

The Gastropod Genus *Nerita* in the Neogene of Tropical America

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The neritid neritaemorph gastropod genus *Nerita* Linnaeus, 1758, is represented by two new species in the Cantaure Formation (Early Miocene: Burdigalian) of Venezuela. *Nerita* (*Nerita*) *rugulosa* n. sp. is the earliest known member of *Nerita* s.s., a clade of tropical American species that also includes the Recent West Indian *N. peloronta* Linnaeus, 1758, and *N. versicolor* Gmelin, 1791, and the eastern Pacific *N. scabricosta* Lamarck, 1822. *Nerita rugulosa* differs from these species by having fewer, more prominent spiral ribs and a conspicuously ridged, pustulose septum. *Nerita* (*Theliostyla*) *paucigranosa* n. sp. is related to the Recent western Atlantic *N. fulgurans* Gmelin, 1791, and the eastern Pacific *N. funiculata* Menke, 1850, but differs from these species by its larger size and by having fewer, more prominent septal pustules. We report *N. (T.) exuvioides* Trechmann, 1935, previously known from the Point Hilaire beds of Carriacou and the Gatun Formation of Panama, from the Baitoa Formation (early Middle Miocene) of the Dominican Republic. *Nerita oligopleura* Dall & Ochsner, 1928, from the Pliocene of the Galápagos Islands, is here tentatively assigned to the subgenus *Ilynerita* von Martens, 1887. Members of the *Nerita ascensionis* Gmelin, 1791, complex in the southwest Atlantic are removed from *Theliostyla* Mörch, 1852, and recognized as related to *N. magdalenae* Gmelin, 1791, from the southwestern Indian Ocean. *Nerita magdalenae* Collignon & Cottreau, 1927, from the Miocene of Madagascar, is renamed *N. valdespinosa*. We assign *Nerita chilensis* Philippi, 1887, from the Navidad Formation of Chile, to the subgenus *Lisanerita* Krijnen, 2002; and we more tentatively assign *Nerita joaquinensis* Addicott, 1970, from the Round Mountain Silt (Middle Miocene) of California to the same subgenus.

KEY WORDS: *Nerita*, systematics, new species.

Introduction

Gastropods characteristic of the rocky intertidal zone are infrequently encountered in the fossil record, but the extremely rich fauna of the Cantaure Formation (Early Miocene: Burdigalian) of Venezuela contains a diverse assemblage of well preserved, hard-bottom, intertidal to shallow-subtidal species of notably modern aspect. These include species of *Thais*, *Acanthais* (as *Stramonita* in Vermeij, 2001), *Stramonita*, *Plicopurpura*, *Neorapana*, *Microrhytis*, *Ocinebrina*, *Macron*, *Hesperisternia*, and various limpets, among others (Jung, 1965; Gibson-Smith *et al.*, 1997; Vermeij & Vokes, 1997; Vermeij, 2001, 2006). An additional rocky-shore genus in the fauna is *Nerita*. Jung (1965) identified the single species he encountered in the Cantaure Formation as *N. fulgurans* Gmelin, 1791, a Recent West Indian species. Here we describe this form as the new species *Nerita* (*Theliostyla*) *paucigranosa* n. sp., and name a second, hitherto unknown form as *N. (Nerita) rugulosa*

n. sp., a phylogenetically informative taxon in *Nerita* s.s., an exclusively tropical American clade. To place these taxa in a broader context, we review other known Recent and Neogene fossil species of *Nerita* in tropical America and comment on the taxonomic assignments and nomenclature of several other species.

Materials and Methods

Most of the fossil material we examined is in the Landau collection, but we have also examined specimens at CAS (California Academy of Sciences, San Francisco) and UCMP (Museum of Paleontology, University of California, Berkeley). All Recent material discussed is in the Vermeij collection.

Shell dimensions measured are as follows: major diameter D_1 more or less perpendicular to the shell's axis of coiling;

minor diameter D_2 more or less parallel to the axis of coiling; and height H , distance from dorsal surface to base. Relative height was calculated as $R = H(D_1 \times D_2)^{1/2}$.

Shell Morphology

In describing shells of the genus *Nerita*, we employ a slightly different terminology from that used by previous authors. In nerites, the outer lip is in the form of a loose spiral, whose growing end is at the adapical end of the shell ventral to the apex. In the abapical direction, the spiral extends around to the abapical end of the aperture and then continues as a more or less distinct ridge. This ridge, which we call the abapertural ridge, marks the abapertural limit of the septum and peters out on the adapical side of the septum. We use the term septum for the convex, flat, or concave surface adjacent to the aperture on the ventral surface of the shell. Other authors have referred to the septum as the parietal shield or columellar area. The abapertural ridge is absent or extremely indistinct in species of the subgenera *Amphinerita* von Martens, 1887, and *Linnerita* Vermeij, 1984. In fact, in *Nerita umlaasiana* Krauss, 1848 (type species of *Amphinerita*) and related Recent Indo-West Pacific species, the septum is covered with an extensive, glossy-smooth callus that extends onto the dorsal side of the last whorl opposite the aperture. This case of partial shell envelopment was overlooked by Vermeij (2005) in his survey of enveloped molluscs.

