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*By Hita Pandita*

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## A new cerithioidean genus *Megistocerithium* (Gastropoda; Mollusca) from the Miocene of Southeast Asia: a possible relict of Mesozoic “Eustomatidae”

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**Abstract.** Based upon large cerithiform gastropod specimens from the middle Miocene beds of Java, Indonesia and the Philippines, a new genus and new species, *Megistocerithium magoi*, is described herein. Ten fragmentary specimens from the lower and upper Miocene beds of the Philippines are tentatively referred to this species. *M. magoi* Kase sp. nov. is amongst the largest fossil cerithioidean gastropods (except for Turritellidae). It was a dweller in intertidal sandy mudflats, probably in close proximity to mangrove forests. No species considered to be congeneric with this species have been found in the Cenozoic. On the other hand, *M. magoi* Kase gen. et sp. nov. shares apertural characters with the Middle Jurassic species *Eustoma tuberculosa*, the type species of a genus belonging to the yet to be well-recognized family Eustomatidae. *M. magoi* Kase gen. et sp. nov. is possibly a relict of the Mesozoic Eustomatidae. It is assumed to have been a grazer on mangrove litter like the potamidid genera *Terebralia* and *Telescopium* in modern mangrove swamps.

**Key words:** Cerithioidea, Gastropoda, Java, *Megistocerithium*, Miocene, Philippines

### Introduction

Cerithioidean gastropods are a diverse group and a major component of younger Cenozoic shallow marine molluscan assemblages in the Indonesian and Philippine archipelagos. They are mostly represented by cerithiform (elongate, multiwhorled, and high-spired) shells with sculpture of spiral rows of granules and/or axial ribs. Nonetheless, unlike modern examples, supraspecific identification of fossil specimens from these areas is often difficult, because the complete outer lips and anterior siphonal canals of the last whorl, important shell characters for supraspecific systematics, are usually destroyed during fossilization or broken during excavation. The majority of fossil cerithioidean species descriptions from tropical Southeast Asia have been based on

shells without complete apertures (e.g. Martin, 1899; Shuto, 1978). Therefore, acquisition of specimens with a complete aperture is indispensable for correct identification as well as for understanding cerithioidean biodiversity in this bioprovince. Our collecting surveys on islands in the Philippines and in Java, Indonesia have resulted in discoveries of complete specimens for many cerithioidean species with previously undetermined generic and/or familial positions.

This paper presents descriptions and a discussion of remarkably large cerithiform gastropod specimens obtained during our collecting surveys of 37 middle to upper Miocene formations in Java and the Philippines. The specimens are very infrequent in occurrence (represented by only 18 specimens) and represented mostly by pieces of spire whorls and/or incomplete last whorls.

However, one specimen from the upper Miocene Nyalindung Formation in West Java has the last whorl almost completely preserved. We are now able to realize that these fragmentary specimens belong to a new genus and species of superfamily Cerithioidea, among the largest Cerithioidea recorded. We suggest that this new genus is not congeneric to any known genera from Cenozoic formations or in modern seas, but can possibly be interpreted as a close relative of the Mesozoic genus *Eustoma* Pilsbry, 1855.

Abbreviations used in this paper are as follows: EM = Geological Collections in the University of Lyon 1, France; NMNS = National Museum of Nature and Science, Tsukuba, Japan; SMNH = Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, Sweden; UMUT = University Museum, the University of Tokyo, Tokyo, Japan.

### Localities and stratigraphy

The specimens discussed in this study were obtained from two localities in West Java, Indonesia and four localities in the Philippines, ranging in age from middle to late Miocene (Figure 1). What follows are brief descriptions of the collecting sites, stratigraphy, lithology, sedimentary environments, and ages.

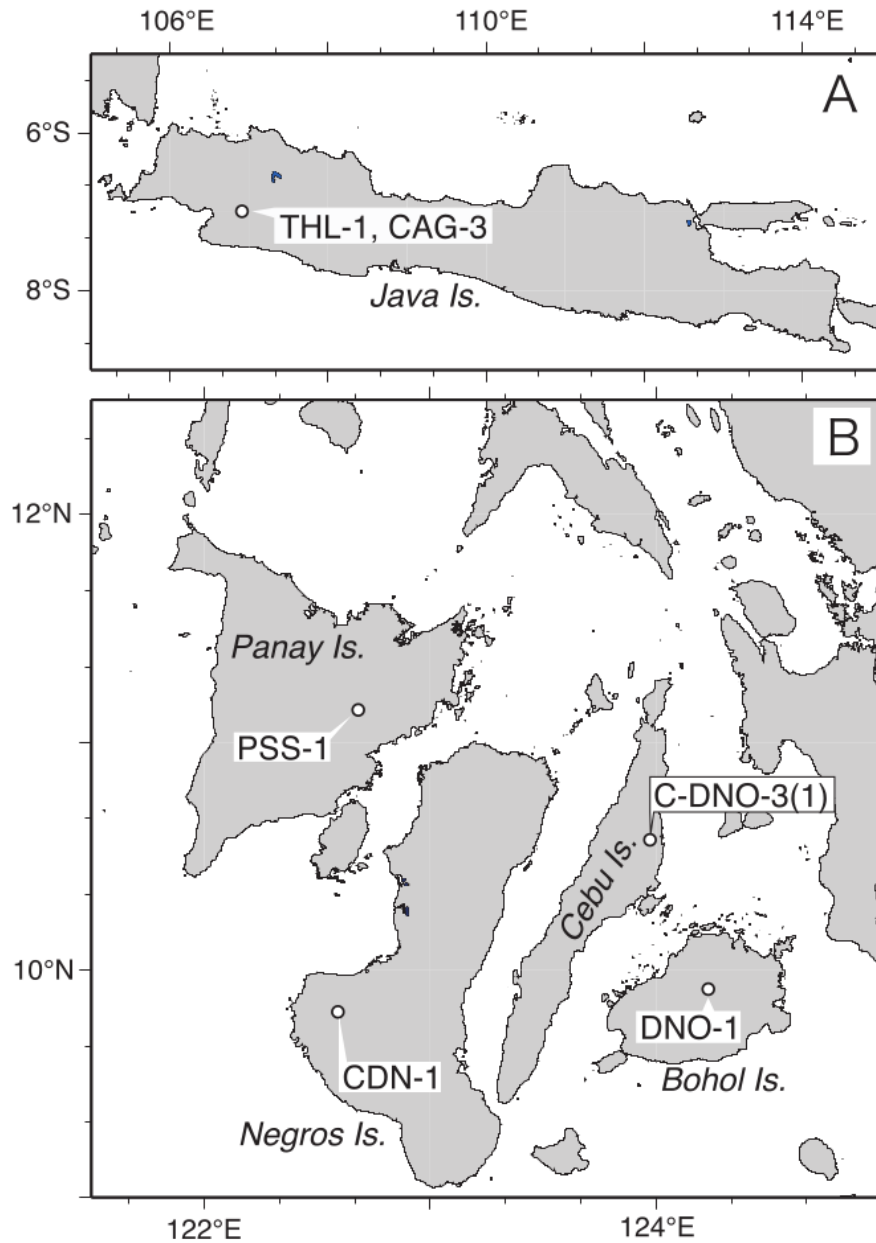
**THL-1.**—A creek bank in Tjitalahab valley in the Nyalindung area of Pelabuhanratu, West Java, Indonesia (7°01'16.3"S, 106°56'35.2"E); Nyalindung Formation (Figure 1A). According to our survey, the Nyalindung Formation exposed in the Tjitalahab valley is about 220 m thick. The lower to middle part of the formation consists of dark sandy siltstone and calcareous sandstone, and contains diverse shallow marine mollusks such as conid, cerithiid and nassariid gastropods, arcid and tridacnid bivalves, and branching corals, suggesting a deposition in a tropical lower intertidal to upper subtidal environment. Oostingh (1938) designated the Nyalindung Formation as the stratotype of the Preangerian Stage, an Indonesian Neogene stage approximately equivalent to the middle Miocene (Bemmelen, 1972). Recently, Batenburg *et al.* (2011) suggested an age of ~10–13 Ma (late Serravallian to earliest Tortonian) for the Nyalindung Formation based on larger foraminifers from the nearby locality Tjiangsana. Planktic foraminifers are very few in this formation and all we found are not age-diagnostic. However, a nannofossil analysis by one of the authors has shown that the mollusk-bearing lower to middle part of the formation in the Tjitalahab valley contains the marker species *Discoaster hamatus*, indicating Martini's (1971) NN9 nannofossil zone (*ca.* 10 Ma; early late Miocene) (A. G. S. Fernando, unpublished data).

