Journal of Paleontology, 86(2), 2012, p. 311–339
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0022-3360/12/0086-0311$03.00

THE FAMILY CANCELLARIIDAE (MOLLUSCA: GASTROPODA) IN THE NEOGENE OF THE BOCAS DEL TORO REGION, PANAMA, WITH THE DESCRIPTION OF SEVEN NEW SPECIES

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ABSTRACT—Twenty four species of Cancellariidae belonging to eleven genera occurring in the Neogene Bocas del Toro assemblages, Caribbean Panama, are discussed and figured. The following seven species are described as new: *Cancellaria pilula* n. sp., *Cancellaria isabelae* n. sp., *Cancellaria stri* n. sp., *Cancellaria axelolssoni* n. sp., *Massyla corpulenta* n. sp., *Aphera trophis* n. sp., *Admetula valientensis* n. sp. The cancellarid genus *Charcolleria* Olsson, 1942 is considered a synonym of *Massyla* H. Adams and A. Adams, 1854. Of the 24 species present in the Bocas del Toro, 12 are known also to occur elsewhere in the tropical American Neogene. This level of endemism is high, but not as high as that reported from other Tropical American Neogene assemblages, probably due to the very central geographic location within the Gatunian Province of the Bocas assemblages.

INTRODUCTION

IN THE last two years more work has been published dealing with the alpha taxonomy of the Neogene gastropods of the Bocas del Toro Region, Caribbean Panama, than in the previous nine decades. Beu (2010) revised the Bocas del Toro tonnoideans in his landmark monograph covering the entire superfamily in the tropical American Neogene, Landau et al. (2011) documented the genus *Strombus* (Gastropoda, Strombidae) in the Bocas assemblages, and Landau and Silva (2011) reported on the genus *Amarophos* (Gastropoda, Buccinidae) in the Caribbean Neogene.

This is the second paper dealing specifically with the Neogene gastropod assemblage found in the Bocas del Toro Region, Caribbean Panama (see Landau et al., 2011). As discussed in Landau et al. (2011), this taxonomic work is greatly facilitated by the huge effort and research which has gone into the Neogene geology and stratigraphy of the region as part of the Panama Paleontology Project (PPP) (Collins and Coates, 1999; Coates et al., 2003, 2005). This preliminary work in surveying and mapping the Neogene of the whole region, naming the physical stratigraphic formations, identifying locations of the richest macrofossil sites and subsequent paleomagnetic and radiometric dating of the deposits is an ideal starting point for taxonomic works. For locality data we refer to Coates in Collins and Coates (1999, p. 287, appendix A, maps).

Here we revise the Cancellariidae occurring in the Bocas del Toro Neogene assemblages. In his monograph on the Costa Rican Miocene, Olsson (1922) recorded four cancellarids from the Bocas del Toro Region: *Cancellaria dariena* Toula, 1909 from the Water and Toro cays (Cayo Agua and Cayo Toro), *Cancellaria mauryae* Olsson, 1922 from Water Cay, *C. toroensis* Olsson, 1922 and *C. plummeri* Olsson, 1922 from Toro Cay. Jung and Petit (1990, p. 96) mentioned a poorly preserved specimen of *C. mauryae* from Water Cay as the only record for the species outside the Dominican Republic. We have not found any further records in the literature for Neogene Cancellariidae from the Bocas area.

The gastropod family Cancellariidae was a characteristic and important constituent of Neogene Caribbean faunas and is highly endemic within assemblages, with a rapid turnover of species. It is also one of the gastropod groups with the highest number of paciphilic species (sensu Woodring, 1966), the importance of which was discussed by Landau et al. (2007, 2010).

As in the previous taxonomic work (Landau et al., 2011), we have adopted the recent recommendation of the International Commission on Stratigraphy—accepted by the IUGS on 30 June 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).

MATERIAL AND METHODS

The material described and discussed here is from the PPP collection 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. Scanning electron micrographs of the protoconchs were taken when sufficiently well preserved material was available. For ages of the Caribbean Neogene assemblages see Landau and Silva (2010).

Abbreviations used.—ANSP, Academy of Natural Sciences, Philadelphia, PA, USA; CAS, California Academy of Sciences, San Francisco, CA, U.S.A.; FMNH, Florida Museum of Natural History, University of Florida, Gainesville, FL, U.S.A.; NHMUK, The Natural History Museum, London, U.K.; NHMW, Naturhistorisches Museum Wien, Austria; NMB, Naturhistorisches Museum Basel, Switzerland; NMW, National Museum of Wales, Cardiff, Wales, U.K.; PPP, Panama Paleontology Project, specimens present in NMB; PRI, Paleontological Research Institute, Ithaca, NY, U.S.A.; SU, Stanford University, Palo Alto, CA, U.S.A. (collections now housed at CAS); USNM, United States National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.; YPM, Peabody Museum of Natural History, Yale University, New Haven, CT, U.S.A.; BL coll., Bernard Landau collection, Albufeira, Portugal.

SYSTEMATIC PALEONTOLOGY

Superfamily CANCELLARIOIDEA Forbes and Hanley, 1851
Family CANCELLARIIDAE Forbes and Hanley, 1851
Subfamily CANCELLARIINAE Forbes and Hanley, 1851

The classification adopted here is according to Harasewych and Petit in Beesley et al. (1998) and Jung and Petit (1990). Most current workers (Ponder and Warén, 1988; Petit and Harasewych, 2005; Bouchet and Rocroi, 2005) follow Ponder (1973) in regarding Cancellarioidea as a superfamily within the Neogastropoda. More recently Kantor and Harasewych (1992) reported similar modifications in the anterior alimentary system of the muricoidean family Volutomitridae and suggested a re-assessment of the taxonomic rank and systematic position of the Cancellarioidea. Rosenberg et al. (1994) suggested the Cancellariidae originated within the Muricoidea on the basis of RNA sequence data.

Landau et al. (2007) adopted a rather conservative approach in considering many of the cancellarid supraspecific taxa as subgenera of *Cancellaria*. In this work we elevate their rank to full genus. As discussed by Beu (2010, p. 131), ranking groups as subgenera of another group expresses a phylogenetic hypothesis about their relationship, which, at the moment within cancellarids cannot be proven, and that narrower genus-rank taxa are more likely to be monophyletic than broader ones.

Genus *CANCELLARIA* Lamarck, 1799

Type species.—*Voluta reticulata* Linnaeus, 1767, by monotypy; Recent, Caribbean.

CANCELLARIA APIMELA Woodring, 1970
Figure 1.1, 1.2

Cancellaria (Cancellaria) apimela WOODRING, 1970, p. 337, pl. 52, figs. 5, 6.

Description.—See Woodring (1970, p. 337).

Types.—Holotype USNM 645720, Caribbean coast east of San Miguel (Río Miguel) station 25 plus 120 meters, Panama, upper Gatun Formation, upper Miocene.

Occurrence.—Middle Miocene, Valiente Formation, Popa Island, Bocas del Toro; upper Miocene, upper Gatun Formation, Caribbean coast, Panama.

Bocas del Toro material.—One specimen NMB H19491, height 22.8 mm, locality PPP 01276 (=NMB 18377), northeast coast of Popa Island, Valiente Formation, Serravalian, middle Miocene.

Discussion.—The single specimen from the middle Miocene Valiente Formation we attribute to *Cancellaria apimela* Woodring, 1970 is similar to the holotype figured by Woodring (1970, pl. 52, figs. 5, 6), but with a slightly wider shell, less scalate spire, and with a slightly greater number of axial ribs. This attribution is made with a little hesitation, as it is difficult to get an idea of the intraspecific variability with the little material available from both the Gatun and Valiente formations. Woodring (1970) did not comment on the columellar folds of this species. The Bocas specimen has a strong, sharp, non-bifid adapical fold and a weak abapical fold. These features are also clearly seen in the holotype. Woodring (1970, p. 337) noted that the protoconch of the Gatun Formation specimens was missing. Unfortunately, the protoconch is also poorly preserved in the Bocas shell.

CANCELLARIA ANOMOIA Woodring, 1970
Figures 1.3–1.14, 7.8, 7.9

Cancellaria rowelli Dall. OLSSON, 1922, p. 256, pl. 6, fig. 7. (not *C. rowelli* Dall, in GUPPY AND DALL, 1896)

Cancellaria rowelli Dall. WEISBORD, 1929, p. 50, pl. 6, figs. 9, 10. (not *C. rowelli* Dall, in GUPPY AND DALL, 1896)

Cancellaria (Cancellaria) anomoia WOODRING, 1970, p. 334, pl. 52, figs. 1, 2.

Description.—See Woodring (1970, p. 334).

Types.—Holotype USNM 645712, Payardi Island, east of Cativa, Panama, lower Gatun Formation, upper Miocene.

Occurrence.—Middle Miocene, lower Gatun Formation, Panama Canal area, Gatun, Panama; upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama; lower Pliocene, Zanclean, Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama, Tuberá Formation, Caribbean Colombia; Pliocene (undetermined), Caribbean, Costa Rica.

Bocas del Toro material.—Two specimens NMB H19492 + H19658, locality PPP 00191 (=NMB 17629), maximum height, 23.5 mm; one specimen NMB H19493, locality PPP 02212 (=NMB 18711), height 18.7 mm; one specimen NMB H19494, locality PPP 01883 (=NMB 18771), height 18.8 mm, Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; two specimens NMB H19495 + H19659 maximum height 18.7 mm, locality PPP 02238 (=NMB 18735); three specimens NMB H19496 + H19660 + H19661; one specimen NMB H19497 height 17.9 mm, locality PPP 02239 (=NMB 18736); one specimen NMB H9498 height 24.3 mm, locality PPP 00326 (=NMB 17822), north side of Nispero Point; two specimens, NMB H19499 + 19662, maximum height 21.6 mm, locality PPP 02234 (=NMB 18731), 400 m from Nispero Point; two specimens NMB H19500 H 19663 height 18.1 mm, locality PPP 02223 (=NMB 18720), east side of Norte Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Discussion.—Jung and Petit (1990) suggested the specimen illustrated by Olsson (1922, pl. 6, fig. 7) as *Cancellaria barretti* Guppy, 1866 (author stated as Dall in error in figure caption) from East Grape Creek, Costa Rica from beds of undetermined age, but probably Pliocene, might represent *Cancellaria anomoia* Woodring, 1970, originally described from the lower Gatun Formation, middle Miocene of Cativa, Panama. We agree with this suggestion, and also record the species from the Cayo Agua Formation, Zanclean, lower Pliocene of Bocas del Toro, Panama.

Cancellaria rowelli Dall, in Guppy and Dall, 1896 has been reported in several Caribbean Neogene assemblages (see Jung and Petit, 1990, p. 99), but we can only confirm its presence in the lower Miocene Baitoa Formation of the Dominican Republic. It differs from *C. anomoia* in having a more fusiform shell shape, with a taller spire, finer and weaker axial sculpture and in having the adapical columellar fold sharp and not clearly bifid, as in *C. anomoia*. *Cancellaria anomoia* has a multispiral protoconch consisting of 3.5 smooth whorls, with a small nucleus (Fig. 7.8, 7.9), similar to that described by Woodring (1970, p. 334) for the Gatun specimens. The shells illustrated by Weisbord (1929, pl. 6, figs. 9, 10) from the Colombian Neogene assemblages as *C. rowelli* are more similar to *C. anomoia* than they are to *C. rowelli*, and we provisionally include them in the chresonymy and distribution.

The material collected from Bocas indicates that *C. anomoia* has a highly variable shell form, as can been seen by the series figured (Fig. 1.3–1.14). The shell width, height of the spire, strength of the axial ribs and the coarseness of the denticles and columellar folds are all variable. Woodring (1970) did not give importance to the character of the columellar folds, which are seldom discussed in his descriptions. In our Bocas material, the adapical columellar fold is always clearly bifid and the mid fold ventrally flattened. The upper Miocene specimens from Bocas (Fig. 1.3–1.8) tend to have fewer and stronger axial ribs than the lower Pliocene ones (Fig. 1.9–1.14), but both forms have a multispiral, dome-shaped protoconch of just under three whorls.

CANCELLARIA PILULA new species
Figures 1.15–1.22, 7.10, 7.11

Diagnosis.—A small *Cancellaria* species, with a very solid, globose shell, spiral sculpture of strap-like cords predominant, a small, narrow aperture with robust armature, broad columellar folds, with adapical fold bifid, and parietal and columellar calluses well developed.

Description.—Shell small, very robust, globose, with a squat conical spire; protoconch consisting of three smooth whorls, nucleus small, transition to teleoconch marked by beginning of spiral sculpture; teleoconch consisting of four depressed, weakly convex whorls, with periphery at abapical suture; sculpture on first and second whorls with 22 narrow prosocline ribs crossed by five narrow spiral cords, forming finely, evenly reticulate sculpture; abapically, axial ribs broaden and weaken, spiral cords become dominant, raised, flattened, strap-like, roughly equal in width to their interspaces; suture impressed; last whorl 82% total height, globose, evenly rounded, hardly constricted at base, bearing 12 flattened cords; aperture narrow, elongate, 50% of total height, outer lip very thick, prosocline, with beveled edge, strongly lirate within; siphonal canal very short, open; parietal callus thickened, broadly expanded, closely adherent, with spiral sculpture showing through; columellar callus greatly thickened, detached abapically, forming medial edge of umbilical chink; three ventrally-flattened, robust columellar folds, adapical fold bifid, middle fold irregular, sinuous, abapical fold weakest; siphonal fasciole not developed, distinct umbilical chink.

Etymology.—Diminutive of Latin "*pila*," a ball.

Types.—Holotype NMB H19501 (Fig. 1.15–1.17), height 14.0 mm, width 9.5 mm, paratype 1 NMB H19502, height 12.6 mm, width 9.0 mm, locality PPP 02212 (=NMB 18711), Finger Island; paratype 2 NMB H19503 (Fig. 1.18, 1.19), height 14.7 mm, width 9.8 mm, paratypes 3 to 6 NMB H19504-H19507 (Fig. 7.10, 7.11) (juveniles), locality PPP 02206 (=NMB 18705), south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula; paratype 7 NMB H19508 (Fig. 1.20–1.22), height 14.0 mm, width 8.8 mm, locality PPP 02207 (=NMB 18706), south coast, about 1.5 km southwest of Punta de Toro, small island 50 m west of coast; paratypes 8 and 9 NMB H19509 and H19510 (juveniles), locality PPP 00191 (=NMB 17629), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—This small, very solid cancellarid, with strap-like, predominant spiral sculpture and strong apertural armature is very distinctive and unlike any other Caribbean living or fossil congener. Paratypes 1 and 2 (Fig. 1.18–1.22) are slightly less robust than the holotype. In sculpture and shape *Cancellaria pilula* n. sp. is similar to a vertically compressed *C. gemmulata* G. B. Sowerby I, 1832, a living species from the Galapagos (see Keen, 1971, left fig. 1451; Hemmen, 2007, fig. 149). The fossil species differs in having a last whorl with a more rounded shoulder and without any constriction behind the siphonal fasciole, the spiral cords are broader and the columellar folds more robust, especially the adapical fold.

CANCELLARIA PETITI Olsson, 1967
Figures 2.1–2.13, 7.12

Cancellaria cossmanni OLSSON, 1922, p. 253, pl. 6, figs. 9, 11. (not *C. cossmanni* MORLET, 1888, p. 209, pl. 9, fig. 10, 10a, 10b)

Cancellaria cossmanni Olsson. MARKS, 1949, p. 459 (list).

?*Cancellaria (Cancellaria) cossmanni* Olsson. ANDERSON, 1929, p. 117.

Not *Cancellaria (Cancellaria) cossmanni* Olsson. OINOMIKADO, 1939, p. 623, pl. 29, fig. 17. (?=juvenile *Distorsio* RÖDING, 1798)

Cancellaria (Cancellaria) petiti OLSSON, 1967, p. 44. (new name for *C. cossmanni* OLSSON, 1922, *non* MORLET, 1888)

Cancellaria barreti (sic) Guppy. GÓMEZ AND VALERIO, 1971, p. 44, fig. 3. (not *C. barretti* GUPPY, 1866)

Cancellaria cossmanni Olsson. GÓMEZ AND VALERIO, 1971, p. 44, fig. 4.

Cancellaria (Cancellaria) petiti Olsson. JUNG AND PETIT, 1990, p. 117, pl. 16, figs. 5–9.

Description.—See Olsson (1922, p. 253) under *Cancellaria cossmanni*.

Types.—Lectotype PRI 20966 (Fig. 2.1, 2.2). Río Banano, Limón Province, Costa Rica, Rio Banano Formation, upper Pliocene.

Occurrence.—Middle Miocene, Valiente Formation, Popa Island, Bocas del Toro, Panama; upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama; lower Pliocene, Zanclean, Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama; upper Pliocene, Piacenzian, Rio Banano Formation, Costa Rica.

Bocas del Toro material.—One specimen NMB H19511, height 23.9 mm (incomplete), locality PPP 01276 (=NMB 18377); one specimen NMB H19512, height 19.6 mm, locality PPP 01277 (=NMB 18378), northeast coast of Popa Island, Valiente Formation, Serravalian, middle Miocene; one specimen NMB H19513, height 23.3 mm, locality PPP 00376 (=NMB 17850); two specimens NMB H19514, locality PPP 00379 (=NMB 17851), maximum height 21.4 mm; three specimens NMB H19515, locality PPP 02227 (=NMB 18724), maximum height 21.8 mm, west side of Bruno Bluff; two specimens NMB H19516, locality PPP 02217 (=NMB 18716), maximum height 26.9 mm, south coast, 5 km southeast of Cayo Patterson, south end of Playa Lorenzo; one specimen NMB H19517, height 18.4 mm, locality PPP 02207 (=NMB 18706); one specimen NMB H19518, locality PPP 02206 (=NMB 18705), height 21.2 mm, south coast, about 1.5 km southwest of Punta de Toro, small island 50 m west of coast; one specimen NMB H19519, locality PPP 00391 = (NMB 17858), height 30.3 mm, west side Shark Hole Point, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; three specimens NMB H19520 height 31.4 mm, locality PPP 02223 (=NMB 18720), east side of Norte Point; 28 specimens NMB H19521, maximum height 26.1 mm, locality PPP 02224 (=NMB 18721), east coast, promontory between Norte and Nispero points; one specimen, NMB H19668, height 22.9 mm, locality PPP 00476 (=NMB 17813), south of Nispero Point; 10 specimens, locality PPP 00200 (=NMB 17634), east coast, south of Norte Point; 10 specimens, locality NMB H19523, PPP 01203 (=NMB 18374), east coast, east of Norte Point; nine specimens (BL coll.), Nispero Point; three specimens NMB H19524, maximum height 20.8 mm, locality NMB 18983; one specimen NMB H19525, height 26.3 mm, PPP 02236 (=NMB 18733),unnamed promontory between Tiburon and Piedra Roja points,W side of Cayo Agua Island,

FIGURE 1—*1, 2, Cancellaria apimela* Woodring, 1970, NMB H19491, height 22.8 mm, PPP 01276 (=NMB 18377), northeast coast of Popa Island, Valiente Formation, Serravalian, middle Miocene; *3, 4, Cancellaria anomoia* Woodring, 1970, NMB H19492, height 21.2 mm, locality PPP 00191 (=NMB 17629), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *5, 6, Cancellaria anomoia* Woodring, 1970, NMB H19493, height 18.7 mm, locality PPP 02212 (=NMB 18711), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *7, 8, Cancellaria anomoia* Woodring, 1970, NMB H19494, height 18.8 mm, locality PPP 01883 (=NMB 18771), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *9–11, Cancellaria anomoia* Woodring, 1970, NMB H19496, height 17.9 mm, locality PPP

all Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Discussion.—*Cancellaria petiti* Olsson, 1967 is the most abundant and widespread cancellarid in the Bocas assemblages. Some of the specimens have a well-preserved, multispiral protoconch, consisting of 3.25 smooth whorls, with a small nucleus (Fig. 7.12). The transition to the teleoconch is sharply delimited by a prosocline scar. For full discussion on the synonymy of this species see Jung and Petit (1990, p. 117), for comparison with related taxa see below.

CANCELLARIA ISABELAE new species

Figures 2.14–2.20, 7.13, 7.14

?*Cancellaria (Cancellaria) barretti* Guppy. WOODRING, 1928 (in part), pl. 12, fig. 6.

Diagnosis.—A medium-sized *Cancellaria* species, with a small multispiral protoconch, a tall, scalate spire, fine evenly reticulate sculpture, regularly rounded last whorl, thin outer lip, and bifurcate columellar folds.

Description.—Shell of medium size and thickness, fusiform, with tall scalate spire, fine evenly-reticulate sculpture; protoconch small, dome-shaped, consisting of three smooth whorls, with very small nucleus, transition to teleoconch delimited by prosocline scar; teleoconch consisting of six weakly convex whorls, periphery at abapical suture; suture impressed, undulating, weakly canaliculate; axial sculpture consisings of close-set, elevated, narrow, rounded, prosocline ribs, roughly equal in width to their interspaces, 12 on first teleoconch whorl, 22–30 on penultimate whorl; spiral sculpture consisting of six flattened cords, slightly narrower than their interspaces, overriding axial sculpture; last whorl 69% total height, convex below shoulder, constricted at base, bearing about 35 axial ribs, becoming crowded behind outer lip, 15 spiral cords, becoming slightly more widely-spaced abapically; aperture elongate, 49% of total height, outer lip not thickened, strongly lirate within; siphonal canal of medium length, open, abaxially pointing; parietal callus reduced to thin callus wash with spiral sculpture showing through; columellar callus weakly thickened, closely adherent; three oblique columellar folds present, weakening rapidly abapically, adapical and mid-fold distinctly bifurcate; siphonal fasciole moderately developed, rounded.

Etymology.—Named after Isabel Fenollera, mother of the senior author.

Occurrence.—Lower Pliocene, Zanclean, Cayo Agua Formation; Pliocene (undetermined), ?Bowden Formation, Jamaica.