In adults of many species of *Nerita* s.l., the septal surface is sculptured with ridges that run from the septal edge of the aperture to the abapertural ridge. These are here called septal ridges. In most cases, these ridges are expressed only on the abapical half to two-thirds of the septal surface. In many groups, the ridges bear granules or pustules. The apertural edge of the septum often bears denticles, but these do not bear a relationship to the septal ridges. In juvenile specimens, septal ridges, septal denticles, and denticles on the inner thickened edge of the outer lip are often absent.

Systematic Paleontology

Genus *Nerita* Linnaeus, 1758

Type species — *Nerita peloronta* Linnaeus, 1758, Recent, West Indies (see Abbott, 1958).

Subgenus *Nerita* Linnaeus, 1758

Remarks — The taxon *Nerita* is based on the Recent West Indian “bleeding tooth”, *Nerita peloronta*, a species living high in the intertidal zone on rocky shores in the West Indies. This species is uniquely characterized by two strong, protruding septal denticles; a concave, nearly smooth septum; and an operculum whose outer surface is marked by a smooth central depression surrounded by a smooth spiral thickening. Most modern authors have considered *Nerita*

s.s. to be monotypic (Vermeij, 1984; Krijnen, 2002). The West Indian *N. versicolor* Gmelin, 1791, has generally been assigned to the subgenus *Ritena* Gray, 1858, a taxon based on the Recent Indo-West Pacific *N. plicata* Linnaeus, 1758 (see Krijnen, 2002); whereas the eastern Pacific *N. scabricosta* Lamarck, 1822, has been placed in either *Ritena* (Keen, 1971) or *Cymostyla* von Martens, 1887, whose Indo-West Pacific type species (*Nerita undata* Linnaeus, 1758) has recently been clarified (Krijnen, 2002; Krijnen *et al.*, 2006).

Molecular phylogenetic analyses now show, however, that Recent high-spired forms of *Nerita* in tropical America form a strongly supported monophyletic clade comprising *N. peloronta*, *N. versicolor*, and *N. scabricosta*. Within this clade, the West Indian *N. peloronta* appears as a sister species to the West Indian *N. versicolor*; together, these species are sister to the eastern Pacific *N. scabricosta* (M. Frey, in preparation). All members of the clade inhabit the upper rocky shore. They have two median teeth as well as a square adapical tooth on the septal edge. The septal surface is typically sculptured with irregular ridges, although in *N. peloronta* it is more or less smooth. The denticles inside the outer lip are always present in adults. In *N. versicolor* and *N. rugulosa* n. sp. (see below), the adapical-most tooth on the outer lip is enlarged and ventrally protruding; in the other species, the enlarged protruding tooth is abapical to a small tooth.

Morphologically, shells of *Nerita* s.s. very closely resemble those of *Cymostyla*. The only consistent difference between these two groups is that the abapical-most outer-lip tooth in *Nerita* s.s. is somewhat enlarged (though not as much as the adapical-most tooth), whereas in species of *Cymostyla* the abapical-most tooth is not enlarged. *Nerita* s.s. resembles *Ritena* in many characters as well, including the heavily ridged septum, number and prominence of teeth on the septal margin, and enlargement of the abapical and adapical teeth. *Nerita* s.s., however, has more numerous outer-lip teeth and spiral ribs. *Nerita versicolor* converges in apertural characteristics on *N. (R.) plicata*, but its apertural teeth are more numerous and smaller, and the teeth on the abapical and adapical end of the outer lip protrude much less than in *N. (R.) plicata*. The new species *N. rugulosa* described below has the high spire, septal ridges, and apertural teeth of Recent members of *Nerita* s.s., and therefore appears to fall within the *Nerita* s.s. clade as defined by molecular criteria. It represents either a direct ancestor or a sister species to the Recent members of *Nerita* s.s.

Regardless of the exact placement of *N. rugulosa* n. sp., the new fossil species yields additional insights into the biogeographic history of high-spired *Nerita* in tropical America. Contemporary geographic ranges of *N. peloronta* and *N. versicolor* extend across the tropical western Atlantic from Bermuda and the east coast of Florida throughout the West Indies to the mainland coast of northern South America (Russell, 1941). *Nerita scabricosta* ranges in the eastern Pacific from the west coast of Baja California and through-

out the Gulf of California to northern Peru (Keen, 1971). While sister species from the Atlantic and Pacific coasts of tropical America often reflect divergence resulting from the uplift of the Isthmus of Panama during the Pliocene, large genetic distances among the Recent species of *Nerita* s.s. indicate that the split between the *N. scabricosta* and *N. peloronta/versicolor* groups is much more ancient (M. Frey, in preparation). Indeed, fossil specimens of *N. scabricosta* have been reported from the Latrania Formation (Late Miocene) of southern California (Deméré & Rugh, 2006), indicating the presence of that species well before the formation of a continuous Panamanian land bridge. *Nerita rugulosa*, which is morphologically closer to *N. versicolor* than to the other species in the tropical American clade, pushes the first appearance of the clade — and perhaps the divergence between *N. peloronta* and *N. versicolor* — back to at least the Early Miocene.

