

Cypraeidae (Mollusca: Gastropoda) from the early Miocene Cantaure Formation of northern Venezuela

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ABSTRACT. This is the first account of the rich assemblage of Cypraeidae from the late early Miocene, Burdigalian Cantaure Formation, Paraguaná Peninsula, Falcón Province, Venezuela. Twelve species are recorded from these deposits, ten of which are new to science; *Luria cantaurana* n. sp., *L. isabellaprimitiva* n. sp., *Trona ingrami* n. sp., *Propustularia longidentata* n. sp., *P. paraganensis* n. sp., *Zonaria pingata* n. sp., *Z. pseudotumulus* n. sp., *Pseudozonaria praeaequinocialis* n. sp., *P. primarobertsi* n. sp. and *P. falconensis* n. sp. Comparative taxon *Muracypraea "henekeni"* of Groves (1997) from the middle to late Miocene Gatun Formation of Panama and Angostura Formation of Ecuador is herein described as *M. woodringi* n. sp. *Cypraea fossula* (Ingram, 1947) is considered a junior subjective synonym of *Trona trinitatensis* (Mansfield, 1925). The type material of *Jousseaumea joossi* Schilder, 1939 and *Pustularia mejasensis* Schilder, 1939 are in very poor condition and do not adequately show species characteristics, and are therefore considered *nomina dubia*.

INTRODUCTION

A rich and varied cypraeid fauna is here reported from the early Miocene (Burdigalian) Cantaure Formation as defined by Hunter and Bartok (1974), Paraguaná Peninsula, Falcón State, Venezuela. Schilder (1939) first documented the family Cypraeidae from these deposits with the report of *Luria (Basilitrona) patrespatriae* (Maury, 1917) and Ingram (1947) described *Cypraea fossula* from the same formation. However, no further cypraeid taxonomic work on the Cantaure Formation has been attempted. Jung's (1965) landmark systematic monograph on the assemblage described and illustrated a specimen identified as *Cypraea* aff. *isabella* Linnaeus, but made no further mention of additional cypraeids in the formation. Herein, these omissions are addressed.

Gibson-Smith & Gibson-Smith (1979) described the presence of 'upper' and 'lower' beds in the Cantaure Formation. The basal unit is defined by a breccia composed of *Balanus* barnacle fragments and blocks of granite overlain by silty and gypsiferous shales with sandy levels (Hunter & Bartok, 1974). They also note rich molluscan levels within the lower unit. The upper level is sandier, and the transition between the two units is unclear. Dr. Emily Vokes, who has also visited the deposits, did not recognize the presence of an 'upper' and 'lower' bed (personal

communication, BL). The gastropod assemblage found in the 'upper' and 'lower' beds is similar, with a predominance of filter-feeding turrillids in the 'upper' beds and a greater number of rocky-bottom dwellers in the 'lower' bed. Cypraeids are not common in the Cantaure Formation, but are found far more often in the 'lower' beds, which are designated as the type locality for the new species.

Material and Methods

The material described here is from the Gibson-Smith 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, Austria. Some specimens are deposited in the Natural History Museum of Los Angeles County, Invertebrate Palaeontology Department (LACMIP coll.). All shells were also examined under UV light as described by Olsson & Petit (1968).

Abbreviations

Abbreviations used for institutional catalogue and/or locality numbers are as follows: ANSP, Academy of Natural Sciences of Philadelphia, USA; BL, Collection of Bernard Landau (Collection now at

NHMW); DFB coll., Dirk Fehse collection, Berlin, Germany; LACMIP Natural History Museum of Los Angeles County, Invertebrate Palaeontology Department, Los Angeles, California, USA; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMB, Naturhistorisches Museum Basel, Switzerland; PPP, Panama Palaeontological Project; TU, Tulane University, New Orleans, USA (Tertiary collections now at the National Museum of Natural History, Smithsonian Institution [USNM]); UCMP, University of California, Museum of Paleontology, Berkeley, California, USA; and USGS, United States Geological Survey, Reston, Virginia, USA.

Systematic Palaeontology

Cypraeids can be a notoriously difficult group to work on, especially the fossils as the surface colour and pattern are usually lost. A single major taxonomic study has been undertaken in recent years on the tropical American Neogene cypraeid assemblages; Dolin (1991) revised the Cypraeoidea from the late early Miocene Chipola Formation of northern Florida, which is roughly contemporaneous with the Cantaure Formation. For the ease of comparison of the two faunas, the morphologic terminology of Dolin (1991: fig. 1) and Dolin & Lozouet (2004: figs. 2a-c) are utilized.

Cypraeid systematics has been greatly enhanced by the works of Meyer (2003, 2004) in particular his molecular data-base for the family. The phylogenetic implications of this new data outlined by Meyer (2004), and the systematic arrangement suggested by López Soriano (2006) based on Meyer's work, are followed here. Higher level systematics follows that of Bouchet, et al. (2005).

The shell formula proposed by Schilder (1935: 327) has been given for each species. This formula is derived from measurements taken from all available fully mature and normally formed specimens. It consists of the following elements: [L (W-H) LT: CT]. L: average length in mm, W: average width/ length ratio in %, H: average height/ length ratio in %, LT: normalized number of labral teeth, CT: normalized number of columellar teeth. The normalized number of teeth – in relation to a shell of 25 mm length – is calculated as follows: $T = 7 + [(c-7) \times \sqrt{(25/L)}]$, T: normalized number of teeth, c: teeth counted, L: length. This shell formula is useful to highlight differences and similarities between species, but should not be used on its own to distinguish between species.

Class **GASTROPODA** Cuvier, 1791

Clade **HYPSOGASTROPODA** Ponder & Lindberg, 1997

Clade **CAENOGASTROPODA** Cox, 1959

Clade **LITTORINIMORPHA** Golikov & Starobogatov, 1975

Superfamily **CYPRAEOIDEA** Rafinesque, 1815

Family **CYPRAEIDAE** Rafinesque, 1815

Subfamily **CYPRAEINAE** Rafinesque, 1815

Genus ***Muracypraea*** Woodring, 1957

Type species: *Cypraea mus* LINNAEUS, 1758, by original designation.

Description. Shell pyriform to triangular of small to moderately large size (30 to 75 mm); posterior part of dorsal surface smooth, roughened, warty, or bituberculate; outer lip, wide, slightly constricted near anterior end; fossula indistinct, wide, shallow, and smooth.

Discussion. A consensus among specialists on the generic assignment for this group of species is lacking as is an agreement of the number of living and fossil species (Woodring, 1959; Petuch, 1979, 1987; Doneddu & Manunza 1996; Lorenz & Hubert, 2000; Meyer, 2004). This may in part be due to the inadequate description of the type species by Woodring (1957). *Muracypraea* was originally proposed as a subgenus of *Cypraea*. Lorenz & Hubert (2000) considered “*Muracypraea*” an informal group within *Siphocypraea* Heilprin, 1887 which was proposed as a subgenus within the genus *Cypraea*. Some species of the *S. problematica* complex have a strongly curled comma-shaped posterior channel that conceals the spire. *Muracypraea* was proposed for the Recent *Cypraea mus* Linnaeus, 1758 and the related fossil species that possess a more normal posterior, wide aperture, and commonly well-developed dorsal callosities, dorsal tubercles, and occasionally a central spike-like dorsal projection. *Siphocypraea* ranges from the early Pliocene to Pleistocene and is restricted to the southeastern United States whereas *Muracypraea* ranges from the early Miocene to Recent of the Caribbean Basin to Peru and southeastern California. Doneddu & Manunza (1996) and Fehse (in press, a) considered *Muracypraea* a junior synonym of *Barycypraea* Schilder, 1927. They drew attention to the long geologic history of the genus with fossil representatives in the Indo-Pacific (see Dharma, 2005; Fehse (in press, b) and the Caribbean Tertiary. Doneddu & Manunza (1996) traced the origins of the *M. mus* complex to *Cypraea* (*Bernayia*) [*sic*] *saltoensis* (Clark in Clark & Durham, 1946) of the Eocene of Colombia. However, close examination of the poorly preserved holotype makes it clear that a conclusive generic assignment is not possible, and determination of a possible new genus is beyond the scope of this paper. Kay (1996) and Groves (1997) used *Muracypraea* as a full genus. Woodring (1959) considered all Miocene specimens from the circum Caribbean basin to be *Cypraea* (*Muracypraea*) *henekeni* (lectotype; Figs 144-145). However, it is notable that specimens from the Miocene Gatun Formation of Panama are different from those of Venezuela, Trinidad, Colombia, and the Dominican Republic. Most specimens from the Gatun Formation examined by the senior author have an

axially striped colour pattern or blotching of dull reddish brown or yellowish orange. Additionally, the marginal callus is extremely thin and poorly delimited, and does not extend onto the dorsum, and the shell periphery of the Gatun shells feel corrugated, whereas they are smooth in *M. henekeni* and *M. hyaena*. We separate two distinct taxa within the Gatun assemblages (see below). The early Pliocene *Muracypraea grahami* (Ingram, 1947) from Cubagua, Venezuela (Figs 29-32) is again different (Landau & Silva, 2010). Ingram (1947) described two *Muracypraea* species from Cubagua; *Cypraea rugosa* [junior homonym of *C. rugosa* Broderip, 1827] and *Cypraea grahami*. Although the holotypes of the two shells look quite different, Landau & Silva (2010) illustrated intermediate forms and recognised a single species in the Cubagua deposits. The shell is very large and solid (63-73 mm in length) and their outline is more triangular and their dorsum even higher than *M. hyaena* (Landau & Silva 2010). The tubercles are staggered on the dorsum in a similar fashion to *M. hyaena*. The margins are corrugated, as in *Muracypraea isthmica* Schilder, 1927, but more coarsely so. In the best preserved specimen from Cubagua an indication of a striped colour pattern is present, akin to that seen in the Gatun Formation shells. On the Pacific side of the Gatunian Province *Muracypraea cayapa* (Pilsbry & Olsson, 1941) from the early Pliocene Jama Formation of Ecuador is a large poorly known species represented by a single broken specimen. Many other taxa of *Muracypraea* have been described from the Caribbean Neogene, which await validation. Species of the extant *Muracypraea mus* complex are known to have an intracapsular larval development (Ranson, 1967; Hoeblich, 1979). This assumption cannot be validated with the fossil taxa, however, this type of development would favour a restricted distribution of species and a high degree of variability between populations. This helps explain the difficulty encountered with the Caribbean Neogene *Muracypraea* populations and may be analogous to the situation among Recent species of the genus *Zoila* Jousseume, 1884 in Australia which also shows intracapsular development. Numerous species of *Zoila* are not only geographically restricted, but numerous intermediate forms are common off the western and southern coasts of Australia (Lorenz, & Hubert, 2000; Lorenz, 2001).

Based on mitochondrial molecular data presented by Meyer (2004), the two extant *Barycypraea* taxa *B. teulerei* (Cazenavette, 1846) and *B. fultoni* (Sowerby, 1903) were placed as sister taxa to *Zoila* Jousseume, 1884, reaffirming the (validity of the subfamilial clade Bernayinae Schilder, 1927, whereas *Muracypraea mus* was placed in the Cypraeinae Gray, 1824. Based on morphological differences, Fehse (in press, a) will reassign the two living *Barycypraea* species and the fossil species *B. zietsmani* (Liltved & LeRoux, 1988) [Pliocene, South Africa], *B. schilderi* (Dey in Schilder, 1941) [Pliocene, India], *B. gendingaensis*

(Martin, 1899) [Pliocene, Indonesia], and *B. kendengensis* (Schilder, 1941) [Pliocene, Indonesia] to a new genus (Dirk Fehse personal communication 2010). Some of the shells of the Indonesian fossil *Barycypraea* group are extremely similar to those of *Muracypraea* in the Tropical American Neogene and could represent a convergent evolutionary process. A morphological feature that helps separate *Muracypraea* from *Barycypraea* are the flattened spatulate horizontal expansions on either side produced from the abapical tips of the inner and outer lips of *M. henekeni* and many related species. Occasionally these spatulate expansions are hyper developed in the Caribbean forms whereas they are somewhat obsolete in the Indonesian species of *Barycypraea*. Although the two genera may have a common Tethyan ancestor, consistent shell differences and the vast geographic separation could justify different genera. Many of the *Muracypraea* shells are lightweight, less callused with a broad aperture and less developed, widely spaced dentition, whereas the shells of *Barycypraea* are heavy, strongly callused with a narrow aperture and a distinct, close-set dentition. The *Muracypraea* exceptions being *M. mus donmorei* (Petuch, 1979), *M. mus bicornis* (Sowerby, 1870), and *M. grahami* (*C. rugosa* Ingram, 1947 junior homonym of *C. rugosa* Broderip, 1827; see Landau & Silva 2010). The dorsal callosities of both genera can be variable even among the same species. However, in *Muracypraea* they tend to be restricted to the posterior portion of the dorsal surface whereas in *Barycypraea* there may be a second set located slightly anterior of the dorsum centre. Because the Miocene fossil record for the central Pacific islands is incomplete, and until a conclusive answer to whether two genera should be used for the two seemingly geographically separated species-groups, the classification of Schilder & Schilder (1971) for *Muracypraea* is used for the Caribbean species.

