

Southeast Asia as the birthplace of unusual traits: the Melongenidae (Gastropoda) of northwest Borneo

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Abstract

In this paper the Miocene to recent melongenid species of northwest Borneo are discussed. The recent fauna is poor with three genera represented by one species each. In the Miocene three (possibly four) genera occur with eight (possibly nine) species of which three are described as new species: *Melongena murifactor*, uniquely characterized by the formation of a septum walling off the adapical sector of the aperture; *Pugilina erecta*, characterized (along with its close Miocene relative from Java, *P. ickei*) by a free-edged, erect inner lip; *Volema goliath*, large for the genus with later whorls progressively covering the upper row of spines of earlier whorls. The apertural septum of *M. murifactor* is unique within Gastropoda, whereas the erect inner lip of *P. erecta* and *P. ickei* is unique within Melongenidae. That these extralimital traits occur exclusively in the Miocene of southeast Asia is consistent with the hypothesis that adaptive innovations are most likely to arise in diverse, productive, shallow-water ecosystems.

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Introduction

The neogastropod family Melongenidae Fischer, 1884, is a relatively small, compact group of 22 recent and at least 42 post-Eocene fossil species and subspecies of medium-sized to very large predators. All species have a tropical to subtropical distribution in shallow waters, and all occur on the shores of continents and continen-

tal islands. In northwest Borneo the recent fauna is poor with three genera represented by one species each. In the Early Miocene three genera occurred with three species, in the Middle-Late Miocene three (possibly four) genera with six (possibly seven) species (Table 1). Three of these Miocene species are described as new species. A short introduction to the area and sampling performed is given in Raven (2002: 3-7).

Although the taxonomic composition of pre-Oligocene members of this family remains unclear, the Oligocene to recent members appear to have ancestors among Late Eocene species of the genus *Pugilina* Schumacher, 1817. Most shells of the group are quite simple, but at least two phenotypes representing significant departures from the standard morphology have evolved, one of which may be unique within Gastropoda. Both of these phenotypes are known only from fossil melongenids in southeast Asia. In the course of a review of melongenid species from the Miocene of Borneo presented in this paper, we document these unusual phenotypes, one of which is associated with a new species and the other with both a new and a previously described Indonesian species. We place these odd morphologies into the broader context of evolution in the highly competitive environment of Neogene marine southeast Asia.

Abbreviations: coll., collection; Fm, Formation(s), fr., fragment(s); H, height; juv., juvenile(s); sp., specimen(s); W, width. For collections and legit: BM, Brunei Museum, Bandar Seri Begawan; BMNH, The Natural History Museum, London; BPM, Bataafsche Petroleum Maatschappij, The Hague, now Royal Dutch Shell; CL, Charlie Lee, Miri; GR, Gerard A. Raven, Leidschendam; MS, Mary Saul, Malvern; N, Novi E. Yusniasita Dols, Seria; PNHS, Panaga Natural History

Table 1. Melongenidae species and stratigraphic distribution based on records from northwest Borneo.

	"Early Miocene, Sibuti Formation"	"Middle Miocene, Lambir Formation"	"Middle-Late Miocene, Miri Formation"	"Late Miocene, Seria Formation"	"Pliocene, Liang Formation"	Pleistocene	Holocene	Recent
<i>Hemifusus ternatanus</i>	■■■■■		?			■■■■■	
<i>Melongena murifactor</i>			■■■■■				
<i>Melongena gigas</i>	■■■■■							
<i>Pugilina spec. A</i>			■■■■■					
<i>Pugilina ickei</i>			■■■■■					
<i>Pugilina erecta</i>	■■■■■							
<i>Pugilina cochlidium</i>			■■■■■					
<i>Volema cf. pyriformis</i>			■■■■■					■■■■■
<i>Volema goliath</i>	■■■■■	■■■■■			■■■■■	■■■■■
<i>Volema myristica</i>								

Society, Seria, Brunei; R, Han Raven, The Hague; RMNH, Nationaal Natuurhistorisch Museum (formerly Rijksmuseum voor Natuurlijke Historie), Leiden; RV, Ricardo Villar, Seria, Brunei; V, Jaap Vermeulen, Leiden; ZMA, Zoologisch Museum Amsterdam.

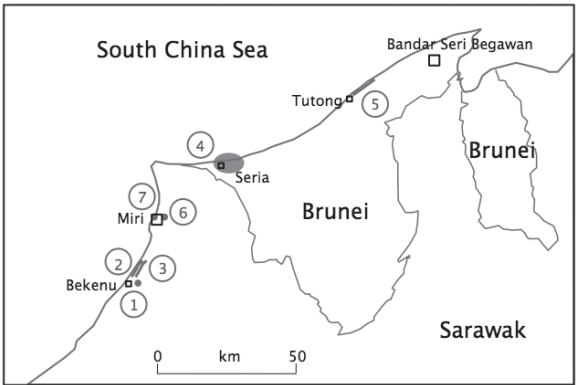
Material is recorded in the following order: COUNTRY, province, locality, geological formation, age, coll. number, number of specimens, leg., size.

Materials and methods

Key localities (see map below) in NW Borneo from which samples are available:

- 1. Kampung Tengah turnoff outcrops C and D (Bungai-Bekenu road km 4.6 measured from Bungai beach side) near Bekenu, 36 km S of Miri, Sarawak,

- Malaysia. The fossiliferous bed is a hardground in the Setap shale, Sibuti Formation (Early Miocene).
- 2. Auban coastal cliffs, 34 km SW of Miri, Sarawak, Malaysia. Individual outcrops are recorded in kilometers distance from Sungei Auban. Fossils collected from silts in the Lower Miri Formation (Middle-Late Miocene).
- 3. Miri-Bekenu road, SW of Miri, Sarawak, Malaysia. Individual outcrops are recorded in kilometers distance from the clock tower roundabout in Miri towncentre, the Kampung Beraya junction being at km 26.9). Fossils collected from silts in the Lower Miri Formation (Middle-Late Miocene).
- 4. The Seria oil field in Brunei – material is limited to small specimens collected from wells drilled in the early 1930’s. Seria Formation (Late Miocene).
- 5. Coastal outcrops NE of Tutong in Brunei. Miri, Seria and Liang Formations (Middle Miocene to Pliocene). Most sampling was done by geologists from the Bataafsche Petroleum Maatschappij (now Royal Dutch Shell) in the 1920s and 1930s. The material was studied in the 1920s to 1940s by K. Martin and C. Beets at the Geological Museum (now the National Museum of Natural History), Leiden.
- 6. 300 m SE of Canada Hill, Miri, Sarawak, Malaysia. Temporary outcrop of tidal flat and coral reef deposits (Holocene, deposited about 6000 years before present).
- 7. Sungei Boang, 250 m WNW of the public pool in Miri, Sarawak, Malaysia. Temporary outcrop of upper shoreface deposits (Holocene, deposited about 5000 years before present).



Sketch map of the areas in Sarawak and Brunei indicating key localities with fossil material discussed in this paper.