Types.—Holotype NMB H19526 (Fig. 2.14–2.16), height 28.6 mm, locality PPP 02239 (=NMB 18736); paratype 1 NMB H19527 (Fig. 2.17, 2.18), height 25.3 mm; paratype 2 NMB H19528, height 24.5 mm; paratype 3 NMB H19529, height 21.7 mm; paratype 9 NMB H19530, height 27.6 mm, locality PPP 01910 (=NMB 18772); paratype 10 NMB H19531 (Fig. 7.13, 7.14), height 24.9 mm, locality PPP 00326 (=NMB 17822), north side of Nispero Point; paratype 4 NMB H19532 (Fig. 2.19, 2.20), height 28.8 mm; paratype 5 NMB H19533, height 23.3 mm; paratype 6 NMB H19534, height 22.6 mm; paratype 7 NMB H19535, height 18.0 mm; paratype 8 NMB H19536, height 15.5 mm, locality PPP 02234 (=NMB 18731), 400 m from Nispero Point; all Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Bocas del Toro (non-type) material.—Three specimens NMB H19537, locality PPP 02239 (=NMB 18736), north side of Nispero Point; six specimens, NMB H19538, locality PPP 02232 (=NMB 18730), maximum height 21.2 mm, Nispero Point; two specimens NMB H19539, maximum height 27.8 mm, locality PPP 00346 (=NMB 17904), unnamed promontory between Tiburon and Piedra Roja Points, west side of Cayo Agua Island, all Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Discussion.—*Cancellaria petiti* Olsson, 1967, *Cancellaria isabelae* n. sp. and *Cancellaria stri* n. sp. are clearly closely related species, which differ subtly in their shell shape and sculpture. *Cancellaria petiti* has the lowest spire and most inflated last whorl. *Cancellaria isabelae* and *C. stri* are higher spired and *C. stri* has a more fusiform shell shape. All three have the reticulate sculpture typical for the genus, but this is finest in *C. isabelae* and rather coarse and horizontally elongated in *C. stri*, with *C. petiti* somewhat intermediate. The adapical and medial columellar folds in both *C. petiti* and *C. stri* are thickened and clearly bifurcate, whereas this is not so evident in *C. stri*, although only one specimen of that species was studied here. The protoconch is not helpful in separating the three species, as all have a small, multispiral, dome-shaped protoconch of 3.0–3.5 whorls with a small nucleus.

Cancellaria barretti Guppy, 1866 from the Pliocene Bowden Formation of Jamaica has a very similar shell to the species discussed above and probably belongs within this group. It has a dense reticulate sculpture most like that of *C. isabelae*. As pointed out by both Woodring (1928, p. 291) and Jung and Petit (1990, p. 117) the species is known from only two shells, the holotype (re-illustrated in Jung and Petit, 1990, pl. 16, figs. 1–4) and the specimen illustrated by Woodring (1928, pl. 12, fig. 6); as pointed out by these authors, the two shells are not identical. The holotype of *C. barretti* has a large barrel-shaped last whorl, whereas the specimen illustrated by Woodring has a shorter, more rounded last whorl. None of the specimens of *C. isabelae* from Bocas have a barrel-shaped last whorl. It is quite possible that the shell illustrated by Woodring (1928, pl. 12, fig. 6) represents *C. isabelae* rather than *C. barretti* but more material is needed to be certain.

CANCELLARIA STRI new species

Figure 3.1–3.5

Diagnosis.—A medium-sized *Cancellaria* species, with a small multispiral protoconch, a tall, scalate spire, coarse, horizontally-elongated reticulate sculpture, non-globular last

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02239 (=NMB 18736), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *12–14, Cancellaria anomoia* Woodring, 1970, NMB H19660, height 17.3 mm, locality PPP 02239 (=NMB 18736), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *15–17, Cancellaria pilula* n. sp., holotype NMB H19501, height 14.0 mm, width 9.5 mm, locality PPP 02212 (=NMB 18711), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *18, 19, Cancellaria pilula* n. sp., paratype 2 NMB H19503, height 14.7 mm, width 9.8 mm, locality PPP 02206 (=NMB 18705), south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *20–22, Cancellaria pilula* n. sp., paratype 7 NMB H19508, height 14.0 mm, width 8.8 mm, locality PPP 02207 (=NMB 18706), south coast, about 1.5 km southwest of Punta de Toro, small island 50 m west of coast, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene.

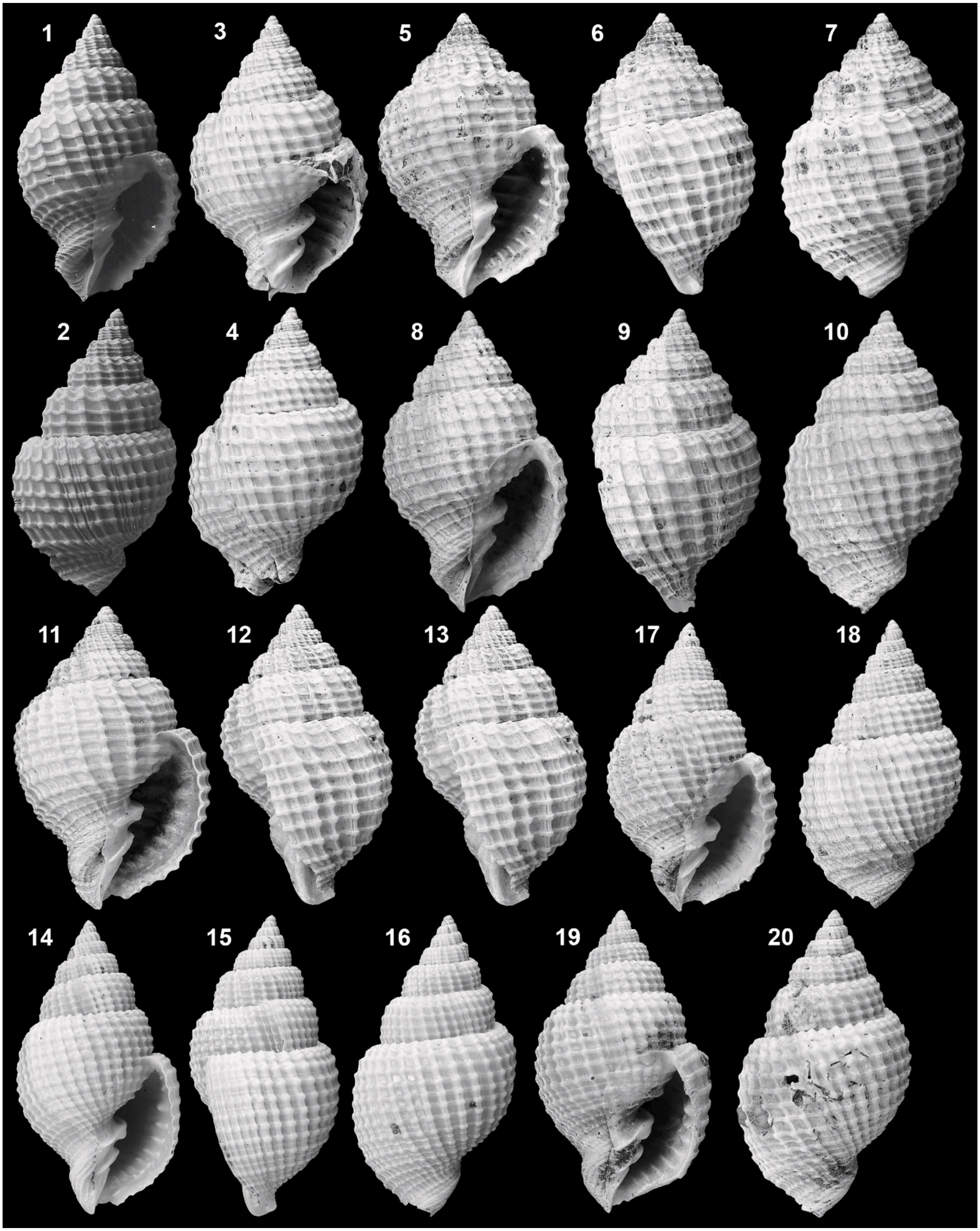

FIGURE 2—*1, 2, Cancellaria petiti* Olsson, 1967, lectotype PRI 20966, Río Banano, Limón Province, Cost Rica, Rio Banano Formation, upper Pliocene; *3, 4, Cancellaria petiti* Olsson, 1967, NMB H19511, height 23.9 mm (incomplete), PPP 01276 (=NMB 18377), northeast coast of Popa Island, Valiente Formation, Serravalian, middle Miocene; *5–7, Cancellaria petiti* Olsson, 1967, NMB H19513, height 23.3 mm, locality PPP 00376 (=NMB 17850), west side of Bruno Bluff, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *8–10, Cancellaria petiti* Olsson, 1967, NMB H19521, height 24.1 mm, locality PPP 02224 (=NMB 18721), east coast, promontory between Norte and Nispero points, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *11–13, Cancellaria petiti* Olsson, 1967, NMB H19525, height 26.3 mm, PPP 02236 (=NMB 18733), unnamed

whorl, thin outer lip, non-bifurcated columellar folds, and a pronounced siphonal fasciole.

Description.—Shell of medium size and thickness, fusiform, with tall scalate spire, coarse, horizontally-elongated, reticulate sculpture; protoconch small, high dome-shaped, consisting of 3.25 smooth whorls, with very small nucleus, transition to teleoconch abrupt, marked by first axial rib; teleoconch consisting of six weakly convex whorls, with narrow, almost horizontal subsutural platform, periphery at abapical suture; suture impressed, undulating, weakly canaliculate; axial sculpture consisting of 14 relatively wide-spaced, elevated, narrow, rounded, weakly prosocline ribs; spiral sculpture consisting of five elevated flattened cords, slightly narrower than their interspaces, overriding axial sculpture; last whorl 69% total height, convex below shoulder, strongly constricted at base, bearing ten spiral cords, becoming slightly more widely-spaced abapically; aperture elongate, 47% of total height, outer lip not thickened, strongly lirate within; siphonal canal of medium length, open, abaxially pointing; parietal callus reduced to thin callus wash with spiral sculpture showing through; columellar callus thickened, detached abapically, forming medial edge of umbilical chink; three oblique, non-bifurcated columellar folds present, weakening rapidly abapically; siphonal fasciole strongly developed, rounded, forming lateral border of deep umbilical chink.

Etymology.—For the Smithsonian Tropical Research Institute (STRI) in recognition of the logistic help given to the authors in the Bocas del Toro area.

Occurrence.—Lower Pleistocene, Gelasian upper Escudo de Veraguas Formation, Bocas del Toro, Panama.

Types.—Holotype, NMB H19540 (Fig. 3.1–3.5), locality PPP 02187 (=NMB 18686), height 29.2 mm, lower Pleistocene, Gelasian, upper Escudo de Veraguas Formation, Escudo de Veraguas Island, south coast, 100 m west of PJ2222, Bocas del Toro, Panama (for age see Coates et al., 2005, p. 382, fig. 5).

Discussion.—Although represented by a single specimen, the shell of *Cancellaria stri* n. sp. is beautifully preserved, with its protoconch intact and well preserved, and clearly distinct from any known cancellarid species. In general shape and sculpture it is closely similar to *Cancellaria petiti* Olsson, 1967, found in the straigraphically older middle Miocene to lower Pliocene Bocas del Toro assemblages, but differs in having a more fusiform shell, and in having fewer and wider spaced axial ribs. *Cancellaria stri* is described as having non-bifurcated columellar folds, although there is a slight thickening of the adapical fold mid-length, which could be interpreted as a trend towards becoming bifurcate. *Cancellaria petiti* usually has a clearly bifurcated adapical columellar fold.

CANCELLARIA AXELOLSSONI new species
Figures 3.6–3.12, 7.15, 7.16

Cancellaria mauryae OLSSON, 1922 (in part), p. 82. (not Dominican material)

Diagnosis.—A medium-sized *Cancellaria* species, with a multispiral protoconch, scalate spire, finely reticulate sculpture with a predominantly axial component, globose last whorl and a subobsolete third columellar fold.

Description.—Shell of medium size and thickness, broadly fusiform, with scalate spire, finely reticulate sculpture, with predominantly axial component; protoconch dome-shaped, consisting of 2.75–3 smooth convex whorls, with small nucleus, transition to teleoconch sharply delimited by beginning of axial sculpture; teleoconch consisting of six whorls, early whorls with narrow, almost horizontal infrasutural platform, roundly angled at shoulder, almost straight below, spire whorls becoming weakly convex abapically; suture impressed, weakly canaliculate; axial sculpture consisting of strongly prosocline, rounded ribs, roughly equal in width to their interspaces, 30 on penultimate whorl, on early whorls two or three cords at the shoulder stronger, with spiral sculpture forming small nodes at intersections; spiral sculpture of weak, narrow spiral cords, 7 to 9 on penultimate whorl, becoming obsolete, or almost so, over axial ribs, single secondary cord in interspaces from penultimate whorl; last whorl globose, about 79% of total height, rounded at shoulder, which is placed a short distance below suture, convex below, strongly constricted at base; axial ribs broaden on last whorl, crowding behind outer lip; aperture broad, ovate, 55% of total height, outer lip slightly prosocline, lirate within, not thickened by varix, stromboid notch shallow; siphonal canal open, short, broad; parietal callus thin, moderately expanded, closely adherent; three columellar folds, adapical fold largest and sharp, middle fold rounded, abapical fold very weak; columellar callus strong, half covering chink-like umbilicus.

Etymology.—For Axel A. Olsson, in recognition of his enormous contribution to our knowledge of the Bocas del Toro assemblages.

Types.—Holotype NMB H19541 (Fig. 3.6–3.8), height 40.6 mm, width 23.9 mm; paratype 1 NMB H19542 (Fig. 3.9), height 35.3 mm, width 20.9 mm; paratype 2 NMB H19543 (Fig. 7.15, 7.16), height 13.6, width 8.1 mm (juvenile), all locality PPP 02236 (=NMB 18733); paratype 3 NMB H19544 (Fig. 3.10–3.12), height 40.0 mm, width 23.4 mm; paratype 4 NMB H19545, height 27.5 mm, width 16.4 mm, both locality PPP 00347 (=NMB 17904); paratype 5 NMB H19546, height 22.6 mm, width 13.5 mm, both locality PPP 00345 (=NMB 17830), unnamed promontory between Tiburon and Piedra Roja points, west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; paratype 6 NMB H19547, height 35.2 mm, width 22.4 mm, locality PPP 00338 (=NMB 17827), east tip of Tiburon Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Occurrence.—Lower Pliocene, Zanclean, Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama.

Discussion.—Olsson (1922) described *C. mauryae* based on material from the upper Miocene Cercado Formation of the

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promontory between Tiburon and Piedra Roja points, west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *14–16, Cancellaria isabelae* n. sp., holotype NMB H19526, height 28.6 mm, locality PPP 02239 (=NMB 18736), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *17, 18, Cancellaria isabelae* n. sp., paratype 1 NMB H19527, height 25.3 mm, locality PPP 02239 (=NMB 18736), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *19–20, Cancellaria isabelae* n. sp., paratype 4 NMB H19532, height 28.8 mm, PPP 02234 (=NMB 18731), 400 m from Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

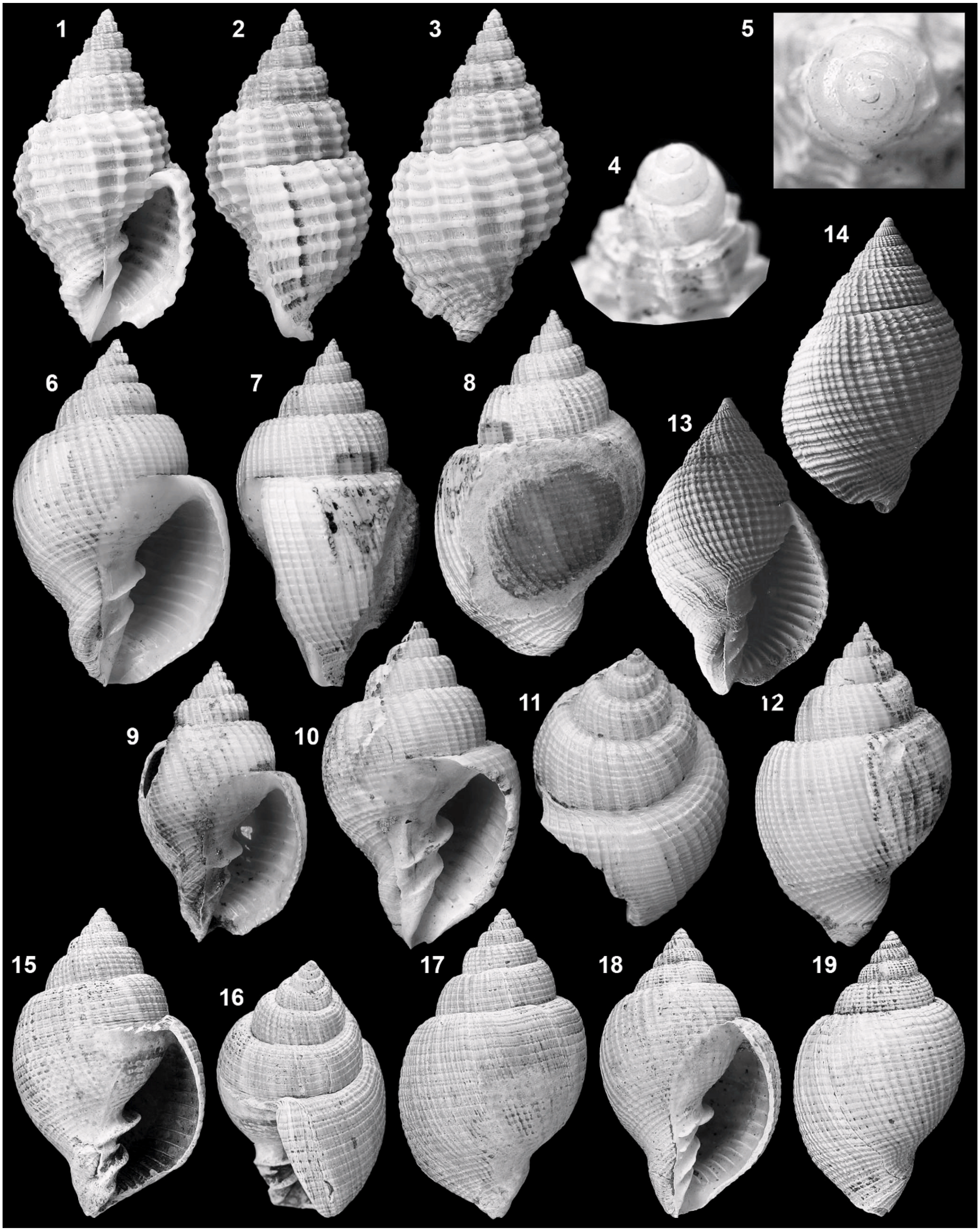

FIGURE 3—*1–5, Cancellaria stri* n. sp., holotype NMB H19540, height 29.2 mm, locality PPP 02187 (=NMB 18686), Escudo de Veraguas Island, south coast, 100 m west of PJ2222, Bocas del Toro, Panama, upper Escudo de Veraguas Formation, Gelasian, lower Pleistocene; *6–8, Cancellaria axelolssoni* n. sp., holotype NMB H19541, height 40.6 mm, width 23.9 mm, locality PPP 02236 (=NMB 18733), unnamed promontory between Tiburon and Piedra Roja points, west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *9, Cancellaria axelolssoni* n. sp., paratype 1 NMB H19542, height 35.3 mm, width 20.9 mm, locality PPP 02236 (=NMB 18733), unnamed promontory between Tiburon and Piedra Roja points,

Dominican Republic. In his discussion, Olsson (1922, p. 83) mentioned the presence of a single incomplete specimen from Water Cay (Cayo Agua). This record undoubtedly refers to the new taxon proposed here which is closely similar to *C. mauryae* but differs mainly in the character of the spire and early teleoconch whorls. *Cancellaria axelolssoni* n. sp. has a scalate spire with a weakly canaliculate suture and a narrow but distinct infrasutural platform whereas the spire whorls in *C. mauryae* (holotype PRI 28661; Fig. 3.13, 3.14) are weakly but regularly convex with no distinct infrasutural area. Other differences can be found in the character of the sculpture, with the axial and spiral element of similar strength, or the spiral cords slightly predominant in *C. mauryae* whereas the axial sculpture is clearly stronger in *C. axelolssoni.* The character of the columellar folds is also different; all three are strongly developed in *C. mauryae* whereas the abapical fold is almost obsolete in *C. axelolssoni*. Specimens of *C. mauryae* from the Cercado Formation are not common but we have examined the five shells listed by Jung and Petit (1990, p. 96) and three further adult specimens (BL coll.) and find these differences to be consistent.

Cancellaria guppyi Gabb, 1873, also from the upper Miocene Cercado Formation of the Dominican Republic differ from *C. axelolssoni* in having a squatter, more globose shell, with a shorter, non-scalate spire and in having a fine, evenly-reticulate sculpture. Most importantly, *C. guppyi* has a bifid adapical columellar fold, which is characteristic of *Cancellaria* sensu stricto. *Cancellaria axelolssoni* is a member of a small group of Caribbean Neogene cancellariid species which do not conform to the generic description in having a sharp non-bifid adapical fold but otherwise share the generic characteristics fairly closely. Another species in this group is *Cancellaria juncta* Jung and Petit, 1990, which differs from its congeners in having extremely fine sculpture.

CANCELLARIA TAPEINA Woodring, 1970
Figure 3.15–3.19

Cancellaria (Cancellaria) tapeina WOODRING, 1970, p. 335, pl. 51, figs. 8, 9.

Description.—See Woodring (1970, p. 335).

Types.—Holotype USNM 645714, Caribbean coast east of San Miguel (Río Miguel) station 25 plus 120 meters, Panama, upper Gatun Formation, upper Miocene.