Muracypraea hyaena (Schilder, 1939)

Figs 1-14

1939 *Siphocypraea angustirima hyaena* Schilder, p. 23, fig. 24.

1971 *Siphocypraea (Muracypraea) angustirima hyaena* Schilder and Schilder, p. 29.

Material. 8 specimens BL coll.; 1 specimen LACMIP 13648 (ex BL coll.).

Description. Shell small to medium, solid, rotund, dorsum very strongly humped $\frac{2}{3}$ distance from the anterior end, in fully adult specimens bearing two small tubercles, right tubercle larger and anterior to left; spire depressed, covered by adapical callus; sides rounded, strongly callused, with the callus ascending progressively adapically to just below the apex posterior to the dorsal hump; ventrum flattened, slightly convex in profile; aperture almost straight,

anterior third weakly dilated; siphonal canal deep, abaxially asymmetrical and abapically orthogonally truncated, flanked on either side by flattened spatulate horizontal expansions produced from the abapical tips of the inner and outer lips; exhalant channel deeper, limited by parallel lips; about 4 mm width weakly concave channel between terminal ridge and first columellar tooth, followed by 13-14 stout, short columellar teeth, extending a short distance onto the

ventrum and into the aperture; terminal ridge obsolete, merged into smooth abapical edge of fossula; fossula small, concave, smooth; labral teeth heavy, 14-16 in number, evenly distributed. Ventral and dorsal zones spotted, marginal callus lighter coloured with larger ocellated spots.

Shell formula. 39.4 (76.9 – 58.2) 16: 15

specimen	collection number	length	width	height	LT	CT
BL coll. 1; (Figs 5-6)		47.2	36.9	26.9	14	14
BL coll. 2; (Figs 1-4)		49.7	37.1	29.8	14	14
BL coll. 3; (Figs 7-8)		44.6	34	25.2	15	14
BL coll. 4		42.9	33.3	25.2	14	13
BL coll. 5		37.8	30	21.5	14	#
BL coll. 6		37.1	29.1	20.4	16	14
BL coll. 7		32.7	24.7	20.5	#	#
BL coll. 8		32	24.5	19.1	13	11
(Figs 9-12)	LACMIP 13648	30.4	23.3	17.7	16	13

Table 1. Dimensions and number of teeth; *Muracypraea hyaena* (Schilder, 1939).

Discussion. *Muracypraea hyaena* (Schilder, 1939) (holotype; Figs 13-14) was described from younger late Miocene beds in the Urumaco area, Falcón Dept., Venezuela (Sánchez-Villagra & Aguilera, 2006). The holotype is in very poor condition, but the general shape, strength of the dorsal hump, disposition of the teeth, and colour markings are consistent. There is some variability as to the presence or absence of tubercles on the dorsal hump; the tubercles usually present only in fully grown specimens, although our largest specimen (Figs 1-4) is devoid of tubercles and the smallest (Figs 9-12) has well developed little tubercles.

Perilliat (1992) figured a fairly well preserved specimen identified as *Siphocypraea (Muracypraea)* sp. cf. *S. (M.) angustirima hyaena* Schilder from the middle Miocene Ferrotepec Formation, Michoacán, southern Mexico. This specimen is indeed a *Muracypraea* somewhat similar to *M. hyaena* but has coarser dentition and has a more produced anterior.

The Ferrotepec Formation shell is more likely an undescribed species.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

Middle Miocene: Urumaco, Venezuela (Schilder, 1939).

Muracypraea woodringi n. sp.

Figs 21-28

1951 *Cypraea* cf. *C. henekeni* Sowerby – Marks, p. 376.

1959 *Cypraea (Muracypraea) henekeni* Sowerby – Woodring, p. 194, pl. 32, figs 1, 4, 6, 9.

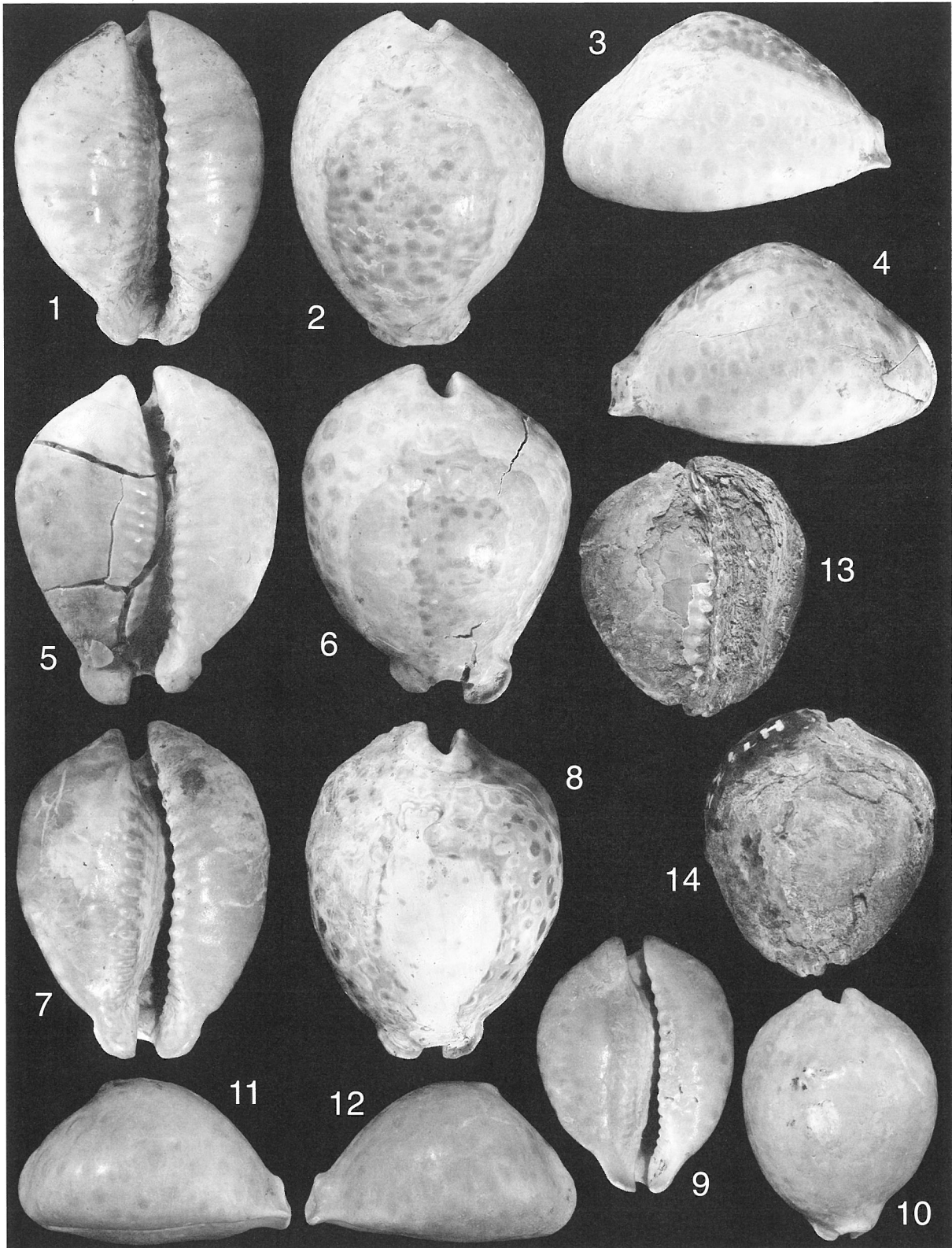
1964 *Siphocypraea (Muracypraea) henekeni* (Sowerby) – Olsson, p. 176, pl. 31, figs 3-3a.

1993 *Cypraea (Muracypraea) henekeni* Sowerby – Pit & Pit, p. 3, pl. 1, fig. 7.

1997 *Muracypraea “henekeni”* (Sowerby, 1850) – Groves, p. 152, pl. 1, figs 4-6.

Figures 1-14

1-4. *Muracypraea hyaena* (Schilder, 1939) NHMW 2010/0036/0024 (NMMW; ex BL coll. no. 2), length 47.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **5-6.** *Muracypraea hyaena* (Schilder, 1939) NHMW 2010/0036/0025 (NMMW; ex BL coll. no. 1), length 47.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **7-8.** *Muracypraea hyaena* (Schilder, 1939) NHMW 2010/0036/0026 (NMMW; ex BL coll. no. 3), length 44.6 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **9-12.** *Muracypraea hyaena* (Schilder, 1939) LACMIP 13648 (LACMIP coll.; ex BL coll.), length 30.4 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela. **13-14.** *Muracypraea hyaena* (Schilder, 1939) Holotype NMB H11272 (NMB coll.), length 31.0 mm. Urumaco area, Falcón Dept., Venezuela, Urumaco Formation, early late Miocene.



Dimensions and type material. Holotype; LACMIP 12431, length 42.1 mm (Figs 23-24); paratype 1 ANSP 315087, length, 42.0 mm (Figs 21-22); paratype 2 USNM 562582, length, 38.5 mm, paratype 3 NHMW 2010/0036/0001 (ex. BL coll.) length 43.4 mm (figs. 25-28).

Other Material. Panama, three incomplete specimens PPP 02168 (NMB 18667); three incomplete specimens PPP 02119 (NMB 17637); two specimens PPP 00490 (NMB 17871); four specimens PPP 00487 (NMB 17868); one specimen PPP 1080 (NMB 18261); one specimen PPP 00224 (NMB 17642); two specimens PPP 01034 (NMB 18258); one incomplete specimen PPP 01078 (NMB 18325) all NMB coll.; one specimen locality ANSP 1731 (internal mould); one specimen locality LACMIP 16936; five specimens locality LACMIP 17908 (= TU 757); five specimens locality LACMIP 17909 (= TU 958); two specimens locality LACMIP 17910 (= TU 960); two specimens locality LACMIP 17911 (= TU 1432); one specimen from LACMIP 17912 (= TU 1433); Cativa, Colón, BL coll. (All Gatun Formation); Colombia, one specimen locality UCMP 154008 (fragment), Nariño Dept.; Ecuador, one incomplete specimen PPP 03391 (NMB 19122); one specimen AGC 99-102, NMB coll.; Baja California Sur, Mexico, one specimen locality USNM 1/1238 (ex USGS), San Ignacio Formation(?).

Type locality. Angostura Formation (late Miocene), Loc. LACMIP 16943 [= TU 1507], just east of Río Verde, approximately 30 km east of Río Esmeraldas Esmeraldas Province, Ecuador.

Type stratum. Angostura Formation (late Miocene).