**CAG-3.**—A small exposure in a small creek, Tjikantjaora, in Tjiangsana village in the Nyalindung area (7°01'53.3"S, 106°55'47.4"E), about 2 km southwest of locality THL-1; Nyalindung Formation (Figure 1A). Calcareous siltstone with larger foraminifers, interbedded with dark silty sandstone. The age is probably the same as THL-1.

**C-DNO-3 (1).**—An abandoned small-scale coal-mining operation, Sitio Capilyahan, Masaba, Danao City, Cebu, Philippines (10°33'18.3"N, 123°57'48.3"E) (Figure 1B). This site appears to be the same as F272 of Smith (1913; Kanno *et al.*, 1980), where Smith (1913, pl. 6, fig. 5) illustrated a fragmentary specimen of *Megistocerithium magoi* Kase gen. et sp. nov. Gray, bituminous sandy siltstone spoil from the mine contains the potamidid *Vicarya verneuili* and small mollusks such as conids, cypraeids, and turrids. Kanno *et al.* (1980) mentioned the occurrence of *Telescopium* and fragments of brackish-water shells from this site, suggesting deposition in an intertidal flat beside a mangrove forest. The site was mapped as the lower Miocene Malubog Formation (Mines and Geosciences Bureau, 1983), and A. G. S. Fernando (unpublished) identified *Sphenolithus belemnoides* among others, indicating that the sediments from this site are within the NN3 nannofossil zone, early Miocene in age.

**CDN-1.**—A creek bed in Palaka Creek, Sitio Palaka, Barangay Bactolon, Sipalay City, Negros Occidental, Philippines (9°48'43.4"N, 122°34'49.6"E) (Figure 1B). Basal part of an unnamed formation consisting of dark-gray silty sandstone interbedded with a thick coal bed in the lower part. Mollusks are prolific, beautifully preserved, and appear to be autochthonous in origin without any indication of strong currents during the deposition. Dominant mollusks are three potamidid species (*Menkrawia callosalabiata*, *Tympanotonus beberkirianus*, and *Vicarya verneuili*), and small cerithiids, *Thais* sp., *Volema* spp., small conids, and oysters. Additionally, *Telescopium titan*, *Rhizophorimurex capucinus* and *Terebralia* sp., whose modern species or congeners are dwellers in mangrove swamps, were also found. The sedimentary facies and fossil mollusks suggest that the mollusk-bearing beds in this locality were deposited on an intertidal flat within or close to a mangrove forest.

H. Hayashi (unpublished) identified planktic foraminifers from the topmost bed of this unnamed formation including age-diagnostic species such as *Menardella praemenardii* and *Paragloborotalia siakensis*, indicating a middle Miocene age spanning 14.50 Ma to 11.50 Ma according to Tian *et al.* (2008). Additionally, A. Gil S. Fernando (unpublished) identified the nannofossil *Sphenolithus heteromorphus*, among others, from a sandy siltstone bed slightly below the topmost bed. This species ranges from Martini's (1971) NN4 to NN5, 17.90 Ma to 13.83 Ma according to Tian *et al.* (2008). In summary,



**Figure 1.** Collecting sites of *Megistocerithium magoi* Kase gen. et sp. nov. in Java, Indonesia (A) and Visayan islands of Philippines (B).

the upper part of the unnamed formation ranges in age from 14.38 Ma to 13.83 Ma, late Langhian.

*DNO-1*.—Bank of the Camansihan Creek, Barangay Poblacion, Danao municipality, Bohol, Philippines

(9°56'27.2"N, 124°13'03.0"E) (Figure 1B). An unnamed formation consisting of dark-gray silty sandstone with mollusks and stony corals (family Poritidae), suggesting an intertidal to upper subtidal environment. Fernando *et*

*al.* (2008) has shown that the formation can be assigned to Martini's (1971) NN11 zone (*ca.* 8 Ma, late Miocene) based on nannofossils.