Systematics

Family Melongenidae Fischer, 1884

Remarks. As Vermeij and Wesselingh (2002) have pointed out, distinctions among the various named genera and subgenera of post-Eocene Melongenidae are not always clear. Although a formal phylogenetic analysis for the family has not yet been attempted, our comparative study of fossil and living melongenids indicates that two morphological groups, perhaps representing sister clades, can be recognized. One is represented in the Recent fauna by *Pugilina*, with species in the Atlantic and Indo-West Pacific regions, and *Hemifusus* Swainson, 1840, known only from southeast Asia. This group is characterized by a relatively high spire, a relatively long siphonal protuberance, the absence of an adapical notch in the outer lip of the adult shell, and usually by the presence of a single row of shoulder nodes or spines (but see below under *P. erecta* n. sp.). The inner side of the outer lip is lirate (spirally ridged) in *P. morio* (Linnaeus, 1758), the type species of *Pugilina*, but smooth in most other species including all *Hemifusus*.

The second group comprises the taxa *Melongena* Schumacher, 1817; *Volema* Röding, 1798; *Rexmela* Olsson and Harbison, 1953; and *Torquifer* Roth, 1981. In this group, the spire is generally low, the siphonal protuberance is short, the outer lip bears a distinct adapical notch in the adult stage, and the fully developed sculpture consists of a row of shoulder tubercles or spines, one or two additional rows of tubercles on the central sector of the last whorl, and a basal row of spines or tubercles immediately adapical to the siphonal protuberance. Any or all of these rows of tubercles may be absent. In the American *Rexmela* (Pleistocene to Recent of Florida) and *Torquifer* (Early to Late Miocene of Atlantic tropical America) there is a pronounced tendency to form imbrications just below the suture, marking previous positions of the adapical end of the shell's outer lip. Subadult shells in the *Melongena* group closely resemble *Pugilina* in lacking basal spines and in the absence of an adapical notch. The inner side of the outer lip is lirate in *Volema* and in some subadult specimens of American *Melongena*.

All living species of *Melongena* and *Rexmela*, as well as the Miocene genus *Torquifer*, are known only from the New World. The living *Melongena melongena* (Linnaeus, 1758) of the Caribbean region and the coast of Atlantic Central America and northern South America to Suriname, and *M. patula* (Broderip and

Sowerby, 1829) from the eastern Pacific (Gulf of California to Ecuador) (Clench and Turner, 1956), are characterized by low-spined shells in which the last whorl of the adult becomes highly expanded and covers part of the spire. Nodes and spines, when developed, are relatively blunt and short. This condition also applies to Miocene and Pliocene representatives of *Melongena* from tropical America. *Rexmela* often has highly elongated, adapically curved spines on the shoulder angulation and a less expanded last whorl and higher spire. In the Old World, all species that have been assigned to *Melongena* are extinct. When spines are developed, they tend to be very long, especially on the shoulder angulation, and the last whorl is distinctly conical rather than broadly inflated as in the tropical American species. The oldest species of *Melongena*, *M. crassicornuta* Conrad, 1848, from the Byram Fm (Early Oligocene) of Mississippi, and *M. laxecarinata* (Bellardi, 1882) from the Early Oligocene of Italy (see MacNeil and Dockery, 1984; Dockery and Lozouet, 2003) may have given rise to the New and Old World groups, respectively. Further work may show that the Oligocene and Miocene species of the Old World that have been assigned to *Melongena*, including *M. cornuta* (Agassiz, 1843) and *M. lainei* (de Basterot, 1825) from Europe, and *M. gigas* (Martin, 1883) from Indonesia, should be separated as a separate genus or subgenus. For now, however, we continue to use the generic name *Melongena* in the broad sense for both the New World lineage, including the type species *M. melongena*, and for the fossil species from Europe and Asia.

Genus *Melongena* Schumacher, 1817

Type species: *Melongena fasciata* Schumacher, 1817 (= *Murex melongena* Linnaeus, 1758)

Melongena gigas (Martin, 1883)

Description. A large species (up to at least 25 cm high) with a very large aperture, a low spire with large spines and a row of smaller spines lower on the neck.

Material. Miocene. MALAYSIA, Sarawak. F97.06 Auban outcrop km 2.68, Middle Miocene, Lower Miri Fm, R F5142: 1 sp., leg R (Fig. 3); Auban outcrop km 3.7, Middle Miocene, Lower Miri Fm, R F5123: 1 large fr., leg. CL (Fig. 4); Miri-Bekenu Road km 27.6 left, Middle Miocene, Lower Miri Fm, R F4498: 1 fr., leg. R; Miri-Bekenu Road km 27.8 left, Middle Miocene, Lower Miri Fm, R F4497: 1 fr., leg. R. BRUNEI,

Tutong. Penanjong beach, Miocene/Pliocene, Seria or Liang Fm, coll. CL: 1, leg. CL (Fig. 5).

Remarks. This species is rare in the studied deposits. Only one fully grown specimen was collected, besides some fragments and a juvenile. The fully grown specimen is 25 cm high, whereas the largest (not fully grown) specimen recorded by Martin (1883: 90) is only 17.5 cm high.

Melongena murifactor n. sp.

= *Melongena* sp. 3, Martin, 1928: 20

Diagnosis. A small species characterized by a strongly convex subsutural region, very low spire, an extremely deep adapical notch on the outer lip, and the presence of periodic septa walling off the adapical sector of the aperture.

Description. Shell thick, relatively small for genus, maximum length 65.7 mm, globose, with a very low spire and markedly convex subsutural ramp; abapical part of last whorl weakly and gradually constricted; sculpture variable: holotype (Fig. 1) smooth, without spines, other specimens from the same sample with three discontinuous spiral rows of nodes (Fig. 2), one at shoulder, one just below shoulder, and one at base of last whorl just above keel-like siphonal fasciole; aperture smooth within; heavy ventral callus; adapical end of outer lip with very deep notch; adapical sector of aperture walled off from part of adapical notch by a septum, whose adapertural edge lies some distance within the aperture; at least one earlier septum also present. There is no evidence of a color pattern, also not in UV light.

Type specimens.

Holotype RMNH: leg. CL, 65.7 mm (Fig. 1).

Paratype R F4089: leg. CL, 43.5 mm (Fig. 2).

Other specimens R F4089: 2 + 4 fr. leg. CL.

Type locality and stratigraphic horizon.

MALAYSIA, Sarawak. Bekenu (36 km S of Miri), Kampung Tengah turnoff outcrops C and D, Early Miocene, Sibuti Fm, hardground in the Setap shale (sequence boundary).

Etymology: *murifactor*, Latin noun for wall-builder.

Remarks. This species is highly distinctive not only because of its globose form and convex subsutural

ramp, but especially because of its extremely deep adapical (anal) notch, which is periodically walled off by a septum forming the adapical side of the aperture. In the specimens from Borneo, the outer lip of the shell has grown beyond the outer edge of the septum, so that the adapical notch remains continuous. In these specimens, there is a second septum, set about 70° to 90° back from the outer lip, indicating that the septum forms periodically.