Description. Shell medium-sized for genus, solid, triangular-shaped, dorsum very strongly humped $\frac{2}{3}$ distance from the anterior end, bearing two groups of small warty tubercles, left group larger and slightly anterior to right; spike-like projection at centre of apex rises 2 mm above dorsal surface; spire depressed, covered by adapical callus; sides rounded, strongly callused, with the callus ascending progressively adapically to just below the apex posterior to the dorsal hump, callus edge poorly delimited; ventrum flattened, slightly convex in profile; aperture almost straight, anterior third weakly dilated; anterior canal deep, abaxially asymmetrical and abapically orthogonally truncated, flanked on either side by flattened spatulate horizontal expansions produced from the abapical tips of the inner and outer lips; posterior channel deeper, limited by parallel lips; about 4 mm width weakly concave channel between terminal ridge and first columellar tooth, followed by 14 stout, becoming weak posteriorly, short columellar teeth, extending a short distance onto the ventrum and into the aperture; terminal ridge obsolete, merged into smooth abapical edge of fossula; fossula small, concave, smooth; labral teeth heavy, 14 in number, evenly distributed, becoming weak posteriorly. Ventral and dorsal zones striped, marginal callus lighter coloured, dorsum with irregular stripes of dull red-orange and tan.

Shell Formula. 45.3 (80.0 – 60.0) 21: 14

specimen	collection number	length	width	Height	LT	CT
holotype (Figs 23-24)	LACMIP 12431	43.5	34.5	27.1	18	#
paratype 1 (Figs 21-22)	ANSP 315087	42.1	34.1	24.6	14	13
paratype 2	USNM 562582	46.0	36.9	24.3	#	#
paratype 3 (Figs 25-28)	NHMW 2010/0036/0001	43.4	31.1	25.6	18	13
	CAS 66589.06	37.5	29.7	22.6	#	#
	USNM 562581	52.7	44.0	31.8	#	#
BL coll. 1		38.4	31.6	21.4	18	13
BL coll. 2		42.4	35.1	23.1	17	12
BL coll. 3		57.6	45.1	31.8	18	12
BL coll. 4		48.8	41.0	28.5	17	13
BL coll. 5		46.6	35.5	26.7	17	12
DFB coll.	No. 7406-1	48.5	39.8	26.3	17	11
DFB coll.	No. 7406-2	38.8	32.7	22.1	16	12

Table 2. Dimensions and number of teeth; *Muracypraea woodringi* n. sp.

Discussion. *Muracypraea woodringi* is described for the forms noted by Groves (1997) as *M. "henekeni"* from the Gatun Formation of Panama, the Angostura Formation of Ecuador, and Miocene strata in southwestern Colombia. A poorly preserved specimen from southern Baja California Sur, Mexico may also represent *M. woodringi*. *Muracypraea woodringi* is most similar to *M. isthmica* (Schilder, 1927) [= *Cypraea henekeni* Sowb. var. of

Brown & Pilsbry (1911:356-357, pl. 26, figs. 9-10)] also from the Gatun Formation, which has a broad, smooth rounded, poorly delimited dorsal gibbosity centrally positioned (Figs 23-24). These shells were illustrated by Woodring (1959: pl. 31, figs 6-10). The specimen illustrated by Brown & Pilsbry (1911: pl. 26, figs. 9-10) clearly has a single dorsal gibbosity. Unfortunately, the holotype is missing. Brown & Pilsbry (1911: 356) noted that the "aperture is like that

of Santo Domingo *C. henikeni* [sic], except that the teeth are more compressed and longer. In a specimen 42.5 mm. long there are 15 teeth on the inner, 19 on the outer lip." The length of the denticles seems variable, but on average *M. isthmica* has fewer denticles on both the inner and outer lips than *M. henikeni* or *M. hyaena*. Woodring (1959: pl. 32, figs. 1, 4, 6, 9) illustrated specimens that are considered true *M. woodringi*. The two Gatun Formation taxa cannot be separated by their dentition or fossula. Landau and Silva (2010) discussed the presence of the genus in the Venezuelan Pliocene assemblages and stressed the need for a full revision of the genus. This much needed revision is again outside the scope of this work, however, at least half a dozen different *Muracypraea* species may occur in the tropical American Neogene.

Etymology. Named for Wendell P. Woodring in recognition of his monumental work on the geology and palaeontology of the Panama Canal Zone region.

Geological and geographical distribution.

Upper Miocene: Angostura Formation, Ecuador; Gatun Formation, Panama.

Miocene (indeterminate): Nariño Dept., Colombia.

Subfamily LURIIINAE Schilder, 1932

Genus *Luria* Jousseume, 1884

Type species: *Cypraea lurida* Linnaeus, 1758, by original designation.

Discussion. Dolin (1991) synonymised the genera/subgenera *Tessellata* Jousseume, 1884 (type species *Cypraea tessellata* Swainson, 1822), *Basilitrona* Iredale, 1930 (type species *Cypraea isabella* Linnaeus, 1758) and *Fossacypraea* Schilder, 1939 (type species *Cypraea hieroglyphica* Schilder, 1923) with *Talparia* Troschel, 1863. Lorenz & Hubert (2000) considered "*Basilitrona*" and "*Tessellata*" as species groups within the genus *Luria* Jousseume, 1884. Dolin & Lozouet (2004) transferred the tropical American species included in *Talparia* by Dolin (1991) to *Luria* (*Tessellata*). Meyer's (2004) molecular data supports the systematic arrangement of Lorenz & Hubert (2000), on the basis of which López Soriano (2006) formally synonymised *Tessellata* with *Luria*. Shells in the genus *Luria* differ from those in *Talparia* in having blunt extremities, short and deep anterior and posterior canals, the anterior canal is straight as opposed to slightly off-set in *Talparia*, and the angulation is more prominent with the labral teeth developed at the angulation running into the aperture

but not onto the ventrum. In *Talparia* the angulation is developed and raised in the anterior portion but not in the mid and posterior portion with the teeth extending a short distance onto the ventrum. The character of the fossula; spoon-like, smooth or weakly ribbed, with denticles on the inner margin, is similar in both genera.

Luria cantaurana n. sp.

Text-figure 1; Figs. 37-44

Dimensions and type material. Holotype; NHMW 2010/0036/0002, length 56.0 mm (Figs 37-40); paratype 1 NHMW 2010/0036/0003, length, 42.0 mm (Figs 41-44); paratype 2 NHMW 2010/0036/0004, length, 38.5 mm.

Type locality. lower shell bed, 1 km southwest of Casa Cantaura, about 10 km west of Pueblo Nuevo, Falcón State, Venezuela (=locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

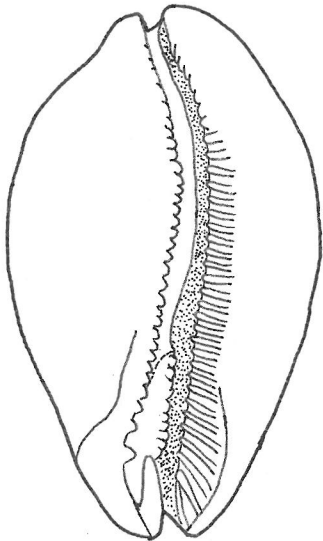
Type stratum. Cantaura Formation (early Miocene: Burdigalian).

Description. Shell medium-sized for genus, solid, subcylindrical, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, callused, the callus extending to between $\frac{2}{3}$ and $\frac{3}{4}$ height; ventrum flattened, especially in the anterior portion, slightly convex in profile in the posterior portion; aperture parasigmoidal, anterior third wider, dilated by hemispherical expansion on the labrum; siphonal canal deep, abaxially asymmetrical and abapically orthogonally truncated; exhalant channel deep, limited by parallel lips; 28-33 very short columellar teeth most clearly developed at the angulation, running a short distance into the aperture, but not onto the ventrum; angulation sharp and ridge-like in the anterior and mid-portions; terminal ridge weakly developed, merged into abapical edge; fossula well-delimited, spoon-like, concave, broad, smooth, fringed with weak denticles at its inner edge; columella peristome smooth; 24-29 labral teeth, anterior third of labral teeth stretched out on constricted, depressed, hemicircular area; remainder sharp, outer lip bevelled inwards, with teeth extending across the bevelled inner portion and a very short distance externally onto the labrum; no colour pattern preserved, under UV light some axially elongated blotches seen in two specimens, but no clear pattern.

Shell Formula. 45.5 (58.0 – 45.7) 20: 24

specimen	collection number	length	Width	Height	LT	CT
holotype (Figs 37-40)	NHMW 2010/0036/0002	56.0	33.3	25.6	29	33
paratype 1 (Figs 41-44)	NHMW 2010/0036/0003	42.0	23.8	18.9	24	29
paratype 2	NHMW 2010/0036/0004	38.5	22.1	17.9	24	28

Table 3. Dimensions and number of teeth; *Luria cantaurana* n. sp.



Text-figure 1. *Luria cantaurana* n. sp. Holotype NHMW 2010/0036/0002 (NMMW coll.; ex. BL coll.), length 56.0 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Luria cantaurana* n. sp. is by far the largest *Luria* species of the Cantaure Formation. As can be seen from the shell formulae, it differs from *L. fossula* (shell formula; 43.0 (60.4 – 48.8) 22: 16) in having significantly fewer columellar teeth, whereas *L. dominicensis* (shell formula; 39.5 (59.4 – 48.1) 30: 25) has a similar number of columellar teeth, but a far greater number of labral teeth. The early Miocene *L. dockeryi* from the Chipola Formation of Florida cannot be separated from *L. dominicensis* on the basis of the shell formula (see below).

Dolin (1991) synonymised *Cypraea fossula* Ingram, 1947 with *Cypraea dominicensis* Gabb, 1873. However, *Cypraea fossula* belongs within the genus *Trona* (see below). *Luria dominicensis* (LT 36, CT 29, Pilsbry, 1922; shell formula 39.5 (58.7 – 48.1) 30: 24), from an unknown locality in the Dominican Republic). The species from the early Miocene Chipola Formation of Florida originally identified as *Luria dominicensis* by Dolin (1991) was renamed

Luria (Tessellata) dockeryi Dolin & Lozouet, 2004. *Luria dockeryi* has numerous short teeth (LT 36, CT 29, Dolin, 1991; shell formula 39.5 (59.4 – 48.1) 30: 25). The shell formula is identical to that of the holotype of *Luria dominicensis*. Unfortunately the holotype (ANSP 3003) illustrated by Pilsbry (1922) cannot be located. Dolin & Lozouet (2004) renamed the Chipola species without mentioning how it differed from the Dominican taxon. There is little to distinguish the two, from the scant material available, and they may be synonyms.

Jousseamea joossi Schilder, 1939 (p. 23, fig. 23) was synonymised with *Luria dominicensis* by Dolin (1991). The holotype is an internal cast from the Miocene of Trinidad representing an indeterminate *Luria* sp., and it should be considered *nomen dubium*.

Etymology. Named for the Cantaure Formation.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

Luria isabellaprimitiva n. sp.

Text-figure 2; Figs 45-53

1965 *Cypraea* aff. *isabella* Linné – Jung, p. 501, pl. 67, figs 7-8.

Dimensions and type material. Holotype; NHMW 2010/0036/0005, length 27.7 mm (Figs 45-49); paratype 1 NHMW 2010/0036/0006, length, 26.6 mm (Figs 50-53); paratype 2 NHMW 2010/0036/0007, length, 26.4 mm.

Other material. 4 specimens BL coll.