***Nerita (Nerita) rugulosa*, n. sp.**

Figures 1-3

Diagnosis — A small, globose *Nerita* with 16 to 18 strongly expressed spiral ribs, well-developed septal ridges, and two strongly expressed pustules on abapical septal ridges.

Description — Shell small for clade, maximum major diameter 22.5 mm, globose (relative height 0.69 to 0.76, mean 0.725); last whorl convex, evenly rounded, bearing 17 to 18 sharp spiral ribs; outer lip thickened within, bearing 12 to 13 denticles; adapical-most denticle largest, protruding ventrally; abapical-most denticle also somewhat enlarged; septal edge with square adapical tooth and two prominent medial teeth; septal surface flat to slightly convex, bearing seven to nine prominent ridges, the abapical five of which bear two well-expressed pustules each; abapertural ridge rounded, indistinct; spire protruding.

Holotype — NHMW 2007z0169/0001: Major diameter 21.1 mm, minor diameter 16.6 mm, height 13.8 mm.

Paratype — Major diameter 22.5 mm, minor diameter 18.9 mm, height 14.2 mm.

Type locality — Casa Cantaure, east of San Jose, Falcón State, Paraguaná Peninsula, Venezuela.

Distribution — Cantaure Formation (Early Miocene: Burdigalian), Venezuela.

Etymology — Latin: roughened, referring to the external sculpture and the well expressed septal ridges.

Remarks — *Nerita rugulosa* n. sp. is a distinctive member of the tropical American clade of *Nerita* s.s., characterized by strong septal ridges bearing distinct pustules and by 17 to 18 strong spiral ribs. No species of *Nerita* s.s. has spiral ribs that are as well developed as does *N. rugulosa*.

Most similar among living species to *N. rugulosa* is *N. versicolor*. In contrast to *N. peloronta* and *N. scabricosta*, both *N. versicolor* and *N. rugulosa* have the adapical-most denticle on the inner side of the outer lip strongest and most protruding. In the other species, the strongest denticle is the second from the adapical end of the lip. *Nerita rugulosa* has 12 to 13 denticles on the outer lip, whereas *N. versicolor* has fewer (usually ten to 11, sometimes 12). The number of spiral ribs in *N. rugulosa* (17 to 18) falls within the wide range of *N. versicolor* (13 to 23). Some specimens of *N. versicolor* throughout its range have a nearly or completely smooth last whorl, with ribs (if present) confined to the adapical sector. This condition is not known in *N. rugulosa*. Available specimens of *N. rugulosa* are much smaller (maximum major diameter 22.5 mm) than *N. versicolor* (maximum 30.5 mm, west coast of Aruba, Netherlands Antilles).

Macsoy & Campos Villaroel (2001) described their new species *Nerita amplisulcata* from empty shells dredged at a depth of nine meters from near Isla Margarita, Venezuela. This taxon is characterized by having 13 strong cords and six to seven large teeth on the outer lip. We have not seen specimens, and illustrations given by the authors are poor, but it is possible that *N. amplisulcata* is a distinct species, possibly an extinct one. It differs from other Atlantic species of *Nerita*, including *N. rugulosa*, by having fewer teeth inside the outer lip.

In the eastern Pacific, shells of the *N. scabricosta* complex differ from *N. rugulosa* by having more numerous spiral ribs (23 to 33 in the typical *scabricosta* form from Mexico; 25 to 28 in the subspecies *N. s. ornata* Sowerby, 1823, from Panama; 23 to 29 in the form from the Galápagos, perhaps belonging to the subspecies *ornata*) and more numerous denticles inside the outer lip (16 to 18 in populations from Mexico to Panama, 15 to 20 in the Galápagos). Typical *N. scabricosta* from Mexico (Pacific coast of Baja California Sur, Gulf of California, Nayarit, and Jalisco) and specimens from Guanacaste Province in northwestern Costa Rica are somewhat less convex (relative height respectively 0.68 ± 0.028 , $n = 12$; and 0.66 ± 0.024 , $n = 5$) than are shells of *N. s. ornata* from Panama (0.725 ± 0.026 , $n = 13$) and the Galápagos (0.72 ± 0.036 , $n = 7$). The southern *ornata* populations are thus of about the same globosity as those of *N. rugulosa*. Like the fossil *N. rugulosa*, *N. s. ornata* has a septal surface sculpture of strongly pustulose ridges. Molecular studies show that Panamanian *N. scabricosta* differ by about 0.5% from Mexican ones but the two populations do not form reciprocally monophyletic groups (Hurtado *et al.*, 2007). *Nerita scabricosta* is one of the largest known nerites (maximum major diameter 50.0 mm, Isla Santa Cruz, Galápagos).

Nerita rugulosa co-occurs in the Cantaure Formation with *N. (Theliostyla) paucigranosa* n. sp. It can be immediately distinguished from *N. paucigranosa* by its globose, higher-spired shell, and by the outer lip dentition.