Occurrence.—Middle Miocene, Valiente Formation, Valiente Peninsula, Bocas del Toro; upper Miocene, upper Gatun Formation, Caribbean coast, Panama.

Bocas del Toro material.—Two specimens NMB H19548 + H19549, maximum height 32.1 mm, locality PPP 02217 (=NMB 18716), south coast, 5 km southeast of Cayo Patterson, south end of Playa Lorenzo, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene.

Discussion.—Two specimens from the middle Miocene Valiente Formation of Bocas are present in the PPP collection, which closely match the holotype of *C. tapeina* Woodring, 1970 (pl. 51, figs. 8, 9) from the upper Gatun Formation of San Miguel, on the Caribbean coast of Panama. Both this species and *Cancellaria apimela* Woodring, 1970, discussed above are present in both the Valiente Formation of Bocas del Toro and the upper Gatun Formation of San Miguel.

Cancellaria tapeina is characterized by its inflated last whorl, very depressed, fine, cancellate sculpture and sharp, non-bifurcate columellar folds. These shell characters place it in a group of Caribbean Neogene cancellarids including *C. mauryae* Olsson, 1922, from the upper Miocene Cercado Formation of the Dominican Republic, which differs in having a more conical spire and more elevated sculpture, *C. juncta* Jung and Petit, 1990 also from the Cercado Formation of the Dominican Republic, which has more rounded spire whorls and a more inflated last whorl, and *C. axelolssoni* n. sp., from the lower Pliocene Cayo Agua Formation, Bocas del Toro, which has more shouldered whorls and a more elevated, reticulate sculpture. Woodring (1970, p. 335) mentioned that the protoconch was missing in the Gatun shells. Unfortunately, the protoconch is also poorly preserved in the Bocas specimens.

Genus EUCLIA H. Adams and A. Adams, 1853

Type species.—*Cancellaria cassidiformis* G. B. Sowerby I, 1832, by subsequent designation Cossmann, 1888. Recent, Panamic-Pacific.

EUCLIA CODAZZII (Anderson, 1929)
Figure 4.1–4.5

Cancellaria codazzii ANDERSON, 1929, p. 116, pl. 14, figs. 4–7.

Cancellaria karsteni ANDERSON, 1929, p. 114, pl. 10, figs. 7–9.

Cancellaria hettneri ANDERSON, 1929, p. 114, pl. 10, figs. 5, 6.

Cancellaria codazzii Anderson. MARKS, 1949, p. 459 (list).

Cancellaria karsteni Anderson. MARKS, 1949, p. 460 (list).

Cancellaria hettneri Anderson. MARKS, 1949, p. 460 (list).

Cancellaria codazzii Anderson. BARRIOS, 1960, p. 291, pl. 11, fig. 5.

Cancellaria (Euclia) cf. *codazzii* Anderson. JUNG, 1969. 541, pl. 58, fig. 8.

Cancellaria (Euclia) codazzii Anderson. WOODRING, 1970, p. 339, pl. 54, figs. 3, 4, 7, 8, 11, 12.

Cancellaria (Euclia) codazzii Anderson. PITT AND PITT, 1993, p. 6, pl. 2, fig. 10.

Cancellaria (Euclia) codazzii Anderson. LANDAU et al., 2007, p. 36, figs. 26–28.

Euclia codazzii (Anderson). LANDAU AND SILVA, 2010, p. 97, pl. 19, fig. 7.

Description.—See Anderson (1929, p. 116).

Types.—Holotype CAS 4645, locality between Chorrera and Cibarco, Departamento del Atlántico, Colombia, Tuberá Formation, lower Pliocene.

Occurrence.—Middle Miocene, lower Gatun Formation, Panama Canal area, Gatun, Panama; upper Miocene, middle Gatun Formation, Panama Canal area, Gatun, Panama;

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west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *10–12, Cancellaria axelolssoni* n. sp., paratype 3 NMB H19544, height 40.0 mm, width 23.4 mm, locality PPP 00347 (=NMB 17904),unnamed promontory between Tiburon and Piedra Roja points, west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *13, 14, Cancellaria mauryae* Olsson, 1922, holotype PRI 28661, height 36.7 mm, Río Mao (exact locality unknown), Dominican Republic, Cercado Formation, upper Miocene; *15–17, Cancellaria tapeina* Woodring, 1970, NMB H19548, height 32.1 mm, locality PPP 02217 (=NMB 18716), south coast, 5 km southeast of Cayo Patterson, south end of Playa Lorenzo, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *18, 19, Cancellaria tapeina* Woodring, 1970, NMB H19549, height 23.7 mm, locality PPP 02217 (=NMB 18716), south coast, 5 km southeast of Cayo Patterson, south end of Playa Lorenzo, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene.

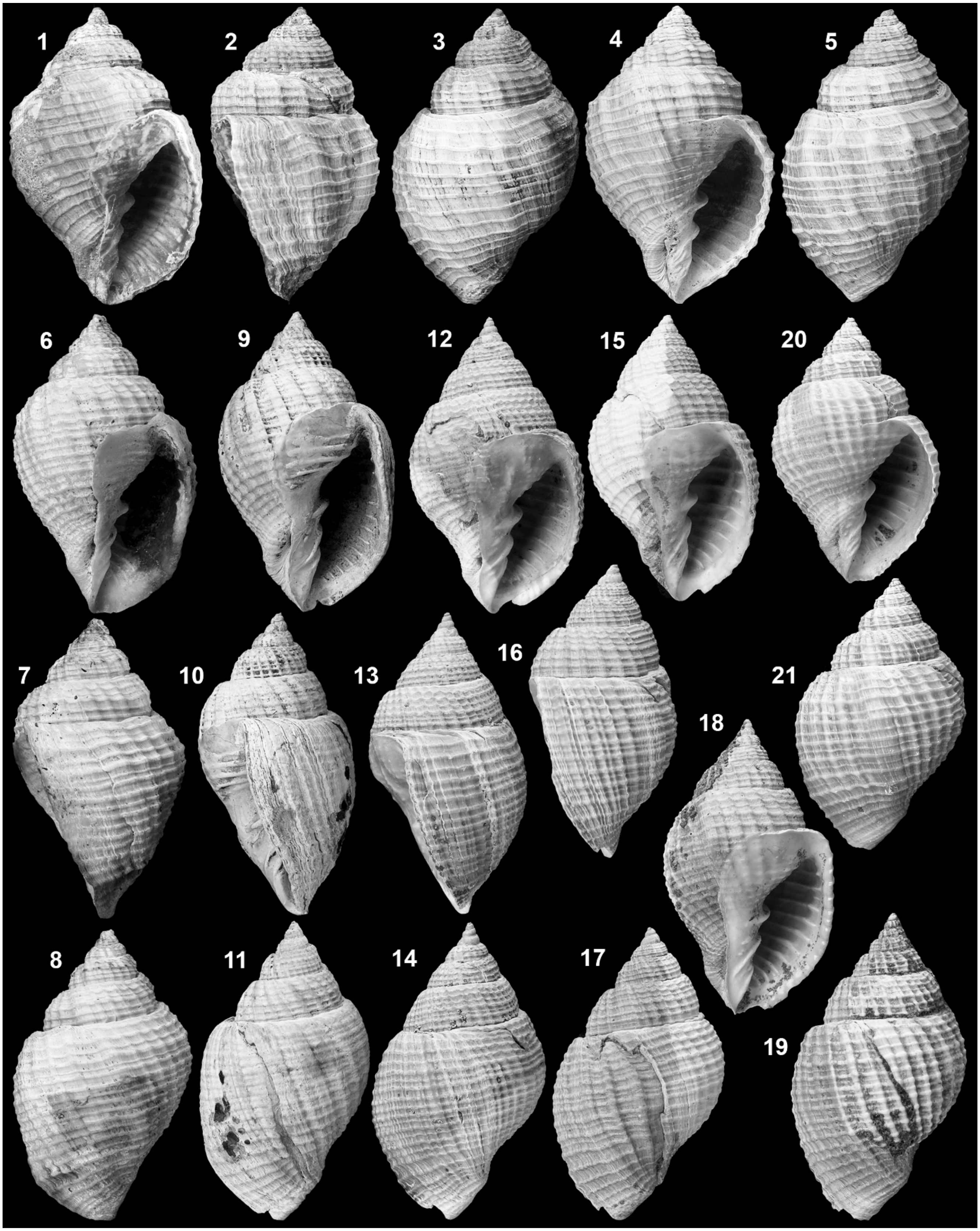

FIGURE 4—*1–3, Euclia codazzii* (Anderson, 1929), NMB H19550, height 32.2 mm, locality PPP 00201 (=NMB 17635), east coast, south of Norte Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *4, 5, Euclia codazzii* (Anderson, 1929). NMB H19551, height 30.7 mm, locality PPP 00201 (=NMB 17635), east coast, south of Norte Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *6–8, Euclia leuzingeri* (Rutsch, 1934), NMB H19613, height 40.8 mm, locality PPP 00326 (=NMB 17822), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *9–11, Euclia leuzingeri* (Rutsch, 1934), NMB H19610, height 46.6 mm, locality PPP 02195 (=NMB 18694),

lower Pliocene, Zanclean, Araya Formation, Cubagua Island, Venezuela; Tuberá Group, northern Colombia; Melajo Clay Member of Springvale Formation, Trinidad; Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama.

Bocas del Toro material.—Four specimens NMB H19550-H19553, maximum height 32.2 mm, locality PPP 00201 (=NMB 17635), east coast, south of Norte Point; one specimen NMB H19554, height 26.9 mm (incomplete), locality PPP 01203 (=NMB 18374), east coast, east of Norte Point; Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Discussion.—As discussed by Woodring (1970), the shells of this species are quite variable with the angulation at the shoulder of the last whorl and the spines more or less developed. Woodring (1970) considered *Euclia karsteni* (Anderson, 1929) and *Euclia hettneri* (Anderson, 1929) to be synonyms of *Euclia codazzii*. As first reviser he selected the name *C. codazzii* as the senior synonym, considering the other two nominal species to represent variability extremes. Woodring (1970) also included in his synonymy *Euclia maldonadoi* Olsson, 1964 from the Pacific upper Miocene Angostura Formation of Ecuador. That synonymy was not accepted by Jung and Petit (1990) as *E. maldonadoi* has a rounded last whorl whereas the shells of *E. codazzii* have a sharp shoulder with a flat or concave area posterior to the shoulder. The specimens from Cayo Agua have a concave shoulder posterior to the angled shoulder and match the type specimen of *E. codazzii*.

Species of the genus *Euclia* H. and A. Adams, 1854 are characterized by having shells with swollen axial ribs on the last whorl with a tendency to form nodules at the shoulder. Both *Euclia* and *Pyruclia* Olsson, 1932 represent species groups which were present in the Neogene Caribbean but are now restricted to the Pacific. In this particular case the lineage starts in the early Miocene with *Euclia werenfelsi* Jung, 1965 represented in the Cantaure Formation of Venezuela. This is a species with a relatively small, elongated shell, with fine axial sculpture and relatively well-developed spines at the shoulder. *Euclia codazzii* was present in both the Atlantic and Pacific in the late Miocene. It gave rise to the Pacific Tropical American species of *Euclia* of which *Euclia balboae* Pilsbry, 1931 is the most similar, but differing in having fewer axial ribs on the spire whorls (Woodring, 1970). The shell of the more common Pacific Pleistocene to Recent *Euclia cassidiformis* Sowerby, G. B. I 1832 is larger, more spinose and has angular spire whorls as well on the last whorl.

Cancellaria epistomifera acuticarinata Weisbord, 1929 (holotype illustrated in Landau and Silva, 2010, pl. 19, fig. 8) was based on a small incomplete shell. It is very similar to *Euclia codazzii* (Anderson, 1929) and possibly conspecific. If this were the case the name *Euclia acuticarinata* would take priority, as Weisbord's work is dated 8 January 1929, whereas Anderson's is dated 29 March 1929. Until better-preserved material from Colombia is available we prefer to keep the well-established name *E. codazzii*.

EUCLIA LEUZINGERI (Rutsch, 1934)

Figures 4.6–4.21, 9.1, 9.2

Cancellaria dariena Toula. WEISBORD, 1929, p. 50. pl. 6, fig. 8. (non *Cancellaria dariena* TOULA, 1909).

Cancellaria reticulata leuzingeri RUTSCH, 1934, p. 89, pl. 7, figs.10, 11, pl. 8, figs. 1, 2, 5.

Cancellaria (Euclia) leuzingeri Rutsch. LANDAU et al., 2007, p. 37, figs. 29–31.

Euclia leuzingeri (Rutsch). LANDAU AND SILVA, 2010, p. 97, pl. 19, fig. 9.

Description.—See Rutsch (1934, p. 89).

Types.—Holotype NMB H1926 (Rutsch, 1934, pl. 8, figs. 1, 2); paratype 1 H1925 (Rutsch, 1934, pl. 7, fig. 11, pl. 8, fig. 5); paratype 2 H1924 (Rutsch, 1934, pl. 7, fig. 10), NMB H1927/1 and NMB 1927/6 (non-figured paratypes), all Punta Gavilán, Falcón Province, Venezuela, Punta Gavilán Formation, lower Pliocene.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Bocas del Toro, Panama; lower Pliocene, Zanclean, Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama; Punta Gavilán Formation, Falcón Province, Araya Formation, Cubagua Island, Aramina Formation, Araya Peninsula, Venezuela; Tuberá Formation, Colombia.

Bocas del Toro material.—Five specimens NMB H19555-H19559, locality PPP 01883 (=NMB 18771), maximum height 37.6 mm; 16 specimens NMB H19560 − H19575, locality PPP 02212 (=NMB 18711), maximum height 37.0 mm; 13 specimens NMB H19576-H19588, locality PPP 00477 (=NMB 17824), maximum height 34.1 mm; three specimens NMB H19589-19591, locality PPP 01996 (=NMB 18375), maximum height 32.6 mm; 13 specimens NMB H19592-19604; one specimen NMB H19605, locality PPP 00191 (=NMB 17629), maximum height, 34.2 mm; two specimens NMB H19606 + H19607, locality PPP 01996 (=NMB 18375), maximum height 29.9 mm, all Finger Island, Valiente Peninsula; two specimens NMB H19608 + H19609, locality PPP 02206 (=NMB 18705), maximum height 36.0 mm, south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula; one specimen NMB H19610, one specimen NMB H19611, height 40.3 mm, height 46.6 mm, locality PPP 02195 (=NMB 18694), Chong Point, northeast of PJ2231, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; one specimen NMB H19612, locality PPP 02225 (=NMB 18722), height 29.8 mm, east side Norte Point; one specimen NMB H19613, height 40.8 mm, locality PPP 00326 (=NMB 17822); two specimens NMB H19614 + H19615 maximum height 30.4 mm, locality PPP 02238 (=NMB 18735); one specimen NMB H19616, height 34.2 mm, locality PPP 02239 (=NMB 18736), north side of Nispero Point, Cayo

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Chong Point, northeast of PJ2231, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *12–14, Euclia leuzingeri* (Rutsch, 1934), NMB H19555, height 32.7 mm, locality PPP 01883 (=NMB 18771), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *15–17, Euclia leuzingeri* (Rutsch, 1934), NMB H19589, height 32.6 mm, locality PPP 01996 (=NMB 18375), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *18, 19, Euclia leuzingeri* (Rutsch, 1934). NMB H19560, height 36.0 mm, locality PPP 02212 (=NMB 18711), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *20, 21, Euclia leuzingeri* (Rutsch, 1934). NMB H19614, height 30.4 mm (subadult), locality PPP 02238 (=NMB 18735), north side of Nispero Point, Cayo Agua Island, Bocas del Toro, Panama, Cayo Agua Formation, lower Pliocene.

Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Discussion.—Originally described as a subspecies of *Cancellaria reticulata* (Linnaeus, 1767), the affinity between the two is superficial. The adapical columellar fold in *C. reticulata* is bifurcate, a character of *Cancellaria* s.s. The form of the columellar folds and the shell outline clearly place *C. leuzingeri* (Rutsch, 1934) in the genus *Euclia*. This is the first record of the species outside the Venezuelan lower Pliocene assemblages. The specimens from Bocas are quite variable, as can be seen in the series illustrated (Fig. 4.6–4.21), and the last whorl can be more or less shouldered, but very few of the Bocas shells attain the large size of the Venezuelan populations from the lower Pliocene of Punta Gavilán and Cubagua.

A characteristic of the shells of most species of the genus is the "stretched out" shape of the aperture, which is especially accentuated in *E. leuzingeri.* This subgenus is particularly well represented in the southern Caribbean Neogene (Landau et al., 2007); *E. codazzii* (Anderson, 1929) from the lower Pliocene of Venezuela and Trinidad is of similar size but is characterized by having a sharp shoulder with a flat or concave infrasutural platform; *E. montserratensis* (Maury, 1925), also of similar size and from the same deposits, has a more scalate spire and coarser sculpture; and *E. werenfelsi* Jung, 1965 from the lower Miocene Cantaure Formation of the Paraguaná Peninsula of Venezuela has a relatively small and elongated shell, with fine axial sculpture and relatively well-developed spines at the shoulder. The protoconch is damaged in all Bocas specimens of *E. leuzingeri*, except a juvenile shell from location PPP 00477, which shows a smooth, relatively tall multispiral protoconch of 3.25 whorls with small nucleus (Fig. 9.1, 9.2).

Weisbord (1929) illustrated a shell from the upper Miocene Tuberá Formation of Colombia as *Cancellaria dariena* Toula, 1909 which is, in our opinion, a specimen of *E. leuzingeri*.

Euclia is a paciphile genus represented today by the Pacific Tropical American species *E. cassidiformis* (G. B. Sowerby, I, 1832), *E. balboae* (Pilsbry, 1931) and *E. laurettae* Petit and Harasewych, 1998.

Genus *BIVETOPSIA* Jousseaume, 1887

Type species.—*Cancellaria chrysostoma* G. B. Sowerby I, 1832, by subsequent designation of Cossmann, 1888; Recent, Panamic-Pacific.

BIVETOPSIA PACHIA (M. Smith, 1940)

Figure 5.1–5.6

Cancellaria (Bivetopsia) moorei pachia M. SMITH, 1940, p. 45 pl. 2, fig. 2.

Cancellaria (Bivetopsia) pachia M. Smith. LANDAU et al., 2007, p. 35, figs. 20–22.

Bivetopsia pachia (M. Smith). LANDAU AND SILVA, 2010, p. 97, pl. 19, fig. 6.

non Bivetopsia pachia (M. Smith). PETUCH, 1994, p. 222, pl. 90, fig. C.

Description.—See Smith (1940, p. 45).

Types.—Holotype FMNH UF 1319 (Fig. 5.4–5.6), dike near Belle Glade, Florida, Plio-Pleistocene (assigned incorrectly to Miocene by M. Smith, 1940).

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama; lower Pliocene, Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Plio-Pleistocene, Florida.

Bocas del Toro material.—One specimen NHMW 2011/0176/0001 (ex BL coll.), height 18.1 mm, upper Miocene, Messinian, Nancy Point Formation, Finger Island, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—Although Jung and Petit (1990) cited *Bivetopsia pachia* (M. Smith, 1940) as a subspecies of *B. moorei* (Guppy, 1866) they are separate species. *Bivetopsia moorei* has a shell with a more attenuate profile lacking the strong shoulder and thickened out lip of *B. pachia*. However, the major and most easily noted difference is the presence of wider spiral cords on the shells of *B. pachia*, all of which are bifurcated by a deep narrow groove, a feature not prominent in other species. This feature of bifurcated spiral cords is clearly developed in our single specimen from Finger Island (Fig. 5.1–5.3). The protoconch of the Bocas specimen is somewhat worn, but it is multispiral, low-domed, consisting of 3.75 whorls with a small nucleus, and the protoconch/teleoconch boundary is marked by the beginning of the spiral sculpture. *Bivetopsia plectilis* (Jung and Petit, 1990) has even heavier spiral cords with multiple grooves. The Recent species *Bivetopsia rugosa* (Lamarck, 1822), distinguished by its rounded form and low sculpture, also has grooves in the spiral cords but they are neither as pronounced nor prominent as they are in the shells of other species and are sometimes absent on most of the cords. The specimen figured by Petuch (1994, pl. 90, fig. C) as *Bivetopsia pachia* does not correspond to that species. It cannot be clearly identified from the illustration, but appears to be either *B. rugosa* (Lamarck, 1822), or a very closely related unnamed species.

Landau et al. (2007) noted that the presence of *B. pachia* in the lower Pliocene of Venezuela made it one of the most long-lived and most widespread Caribbean Neogene cancellarids. This record for the Nancy Point Formation of Bocas del Toro further extends the chronological range of this species from upper Miocene to Pleistocene. For further discussion on the genus see Landau et al. (2007).

Genus *HERTLEINIA* Marks, 1949

Type species.—*Cancellaria mitriformis* G. B. Sowerby I, 1832, by original designation, Recent, Panamic-Pacific.

HERTLEINIA ANGOSTURANA Marks, 1949

Figure 5.7–5.16

Cancellaria (Hertleinia) angosturana MARKS, 1949, p. 463, pl. 78, figs. 1, 2.

Cancellaria (Hertleinia) angosturana Marks. OLSSON, 1964, p. 125, pl. 37, fig. 12.

Cancellaria (Hertleinia) angosturana Marks. JUNG AND PETIT, 1990, p. 108, pl. 23, figs. 6–8.

Description.—See Marks (1949, p. 463).

Types.—Holotype PRI 20387 (Fig. 5.14–5.16); specimen figured by Marks, 1949, pl. 78, figs. 1, 2 (re-illustrated Jung and Petit, 1990, pl. 23, figs. 6–8); paratype 1, CAS 71597 (ex SU 7964), upper Miocene, Angostura Formation, Angostura Cave on Río Santiago, Esmeraldas Province, Ecuador, planktonic foraminiferal zone N.16 (Pitt and Pitt, 1992).

