Cainozoic Research, **9**(1), pp. 121-133, June 2012

The genera *Engina* and *Ameranna* nov. gen. (Mollusca: Gastropoda, Buccinoidea, Buccinidae, Pisaniinae) from the Western Atlantic Neogene

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Received: 16 April 2012; revised version accepted 20 April 2012

The first occurrence of the cosmotropical pisaniine buccinid gastropod genus *Engina* Gray, 1839 was previously in the lower Gatun Formation (late Miocene) of Panama. Here we describe four new fossil species: *E. cantaurana* nov. sp., from the early Miocene of Venezuela (the oldest known species of *Engina*, with an unusually high spire), *E. gigas* nov. sp., from the late Miocene and early Pliocene of the Dominican Republic (the largest known *Engina*, with an erect inner lip and obsolete parietal denticle), *E. latior* nov. sp. from the late Miocene and early Pliocene of the Dominican Republic (a more typical species of *Engina* in terms of apertural dentition) and *Engina moinensis* nov. sp from the Pleistocene of Costa Rica and the Bocas del Toro Area (a species with possible paciphile affinities). We propose the new pisaniine genus *Ameranna* (type species: *Anna florida* García, 2008) for four living Caribbean species and for two fossil species: *A. primitiva* nov. sp., from the early Miocene of Venezuela (the oldest known species of *Ameranna*) and the new Pliocene species *A. minuscula* nov. sp. from the Dominican Republic. The new genus differs from the early Oligocene to Recent eastern Atlantic genus *Anna* by having a lirate rather than denticulate outer lip.

KEY WORDS: Neogene, tropical America, Gastropoda, Pisaniinae, new genus, new species

Introduction

Despite years of taxonomic study, the fossil record of tropical America still contains many undescribed species. This situation applies especially to hard-bottom taxa, which preserve less reliably than those from sand or mud bottoms. To help redress this lack of taxonomic work, we here describe six new fossil species from hard-bottom habitats in the Neogene of tropical America. All the species in question belong to the buccinid neogastropod subfamily Pisaniinae.

Vermeij (2001, 2006) informally recognized three morphological groups within Pisaniinae, those centered on the genera *Pisania* Bivona-Bernardi, 1832, *Cantharus* Röding, 1798; and *Engina* Gray, 1839. The *Engina* group, characterized by a shell with a narrow, strongly denticulate aperture and the presence of distinct columellar folds, is the least well represented in the fossil record but the most species-rich in the Recent fauna. Four of the six species we describe here belong to *Engina* in the broad sense, and thus add significantly to the fossil record of that group.

Material and methods

The material described here is from the Panama Paleontology Project (PPP) collection and the Gibson-Smith collection, both housed in the Naturhistorisches Museum Basel (NMB coll.), Switzerland and the Bernard Landau collection (BL coll.), now deposited in the Naturhistorisches Museum Wien (NHMW coll.), Vienna, Austria. We have also consulted the collections in the Zoological Museum, University of Amsterdam (ZMA), The Netherlands.

We have adopted the recent recommendation of the International Commission on Stratigraphy – accepted by the IUGS on June 30, 2009 – on the redefinition of the Pleistocene (now including the Gelasian Stage/Age as its lowermost unit), and the concomitant formal redefinition of the base of the Quaternary System/Period (and thus the Neogene/Quaternary boundary) by the Monte San Nicola GSSP and thus to be coincident with the bases of the Pleistocene and Gelasian. The Plio-Pleistocene boundary is now pushed back to 2.59 Ma (Riccardi, 2009).

Systematic Palaeontology

Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815
Subfamily Pisaniinae Gray, 1857
Genus *Engina* Gray, 1839

Type species – *Engina zonata* Gray, 1839 by subsequent designation Gray, 1847 = *Purpura turbinella* Kiener, 1836 (see Orr, 1962), Recent, Caribbean.

Remarks – As currently understood, *Engina* comprises a cosmotropical and warm-temperate southern-hemisphere group of small, thick-shelled, determinately growing gastropods found on intertidal and shallow subtidal rocky bottoms (Cernohorsky, 1971, 1975; Ponder, 1972). *Engina turbinella* Kiener, 1836 (the type species) and other typical members of the genus have shells with a biconic shape, weak abapical constriction, a relatively short siphonal protuberance whose axis more or less parallels that of the shell, and teleoconch sculpture consisting of narrowly rounded axial ribs overridden by spiral cords and threads. The aperture is narrow and more or less parallel-sided or elongate pyriform, bordered abaxially by a slightly expanded and thickened terminal varix and on its adaxial side by an adherent inner lip. At the adapical end of the aperture, a distinct anal canal is formed between the adapicalmost (anal) tooth on the outer lip and a parietal tooth on the inner lip, but there is no adapical notch in the outer lip. Adults bear five or more teeth on the inner side of the outer lip some distance in from the edge. There is typically a gap between these teeth and the anal tooth, and the adapical outer-lip tooth is larger than the others. The edge of the outer lip is erect, sharp, and slightly crenulated by the ends of the external spiral cords. There are no spiral ridges (lirae) on the inner side of the outer lip. The adult inner lip bears small denticles along its edge, and has two abapical spiral folds, an entrance fold to the siphonal canal and, immediately adapical to it, a much weaker second fold. Cernohorsky (1975) described radial lirae, present on the parietal callus, as a characteristic feature of the genus. However, these parietal lirae are not present in all *Engina* species.

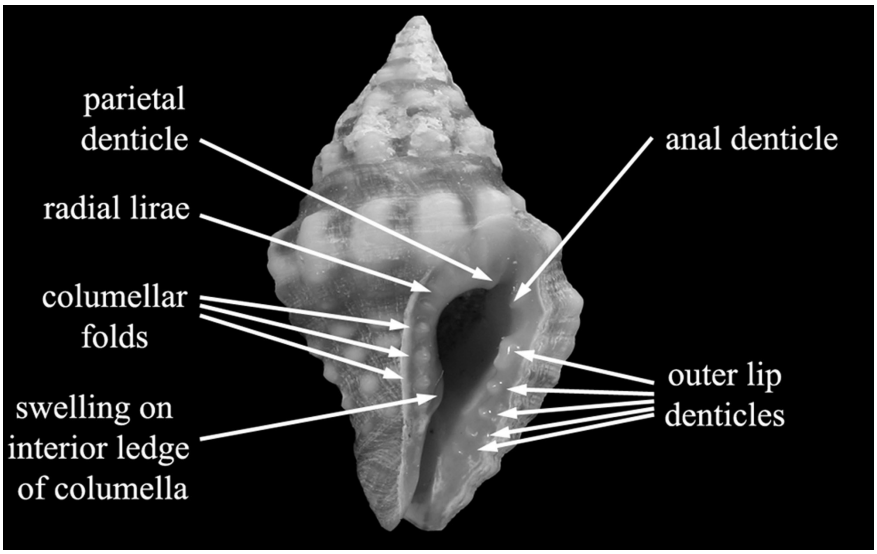

Figure 1. *Engina turbinella* (Kiener, 1836), illustrating terminology of apertural features for the genus (adapted from Cernohorsky, 1975).