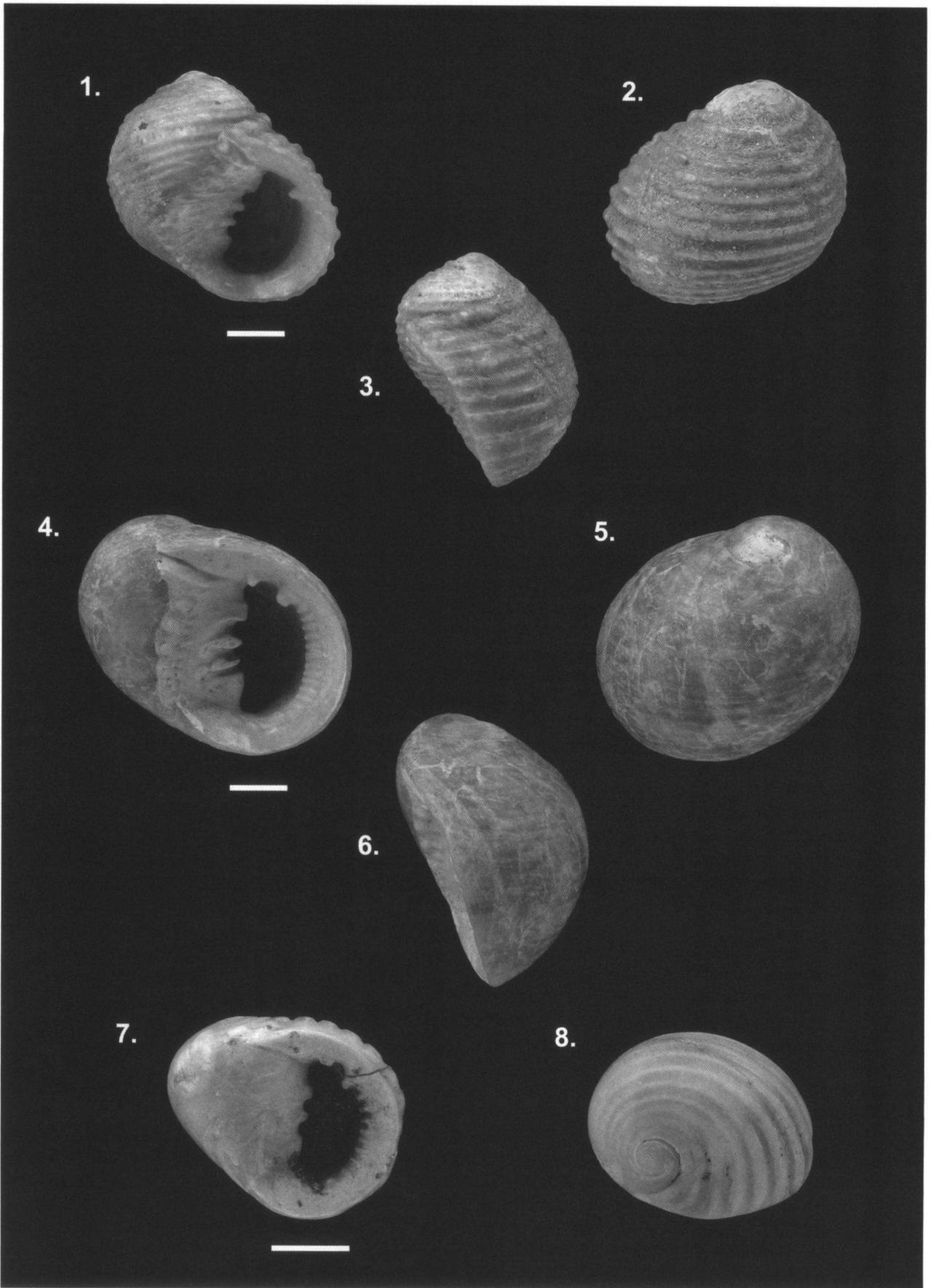


Figure 1-8.

Figures 1-3. NHMW 2007z0169/0001 *Nerita rugulosa* n. sp., holotype. Miocene, Cantaure Formation, Paraguaná Peninsula, Venezuela. Scale bar 5 mm; (1) frontal view, (2) rear view, (3) side view.

Figures 4-6. NHMW 2007z0168/0002 *Nerita paucigranosa* n. sp., holotype. Miocene, Cantaure Formation, Paraguaná Peninsula, Venezuela. Scale bar 5 mm; (4) frontal view, (5) rear view, (6) side view.

Figures 7-8. BML n.n. *Nerita exuvioides*. Miocene, Baitoa Formation, Rio Yaque del Norte, Dominican Republic. Scale bar 5 mm; (7) frontal view, (8) top view.

In *N. rugulosa*, the adapical-most and to a lesser extent the abapical-most tooth are enlarged and protruding; in *N. paucigranosa*, the adapical two teeth are enlarged. The aperture of *N. rugulosa* is relatively smaller than that of *N. paucigranosa*, and the more convex septum bears strong ridges with two pustules, whereas the septum of *N. paucigranosa* is flat to concave and has ridges with three prominent pustules. The abapertural ridge of *N. rugulosa* is much less distinct than that in *N. paucigranosa*.