*PSS-1*.—A small sand quarry in Barangay Bacuranan, Passi City, Panay, Philippines (11°08'35.8"N, 122°39'03.7"E) (Figure 1B). Dingle Formation. Calcareous silty sandstone about 10 m thick, with a 40 cm-thick lignite bed at the base. The sandstone contains cerithiid, conid and large strombid gastropods and fragments of corals, all allochthonous in occurrence, suggesting deposition in a shallow marine environment. Mines and Geosciences Bureau (2010) assigned the Dingle Formation to the upper Miocene, and H. Hayashi (unpublished) identified *Globorotalia plesiotumida* and *Globoturborotalia nepenthes*, among others, from this locality, also suggesting a late Miocene age between 8.58 Ma and 4.43 Ma based on Tian *et al.* (2008) and Hilgen *et al.* (2012).

### Systematic description

(Tomoki Kase)

?Family Eustomatidae Cossmann, 1906  
Genus *Megistocerithium* Kase gen. nov.

**2** *Type species*.—*Megistocerithium magoi* Kase sp. nov. from the Miocene of Java, Indonesia and the Philippines.

*Diagnosis*.—Shell very large, elongate cerithiform; later whorls seven-sided pyramidal in shape formed by juxtaposed, weakly opisthocline, prominent axial ribs. Spiral sculpture of sharp primary cords, their interspaces densely packed with one to several secondary cords, all crossed by axial ribs. Aperture elliptical, flared, plane of aperture almost orthocline to shell axis. Last whorl constricted anteriorly, with an obtuse ventrolateral varix. Outer lip thick, flaring, varix-like, beveled, and smooth within, crenate outside in accordance with strong spiral cords on last whorl; adapical end of outer lip well extended onto last whorl, forming flat triangular area, with a shallow groove due to deposition of shell material defined by a parietal plait extending from posterior anal canal. Anterior siphonal canal long, tube-like, extending antero-dorsally. Parietal area smooth with thick callus. Columellar lip covered with thick, expanded, reflected inductura, being broadly concave dorsally.

*Etymology*.—The genus name comes from the combination of the Greek *megistos*, meaning greatest, and *cerithium*, in reference to it having the largest shell size among cerithioideans.

*Remarks*.—The genus is monotypic at present. For comparison and relationship with other cerithioidean genera, see "Discussion" below.

### *Megistocerithium magoi* Kase sp. nov.

Figures 2, 3

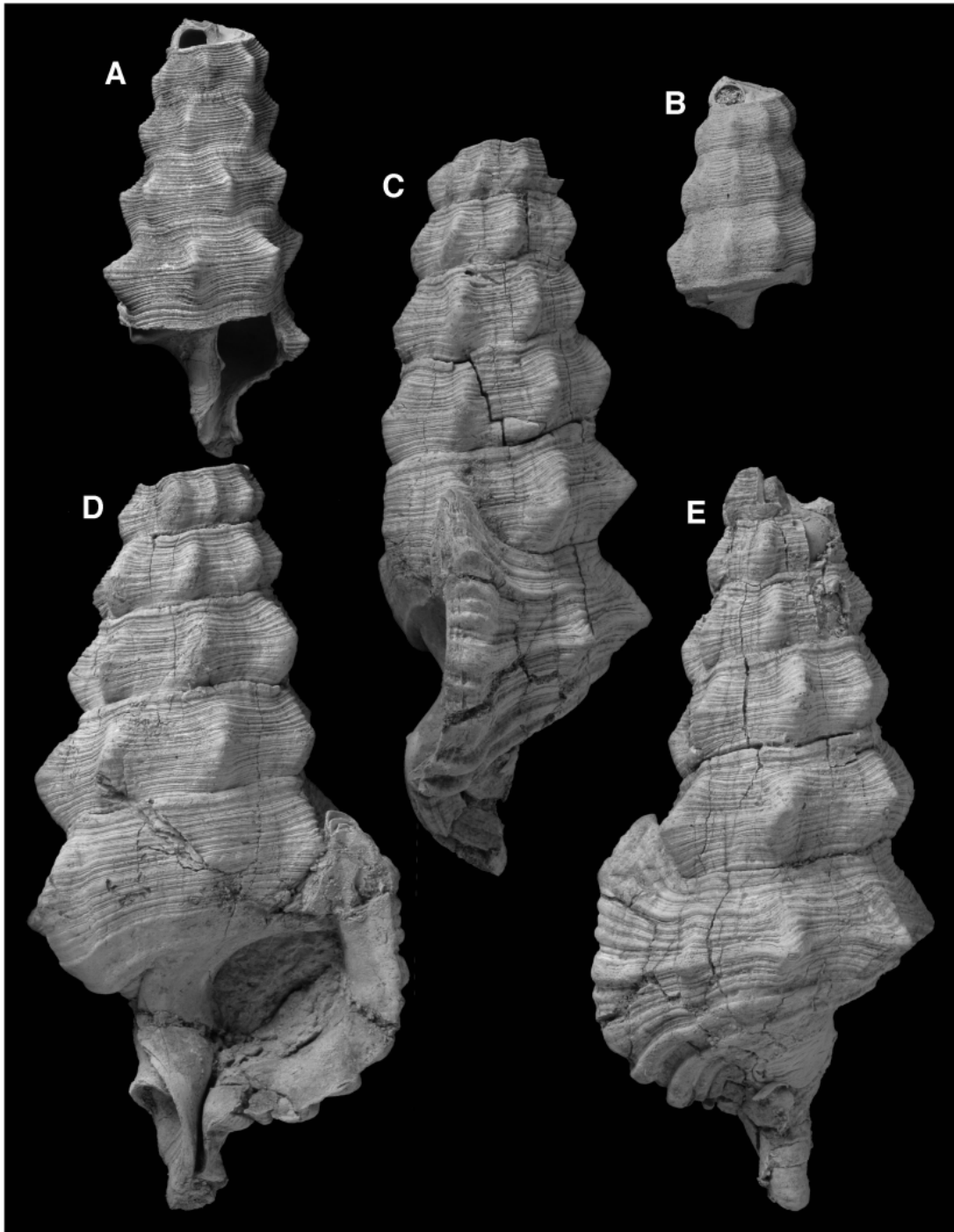
*Cerithium* (*Campanile*) sp. Smith, 1913, p. 269, pl. 4, fig. 5.  
?*Pyrazus* sp. 3. Dharma, 2005, p. 308, pl. 119, fig. 3a, b.