Besides *E. turbinella*, which is a species (or species complex) in the Caribbean with low axial ribs and very weak spiral cords, at least two other Recent tropical American species conform to this general description, except that their spiral sculpture and axial ribs are considerably more prominent. These are the eastern Pacific *E. maura* (Sowerby, 1832) and *E. tabogaensis* Bartsch, 1931. In the Indo-West Pacific, species with similar outer-lip dentition have a notably thickened outer lip and low axial and spiral sculpture. They include, among others, the widespread *E. mendicaria* (Linnaeus, 1758) and *E. phasinola* (Duclos, 1840).
Not all species placed in *Engina* conform to this characterization. In these species, the outer-lip denticles are more numerous and less differentiated in size, and the siphonal protuberance is often longer than in typical *Engina*, and, as previously mentioned, the parietal lirae are not present in all species. A wide range of shell form is seen in the Recent American species, which include the very short and squat *E. pulchra* (Reeve, 1846), strongly shouldered *E. pyrostoma* (Sowerby I, 1832), both of which are from the eastern Pacific, and the elongate Floridian *E. corinnae* Crovo, 1971. The Brazilian *E. goncalvesi* Coltro, 2005 is an outlier, with a less biconic shell, with much weaker sculpture, more rounded, less angular whorls and a wider pyriform aperture, but the character of the apertural denticles and folds is characteristic for the genus. In all Recent Caribbean members of the genus, including *E. goncalvesi*, the protoconch is paucispiral, consisting of 1.5 whorls. Watters (2009)

described *Hesperisternia itzamnai*, a very rare Recent shell from eastern Mexico and compared it to the eastern Pacific *H. jugosa* (Adams, 1852) and placed this and the Brasilian *Engina janowskyi* Coltro, 2005 in the genus *Hesperisternia*, which was reviewed by Vermeij (2006). Both these species show shell features characteristic of *Engina*, and should be included in this genus.

Numerous Indo-West Pacific species also diverge from the typical form (see also Ponder, 1972). The species we describe in this paper fall into several categories, including typical *Engina* (see *E. latior* nov. sp.). As discussed below, we consider all of them to belong to *Engina* in the broad sense.

Our assignment of the three new *Engina* species to *Engina* rests on comparisons with other genera that resemble, and may be related to that genus. The Indo-West Pacific genus *Clivipollia* Iredale, 1929, has shells characterized by broad, rounded axial ribs, a glossy surface, and a terminal varix with denticles of relatively even size situated on its inner side very close to the slightly convex, crenulated edge. Further inside the aperture, the outer lip bears long, prominent spiral lirae. There is no parietal denticle. The siphonal protuberance is demarcated from the rest of the shell by a well-marked constriction, and shows a strong dorsal curvature, unlike the nearly straight canal of *Engina*. In the deepwater Indo-West Pacific genus *Falsilatirus* Emerson & Moffitt, 1988, which Vermeij (2001) assigned to the *Engina* group instead of to the Fasciolariidae where Emerson & Moffitt (1988) had assigned it, the terminal varix bears two very prominent central denticles, five weaker abapical denticles, and three very weak spirally elongated, adapical denticles bordering a very weak parietal denticle at the posterior end of the aperture. There is no anal canal, and lirae are absent on the inner side of the outer lip. The two abapical columellar folds are prominent. As in *Clivipollia*, the siphonal protuberance is relatively long and dorsally recurved, and the exterior shell surface is glossy. The shell characters of *Clivipollia* and *Falsilatirus* exclude these taxa as suitable placements for any of the fossil American species we discuss in this paper.

In tropical America, the genus *Engina* in the broad sense is represented by fourteen living species, nine in the eastern Pacific: *Engina solida* Dall, 1917, *E. macleani* Olsson, 1971, *E. mantensis* Bartsch, 1928, *E. maura* (Sowerby, 1832), *E. pulchra* (Reeve, 1846), *E. pyrostoma* (Sowerby, 1832), *E. tabogaensis* Bartsch, 1931, one endemic to the Galapagos Islands, *E. pyrostoma* (Sowerby I, 1832), and six in the western Atlantic: *E. turbinella*, *E. corinnae*, *E. demani* de Jong & Coomans, 1988, *E. goncalvesi*, *E. janowskyi* Coltro, 2005 and *E. itzamnai* (Watters, 2009).

Until now, there was almost no fossil record for the genus *Engina*. Woodring (1973) considered a specimen from the lower Gatun Formation (late Miocene) of Panama to belong to the living Caribbean species *E. turbinella*. Olsson & Harbison (1953) described *E. floridana* (Figs 20-21) from beds at St. Petersburg, Florida, of early Pleistocene (Caloosahatchee Formation) age. The species has also been found in the underlying (Pliocene) Pinecrest beds. The genus *Engina* remains almost unrecorded from the fossil record of the Indo-West Pacific. The only record of which we are aware is that of van Regteren Altena (1950), who recorded *E. sinensis* Melvill, 1895 [a synonym of *E. curtisiana* (E.A. Smith, 1884) according to Wilson (1994)] from the Kendeng Beds (Pucangan Formation, early Pleistocene) of Java, Indonesia.

***Engina cantaurana* nov. sp.**

Figs 2-7

Dimensions and type material – Holotype NHMW 2010/0124/0001, height 18.6 mm, width 9.8 mm (Figs 2-4); paratype 1 NHMW 2010/0124/0002, height 16.8 mm, width 9.7 mm (Figs 5-7); paratype 2 NHMW 2010/0124/0003, height 21.4 mm; paratype 3 NHMW 2010/0124/0004, height 21.4 mm.

Etymology – From the locality of Casa Cantaure, Paraguaná Peninsula, where this species is found.

Type locality – 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (= locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

Type stratum – Lower shell bed, Cantaure Formation (early Miocene; late Burdigalian).

Diagnosis – A large, slender, biconic *Engina* species, with a high spire, multispiral protoconch, flattened ribs, prominent spiral cords, pyriform aperture, weakly developed dentition and a poorly developed parietal callus with radial ribs absent.