Subgenus *Theliostyla* Mörch, 1852

Type species — *Nerita albicilla* Linnaeus, 1758, Recent, Indo-West Pacific.

Remarks — Three Recent tropical American species and the Recent eastern Atlantic *Nerita senegalensis* Gmelin, 1791, form a distinct clade (M. Frey, in preparation) whose members have generally been assigned to the subgenus *Theliostyla*, a taxon based on the Recent Indo-West Pacific *Nerita albicilla*. The West Indian *N. fulgurans* Gmelin, 1791, and *N. tessellata* Gmelin, 1791, the Eastern Pacific *N. funiculata* Menke, 1850, and the West African *N. senegalensis* are all characterized by a flat to concave septum, pustules on the adapical septal ridges, prominent abapertural ridge, and denticles inside the outer lip of which the two adapical-most teeth are enlarged and protruding. The septal margin bears two small central teeth. The spire is either slightly protruding or flat. All American species have spiral ribs that often bifurcate, whereas *N. senegalensis* is either entirely smooth or, in populations from Sierra Leone to Cameroon, very weakly ribbed.

The widespread Indo-West Pacific *N. albicilla*, type species of *Theliostyla*, resembles the species in the American clade in most respects. It differs slightly by having the second tooth from the adapical end of the outer lip enlarged, whereas the first tooth, though present, remains small. The septal margin bears two to three small denticles. *Nerita albicilla* tends to have weakly expressed, distant, rounded ribs, and in large adults has the edge of the outer lip polished. In the Atlantic and eastern Pacific species mentioned, the lip edge is always sharp and, where spiral ribbing is well developed, is distinctly crenulated.

Two previously described fossil species from tropical America also belong to *Theliostyla*. *Nerita exuvioides* Trechmann, 1935, from the Point Hilaire beds (Middle Miocene) of Carriacou (Trechmann, 1935) and the Gatun Formation (Late Miocene) of Panama (Vokes, 1983) has a large shell (maximum major diameter 33.0 mm) with 11 to

12 prominent, slightly overhanging spiral ribs and a finely denticulated outer lip (see also Jung, 1971). *Nerita (T.) fortidentata* Vermeij & Collins, 1988, known only from the Cayo Agua Formation (Early Pliocene) of Panama, is smaller (21.3 mm) and has 21 strong, slightly overhanging spiral ribs and very strongly expressed outer-lip teeth. Other fossils were questionably referred to *N. fulgurans* by Jung (1965, 1969). Careful examination of numerous specimens from the Cantaure Formation of Venezuela, however, persuades us that these represent a previously unrecognized species, which we here name *Nerita (Theliostyla) paucigranosa* n. sp. We also report a new occurrence of *N. exuvioides*.

Another fossil member of the clade to which the American species of *Theliostyla* belong is the Mediterranean Early Pliocene *Nerita emiliana* Mayer, 1872 (for a thorough review see Landau *et al.*, 2004). This species is extremely close to, or perhaps even identical with, the living *N. senegalensis*. It shares with *N. senegalensis* and the American forms the two prominent adapical teeth on the outer lip. Like *N. senegalensis*, the Pliocene *N. emiliana* varies from being almost wholly smooth to very weakly ribbed.

Vermeij (1970) tentatively assigned *Nerita ascensionis* Gmelin, 1791, and its subspecies *N. a. chlorostoma* Lamarck, 1816 (as *N. a. deturpensis* and *N. a. trindadeensis*, both of Vermeij, 1970) from the western South Atlantic to *Theliostyla* because of their very weakly pustulose septum and granulose operculum. This complex of forms, however, differs strikingly from *Theliostyla* in having only one strong adapical tooth inside the outer lip, in having a glossy-smooth, flat septal surface bounded abaperturally by an indistinct rounded ridge, and a flat instead of convex operculum. Shell characters indicate that *N. ascensionis* is closely related to *N. magdalenae* Gmelin, 1791, a Recent species from Mauritius and Reunion in the southwestern Indian Ocean.

We note in passing a primary homonymy of *Nerita magdalenae* Collignon & Cottreau, 1927. The latter, and Early Miocene (Aquitanian) species with strongly expressed spines from Marofototra, Madagascar, is here renamed *Nerita* (s.l.) *valdespinosa*.

Nerita (Theliostyla) exuvioides Trechmann, 1935 Figures 7-8

Nerita exuvioides Trechmann, 1935: p. 551, pl. 20, fig. 30.
Nerita (Nerita) exuvioides Trechmann: Jung, 1971, p. 175, pl. 6, figs 1-2.

Nerita (Theliostyla) exuvioides Trechmann: Vokes, 1983, p. 133, pl. 1, fig. 1a, b.

Remarks — Trechmann (1935) described *Nerita exuvioides* from an incomplete specimen from the Point Hilaire beds on the island of Carriacou in the Grenadines. Jung (1971) further discussed this species from Carriacou and inferred its age to be early Middle Miocene. Vokes (1983) described a well preserved specimen of *N. exuvioides* from the Gatun Formation (Late Miocene) of Panama.