*Material*.—Holotype, NMNS PM26959, *ca.* 190 mm long (reconstructed), loc. CAG-1, Nyalindung Formation, late Miocene, West Java; five paratypes, NMNS PM26960–26964, fragmentary specimens, loc. THL-1, Nyalindung Formation, late Miocene, West Java; two specimens, NMNS PM26965, 26966, loc. CDN-1, middle Miocene, Philippines. Ten specimens are tentatively referred to this species: one fragmentary specimen, loc. C-DNO-3(1), NMNS PM26967, Malubog Formation, early Miocene, Philippines; eight specimens, BMNS PM26968–26975, all fragmentary, loc. PSS-1, late Miocene, Philippines; one specimen, NMNS PM26976, incomplete specimen without most of the last whorl, loc. DNO-1, late Miocene, Philippines.

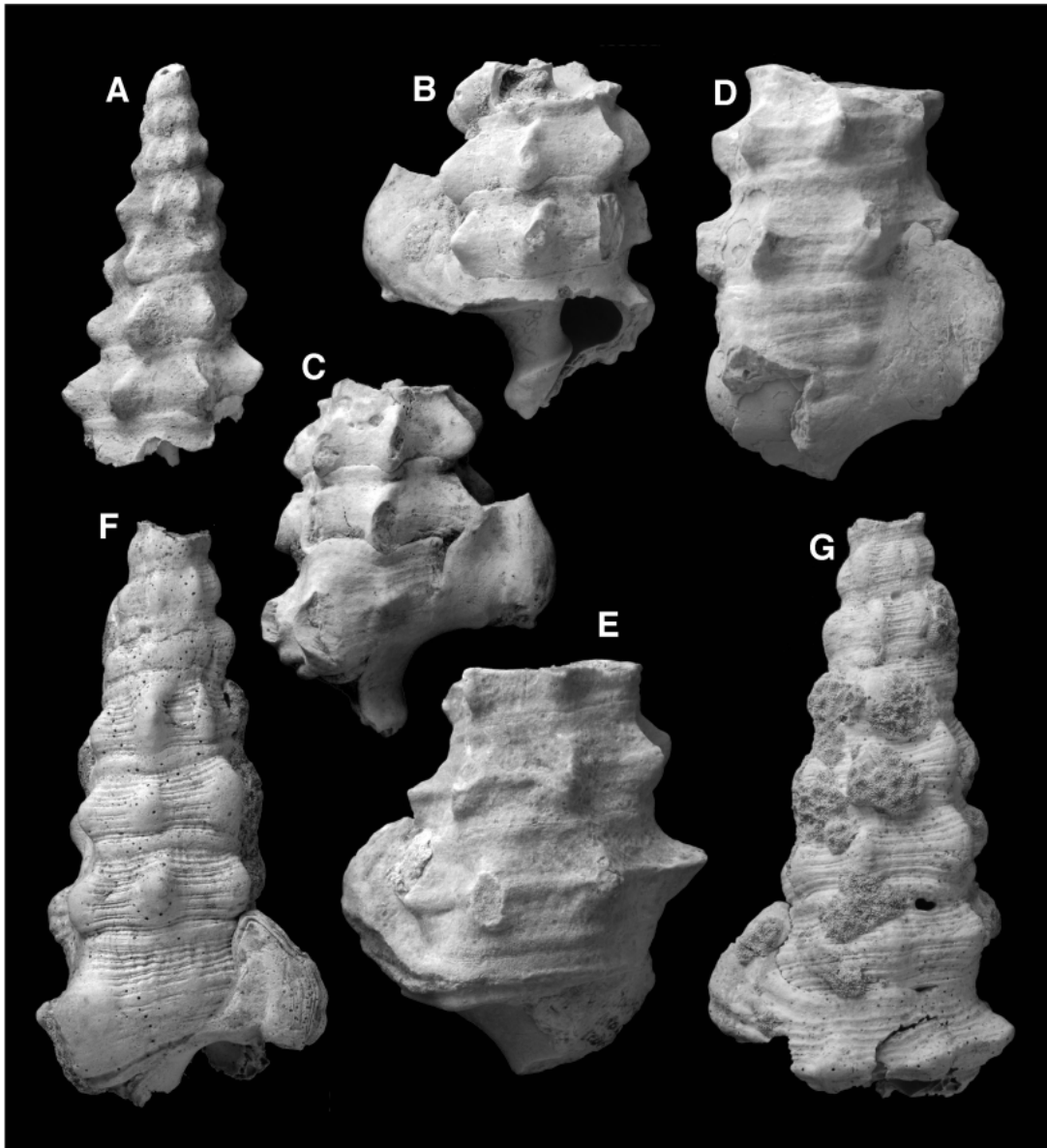
*Etymology*.—Named after Wency Mago of Mining and Geosciences Bureau, Quezon City, Philippines for his assistance during our more than seven years of field work.

*Diagnosis*.—Same as for the genus.

*Description*.—Holotype (Figure 2C–E). Shell of five whorls preserved, very large (probably reaching 190 mm in height if complete), high-spined, cerithiform, pleural angle about 25°. Protoconch and early teleoconch whorls missing. Suture shallow, somewhat undulated. Spire whorls weakly convex in profile. Last three spire whorls with seven prominent axial ribs and much wider interspaces; axial ribs strong, round-topped, weakly opisthocline (extent of inclination slightly variable), becoming spiny at mid-whorl toward last whorl. Spire whorls covered with dense, slightly wavy spiral sculpture, consisting of spiral cords or threads of variable prominence; those just adapical and abapical to suture and at mid-whorl more prominent than others. Last whorl with one abapically thickened ventrolateral varix located about 270° volution back from outer lip; axial ribs on last whorl spiny, becoming gradually shorter and less prominent toward outer lip; spiral cords becoming thicker, two on base and one on mid-whorl prominent. Aperture elliptical; anterior siphon long, tube-like, extending antero-dorsally, narrowly open. Parietal lip broadly concave, covered with smooth, thin callus, fading gradually into last whorl, with small parietal plate. Columella covered with thick, reflected, rimmed inductura, dorsally concave as a whole. Outer lip flared and varix-like, rugged externally, smooth and beveled within due to thick callus; adapical part of outer lip forming triangular wedge covered by thick callus, flattened dorsally, with shallow