Martin (1928: 20) referred to an unnamed species of *Melongena* from the Late Miocene of Atjeh (= Aceh), northern Sumatra, as *Melongena* sp. 3. Inspection of this specimen (RGM 675) indicates that it belongs to *M. murifactor*. Although its aperture is not well preserved, the remains of a septum are clearly evident. In his brief discussion of this specimen, Martin (1928) noted that the globose form, especially of the adapical sector of the last whorl, was distinctive; but he did not mention the septum.

As Martin (1928) pointed out, the present species resembles spiny members of the southeast Asian species *Volema myristica* Röding, 1798 (see below). We use this name for the taxon Martin (1928) and most other authors have called *Melongena galeodes* (Lamarck, 1822). *Volema myristica* differs from *M. murifactor* by lacking the adapical septum and by having intermittent spiral ridges on the inner side of the outer lip.

The only species that appears to resemble *M. murifactor* is *Cassidea acanthina* Dalton, 1908, which Vredenburg (1922) reassigned to *Melongena*. This species, from the Late Oligocene of Birma (= Myanmar), is globose, with a reflected inner-lip callus and a shallow umbilicus. The spines are described as large, irregular, and robust. There is no mention of an adapical notch or septum.

Melongena murifactor is not similar to any other Old World species of *Melongena*, but it does resemble some New World species in its very low spire and globose form. No American species of *Melongena* s.s., however, possesses an adapical septum of the kind seen in *M. murifactor*.

Our examination of nearly all living and fossil melongenid species reveals that adapical septa occur in highly reduced form in some individuals of only two taxa, *Melongena (Rexmela) corona corona* (Gmelin, 1791) from the west coast of Florida, and *M. (R.) c. johnstonei* Clench and Turner, 1956, from northwestern Florida. Specimens of these taxa in the Vermeij collection show the formation of a septum closing off

the last-formed shoulder spine at the outer lip. Only one septum is present in any given specimen, and the edge of the septum is flush with the edge of the rest of the outer lip. This is unlike the situation in *M. murifactor*, in which the outer lip has grown beyond the edge of the most recently formed septum. To our knowledge, there are no previous descriptions of the adapical septum in the literature, likely because it is a subtle feature that could be easily interpreted as a gerontic aberration.

All kinds of apertural elaborations — notches, sinuses, canals, and spine-like extensions — are known in gastropods. When these form periodically during shell growth, the most recently formed structure is initially almost always hollow on its adapertural side. During the next growth cycle, or when the aperture remains in the same position for a long interval of time, its connection with the apertural cavity is usually severed by a general infilling of the hollow structure with shell material secreted by the mantle surface on the shell's interior. The extent of this infilling varies within and among species. The spines of many busyconine whelks, coralliophiline and muricine muricids, columbariids, and the turbinid *Astraea*, remain adaperturally hollow, and only the base of the structure is closed off by a thin layer of shell material. This layer is not, however, a septum, because its formation occurs within the broad entrance of the spine in the apertural cavity. The hollow entrance is itself gradually filled in with additional shell material. In many thick-shelled muricids, as well as in the spinose strombids *Lambis* and *Harpago*, the long-spined turbinid *Guildfordia*, and spiny species of *Vasum* in the Vasidae, the open edges of the spine are often closed in conjunction with the basal infilling of the hollow spine (see also Savazzi and Sasaki, 2004). In members of the Bursidae, whose adapical notch forms periodically when a varix is produced, the old adapical notch is succeeded in growth by a new thin lip that reaches to the penultimate whorl without forming a notch; only the formation of the next varix initiates a new notch. In most gastropods, old siphonal canals are typically left open to the aperture and are never sealed off by a septum or infilling.

Our discovery of septa in *Melongena murifactor* and our preliminary studies of how periodically formed apertural extensions are walled off or filled in has exposed an aspect of shell morphology and growth about which very little appears to be known. We hope the present paper draws attention to the topic of secondary shell secretion and resorption within the gas-

tropod shell aperture.

In his note on the fossils from Brunei (Martin, 1932: 3) a '*Melongena* 3' is reported from well 13 in the Seria oil field (340-350 m depth). On p. 6 Martin states that it concerns a very young specimen. In the RMNH collection the box with the label '*Melongena* spec. 3' comprises a glass tube with another label inside stating 'Seria-13 340-350 m' and a single shell of a juvenile *Eucithara* (Clathurellinae, Conidae), unrelated to *Melongena* sp. 3 from Aceh.

Genus *Pugilina* Schumacher, 1817

Type species: *Pugilina fasciata* Schumacher, 1817 (= *Murex morio* Linnaeus, 1758)

Pugilina erecta n. sp.

= *Melongena* (*Pugilina*) *madjalengkensis* of Martin, 1928: 19, not *Pyrula* (*Melongena*) *madjalengkensis* Martin, 1895

Diagnosis. Small *Pugilina* with a single row of shoulder tubercles and an erect inner lip.

Description. Shell moderately small for genus, maximum length 62.1 mm, fusiform; body whorl with eight to ten shoulder spines, extended abapically as narrowly rounded axial ribs, which reach to the constriction; spiral sculpture consisting of a continuous subsutural cord, ten cords on the steep shoulder slope, ten between the spines and the basal constriction, and 12 on the constriction and siphonal protuberance; aperture adapically broad, smooth within; outer lip adapically forming short narrow channel with parietal wall, but without notch; inner lip erect and expanded along most of its length.

Type specimens.

Holotype. Auban outcrop km 3.55, RMNH: leg. CL, 47.5 mm (Fig. 6).

Paratype 1. Auban outcrop km 3.55, F R5135: leg. CL, 47.5 mm.

Paratypes 2-3. Auban outcrop km 3.45, R F5136: leg. CL, 57.5+ mm (Fig. 7) and 62.1 mm (Fig. 8).

Paratype 4. Auban outcrop lower part of section, R F4023: leg. CL, 51.8 mm (Fig. 9).

Type locality and stratigraphic horizon.

MALAYSIA, Sarawak. Auban coastal outcrop between Tanjing Batu and Sungei Kadulit, 34 km southwest of Miri, Sarawak, Malaysia; Middle Miocene, Lower Miri Fm.



Figs. 1-2. *Melongena murifactor* n. sp. East of Kampung Tengah turnoff near Bekenu, Sibuti Fm, Setap Shale. Fig. 1 Holotype, RMNH: H 65.7 mm; Fig. 2 Paratype, R F4071: H 43.5 mm.

Figs. 3-5. *Melongena gigas*. Fig. 3 Auban outcrop, km 2.68 km, Lower Miri Fm, R F5142: H 25 cm. Fig. 4 Auban outcrop km 3.7, Lower Miri Fm, R F5123: W 132 mm. Fig. 5 Penanjong Beach (on beach itself), Seria or Liang Fm, coll. CL.

Other material.

