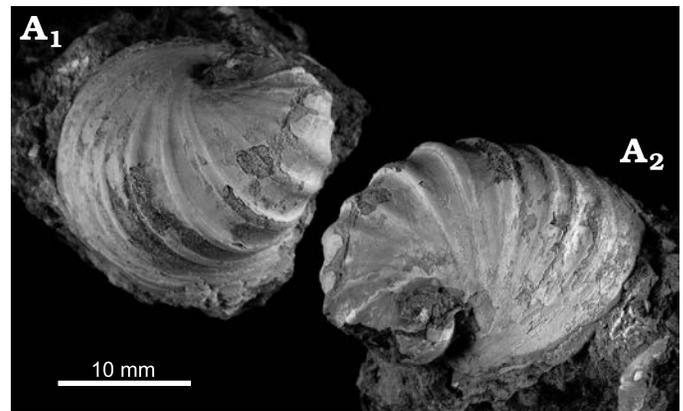


Fig. 19. The phenacolepadid gastropod *Thalassonerita hagai* sp. nov., from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. NIGSPAL-032, holotype, in abapertural view (A₁) and apical view (A₂).

Remarks.—The specimens have a thin outer layer that appears to differ in mineralogy from the remaining shell material, and such a layer has not been observed in other gastropods from the Northern Cement Corporation quarry. It is here interpreted as the calcitic outer layer typical of neritimorph gastropods. This is the first fossil record of *Thalassonerita* from the central Indo-West Pacific and with a width of 25.0 mm it is by far the largest *Thalassonerita* reported to date. Both the middle Eocene *Thalassonerita eocenica* Squires and Goedert, 1996, from the Humptulips Formation in western Washington state, USA (Squires and Goedert 1996; Hybertsen and Kiel 2018), and the type species *Thalassonerita megastoma* Moroni, 1966, from the Upper Miocene of Italy, also reported from the Miocene of Barbados, reach only 10.0 mm in width (Moroni 1966; Gill et al. 2005). An early Oligocene neritid reported from seep deposits in Peru reaches 8.5 mm in width (Kiel et al. 2020b), and the extant *Thalassonerita naticoides* (Clarke, 1989) has a maximum width of 12.5 mm (Clarke 1989). Furthermore, all above mentioned species have less distinctive axial ornament than *Thalassonerita hagai*; the extant *T. naticoides* is nearly smooth. An Early Cretaceous neritid reported from a seep deposit on the Crimean Peninsula reaches just over 20.0 mm in width, but is nearly smooth and might not have any direct phylogenetic relationships to *Thalassonerita* (Kiel and Peckmann 2008).

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines.

Subclass Caenogastropoda Cox, 1960

Family Naticidae Guilding, 1834

Naticidae gen. et sp. indet.

Fig. 20A.

Material.—One specimen from block B (NRM Mo 192628: H = 21.3 mm, W = 21.2 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—Unfortunately, the umbilical area of this specimen is damaged, preventing a generic assignment.

Family Fasciolaridae Gray, 1853

Genus *Fusinus* Rafinesque, 1815

Type species: *Murex colus* Linnaeus, 1758, by typification of replaced name; Recent, Indo-West Pacific Ocean.

Fusinus? sp.

Fig. 20B, C.

Material.—Two large specimens from block I (NRM Mo 192662, 192663). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192662: H = 73.2, W = 52.0; NRM Mo 192663: H = 90.8, W = 45.0.

Remarks.—*Fusinus* is widespread in the Indian and Pacific Oceans today (Okutani and Tsuchiya 2000; Callomon and Snyder 2007, 2019; Couto et al. 2016), but its fossil record from this area is meager at best. Although the preservation of the two *Fusinus?* sp. specimens is not ideal, they clearly lack the granulate sculpture typical for *Granulifusus*, a genus common in the Indo-West Pacific and known from several fossils, especially in Japan (Shuto 1958; Hadorn and Fraussen 2005). With their evenly convex whorls, the two *Fusinus?* sp. specimens are clearly different from those of several deep-water fusinins inhabiting deeper water around the Philippines today, such as species of *Latirus* Montfort, 1810, and *Fusolatirus* Kuroda and Habe in Kuroda et al., 1971 (Garcia 2001; Snyder and Bouchet 2006).