Occurrence.—Upper Miocene, Tortonian, Angostura Formation, Ecuador; lower Pliocene, Zanclean, Cayo Agua Formation, Cayo Agua Island, Bocas del Toro, Panama.

Bocas del Toro material.—One specimen NMB H19617, locality PPP 00326 (=NMB 17822), height 27.3 mm; one specimen NMB H19618, locality PPP 02240 (=NMB 18737), height 29.2 mm, north side Nispero Point, Cayo Agua Island, Bocas del Toro, Panama.

Discussion.—This species in the Bocas del Toro assemblages is represented by two specimens in excellent state of preservation. The shell is characterized by its relatively small size, slender form, weak subsutural collar, finely cancellate sculpture consisting of seven spiral cords and 34 axial ribs on the penultimate whorl, both ribs and cords flattened, narrow aperture, crenulate outer lip and prominent stromboid notch. The protoconch (Fig. 5.10) is multispiral and of inferred planktotrophic type, consisting of 2.75 smooth whorls with a very small nucleus, similar to that described by Marks (1949, p. 463).

We report this species from the Bocas Neogene with some surprise, as it was previously known only from the Pacific portion of the Neogene Gatunian Province. However, it is very similar to the Ecuadorian holotype (Jung and Petit, 1990, pl. 23, figs. 6–8; Fig. 5.14–5.16). There is a slight difference in the strength of the columellar folds, which are slightly smaller in the Bocas specimen but still clearly bifid. With the material available, it is not possible to judge on the range of variability of these folds.

The genus is not speciose. A species present in the Dominican upper Miocene Cercado Formation, *Hertleinia miranda* Jung and Petit, 1990 can be immediately separated from *H. angosturana* by its broader shape, less dense cancellate sculpture composed of sharper cords and ribs and the absence of a well-defined subsutural collar. Another species occurs in the Pacific Ecuadorian upper Miocene Esmeraldas beds, Onozole Formation; *Hertleinia marksi* Olsson, 1964, which has a broader shell, with a more inflated last whorl and a more strongly delimited and angular subsutural collar. *Hertleinia marksi* is the most similar to the only living member of the genus, the eastern Pacific *H. mitriformis* (G. B. Sowerby I, 1832), which has an even wider concave subsutural collar and tabulate whorls.

Genus *Massyla* H. Adams and A. Adams, 1854

Type species.—*Cancellaria corrugata* Hinds, 1843, by monotypy. Recent, Panamic-Pacific.

Charcolleria Olsson, 1942, type species *Cancellaria (Charcolleria) perdiciana* Olsson, 1942, by original designation, is here considered a junior synonym (see under discussion of *M. corpulenta* n. sp.).

Massyla cumingiana (Petit de la Saussaye, 1844)
Figures 5.17–5.24, 9.3.

Cancellaria cumingiana Petit de la Saussaye, 1844, unnumbered page, pl. 112.

Cancellaria cumingiana Petit de la Saussaye. Sowerby, 1849, p. 440, pl. 93, fig. 20.

Cancellaria cumingiana Petit. Reeve, 1856, spec. 1, pl. 1, figs. 1a, 1b.

Cancellaria cumingiana var. *subobtusa* Crosse, 1863, p. 62, pl. 2, fig. 9.

Cancellaria cumingiana Petit de la Saussaye. Tryon, 1885, p. 68, pl. 1, fig. 12, pl. 2, fig. 13.

Cancellaria cumingiana Petit de la Saussaye. Loebbecke, 1886, p. 46, pl. 14, figs. 1, 2.

Cancellaria cumingiana var. *subobtusa* Crosse. Loebbecke, 1886, p. 59, pl. 17, fig. 1.

Cancellaria (Ovilia?) cumingiana Petit. Pilsbry and Olsson, 1941, p. 24.

Cancellaria (Olivia) cumingiana Petit de la Saussaye. Keen, 1971, p. 653, fig. 1471.

Cancellaria (?Massyla) cumingiana Petit de la Saussaye. Hemmen, 2007, p. 114, 115, unnumbered fig.

Cancellaria (Massyla) cumingiana Petit de la Saussage (sic). Mogollón, 2001, p. 102, pl. 3, fig. 5.

Description.—See Keen (1971, p. 652).

Types.—Two syntypes, NHMUK 1966441 (Fig. 5.24); syntype of *Cancellaria cumingiana* var. *subobtusa* NMW1955.158.02198 (Melvill-Tomlin coll.).

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama; Pliocene (undetermined), Jama Formation, Ecuador; Pleistocene, Armuelles Formation, Burica Peninsula, Panama (NHMW 2011/0176/0002, ex BL coll.); Recent, west Mexico (Keen, 1971).

Bocas del Toro material.—Two specimens NMB H19619 + H19620, locality PPP 00191 (=NMB 17629), maximum height 23.6 mm; one specimen NMB H19621, locality PPP 00477 (=NMB 17824), height 18.3 mm; one specimen NMB H19622, locality PPP 01996 (=NMB 18375), height 17.6 mm; one specimen NMB H19623, locality PPP 01883 (=NMB 18771), height 17.2 mm; five specimens NMB H19624, locality PPP 02212 (=NMB 18711), maximum height 19.6 mm; one specimen NHMW 2011/0176/0003 (ex BL coll.), height 22.4 mm; upper Miocene, Messinian, Nancy Point Formation, Finger Island, Valiente Peninsula, Bocas del Toro, Panama; one specimen NMB H19625, locality PPP 02206 (=NMB 18705), maximum height 18.5 mm; upper Miocene, Messinian, Nancy Point Formation, south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—Three similar *Massyla* species have been described in the Recent Tropical American Pacific: *M. obtusa* (Deshayes, 1830) (holotype NHMUK 1964454, Fig. 5.25, 5.26); *M. cumingiana* (Petit de la Saussaye, 1844) (syntype NHMUK 1966441, Fig. 5.24); and *M. cumingiana subobtusa* (Crosse, 1863) (holotype NMW [unnumbered], Fig. 6.1, 6.2). The more southern forms from Peru described as *M. obtusa* have a very low spire and are extremely thick-shelled but are otherwise indistinguishable from the more northern forms. *Massyla subobtusa* is probably a synonym of *M. cumingiana*. It may well be that all these Recent forms represent a single species but unfortunately these specimens are uncommon and until further study of the Recent taxa is done we provisionally consider *M. cumingiana subobtusa* a junior subjective synonym of *M. cumingiana*, and we separate the thick-shelled, low-spired forms as *M. obtusa*.

The fossil shells from the Valiente Peninsula are well within the range of variability seen in the Recent Pacific *M. cumingiana*. The axial folds in the fossil shells are relatively strong but this can also be the case in some of the Recent specimens. The protoconch is well-preserved in some of the specimens in Lot NMB H19624 from Finger Island and shows a multispiral protoconch of about 3.5 whorls with a very small nucleus (Fig. 9.3). *Massyla cumingiana* must be added to the short list of Paciphile species listed by Landau et al. (2009, appendix 3).

Massyla corpulenta new species
Figure 6.3–6.7

Diagnosis.—A large *Massyla* species, with an elevated spire, strongly convex whorls, a finely reticulated sculpture, with a predominantly spiral component on later whorls.

Description.—Shell large, of medium-thickness, fusiform, with elevated spire, sculpture reticulate, spiral component predominant; protoconch not preserved; teleoconch consisting

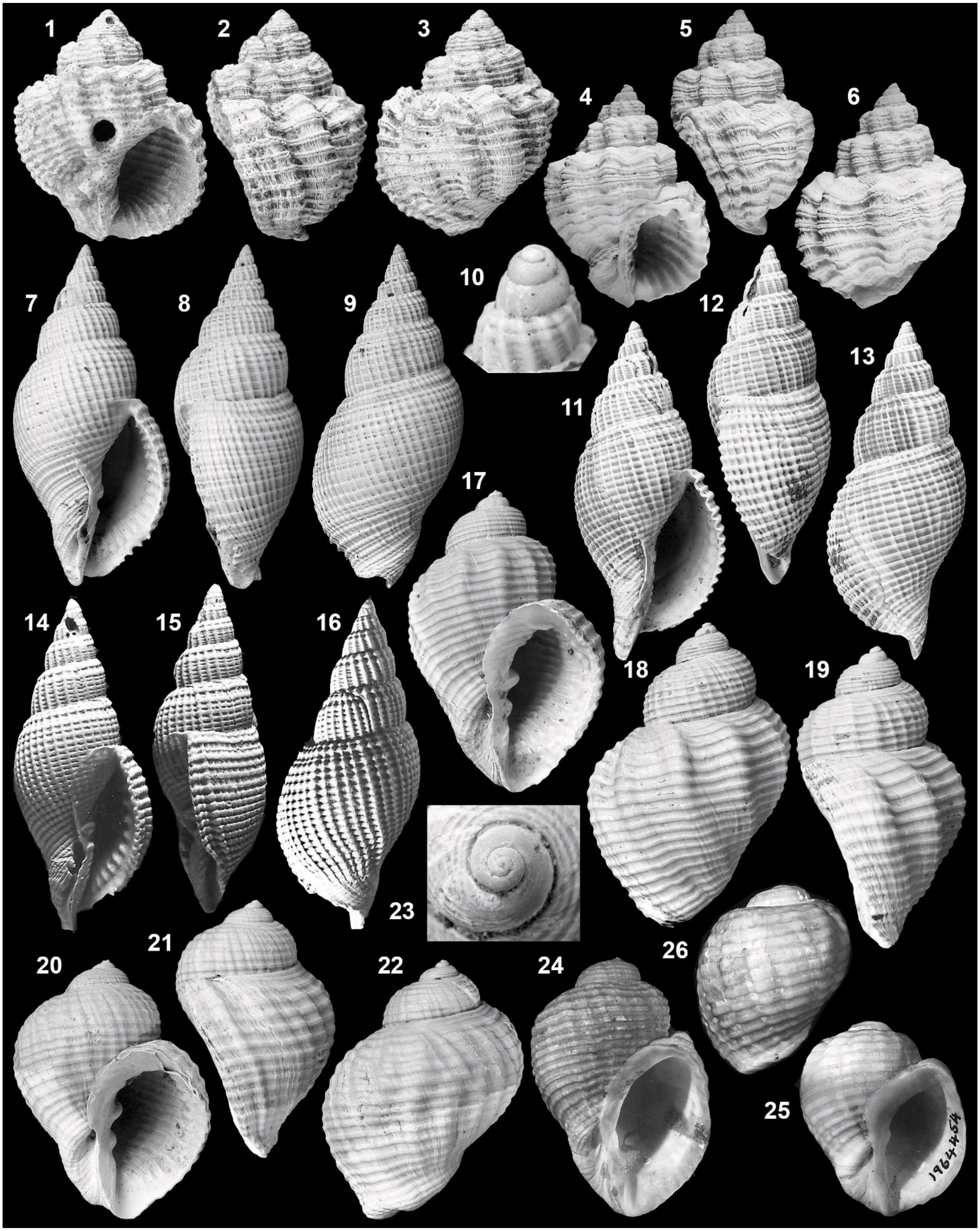

FIGURE 5—*1–3, Bivetopsia pachia* (M. Smith, 1940). NHMW 2011/0176/0001 (ex BL coll.), height 18.1 mm, Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *4–6, Bivetopsia pachia* (M. Smith, 1940), holotype FMNH UF 1319, height 18.4 mm, dike near Belle Glade, Florida, Plio-Pleistocene (assigned incorrectly to Miocene by M. Smith, 1940); *7–10, Hertleinia angosturana* Marks, 1949, NMB H19617, height 27.3 mm, locality PPP 00326 (=NMB 17822), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *11–13, Hertleinia angosturana* Marks, 1949, NMB H19618, height 29.2 mm, locality PPP 02240

of five strongly convex whorls, periphery just above abapical suture; suture deeply impressed, linear, narrowly canaliculate on later whorls; axial sculpture consisting of numerous narrow, irregular, close-set, weakly elevated ribs, weakening further abapically; spiral sculpture consisting of seven flattened cords, overriding axial ribs, narrower than their interspaces; last whorl relatively globose, 74% of total height, regularly convex, moderately constricted at the base; aperture 48% of total height, wide, ovate; outer lip not thickened, regularly convex, lirate within; siphonal fasciole open, narrow, relatively long; parietal callus thickened, well delimited, weakly expanded; columellar callus thickened, erect, forming medial wall of umbilical chink; two narrow, oblique columellar folds, adapical fold strongest, a third fold poorly developed, bordering the siphonal canal; siphonal fasciole narrow, rounded, forming lateral border of umbilical chink.

Etymology.—From the Latin *corpulentus,* meaning solid, massive, heavily-built, reflecting the large body size of the species.

Types.—Holotype NMB H19626 (Fig. 6.3–6.5), locality PPP 01883 (=NMB 18771), height 48.5 mm; paratype 1 NMB H 19669 (Fig. 6.6, 6.7), locality PPP 02197 (=NMB 18696), height 19.2 mm (incomplete), upper Miocene, Messinian, Nancy Point Formation, Finger Island, west of finger, Valiente Peninsula, Bocas del Toro, Panama.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—This species is represented in the Bocas assemblages by a single well-preserved adult specimen, and one broken juvenile. Nevertheless, it is a very distinctive and interesting species, which merits description.

Massyla corpulenta n. sp. blurs the boundary between the genera *Massyla* H. Adams and A. Adams, 1854 and *Charcolleria* Olsson, 1942. *Massyla* tends to have a rather flattened spire whereas *Charcolleria* has a tall protracted spire and rather disjunct whorls. These characters are clearly developed in *Charcolleria perdiciana* Olsson, 1942, the type species from the lower Miocene Las Perdices Formation of Colombia, and *Charcolleria terryi* Olsson, 1942, found in the Panamanian, Venezuelan and Ecuadorian Neogene, but less accentuated in *Charcolleria distinguenda* Petit, 1970 from the lower Miocene Chipola Formation of Florida. This latter species could be placed in the genus *Massyla* and is most similar in shape to *M. corpulenta*, but it is smaller shelled and has a coarser sculpture. The character of the columellar folds; two folds developed, with a third very weak fold bordering the siphonal canal in some species, is common to both genera. The height of the spire alone cannot be used as a generic character in cancellarids, and in view of the lack of other criteria by which to separate the two genera, we consider *Charcolleria* to be a junior synonym of *Massyla*.

The tropical American *Massyla* species can be separated into two main groups. One consisting of those with solid, squat shells, strongly depressed spires and strap-like spiral cords, such as the living American Pacific *M. obtusa* (Deshayes, 1830) and *M. cumingiana* (Petit de la Saussaye, 1844), including the fossil *M. lopezana* Jung and Petit, 1990 from the lower Miocene Baitoa Formation of the Dominican Republic, *M. cantaurana* Landau and Petit, 1997 from the lower Miocene Cantaure Formation of Venezuela, and *M. cubaguaensis* Landau, Petit and Silva, 2007 from the lower Pliocene Araya Formation of Cubagua Island, Venezuela. Species in the other group have rather less solid, more fusiform shells, with more elevated spires such as *M. venusta* (Tuomey and Holmes, 1856) and *M. propevenusta* (Mansfield, 1929) both from the Plio-Pleistocene of the Carolinas and Florida, and *M. distinguenda*. Interestingly, *M. corpulenta* n. sp. is more similar to the Floridian group than the Panamic species. It is similar in size to *M. propevenusta*, which has a squat spire and a proportionately larger last whorl, and similar in shape to *M. venusta* which is smaller, more fusiform, with a pointed spire, but again a proportionately larger last whorl.

Genus *Aphera* H. Adams and A. Adams, 1854

Type species.—*Cancellaria tessellata* G. B. Sowerby I, 1832, by monotypy; Recent, Panamic-Pacific.

APHERA TROPHIS new species
Figure 6.8–6.11

Diagnosis.—A small *Aphera* species with broadly ovate shell, a paucispiral protoconch, a depressed conical spire, relatively coarse, horizontally-elongated reticulate sculpture, and a strongly thickened parietal and columellar calluses, which do not developed into a shield.

Description.—Shell small, solid, broadly ovate, with depressed conical spire; protoconch paucispiral, consisting of 1.5 smooth whorls, nucleus large, bulbous, transition to teleoconch delimited by elevated prosocline scar; teleoconch consisting of three whorls; spire whorls depressed, weakly convex, with periphery at abapical suture; suture impressed, linear; axial sculpture consisting of narrow, close-set, prosocline ribs, 35 on penultimate whorl, becoming more widespaced abapically; spiral sculpture consisting of five flattened cords, slightly wider than their interspaces, overrunning the axial sculpture; last whorl globose, 90% of total height, regularly convex, bearing 24 axial ribs and 23 spiral cords, forming horizontally elongated reticulate sculpture, with a further three close-set cords immediately below the suture; aperture 62% of total height, elongate, inside obscured by hard matrix; outer lip thickened, most of the thickening occurring inside the aperture, edge of outer lip bearing nine coarse denticles; siphonal canal short, open; parietal and columellar calluses strongly thickened, moderately expanded, closely adherent, bearing short secondary folds and pustules; columella with two strong folds, the adapical being larger, both incipiently bifid; no umbilicus.

Etymology.—Greek, "*trophis*," plump or stout.

Types.—Holotype NMB H19627 (Fig. 6.8–6.11), locality PPP 02232 (=NMB 18730), height 11.1 mm, Nispero Point;

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(=NMB 18737), north side of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene; *14–16, Hertleinia angosturana* Marks, 1949, holotype PRI 28307, height 21.7 mm, Angostura Cave on Río Santiago, Esmeraldas Province, Ecuador, Angostura Formation, upper Miocene; *17–19, Massyla cumingiana* (Petit de la Saussaye, 1844). NMB H19619, height 23.6 mm, locality PPP 00191 (=NMB 17629), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *20–23, Massyla cumingiana* (Petit de la Saussaye, 1844), NHMW 2011/0176/0003 (ex BL coll.), height 22.4 mm, Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *24, Massyla cumingiana* (Petit de la Saussaye, 1844), syntype NHMUK 1966441, height 46.5 mm, Recent, locality "Payta" (=Paita, Peru); *25, 26, Massyla obtusa* (Deshayes, 1830), syntype NHMUK 1964454, height 27.8 mm, Recent, locality unknown.

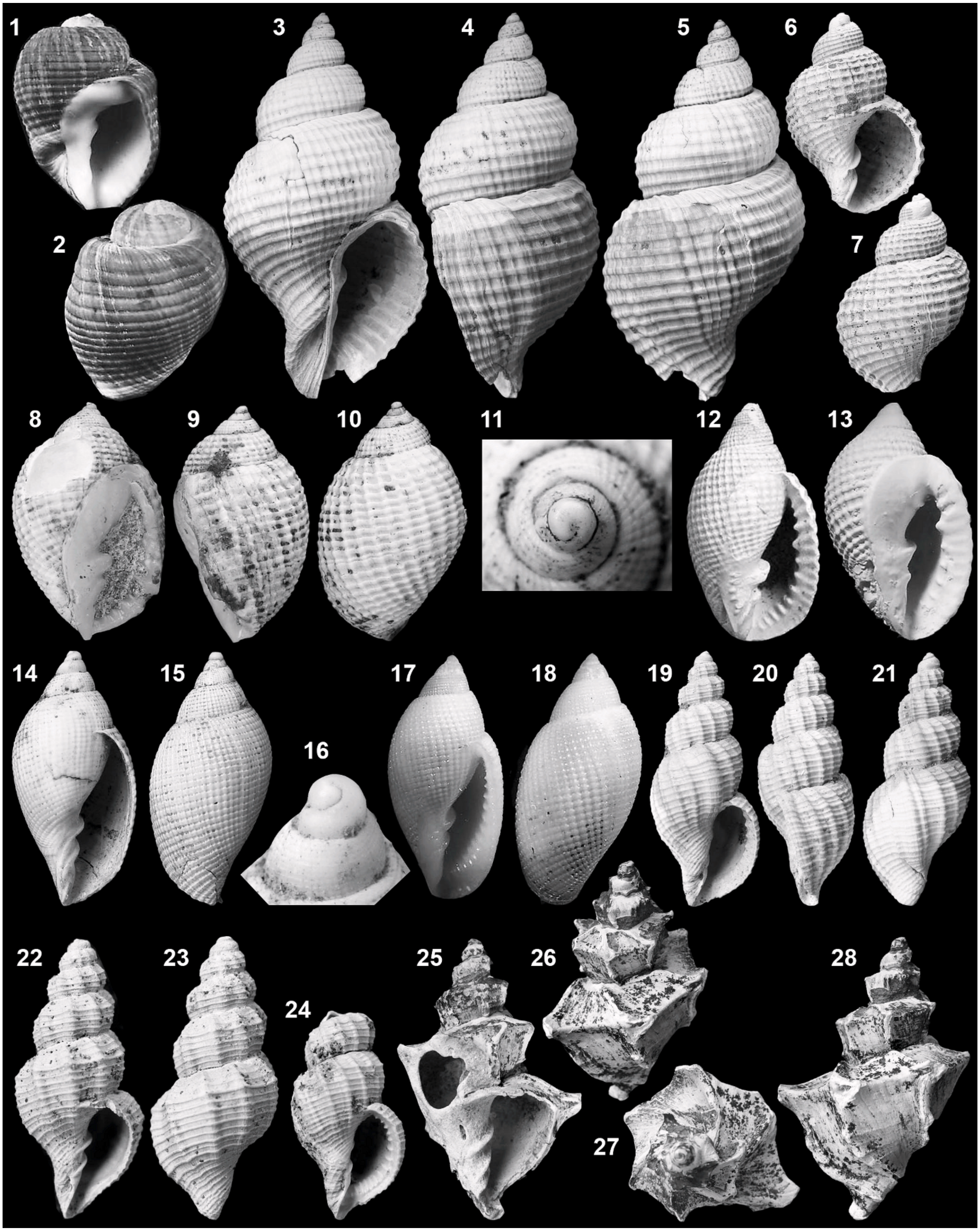

FIGURE 6—*1, 2, Massyla cumingiana subobtusa* (Crosse, 1863), height 32.5 mm, Recent, locality "Payta" (=Paita, Peru); *3–5, Massyla corpulenta* n. sp., holotype NMB H19626, height 48.5 mm, locality PPP 01883 (=NMB 18771), Finger Island, west of finger, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *6, 7, Massyla corpulenta* n. sp., paratype 1 NMB H19669, height 19.2 mm (incomplete), locality PPP 02197 (=NMB 18696), Finger Island, west of finger, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *8–11, Aphera trophis* n. sp., holotype NMB H19627, height 11.1 mm, locality PPP 02232 (=NMB 18730), Nispero Point; Cayo Agua

Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene.