MALAYSIA, Sarawak. Auban outcrop, Middle Miocene, Lower Miri Fm. Km 1.2 km, R F5139: 1 juv., leg. CL; Km 2.0 km, R 4761: 2, leg. R. Km 2.68 km, R F5137: 1, leg. R. Km 3.60, R F5135: 1 + 1 broken, leg. CL. Km 3.65, R F5138: 1 juv., leg. CL. Km 4.35, R F5141: 4 broken, 1 in stone, leg. R. Miri-Bekenu Road, Middle Miocene, Lower Miri Fm. Km 27.6 (right), R F4460: 1 broken + fr., leg. R. Km 30.1 (left), R F4365: 1, leg. R. Same outcrop, *P. cf. erecta*. Km 27.8 (left): 1 broken, not kept, leg. R. Km 28.4 (right) R F4300: 2 juv., leg. R. Km 28.5 (left), R F4671: 1 fr, leg. R. Km 27.8 (left), R F4671: 1 fr, leg. R.

Etymology. Latin adjective *erecta*, standing up, referring to the free-edged inner lip.

Remarks. The new species *Pugilina erecta* displays some variation. The two largest specimens (lengths 57.5+ (Fig. 7) and 62.1 mm (Fig. 8)) differ from the holotype (Fig. 6) and a second specimen of identical length (47.5 mm) by having the inner lip adherent instead of erect. We interpret this difference as reflecting a subadult stage despite the larger size of these specimens. Another specimen, of length 51.8 mm (Fig. 9), has spiral ridges on the inner side of the outer lip. This specimen resembles the holotype and the other small specimen in having an erect inner lip. In UV light the shells have a pattern of fine radial lines with pale riblets and darker interspaces.

Pugilina erecta is most similar to *P. ickei* (Martin, 1906) from the Middle and Late Miocene of Java. The latter species is larger (maximum length 113 mm in a specimen with incomplete spire and siphonal protuberance), from Tji Angsana-Merang (= Ciangsana-Merang), and is characterized by either a row of tubercles or a continuous angulation at the abapical end of the axial ribs. This angulation or second row of tubercles is absent in *P. erecta*. Both species have an erect inner lip, a character otherwise unknown in *Pugilina* and indeed in the family Melongenidae.

A specimen identified by Martin (1928: 19) as *Melongena (Pugilina) madjalengkensis* (Martin, 1895) from the Late Miocene of Aceh in northern Sumatra has a discontinuous row of shoulder nodes and obsolete spiral sculpture on the central sector of the body whorl between the shoulder nodes and the basal constriction which is spirally threaded. Like most of our Borneo specimens, the Aceh specimen (H 94.5 mm) has an erect inner lip. The taxon *Pyrula (Melongena) madjalengkensis* Martin, 1895, was originally de-

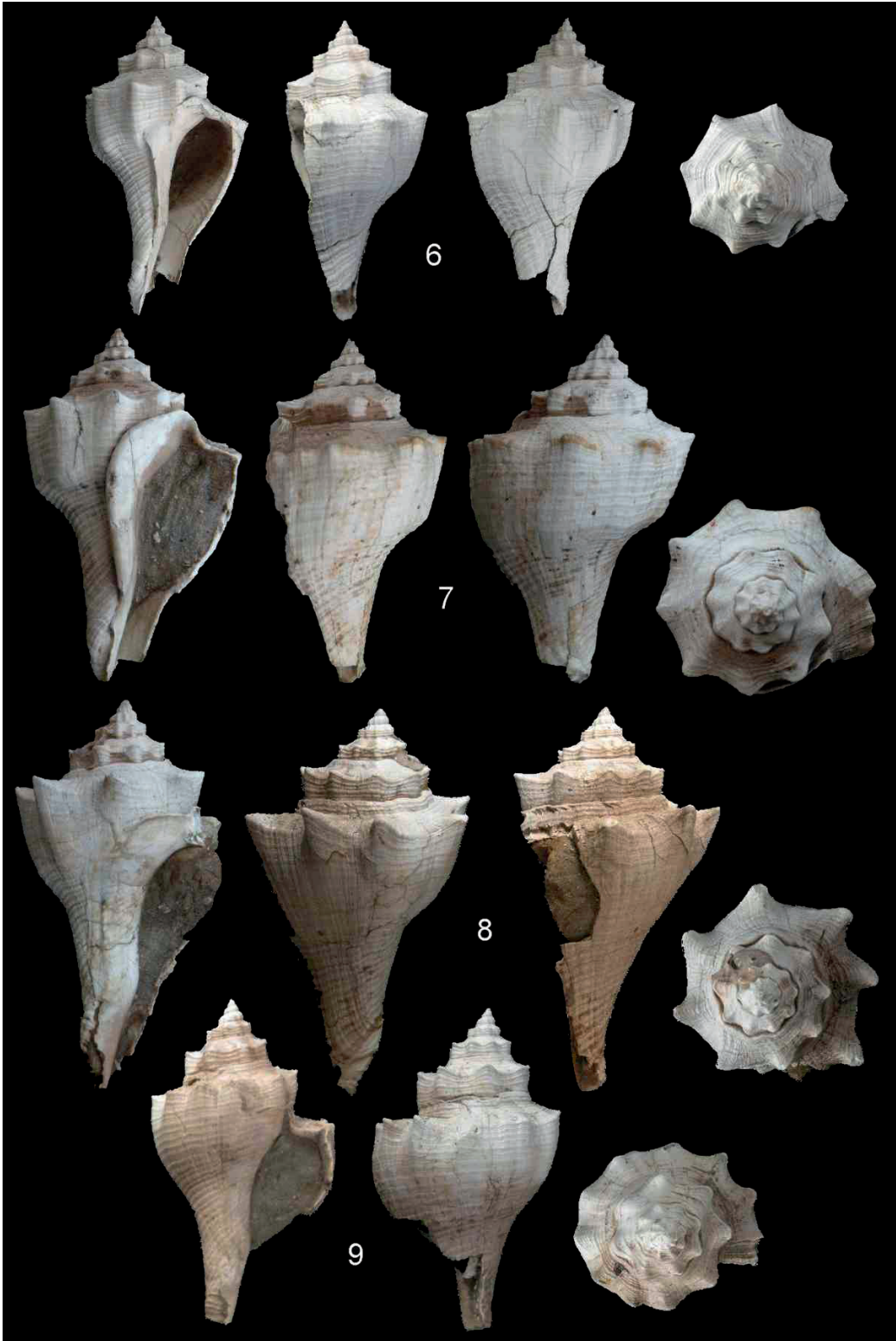
scribed from the Pliocene of Java. Oostingh (1935) and van Regteren Altena (1950) considered it a stratigraphic subspecies of the Pleistocene to Recent *P. cochlidium* (Linnaeus, 1758) (as *P. pugilina* (Born)). True *P. madjalengkensis* resembles the living *P. cochlidium* in almost all characters, including the presence of a consistently adherent inner lip. We therefore tentatively assign Martin's (1928) specimen from Aceh as *P. erecta* even though his specimen is larger and smoother than our specimens from Borneo.

Juvenile specimens can be differentiated from those of *P. cochlidium* by the lower number, larger and more pointed shoulder spines in *P. erecta*.