One of us (BML) has collected an additional worn specimen of this uncommon species at Río Yaque del Norte, López section (location equivalent to NMB 17281) in the Baitoa Formation (Early Miocene) of the Dominican Republic. The specimen is small (major diameter 15.7 mm, minor diameter 13.5 mm, height 9.8 mm) and has 12 very strong ribs separated by deep interspaces. Its septum is sculptured by abapical ridges each bearing three pustules, bounded by a distinct abapertural ridge. The septal edge bears one small medial tooth. The spire is flat, and the outer lip bears ten prominent teeth on its inner surface, of which the adapical-most tooth is protruding. This specimen is considerably smaller than other known specimens (Vokes's shell from the Gatun Formation being 33.0 mm in major diameter and 28.3 mm in minor diameter). The number of ribs (12) is the same as in the Carriacou material but one more than in Vokes's specimen.

The small size, together with characters of the apertural dentition, indicates that the specimen from the Baitoa Formation is subadult. Vokes's specimen (USNM collections) of *N. exuvioides* has two very strong adapical teeth on the outer lip (as in other American species of *Theliostyla*) and two strong teeth on the central sector of the septal margin. The Baitoa specimen has just one adapical tooth enlarged and bears a single small medial tooth on the septal margin.

Nerita exuvioides differs from *N. fortidentata* Vermeij & Collins, 1988, from the Cayo Agua Formation (Early Pliocene) of Panama by having 11 or 12 instead of 21 prominent spiral ribs and by having the strongest abapical tooth in the most abapical position instead of in the third position from the abapical end.

Trechmann (1935) and Vokes (1983) drew attention to the very close similarity between *N. exuvioides* and the Recent western Pacific *N. exuvia* Linnaeus, 1758. Examination of Recent specimens of *N. exuvia* from the Philippines, Papua New Guinea, and Indonesia reveals that this species reaches a maximum size (major diameter 35.7 mm, Moti, Maluku, Indonesia) comparable to that of *N. exuvioides*. As noted by Vokes (1983), *N. exuvia* differs by having somewhat more numerous ribs (13 to 14 as compared to 11 to 12) and outer-lip teeth (15 as compared to 10). The two adapical-most teeth in *N. exuvia* are enlarged, not just one as in *N. exuvioides*. The septum has two medial teeth at its edge, and ridges bearing eight pustules each on its surface. *Nerita exuvioides* has only three pustules on the septal ridges. Another similar species is *N. textilis* Röding, 1798,

from the Indian Ocean, which, however, has fewer, almost tuberculate ribs.

Nerita (Theliostyla) paucigranosa, n. sp.
Figures 4-6

Nerita (Nerita) fulgurans Gmelin: Jung, 1965: 479, pl. 62, fig. 14.

Diagnosis — Large *Theliostyla* with 19 to 21 strong spiral ribs, 11 to 13 teeth inside the outer lip of which the two adapical-most ones are largest and often protruding, and a strongly ridged concave septal surface with three large pustules per ridge.

Description — Shell large for subgenus, maximum major diameter 32.2 mm; globose (relative shell height 0.68 ± 0.032 , $n = 20$); spire flat or very slightly protruding, eroded; last whorl with 19 to 21 strong spiral ribs; outer lip crenulated at edge, bearing 11 to 13 prominent denticles on its inner side; two adapical denticles (especially the second from the adapical end) larger than others, protruding ventrally; septum distinctly set off by abapertural ridge, concave, bearing seven to ten septal ridges each bearing up to three large pustules; septal edge with two prominent medial teeth.

Holotype — NHMW 2007z0168/0002: Major diameter 21.2 mm, minor diameter 16.4 mm, height 12.5 mm.

Paratype — NHMW 2007z0168/0001 and NHMW 2007z0160/0180: major diameter 25.4 mm, minor diameter 19.6 mm, height 15.3 mm.

Type locality — Casa Cantaure, east of San Jose, Falcón State, Paraguaná Peninsula, Venezuela.

Distribution — Cantaure Formation (Early Miocene, Burdigalian), Venezuela.

Etymology — Latin, few-grained, referring to the small number of pustules (or granules) on the septum.

Remarks — This large nerite is so similar to the Pliocene to Recent western Atlantic *N. fulgurans* Gmelin, 1791, that Jung (1965) considered it to belong to the latter taxon, although he did observe some differences. Recent specimens of *N. fulgurans* reach a somewhat smaller maximum size; the neotype, from Cartagena (Colombia), has a major diameter of 29.1 mm, whereas the largest specimen in the Vermeij collection (Jupiter, Florida) is 28.7 mm. *Nerita fulgurans* has less prominent and more numerous pustules on the septum (four to six as compared to three in *N. paucigranosa*) and usually has more numerous, much less prominent spiral ribs (16 to 35 in *N. fulgurans*, 19 to 21 in *N. paucigranosa*). The ribs in *N. fulgurans* tend to bifurcate toward the outer lip, whereas in *N. paucigranosa* they do not. The range in the number of teeth on the outer lip in *N. fulgurans* (10 to 16) encompasses that in *N. pauci-*

granosa (11 to 13). A fossil specimen of *N. fulgurans* is known from the Mao Formation (Pliocene) of the Dominican Republic (Costa *et al.*, 2001).