Description – Shell medium-sized for genus, biconic; protoconch multispiral, low dome-shaped, of 3.5 smooth convex whorls, with periphery at abapical suture, nucleus small, 4-5 prosocline axial riblets on last ¼ protoconch whorl, protoconch boundary sharply delimited by prosocline scar; teleoconch of 4.5 weakly convex whorls; suture impressed, undulating; axial sculpture of 8-9 broad rounded ribs, wider than their interspaces; spiral sculpture on first teleoconch whorl of three narrow, elevated, rounded cords; cords override and become strongly swollen over axial ribs; secondary spiral sculpture present in interspaces from third teleoconch whorl; on later adult whorls adapical cord placed immediately below adapical suture, a wider gap develops between the adapical and two lower cords, which become placed more abapically, the abapical cord forming whorl periphery, placed just above abapical suture; last whorl rounded, weakly constricted at base, bearing 8-9 primary spiral cords with secondary and tertiary threads in interspaces; aperture elongate-ovate, outer lip sharp, weakly crenulated by primary spiral cords, relatively strongly denticulate within; anal denticle strongly developed; 5-6 outer lip denticles, weakening abapically, in some specimens extending a short distance within the aperture; anal canal strongly developed, forming very deep, nar-

row groove in labral callus; siphonal canal open, moderate length, hardly posteriorly recurved; columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; parietal denticle well-developed; five prominent columellar folds present below mid-aperture; small swelling developed on interior ledge of the columella; siphonal fasciole rounded, bearing irregular spiral cords and threads.

Discussion – With its early Miocene age, *Engina cantaurana* is the oldest known species of *Engina.* Relative to other members of the genus in tropical America, *E. cantaurana* is unusually slender and high-spired (mean width/height = 0.50, range 0.47 to 0.53, n = 4) and its aperture is more pyriform than that of most of the other Recent species. Its outer lip denticles are less strongly developed than in typical Recent members of *Engina*, including *E. turbinella*, *E. maura* and *E. tabogaensis*. There are no modern western Atlantic *Engina* species which can be compared with this new taxon.
Engina cantaurana differs from *E. gigas* nov. sp. (see below) by its smaller size, more prominent parietal denticle, more numerous axial ribs, more numerous columellar folds, and an adherent instead of an erect inner lip edge. *Engina cantaurana* differs from *E. floridana* (Figs 20-21) by having a more slender shell with a rounded instead of an angular periphery and by having a longer siphonal protuberance.

Distribution – Early Miocene**;** Cantaure Formation, Venezuela.

***Engina gigas* nov. sp.**
Figs 8-13

Dimensions and type material – Holotype NMB H18437, height 24.4 mm, width 12.1 mm (Figs 8-10); paratype 1 NMB H18438, height 22.5 mm, width 10.7 mm (Figs 11-12); paratype 2 NMB H18439, height 20.7 mm, width 11.2 mm; paratype 3 NMB H18440, height 20.3 mm, width 9.8 mm; paratype 4 NMB 1 H18441, height 19.1 mm, width 10.0 mm; paratype 5 NHMW 2010/0124/0005 (NHMW coll., ex BL coll.), height 18.6 mm (Fig. 13). Paratypes 1-5 locality TU 1215, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

Other material – One specimen, NMB H18442, height 24.4 mm, width 11.8 mm, locality NMB 18272 (= TU 1422) Arroyo Bellaco, Rio Cana, Cercado Formation, late Miocene; 9 specimens BL coll., locality TU 1215, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

Etymology – From L. *Gigas* = a mythical giant, huge, gigantic; name reflecting the large size of the shell.

Type locality – Locality NMB 18581 (= TU 1215), Gurabo River, Dominican Republic.

Type stratum – Gurabo Formation, early Pliocene.

Diagnosis – A very large, relatively slender *Engina* species, with a multispiral protoconch, long siphonal protuberance, parietal and anal denticles poorly developed, two folds in the central portion of the columella and poorly developed columellar and parietal calluses, with parietal radial lirae present.

Description – Shell large for genus, biconic; protoconch multispiral, elevated, of at least three tall convex whorls, with periphery at abapical suture; nucleus missing in all specimens, protoconch boundary sharply delimited by sinusoid scar; teleoconch of seven compressed angular whorls; suture impressed, deeply undulating; axial of six broad rounded, elevated ribs, narrower than their interspaces, winding around shell in a slightly anticlockwise direction on apical view; spiral sculpture overrides axial ribs, consists on first teleoconch whorl of two elevated, rounded cords, the abapical cord forming the whorl periphery; abapically, whorls develop broad, shallow, sutural ramp delimited by the adapical primary spiral cord, profile concave between adapical and abapical cords and between abapical cord and suture; secondary and tertiary spiral sculpture develops between primary cords from second teleoconch whorl; on penultimate whorl secondary cord on sutural ramp strengthens, and a further primary cord appears at the adapical suture; last whorl rounded, weakly constricted at base, bearing 12-13 primary spiral cords with up to four secondary threads in interspaces; fine, close-set axial growth lines interrupt spiral sculpture developed to a varying degree, in some specimens giving surface a very finely scabrose appearance; aperture narrow, elongate, outer lip sharp, weakly crenulated by primary spiral cords, relatively strongly denticulate within; anal denticle weak or absent; six outer lip denticles, weakening abapically; anal canal hardly developed; siphonal canal open, long, weakly posteriorly recurved; columellar callus sharply delimited, erect, hardly expanded over venter of last whorl, detached in abapical portion; parietal denticle hardly developed; two broad, oblique columellar folds developed mid-height; five or six parietal lines present in some specimens formed by callus slightly thickened and elevated over primary spiral cords; siphonal fasciole flattened, bearing irregular spiral cords and threads.

Discussion – *Engina gigas* nov. sp. is the largest known species of *Engina*, living or fossil. Next to *E. cantaurana*, it is the most slender tropical American species (mean width/length 0.52, range 0.50 to 0.54, n = 5). The apertural features of *E. gigas* do not conform to those of typical members of *Engina*, but they are still consistent with placement in *Engina* in the broad sense. The columellar callus is hardly expanded, the parietal denticle is poorly expressed, and the parietal area lacks radial lirae. There are only two columellar folds located on the central sector of the inner lip, and the edge of the inner lip is erect, not adherent as in other species of *Engina*. The siphonal protuberance is also long relative to that of most other species in the genus. There are no modern western

Atlantic *Engina* species which can be compared with this new taxon.

Distribution – Early Miocene; Cercado Formation, Dominican Republic. Late Pliocene: Gurabo Formation, Dominican Republic.

***Engina latior* nov. sp.**
Figs 14-19

Dimensions and type material – Holotype NMB H18444, height 10.0 mm, width 5.9 mm (Figs 14-16); paratype 1 NMB H18443, height 10.0 mm, width 6.0 mm (Figs 17-19); paratype 2 NMB16934 (=PJ 1688), height 9.9 mm, width 6.0 mm.