To our knowledge, *P. erecta* and *P. ickei* are the only fossil or living melongenids with an erect inner lip. All other species have the inner lip fully attached to the abapertural side of the body whorl. The erect inner lip is therefore the second unique departure by a southeast Asian species from the standard shell morphology of melongenids.

Gastropods with an erect inner lip are found mainly on soft bottoms. Those rock-dwelling muricids that possess an erect inner lip tend to have a small, nearly round aperture with an effectively continuous rim that adheres closely to the substratum. Muricids as a whole are slow-moving snails, and it is possible (but unproven) that those with an erect aperture are sedentary, perhaps even parasitic, in habit.

Mud-dwelling and sand-dwelling gastropods with an erect inner lip do not burrow completely. Indeed, an inner-lip edge that is almost vertically oriented with respect to the sediment surface would seem to prevent active burrowing, and points instead to a relatively sedentary, mostly surface-dwelling habit. Compared to gastropods in which the inner lip merges gradually with the outer surface of the shell, gastropods with an erect inner lip have a larger volume between the shell's ventral side and the sediment surface. An erect inner lip could thus contribute to a prey-trapping or prey-enveloping method of predation, as proposed for long-spined species of *Murex* by Paul (1981). No observations have been made on any living gastropod to evaluate such a suggestion. Prey-trapping of crabs beneath the shell has been described for species of *Harpa*, which have a very large aperture and foot but an adherent inner lip (Rehder, 1973). It is conceivable that wide-apertured species of *Melongena* also use trapping to prey on bivalves, and that species of such melongenid genera as *Pugilina* and *Volema*, whose apertures are narrower, would have to resort to an erect inner lip to construct an adequate cage for trapping prey.



Figs. 6-9. *Pugilina erecta* n. sp., Auban outcrop, Lower Miri Fm. Fig. 6 Holotype km 3.55, RMNH: H 47.5 mm. Figs. 7-8 Paratypes 2-3 km 3.45, R F5136: H 57.5+ mm and 62.1 mm. Fig. 9 Paratype 4 Auban outcrop lower part of section, R F4023: H 51.8 mm.

Pugilina ickei (Martin, 1906)

Material. MALAYSIA, Sarawak. Auban outcrop km 0.6, Middle Miocene, Lower Miri Fm, R F5140: 1, leg. CL (Fig. 10). BRUNEI, Tutong. Tutong sample 11B, Late Miocene, Miri Fm, RMNH: 1 juv., leg. BPM (Fig. 11); Tutong sample 11A, Middle-Late Miocene, Miri Fm, RMNH: 1, leg. BPM.

Remarks. Like *P. erecta* this species often, but not always, has an erect inner lip. It can be differentiated from *P. erecta* as it has fewer spines, which are also shorter and rounder.

A few specimens of this species have been collected in NW Borneo. The specimens from Tutong were identified by Martin (1931: 6) as '*Melongena cochlidium*' (sample 11B) and '*Melongena* spec. 2, related to *M. cochlidium*' (sample 11A). Both specimens differ substantially from *P. cochlidium*, especially by having far fewer and larger, more pointed spines (Figs. 10-11).

Pugilina sp. A

Material. MALAYSIA, Sarawak. Bekenu, Kampung Tengah turnoff outcrops C and D, Early Miocene, Sibuti Fm, hardground in the Setap Shale, R F4089: 2, leg. CL (Figs. 12-13).

Remarks. Two shells from the Sibuti Fm (Early Miocene) of Borneo, measuring 54.6 and 47.4 mm in length (Figs. 12-13), may represent a third new species of Melongenidae, but we hesitate to describe these formally as a distinct taxon. They are characterized by prominent shoulder spines oriented adapically, which may be absent over distances of less than a quarter to almost half a whorl. Axial ribs extend from the spines to the basal constriction. Spiral sculpture is weak, being wholly absent from the central sector of the last whorl from the spines to the constriction. The aperture is smooth within, and the inner lip is adherent.

This specimen looks like a miniature *P. ponderosa* (Martin, 1895), a large species (shell length 116 mm) from the Late Miocene of Java, which like our specimen has adapically oriented spines and a smooth inner lip. More material will be needed to clarify the status of the taxon from the Sibuti Fm.

Pugilina cochlidium (Linnaeus, 1758)

Description. An intermediate sized species (up to 11 cm high) with solid shell, moderately high spire,

shouldered whorls with short and rounded nodes (Fig. 14). Juveniles have spiral sculpture or variable strength all over the shell, whereas in adults this sculpture is only noted on the neck. Strong, brown periostracum.