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

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

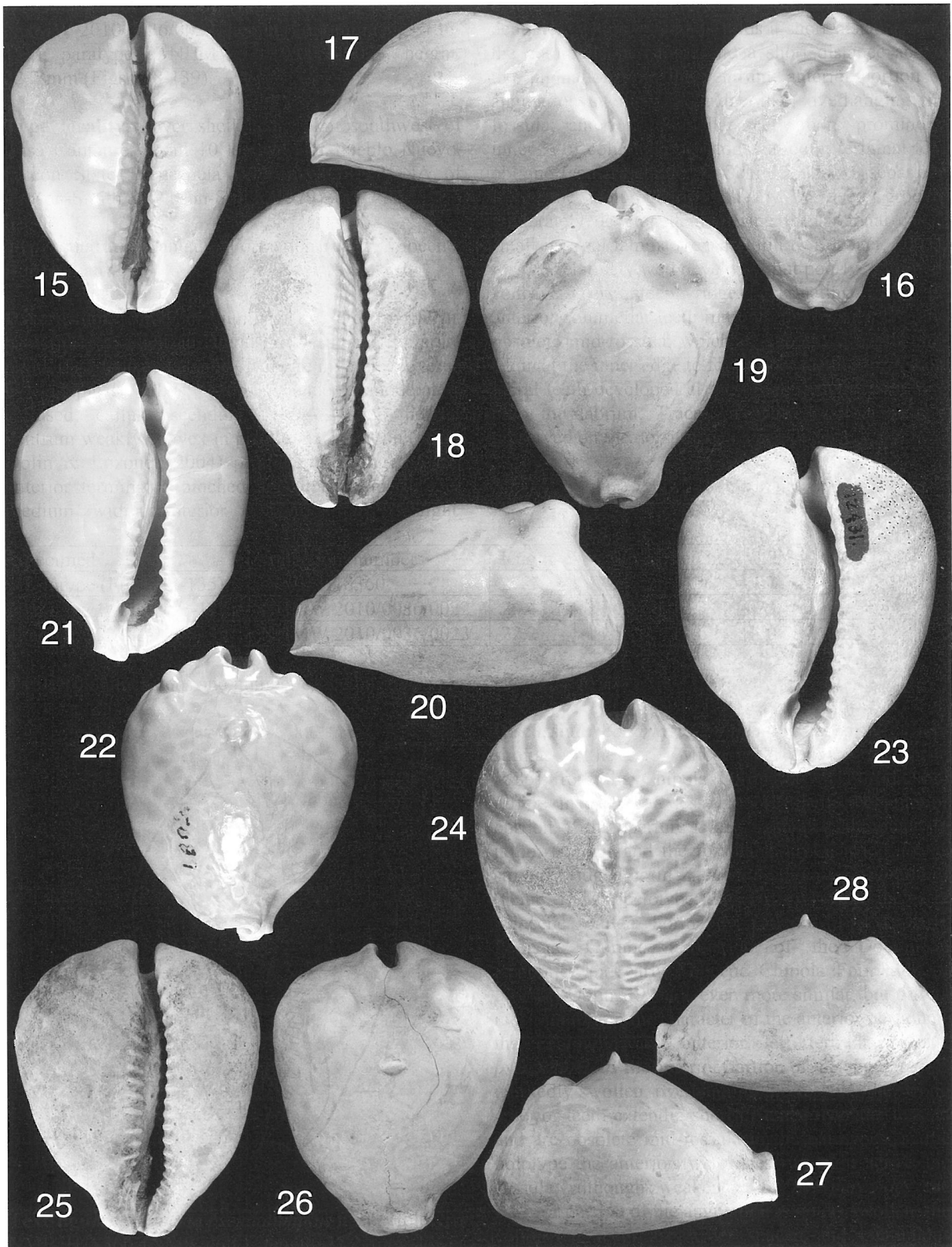
Figures 15-28

15-17. *Muracypraea henekeni* (G. B. Sowerby I, 1850) NHMW 2010/0036/0027 (NMMW; ex. BL coll.), length 53.6 mm. TU1219, lower Gurabo Formation, early Pliocene, Gurabo River, Dominican Republic;

18-20. *Muracypraea henekeni* (G. B. Sowerby I, 1850) NHMW 2010/0036/0028 (NMMW; ex. BL coll.), length 51.7 mm. TU1219, lower Gurabo Formation, early Pliocene, Gurabo River, Dominican Republic;

21-22. *Muracypraea woodringi* n. sp. Paratype 1 ANSP 315087, length 42.1 mm. Lower Gatun Formation (middle Miocene), Cativa, Colón Province, Panama (photo Lindsey Groves); **23-24.** *Muracypraea woodringi* n. sp. Holotype LACMIP 12431, length 42.1 mm. Angostura Formation (upper Miocene), Loc. LACMIP 16943 [=

TU 1507], just east of Río Verde, approximately 30 km east of Río Esmeraldas Esmeraldas Province, Ecuador (photo Lindsey Groves); **25-28.** *Muracypraea woodringi* n. sp. Paratype 3 NHMW 2010/0036/0001 (NMMW; ex. BL coll.), length 43.4 mm. Lower Gatun Formation (middle Miocene), Loc TU 961, roadcuts both sides of Boyd-Roosevelt Highway, just east of Cativa (= Woodring locality no. 138e), Colón Province, Panama.



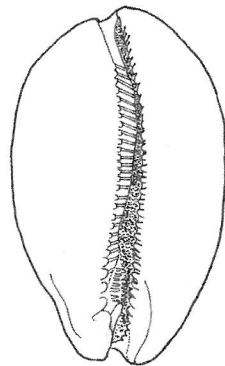
Description. Shell small for genus, solid, subcylindrical, slightly posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, callused, the callus extending to $\frac{1}{3}$ height; ventrum flattened, very slightly convex in profile at the extremities; aperture straight, weakly curved to the left in the posterior portion, anteriorly somewhat dilated by hemispherical expansion on the labrum; siphonal canal deep and narrow, abaxially asymmetrical and abapically orthogonally truncated; exhalant channel deep and narrow, limited by parallel lips; 25-30 very short columellar teeth running deep into the aperture from the angulation across the columellar peristome, but not onto the ventrum;

angulation relatively sharp; terminal ridge weakly developed, merged into abapical edge; fossula well-delimited from the columellar peristome by an oblique ridge, spoon-like, concave, strongly ridged, ridges ending as denticles at its inner edge; columella peristome very steep, ridged; 20-25 very short, sharp, labral teeth, abapically teeth not stretched out onto constricted, depressed, hemicircular area; teeth extending across inner portion of lip, but not externally onto the labrum; colour pattern indicating preserved spots on margins and rings on the dorsum (Fig. 49).

Shell Formula. 25.8 (64.7 – 51.6) 27: 25

Specimen	collection number	Length	Width	height	LT	CT
holotype (Figs 45-49)	NHMW 2010/0036/0005	27.7	17.0	14.2	30	24
paratype 1 (Figs 50-53)	NHMW 2010/0036/0006	26.6	16.9	13.4	28	25
paratype 2	NHMW 2010/0036/0007	26.4	17.2	14.1	24	27
BL coll. 4		28.8	17.6	14.2	29	25
BL coll. 5		27.9	17.2	12.8	26	25
BL coll. 6		26.3	15.9	13.1	28	#
BL coll. 7		22.1	15.0	11.4	23	#

Table 4. Dimensions and number of teeth; *Luria isabellaprimtiva* n. sp.

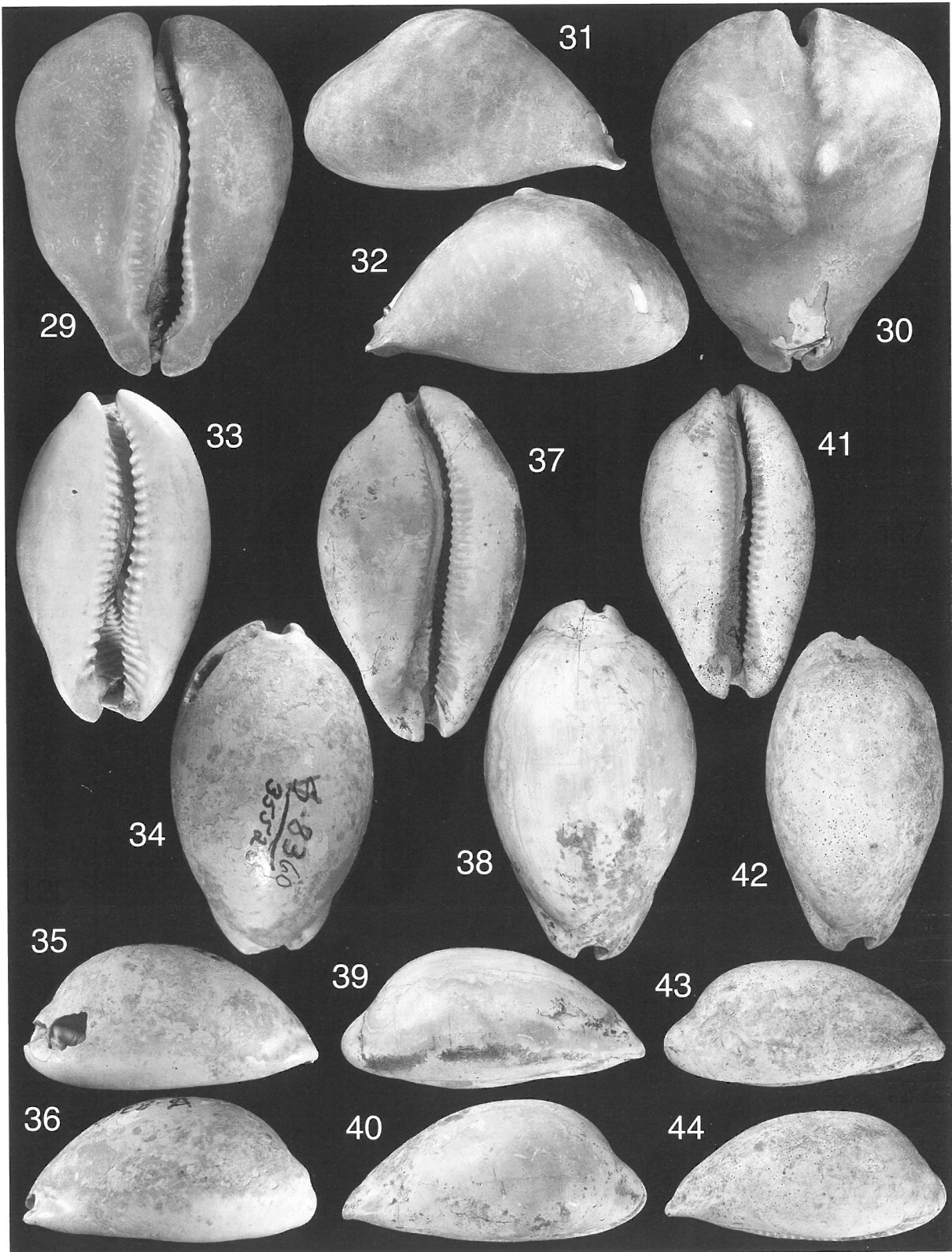


Text-figure 2. *Luria isabellaprimtiva* n. sp. Holotype NHMW 2010/0036/0005 (NMMW coll.; ex. BL coll.), length 27.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Luria isabellaprimtiva* n. sp. differs from its Cantaure Formation congener *L. cantaurana* n. sp. in having a smaller, more subcylindrical shell, with shorter extremities, and a smaller, deeper fossula. The colour pattern is somewhat unusual in consisting of circles, similar to that seen in the Recent *Arestorides argus* (Linnaeus, 1758). This is not a colour pattern present in any living or fossil species of *Luria*. The ocellated spots are not very clear and only visible on part of the holotype, and not on any of the paratypes. If this pattern were found on more specimens placement within the genus *Arestorides* Iredale, 1930 might be supported, although there is no record so far of this genus in the American Neogene to Recent faunas.

Figures 29-44

29-32. *Muracypraea grahami* (Ingram, 1947) NHMW 2010/0036/0029 (NMMW; ex. BL coll.), length 63.2 mm. Araya Formation, Cubagua Group, early Pliocene, Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela; **33-36.** *Trona trinitatensis* (Mansfield, 1925). UCMP 35536, holotype of *Cypraea fossula* Ingram, 1947. length 43.0 mm. 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **37-40.** *Luria cantaurana* n. sp. Holotype NHMW 2010/0036/0002 (NMMW; ex. BL coll.), length 56.0 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **41-44.** *Luria cantaurana* n. sp. Paratype 1 NHMW 2010/0036/0003 (NMMW; ex. BL coll.), length 42.0 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.