Another extremely similar species is *N. funiculata* Menke, 1850, from the eastern Pacific. This species, which is also known from the Latrania Formation (Late Miocene) of southern California (Deméré & Rugh, 2006), is relatively small (maximum major diameter 22.0 mm, Isla Perico, Panama), but overlaps broadly with *N. fulgurans* in number of ribs (15 to 38) and number of outer-lip denticles (nine to 14). It has more pustules on the septal surface (six to eight per septal ridge) than either *N. fulgurans* (four to six) or *N. paucigranosa* (three). *Nerita funiculata* is slightly less globose (relative shell height 0.655 ± 0.030 , $n = 7$) than either *N. fulgurans* (0.67 ± 0.020 , $n = 8$) or *N. paucigranosa* (0.68 ± 0.032 , $n = 20$).

Vermeij & Collins (1988) suggested that the species here distinguished as *N. paucigranosa* should be included in *N. fortidentata*. We reject this suggestion. The two species are indeed very similar in the number of septal pustules, spiral ribs, and outer-lip teeth; but *N. paucigranosa* has much less prominent, narrower ribs separated by shallower interspaces, a more steeply excavated septum, and different abapical teeth on the outer lip. In *N. fortidentata*, the abapical-most tooth is small, and it is the third tooth from the abapical end that is most enlarged; whereas in *N. paucigranosa*, the enlarged tooth is at the most abapical position on the outer lip.

Subgenus *Ilynerita* von Martens, 1887

Type species — *Nerita planospira* Anton, 1838, Recent, Indo-West Pacific.

Remarks — The type and only Recent species of *Ilynerita*, *Nerita planospira* Anton, 1838, resembles *Theliostyla* in shell characters but is immediately distinguished from *Theliostyla* by its entirely smooth instead of externally granulated operculum. *Nerita planospira* has a flat to immersed spire; its spiral sculpture consists of 14 to 15 prominent ribs, of which the fourth or fifth from the adapical end is somewhat enlarged to form a weak angulation. The adapical face of the shell is therefore more or less flattened. The adult outer lip is thickened within and bears 25 extremely weak denticles, none of which is enlarged. The broad septum is flat to concave and bears distinct ridges, each with four to five prominent pustules, which like the ridges are largely confined to the abapical sector of the septal surface. The septal edge uniquely bears a prominent abapical tooth, and a variably developed number (usually two, sometimes four) number of medial teeth, as well as a broad adapical tooth. In specimens from eastern Papua New Guinea, there is a prominent adapical fold on both the outer lip and the septum. This fold is weak or absent in specimens from Okinawa, the Philippines, eastern Indonesia, and Singapore. The largest specimen we have seen has a major diameter of 32.5 mm (collected by M. Frey at Nagaji-Jima, Okinawa).

Ilynerita bears some resemblance to the monotypic Recent genus or subgenus *Adenerita* Dekker, 2000, based on *Nerita adenensis* Mienis, 1978, from the southern Red Sea and Arabian Gulf. Like *Ilynerita*, *Adenerita* has an entirely smooth operculum, but *Adenerita* differs by having very weak spiral ribs and a very small, concave, finely granulated septum. *Adenerita* has two small denticles on the medial sector of the septal edge, and lacks denticles on the outer lip.

Although *Ilynerita* is represented in the Recent fauna by a single Indo-West Pacific species, the taxon appears to have had a much broader distribution in the past. *Nerita listrota* Woodring, 1973, from the Gatuncillo Formation (Late Eocene) of Panama, appears to belong to *Ilynerita* (Vermeij & Collins, 1988). It has a pustulose septum whose edge bears one abapical tooth, five medial teeth, and an adapical tooth situated at the end of an adapical septal fold. There is an angulation demarcating a nearly flat adapical shell face from the rest of the shell, as in *N. planospira*. The lip of *N. listrota* is described as “finely striate” (Woodring, 1973). Our examination of the holotype (USNM 646646) indicates that dentition on the inner side of the outer lip is obsolete, and that, as in living *N. planospira*, the abapertural ridge is indistinct.

Shells of similar form occur in Europe. These include *Nerita plutonis* Basterot, 1825, from the Late Oligocene to Middle Miocene of France; and the Middle Miocene *N. asperata* Dujardin, 1837, *N. funata* Dujardin, 1837, and *N. proserpinae* Mayer, 1895, all from the Touraine basin of France. Although the sculpture varies among and within these species, there is always an angulation separating a nearly flat adapical shell face from the rest of the shell. The outer lip in these species is thickened and smooth (not denticulate) within. The septum is pustulose, its edge typically bearing two weak central denticles. Glibert (1949, 1962) assigned these species to *Theliostyla*, presumably because of the pustulose septum. We tentatively assign these European fossils to *Ilynerita* because of the presence of the angulation and the absence of outer-lip denticles. The discovery of opercula would settle the matter.