Other material – Two specimens, locality NMB18993 (= TU 1422), maximum height 11.5 mm, Arroyo Bellaco, Rio Cana, Cercado Formation, late Miocene; 9 specimens BL coll., maximum height 10.0 mm, locality TU 1215, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene; 1 specimen locality NMB 16982, height 8.4 mm, Cana River, Cercado Formation, Dominican Republic.

Etymology – From L. *latus* (adj.) = broad, wide; name reflecting the somewhat convex shape of the outer lip.

Type locality – Locality NMB16934 (=PJ 1688), Gurabo River, Dominican Republic.

Type stratum – Gurabo Formation, early Pliocene.

Diagnosis – A small, relatively broad, biconic *Engina* species, with the last whorl relatively strongly constricted at the base, dentition as typical for genus, but with only four outer lip denticles, the adapical one far more strongly developed, no parietal radial lirae present.

Description – Shell small for genus, biconic; protoconch paucispiral, smooth, of 1.5 convex whorls, with medium-sized nucleus, protoconch boundary sharply delimited by sinusoid scar; teleoconch of 4.5-5 compressed angular whorls with a very broad, concave sutural ramp, sharply angular at shoulder, weakly convex to abapical suture; suture impressed, undulating; axial sculpture of nine broad rounded ribs, slightly narrower than their interspaces, subobsolete on sutural ramp, strongly developed below shoulder; spiral sculpture overrides axial ribs, on first teleoconch whorl consists of four rounded cords, roughly equal in width to their interspaces, abapically, further cords develop on sutural ramp, six on penultimate whorl, and three very slightly stronger cords below shoulder from third teleoconch whorl; last whorl with strongly concave sutural ramp, angled at shoulder, convex below, weakly constricted at base, bearing seven spiral cords on sutural ramp; below shoulder spiral cords of irregular strength, six or seven, strengthening to form primary cords; fine, close-set axial growth lines interrupt spiral sculpture developed to a varying degree, in some specimens giving surface a very finely scabrose appearance; aperture narrow, elongate, outer lip sharp, weakly crenulated by primary spiral cords, relatively strongly denticulate within; anal denticle well developed; three to five outer lip denticles, adapical two much stronger, weakening abapically; anal canal well developed, forming a relatively deep groove in labral callus; siphonal canal open, long, weakly posteriorly recurved; columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; parietal denticle weakly developed; 5-7 short, horizontal, tubercle-like columellar folds, strongest mid-height developed close to outer edge of columellar callus; siphonal fasciole flattened, bearing spiral cords.

Discussion – *Engina latior* nov. sp. is a distinctive species characterized by the presence of only four outer lip denticles (not counting the anal denticle), of which the posterior one is by far the largest. This dentition is like that of typical members of *Engina*. As its name implies, *E. latior* is broader (width/length mean 0.57, range 0.53 to 0.60) than the co-occurring *E. gigas*. It further differs from *E. gigas* in having a parallel-sided aperture instead of a slightly pyriform one, a well developed anal canal, and more numerous columellar folds. *Engina floridana* from the Pliocene and early Pleistocene of Florida is larger than *E. latior* (up to 19 mm in length) and has a more prominent parietal tooth, more numerous outer-lip denticles (five to six instead of four), and the outer-lip denticles more even in size than in the Dominican species.
Compared to its living western Atlantic congeners, *Engina latior* is most similar in shape to *E. corinnae* Crovo, 1971 found in waters around Florida (Coltro, 2005), but differs in being more constricted at the base, and having four instead of five labral denticles (excluding anal denticle). It is also similar to *E. janowskyi* Coltro, 2005 from Brazil, which can have four or five labral denticles, but has fewer, more prominent axial ribs (7 vs. 9) and has more prominent primary spiral cords with weaker secondary sculpture. We (BL) have also examined specimens of *E. demani* present in the ZMA coll. (2 unnumbered lots, 10 specimens) from Aruba.
This species belongs within the same group of *Engina* species as *E. turbinella, E. latior*, *E. corinnae*, *E. janowskyi* and *E. demani* (*i.e.* typical *Engina* as described by Cernohorsky, 1975), but differs in having a slightly more elongated shell, even less constricted at the base, seven axial ribs, and the denticles on the outer lip and columellar folds, although typical in number and position for this group of *Engina*-species, are more weakly developed than in any of the preceding species. Although de Jong & Coomans (1988, p. 83) described the protoconch of *E. demani* as consisting of 2½ whorls, all the specimens seen in the ZMA coll. have just under two whorls, with a large nucleus. Indeed, all four species, *E. latior*, *E. corinnae*, *E. janowskyi* and *E. demani* have a paucispiral protoconch with a medium to large sized nucleus, suggesting a direct method of development, as does the type species; *E. turbinella*.

Distribution – Late Miocene; Cercado Formation, Dominican Republic. Early Pliocene; Gurabo Formation, Dominican Republic.

***Engina moinensis* nov. sp.**
Figs 22-29, 40

Dimensions and type material – Holotype NHMW 2010/0124/0006, height 13.1 mm, width 8.2 mm (22-23); paratype 1 NHMW 2010/0124/0007, height 14.5 mm, width 7.6 mm (Figs 23-24); paratype 2 NHMW 2010/0124/0011, height 15.1 mm, width 9.2 mm; paratype 3 NHMW 2010/0124/0012, height 10.1 mm, width 6.6 mm; paratype 4 NHMW 2010/0124/0013, height 11.6 mm, width 7.0 mm (all NHMW coll., ex BL coll.).

Other material – One specimen NMB H19478 (Figs 26-27), early Pleistocene, Swan Cay Formation, Bocas del Toro area, Panama; three specimens NMB H19477 (Figs 28-29), Gelasian-Calabrian, Ground Creek Formation, Isla Colon, Bocas del Toro area, Panama.

Etymology – Named after the Moin Formation of Costa Rica.

Type locality – Locality TU 1240, Los Corales, Puerto Limon, Costa Rica.

Type stratum – Moin Formation, early Pleistocene.

Diagnosis – A medium to small-sized *Engina* species with a protoconch of 2.5 whorls, last half protoconch whorl with prosocline riblets, teleoconch whorls with seven ribs, apertural dentition strongly developed, with four upper outer lip denticles strongly developed forming a dental ridge mid-aperture.