**Figure 2.** *Megistocerithium magoi* Kase gen. et sp. nov. **A**, NMNS PM26965, shell height 78.4 mm, middle Miocene unnamed formation, Loc. CDN-1, Negros, Philippines; **B**, NMNS PM26960, paratype, shell height 46.5 mm, Nyalindung Formation, THL-1, West Java, Indonesia; **C–E**, NMNS PM26959, holotype, shell height 133.0 mm, upper Miocene Nyalindung Formation, CAG-3, West Java, Indonesia; **C**, lateral view; **D**, apertural view; **E**, adapertural view.



**Figure 3.** *Megistocerithium magoi* Kase gen. et sp. nov. **A**, NMNS PM26968, shell height 65.3 mm, upper Miocene Dingle Formation, Loc. PSS-1, Panay, Philippines; **B**, **C**, NMNS PM26969, shell height 58.5 mm, upper Miocene Dingle Formation, Loc. PSS-1, Panay, Philippines; **B**, adapertural view; **C**, apertural view; **D**, **E**, NMNS PM26967, shell height 67.6 mm, lower Miocene Malubog Formation, Loc. C-DNO-3(1), Cebu, Philippines; **D**, apertural view; **E**, adapertural view; **F**, **G**, NMNS PM26976, apertural and adapertural views, shell height 95.4 mm, unnamed upper Miocene formation, loc. DNO-1, Bohol, Philippines; **F**, apertural view; **G**, adapertural view.

groove extending from adapical notch of aperture.

*Dimensions*.—NMNS PM26959, holotype, height 133 mm, width 61.6 mm; NMNS PM26960, paratype,

height 46.5 mm, width 27.1 mm; NMNS PM26965, paratype, height 78.4 mm, width 36.3 mm; NMNS PM26969, height 58.5 mm, width 49.6 mm; NMNS PM26976,



height 17.95.4 mm, width 47.8 mm.

**Remarks.**—The occurrence of this species is very infrequent both in Java and in the Philippines. Other than the holotype and the five paratypes, Smith (1913, pl. 6, fig. 5) illustrated a fragmentary specimen identified as *Cerithium (Campanile)* sp. from Cebu, Philippines and Dharma (2005, pl. 119, fig. 3a, b) illustrated two specimens of this species identified as *?Pyrazus* sp. from the Nyalindung Formation in Tjitalahab, West Java. We here refer eleven fragmentary specimens from three localities in the Philippines to this species, ranging in age from the early to late Miocene. Two specimens from the unnamed middle Miocene formation at locality CDN-1, Negros have six and four preserved whorls, respectively, and are sculptured with densely packed fine spiral cords, as on the holotype and paratypes from Java (Figure 2A). In these specimens, the axial ribs are more angulated at the mid-whorl compared to the early whorls on the holotype. However, this difference is too minor to separate the specimens from CDN-1 as a different species.

We tentatively refer the ten fragmentary specimens from the three localities in the Philippines to *Megistocerithium magoi* Kase gen. et sp. nov. (Figure 3A–G). NMNS PM30009 from the Malubog Formation at locality C-DNO-3 (1) is a silicified specimen with only three preserved whorls including the posteriorly expanded outer lip of the last whorl (Figure 3D, E). The spiral sculpture of this specimen is composed of thick cords, unlike the densely packed fine spirals in addition to some thicker cords in the holotype. However, in silicified specimens found in coal-mining sites in the Philippines, the surface shell layer of many gastropods is unsilicified and easily eroded away, particularly in float specimens. We suggest that NMNS PM26967 is a case of such selective silicification and subsequent erosion.

Seven specimens from the upper Miocene Dingle Formation at locality PSS-1 are all fragmentary and their shell surfaces are strongly eroded. Two of the specimens have a preserved last whorl and have a posteriorly expanded outer lip as in the holotype (Figure 3B, C). The densely packed fine spiral cords still remain but are obscure in three specimens, and the axial ribs are pyramidal in early spire whorls with seven ribs per whorl (Figure 3A). In these specimens the axial ribs are laterally flattened unlike those in the holotype.

One specimen, NMNS PM26976, from the unnamed upper Miocene formation at locality DNO-1 in Bohol, has seven preserved whorls including the last whorl and a posteriorly expanded outer lip (Figure 3F, G). The shell surface is sculptured with densely packed fine spiral cords and strong axial ribs. However, the shell is more slender, the crests of the axial ribs are more rounded and not angulated at the middle of the whorls, and the spiral

band below the suture is thicker than those of the holotype. Taking a wide variability of shell sculpture in cerithioidean gastropods into consideration (e.g. Houbriek, 1992), it seems likely that the differences are within the morphological variation of *Megistocerithium magoi* Kase gen. et sp. nov.

To the best of our knowledge, no species definitely congeneric to *Megistocerithium magoi* Kase gen. et sp. nov. is known from the Cenozoic and Mesozoic formations or modern seas. *Pyrazus protebeninus* Vredenburg, 1928 from the lower Miocene of Gaj in Sindh, Pakistan, resembles *M. magoi* Kase sp. nov. Harzhauser (2007) reassigned *P. protebeninus* to the genus *Pyrazisinus* Heilprin, 1887, and also suggested that it was closely related to *Pyrazisinus monstrosus* (Grateloup, 1847) (Lesport and Cahuzac, 2002). Two specimens illustrated by Vredenburg (1928, pl. 18, figs. 6, 7) may attain well over 100 mm in shell length when complete, and have eight prominent opisthocline axial ribs that are raised into spines where they are crossed by rather strong spiral cords. However, assignment of this Pakistan species either to *Pyrazisinus* or to *Megistocerithium* Kase gen. nov. is difficult because the shells of the Pakistan species are too poorly preserved and their apertures are completely missing.