Occurrence.—Lower Pliocene, Zanclean, Cayo Agua Formation, Bocas del Toro, Panama.

Discussion.—Although represented by only a single specimen from the lower Pliocene Cayo Agua Formation on Cayo Agua Island, *Aphera trophis* n. sp. is so distinctive as to deserve description.

Jung and Petit (1990) discussed the presence of *Aphera* H. Adams and A. Adams, 1854 in the Caribbean Neogene and suggested that the genus may be more speciose than previously recognized. This is indeed the case as demonstrated by the description of this new species and the confirmation that the Gatun shells referred to by Woodring (1970, pl. 56, figs. 1, 2) as *Aphera islacolonis* (Maury, 1917) does not correspond to that species.

Aphera islacolonis (lectotype, Fig. 6.12) from the Dominican Neogene upper Miocene and lower Pliocene Cercado and Gurabo formations assemblages differs from *Aphera trophis* in having a protoconch composed of 2.5 whorls, with a small nucleus (see Jung and Petit, 1990, pl. 26, figs. 8–11), in having a narrower, more elevated spire, less globose last whorl and the parietal and columellar calluses are usually developed into a ventral shield (not seen in the lectotype but present in most adult specimens; see Jung and Petit, 1990, pls. 24, 25). The *Aphera* specimens from the middle Gatun Formation of Panama (Woodring, 1970, pl. 56, figs. 1, 2) are similar in shape to *A. islacolonis*, but are thicker shelled, with larger and heavier columellar folds, and coarser sculpture. We here confirm that the Gatun shells are undoubtedly distinct from those of the Dominican Republic, having an inferred planktotrophic type protoconch consisting of three whorls, with a very small nucleus. These Gatun specimens are immediately separated from *Aphera trophis* by the character of the protoconch and the more elongated shell and higher spire. The Gatun *Aphera* will be formally described in a subsequent paper updating our knowledge of the Gatun Cancellariidae. *Aphera peruana* Nelson, 1870 (holotype, Fig. 6.13) from the ?lower Miocene, lower Zorritos Formation and upper Miocene Tumbes Formation of northern Peru differs from *A. islacolonis* and *A. trophis* in having a much coarser sculpture, in having a heavier columellar callus shield, in having a strong denticle on the adapical portion of the columella, and in having the adapical columellar fold broadly shelved. For comparison with *A. lindae* Petuch, 1987, see below.

APHERA cf. LINDAE Petuch, 1987
Figures 6.14–6.16, 9.4, 9.5

Bocas del Toro material.—Four specimens (all immature or broken), NMB H19628 + H19664 + H19665 + H19666, locality PPP 02127 (=NMB 18671), maximum height 13.5 mm, lower Pleistocene, Gelasian, upper Escudo de Veraguas Formation, Escudo de Veraguas Island, northwest coast, small island approximately 600 m west of PPP 02207, Bocas del Toro, Panama (for age see Coates et al., 2005, p. 382, fig. 5).

Occurrence.—Lower Pleistocene, Gelasian, upper Escudo de Veraguas Formation, Escudo de Veraguas Island, Bocas del Toro, Panama.

Discussion.—Unfortunately, all four specimens available to us are immature, not having developed the thickened, denticulate outer lip and very thickened parietal shield characteristic of the genus. However, the sculpture seems to be relatively finely reticulate. All four shells do have their protoconch preserved, which is of an inferred non-planktotrophic type; bulbous, paucispiral, consisting of 1.5 smooth whorls (Fig. 9.4, 9.5).

Aphera was considered extinct in the Caribbean until Petuch (1981) reported a single specimen trawled from the coast off Venezuela as conspecific with the fossil *A. islacolonis*. The specimen was stated to have been "trawled by commercial shrimp boats, from 35 m depth, in Golfo de Triste, Venezuela, March 1979." The specimen was placed in the USNM as number 784467 and has a label with the shell bearing this data, written and signed by the author.

A photograph of specimen USNM 784467was requested (by REP) and was received in December 1978. The photograph is marked "Barbados" and the locality was subsequently independently confirmed. Although this was immediately discussed with the author, no mention was made when the specimen was considered distinct from *A. islacolonis* and described as *A. lindae* (Petuch, 1987, p. 109, pl. 13, fig. 11; holotype USNM 784467; Figs. 6.17, 6.18, 9.6, 9.8). Unfortunately, the incorrect type locality of Golfo de Triste, Venezuela was repeated.

Petuch (1988, p. 160) corrected the type locality of *A. lindae* in a footnote stating that there was a mistake in his field notes. This probably led to Hemmen (2007, p. 194) to repeat the incorrect type locality and stating that Petit and Harasewych (1990, p. 27) "gave a wrong distribution: Barbados." We would here like to clarify that the type locality of *A. lindae* is "200 meters depth off St. James, Barbados."

The Recent *A. lindae* Petuch, 1987 is slimmer and more finely sculptured than *A. islacolonis* or the unnamed Gatunian species (discussed above). Protoconch details were not given by Petuch (1981, 1987), however, the protoconch of *A. lindae* is somewhat eroded, low, conical, increasing in diameter from 370 μm to 780 μm in 1.25 whorls, deflected from coiling axis of shell by about 30°. The transition to the teleoconch is abrupt, marked by weakly flared lip, followed by the onset of spiral and then axial sculpture, producing a weakly cancellate surface (M. G. Harasewych, personal commun., 2011; Fig. 9.6–9.8). This paucispiral protoconch is similar to that

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Island, Cayo Agua Formation, Zanclean, lower Pliocene; *12, Aphera islacolonis* (Maury, 1917), lectotype PRI 28960, height 16.8 mm, Maury's Bluff 2 on Río Mao, Dominican Republic, Cercado Formation, upper Miocene; *13, Aphera peruana* Nelson, 1870, holotype YPM 525, height 16.5 mm, Quebrada Tucillal at Zorritos, northern Peru, Tumbes Formation, upper Miocene; *14–16, Aphera* cf. *lindae* Petuch, 1987, NMB H19628, height 13.5 mm, locality PPP 02127 (=NMB 18671) northwest coast Escudo de Veraguas Island, small Island approximately 600 m west of PPP 02207, Bocas del Toro, Panama, upper Escudo de Veraguas Formation, Gelasian, lower Pleistocene; *17, 18, Aphera lindae* Petuch, 1987, holotype USNM 784467, height 10 mm, Recent, 200 meters depth off St. James, Barbados (photograph M. G. Harasewych); *19–21, Narona decaptyx* (Brown and Pilsbry, 1911). NMB H19629, height 13.5 mm, locality PPP 00191 (=NMB 17629), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; *22, 23, Narona decaptyx* (Brown and Pilsbry, 1911). NMB H19632, height 9.7 mm, locality PPP 00376 (=NMB 17850), west side of Bruno Bluff, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *24, Narona decaptyx* (Brown and Pilsbry, 1911), NMB H19633, height 9.1 mm, locality PPP 02206 (=NMB 18705), west side of Bruno Bluff, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *25–28, Sveltia zahni* (Böse, 1910), NMB H19634, height 25.8 mm, locality PPP 00397 (=NMB 17859), tip of Chong Point, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene.

seen in *A. trophis* n. sp., from the lower Pliocene, Zanclean, Cayo Agua Formation of Bocas del Toro, but this can be immediately separated by its much broader shell, squatter spire and coarser sculpture. Based on the fine sculpture and protoconch type, we provisionally approximate our Escudo de Veraguas shells to *A. lindae*.

Aphera tessellata (G. B. Sowerby I, 1832) from the Recent Tropical American Pacific has a much slimmer shell than its congeners and the columellar callus is not as strongly developed. *Aphera tessellata* has an inferred planktotrophic type, dome-shaped protoconch, consisting of three whorls, with a very small nucleus.

Genus *NARONA* H. Adams and A. Adams, 1854

Type species.—*Cancellaria clavatula* G. B. Sowerby I, 1832, by subsequent designation of Jousseaume (1887b, p. 222); Recent, Panamic-Pacific.

Narona decaptyx (Brown and Pilsbry, 1911)

Figures 6.19–6.24, 9.9, 9.10

Cancellaria decaptyx Brown and Pilsbry, 1911, p. 346, pl. 24, figs. 5, 6.

Cancellaria (Narona) decaptyx Brown and Pilsbry, 1911. Marks, 1949, p. 460 (list).

Cancellaria (Narona) decaptyx Brown and Pilsbry, 1911. Woodring, 1970, p. 342.

Revised description.—Shell small, fusiform with an elevated scalate spire; protoconch dome-shaped, consisting of 3.25 to 3.5 smooth, convex whorls, nucleus very small, transition to teleoconch marked by beginning of axial sculpture; teleoconch of five angular to weakly angular whorls with broad, steep, weakly convex infrasutural ramp above the carina, whorl slightly convex below; suture superficial, weakly undulating; axial sculpture consisting of eight, prosocline, rounded ribs, narrower than their interspaces; spiral sculpture consisting of three sharp, narrow spiral cords below the carina, with one strong secondary spiral cord developed in each interspace, three further slightly weaker cords on the infrasutural ramp, cords overrun axial sculpture, cord at carina delimiting infrasutural ramp slightly more strongly developed; last whorl 64% total height, weakly angled at carina, constricted at base, bearing eight primary cords below carina with strong secondary cords in the interspaces, three cords on the sutural ramp; aperture, ovate, 40% of total height; outer lip not thickened, angled at carina, convex below, lirate within; siphonal canal open, narrow, abaxially pointing; columella weakly excavated, bearing two narrow, oblique folds of equal strength; columellar and parietal callus hardly developed; small umbilical chink present; siphonal fasciole relatively long, bearing well-developed spiral cords.

Types.—Holotype ANSP 1701, Gatun Locks excavation, Panama Canal area, middle Gatun Formation, upper Miocene.

Bocas del Toro material.—NMB H19629 (Fig. 6.19–6.21), height 13.5 mm, width 5.4 mm, NMB H19630/NMB H19631 (Fig. 9.9, 9.10) (juveniles), locality PPP 00191 (=NMB 17629), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene; NMB H19632 (Fig. 6.22, 6.23), locality PPP 00376 (=NMB 17850), height 9.7 mm, west side of Bruno Bluff; NMB H19633 (Fig. 6.24), locality PPP 02206 (=NMB 18705), height 9.1 mm (broken), south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, all upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Occurrence.—Upper Miocene, upper Gatun Formation, Gatun, Panama Canal area, Panama; Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—Until now *Narona decaptyx* (Brown and Pilsbry, 1911) was known only from the holotype collected from the Gatun Locks excavation, Canal Zone (Panama Canal area) of Panama. Woodring (1970, p. 342) in his extensive monograph covering the cancellarids of the Panama Canal area did not find any further specimens of this elusive species. We therefore find it useful to offer an updated description of this species.

The cancellarid genus *Narona* H. Adams and A. Adams, 1854 is poorly represented in the Caribbean Gatunian Neogene. *Narona barystoma* Woodring, 1970 was described from the lower Pliocene Gatun Formation of Panama. It was subsequently reported from the lower Miocene Cantaure Formation of Venezuela (Landau and Petit, 1997), and has also been found in the upper Miocene Cercado Formation of the Dominican Republic (Landau, unpublished data). *Narona barystoma* is much larger shelled than *N. decaptyx*, with more rounded, less angular whorls, more numerous axial ribs, broader folds on the columella and heavier denticulation within the aperture. *Narona semota* Jung, 1969 from the lower Pliocene Melajo Clay member of the Springvale Formation of Trinidad is closely similar in shape but has fewer spiral cords and axial ribs. *Narona bullbrooki* (Mansfield, 1925), also from the Miocene of Trinidad, was based on an immature specimen. We have not seen this specimen, but Jung (1969) commented that the axis of the protoconch of *N. bullbrooki* was even more oblique than that of *N. semota*, and that although the early sculpture was the same in both species, additional spirals appeared later in *N. semota*. It is difficult to compare the specimen of *N. bullbrooki* with other congeners due to its very immature state, but it seems to have far more angular whorls and more scalate spire than either *N. semota* or *N. decaptyx*.

In the Pacific side of the Gatunian Province two species have been described: *N. trema* (Olsson, 1932) from the upper Miocene Tumbes Formation of Peru and *N. pajana* (Pilsbry and Olsson, 1941) from the Pliocene Canoa Formation of Ecuador. The latter is based on an incomplete shell but both have more rounded whorls, a more superficial suture and far more numerous axial ribs than *N. decaptyx*, *N. semota* or *N. bullbrooki*.

Two species have been described from the neighboring Caloosahatchian province; *Narona agria* Mansfield, 1930 and *N. coensis* Mansfield, 1930, from the Pliocene of Florida. Both of the Floridian species have shells with a more rounded last whorl, a greater number of axial ribs and a spiral sculpture composed of only primary cords as opposed to primary and secondary cords as in *N. decaptyx*. *Narona agria* differs from *N. coensis* primarily in having a greater number of spiral cords.

Narona is a paciphile genus, now restricted to the tropical American Pacific (Jung and Petit, 1990; Landau et al., 2009), where it is represented by two species; *N. clavatula* (Sowerby, G. B. I, 1832) and *N. exopleura* (Dall, 1908). Both of these species are larger shelled than *N. decaptyx* and differ in their shell shape; more rounded whorls, more inflated last whorl, making them more closely related to *N. barystoma*.

Genus *Sveltia* Jousseaume, 1887

Type species.—"*Sveltia varicosa* Brocc." (=*Voluta varricosa* Brocchi, 1814), by original designation; Pliocene, Italy.

SVELTIA ZAHNI (Böse, 1910)
Figure 6.25–6.28

Cancellaria zahni BÖSE, 1910, p. 239, pl. 13, fig. 16.
Cancellaria (Calcarata) zahni Böse. PERRILLIAT, 1973, p. 26, pl. 12, figs. 1, 2.

Description.—See Böse (1910, p. 239) and Perrilliat (1973, p. 26).

Types.—According to Böse (1910, p. 273), the type material described in the paper was housed in the Prof. Dr. E. Philippi Collection in the Museum der königl. preuß. Geologischen Landesanstalt, which is now the Bundesanstalt für Geowissenschaften und Rohstoffe Berlin (BGR). However, inquiries to this museum reveal that the holotype is not in the Philippi Collection, BGR (A. Ehling, personal commun.), nor in the Museum für Naturkunde, Berlin (M. Aberhan, personal commun.), nor in the NHMW, Vienna (M. Harzhauser, personal commun.). We therefore consider the type material as lost.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama; upper Pliocene, Piacenzian, Agueguexquite Formation, Santa Rosa, Veracruz, 2.9–2.5 Ma (Cotton in Collins and Coates, 1999).

Bocas del Toro material.—One specimen NMB H19634, locality PPP 00397 (=NMB 17859), height 25.8 mm, upper Miocene, Messinian, Nancy Point Formation, tip of Chong Point, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—*Sveltia zahni* (Böse, 1910) is represented in the Bocas del Toro assemblages by a single, poorly preserved specimen. The shell is characterized by its strongly angular, tabulate whorls, almost horizontal infrasutural platform, widely spaced sharp axial ribs, forming spines at the shoulder and very weak spiral sculpture, reduced to one thread abapically on the spire whorls and a few spiral threads on the abapical half of the last whorl. The Bocas specimen differs from that illustrated by Perrilliat (1973) from the upper Pliocene Agueguexquite Formation of Mexico in being slightly broader, the infrasutural platform is more horizontal and the spiral sculpture is even weaker. However, with the very scant material available to us we consider the Bocas shell to fit within the variability of this species.

Sveltia zahni belongs to a small group of *Sveltia* species with shells similar to those belonging to the Neogene-Recent European-West African genus *Calcarata* Jousseaume, 1887 in having strongly tabulate whorls and long spines developed at the shoulder on the last whorl. However, in *Calcarata* species a secondary cord on the last whorl is strongly developed making the last whorl markedly biangular. This is absent in the Tropical American species.

Sveltia inquilinus Jung and Petit, 1990 from the lower Pliocene Gurabo Formation of the Dominican Republic is immediately distinguished in having more numerous axial ribs, stronger and denser spiral sculpture, less tabulate whorls and a narrower less flattened infrasutural platform. *Sveltia trochilia* (Olsson, 1964) from the upper Miocene Esmeraldas beds, Onozole Formation, Ecuador, is most similar to the Bocas shell in shape and the nature of the flattened infrasutural platform. The holotype figured by Olsson (1964; pl. 22, fig.5) has two more axial ribs on the last whorl than the Bocas shell and the spiral threads are denser on the spire and last whorls and do not seem to form a small spine where they cross the axial ribs on the last whorl as seen in the Bocas shell and the Mexican specimens. More material may show *S. trochilia* and *S. zahni* to be conspecific.

In the Tropical American Pacific this group is represented by *Sveltia centrota* (Dall, 1896), which differs in having less tabulate whorls, more numerous axial ribs and stronger spiral sculpture, and *Sveltia gladiator* Petit, 1976 from the Galapagos Islands, which differs from S. *zahni* in having a more fusiform shell shape, with more numerous axial ribs and longer spines formed at the aperture resulting from extensions of the first and second adapical spiral cords.

Until very recently this genus was included within the group of paciphile cancellarids. However, it is now known in the Recent Caribbean faunas with the description of *Sveltia yoyottei* Petit and Harasewych, 2011 from bathyal depths off Guadeloupe, French West Indies. As discussed by Petit and Harasewych (2011) while sharing characters with S. *zahni*, *S. yoyottei* is most similar to *S. inquilinus* but differs in being slightly shorter, with a more gradate spire, narrower pseudoumbilicus, and fewer, stronger denticles along the outer lip. *Sveltia inquilinus* has more inflated whorls with finer and more numerous spiral sculpture. Finding *Sveltia* living in the Caribbean could have been expected based on the succession of ecostratigraphic units proposed for the Caribbean Neogene by Landau et al. (2009). The paciphilic cancellarids disappeared from the Caribbean at the end of GNPMU1. The presence of *Sveltia* in the Mexican upper Pliocene assemblages, which fall within GNPMU2, did not fit with the genus being paciphilic. Its presence in the Recent Caribbean supports the validity of GNPMUs within the Caribbean Neogene.

Genus ADMETULA Cossmann, 1889

Type species.—*Buccinum evulsum* Solander, 1766, by original designation; Eocene, England.

ADMETULA VALIENTENSIS new species
Figure 7.1–7.7

Diagnosis.—Small *Admetula* species, with a paucispiral protoconch, relatively wide spaced axial ribs, weak varices, strong spiral cords and almost without secondary spiral sculpture.

Description.—Shell small, fragile, relatively globose, with conical spire; protoconch paucispiral, consisting of two smooth whorls, nucleus of medium size, transition to teleoconch marked by prosocline riblets; teleoconch consists of 4.5 angular whorls, with relatively broad, shallow, infrasutural ramp, periphery mid-whorl; suture superficial, undulating; axial sculpture consists of ten relatively narrow, rounded, prosocline ribs; spiral sculpture of very narrow elevated cords overriding axial ribs, consists of two weaker cords on infrasutural platform, three narrow primary cords below, adapical cord delimits infrasutural ramp, abapical two cords more close-set mid-whorl; secondary spiral sculpture absent, except one very weak thread in one interspace in the holotype; one weak varix developed per whorl; whole teleoconch surface covered in fine, close-set prosocline growth lines; last whorl globose, about 68% total height, angled at the infrasutural ramp, convex below, weakly constricted at the base, bearing 12 primary spiral cords below infrasutural ramp; aperture broadly ovate, about 50% of total height; outer lip regularly convex, not thickened by labial varix, dentate to lirate within; siphonal canal open, short and pointing abaxially; columella excavated, bearing three parallel oblique folds, the abapical two slightly more close-set, third fold forming medial edge of siphonal canal; columella and parietal callus hardly developed; umbilicus closed.