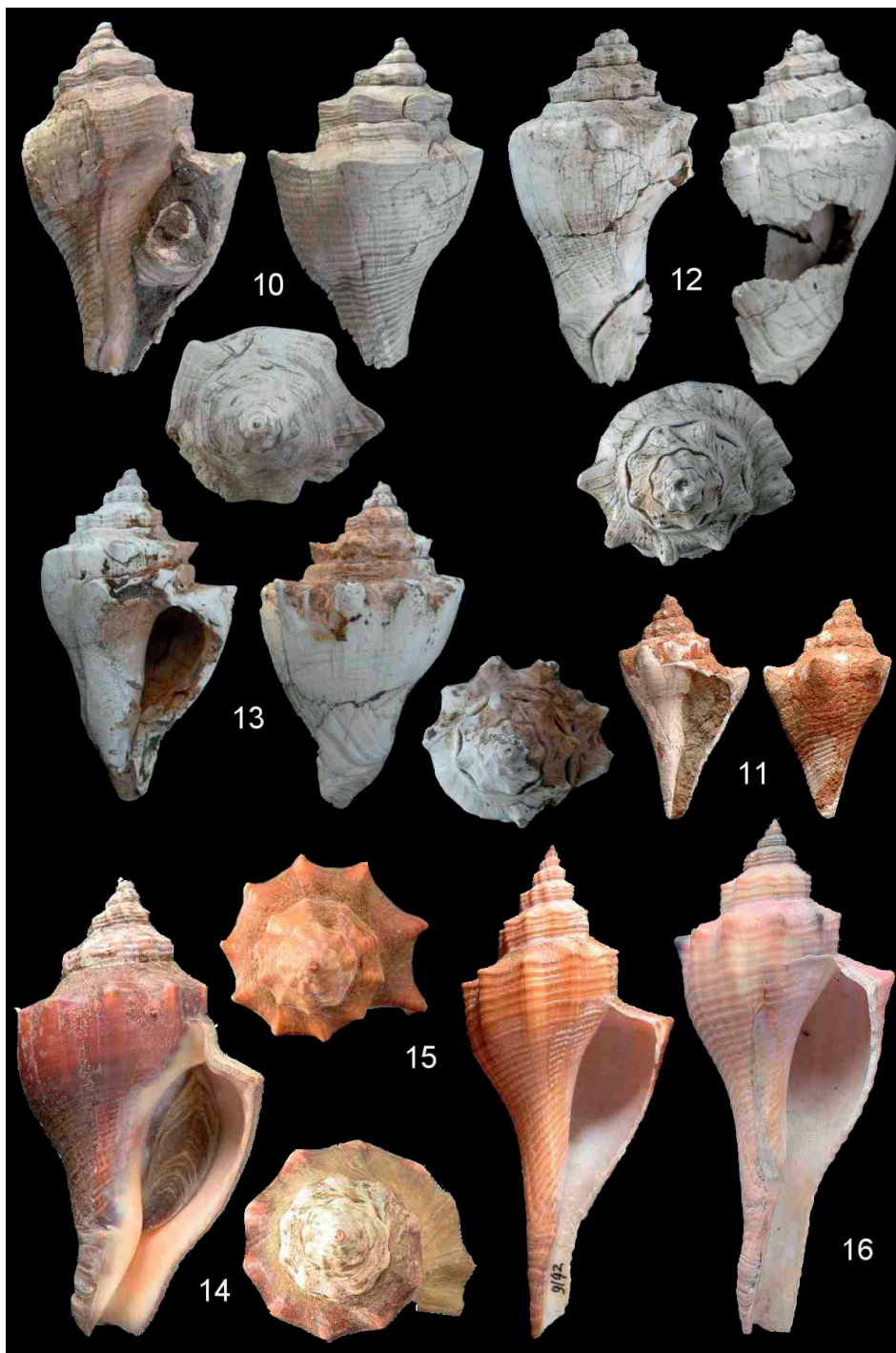
Material. Recent. MALAYSIA, Sarawak. Bako National Park, Teluk Pandan Besar, beach, R T7133: 1, vii.2003, leg. V; Miri, Piasau & Miri beaches, found alive on objects low on beach, R T0615: 6 + 18 juv., 1992-1997, leg. R; Miri, Tanjing Lobang, intertidal area with sandstone, abundant alive on/under rocks in lower half of tidal zone, R T1732: 14 + 4 juv., 1992-1997, leg. R (Fig. 14); 6km W of Bekenu, Tanjung Batu, sandy beach, 1 sp. not kept, 07.x.92, leg. R; Damai Beach NW of Santubong, near rocky area, R T3417: 1, 31.viii.1996, leg. R. Sabah. Labuan Island, 1 km N of Tanjing Aru, on tidal flat area near Sungei Ganggarok, few sp., not kept, 20.vi.1993, leg. R. Kedah. Langkawi Island, Pantai Cenang, sandy and muddy tidal flat in large lagoon behind island and corals, several sp. alive in muddy sand (not collected), R T2059: 3 juv., iii.1994, leg. R. Penang, 2 km W of Teluk Kumbar, small rocky promontory with sandy beaches, 1 sp., not collected, 2.ii.1996, leg. R. BRUNEI: Belait. Left bank of Sungei Seria estuary, tidal flat with local wooden piles and stones, R T2457: 1 + 2 juv., 01.ii.1995, leg. R; S92.26, Anduki, estuary of Sungei Bera with nipah palm and mangrove swamp, PNHS: 2, 1990, leg. RV. Tutong. Jerudong, alive in intertidal zone on rocks near cape, R T1617: 3 + 4 juv., ix.1993, leg. R. Muara. Kampung Sungei Besar, mangrove forest along huge estuary, few sp., not kept, 11.ix.1993, leg. R. SINGAPORE. Changi Beach, R T5588: several juv., 16.iii.2003, leg. V.

Remarks. This is the most abundant and widely spread recent species. It occurs from low in the intertidal zone to shallow subtidal, especially between rocks. After death of the mollusc the shells are often inhabited by large hermit crabs which may take the shells to different depositional environments, such as beaches and estuaries.

Genus *Hemifusus* Swainson, 1840 (as *Semifusus*)

Type species: *Fusus colosseus* Lamarck, 1816

Remarks. The genus is characterized by a much more elongate shell, which is also thinner than that of the other genera mentioned in this paper. Living speci-



Figs. 10-11. *Pugilina ickei*. Fig. 10 Auban outcrop km 0.6, Lower Miri Fm, R F5140: H 51.6 mm. Fig. 11 Tutong sample 11B, Miri Fm, RMNH: H 26.3 mm.

Figs 12-13. *Pugilina* spec. A East of Kampung Tengah turnoff near Bekenu, Sibuti Fm, Setap Shale, R F4089. Fig. 12 H 54.6 mm. Fig. 13 H 47.4 mm.

Fig. 14. *Pugilina cochlidium*. Tanjing Lobang, Miri, Recent, R T1732: H 89.4 mm.

Figs. 15-16. *Hemifusus ternatanus*. Fig. 15 Piasau Beach, Miri, Recent, R T0613: H 87.4 mm. Fig. 16 Sungei Boang, Miri, Holocene, R H1489: H 109.6 mm.

mens are found subtidally, but empty shells do wash up on the shore.

Hemifusus ternatanus (Gmelin, 1791)

Material. Holocene. MALAYSIA, Sarawak. Miri, 300 m SE of Canada Hill, Holocene, R H1111: 2 + 1 fr., leg. R; Sungei Boang, 250 m WNW of public pool in Miri, Holocene, R H1489: 1, leg. R (Fig. 16).

Recent. MALAYSIA, Sarawak. Miri Marina, sand dredged from about -15 m offshore used to construct pier of Miri river mouth and Miri marina, R T6350: 1, xi.2005, leg. R; Piasau and Miri beaches, Miri, IX.1992, R T0613: 1 + 2 juv., leg. R (Fig. 15); Tanjing Lobang, Miri, intertidal zone with sandstone rocks, 1992-1997, R T3733: 2, leg. R; Kg.Ra'an, S of Miri, beach, not kept: 1 fr., 1992-1997, leg. R.; Miri, Tyre Reef, sand bottom at 14 m water depth, R T4379: 1 operculum and trails on sea floor, 06.iv.1997, leg. R. Sabah. Kota Kinabalu, coral rubble and fine sand dredged SW of Pulau Gaya W of city for harbour resort construction, R T3919: 1, iii.1996, leg. R. Kedah. Kedah, SW Langkawi, Pantai Cenang, sandy beach along tidal flats in large lagoon behind island and corals, R T2015: 1, iii.1994, leg. R. BRUNEI, Seria. Seria, Panaga beach, PNHS: several, 2006, leg. N. Tutong. Tutong, Penanjong beach, not kept: 1996, leg. R; Jerudong beach, sand supplied from offshore, R T1856: 22, ix.1993, leg. R. Muara. Muara, Tanjing Batu, between littoral rocks in muddy water, R T3848: 1, 4.v.1996, leg. R.

Remarks. Nuttall (1961: 75) recorded *Pugilina* (*Hemifusus*) cf. *ternatana* from the Lower Miri Fm at Penanjong, Tutong, Brunei, Miocene. As there is no figure nor a description, it is impossible to check the identification.

'*Hemifusus* ?' was recorded by Martin (1931: 3) from Tutong outcrop 8 (Seria Fm) in Brunei. No description or illustration was provided, and the specimen is not present in the collection of RMNH, therefore it is impossible to know which species this could be, or even whether the material really belongs to this genus.