## Discussion

**Generic comparison to Cenozoic cerithiform gastropods.**—*Megistocerithium magoi* Kase gen. et sp. nov. is remarkably large. Cerithiform gastropods (gastropods of widely separated taxonomic groups similar in shell form to the genus *Cerithium*; Sälgeback and Savazzi, 2006) that approximate or exceed the shell height of this genus are known sporadically from the Cenozoic. A well known example is *Campanile giganteum* (Lamarck, 1804) from the Eocene of France, which attains over a meter in length, while during the Neogene and Quaternary, the largest species of *Campanile*, *C. symbolicum* Iredale, 1917 from the Pleistocene to Recent of southwestern Australia, is 244 mm long (Houbriek, 1981, 1984). *Campanile* is currently classified as Campanilidae of the superfamily Campaniloidea based on its anatomical characters (e.g. Szprunar, 1988; Healy and Wells, 1998). *Campanile* is similar in shell characters to species of the superfamily Cerithioidea but differs in having an unflared opisthocline outer lip that sweeps backwards in a broad sinus abapical to the suture, and a calcified periostracum (usually not preserved in fossil species). *Megistocerithium* Kase gen. nov. is not related to *Campanile* because the outer lip is expanded and almost orthocline, without the backward-directed sinus abapical to the suture.

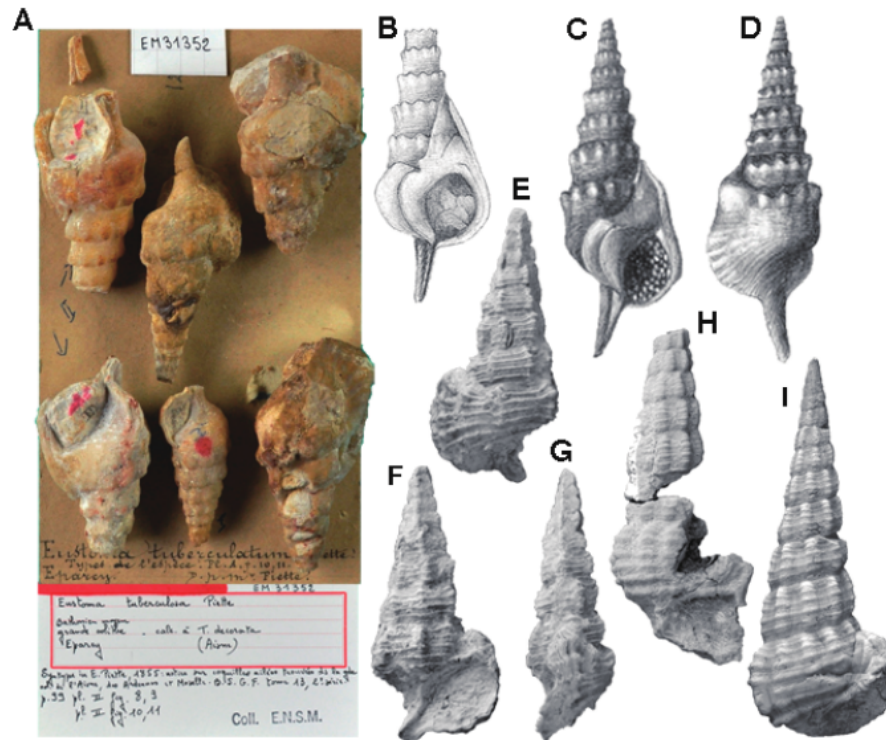
The younger Cenozoic shallow-marine carbonate sedimentary basins of southern Australia are known for the occurrence of large cerithiform gastropods (Ludbrook, 1971). Aside from two campanilid species, *Thericium* (*Chavanicerithium*) *torri* (Tate, 1899), *Thericium* (*Chavanicerithium*) *pritchardi* (Harris, 1897) and *Jetwoodsia* *apheles* (Tenison-Woods, 1879) reach over 100 mm in length. These species have a short, twisted anterior siphon and an unflared, simple outer lip, indicating that they are not related to *Megistocerithium* Kase gen. nov. In modern seas, the largest cerithiid species is *Pseudovergatus* (s. s.) *nobilis* (Reeve in Sowerby, 1855) in the tropical Indo-West Pacific, which reaches up to 167 mm in length (Houbriek, 1978). This species is not congeneric with *Megistocerithium* Kase gen. nov. as it has a smooth shell, a simple, unflared outer lip and a short twisted anterior canal. *Cerithium nodulosum* Bruguière, 1792 (type species of the genus) in the tropical Indo-West Pacific reaches 114 mm in length (Houbriek, 1992), has a slightly flared outer lip and thick axial ribs that are nodulous on later whorls as in *Megistocerithium magoi* Kase gen. et sp. nov., but this similarity is only superficial. The aperture has a distinct spout at the anal canal, the outer lip has deep spiral grooves interiorly and a claw-like anterior extension that crosses over the short anterior siphonal canal slightly reflexed to the left in *C. nodulosum*. In contrast, the anal canal is indistinct and the outer lip is smooth within and merges into the anteriorly extended siphonal canal in *M. magoi* Kase gen. et sp. nov. *Megistocerithium* Kase gen. nov. has a remarkable shell character unknown in Cerithiidae: a triangularly projected posterior margin of the outer lip lined internally with thick callus deposits and a shallow furrow within, indicating that this new genus may not belong to Cerithiidae.

Cerithiform gastropods with an expanded outer lip such as *Megistocerithium* Kase gen. nov. are also known in Potamididae and Batillariidae. The best example is the Miocene potamidid genus *Vicarya* d'Archiac and Haime, 1854, thought to have been an inhabitant of mangrove swamps in Southeast Asia and Japan (e.g. Oyama, 1950; Chinzei, 1978; Tojo and Masuda, 1999). Like *Megistocerithium* Kase gen. nov., the outer lip of *Vicarya verneuli* (d'Archiac, 1851) and *V. yokoyamai* Takeyama, 1933 is well expanded posteriorly to form a triangular projection with a thick callus lining internally and a shallow furrow within (Kanno, 1986; Sälgeback and Savazzi, 2006, fig. 13D). *Vicarya* clearly differs from *Megistocerithium* Kase gen. nov. in having a very short siphonal canal, a claw-like basal lip, a remarkable knob-like swelling of callus on shell base and a different type of shell sculpture that consists of a subsutural spiral row of spiny tubercles and some beaded spiral cords. *Pyrazus*

*ebeninus* (Bruguière, 1792), the largest modern species of Batillariidae, living in the tidal flats and estuaries of Australian and Tasmanian waters, has strong axial and spiral sculpture similar to that of *M. magoi* Kase sp. nov. *P. ebeninus* also possesses a posteriorly projected outer lip but the outer lip is less extended than in *M. magoi* Kase gen. et sp. nov., and does not have a shallow groove within the interior surface. *P. ebeninus* clearly differs from *M. magoi* Kase sp. nov. in having a very short anterior siphon and a wide backward-directed sinus in the upper part of the outer lip.