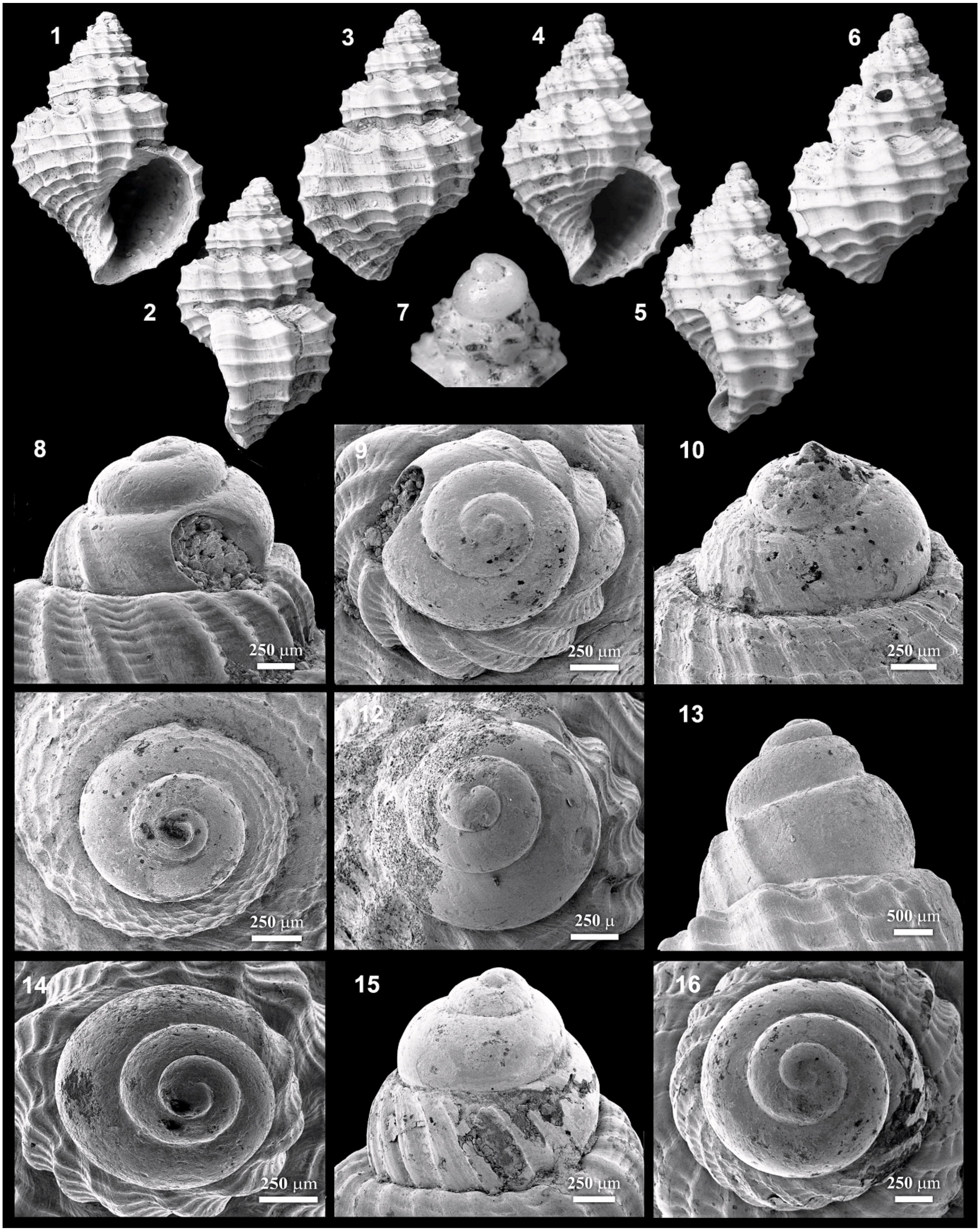

FIGURE 7—*1–3, Admetula valientensis* n. sp., holotype NMB H19635, height 11.8 mm, locality PPP 02189 (=NMB 18688), banana-shaped island at northern end of Nancy Point, Valiente Peninsula, Bocas del Toro, Panama. Nancy Point Formation, Messinian, upper Miocene; *4–7, Admetula valientensis* n. sp., paratype 1 NMB H19636, height 8.7 mm, locality PPP 00296 (=NMB 17811), (5.0–3.5 Ma; Collins and Coates, 1999), Tiburon Point, Cayo Agua Island, Bocas del Toro, Panama, Cayo Agua Formation, Zanclean, lower Pliocene; *8, 9, Cancellaria anomoia* Woodring, 1970, NMB H19659, locality PPP 02238 (=NMB 18735), north side of Nispero Point, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene, SEM photograph showing detail of protoconch; *10, 11, Cancellaria pilula* n. sp., paratype 6 NMB H19507, locality PPP 02206 (=NMB 18705), south coast,

Etymology.—After the Valiente Peninsula, Bocas del Toro Area, Panama, the type locality.

Types.—Holotype NMB H19635 (Fig. 7.1–7.3) height 11.8 mm, width 8.0 mm, locality PPP 02189 (=NMB 18688), banana-shaped island at northern end of Nancy Point; paratype 1 NMB H19636 (Fig. 7.4–7.7), height 8.7 mm, width 5.4 mm, locality PPP 02206 (=NMB 17851), small island 50 m west off coast approximately 1.5 km southwest of Punta de Toro; paratype 2 NMB H19637, height 16.1 mm, width 10.3 mm; paratype 3 NMB H19638, height 11.8 mm, width (incomplete); paratype 4 NMB H19639, height 9.3 mm, width 7.0 mm, locality PPP 02195 (=NMB 18694), Chong Point, northeast of PJ2231; paratype 5 NMB H19640, height 13.0 mm, width 8.6 mm, locality PPP 00397 (=NMB 17859), height 13.0 mm, tip of Chong Point.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Other Bocas del Toro material.—Three specimens, NMB H19641-H19643, locality PPP 02189 (=NMB 18688), maximum height 9.9 mm, banana-shaped island at northern end of Nancy Point; one specimen, NMB H19644, locality PPP 00379 (=NMB 18705), height 6.1 mm, northwest side of Bruno Bluff; one specimen NMB H19645, locality PPP 01883 (=NMB 18771), height 7.7 mm; Finger Island, Valiente Peninsula; all upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—This species is characterized by its relatively wide spaced axial ribs, strong spiral cords almost without secondary spiral sculpture and having weak varices. The protoconch is paucispiral, consisting of two smooth whorls, the transition to the teleoconch marked by prosocline riblets.

Most fossil Caribbean *Admetula* species have varices developed, especially prominent on the last whorl. *Admetula zalayana* Jung and Petit, 1990 from the lower Pliocene Gurabo Formation of the Dominican Republic is closely similar in shape to our Bocas shells and also has a paucispiral protoconch, but differs in having more numerous axial ribs and strong secondary spiral sculpture in the interspaces between the primary cords. *Admetula zapoteca* (Böse, 1910) from the upper Pliocene Agueguexquite Formation of Mexico has weaker, more numerous axial ribs and prominent secondary spiral sculpture. Both these species have stronger varices.

Two Recent Caribbean species have been described without varices; *Admetula bayeri* Petit, 1976 from the Gulf of Mexico is quite different with crowded axial and spiral sculpture and *A. vossi* Petit, 1976 from the Bahamas, which is similar to the Bocas specimens, but has a more solid shell and secondary spiral sculpture. *Admetula deroyae* (Petit, 1970) from the Galapagos Islands is also devoid of varices, but is immediately distinguished by having more numerous axial ribs and very close-set spiral cords.

Genus AGATRIX Petit, 1967

Type species.—*Cancellaria agassizii* Dall, 1889, by original designation; Recent, western Atlantic.

AGATRIX EPOMIS (Woodring, 1928)

Figures 8.1–8.8, 9.11, 9.12

Tribia epomis WOODRING, 1928, p. 223, pl. 12, fig. 10.

Cancellaria (Tribia?) epomis Woodring. MARKS, 1949, p. 460 (list).

Agatrix epomis (Woodring). PETIT, 1976, p. 38, pl. 1, fig. 3.

Agatrix epomis (Woodring). HEMMEN, 2007, p. 131, unnumbered fig.

non Agatrix epomis (Woodring). PETUCH, 1981, p. 333, figs. 79, 80 (=*Axelella smithii* DALL, 1888)

Description.—See Woodring (1928, p. 223) and Petit (1976, p. 38).

Types.—Holotype USNM 747976, Pliocene, Bowden Formation, Bowden, Jamaica (Fig. 8.1, 8.2).

Occurrence.—Lower Pliocene, Zanclean, Cayo Agua Formation, Bocas del Toro, Panama; Pliocene (undetermined), Bowden Formation, Jamaica; lower Pleistocene, Gelasian, upper Escudo de Veraguas Formation, Bocas del Toro, Panama; Moin Formation, Costa Rica; Recent, 60 to 68 meters off coast of Venezuela.

Bocas del Toro material.—Two specimens, NMB H19646 + H19670, locality PPP 00296 (=NMB 17811), height 8.7 mm, Tiburon Point, Area F (Collins and Coates, 1999; map 6, p. 292; Coates et al., 2005); one specimen, NMB H19647, locality PPP 02232 (=NMB 18730), height 10.2 mm, Nispero Point; two specimens, NMB H19648 + H19649, locality PPP 00197 (=NMB 17630), height 9.5 mm, 350 m southwest of Punta Norte, Area A (Collins and Coates, 1999; map 6, p. 292; Coates et al., 2005); Cayo Agua Island, Cayo Agua Formation, (5.0–3.5 Ma; Collins and Coates, 1999), Zanclean, lower Pliocene; one specimen, NMB H19650, locality PPP 02187 (=NMB 18686), height 10.1 mm, lower Pleistocene, Gelasian, upper Escudo de Veraguas Formation, Escudo de Veraguas Island, south coast, 100 m west of PJ2222, Bocas del Toro, Panama (for age see Coates et al., 2005, p. 382, fig. 5).

Other material.—Forty specimens, Los Corales, Puerto Limon, lower Pleistocene, Gelasian, Moin Formation, Costa Rica (BL coll.).

Discussion.—*Agatrix epomis* (Woodring, 1928) differs from the Recent *A. agassizii* (Dall, 1889), found from North Carolina south into the Caribbean to Puerto Rico, in having a smooth area between the shoulder nodes and the suture, in having a less deeply impressed suture, and in having more widely spaced spiral cords. *Agatrix losquemadica* Jung and Petit, 1990 from the lower Pliocene Gurabo Formation of the Dominican Republic has a greater number of spiral cords and stronger secondary sculpture between the primary spiral cords, making the shell more finely sculptured. *Agatrix epomis* is also closely similar in teleoconch characteristics to *Agatrix beatrix* (Olsson, 1964) from upper Miocene Nancy Point Formation, Valiente Peninsula, Bocas del Toro, but the latter has a multispiral protoconch, whereas *A. epomis* has a paucispiral protoconch consisting of two whorls (Fig. 9.11, 9.12). The Recent Tropical American Pacific *A. strongi* (Shasky, 1961)

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approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene, SEM photograph showing detail of protoconch; *12, Cancellaria petiti* Olsson, 1967, NMB H19668, locality PPP 00476 (=NMB 17813), south of Nispero Point, Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene, SEM photograph showing detail of protoconch; *13, 14, Cancellaria isabelae* n. sp., paratype 10 NMB H19531, locality PPP 00326 (=NMB 17822), north side of Nispero Point, Cayo Agua Formation, Zanclean, lower Pliocene, SEM photograph showing detail of protoconch; *15, 16, Cancellaria axelolssoni* n. sp., paratype 2 NMB H19543, locality PPP 02236 (=NMB 18733), unnamed promontory between Tiburon and Piedra Roja points, west side of Cayo Agua Island, Cayo Agua Formation, Zanclean, lower Pliocene, SEM photograph showing detail of protoconch.

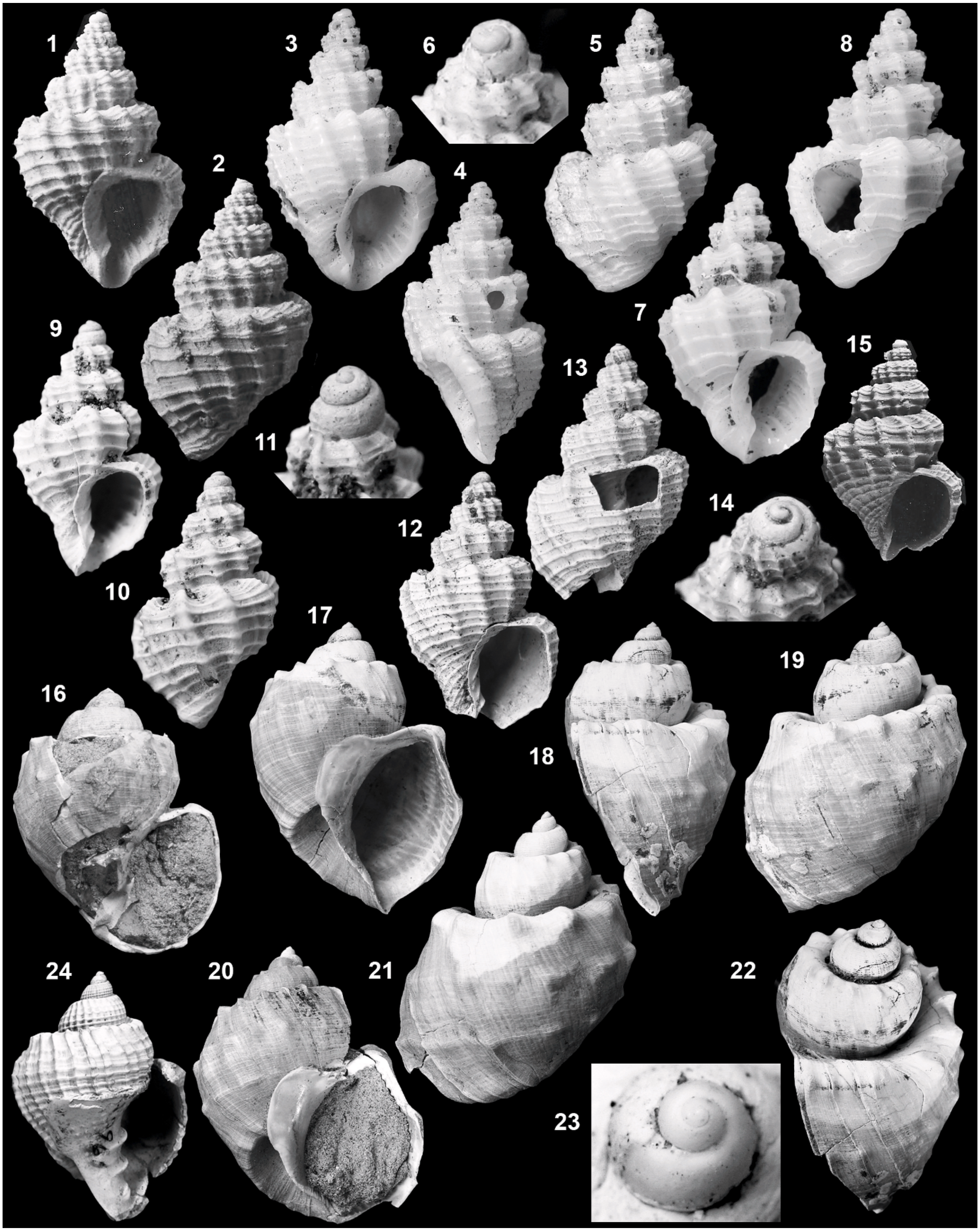

FIGURE 8—*1, 2, Agatrix epomis* (Woodring, 1928), holotype USNM 747976, height 11.8 mm, Bowden, Jamaica, Bowden Formation, Pliocene; *3–6, Agatrix epomis* (Woodring, 1928), NMB H19650, height 10.1 mm, locality PPP 02187 (=NMB 18686), Escudo de Veraguas Island, south coast, 100 m west of PJ2222, Bocas del Toro, Panama, upper Escudo de Veraguas Formation, Bocas del Toro, Panama, Gelasian, lower Pleistocene; *7, 8, Agatrix epomis* (Woodring, 1928). NMB H19670, height 10.1 mm, locality PPP 00397 (=NMB 17859), tip of Chong Point, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *9–11, Agatrix* aff. *epomis* (Woodring, 1928), NMB H19651, height 10.9 mm, locality PPP

has a more rounded shoulder, less canaliculate infrasutural platform, and a larger, rounder aperture.

AGATRIX aff. EPOMIS (Woodring, 1928)
Figure 8.9–8.11

Description.—Shell small, solid, fusiform with elevated scalate spire; protoconch consisting of 2.5 convex whorls, dome-shaped, nucleus medium-sized, junction with teleoconch marked by beginning of spiral sculpture; teleoconch consisting of four convex whorls, with narrow subsutural platform, relatively steep on first two teleoconch whorls, shallowing abapically, almost horizontal on last whorl, whorl periphery above mid-whorl; suture very superficial, undulating; axial sculpture consisting of seven elevated, rounded, prosocline ribs, half the width of their interspaces; spiral sculpture overrides axial ribs, consisting of three narrow primary cords below carina, two weaker cords on infrasutural ramp, cords slightly horizontally thickened over the axial ribs, no secondary sculpture; last whorl about 66% total height, strongly shouldered just below suture, moderately constricted at base, bearing 6 primary spiral cords below carina, four weaker cords on almost horizontal infrasutural platform; aperture subtrigonal, about 40% of total height; outer lip convex, angled at shoulder, not thickened by labial varix, lirate within; siphonal canal moderately long, open, pointing abaxially; columella broadly excavated, bearing three parallel, narrow oblique folds, abapical fold forming medial edge of siphonal canal; columella callus strongly developed, thickened, weakly expanded, erect, forming medial border of columellar chink; parietal callus weakly developed; siphonal fasciole clearly developed and delimited from base, bearing weak spiral sculpture.

Bocas del Toro material.—One specimen NMB H19651, locality PPP 00379 (=NMB 17851), height 7.2 mm, width 4.1 mm; upper Miocene, Messinian, Nancy Point Formation, northwest side of Bruno Bluff, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—*Agatrix* aff. *epomis* differs from *Agatrix epomis* (Woodring, 1928) in being smaller-shelled and in having fewer axial ribs, but most importantly, in having an extra protoconch whorl. *Agatrix* aff. *epomis* has no secondary spiral sculpture, which is but not always, present in *A. epomis.* This may be a distinct species, but we lack sufficient material to be sure.

AGATRIX BEATRIX (Olsson, 1964)
Figure 8.12–8.15

Admete (Bonellitia) beatrix OLSSON, 1964, p. 128, pl. 22, fig. 9.

Description.—See Olsson (1964, p. 128).

Types.—Holotype USNM 644118 (Fig. 8.15); specimen figured by Olsson, 1964, pl. 22, fig. 9; paratype 1, USNM 644119, upper Miocene, Tortonian, Angostura Formation, Punta Gorda, Esmeraldas Province, Ecuador, planktonic foraminiferal zone N.16 (Pitt and Pitt, 1992).

Occurrence.—Upper Miocene, Torotonian, Angostura Formation, Ecuador; Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Bocas del Toro material.—One specimen, NMB H19652, locality PPP 02206 (=NMB 18705), height 10.9 mm; upper Miocene, Messinian, Nancy Point Formation, south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—A single, broken specimen from the upper Miocene of Valiente Peninsula is present in the PPP collection, which represents a relatively thin shelled *Agatrix* species, with a multispiral protoconch consisting of about three whorls with a small nucleus. The teleoconch is weakly canaliculate for the genus, with 12 axial ribs and ten spiral cords between the shoulder and the base on the last whorl, and with a relatively large aperture with weak folds and denticles within. The Bocas shell matches the description and illustration of the *Agatrix beatrix* (Olsson, 1964) from the upper Miocene Angostura Formation of Ecuador. Unfortunately, there is no reference to the protoconch type in the description but the shell shape and number of ribs and cords match. The spiral cords seem to be of alternate strength in the Ecuadorian shell, whereas all the cords are of roughly equal strength in the Bocas shell, but this feature can vary somewhat intraspecifically. Until further material becomes available, we provisionally consider the Bocas and Ecuadorian shells conspecific. *Agatrix beatrix* differs from both *A. epomis* (Woodring, 1928) and *A.* aff. *epomis* in being thinner and broader shelled, having more numerous spiral cords and a larger aperture.

Olsson (1964, p. 128) mentioned that a single specimen apparently belonging to the same species was dredged off Zorritos, Peru. We have not found any further reference to this species in recent literature but it probably relates to *Agatrix strongi* Shasky, 1961, which is very similar to the fossil *A. beatrix*, differing in having a taller, more scalate spire and more angular whorls, with a sharper shoulder.

Genus VENTRILIA Jousseaume, 1887

Type species.—*Ventrilia ventrilia* Jousseaume, 1887a, by monotypy; Recent, Caribbean.

VENTRILIA PLUMMERI (Olsson, 1922)
Figure 8.16–8.23

Cancellaria Plummeri OLSSON, 1922, p. 85, pl. 6, figs. 2, 3.
Trigonostoma plummeri Olsson. MARKS, 1949, p. 460 (list).

Description.—See Olsson (1922, p. 85).

Types.—Holotype PRI 20960; specimen figured by Olsson, 1922, pl. 6, figs. 2, 3 (Fig. 8.16); Toro Cay (Cay Toro), Bocas del Toro, Panama, Miocene.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Bocas del Toro material.—Three specimens, one complete, two broken NMB H19653-H19655, locality PPP 00477

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02206 (=NMB 18705), locality PPP 00379 (=NMB 17851), height 7.2 mm; northwest side of Bruno Bluff, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *12–14, Agatrix beatrix* (Olsson, 1964). NMB H19652, height 10.9 mm, locality PPP 02206 (=NMB 18705), south coast, approximately 1.5 km SW of Punta de Toro, small island 50 m west off coast, 50 m east of PJ2241, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *15, Agatrix beatrix* (Olsson, 1964), holotype USNM 644118, height 15.0 mm, Punta Gorda, Esmeraldas Province, Ecuador, Angostura Formation, upper Miocene; *16, Ventrilia plummeri* (Olsson, 1922), holotype PRI 20960, height 34.0 mm, Toro Cays, Bocas del Toro, Panama, upper Miocene (Photo PRI database); *17–19, Ventrilia plummeri* (Olsson, 1922), NHMW 2011/0176/0004 (ex BL coll.), height 36.2 mm, Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *20–23, Ventrilia plummeri* (Olsson, 1922), NMB H19653, height 37.0 mm, locality PPP 00477 (=NMB 17824), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene; *24, Ventrilia toroensis* (Olsson, 1922), holotype PRI 20961, height 29.0 mm, Toro Cays, Panama upper Miocene (photo PRI database).