Another recent species of this genus (*Hemifusus elongatus* (Lamarck, 1822)) has been reported from Singapore (Chan, 2009: 64) but that record requires confirmation. The second author of the present paper has collected a fossil-looking (Holocene?) specimen at Tanjing Kling, 10 km NW of Malacca, Malaysia, 26.xii.1996.

Genus *Volema* Röding, 1798.

Type species: *Volema paradisiaca* Röding, 1798 (= *Buccinum pyrum* Gmelin, 1791)

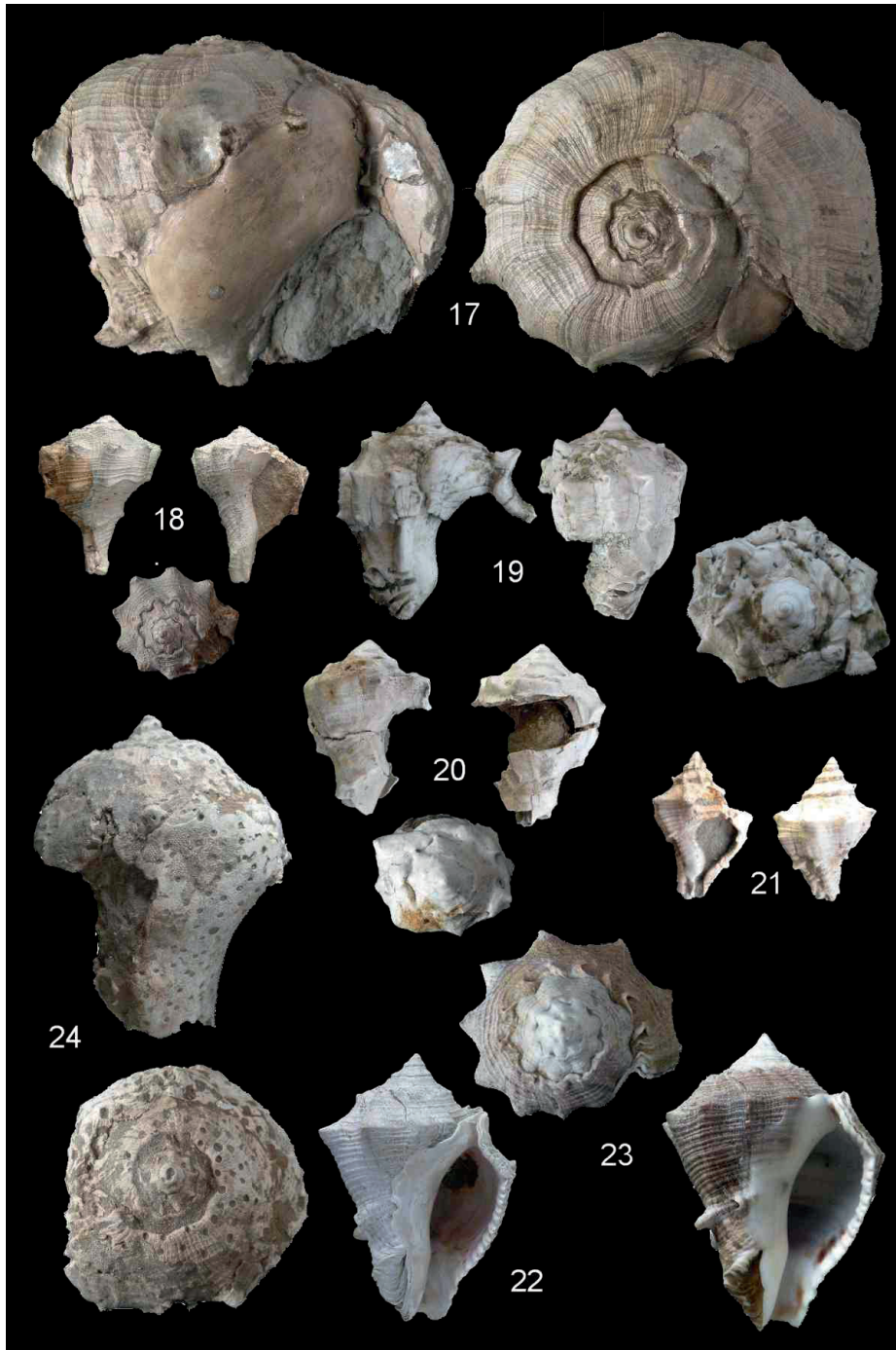
Volema myristica Röding, 1798

Material. Miocene. MALAYSIA, Sarawak. Bekenu, Kampung Tengah turnoff outcrops C and D, Early Miocene, Sibuti Fm, hardground in the Setap Shale, R F4141: 1 broken, 1 fr., leg. CL (Fig. 19); Auban outcrop km 4.35, Middle Miocene, Lower Miri Fm, R F4198: 1 broken, 1 juv., leg. R (Figs. 20-21).

Holocene. MALAYSIA, Sarawak. Miri, 300 m SE of Canada Hill, Holocene, R H1112: 9 + 4 juv., leg. R (Fig. 23).

Recent. MALAYSIA, Sabah. Kota Kinabalu, Tanjung Aru, mud flat with brackish water influx and some mangroves, few sp., not collected, 1995-1997, leg. R; Kota Kinabalu, coral rubble dredged from SW of Pulau Gaya, 1 sp., not collected, iii.1996, leg. R; Labuan Island, Membendai, tidal flat area north of rocky area, few sp., not collected, 19.vi.1993, leg. R; Labuan Island, Tanjing Layang Layangan, small mangrove area behind sandstone rocks, R T1484: 2, 19.vi.1993, leg. R; Labuan Island, Kampung Pohon Batu, beach along sandy lagoon behind coral reef, R T3137: 21 shells from fresh midden, 19.vi.1993, leg. R (Fig. 24); Labuan Island, 1 km N of Tanjing Aru, alive in sand of tidal flat area near Sungei Ganggarok, R T1521: 6, 20.vi.1993, leg. R. BRUNEI, Belait. Seria, Panaga beach, PNHS: 1 sp. worn, 2006, leg. N. Muara. Muara, 1 km W of Tanjing Batu, sandy beach, PNHS: 2 sp. not fresh, 1990, leg. RV.

Remarks. We have one complete juvenile specimen and several larger incomplete specimens (Figs. 19-21) from the Sibuti and Miri Fms of Borneo. These specimens have sculpture consisting of four spiral rows of spines, one situated immediately beneath the suture, the second on the shoulder angulation, and two others more basal. This pattern is identical to that of Recent specimens we have seen from southwestern Sulawesi, Borneo, and the Moluccas. As currently understood, *V. myristica* is a highly variable species. In some populations from southwestern Sulawesi there are no spines at all on the last whorl, whereas in others, such as those from north Java and Bohol (the Philippines), there is a single peripheral row of spines with sometimes a sub-



Figs. 17-18. *Volema goliath*. Fig 17 Holotype, Auban outcrop km 3.65, Lower Miri Fm, RMNH: H 65.7+ mm, W 83.8 mm; Fig. 18 Paratype, Tutong sample 11B, NE of Tutong, Miri Fm, RMNH: H 25.2, W 19.4 mm.