*Comparison to Mesozoic cerithiform gastropods.*—As discussed above, no species considered to be congeneric with *Megistocerithium magoi* Kase gen. et sp. nov. have been found in the Cenozoic in spite of the rich fossil records of tropical faunas of this age. On the other hand, *Megistocerithium* Kase gen. nov. has apertural characters quite similar to *Eustoma* Piette, 1855, of which the type species is *E. tuberculosa* Piette, 1855 from the Bathonian (Jurassic) of France (Figure 4A). Cossmann (1906) proposed the new family Eustomatidae (as Eustomidae) with *Eustoma* as the type genus, and renamed it *Diatinostoma* because *Eustoma* and *Eustomum* Leidy, 1851 (a flatworm) appeared to be in homonymy. However, the latter name, according to Cossmann (1906), was a misspelling. Wenz (1940) regarded *Eustomum* as a senior homonym of *Eustoma*, and Williams and Richards (1968, p. 217) took the same view. However, *Eustoma* is not a homonym of *Eustomum* based on the current code (ICZN, 4th ed., 1999, Art. 32.2 and 32.5); *Diatinostoma* is, therefore, an unnecessary name.

Piette (1855) described *Eustoma tuberculosa*, accompanied with line drawings of two specimens (Figure 4B), and Piette (1856) described it again with more elaborate line drawings (Figure 7, D). Six syntypes of *E. tuberculosa*, all incomplete specimens, are stored in the Geological Collections of the University of Lyon 1, France (Figure 4A). The shell may attain over 60 mm in height, is elongate cerithiform and has a long, anteriorly extended, tube-like siphonal canal. The outer lip is well expanded, its posterior tip reaches the penultimate whorl, and the posterior portion of the outer lip forms a triangular projection. This projection is lined internally with a thick callus deposit, with a shallow groove extending from the posterior corner of the aperture to the posterior tip of the outer lip. The parietal area is covered with a thick inductura that spreads over the basal area of the last whorl. The exterior sculpture is comprised of rounded topped axial ribs on the adapical half of each whorl in addition to fine spiral cords. Although the shell size is smaller and the exterior sculpture is different, the other shell characteristics of *E. tuberculosa* fit well with those of *Megistocerithium magoi* Kase gen. et sp. nov., sug-



**Figure 4.** **A**, Six syntypes of *Eustoma tuberculosa* Piette, 1855, EM 31352, in the Geological Collections of the University of Lyon 1, France (courtesy of E. Robert); cardboard mount of syntypes 120 mm high and 70 mm wide, Bathonian of France; **B**, hand drawing of *E. tuberculosa* Piette, 1855, seemingly based on two of the syntypes (upper left and lower left in A) (after Piette, 1855, pl. 31, fig. 2); **C**, **D**, hand drawings of *E. tuberculosa* Piette (after Piette, 1856, pl. 2, fig. 10, 11); **E–G**, *Pyrazopsis* sp., previously identified by Sälgeback and Savazzi (2006) as *?Diatinostoma* sp., SMNH Mo 113872, apertural, lateral and adapertural views, shell height 43.5 mm, Upper Cretaceous of Syria; **H**, **I**, *Pyrazus? scalariformis* Nagao, 1934, Aptian Miyako Group, Japan; **H**, UMUT MM15695, shell height 69.5 mm, apertural view; **I**, UMUT MM 15694 shell height 58.8 mm, apertural view.

gesting that the two species might be related to each other.

Cossmann (1906, p. 12–13) listed ten species referable to *Eustoma* (as *Diatinostoma*) ranging in age from Bathonian to Turonian (Cretaceous). However, complete apertures are unknown in all these species, so that the assignment of these species to *Eustoma* remains unconfirmed. Hikuroa and Kaim (2007) consider the genus *Silberlingiella* Frýda and Blodgett, 2003 (originally placed in the family Purpurinidae of Littorinoidea) to be a member of *Eustoma* (11). *Silberlingiella ornata* Frýda and Blodgett, 2003 (the type species of the genus) from the Norian (Triassic) of Nevada, USA and *Silberlingiella latadyensis* Hikuroa and Kaim, 2007 from the Middle/Upper Jurassic of Antarctica are both characterized by a small, elongate, turriculate shell with a row of nodes or spines at the narrow ramp angle slightly abapical to the

upper suture, a concave and vertical whorl surface and a keeled basal periphery. According to Hikuroa and Kaim (3407), the outer lip is expanded and sinuous, and the anterior margin is notched to form an incipient siphonal canal in *S. latadyensis*. These shell characteristics in *Silberlingiella* are quite different from *Megistocerithium magoi* Kase gen. et sp. nov.

*Diatinostoma? eximium* Sayn, 1932 from the Urgonian (Lower Cretaceous) of Spain is likely to be related to *Eustoma tuberculosa* and *Megistocerithium* (12) *igoi* Kase gen. et sp. nov. In addition to the pyramidal spire whorls, the outer lip of this species is expanded onto the penultimate whorl, covered with a thick callus internally, and has a gutter-like groove extending from the posterior corner of the aperture to the posterior tip of the outer lip. Two more species worth mentioning are *Pyrazus? scalariformis* Nagao, 1934 (Kase, 1984) from the Aptian

(Cretaceous) of Japan (Figure 4H, I) and *Pyrazus stueri* Cossmann (1906) from the Coniacian (Cretaceous) of France. These two species have a pyramidal upper spire and an internally callused posterior projection of the outer lip with an indistinct shallow groove within like that of *Megistocerithium* Kase gen. nov. However, the complete anterior siphonal canal is not known in these three species.