Dall & Ochsner (1928) described a peculiar nerite from the upper (Pliocene) horizons of Seymour (= Santa Cruz) island in the Galápagos. Examination of the heavily worn holotype (CAS 2937) indicates that the spiral sculpture consists of four angulations, the abapical-most one being distant from the other three. The adapical-most angulation is the most prominent, and sets off a more or less flat adapical shell face from the rest of the shell. The septum appears to be pustulose and bears two central denticles. The outer lip appears to have one small denticle at both the adapical and abapical end, but is otherwise smooth within. This species differs strikingly from all Neogene to Recent tropical American nerites, as already noted by Dall & Ochsner (1928). It does, however, bear a close resemblance to the European species discussed in the preceding paragraph. We therefore tentatively assign *N. oligopleura* to the

subgenus *Ilynerita*.

Subgenus *Lisanerita* Krijnen, 2002

Type species — *Nerita lirellata* Rehder, 1980, Recent, Easter Island.

Remarks — Krijnen (2002) proposed his subgenus *Lisanerita* for several subtropical and warm-temperate species from Easter Island, New Zealand, and Australia (for detailed treatment of Recent species see Spencer *et al.*, 2007). Species in the group are characterized by strongly reduced spiral sculpture, a flat to concave, smooth to weakly pustulose septum with a smooth edge or with up to two weak medial teeth, an outer lip with thickened, finely denticulate inner side, and a smooth to weakly granulose operculum. The septum is broad and not distinctly set off by an abapertural ridge.

In the Navidad Formation of central Chile, *Nerita chilensis* Philippi, 1887, occurs as one of several warm-water littoral molluscs. According to Finger *et al.* (2007), the shallow-water molluscs of the Navidad Formation are older (Late Oligocene to Early Miocene) than are the deep-water, cooler-climate microfossils and molluscs in that formation. These latter elements are of Late Miocene to Early Pliocene age. According to Finger *et al.* (2007), shallow-water species would have been carried in reworked condition from shallow-water sediments laid down during the early Neogene and redeposited at bathyal depths later.

Nielsen *et al.* (2004) assigned *Nerita chilensis* to the subgenus *Heminerita* von Martens, 1887, on the grounds that *N. chilensis* strongly resembles *N. lirellata*. In his original description of the latter species, Rehder (1980) placed *N. lirellata* from Easter Island in *Heminerita*, an assignment affirmed by Nielsen *et al.* (2004). *Nerita japonica* Dunker, 1860, the type (and, in our view, the only) species of *Heminerita*, is a Japanese species characterized by a globose, smooth shell with a raised, blunt apex, steeply inclined smooth septum distinctly set off by an abapertural ridge, smooth or very weakly denticulate septal edge, and internally thickened smooth outer lip. By contrast, *N. chilensis* has 38 to 45 flattened spiral ribs. Rehder (1980) and Nielsen *et al.* (2004) interpreted *Heminerita* broadly to include species that we would assign to other subgenera including *Amphinerita* and *Lisanerita*. On molecular grounds, *N. japonica* forms a clade distinct from both *Amphinerita* and *Lisanerita* (Frey, in preparation). Given its morphological similarity to *N. lirellata*, the type species of *Lisanerita*, we assign *N. chilensis* to the latter subgenus. Biogeographically, a subtropical Early Miocene South American occurrence of an otherwise Indo-West Pacific and Australasian clade of nerites has parallels in at least two other gastropod families, the Trochidae (DeVries and Hess, 2004) and Turritellidae (DeVries, 2007), and perhaps also the Turbinidae (DeVries, 2006). The nerite, trochid, and turritellid clades are now all extinct in South America.

We tentatively assign two additional fossil species from North America to the subgenus *Lisanerita*. One is *Nerita joaquinensis* Addicott, 1970, from the lower Round Mountain Silt (Middle Miocene) of the Kern River area of California. The holotype (USNM 650051) is a small (13.9 mm) shell with an immersed spire, a thickened denticulate outer lip, two median denticles on the septal margin, and three granules on the preserved part of the septal surface. Sculpture of the last whorl consists of fine incremental lines only (Addicott, 1970). The abapertural ridge is well developed. Squires & Saul (2002) placed this species in the subgenus *Theliostyla*, presumably because of its granulose septum. Its shell characters fit better with those of *Lisanerita*. If this allocation is correct, *Lisanerita* would have been represented in the northern hemisphere.

This interpretation is strengthened by our tentative assignment of *Nerita tampaensis* Dall, 1892, from the Silex beds of the Tampa Limestone (latest Oligocene or earliest Miocene) of Florida, to the subgenus *Lisanerita*. Its holotype (USNM 112663, illustrated by Mansfield, 1937) is strongly eroded, but it shows two central denticles on the septal margin, at least two granules on the septal surface, and obsolete spiral elements on the shell exterior. The inner side of the outer lip is not thickened and lacks denticles, perhaps indicating that the specimen is not an adult. No similar species is known from the Miocene to Recent on the Atlantic coast of the Americas.

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