Figs. 19-23. *Volema myristica*. Fig. 19 East of Kampung Tengah turnoff near Bekenu, Sibuti Fm, Setap Shale, R F4141: H 30.7 mm. Figs 20-21 Auban outcrop km 4.35, Middle Miocene, Lower Miri Fm, F4198. Fig. 2, H 32.7 mm. Fig. 3, H 14.1 mm. Fig. 22 300 m SE of Canada Hill, Miri, Holocene, R H1112: H 40.7 mm. Fig. 23 Kampung Pohon Batu, Labuan Island, Recent, R T3137: part of group of shells of various species eaten by men, 54.1 mm.

Fig. 24. *Volema* n. sp., to be described by Kurihara & Kase (pers. comm. to GJV, Oct, 2008), Auban outcrop lower part of section, Lower Miri Fm, R F4109: H 54.3+ mm.

sutural row. The species always possesses strong cords, unlike the nearly smooth type species of *Volema*, *V. pyrum* (Gmelin, 1791) (see also Cernohorsky, 1974).

The form described by Vredenburg (1925) as *Melongenella galeodes* var. *sindiensis* from the Gaj beds (Early Miocene) of Pakistan closely resembles our spiny form. It has one subsutural row of projections, a row of widely spaced spines at the shoulder angulation, and another near the base. According to Vredenburg (1925), the spiral cords are weaker than in the Recent *V. galeodes* (Lamarck, 1822) (= *V. myristica*). More material is needed to confirm that *V. g. sindiensis* is really distinct from *V. myristica*.

Volema n. sp., to be described by Kurihara & Kase (pers. comm. to GJV, Oct. 2008)

Material. Miocene. MALAYSIA, Sarawak. Auban outcrop – lower part, Middle Miocene, Lower Miri Fm, R F4109: 1 broken, leg. CL (Fig. 24).

Remarks. We have one damaged specimen (54.3 mm high, Fig. 24) from the Miri Fm of Borneo that we provisionally assign this species. The overall shape is similar, as are the narrow whorls of the spire and the sculpture.

Volema goliath n. sp.

Diagnosis. A large species with a strongly convex subsutural region, very low spire, three rows of spines, with later whorls progressively covering the upper row of spines of earlier whorls.

Description. Shell thick, large for the genus (Fig. 17), maximum width 119 mm, globose, with a very low spire; abapical part of the whorl concave; sculpture comprises three rows of nodes, the most marked at the shoulder (about ten per whorl in juvenile (Fig. 18), up to 12 per whorl in adult shells), one just below the shoulder and row of weak nodes lower on the neck; the upper row of spines is very marked in juvenile shells, especially in adapical view, but the spines become less marked in adult shells, whereas later whorls progressively cover the upper row of spines of earlier whorls; the outline between the middle rows is markedly straight, especially in the juvenile paratype; spiral sculpture of stronger ridges with weaker ones in between extends over the entire shell and is intersected with closely spaced growth lines that interrupt the spi-

ral; aperture relatively small, smooth within; heavy ventral callus; strong adapical apertural channel; no evidence of a color pattern, also not in UV light.

Type specimens.

Holotype. Miocene. MALAYSIA, Sarawak. Auban outcrop km 3.65, Middle Miocene, Lower Miri Fm, RMNH: 1 broken, leg. CL (Fig. 17).

Paratype. Miocene. BRUNEI, Tutong. Tutong sample 11A, Middle-Late Miocene, Miri Fm, RMNH: 1, leg. BPM (Fig. 18).

Type locality and stratigraphic horizon.

Auban coastal outcrop between Tanjing Batu and Sungei Kadulit, 34 km southwest of Miri, Sarawak, Malaysia; Middle Miocene, Lower Miri Fm.

Material: F97.06 Auban outcrop km 2.35, Middle Miocene, Lower Miri Fm, R F5144: 1 large mould (W 119 mm), leg R

Etymology: *goliath*, after the biblical figure, a giant.

Remarks. This species is distinctive because of its size and globose outline. The holotype is by far the largest specimen of the genus (H 65.7+ mm, W 83.8 mm) that we have seen. Regrettably it is damaged, but additional characteristics are represented in the paratype, which is a juvenile specimen (H 25.2, W 19.4 mm). The juvenile specimen has similarities to spiny specimens of *V. junghuhni* but has a much lower spire.

Martin (1931: 6) reviewed this specimen and listed it as '*Melongenella* sp. 1'. C. Beets studied the paratype and recognized it as a new species which he intended to call *M. fascioplexiformis*, but never published his description.

Both specimens have barnacles on the shell. Beets removed the one from the juvenile. The adult specimen has one barnacle, the base of another and a few juvenile oysters.

Discussion

The melongenids we have described in this paper exhibit two features that are otherwise unknown in the family, namely, an adapical septal wall in the aperture (*Melongenella murifactor*) and an erect inner lip (*Pugilina erecta* and *P. ickei*). Although the latter feature is common in many gastropod families (see above under *P. erecta*), it is unknown in any other living or fossil

melongenids. The septum of *M. murifactor* is unique among gastropods.

Phylogenetic and geological studies (Wilson and Rosen, 1998; Meyer, 2003; Wilson and Vecsei, 2005; Frey and Vermeij, 2008; Renema *et al.*, 2008; Williams and Duda, 2008) indicate that the shallow-water marine faunas of southeast Asia underwent dramatic diversification during the early Neogene, as the area of shallow habitat increased by a factor ten and as productivity due to upwelling and runoff increased. Much of the distinctive character of shallow-water Indo-West Pacific faunas, including the high incidence of shell defenses in molluscs, dates from this expansive phase. These conditions — intense predation and competition, high productivity, and extensive habitats — are ideal for the evolution of adaptive novelties (Vermeij, 2003). Similar favourable conditions may have existed elsewhere during this time interval as well, but the adaptive departures and specializations seen in central Indo-West Pacific faunas of the Neogene are unrivaled in other regions. We therefore suggest that southeast Asia was exceptionally favourable to the establishment of traits that expanded the phenotypic range of the clades in which they arose. Vermeij (2001) already pointed to this time interval in southeast Asia as a time and place in which many gastropod lineages (at least four in greater southeast Asia) independently evolved a labral tooth, a structure on the outer shell lip that speeds up predation on hard-shelled prey.

Among species of the gastropod genus *Nerita*, a partially enveloped shell (subgenus *Amphinerita*) and the sand-dwelling habit (subgenus *Linnerita*) are unique to the Indo-West Pacific, with envelopment being confined to its inner portions (Frey and Vermeij, 2008). Preliminary data from a survey of Neogene clade-specific innovations of molluscs by one of us (GJV) indicate that 32 ecologically or morphologically unique innovations evolved in the Indo-West Pacific, of which at least 15 are restricted to greater southeast Asia. Only ten comparable innovations have been identified for the Neogene to Recent time interval in the tropical Atlantic and eastern Pacific. Further work on this topic is in progress and will be presented in a future paper.

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