Description – Shell medium to small for genus, biconic; protoconch smooth, of 2.5 convex whorls, with medium-sized nucleus, last half whorl bearing 3-4 prosocline riblets; protoconch boundary sharply delimited by sinusoid scar; teleoconch of five compressed angular whorls with a very broad, concave sutural ramp, sharply angular at shoulder, weakly convex to abapical suture; suture impressed, undulating; axial sculpture of seven broad rounded, ribs, about equal in width to their interspaces, subobsolete on sutural ramp, strongly developed below shoulder; spiral sculpture overrides axial ribs, on first teleoconch whorl consists of three rounded cords, roughly equal in width to their interspaces, abapically, further weaker irregular cords develop on sutural ramp; last whorl with strongly concave sutural ramp, angled at shoulder, convex below, weakly constricted at base, bearing irregular cords on sutural ramp, one of which abapically is stronger; mid-section six primary spiral cords, three over shoulder node, three below, with five secondary cords in each interspace, two further primary cords on base; fine, close-set axial growth lines interrupt spiral sculpture developed to a varying degree, giving surface a very finely scabrose appearance; aperture narrow, elongate, outer lip sharp, weakly crenulated by primary spiral cords, strongly denticulate within; anal denticle strong; four mid-aperture denticles well-developed, two adapical denticles much weaker; anal canal well developed, forming a deep groove in labral callus; siphonal canal open, long, weakly posteriorly recurved; columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; parietal denticle strong; parietal lirae present; 2-6 short, horizontal, tubercle-like columellar folds, strongest mid-height developed close to outer edge of columellar callus; siphonal fasciole flattened, bearing spiral cords.

Discussion – *Engina moinensis* nov. sp. found in the Caribbean Pleistocene assemblages of Costa Rica and the Bocas del Toro area of Panama, is similar in shape to several Recent Caribbean small to medium-sized *Engina* species, but is immediately distinguished by having one extra protoconch whorl, with riblets on the last half whorl, a feature we have not seen in any of the living Caribbean *Engina* species, which all have a paucispiral protoconch consisting of 1.5 smooth whorls, with a clearly delimited scar marking the protoconch-teleoconch boundary. The type material shows some intraspecific variability; paratype 1 (Figs 23-24) is somewhat more slender.
The Recent *Engina janowskyi* described from Brazil is most similar in shell shape, length of siphonal protuberance and number of axial ribs to *E. moinensis*. However, *E. janowskyi* does not have the strong ridge of outer lip denticles seen *E. moinensis*, instead the adapical outer lip denticle in *E. janowskyi* is strongest, weakening rapidly abapically. The Recent Floridian *E. corinnae* is also similar in size, but has a more elongated shape, the shoulder is less prominent, and although the outer lip denticles are strongly developed, they weaken regularly abapically and do not form the mid-height dental ridge seen in *E. moinensis.*
Engina moinensis nov. sp. may be more closely related to the tropical American Pacific *E. tobagoensis* Bartsch, 1931, which also has a mid-height dental ridge within the outer lip. However, in this species the single strong cord on the sutural ramp is more strongly developed and the outer lip forms a small adapical wing-like projection. The holotype of *E. moinensis* (Figs 22-23) shares these features, but much more weakly developed. The sutural ramp cord is even more weakly developed in the paratypes. Unfortunately we have not found a specimen of *E. tobagoensis* in our collections or in the ZMA with the protoconch preserved to compare with *E. moinensis*.

Distribution – Moin Formation, Costa Rica; Swan Cay Formation, Bocas del Toro area, Panama, early Pleistocene; Ground Creek Formation, Isla Colon, Bocas del Toro area, Panama, late Pleistocene.

***Engina turbinella* Kiener, 1836**
Figs 30-33

*1836 *Purpura turbinella* Kiener, p. 29, pl. 9, fig. 25.
1954 *Engina turbinella* Kiener – Abbott, p. 232, pl. 25W.

1959 *Engina turbinella* var. *cruzana* Usticke, p. 68.
1961 *Engina turbinella* Kiener, 1936 [*sic*] – Warmke & Abbott, p. 116, pl. 21d.
1962 *Engina?* species – Weisbord, p. 338, pl. 29, figs 25-26.
1973 *Engina turbinella* (Kiener) – Woodring, p. 477, pl. 74, figs 4-5.
1974 *Engina turbinella* (Kiener, 1835) – Abbott, p. 218, fig. 2399.
1988 *Engina turbinella* (Kiener, 1835) – de Jong & Coomans, p. 82, pl. 38, fig. 450.
1994 *Engina turbinella* (Kiener, 1835) – Díaz & Puyana, p. 187, fig. 710.
2001 *Engina turbinella* (Kiener, 1835) – Redfern, p. 93, pl. 43, fig. 396.
2009 *Engina turbinella* (Kiener, 1835) – Rios, p. 233, fig. 577.

Material and dimensions – Two specimens, NHMW 2010/0124/0008 (Figs 30-31) and NHMW 2010/0124/0009 (Figs 32-22) (NHMW coll., ex BL coll.).

Discussion – Woodring (1973) illustrated a single specimen from the middle Miocene Lower Gatun Formation of Panama as *Engina turbinella*, although he noted that the primary cords on his specimen were even more than those of many Recent specimens. Nevertheless, the shell illustrated probably falls within the range of variability for this species. *Engina turbinella* seems to be exceptionally rare in the Gatun deposits, as we have not collected any further specimens, nor are there any present in the Basel collections. There are no further fossil records for the species until the late Pleistocene.
Engina turbinella occurs in the fossil assemblage at La Isabella, Dominican Republic. This locality was first reported by Marcano & Tavares, 1982, and is probably late Pleistocene in age. The assemblage is very similar to that found in the area today, with a single extinct species described to date (Landau, 2003). We have examined two specimens from the assemblage which we ascribe to *Engina turbinella*. The shells show the same squat shape, nodules at the periphery and remnants of a colour pattern similar to that seen in shells of the species today.

Distribution – Middle Miocene; Lower Gatun Formation (Woodring, 1973). Late Pleistocene; Isabella Formation, Dominican Republic. Recent; Atlantic, Florida, Caribbean, southwards to Rio de Janeiro, Brazil.

Genus *Ameranna* nov. gen.

Type species – *Anna florida* García, 2008 (Recent, Florida).

Diagnosis – Pisaniine characterized by a small size, paucispiral protoconch, tall spire, axial sculpture of relatively wide-spaced axial ribs (7-13 on last whorl), a finely crenulated outer lip, and an aperture lirate within.

Description – Shell small, maximum height 16.2 mm, fusiform, constricted at base; protoconch paucispiral, smooth, rounded; teleoconch with high spire, often more than half the total shell height; teleoconch numbering five to six rounded whorls; spiral sculpture of last whorl consisting of eight to sixteen rounded cords with intercalated threads, cords somewhat more prominent on siphonal protuberance; axial sculpture consisting of seven to thirteen rounded ribs on last whorl, as well as a terminal varix; outer lip ventrally convex in profile, its edge finely crenulated, its inner side with six to nine lirae; inner lip partially erect, with three to six minute denticles along its length; columella abapically bearing an entrance fold to the siphonal canal and one to two subsidiary folds; parietal denticle present; siphonal canal open.