Sälgeback and Savazzi (2006, fig. 16A) illustrated an almost complete cerithiform shell from the Upper Cretaceous of Syria and identified it as ?*Diatinostoma* sp. This specimen has five-sided pyramidal upper spire whorls, an obliquely elongate aperture rimmed with a callus deposit along the parietal and columellar arc, an expanded outer lip, an obscurely defined notch at the posterior end of the aperture, and a moderately long, twisted, open siphonal canal (Figure 4E–G). The posterior part of the outer lip appears to form a small triangular projection that is not covered by a callus deposit. This Syrian specimen has many shell characters much in common with the Eocene species *Pyrazopsis pentagonatus* (Schlotheim, 1820) and *Pyrazopsis angulatus* (Solander in Brander, 1766) except that the anterior canal is longer, suggesting that it belongs to the Batillariidae. As already pointed out by Saul and Squires (2003), the shell apertures of *Pyrazopsis quinquecostatus* (Egojan, 1955) from the Upper Cretaceous of Armenia, the type species of *Pyrazopsis* Akopjan, 1972, and of seven other Cretaceous species Akopjan (1972, 1976) referred to *Pyrazopsis* are all unknown. Therefore, it is not known whether *P. pentagonatus* and *P. angulatus* belong to *Pyrazopsis*.

Saul and Squires (2003) described a remarkable new genus and species, *Alamirifica corona*, of unknown systematic position, based on a complete specimen from the Turonian of California. Interestingly, this specimen has an elongate cerithiform shell and pyramidal upper spire whorls like the above-mentioned Cretaceous species, which Akopjan (1972, 1976) referred to *Pyrazopsis*, but surprisingly its aperture is circular and rimmed without a posterior notch and has a moderately long, closed anterior siphonal canal. Their finding suggests that, without the complete aperture, the systematic position of cerithiform gastropods with pyramidal spire whorls from the Mesozoic cannot be determined definitely.

Cossmann (1906) pointed out that species of Eustomatidae have shell characteristics (expanded outer lip and straight, tube-like anterior canal) intermediate between those of Stromboidea (Alatacea of Cossmann) and Cerithioidea. However, recent anatomical and molecular phylogenetic analyses do not support such a close relationship between Cerithioidea and Stromboidea (e.g. Colgan *et al.*, 2007). Wenz (1940) placed Eustomatidae in the Cerithioidea with a query, and Sälgeback and

Savazzi (2006) placed *Eustoma* (as *Diatinostoma*) in the Procerithiidae. More recently, Hikuroa and Kaim (2007) suggested that Eustomatidae was an ancestor of Batillariidae or Potamididae. Eustomatidae is a poorly known family based only on a few morphological characters. Therefore, the status of Eustomatidae as a family-group taxon and the reciprocal relationships with other cerithioidean families require additional information on included species and genera and morphological characters such as larval shells. We agree with Hikuroa and Kaim (2007) that Eustomatidae is either a family close to Batillariidae or Potamididae, or assume that it is a clade within Potamididae because of the morphological similarity to some members of this family.

In conclusion, *Megistocerithium magoi* Kase gen. et sp. nov. is not related to any cerithioidean species from the Cenozoic, and is possibly related to or is a relict of the poorly known Mesozoic family Eustomatidae.

*Paleoecology.*—Most modern cerithioideans are herbivores and detritus feeders (Healy and Wells, 1998), and it may have been the same for *Megistocerithium magoi* Kase gen. et sp. nov. The possible affinity to Batillariidae or Potamididae as well as the sedimentary facies and associated autochthonous mollusks of the host sediments suggest that *M. magoi* Kase gen. et sp. nov. was an intertidal sandy mudflat dweller within or close to mangrove forests. The long, antero-dorsally extended siphonal canal further suggests a semi-infaunal mode of life, but this may have been facultative because the unflattened dorsal region of the last whorl and the prominent axial sculpture appear unsuitable for continuous burrowing in sediment (Sälgeback and Savazzi, 2006). The shallow groove in the triangular projection of the outer lip may have functioned as an exhalent sinus during an inactive semi-burrowing phase.

*Megistocerithium magoi* Kase gen. et sp. nov. is very large and is suggested to have been a dweller within or close to mangrove swamps. Today, the potamidid species *Terebralia palustris* and *Telescopium telescopium* and the corbiculid bivalve *Geloina* are core species in the Indo-West Pacific mangrove molluscan communities (Plaziat, 1984, 1995; Plaziat *et al.*, 2001), and are extraordinarily large compared with other potamidid species and bivalves in the community. Analogous assemblages with large potamidids (e.g. *Telescopium titan* Martin, 1890a and *Terebralia wichmanni* Martin, 1890b) and *Geloina* (e.g. *G. stachi* Oyama, 1950) are known from deposits of the latest Oligocene onwards in the Philippines (Iwasaki, 1970; Kanno, 1986; unpublished data) and from the middle Miocene of Japan (Oyama, 1950; Chinzei, 1978; Itoigawa, 1978; Ozawa *et al.*, 1986; Tsuda *et al.*, 1986; Inoue, 2007; etc.), whereas *Terebralia* and other potamidid gastropods during the Paleogene are not as large

as those from the Miocene onwards (e.g., Kowalke, 2001, 2003; *Terebralia subcorvina* is an exception). Interestingly, ecological observations and isotope and fatty acid marker analyses have demonstrated that in modern mangrove swamps, these large mollusks exploit food resources mostly from mangrove litter such as leaves and fruits or detritus derived from mangrove trees (Alexander *et al.*, 1979; Nishihara, 1983; Rodelli *et al.*, 1984; Houbriek, 1991; Slim *et al.*, 1997; Bachok *et al.*, 2003; Bouillon *et al.*, 2004; Fratini *et al.*, 2004). Vermeij (2011, 2012) discussed how the body size of the largest species in shallow marine molluscan guilds (group of species with a similar habit and trophic role) reflects the relative amount of available food supply, and that a change in the maximum size within a guild over time chronicles a change in productivity. We here suggest that the appearance of large mangrove mollusks from the latest Oligocene onwards indicates an increase in mangrove litter in the tropical West Pacific. We assume that *M. magoi* Kase sp. nov. was another gastropod exploiting mangrove litter as a major food resource during the Miocene.

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