In the character of its subcylindrical shape and very short extremities Jung (1965) was correct to suggest that *L. isabellaprimtiva* belonged within the *L. isabella*-group. This is represented in the tropical American fossil assemblages by *L. patrespatriae* (Maury, 1917) (holotype; Fig. 146), which is found in the Lower Pliocene Gurabo Formation of the Dominican Republic. Schilder (1939) recorded *L. patrespatriae* in the Cantaure Formation. Pilsbry (1922) synonymised this taxon with the living *L. isabella* (Linnaeus, 1758), which today is widespread in the Indo-Pacific (Lorenz & Hubert, 2000). Ingram (1947) reaffirmed the synonymy whilst Woodring (1928) considered it a subspecies of *L. isabella*.

We have compared specimens of *L. patrespatriae* from the early Pliocene Gurabo Formation of the Dominican Republic with specimens *L. isabella* from the Red Sea (BL coll.). Unfortunately, the Dominican shells are fragile, including the holotype, and in almost all our specimens the columella is pushed inwards and the teeth are uncountable. We have one undamaged specimen in which the apertural characters are well preserved (Figs 54-57). The shell formula for *L. patrespatriae* [32.4 (54.0 – 44.0) 32: 29] is almost identical to that of *L. isabella* [35 (52.9 – 44.0) 34: 29]. One specimen from the Dominican Republic has the colour pattern preserved, which shows the same orange coloured tips seen in Recent *L. isabella*, but no black striping. On ventral view the columella is slightly more sinuous in *L. patrespatriae* and the terminals, especially the posterior terminal, is slightly more produced. The relationship between these species within the *L. isabella* group is unclear, we therefore consider them distinct at full species level. *Luria isabella* has a long geologic history in the Indo-Pacific, first recorded from the early Miocene of Fiji (Ladd, 1977) as *Cypraea (Talparia) isabella lekalekana* Ladd, 1934. This taxon was synonymised with *L. isabella* by Lorenz & Hubert (2000).

This species group is represented today in the tropical American Pacific by *Luria isabellamexicana* (Stearns, 1893), which differs from *L. isabella* in having a more pyriform, less subcylindrical shell shape, fewer teeth on both inner and outer lips, more protracted terminals and a somewhat different colouration [shell formula for *L. isabellamexicana* from Île de Clipperton; ZMA coll. unnumbered lot; 39.7 (54.4 – 46.6) 29: 27]. There are also radular differences (Burgess, 1985, Lorenz, 2002).

It seems, therefore, that during the Pliocene *L. patrespatriae* was present in the Caribbean portion of the Neogene Gatunian Province and *L. isabella* in the Indo-Pacific. Following the closure of the Central American isthmus, the *L. isabella*-group disappeared from the Caribbean, and its populations in the Pacific became fragmented into a questionable number of Indo-Pacific species/subspecies with restricted geographic distributions (see Lorenz & Hubert, 2000; Lorenz, 2002) and *L. isabellamexicana* restricted to the tropical American Pacific, which is unquestionably a valid taxon. Interestingly, *L. isabellamexicana* is present and common in the Lower Pleistocene Moin Formation of Costa Rica (BL collection). At this time connections between the Pacific and Caribbean, albeit intermittent, still existed and is an example of a paciphile species (see Landau et al., 2009). The *L. isabella*-group has not so far been found in the neighbouring northern Atlantic Caloosahatchian Province.

The early Miocene shells from the Cantaure Formation were synonymised with *L. patrespatriae* by Schilder (1939). However, the two populations are different; the Cantaure shells are never as cylindrical or elongated as those of *L. isabella*, and the teeth are far less numerous and stronger than in *L. isabella* (see shell formulae above). The Cantaure Formation shells are closer in shape to those of *L. isabellamexicana*, but differ in having less protracted terminals and again fewer columellar and labral teeth. We therefore consider the Cantaure shells a distinct species *L. isabellaprimtiva* n. sp.

The genus *Luria* has also been recorded from the mid-Atlantic middle Miocene Madeira Archipelago (Lorenz & Groh, 1998). The shell of *Luria santoensis* Lorenz & Groh, 1998 is not unlike that of *L. isabellaprimtiva* in general shape, but with relatively fewer columellar teeth, a wider aperture and smooth fossula. Indeed, in the character of the fossula *L. isabellaprimtiva* does not conform well within the genus, which is characterised by shells with a smooth fossula, or almost so.

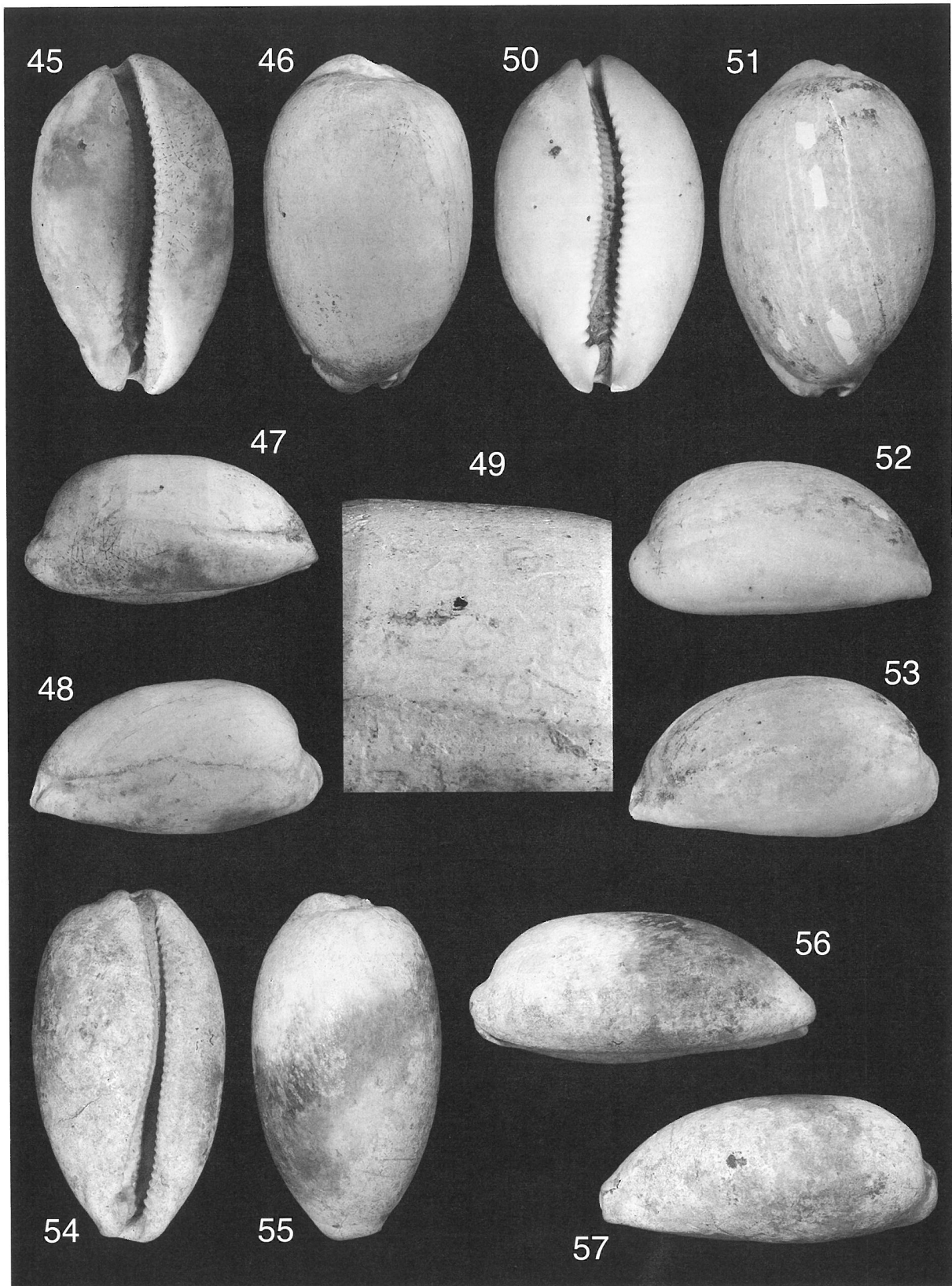
Etymology. The name indicates an early member of the *L. isabella* species-group.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

Figures 45-57

45-49. *Luria isabellaprimtiva* n. sp. Holotype NHMW 2010/0036/0005 (NMMW; ex. BL coll.), length 27.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **50-53.** *Luria isabellaprimtiva* n. sp. Paratype 1 NHMW 2010/0036/0006 (NMMW; ex. BL coll.), length 26.6 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **54-57.** *Luria patrespatriae* (Maury, 1917) NHMW 2010/0036/0030 (NMMW; ex. BL coll.), length 30.0 mm. TU1215, lower Gurabo Formation, early Pliocene, Gurabo River, Dominican Republic.



Genus *Trona* Jousseume, 1884

Type species: *Cypraea stercoraria* Linnaeus, 1758, by original designation.

Discussion. The genera *Trona* and *Macrocypraea* Schilder, 1930, traditionally considered to be closely related and within the Cypraeinae (Lorenz & Hubert, 2000) were shown by Meyer (2004) to belong to different subfamilies; *Trona* within the Luriinae and *Macrocypraea* within the Cypraeinae. The shell characteristics of the two genera are quite different. *Macrocypraea* has a rather light shell, as opposed to the very heavy shell of *Trona*. The shell of *Macrocypraea* is elongate rather than globose, they rarely have a marginal callus as opposed to the heavy callus seen in most *Trona* species, the base is far less flattened than in *Trona*, the apertures are wide with spiny extremities, not seen in *Trona*, and the shape of the anterior expansion of the aperture is quite different. The fossula in *Macrocypraea* is not as large or spoon-shaped, nor as strongly sculptured as in *Trona* and the terminal ridge is much more prominent in *Macrocypraea*.

The genus *Trona* was previously represented by a single subspecies in the Western Hemisphere. Dolin (1991) described *Trona leporina calhounensis* from the Chipola Formation of Florida based on two specimens. *Trona* is also a characteristic component within the European Miocene cypraeid fauna. *Trona leporina* (Lamarck, 1810) from contemporary late early Miocene (Burdigalian) deposits in France (Moulin de Cabannes, St Paul-les-Dax, Landes, France; BL coll.) differs from *T. leporina calhounensis* in having a less basally flattened shell, a thicker marginal callus and thicker anterior channel callus, a more rounded inner lip, a poorly developed basal angulation with narrow adapical denticles, fossula sculptured with alternate interrupted ridges and rows of pustules, more rounded outer lip, and shorter adapical denticles. Specimens from the early Burdigalian of Le Peloua, France (BL coll.), seem slightly different, more ovate with rows of very small

pustules on the fossula. Dolin (1991) commented on these small differences in fossular sculpture between populations and postulated these may be an expression of ecophenotypic variation or reproductive isolation and opted to name the Chipola Formation shells *T. leporina calhounensis* a subspecies of the European taxon without implying a close phylogenetic link between the two populations. This approach is confusing and in view of the taxonomic problems still to be resolved within the European populations and the presence of additional species in the Caribbean Neogene we consider this taxon distinct at full specific rank. *Trona trinitatis* (Mansfield, 1925) is found in the early and middle Miocene of Venezuela, Trinidad, and Carriacou, Grenadine Islands, Lesser Antilles. *Trona trinitatis* differs from *T. ingrami* and *T. calhounensis* in having a smaller, more elongated shell, in having much less sinuous and narrower aperture, and somewhat more crowded teeth on both labral and columellar sides (see below under *Trona trinitatis*)

***Trona ingrami* n. sp.**

Text-figure 3; Figs 58-70

Dimensions and type material. Holotype; NMB H18402, height 53.1 mm (Figs 58-60); paratype 1 NHMW 2010/0036/0008, height, 48.2 mm (Figs 61-64); paratype 2 NHMW 2010/0036/0009, height, 47.2 mm (Figs 65-68); paratype 3 NHMW 2010/0036/0010, height, 49.7 mm (Figs 69-70).