Etymology – A combination of *Anna*, a related genus, and America, referring to the distribution of the genus.

Included species – *Anna florida* García, 2008; *Bailya milleri* Usticke, 1959; *Anna royalensis* Watters, 2009; *Engina willemsae* de Jong & Coomans, 1988; *Ameranna minuscula* nov. sp.; *Ameranna primitiva* nov. sp.

Discussion – In his excellent paper on small Recent western Atlantic pisaniine and photine buccinids, Watters (2009) revised four species that he assigned with reservation to the genus *Anna* Risso, 1826. He noted that these four species differ from early Oligocene to Recent species in the eastern Atlantic *Anna* (see Vermeij, 2006) by generally having fewer axial ribs on the last whorl (seven to thirteen as compared with ten to more than twenty) and by having lirae instead of denticles on the inner side of the outer lip. Although these differences (especially the axial rib number) seem slight, the geographic separation and the lirate instead of denticulate outer lip distinguish Watters's four species in the western Atlantic from the many fossil and living species of *Anna*. We therefore propose the new genus *Ameranna* for these four western Atlantic taxa. Moreover, we describe two new species, one from the early Miocene of Venezuela and one from the early Pliocene of the Dominican Republic, showing that *Ameranna*, like *Engina* were already present in the Gatunian tropical American assemblages by the early Miocene.

***Ameranna primitiva* nov. sp.**
Figs 34-35

Dimensions and type material – Holotype NHMW 2010/0124/0010, height 21.2 mm, width 10.0 mm (Figs 34-35).

Etymology – Reflecting earliest known member of the genus.
Type locality – One km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (= locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

Type stratum – Lower shell bed, Cantaure Formation (early Miocene; late Burdigalian).

Diagnosis – A large, fusiform *Ameranna* species, with convex whorls, lirae arranged in pairs within the outer lip and columellar callus and dentition very weakly developed.

Description – Shell large for genus, fusiform; protoconch missing; six convex teleoconch whorls preserved, with broad, poorly-delimited, steeply sloping sutural ramp; whorl periphery a short distance above abapical suture; suture impressed, undulating; axial sculpture of weakly prosocline, rounded ribs, broader than their interspaces, 15 on penultimate whorl, 11 on last whorl, excluding terminal varix; spiral sculpture of narrow elevated cords, narrower than their interspaces, five cords on third teleoconch whorl (first well-preserved whorl), 13 on last whorl, second cord from adapical suture slightly weaker, third cord weakly delimits sutural ramp; secondary cords appear in interspaces on fourth whorl, tertiary threads in all primary and secondary cord interspaces on last whorl; spiral sculpture overrides and slightly swollen over axial ribs; last whorl evenly rounded, sutural ramp hardly developed, weakly constricted at base; terminal varix well-developed; aperture elongated-ovate, outer lip sharp, weakly crenulated by primary spiral cords, strongly and deeply lirate within, 14 lirae arranged in pairs; anal denticle hardly developed; outer lip denticles absent; anal canal narrow, forming small groove in labral callus; siphonal canal open, short, weakly posteriorly recurved; columellar callus poorly developed, reduced to thin glaze adjacent to aperture; parietal denticle present, weak; columella with two placations abapically.

Discussion – Although represented by only one specimen, the description of this new taxon is important, as it is the first known occurrence of the genus in tropical America. The new taxon clearly shows the characteristics of the new genus: relatively few axial ribs on the last whorl and lirae as opposed to denticles within the outer lip.
Ameranna primitiva nov. sp. is most similar in shape and sculpture to the type species for the genus, *A. florida* (García, 2008), but differs in being larger, with more numerous axial ribs on the penultimate whorl (15 vs. 9-13 in *A. florida* fide Watters (2009. p. 227), but fewer on the last whorl (11 vs. 13 in *A. florida* fide Watters (2009, p. 227), the suture in *A. florida* is deeper, almost canaliculate, *A. florida* has fewer lirae within the outer lip 7-9, which are not arranged in pairs as they are in *A. primitiva*, the columellar callus and columellar denticles and plicae, well-developed in *A. florida*, are weakly developed in *A. primitiva*. The other living Caribbean congeners: *Ameranna milleri* (Usticke, 1959), *A. royalensis* (Watters, 2009) and *A.willemsae* (de Jong & Coomans, 1988) all have smaller shells, with more angular whorls and fewer axial ribs on the last whorl.

***Ameranna minuscula* nov. sp.**
Figs 35-38

Dimensions and type material – Holotype NMB H18435, height 11.7 mm, width 6.4 mm (Figs 35-36); paratype 1 NMB H18436, height 9.6 mm, width 5.5 mm (Figs 37-38).

Etymology – Name reflecting the small size of the shell.

Type locality – Locality NMB 15858 (= PJ 1484), Gurabo River, Dominican Republic.

Type stratum – Gurabo Formation, early Pliocene.

Diagnosis – A small, stocky, solid-shelled *Ameranna* species with relatively few axial and spiral elements, and a narrow but pronounced, slightly concave sutural ramp.

Description – Shell small for genus, solid, fusiform; protoconch missing; 4.5 compressed, angularly-convex teleoconch whorls preserved, with a steep, narrow, weakly concave sutural ramp, convex below, with periphery a short distance above abapical suture; suture impressed, weakly undulating; axial sculpture of seven broad, rounded ribs, slightly broader than their interspaces, subobsolete on sutural ramp, strongly developed below shoulder; three rounded spiral cords on first teleoconch whorl preserved, slightly swollen where they override axial sculpture; secondary threads develop in interspaces from third teleoconch whorl; last whorl with narrow, concave sutural ramp, angled at shoulder, convex below, moderately constricted at base, bearing 7-8 primary spiral cords, with secondary and tertiary cords in interspaces; aperture ovate, outer lip sharp, weakly crenulated by primary spiral cords, strongly and deeply lirate within; anal denticle narrow, well developed; outer lip denticles absent; anal canal well-developed, narrow, forming small groove in labral callus; siphonal canal open, of medium length, weakly posteriorly recurved; columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; parietal denticle well-developed, narrow; numerous, irregular, interrupted columellar denticles along entire columellar length; small swelling on interior ledge of columella developed; siphonal fasciole flattened, bearing spiral cords.