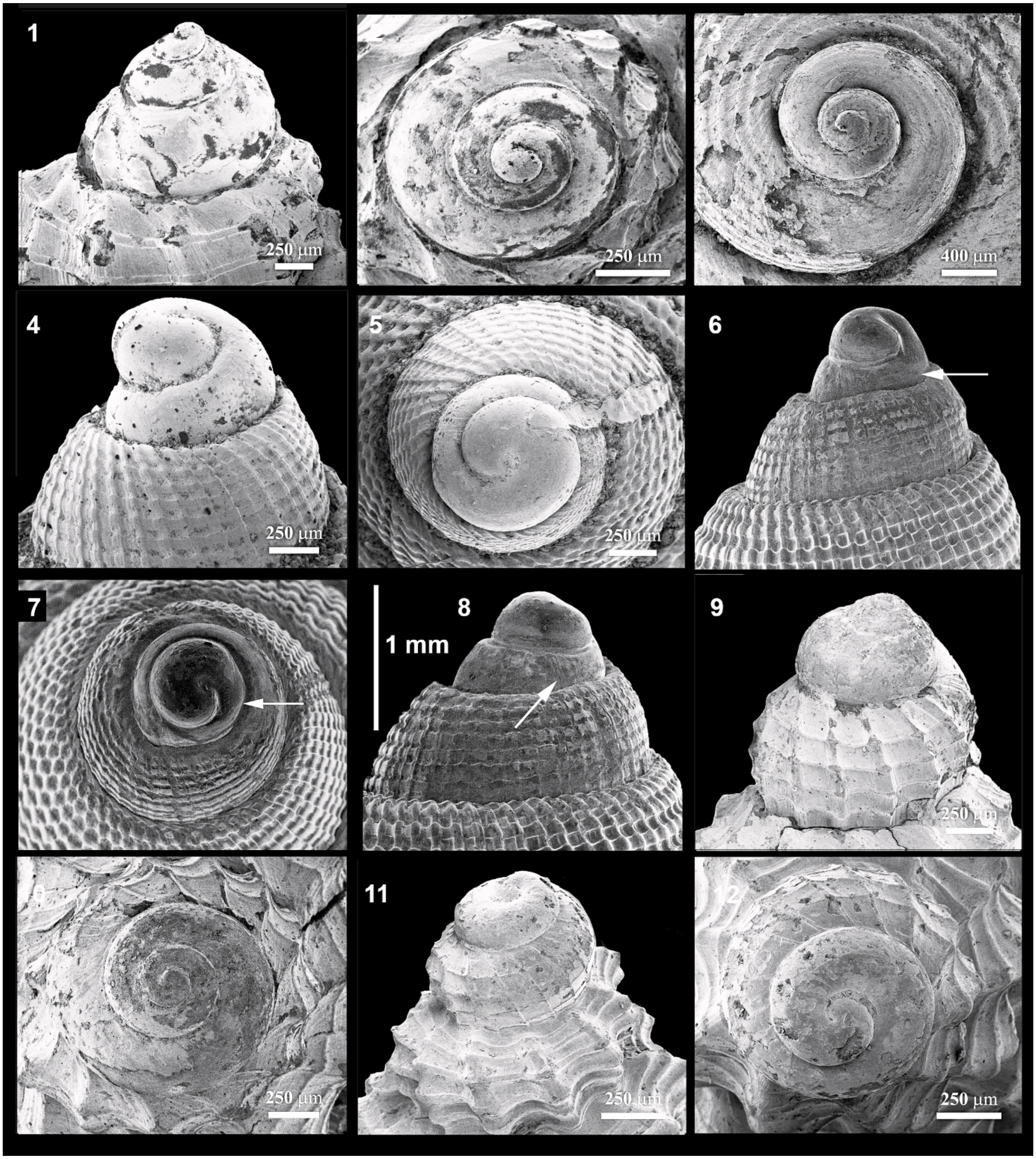

FIGURE 9—*1, 2, Euclia leuzingeri* (Rutsch, 1934), NMB H19576, locality PPP 00477 (=NMB 17824), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene, SEM photograph showing detail of protoconch; *3, Massyla cumingiana* (Petit de la Saussaye, 1844), NMB H19621, locality PPP 00477 (=NMB 17824), Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Nancy Point Formation, Messinian, upper Miocene, SEM photograph showing detail of protoconch; *4, 5, Aphera* cf. *lindae* Petuch, 1987, NMB H19666, locality PPP 02127 (=NMB 18671) northwest coast Escudo de Veraguas Island, small Island approximately 600 m west of PPP 02207, Bocas del Toro, Panama, Escudo de Veraguas Formation, Piacenzian, upper Pliocene, SEM photograph showing detail of protoconch; *6–8, Aphera lindae* Petuch, 1987, holotype USNM 784467, Recent, 200 meters depth off St. James, Barbados, SEM photograph showing detail of protoconch (photograph M. G. Harasewych); *9, 10, Narona decaptyx* (Brown and Pilsbry, 1911), NMB H19631, locality PPP 00191 (=NMB 17629), Finger Island, Valiente Peninsula, Nancy Point Formation, Messinian, upper Miocene, SEM photograph showing detail of protoconch; *11, 12, Agatrix epomis* (Woodring, 1928), NMB H19647, locality PPP 02232 (=NMB 18730), Nispero Point, Cayo Agua Formation, Zanclean, lower Pliocene, SEM photograph showing detail of protoconch.

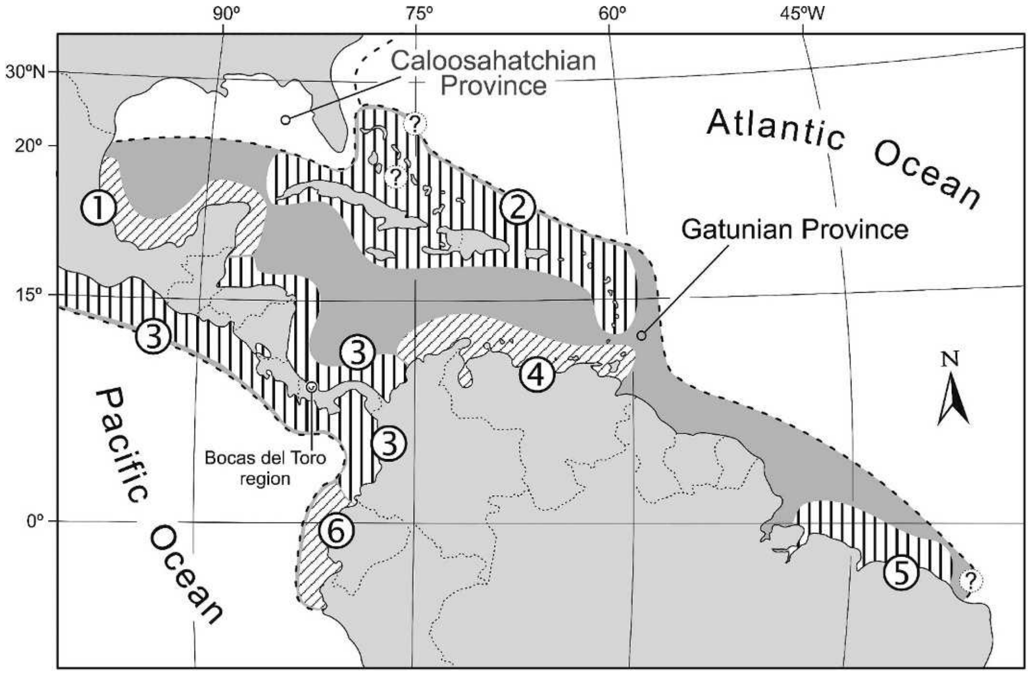

FIGURE *10*—Neogene Tropical American Provinces. Gatunian and Caloosahatchian Provinces of Petuch (1982), subprovinces follow Woodring (1974): *1*, Mexican; *2*, West Indian; *3*, Central American-northern South American; *4*, Colombian-Venezuelan-Trinidad; *5*, Brasilian; *6*, Ecuadorian-Peruvian.

(=NMB 17824), height complete specimen 37.0 mm; two specimens, one complete, one broken NMB H19656 + H19657, locality PPP 00191 (=NMB 17629), height complete specimen 25.5 mm; one specimen NHMW 2011/0176/0004 (ex BL coll.), height 36.2 mm, all Finger Island, west of south tip of Cayo Toro, Valiente Peninsula, Bocas del Toro, Panama, Messinian, Nancy Point Formation, upper Miocene.

Discussion.—*Ventrilia plummeri* (Olsson, 1922) clearly belongs to the *Ventrilia tenera* (Philippi, 1848) species group, characterized by their thin shell, weak sculpture and relatively strongly canaliculated infrasutural platform. *Ventrilia plummeri* is characterized by having a very light shell which is more tightly coiled than other members of the species-group, resulting in a relatively fusiform shape and a narrower infrasutural platform than other members. The sculpture is obsolete, or almost so, with four very weak spiral cords on the last whorl, the adapical two bearing small sharp tubercles. The protoconch is multispiral and of inferred planktotrophic type, consisting of three smooth whorls with a very small nucleus (Fig. 8.23).

This species group is well represented in the Plio-Pleistocene of Florida and in the neighboring northern biogeographic Caloosahatchian Province (see Petuch, 1994) but occurrences are scarce in the Gatunian Province and individuals always rare. Landau et al. (2007) reported the presence of the species group in the southern Caribbean Neogene of Venezuela, with one shell from the Punta Gavilán Formation and a second from the Araya Formation, both lower Pliocene. Those shells are indistinguishable from, and were synonymized with, the Floridian shells described by Petuch (1994) as *Ventrilia kissimmeensis* and *V. rucksorum*. The trivial name *V. rucksorum* was selected in preference over *V. kissimmeensis* as the latter is considered an unusually smooth form (Landau et al., 2007). *Ventrilia plummeri* is similar to *V. rucksorum* and is the same size. However, it has a more elongated fusiform shell, the knobs formed on the spiral cords on the last whorl are stronger and sharper in *V. plummeri* and, most importantly, the infrasutural platform is narrower.

Today the species group is represented in the Caribbean by *V. tenera*, which differs from *V. rucksorum* in having slightly stronger sculpture and a flatter infrasutural platform. *Ventrilia tenera* differs from *V. plummeri* in having a much more uncoiled shell, which is therefore broader, with a wider, almost flat, infrasutural platform. The spiral cords are subdued but present in *V. tenera*, whereas in *V. plummeri* they are subobsolete.

Petit (1976) described *Ventrilia sacellum* from the Miocene Gatun Formation of Panama. This species should probably be included in the *V. tenera* species group, but is rather unusual in having the shoulder compressed, an elevated spire, and an almost total lack of axial sculpture.

VENTRILIA TOROENSIS (Olsson, 1922)
Figure 8.24

Cancellaria toroensis OLSSON, 1922, p. 84, pl. 6, fig. 4.
Trigonostoma toroenis Olsson. MARKS, 1949, p. 460 (list).

Description.—See Olsson (1922, p. 84).

Types.—Holotype PRI 20961; specimen figured by Olsson, 1922, pl. 6, fig. 4 (Fig. 8.24), Toro Cay (Cayo Toro), Bocas del Toro, Panama, Miocene.

Occurrence.—Upper Miocene, Messinian, Nancy Point Formation, Valiente Peninsula, Bocas del Toro, Panama.

Discussion.—*Ventrilia toroensis* (Olsson, 1922) was described based on a single broken specimen from the upper Miocene Nancy Point Formation of the Valiente Peninsula. No further specimens are present in the collections examined. It is characterized by its convex spire whorls and relatively evenly reticulate sculpture. The character of this sculpture immediately distinguishes *V. toroensis* from the *Ventrilia tenera* species group discussed above. Olsson (1922, p. 85) compared the new taxon to *V. insulare* (Pilsbry and Johnson, 1917) from the Neogene, locality unknown, of the Dominican Republic, but this species does not have a reticulate sculpture

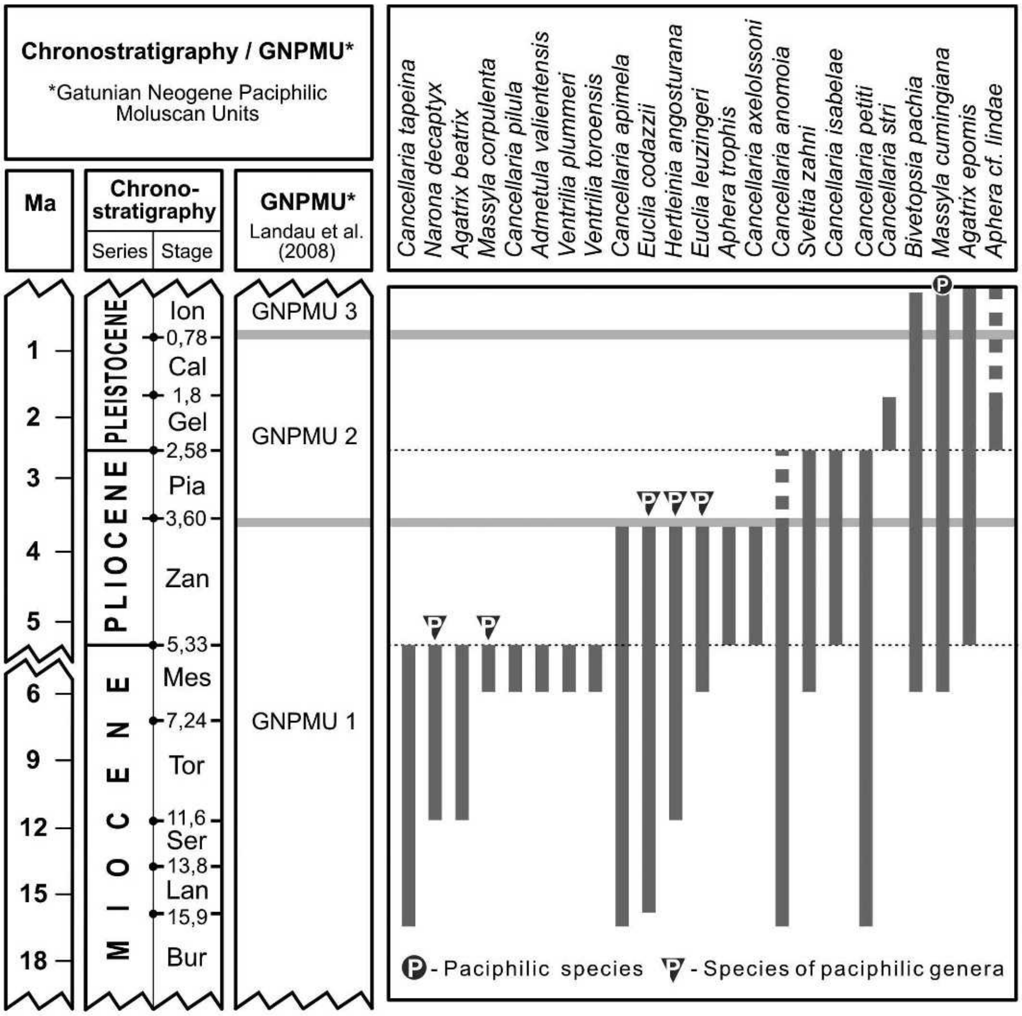

FIGURE 11—Chronological distribution of Neogene cancellariid species from the Bocas del Toro region.

(see Jung and Petit, 1990, pl. 27, figs. 13–15). Woodring (1970, p. 345, pl. 63, figs. 14, 15) described but did not name a *Trigonostoma* species from the lower Pliocene Chagres Formation of Panama. The shell is somewhat worn but its sculpture is closer to that of *V. insulare* than *V. toroensis*. *Ventrilia gurabis* Jung and Petit, 1990 from the lower Pliocene Gurabo Formation of the Dominican Republic has more angular spire whorls than *V. toroensis*, and a reticulate sculpture composed of ribs and cords of very irregular strength.

DISCUSSION

This paper records 24 cancellarid species present in the Bocas del Toro assemblages, representing 11 genera. Seven species; *Cancellaria pilula* n. sp., *Cancellaria isabelae* n. sp., *Cancellaria stri* n. sp., *Cancellaria axelolssoni* n. sp., *Massyla corpulenta* n. sp., *Aphera trophis* n. sp. and *Admetula valientensis* n. sp. are new. The cancellarid genus *Charcolleria* Olsson, 1942 is considered a junior synonym of *Massyla* H. Adams and A. Adams, 1854.

Cancellarids were far more diverse in the Tropical American Neogene in the Miocene and Pliocene than they are today. The diversity reported here for the Bocas assemblages is similar to that reported from other well-studied Caribbean assemblages (i.e., Dominican Republic–20 species [Jung and Petit, 1990]; Venezuelan assemblages–23 species [Jung, 1965; Landau and Petit, 1997; Landau et al., 2007]; Ecuador–27 species [Olsson, 1942, 1964]; Gatun area of Panama–21 species [Woodring, 1970; Petit, 1976]). If we compare that with the six shallow water cancellarids living in the Caribbean today (*Cancellaria reticulata* [Linnaeus, 1767], *Agatrix agassizi* [Dall, 1889], *Axelella smithii* [Dall, 1888], *Tritonoharpa lanceolata* [Menke, 1828], *Bivetopsia rugosa* [Lamarck, 1822], *Ventrilia tenera* [Philippi, 1848]), it is clear that the modern fauna is severely depleted at both the species and genus levels. This is not the case in the tropical American Pacific, where 41 species representing 19 different genera/subgenera were listed by Keen (1971).

Jung and Petit (1990) commented on the highly endemic nature of the cancellarids found in the Dominican Neogene where only one of the twenty species is known to occur outside the Dominican Republic. In the Bocas assemblages endemism is far less, with only nine (37.5%) species known only from the Bocas assemblages.

For our paleobiogeographic study we use Petuch's (1982) Gatunian Province over Woodring's (1974) Miocene Caribbean Province but prefer Woodring's biogeographic model for the Tropical American subprovinces over those of Petuch (1988, 2004). (For further discussion on ages of Caribbean assemblages and the use of Woodring's [1974] biogeographic model versus those of Petuch [1982, 1988, 2004], see Landau et al., 2008; Landau and Silva, 2010). The Bocas region lies within the Central American-northern South American paleobiogeographic subprovince (Fig. 10).

At genus level, the cancellarid fauna shared nine (82%) genera with the Ecuadorian-Peruvian Subprovince on the Pacific side of the Neogene Gatunian Province, nine (82%) with the West Indian Subprovince, six (54.5%) with the neighboring Colombian-Venezuelan-Trinidad Subprovince, six (54.5%) with the Mexican Subprovince, and one (9%) with the Brazilian Subprovince. This would indicate that the provinces directly within the Central American Seaway shared most genera in common, with the number of shared genera decreasing in the more outlying subprovinces.

At species level, the cancellarid fauna shared three (12.5%) species with the Ecuadorian-Peruvian Province, three (12.5%) with the Colombian-Venezuelan-Trinidad Subprovince, one (4%) with the Mexican Subprovince, one (4%) with the West Indian, and had no species in common with the Brazilian Subprovince. None of the species occur in more than two subprovinces. The level of endemism is high but not as high as that reported by Jung and Petit (1990), probably due to the very central geographic location within the Gatunian Province of the Bocas assemblages. Our comments on the Brazilian Subprovince fauna must be treated with some reservation as the material from this region is very poorly preserved.

Many of the cancellarid genera that disappeared from the Caribbean during or after the closure of the Central American Seaway are still present on the Pacific side of the Isthmus of Panama, and therefore suffered a range contraction following the uplift of the Isthmus of Panama, becoming restricted to the Pacific side of their original wider distribution in the Neogene, which was throughout the Gatunian Paleobiogeographic Province (see Vermeij and Petuch, 1986; Landau et al., 2008). These are the taxa known as paciphiles (Woodring, 1966). The paciphilic cancellarids listed by Jung and Petit (1990, p. 91) are still valid; although *Sveltia* must be removed, which was recently found living in deep waters in the Caribbean (Harasewych and Petit, 2011).

The disappearance of the paciphiles from the Caribbean did not occur gradually but in distinct pulses (Landau et al., 2009; Landau and Silva, 2010). Landau et al. (2009) constructed a chronological succession of ecostratigraphic units for the Caribbean Neogene (Gatunian Neogene Paciphile Molluscan Units) based on the presence/absence of paciphiles. The paciphilic cancellarids played an important role in this model, their disappeance marking the end of GNPMU1, at the Pliocene Zanclean/Piacenzian boundary.

This revision of virtually unknown Neogene cancellarids from the Bocas del Toro region provides an opportunity to test the ecostratigraphic model proposed by Landau et al. (2009) because the Bocas assemblages span from middle Miocene to upper Pliocene (i.e., both GNPMU1 and GNPMU2 are represented). According to this model, assemblages older than the Pliocene Zanclean/Piacenzian boundary should be rich in paciphilic cancellarid genera whereas those younger than lowermost Piacenzian should not have any paciphilic cancellarids. Four paciphile cancellarid genera are present in the Bocas assemblages: *Euclia*, *Hertleinia*, *Massyla* and *Narona*. As can be seen in Figure 11, none of these genera is present in the Caribbean portion of the Gatunian Province in beds later than lower Pliocene which is the scenario predicted by the ecostratigraphic model proposed by Landau et al. (2009). Although *Massyla cumingiana* is shown to extend to the present day in Figure 11, it is only present in the Pacific portion of the Gatunian Province after the lower Pliocene.

ACKNOWLEDGMENTS

Thanks go to W. Etter, O. Schmidt and F. Wiedenmeyer of the Naturhistorisches Museum Basel (NMB), Switzerland for help with access to the Panama Paleontology Project (PPP) collection. The authors thankfully acknowledge the following Panamian entities for greatly facilitating field work and for granting the necessary permits to conduct it in the Republic of Panama: Autoridad del Canal de Panamá/Panama Canal Authority (ACP) and Dirección de Recursos Minerales del Ministerio de Comercio e Industria (MICI). The authors would also like to thank the Smithsonian Tropical Research Institute in Panama, both at Panamá City and at the STRI Bocas del Toro Research Station, for their help and guidance in obtaining the necessary permits and for all the logistical—laboratorial and field—support. REP thanks S. Kaicher for providing a photograph of USNM 784467. M. G. Harasewych of the National Museum of Natural History, Smithsonian Institution is thanked for supplying SEM photograph of the protoconch of *Aphera lindae*. Our thanks also to G. Dietl of the Paleontological Research Institution for permission to reproduce some images of type material from their database.

REFERENCES

ADAMS, H. AND A. ADAMS. 1853–1858. The genera of Recent Mollusca; Arranged according to their organization. John van Voorst, London. 2 Vols. (1, 1–256, pls. 1–32 (1853); 1, 257–484, 2, 1–92, pls. 33–72 [1854]; 2, 93–284, pls. 73–96 [1855]; 2, 285–412, pls. 97–112 [1856]; 2, 413–540, pls. 113–128 [1857]; 2, 541–660, pls. 129–138 [1858].)