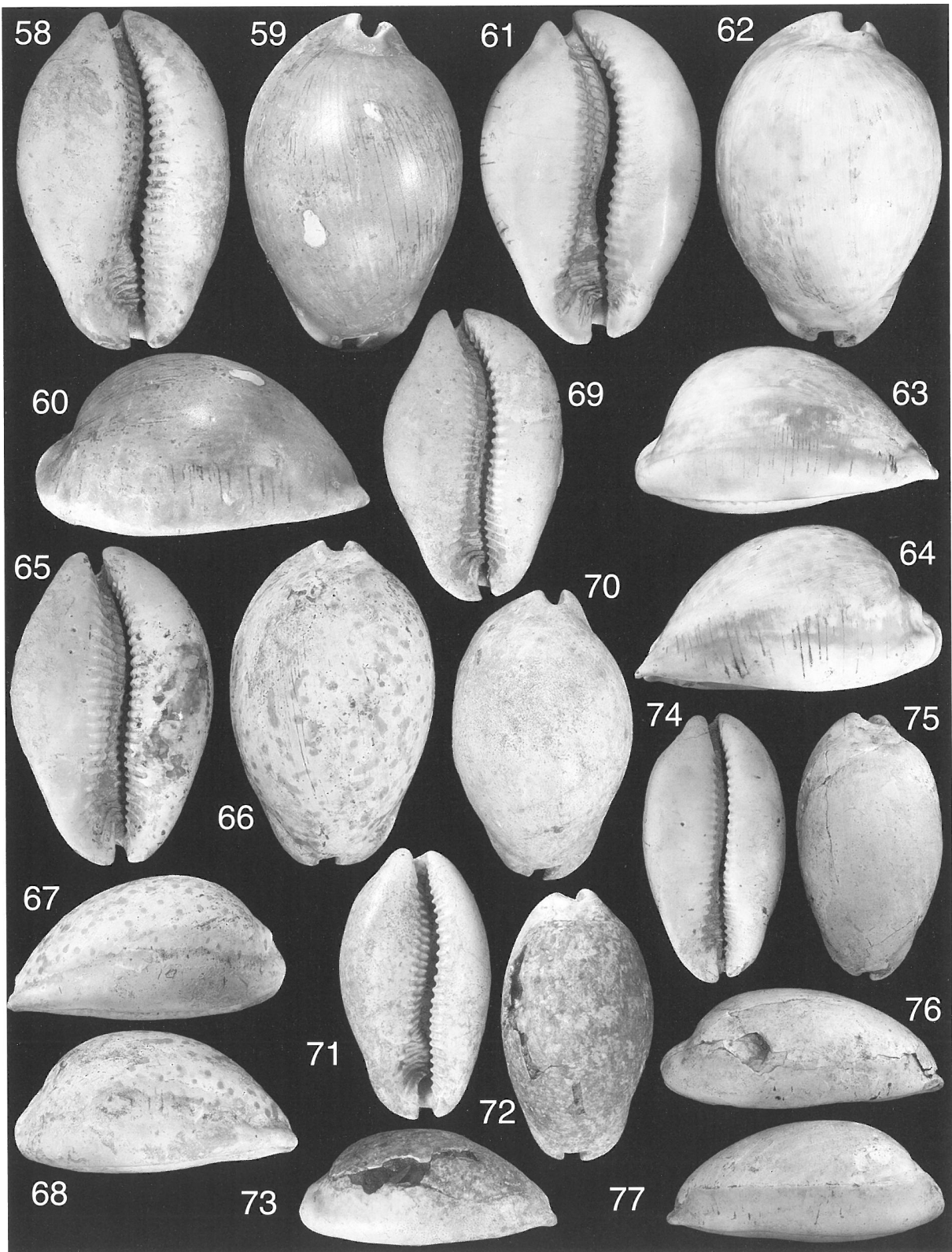
Other material. 3 specimens NMB coll.; 18 specimens BL coll.; 1 specimen DFB, no. 6578.

Type locality. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela (=locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Figures 58-77

58-60. *Trona ingrami* n. sp. Holotype NMB H18402 (NMB coll.), length 53.1 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **61-64.** *Trona ingrami* n. sp. Paratype 1 NHMW 2010/0036/0008 (NMMW; ex. BL coll. no. 9), length 48.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **65-68.** *Trona ingrami* n. sp. Paratype 2 NHMW 2010/0036/0009 (NMMW; ex. BL coll. no. 10), length 47.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **69-70.** *Trona ingrami* n. sp. Paratype 3 NHMW 2010/0036/0010 (NMMW; ex. BL coll. no. 15), length 49.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **71-73.** *Trona trinitatis* (Mansfield, 1925) NMB H18403 (NMB coll.), length 33.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **74-77.** *Trona trinitatis* (Mansfield, 1925) NHMW 2010/0036/0011 (NMMW; ex. BL coll.), length 33.0 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.



Description. Shell medium-sized for genus, solid, subcylindrical to rotund, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire weakly projecting, covered by adapical callus; sides rounded, weakly callused; ventrum flattened, slightly convex in profile; aperture parasigmoidal, anterior third dilated by hemispherical expansion; siphonal canal deep, abaxially asymmetrical and abapically orthogonally truncated; exhalant channel deeper, limited by parallel lips; four or five anterior columellar teeth, most anterior thinnest, strengthening adapically; other numerous inner teeth parallel, extending deep within the aperture, bituberculate, about 6 mm in length in the columellar area, abrupt, extending a short distance over the angulation of the basal and columellar planes

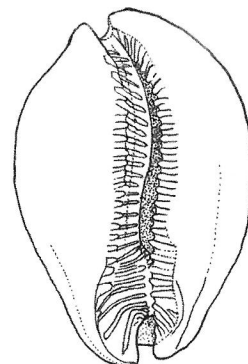
onto the ventrum where they are slightly coarser; terminal ridge obsolete, merged into abapical edge, fringed with denticles from fossula on inner margin; fossula deep, concave, spoon-like, covered by narrow ridges, sometimes interrupted, joining fossular denticulation to anterior columellar teeth; 22-30 labral teeth, anterior third of labral teeth stretched out on constricted, depressed, hemicircular area; remainder heavier, outer lip bevelled inwards, with teeth extending across the bevelled inner portion, 3-4 mm in length; ventral and dorsal zones spotted, marginal callus lighter coloured, under UV light spire blotch present.

Shell Formula. 48.7 (63.0 – 50.1) 20: 18

Specimen	collection number	length	width	height	LT	CT
holotype (Figs 58-60)	NMB H18402	53.1	34.5	29	23	20
NMB lot 17516		35.3	22.4	18.2	22	17
NMB lot 17516		35.7	22	18.7	#	#
NMB lot 17516		43	26.8	#	23	26
paratype 1 (Figs 61-64)	NHMW 2010/0036/0008	48.2	32.6	25.7	23	23
paratype 2 (Figs 65-68)	NHMW 2010/0036/0009	47.2	29.7	23.2	23	25
paratype 3 (Figs 69-70)	NHMW 2010/0036/0010	49.7	30.4	26.3	25	24
BL coll. 1		57.9	36.7	28.3	26	23
BL coll. 2		56.1	34.6	26.9	27	21
BL coll. 3		55.8	35.4	28.2	27	24
BL coll. 4		58.9	36.3	29.7	24	23
BL coll. 5		57.4	39.4	31.1	23	20
BL coll. 6		55.9	34.3	27.6	23	21
BL coll. 7		55.6	36	29.7	26	23
BL coll. 8		60.2	37.5	29.4	30	28
BL coll. 11		48.7	30.9	25.1	22	25
BL coll. 12		47.8	31.8	24	23	20
BL coll. 13		45.1	30.6	25.3	23	20
BL coll. 14		44.2	28.2	22	24	22
BL coll. 16		44.8	27.2	20.9	25	26
BL coll. 17		51.5	31.4	25.2	25	23
BL coll. 18		49.5	32.8	25.3	24	21
BL coll. 19		40.1	24.3	18.9	25	22
BL coll. 20		37.1	22	17.3	24	26
BL coll. subadult 21		39.5	25.1	18.8	25	24
DFB coll.	no. 6578	55.1	38.4	30.4	24	17

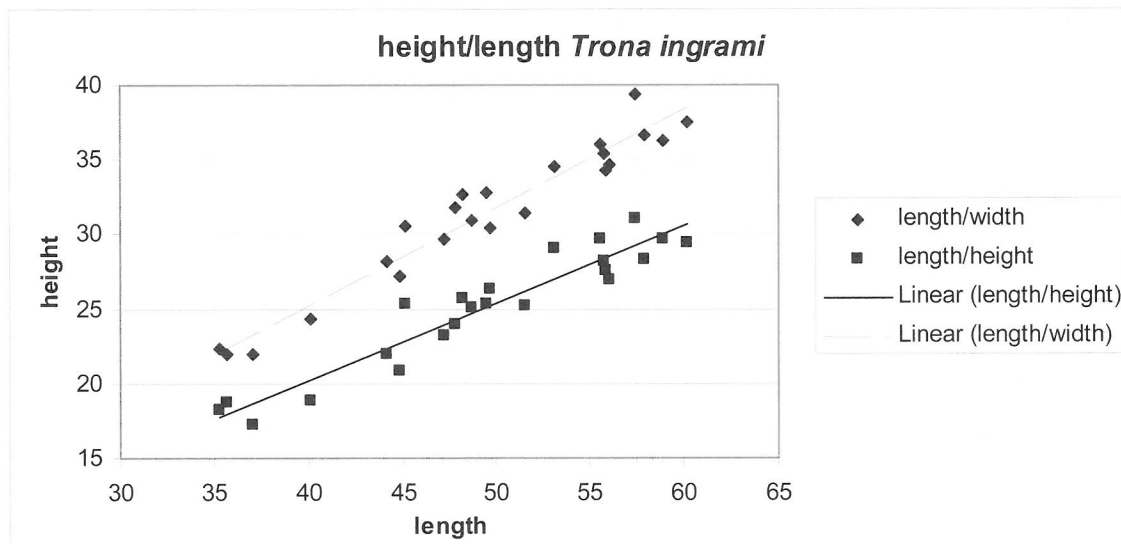
Table 5. Dimensions and number of teeth; *Trona ingrami* n. sp.

Text-figure 3 (opposite). *Trona ingrami* n. sp. Paratype 1 NHMW 2010/0036/0008 (NMMW coll.; ex. BL coll. no. 9), length 48.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela



Discussion. *Trona ingrami* n. sp. has a rather variable shell shape. The larger specimens tend to be more rotund and broad (Figs 58-64), whereas the smaller specimens have a more elongated aspect and a less sinuous aperture, but intermediate specimens also occur (see Text-figure 4). The single living representative of the genus *Trona stercoraria*

(Linnaeus, 1758) distributed today along the coast of tropical West Africa also has a variable shell shape (Lorenz & Hubert, 2000; pl. 11). Dolin (1991) hints at sexual dimorphism in the species without elaborating, however, in Cypraeidae as well as in Ovulidae male shells tend to be smaller than females.



Text-figure 4. Height/ Length; *Trona ingrami* n. sp.

Dolin (1991) describes a light-weight shell with uncalled margins, whereas the *Cantaure* shells are very solid with a weakly developed marginal callus. His description and figure clearly show the labral teeth to be restricted to the inside of the aperture, whereas the teeth in *T. ingrami* extend a short distance over the basal plane onto the ventrum where they become somewhat coarser. On the labral side the teeth abapically are described as short, whereas in *T. ingrami* the outer lip is bevelled inwards with the teeth extending across the bevelled inner portion. The fossula in *T. ingrami* has few elongated denticles which tend to be continuous and rarely tubercles as compared to the specimens of *T. calhounensis* figured by Dolin (1991) (fig. 22a) which has the fossula crowded with interrupted ridges and elongated tubercles.

Etymology. Named for William Marcus Ingram in recognition of his pioneering work on Caribbean Neogene cypraeids.

Geological and geographical distribution.

Lower Miocene: *Cantaure* Formation, Venezuela.