Discussion – Among living species of *Ameranna*, the most similar to *A. minuscula* is *A. willemsae* (de Jong & Coomans, 1988) from the southern Caribbean. Both species have relatively few (seven and seven to eight, respectively) axial ribs, but *A. minuscula* has fewer spiral cords (seven to eight) than *A. willemsae* or any other species of *Ameranna*. Moreover, the shoulder on the last whorl of *A. minuscula* is placed higher, resulting in a relatively narrow, slightly concave sutural ramp, whereas the sutural ramp in all living *Ameranna* species is broader, with a convex profile.
All the Recent *Ameranna* species have a paucispiral protoconch, which infers a direct mode of development. This type of reproduction is consistent with the restricted distribution recorded for the living species by Watters (2009, fig. 16). Unfortunately the protoconch is lost in our specimens.

Distribution – Early Pliocene; Gurabo Formation, Dominican Republic.

Acknowledgments

We wish to thank Walter Etter and Olivier Schmidt of the Naturhistorisches Museum Basel (NMB), Switzerland for help with access to the Gibson-Smith collection and the Panama Paleontology Project (PPP) collection, and for the loan of type specimens from the NMB collection. Thanks also to Robert Molenbeek for allowing access to the collections of the Zoological Museum, University of Amsterdam, The Netherlands (ZMA).

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Figures 2-19.

2-4. *Engina cantaurana* nov. sp. **Holotype** NHMW 2010/0124/0001 (NHMW coll., ex BL coll.), height 18.6 mm, width 9.8 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, late Burdigalian, early Miocene.

5-7. *Engina cantaurana* nov. sp. **Paratype** 1 NHMW 2010/0124/0002 (NHMW coll., ex BL coll.), height 16.8 mm, width 9.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, late Burdigalian, early Miocene. Fig 6, detail of protoconch.

8-10. *Engina gigas* nov. sp. **Holotype** NMB H18437 (NMB coll.), height 24.4 mm, width 12.1 mm. Locality NMB 18581, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

11-12. *Engina gigas* nov. sp. **Paratype** 1 NMB H18438 (NMB coll.), height 22.5 mm, width 10.7 mm. Locality NMB 18581, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

13. *Engina gigas* nov. sp. **Paratype** 5 NHMW 2010/0124/0005 (NHMW coll., ex BL coll.), height 18.6 mm. Locality TU 1215, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene. Detail of protoconch.

14-16. *Engina latior* nov. sp. **Holotype** NMB H18444 (NMB coll.), height 10.0 mm, width 5.9 mm. Locality NMB 16934, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

17-19. *Engina latior* nov. sp. **Paratype** 1 NMB H18443 (NMB coll.), height 10.0 mm, width 6.0 mm. Locality NMB 16934, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

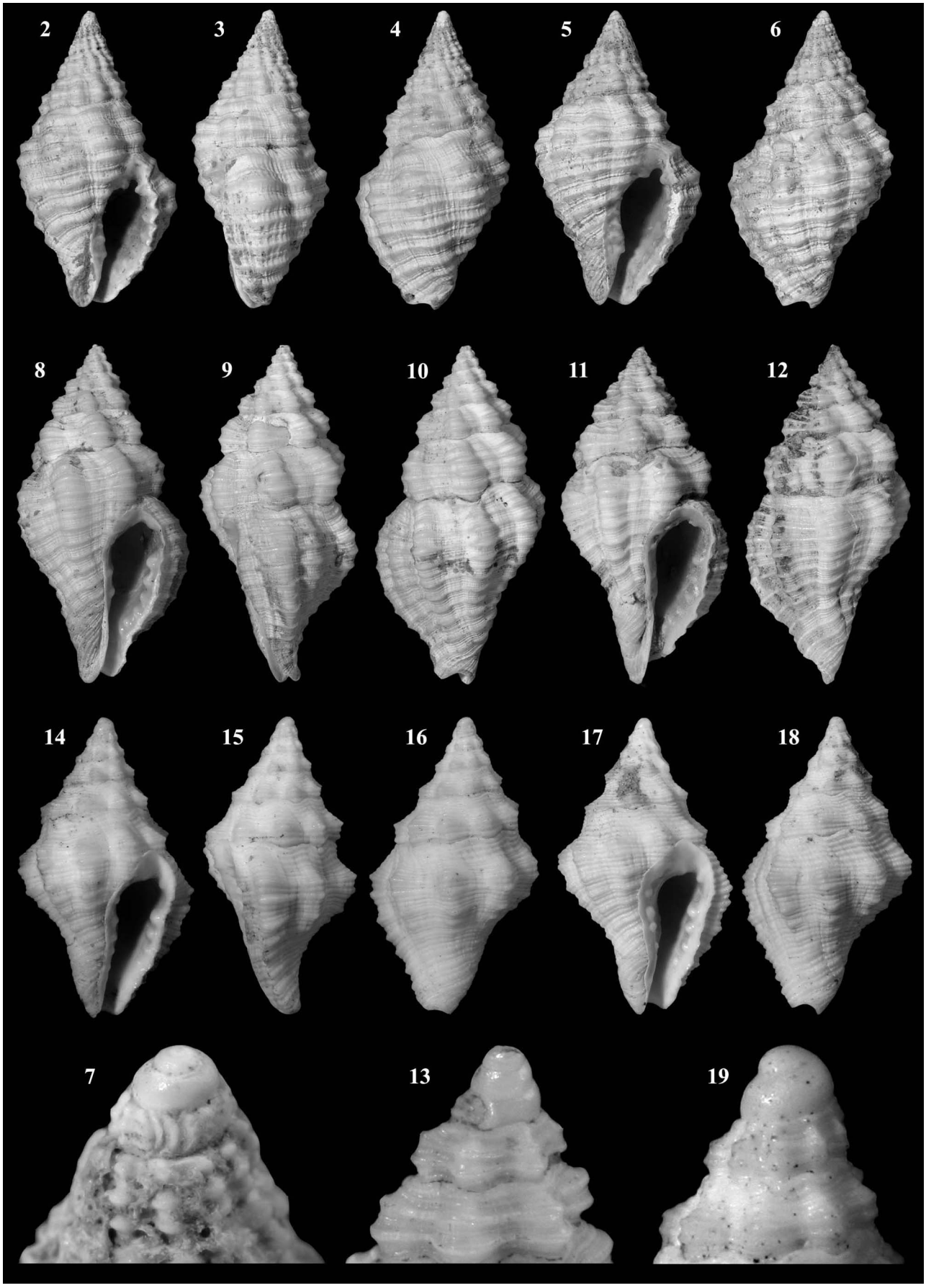


Figure 2-19.

Figures 20-40.

20-21. *Engina floridana* Olsson & Harbison, 1953. NHMW 2010/0124/0011 (NHMW coll., ex BL coll.), height 16.3 mm, width 8.7 mm. Quarry on Golf Road, east of turnoff to Punta Gorda, Charlotte County, Florida, USA, Caloosahatchee Formation, early Pleistocene.