ANDERSON, F. M. 1929. Marine Miocene and related deposits of north Colombia. Proceedings of the California Academy of Sciences, Fourth Series, 18:73–213, pls. 8–23.

BARRIOS, M. M. 1960. Algunos moluscos del Terciario medio de Colombia. República de Colombia, Servicio Geológico Nacional, Boletín Geológico, 6:213–306.

BEESLEY, P. L., G. J. B. ROSS, AND A. WELLS, (eds.). 1998. Mollusca: The Southern Synthesis. Fauna of Australia, Vol. 5. Australian Biological Resources Study, Canberra. CSIRO Publishing, Melbourne. Part A, i–xvi, 1–563; Part B, i–viii, 565–1234.

BEU, A. G. 2010. Neogene tonnoidean gastropods of tropical and South America: Contributions to the Dominican Republic and Panama Paleontology Projects and uplift of the Central American Isthmus. Bulletins of American Paleontology, 377–378:1–550, figs. 1–6, pls. 1–79.

BÖSE, E. 1910. Zur jungtertiären Fauna von Tehuantepec. I. Stratigraphie, Beschreibung und Vergleich mit amerikanischen Tertiärfaunen. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, 60:215–255, pls. 12–13.

BOUCHET, P. AND J.-P. ROCROI. 2005. Classification and nomenclator of gastropod families. Malacologia, 47:1–397.

BROCCHI, G. B. 1814. Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente. Stamperia Reale, Milano. 2 Vols., 1:1–240; 2: 241–712, pls. 1–16.

BROWN, A. P. AND H. A. PILSBRY. 1911. Fauna of the Gatun Formation, Isthmus of Panama. Proceedings of the Academy of Natural Sciences of Philadelphia, 63:336–373, figs. 1–3, pls. 22–29.

COATES, A. G., M. P. AUBRY, W. A. BERGGREN, L. S. COLLINS, AND M. KUNK. 2003. Early Neogene history of the Central American Arc from Bocas del Toro, western Panama. Geological Society of America Bulletin, 115:271–287, figs. 1–7.

COATES, A. G., D. F. MCNEILL, M. P. AUBRY, W. A. BERGGREN, AND L. S. COLLINS. 2005. An introduction to the Geology of the Bocas del Toro Archipelago, Panama. Caribbean Journal of Science, 41:374–391.

COLLINS, L. S. AND A. G. COATES. 1999. Introduction. *In* L. S. Collins and A. G. Coates (eds.), A paleobiotic survey of the Caribbean faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, 357:5–13, figs. 1–13.

COSSMANN, M. 1888. Mollusques: Gastéropodes. *In* Revue de Paléontologie pour l'année 1887, dirigée par M. H. Douvillé. Annuaire Géologique Universel, Revue de Géologie et Paléontologie, 4:765–785.

COSSMANN, M. 1889. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. Quatrième Fascicule. Annales de la Société Royale Malacologique de Belgique, 24:3–381, pls. 1–12. (Also issued as a separate, p. 7–385, 12 pls.)

CROSSE, H. 1863. Étude sur le genre cancellaire, et description d'espèces nouvelles (suite). Journal de Conchyliologie, 11:58–69, pl. 2.

DALL, W. H. 1888. *Gastropods and lamellibranchs,* Vol. 2, p. 62–76. *In* A. Agassiz (ed.), Three cruises of the United States Coast and Geodetic Survey Steamer "Blake" in the Gulf of Mexico, in the Caribbean Sea, and along the Atlantic Coast of the United States, from 1877 to 1880. Houghton, Mifflin and Company, Boston and New York. Two volumes.

DALL, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–1878) and in the Caribbean Sea (1879–1880) by the U.S. Coast Survey Steamer "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology, 18(1034):1–492, pls. 10–40.

DALL, W. H. 1896. Diagnoses of new species of mollusks from the west coast of America. Proceedings of the United States National Museum, 18:7–20.

DALL, W. H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XXXVII. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," from October 1904, to March 1905, Lieut. Commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and the Brachiopoda. Bulletin of the Museum of Comparative Zoology, 43(6):205–487, pls. 1–22.

DESHAYES, G. P. 1830. *Encyclopédie Méthodique. Histoire naturelle des vers*. Mme Veuve Agasse, Paris, 2(1):1–256.

FORBES, E. AND S. HANLEY. 1848–1853. A history of British Mollusca and their shells. van Voorst, London. 4 Vols. (Published in parts; for dates of parts see Fisher and Tomlin, 1935, Journal of Conchology, 20:150–151.)

GABB, W. M. 1873. On the topography and geology of Santo Domingo. Transactions American Philosophical Society, new series, 15:49–259, 2 maps.

GÓMEZ, P. L. D. AND G. C. E. VALERIO. 1971. Lista preliminar illustrada de los moluscos fósiles de la formación Río Banano (Mioceno), Limón, Costa Rica. Instituto Geografico Nacional (Costa Rica), Informe Semestral, Enero a Junio, 1971:43–62.

GUPPY, R. J. L. 1866. On the Tertiary Mollusca of Jamaica. Quarterly Journal of the Geological Society of London, 22:281–295, pls. 16–18.

GUPPY, R. J. L. AND W. H. DALL. 1896. Descriptions of Tertiary fossils from the Antillean region. Proceedings of the United States National Museum, 19(1110):303–331, pls. 27–30.

HEMMEN, J. 2007. Annotated and illustrated calatlogue of Recent Cancellariidae. Privately published, Weisbaden, Germany, 428 p.

HINDS, R. B. 1843. Description of ten new species of *Cancellaria*, from the collection of Sir Edward Belcher. Proceedings of the Zoological Society of London, 1843:47–49.

JOUSSEAUME, F. P. 1887a. Diagnoses de coquilles nouvelles de la famille des Cancellariidae (Mollusques gastéropodes). Le Naturaliste, Année 9, 2e Série Année, 1:163–165.

JOUSSEAUME, F. P. 1887b. La famille des Cancellariidae (Mollusques gastéropodes). Le Naturaliste, Année 9, 2e Série (Année 1), p. 155–157, 192–194, 213–214, 221–223.

JOUSSEAUME, F. P. 1888. La famille des Cancellariidae (Mollusques gastéropodes). Paris, 31 p. (Reprint of 1887a and 1887b above, combined into one paper; type reset in reduced size.)

JUNG, P. 1965. Miocene Mollusca from the Paraguana Peninsula, Venezuela. Bulletins of American Paleontology, 49(223):387–652, figs. 1, 2, pls. 50–79.

JUNG, P. 1969. Miocene and Pliocene mollusks from Trinidad. Bulletins of American Paleontology, 55(247):289–657, figs. 1–4, pls. 13–60.

JUNG, P. AND R. E. PETIT. 1990. Neogene Paleontology in the northern Dominican Republic. 10. The Family Cancellariidae (Mollusca: Gastropoda). Bulletins of American Paleontology, 98(334):87–144, figs. 1–18, pls. 15–29.

KANTOR, Y. I. AND M. G. HARASEWYCH. 1992. Morphology of the digestive system of Volutomitra alaskana Dall, 1902 (Gastropoda, Pectinibranchia, Volutomitridae) with notes on the possible mechanism of feeding. Ruthenica, 2:45–53, figs. 1–5.

KEEN, A. M. 1971. Sea shells of Tropical West America. Marine mollusks from Baja California to Peru. Second edition. Stanford University Press, Stanford, California, xiv + 1064 p, numerous non-consecutive figs., pls. 1–22.

LAMARCK, J. B. P. A. 1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. Société d'Histoire Naturelle de Paris Mémoire, 1:63–91.

LAMARCK, J. B. P. A. 1822. Histoire naturelle des animaux sans vertèbres. Paris, 7:1–711.

LANDAU, B. M., G. C. KRONENBERG, G. S. HERBERT, AND C. M. DA SILVA. 2011. The genus Strombus (Mollusca: Caenogastropoda: Strombidae) in the Neogene of the Bocas del Toro area, Panama, with the description of three new species. Journal of Paleontology, 85:337–352, figs. 1–9.

LANDAU, B. M. AND R. E. PETIT. (1996) 1997. New species of Cancellarioidea (Mollusca: Gastropoda) from the lower Miocene Cantaure Formation of Venezuela. Tulane Studies in Geology and Paleontology, 29:45–150, pl. 1. (Separates dated 26 February 1996 instead of 26 February 1997 in error.)

LANDAU, B. M., R. E. PETIT, AND C. M. DA SILVA. 2007. The Pliocene Cancellariidae (Mollusca: Gastropoda) of the Cubagua Formation (Cerro Negro Member) from Cubagua Island, with a new species from the Miocene Cantaure Formation, Venezuela. The Veliger, 49:27–43, figs. 1–48.

LANDAU, B. M. AND C. M. DA SILVA. 2010. Early Pliocene gastropods of Cubagua, Venezuela: Taxonomy, palaeobiogeography and ecostratigraphy. Palaeontos, 19:1–221, figs. 1–20, pls. 1–23.

LANDAU, B. M. AND C. M. DA SILVA. 2011. The genus *Amarophos* Woodring, 1964 (Gastropoda: Buccinoidea) in the tropical American Neogene, with the description of two new species. The Veliger, in press.

LANDAU, B. M., G. J. VERMEIJ AND C. M. DA SILVA. 2008. Southern Caribbean Neogene palaeobiogeography revisited. New data from the Pliocene of Cubagua, Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology, 257:445–461, figs. 1, 2.

LANDAU, B. M., G. J. VERMEIJ AND C. M. DA SILVA. 2009. Pacific elements in the Caribbean Neogene gastropod fauna: the source-sink model, larval development, disappearance, and faunal units. Bulletin de la Société géologique de France, 180:249–258.

LINNAEUS, C. 1767. Systema naturae per regna tria naturae. Editio duodecimo reformata. Stockholm, 1(2):533–1327.

LÖBBECKE, T. 1881–1887. Das genus *Cancellaria*. Systematisches Conchylien-Cabinet von Martini und Chemnitz, 4:1–96, pls. 1–23. (Issued in parts: pt. 309, 1–16, pls. 1–5 [1881]; pt. 335, 17–32, pls. 6–10 [1885]; pt. 340, 33–56, pls. 11–15 [1886]; pt. 343, 57–80, pls. 16–20 [1886]; pt. 346, 81–96, pls. 21–23 [1887].)

MANSFIELD, W. C. 1925. Miocene gastropods and scaphopods from Trinidad, British West Indies. Proceedings of the United States National Museum, 66(2559):1–65, pls. 1–10.

MANSFIELD, W. C. 1929. Plates 16–21. *In* C. W. Cooke and S. Mossom (eds.), Geology of Florida. Florida State Geological Survey, Twentieth Annual Report: 31–227, pls. 1–28.

MANSFIELD, W. C. 1930. Miocene gastropods and scaphopods of the Choctawhatchee Formation of Florida. Florida State Geological Survey Bulletin, 3:1–185, pls. 1–21.

MARKS, J. G. 1949. Nomenclatural units and tropical American Miocene species of the gastropod family Cancellariidae. Journal of Paleontology, 23:453–464, pl. 78.

MAURY, C. J. 1917. Santo Domingo type sections and fossils. Part 1. Mollusca. Bulletins of American Paleontology, 5(29):165–415, pls. 29–65.

MAURY, C. J. 1925. A further contribution to the paleontology of Trinidad (Miocene horizons). Bulletins of American Paleontology, 10(42):153–402, pls. 12–54.

MENKE, C. T. 1828. Synopsis methodica molluscorum generum omnium et specierum earum, quae in Museo Menkeano adservantur; cum synonymia critica et novarum specierum diagnosibus, auctore Carolo Theodoro Menke. M. Dre. Henrici Gelpke, Pyrmonti, xii + 91 p.

MOGOLLÓN, V. A. 2001. Moluscos marinos del Perú: Nuevos registros y datos sobre especies poco conocidas. Wiñay Yachay, 5:93–115.

MORLET, L. 1888. Catalogue des coquilles fossiles recueillies dans quelques localités récemment exploitées du Bassin de Paris et description des espèces nouvelles. Journal de Conchyliologie, 36:136–220, pls. 8–10.

NELSON, E. T. 1870. On the molluscan fauna of the later Tertiary of Peru. Transactions of the Connecticut Academy of Arts and Science, 2:186–206, pls. 6–7. (Also issued as a separate, p. 3–23, pls. 6–7.) (A Spanish translation of this work was published in 1980 [Sobre la fauna de moluscos del Terciario Superior DEL Peru. Boletín de la Sociedad Geológica del Peru, 66:67–81, illustr.; not seen] and the taxa were listed by the Zoological Record in 1984 as having been described in 1980.)

OINOMIKADO, T. 1939. Miocene Mollusca from the neighbourhood of Cucurrupi, Department of Choco, Colombia. Journal of the Geological Society of Japan, 46:103–116, pl. 15.

OLSSON, A. A. 1922. The Miocene of northern Costa Rica. With notes on its general stratigraphic relations. Bulletins of American Paleontology, 9(39):174–482, pls. 4–35.

Olsson, A. A. 1932. Contributions to the Tertiary paleontology of northern Peru: Part 5, The Peruvian Miocene. Bulletins of American Paleontology, 19(68):1–272, pls. 1–24.

Olsson, A. A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. Bulletins of American Paleontology, 27(106):153–258, pls. 14–25.

Olsson, A. A. 1964. Neogene mollusks from northwestern Ecuador. Paleontological Research Institution, Ithaca, New York, 1–256, pls. 1–38.

Olsson, A. A. 1967. Some Tertiary mollusks from south Florida and the Caribbean. Paleontological Research Institution, Ithaca, New York61 p., 9 pls. (Reprinted 1993 in Paleontological Research Institution Special Publication No. 19.)

Perrilliat, M. del C. 1973. Monografia de los moluscos del Mioceno Medio de Santa Rosa, Veracruz, México. Parte II. (Gasterópodos: Mitridae a Terebridae). Paleontología Mexicana, 35:1–97.

Petit, R. E. 1967. Notes on Cancellariidae (Mollusca: Gastropoda). Tulane Studies in Geology, 5:217–219, fig. 1.

Petit, R. E. 1970. Notes on Cancellariidae (Mollusca: Gastropoda)—II. Tulane Studies in Geology and Paleontology, 8:83–88, pl. 1.

Petit, R. E. 1976. Notes on Cancellariidae (Mollusca: Gastropoda)—III. Tulane Studies in Geology and Paleontology, 12:33–43, pls. 1–2.

Petit, R. E. and M. G. Harasewych. 1990. Catalogue of the Superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia). The Nautilus, Supplement 1:1–69.

Petit, R. E. and M. G. Harasewych. 1998. Cancellaria (Euclia) laurettae, a new species of Cancellariidae (Mollusca: Neogastropoda) from western Panama. The Nautilus, 112:113–116, figs. 1–4.

Petit, R. E. and M. G. Harasewych. 2005. Catalogue of the superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia)—Second edition. Zootaxa, 1102:1–161.

Petit, R. E. and M. G. Harasewych. 2011. A new *Sveltia* (Gastropoda: Cancellariidae) from off Guadeloupe, French West Indies. The Nautilus, 125:72–74.

Petit de la Saussaye, S. 1844. *Cancellaria cumingiana* n. sp. Magasin de Zoologie, Deuxième Série, 6:1 unnumbered page, pl. 112.

Petuch, E. J. 1981. A relict Neogene Caenogastropod fauna from northern South America. *Malacologia*, 20:307–347, figs. 1–130.

Petuch, E. J. 1982. Geographical heterochrony: Comtemporaneous [sic] coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology, 37:277–312, figs. 1–12.

Petuch, E. J. 1987. New Caribbean molluscan faunas. The Coastal Education and Research Foundation, Charlottesville, Virginia. 1–154 + A1–4 p, 29 pls.

Petuch, E. J. 1988. Neogene history of tropical American mollusks. Biogeography and evolutionary patterns of tropical western Atlantic Mollusca. Coastal Education and Research Foundation, Charlottesville, Virginia, 217 p, 23 figs., 39 pls.

Petuch, E. J. 1994. Atlas of Florida fossil shells (Pliocene and Pleistocene marine gastropods). Chicago Spectrum Press, 394 p, 20 figs., 100 pls.

Petuch, E. J. 2004. Cenozoic seas. The view from eastern North America. CRC Press, Boca Raton, Louisiana. 308 p, 34 figs., 98 pls.

Philippi, R. A. 1848. Testaceorum novorum centuria. (Continuatio.). Zeitschrift für Malakozoologie, 5(2):17–27.

Pilsbry, H. A. 1931. The Miocene and Recent Mollusca of Panama Bay. Proceedings of the Academy of Natural Sciences of Philadelphia, 83:427–440, figs. 1–5, pl. 41.

Pilsbry, H. A. and C. W. Johnson. 1917. New Mollusca of the Santo Domingan Oligocene. Proceedings of the Academy of Natural Sciences of Philadelphia, 69:150–202.

Pilsbry, H. A. and A. A. Olsson. 1941. A Pliocene fauna from western Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia, 93:1–79, pls. 1–19.

Pitt, W. D. and L. Pitt. 1992. Naticidae (Mollusca: Mesogastropoda) from the Neogene of northwestern Ecuador. Tulane Studies in Geology and Paleontology, 25:109–138.

Pitt, W. D. and L. Pitt. 1993. Ultra-violet light as a useful tool for identifying mollusks, with examples from the Gatun Formation, Panama. Tulane Studies in Geology and Paleontology, 26:1–13, pls. 1–4.

Ponder, W. F. 1973. The origin and evolution of Neogastropoda. Malacologia, 12:295–338, figs. 1–6.

Ponder, W. F. and A. Warén. 1988. Classification of the Caenogastropoda and Heterostropha—A list of the family-group names and higher taxa, p. 288–328. *In* W. F. Ponder (ed.), Prosobranch Phylogeny. Malacological Review, Supplement 4 Appendix.

Reeve, L. A. 1856. Monograph of the genus *Cancellaria*. Conchologia Iconica, 10, (unpaginated text), pls. 1–18.

Riccardi, A. C. 2009. "IUGS ratified ICS Recommendation on redefinition of Pleistocene and formal definition of base of Quaternary." International Union of Geological Sciences. http://www.stratigraphy.org/upload/IUGS%20Ratification_Q%20&%20Pleistocene.pdf.

Röding, P. F. 1798. Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Fried Bolten, M.D.p.d. Pars Secunda continens conchylia sive testacea univalvia, bivalvia and multivalvia. Johan. Christi. Trappii., Hamburgi, viii + 199 p. (Reprinted 1906 by Sherborn, C.D. and Sykes, E.R.; 1986 by American Malacological Union, Inc.).

Rosenberg, G., R. S. Kuncio, G. M. Davis, and M. G. Harasewych. 1994. Ribosomal RNA phylogeny of selected gastropod and unionacean bivalve mollusks, p. 111–121. *In* M. G. Harasewych and S. Tillier (eds.), Molecular Techniques and Molluscan Phylogeny. Proceedings of a symposium held at the 11th International Malacological Congress, Siena, 1992. The Nautilus, Supplement 2.

Rutsch, R. F. 1934. Die Gastropoden aus dem Neogen der Punta Gavilan in Nord-Venezuela. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft, 54–55:1–169, pls. 1–9.

Shasky, D. R. 1961. New deep water mollusks from the Gulf of California. The Veliger, 4:18–21, pl. 4, figs. 1–10.

Smith, M. 1940. New Recent and fossil molluscs from Florida. The Nautilus, 54:44–46, pl. 2.

Solander, D. C. 1766. (Descriptions of species). *In* G. Brander, Fossilia hantoniensia collecta, et in Musaeo Britannico deposita, a Gustavo Brander. Londini. vi + 43 p, 9 pls.

Sowerby, G. B. 1832. I. Characters and descriptions of new species of Mollusca and Conchifera collected by Mr. Cuming. Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832:50–61.

Sowerby, G. B. 1849. II. Monograph of the genus *Cancellaria*. Thesaurus Conchyliorum, 2:439–461, pls. 92–96. (Reprinted 1985 by Luis Pisani Burnay, Lisboa.)

Toula, F. 1909. Eine jungtertiäre Fauna von Gatun am Panama-Kanal. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, 58:673–760, pls. 25–28.

Tryon, G. W. 1885. Family Cancellariidae. Manual of Conchology, 7:65–98, pls. 1–7.

Tuomey, M. and F. S. Holmes. 1855–1857. Pleiocene fossils of South Carolina. Russell and Jones, Charleston, xvi + 152 p, 30 pls. (1–30, pls. 1–12 [1855]; 31–144, pls. 13–28 [1856]; 145–152, i–xvi, pls. 29–30 [1857].) (Reprinted 1974, Paleontological Research Institution, Ithaca, N. Y.)

Vermeij, G. J. and E. J. Petuch. 1986. Differential extinction in tropical American molluscs: Endemism, architecture, and the Panama land bridge. Malacologia, 27:29–41.

Weisbord, N. E. 1929. Miocene Mollusca of northern Colombia. Bulletins of American Paleontology, 14(54):233–306, pls. 36–43.

Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part II, Gastropods and discussion of results. Carnegie Institution of Washington Publication, 385:i–vii, 1–564, figs. 1, 2, pls. 1–40.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society, 110:425–433, figs. 1–3.

Woodring, W. P. 1970. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of the Tertiary Mollusks (Gastropods: Eulimidae, Marginellidae to Helminthoglyptidae). United States Geological Survey Professional Paper, 306-D:iii + 299–452, pls. 48–66.

Woodring, W. P. 1974. The Miocene Caribbean Faunal Province and its subprovinces. Contributions to the geology and paleobiology of the Caribbean and adjacent areas. Verhandlungen der Naturforschenden Gesellschaft in Basel, 84:209–213, fig. 1.

Accepted 15 September 2011