Trona trinitatis (Mansfield, 1925)

Text-figure 5; Figs 71-77

- 1925 *Cypraea trinitatis* Mansfield, p. 49, pl. 8, fig. 10.
 1939 *Trona (Macrocypraea) trinitatis* Mansfield, 1925 – Schilder (partim?), p. 30, fig. 32.
 1947 *Cypraea fossula* Ingram, p. 4 (128), pl. 1 (8), fig. 3.
 1971 *Macrocypraea cervinetta fossula* Ingram, 1947 – Schilder & Schilder, p. 33.
 1971 *Macrocypraea trinitatis* Mansfield, 1925 – Schilder & Schilder (partim?), p. 164.
 ?1971 *Macrocypraea* aff. *zebra* (Linné) – Jung, p. 181, pl. 8, figs 1-3.
 1993 *Macrocypraea trinitatis* (Mansfield, 1925) – Lorenz & Herbert, pl. 121, fig. 3.
 2000 *Macrocypraea trinitatis* (Mansfield, 1925) – Lorenz & Herbert, pl. 121, fig. 3.
 2004 *Luria (Tessellata) fossula* (Ingram, 1947) – Dolin & Lozouet, p. 20.

Material. 1 specimen NMB H18403, NMB coll. (Figs 71-73); 1 specimen NHMW 2010/0036/0011, NHMW coll. (ex. BL coll.) (Figs 74-77). Holotype of *C. fossula*; UCMP 35536.

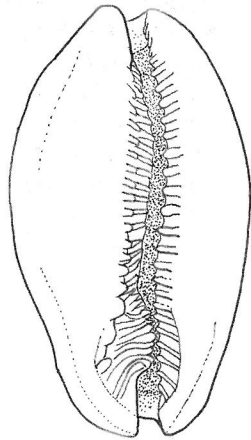
Description. Shell small for genus, solid, subcylindrical, weakly posteriorly swollen, spire projecting, covered by adapical callus; sides angular to rounded, callused; ventrum almost flat; aperture weakly parasigmoidal, anterior third dilated by hemispherical expansion; siphonal canal deep, abaxially asymmetrical and abapically orthogonally truncated; exhalant channel deeper, limited by parallel lips; four anterior columellar teeth; other numerous inner teeth parallel, extending deep within the aperture, bituberculate, abrupt, not extending over the angulation onto the ventrum; terminal ridge obsolete,

merged into abapical edge, fringed with denticles from fossula on inner margin; fossula deep, concave, spoon-like, covered by narrow ridges, sometimes interrupted, joining fossular denticulation to anterior columellar teeth; 22-27 labral teeth, anterior third of labral teeth stretched out on constricted, depressed, hemicircular area; remainder heavier, outer lip bevelled inwards, with teeth extending across the bevelled inner portion; no colour pattern preserved, under UV light spots present on marginal callus.

Shell Formula. 33.2 (55.8 – 44.0) 22: 20

specimen	collection number	length	Width	height	LT	CT
Figs 71-73	NMB H18403	33.3	18.8	15.3	22	21
Figs 74-77	NHMW 2010/0036/0011	33.0	18.3	13.9	27	22
Figs 33-36	UCMP 35536	43.0	26.0	21.0	27	19

Table 6. Dimensions and number of teeth; *Trona trinitatensis* n. sp.

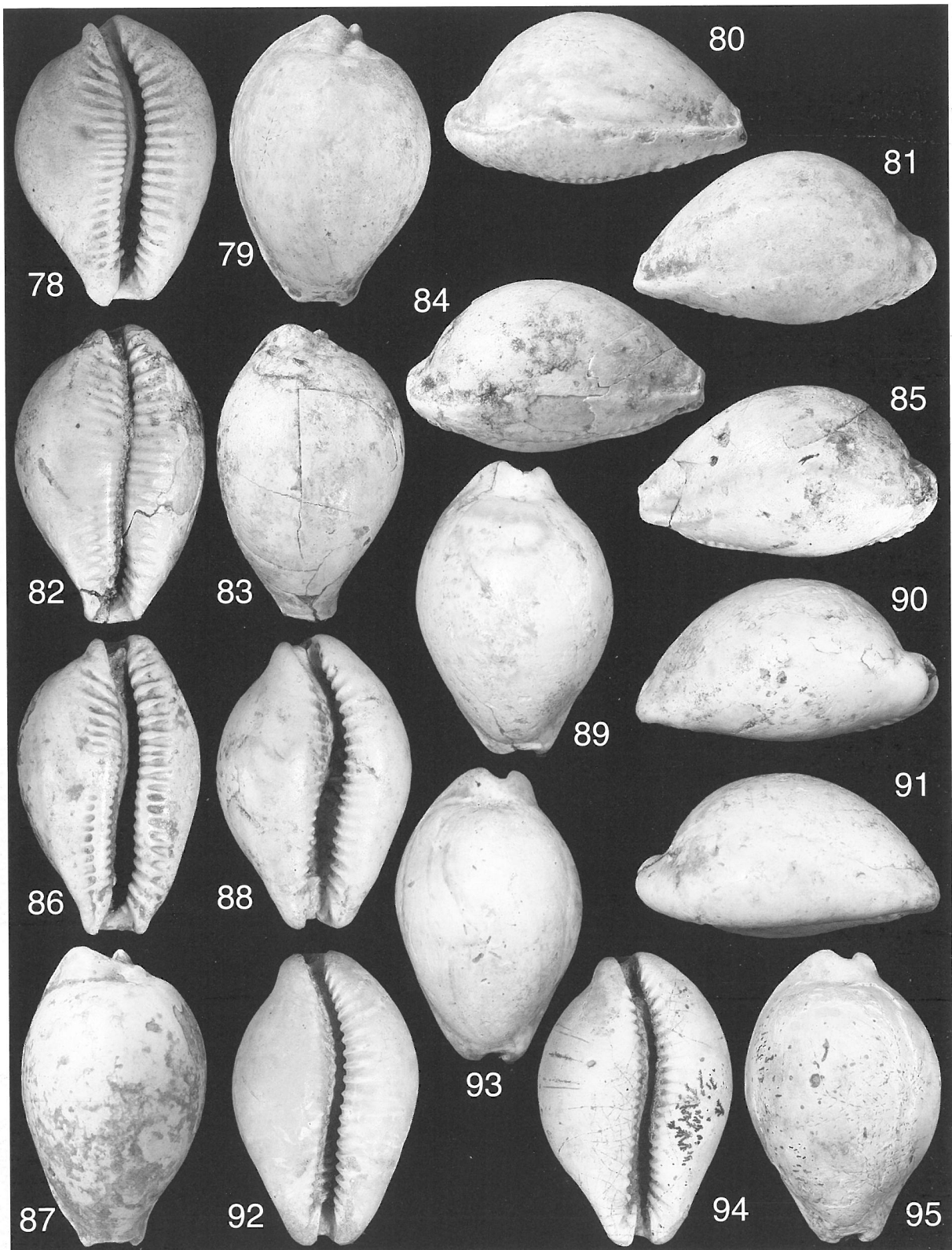


Text-figure 5. *Trona trinitatensis* (Mansfield, 1925) NMB H18403 (NMB coll.), length 33.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. The holotype of *Trona trinitatensis* (Mansfield, 1925) is an internal mould collected from the Guaracara Limestone Member of the late early to early middle Miocene Tamana Formation of Trinidad and is difficult to identify with any certainty. According to Jung (1971), all the other specimens from Trinidad recorded by Schilder (1939) are also internal moulds. Schilder (1939) also identified specimens from the middle Miocene Grand Bay Formation of Carriacou as *Trona (Macrocypraea) trinitatensis*. According to Jung (1971) it was unlikely that the Carriacou shells were conspecific with those from Trinidad and that the larger Carriacou shells were closer to the living *Macrocypraea zebra*. According to Jung they differed 'morphologically' from the shells from *T. trinitatensis* from Trinidad, but he did not specify what these differences were.

Figures 78-95

78-81. *Propustularia longidentata* n. sp. Holotype NHMW 2010/0036/0012 (NMMW; ex. BL coll.), length 15.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **82-85.** *Propustularia longidentata* n. sp. Paratype 1 NHMW 2010/0036/0013 (NMMW; ex. BL coll.), length 14.5 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **86-87.** *Propustularia longidentata* n. sp. Paratype 2 NHMW 2010/0036/0014 (NMMW; ex. BL coll.), length 12.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **88-91.** *Propustularia paraguanensis* n. sp. Holotype NHMW 2010/0036/0015 (NMMW; ex. BL coll.), length 17.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **92-93.** *Propustularia paraguanensis* n. sp. Paratype 1 NHMW 2010/0036/0016 (NMMW; ex. BL coll.), length 17.8 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **94-95.** *Propustularia paraguanensis* n. sp. Paratype 2 NHMW 2010/0036/0017 (NMMW; ex. BL coll.), length 16.1 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.



Although ascribed by various authors to the genus *Macrocypraea*, *Cypraea trinitatensis* belongs within the genus *Trona* (see generic discussion above). Unfortunately the fossula is covered by matrix in the Schilder (1939) and Jung (1965) specimen from Carriacou, however, the shape of the dilated hemispherical expansion on anterior third of the aperture and the absence of spines on the siphonal canal indicate they are also *Trona*. *Trona trinitatensis* differs from *T. ingrami* by its smaller shell (at least in Cantaure, although the Trinidad and Carriacou shells are larger), more elongated cylindrical shape, much less sinuous and narrower aperture, and somewhat more crowded teeth on both labral and columellar sides. The re-illustration of the holotype of *Cypraea fossula* Ingram, 1947 (Figs 33-36) clearly show it to belong within the genus *Trona* and not *Luria* as suggested by Dolin (1991) and Dolin & Lozouet (2004). The shell is slightly broader than our other two specimens of *T. trinitatensis*, but less inflated than *T. ingrami*, also the columellar density is slightly less than typical *T. trinitatensis*, but probably within the variability of this species. We therefore consider *C. fossula* a junior subjective synonym of *T. trinitatensis*.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela; Tamana Formation, Trinidad.

Middle Miocene: Grand Bay Formation of Carriacou.

Subfamily **EROSARIINAE** Schilder, 1924

Genus ***Propustularia*** Schilder, 1927

Type species: *Cypraea surinamensis* Perry, 1811, by original designation.

Discussion. Schilder (1939) and Schilder & Schilder (1971) assigned a small group of tropical American cypraeids to the genus *Pustularia* Swainson, 1840 (ie., *P. mejasensis*, *P. americana*, *P. caribaea* all Schilder, 1939, and *C. gurabonis* Ingram, 1939). However, their shells do not conform to the generic characteristics of the Recent Indo-Pacific *Pustularia* species. The fossil taxa all have shells with far less pronounced rostration of the extremities which do not carry the spines so characteristic of the Recent species. Lorenz (1999) also observed that the posterior extremity composed of a callus-accumulation and two marginal spines formed by the posterior terminal ridges, seen in the Recent species, is not found in any of the Caribbean fossil species assigned by Schilder & Schilder (1971) to *Pustularia*. The fossula is narrow and smooth in all Recent *Pustularia* species, whereas it is denticulate in the Neogene Caribbean species. Most of this group of species share more shell characteristics with the genus *Propustularia* Schilder, 1927, which is today represented by a single taxon *Propustularia surinamensis* (Perry, 1811) found in the Caribbean. *Propustularia* is characterised by pyriform-inflated shells, with somewhat rostrate extremities, a weakly

produced spire and fine teeth. *Pustularia americana* (holotype; Figs 147-150), on the other hand, shows the shell characteristics of the genus *Erosaria* Schilder, 1924. Lorenz (1999) and Lorenz & Hubert (2000) synonymised *Propustularia* with *Proadusta* Sacco 1894, and suggested *Pustularia* might have evolved from *Proadusta*-like forms. *Propustularia longidentata* n. sp. (herein) also shares some shell characteristics with the deep water Indo-Pacific and southeast African genus *Nesiocypraea* Azuma & Kurohara, 1967, particularly the species *N. lisetae* Kilburn, 1972. These characteristics include globular shape, distinctly curved aperture in the posterior third, denticulate fossula, and a callus bridge, in *Nesiocypraea* connecting both, labral and columellar teeth. In *Nesiocypraea*, however, the teeth are short and do not extend onto the ventrum or outer lip. Meyer's (2004) molecular work on cypraeids placed the clade consisting of *Propustularia*, *Nesiocypraea* and *Ipsa* as basal to all cowries.