Vermeij and Snyder (2018) reviewed large fasciolarid genera (Fusininae) and introduced several genera for tall species with strongly convex whorls and distinct axial ribs resembling *Fusinus?* sp. reported here. Among these, *Apertifusus* includes three or four tropical Atlantic species, and *Lyonsifusus* consists of a few species from the southern Caribbean, including Miocene fossils. Lastly, *Ariefusus* was introduced for an extant West African species and for the Miocene *Fusus prevosti* Partsch in Hörnes, 1856, whose whorls are more constricted near the suture (Hörnes 1856) and consequently have somewhat pointed ribs on the center of the whorls, unlike the Philippine specimens.

Family Buccinidae Rafinesque, 1815

Genus *Enigmaticolus* Fraussen, 2008

Type species: *Enigmaticolus monnieri* Fraussen, 2008, by original designation; Recent, Madagascar.

Remarks.—Six species and two unnamed records of this genus are known from the Indian and western Pacific Oceans (Fraussen 2008; Fraussen and Stahlschmidt 2016; Zhang et al. 2020b; Chen et al. 2021). Here we transfer a species formerly reported as *Siphonalia semisulcata* Martin, 1933, and *Siphonalia (Pseudoneptunea) semisulcata*, from the Upper Miocene of Buton, Indonesia, to *Enigmaticolus*, report it

also from the Upper Miocene of the Philippines, and regard it as the first fossil record of this genus.

Enigmaticolus semisulcata (Martin, 1933) comb. nov.

Fig. 20D–F.

1933 *Siphonalia semisulcata* sp. nov.; Martin 1933: 25, pl. 3: 24, 25.
1942 *Siphonalia (Pseudoneptunea) semisulcata* Martin; Beets 1942: 281, pl. 28: 38.

Description.—High-spired fusiform shell, whorls gently convex with fine constriction below suture; sculpture of flat spirals crossed by numerous fine axial (slightly opisthocyrt) growth increments, giving the spirals a beaded appearance; sculpture most prominent on early whorls and base; inner lip with thin callus.

Material.—Two specimens from block B (NRM Mo 192586, 192587), three specimens from block I (NRM Mo 192631–192633). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192586: H = 30.0, W = 21.5; NRM Mo 192586: H = 17.7, W = 11.8; NRM Mo 192632: H = 36.8, W = 24.0; NRM Mo 192632: H = 34.0, W = 21.0.

Remarks.—The specimens illustrated by Martin (1933) from the Upper Miocene of Buton, Indonesia, resemble the Philippine specimens reported here in general shape and in having flat, beaded spiral ornament that becomes more prominent on the base. They differ by having more distinctive axial ribbing in the upper part of the whorls, especially on the early whorls (Martin 1933), whereas the Philippine specimens show more distinctive beaded spiral ornament. Even more similar to the Philippine specimens is another specimen from Buton, referred to as “*Siphonalia (Pseudoneptunea) semisulcata* Martin” by Beets (1942), due to its lack of the strong axial ribs on the upper part of the whorls.

Species of *Siphonalia* and *Pseudoneptunea* have more convex whorls with much stronger axial ornament than “*Siphonalia semisulcata* Martin, 1933”; hence the species is unlikely to belong to either of these genera (Makiyama 1941; Cernohorsky 1975; Robba et al. 2004; Zhang and Zhang 2018). Rather, the habitus of the shell, the flat spiral ornament on the upper part of the whorls and the base, the indistinct axial ribs, and fine constriction below the suture, indicate affinities to *Enigmaticolus*, to which this species is herein re-assigned. Among the extant species of *Enigmaticolus*, the most similar to *E. semisulcata* is the type species with its slender shell.

Stratigraphic and geographic range.—Upper Miocene of Luzon, Philippines and Buton, Indonesia.

Enigmaticolus sp.

Fig. 20G.