22-23. *Engina moinensis* nov. sp. **Holotype** NHMW 2010/0124/0006 (NHMW coll., ex BL coll.), height 13.1 mm, width 8.2 mm. Locality TU 1240, Los Corales, Puerto Limon, Costa Rica, Moin Formation, early Pleistocene.

24-25. *Engina moinensis* nov. sp. **Paratype** 1 NHMW 2010/0124/0007 (NHMW coll., ex BL coll.), height 14.5 mm, width 7.6 mm. Locality TU 1240, Los Corales, Puerto Limon, Costa Rica, Moin Formation, early Pleistocene.

26-27. *Engina moinensis* nov. sp. NMB H19478 (NMB coll.), height 15.3 mm, width 9.5 mm. Swan Cay locality PPP02246 (= NMB 18743), Swan Cay Formation, early Pleistocene (1.77-0.78 Ma; see Coates *et al*., 2005)

28-29. *Engina moinensis* nov. sp. NMB H19477 (NMB coll.), height 15.1 mm, width 8.6 mm. Isla Colon locality PPP02251 (= NMB 18748), Ground Creek Formation, Pleistocene (Gelasian-Calabrian; see Coates *et a*l., 2005)

30-31. *Engina turbinella* (Kiener, 1835) NHMW 2010/0124/0008 (NHMW coll., ex BL coll.), height 11.7 mm, width 7.1 mm. La Isabella, Dominican Republic, La Isabella Formation, late Pleistocene.

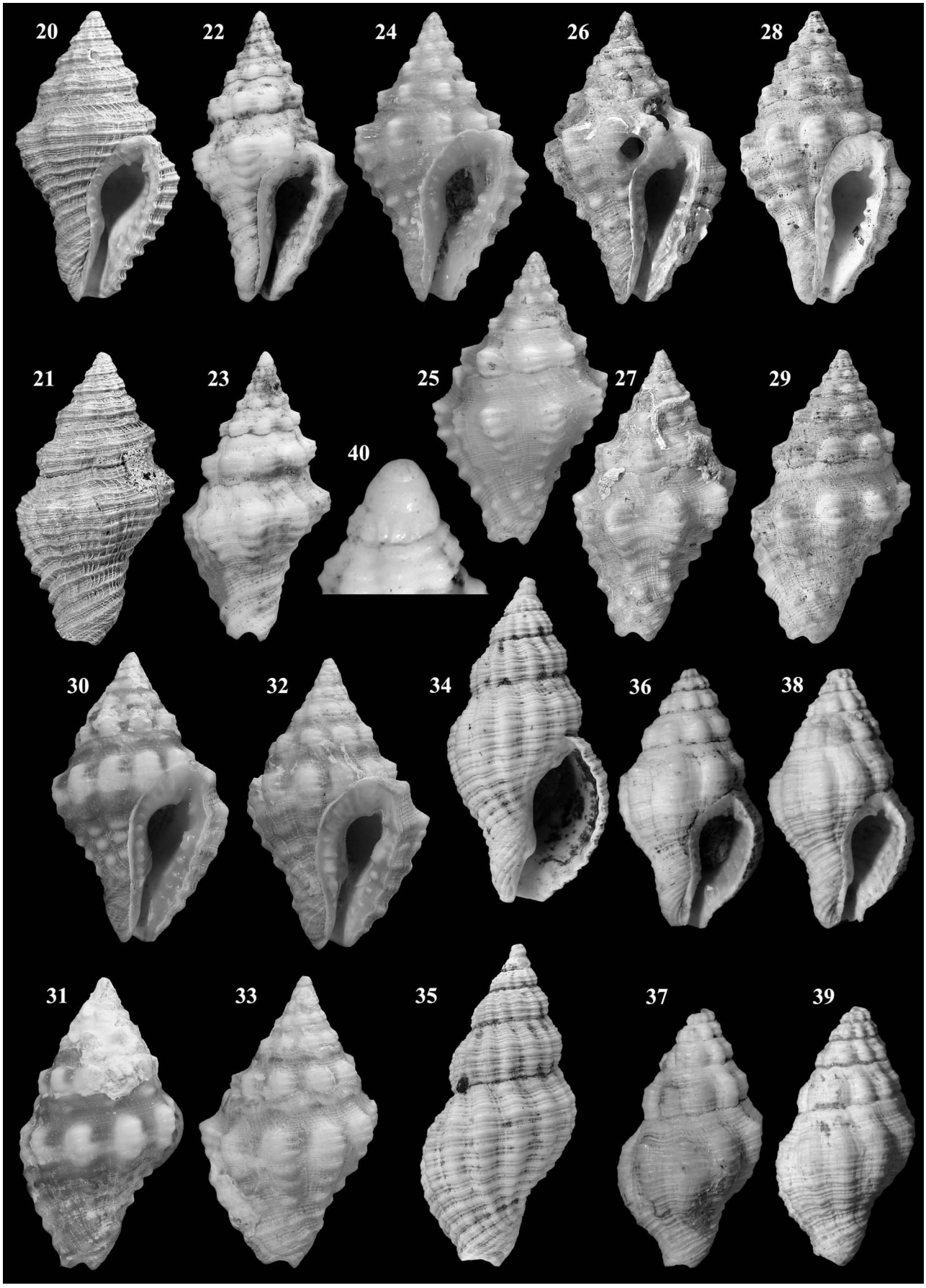
32-33. *Engina turbinella* (Kiener, 1835) NHMW 2010/0124/0009 (NHMW coll., ex BL coll.), height 15.0 mm, width 8.8 mm. La Isabella, Dominican Republic, La Isabella Formation, late Pleistocene.

34-35. *Ameranna primitiva* nov. sp. **Holotype** NHMW 2010/0124/0010 (NHMW coll., ex BL coll.), height 21.2 mm, width 10.0 mm. Lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, late Burdigalian, early Miocene.

36-37. *Ameranna minuscula* nov. sp. **Holotype** NMB H18435 (NMB coll.), height 11.7 mm, width 6.4 mm. Locality NMB 15858, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

38-39. *Ameranna minuscula* nov. sp. **Paratype** 1 NMB H18436 (NMB coll.), height 9.6 mm, width 5.5 mm. Locality NMB 15859, Gurabo River, Dominican Republic, Gurabo Formation, early Pliocene.

40. *Engina moinensis* nov. sp. **Paratype** 3 NHMW 2010/0124/0012 (NHMW coll., ex BL coll.), height 10.1 mm, width 6.6 mm. Locality TU 1240, Los Corales, Puerto Limon, Costa Rica, Moin Formation, early Pleistocene. Detail of protoconch.



Figures 20-40.