Material.—One specimen from block I (NRM Mo 192640: H = 23.8 mm, W = 12.0 mm). Upper Miocene of the “shale

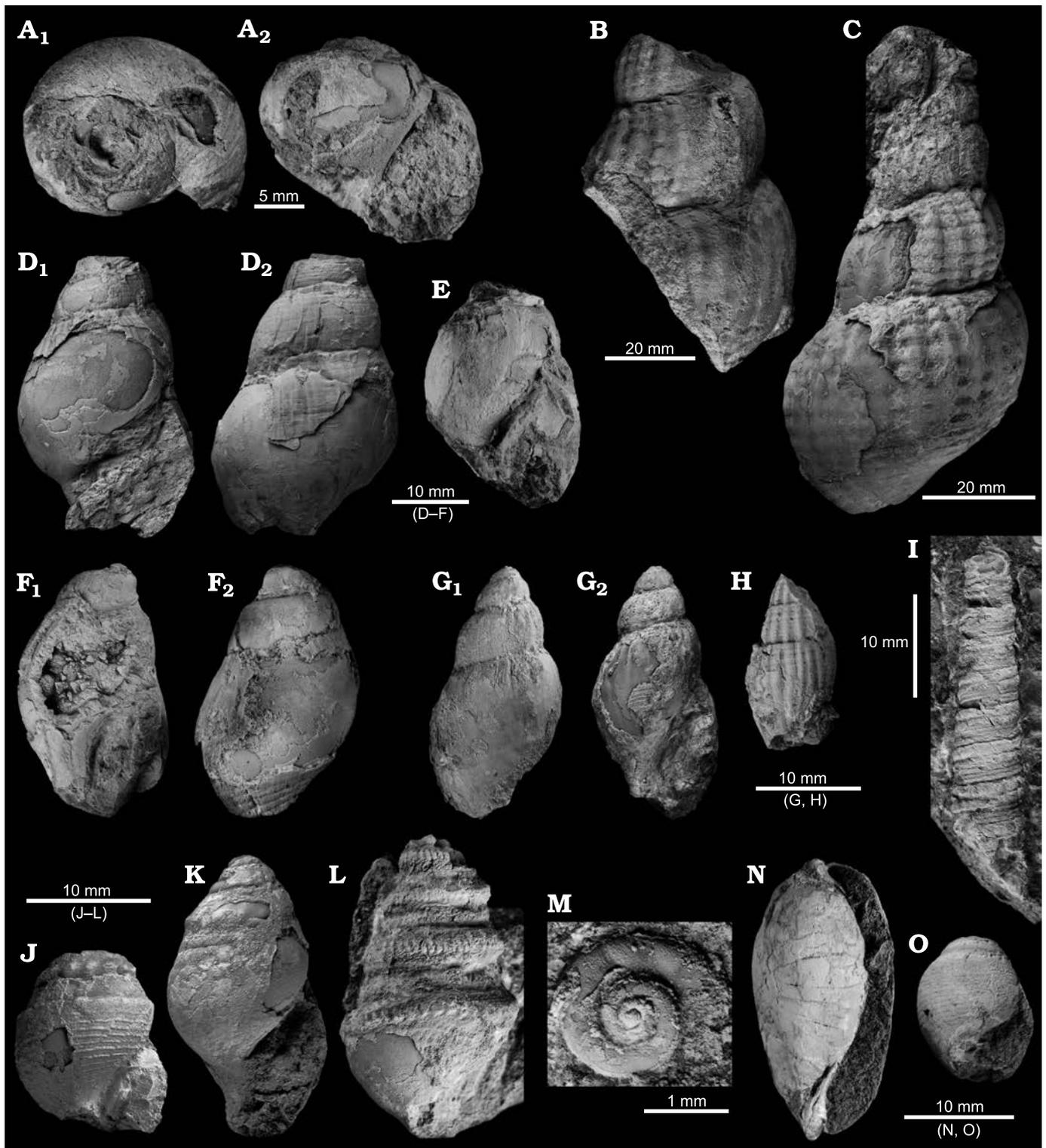


Fig. 20. Caenogastropoda and Opisthobranchia from Upper Miocene seep deposits of the Amlang Formation in Pangasinan province, Luzon, Philippines. **A.** Naticidae gen. et sp. indet., NRM Mo 192628, imperfect specimen in apical and apertural views. **B, C.** Very large *Fusinus*? sp., imperfect specimens in abapertural view. **B.** NRM Mo 192662. **C.** NRM Mo 192663. **D–F.** *Enigmaticolus semisulcata* (Martin, 1933), imperfect specimens in apertural and abapertural views. **D.** NRM Mo 192632. **E.** NRM Mo 192586. **F.** NRM Mo 192633. **G.** *Enigmaticolus* sp., NRM Mo 192640, specimen with broken apertural base, abapertural and apertural view. **H.** Mitridae gen. et sp. indet., NRM Mo 192639, imperfect specimen, abapertural view. **I.** Terebridae gen. et sp. indet., NRM Mo 192627, fragment of spire, lateral view. **J, K.** *Acanthodaphne*? sp., imperfect specimens in apertural view. **J.** NRM Mo 192637. **K.** NRM Mo 192638. **L.** *Gemmula* sp., NRM Mo 192417, imperfect specimen, apertural view. **M.** *Xylodiscula*? sp., NRM Mo 192619, specimen embedded in rock matrix in apical view. **N.** *Volvulella* aff. *minoensis* Itoigawa, 1958, NRM Mo 192641, nearly complete specimen, apertural view. **O.** Ringiculidae gen. et sp. indet., NRM Mo 192642, imperfect specimen, apertural view.

quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—This specimen differs from *Enigmaticolus semisulcata* by being smaller and by having more distinct axial ribs on the whorl’s shoulder. In the latter respect it resembles *Enigmaticolus nipponensis* (Okutani and Fujiwara, 2000) from methane seeps in the South China Sea (Chen et al. 2021).

Family Mitridae Swainson, 1831

Mitridae gen. et sp. indet.

Fig. 20H.

Material.—One specimen from block I (NRM Mo 192639: H = 17.0 mm, W = 9.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—This poorly preserved specimen consists of 2.5 whorls, has straight axial ribs, fine spirals, and two columellar folds. It certainly belongs to the Mitridae, but a genus- or species-level identification is not possible.

Family Terebridae Mörch, 1852

Terebridae gen. et sp. indet.

Fig. 20I.

Material.—One specimen from block I (NRM Mo 192627: H = 36.6 mm, W = 8.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—A similar species is *Gemmaterebra bicorona* (Hutton, 1885) as illustrated in Beu and Maxwell (1990: 269, pl. 30: O) from the Middle–Upper Miocene of New Zealand.

Family Raphitomidae Bellardi, 1875

Genus *Acanthodaphne* Bonfitto and Morassi, 2006

Type species: *Acanthodaphne sabellii* Bonfitto and Morassi, 2006, by original designation; Recent, Gulf of Aden.

Remarks.—This genus of deep-water raphitomids is known from a few extant species from the Indian and West Pacific Oceans; its fossil record is considered to include *Puha pusula* Laws, 1947, from the Lower Miocene of New Zealand, and possibly *Pseudoinquisitor?* cf. *P.? pulchra* (Schepman, 1913) reported by MacNeil (1960) from the Middle Miocene of Okinawa, Japan (Bonfitto and Morassi 2006; Morassi and Bonfitto 2010).

Acanthodaphne? sp.

Fig. 20J, K.

Material.—Three specimens from block I (NRM Mo 192636–192638). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Dimensions (in mm).—NRM Mo 192636: H = 17.0, W = 9.8;

NRM Mo 192637: H = 16.0, W = 12.8; NRM Mo 192638: H = 22.8, W = 12.0.

Remarks.—These three specimens have the general shell outline and ornament of species of *Acanthodaphne*, but with its protoconch morphology unknown, their assignment to this genus remain somewhat uncertain. The Miocene *Pseudoinquisitor?* cf. *P.? pulchra* from the Yunabaru clay on Okinawa (MacNeil 1960: pl. 5: 13) has fewer but more distinct spirals on the lower part of the whorls.

Family Turridae Adams and Adams, 1853

Genus *Gemmula* Weinkauff, 1875

Type species: *Gemmula hindsiana* Berry, 1958, by subsequent designation; Recent, eastern Pacific Ocean.

Gemmula sp.

Fig. 20L.

Material.—One specimen from block E (NRM Mo 192417: H = 24.5 mm, W = 14.0 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—This fragmentary specimen (3.5 whorls) is quite similar to *Gemmula* sp. indet. illustrated by Matsubara (2011: pl. 3: 7) from Miocene shallow marine deposits of the Hokutan Group in the Tajima area, Hyōgo Prefecture, southwest Japan. *Gemmula osawanoensis* Tsuda, 1959, from Middle Miocene deep-water sediments of the Higashibessho Formation in Toyama Prefecture, central Japan (Amano et al. 2004: fig. 5.15), appears to have more distinctive spiral ornament on the base, though the absence of such ornament from the Philippine specimen might be a preservational artifact. The *Gemmula* species from the Miocene Yunabaru clay on Okinawa illustrated by MacNeil (1960: pl. 5) have fewer but stronger axial ribs on the central spiral cord than the specimens reported here. Further similar fossil species include *Gemmula granosus* (Helbling, 1779) illustrated in Noda (1988: pl. 13: 9a, b) from the Pliocene of Okinawa, Japan, and *Pleurotoma woodwardi* Martin, 1883 from Java, Indonesia (Martin 1891–1906: 37, pl. 4: 91–96). A bit more compact are *Bathytoma hetzeli* Martin, 1933, from the Upper Miocene of Buton, Indonesia (Martin 1933: 21, pl. 3: 16), and *Cosmasyrinx monilifera* Marwick, 1931 from Miocene bathyal deposits in New Zealand (Beu and Maxwell 1990: 250, pl. 27: S). Among extant taxa, perhaps most similar are *Gemmula cosmoi* (Sykes, 1830), which occurs from Sagami Bay to Kyushu, in 50–350 m depth, and *G. kieneri* (Doumet, 1840), which occurs from Choshi (Pacific central Honshu) southward to the Philippines (Hasegawa et al. 2000).

Subclass Heterobranchia Burmeister, 1837

Family Xylodisculidae Warén, 1992

Genus *Xylodiscula* Marshall, 1988

Type species: *Xylodiscula vitrea* Marshall, 1988, by original designation; Recent, SE Australia.

Xylodiscula? sp.

Fig. 20M.

Material.—Four specimens from block B (NRM Mo 192619–192622), one specimen from block I (NRM Mo 192626). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—These small (up to 2.0 mm diameter), poorly preserved, low-spired shells most closely resemble species of the heterobranch *Xylodiscula*, but the imperfectly preserved protoconch prevents a more certain assignment. *Xylodiscula* occurs on sunken wood, both recent (Marshall 1988) and fossil (Kiel and Goedert 2007), but is also known from hydrothermal vents (Warén and Bouchet 1993) and other reducing environments (Høisæter and Johannessen 2001; Hawe et al. 2014).

Family Rhizoridae Dell, 1956

Genus *Volvulella* Newton, 1891

Type species: *Bulla acuminata* Bruguière, 1792, by typification of replaced name; Recent, European waters.

Volvulella aff. *minoensis* Itoigawa, 1958

Fig. 20N.

Material.—One specimen from block I (NRM Mo 192641: H = 12.8 mm, W = 7.4 mm). Upper Miocene of the “shale quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—The pointed apex characteristic for *Volvulella* is eroded away in the only available specimen, but its former presence is indicated by the blunt apical peg and the apically broken aperture. The type specimens of *V. minoensis* illustrated by Itoigawa (1958: 178, pl. 26: 8, 9) from the Middle Miocene Mizunami Group in south-central Honshu, are reported to have fine incisions at both ends; these, too, may have been eroded away in NRM Mo 192641. The other Miocene Japanese *Volvulella* species reported by Itoigawa (1958) are more slender than *V. minoensis*.

Similar in shape, size and having a smooth shell is the extant *Volvulella ovulina* (Adams in Sowerby, 1850) which occurs in 10–477 m depth, from Japan to southeastern Indonesia (Valdés 2008). Slightly more globular and with fine incisions near the base is *Volvulella volvulaeformis* (Seguenza, 1879) from the Italian Pliocene (Brunetti 2020), whereas the Early Miocene *V. staphyleomorpha* Harzhauser, 2014, from shallow-marine deposits in Kerala, SW India, has a more slender shell (Harzhauser 2014).

Family Ringiculidae Philippi, 1853

Ringiculidae gen. et sp. indet.

Fig. 20O.

Material.—One specimen from block I (NRM Mo 192642: H = 6.2 mm, W = 5.2 mm). Upper Miocene of the “shale

quarry” within the Northern Cement Corporation quarry in Pangasinan province, Luzon, Philippines.

Remarks.—This small globular shell with about two whorls preserved shows 17 fine spiral incisions on the last whorl and three folds on the parietal and columellar lip, suggesting affinities to *Ringicula*. Helwerda (2015) reported numerous species of *Ringicula* from Plio-Pleistocene strata in the Philippines, but the poor preservation of the present specimen does not allow a more detailed comparison.

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