***Propustularia longidentata* n. sp.**

Text-figure 6; Figs 78-87

Dimensions and type material. Holotype; NHMW 2010/0036/0012, height 15.2 mm (Figs 78-81); paratype 1; NHMW 2010/0036/0013, height 14.5 mm (Figs 82-85); paratype 2; NHMW 2010/0036/0014, height 12.2 mm (Figs 86-87).

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

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Description. Shell small for genus, fragile, globular, posteriorly swollen, spire weakly projecting, covered by adapical callus, extremities moderately projecting; sides rounded, moderately callused, lip marginal callus sharply delimited and slightly raised; ventrum flattened, convex in profile; aperture narrow, edges parallel, conspicuously curved to the left in the posterior third; siphonal canal moderately long, externally barely margined; exhalant channel moderately produced, strongly bent adaxially, externally barely margined; terminal ridge well-developed, tooth-like at its inner extremity; fossula narrow, hardly delimited from the rest of the columella, bearing narrow elongated extensions of the labral teeth; teeth on both sides well developed, 21-22 columellar teeth, anterior columellar teeth fused at the angulation, forming an elevated vertical callus bridge, mid-height the teeth weaken or subobsolete, again strongly developed in the posterior portion, teeth extending onto the ventrum especially in the anterior and posterior portions, inwards the teeth hardly extend onto the columella, columella smooth; 20-23 labral

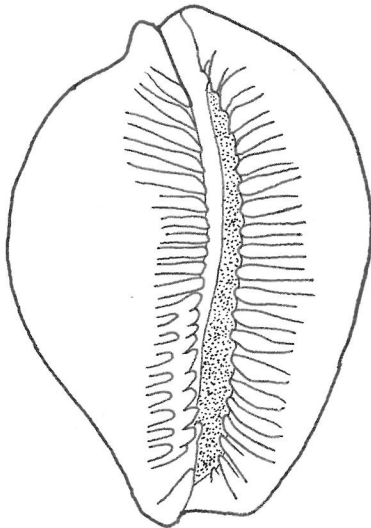
teeth extending just over half of the labral width. No dorsal sulcus, pustules or pitting present. Colour pattern not preserved, under UV light suggestion of

large spots on the dorsum.

Shell Formula. 14.0 (66.4 – 55.7) 26: 26

Specimen	collection number	length	width	height	LT	CT
Holotype (Figs 78-81)	NHMW 2010/0036/0012	15.2	10.8	8.7	20	22
Paratype 1 (Figs 82-85)	NHMW 2010/0036/0013	14.5	9.4 (distorted)	8.3	23	21
Paratype 2 (Figs 86-87)	NHMW 2010/0036/0014	12.2	7.6	6.5	20	21

Table 7. Dimensions and number of teeth; *Propustularia longidentata* n. sp.



Text-figure 6. *Propustularia longidentata* n. sp. Holotype NHMW 2010/0036/0012 (NMMW coll.; ex. BL coll.), length 15.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. Several Neogene Caribbean forms have been described. *Pustularia mejasensis* Schilder, 1939 from Trinidad is represented by a single internal mould. However, because it is impossible to determine what taxon this represents it should be considered *nomen dubium*. *Pustularia americana* Schilder, 1939 from the early Miocene of Cuba has a more solid shell, with less produced, extremities, wider siphonal channel, fewer columellar and labral teeth, which on the columellar side do not extend onto the ventrum and pustules on the dorsum adjacent to the labral marginal callus, and is better placed in the genus *Erosaria*. *Propustularia caribaea* (Schilder, 1939) (holotype; Figs 151-154) from the early Middle Miocene Grand Bay Formation of Carriacou is extremely similar to *P. longidentata* [shell formula 13.5 (64 – 50) 28: 23], but no bridge is developed between the anterior columellar teeth.

Etymology. named for the long teeth, seen especially in the holotype.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela

Propustularia paraganensis n. sp. Text-figure 7; Figs 88-95

Dimensions and type material. Holotype; NHMW 2010/0036/0015, height 17.2 mm (Figs 88-91); paratype 1; NHMW 2010/0036/0016, height 17.8 mm (Figs 92-93); paratype 2; NHMW 2010/0036/0017, height 16.1 mm (Figs 94-95).

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

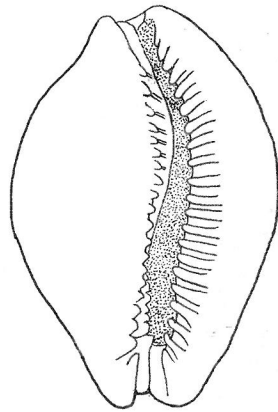
Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Description. Shell small for genus, solid, globular, weakly swollen posteriorly, spire involute, covered by adapical callus, extremities weakly projecting; sides rounded, moderately callused, lip marginal callus sharply delimited and slightly thickened; ventrum flattened, weakly convex in profile; aperture narrow, edges parallel, conspicuously curved to the left in the posterior third; siphonal canal moderately long, externally barely margined; exhalant channel moderately produced, strongly bent adaxially, externally barely margined; terminal ridge well-developed, tooth-like at its inner extremity; fossula narrow, weakly delimited from the rest of the columella, labral teeth extend across the fossula as elevated ridges and form teeth again at the inner edge of the fossula; 19-20 short columellar teeth, not extending past the angulation onto the ventrum; 20-22 labral teeth extending less than half of the labral width. No dorsal sulcus, pustules or pitting present. Colour pattern not preserved, under UV light suggestion large irregular spots on the posterior portion of the dorsum, the spots much wider than the distance between them.

Shell Formula. 17.0 (67.1 – 51.8) 25: 22

specimen	collection number	length	width	height	LT	CT
Holotype (Figs 88-91)	NHMW 2010/0036/0015	17.2	11.7	9.1	20	19
Paratype 1 (Figs 92-93)	NHMW 2010/0036/0016	17.8	11.5	9.0	22	20
Paratype 2 (Figs 94-95)	NHMW 2010/0036/0017	16.1	11.0	8.3	22	20

Table 8. Dimensions and number of teeth; *Propustularia paraguayensis* n. sp.



Text-figure 7. *Propustularia paraguayensis* n. sp. Holotype NHMW 2010/0036/0015 (NMMW coll.; ex. BL coll.), length 17.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Propustularia paraguayensis* n. sp. differs from *P. longidentata* n. sp. in its less posteriorly swollen shell shape, more strongly sculptured fossula and shorter teeth on both labral and columellar sides. There is no trace of the callus bridge so prominently developed in *P. longidentata*. *Propustularia bartschi* (Ingram, 1939) (holotype; Figs 155-156) from the early Pleistocene of Costa Rica is most similar to paratype 2 of *P. paraguayensis* (Figs 94-95) in overall shape but the widest portion of the shell is more posterior in *P. bartschi*. The dentition seems to be the same in all of the figured type specimens but the aperture is most similar to paratype 1 (Figs 92-93). In the lateral views *P. bartschi* is much more tapered towards the anterior than *P. paraguayensis*.

Etymology. named after the Paraguaná Peninsula, location of the Cantaure deposits.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela

Subfamily **ZONARIINAE** Schilder, 1932

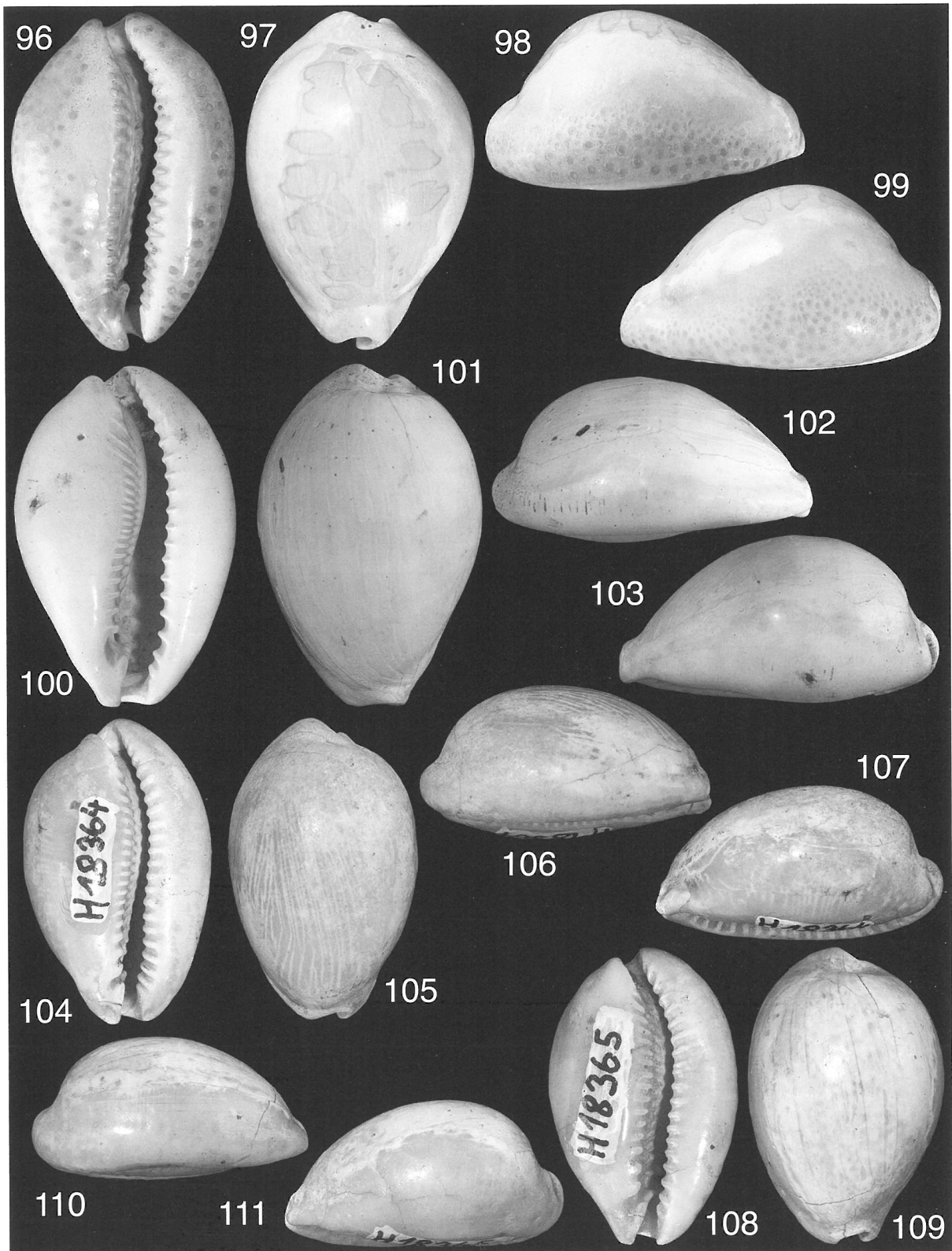
Genus *Zonaria* Jousseaume, 1884

Type species: *Cypraea zonaria* Gmelin, 1791, by original designation.

Zonaria is traditionally assigned to the subfamily Erroneinae Schilder, 1927. However, based on mitochondrial molecular data Meyer (2004) demonstrated that the genus belongs within a separate group; Zonariinae Schilder, 1932. *Zonaria* is characterized by species with oval to pyriform, small to moderate-sized shells, the teeth are fine and widely spaced, the fossula is much reduced, the columellar area is smooth, the callus collar surrounding the siphonal canal is well-developed and the colour pattern consists of marginal spotting and a dorsum with irregular or interrupted mottled banding. *Zonaria* has been known in Europe since the early Miocene and is distributed today in the Mediterranean and West Africa (Lorenz & Hubert, 2000). Groves (1997) reported the genus in the Pacific tropical American Neogene assemblages with the description of *Z. pittorum* Groves, 1997 (holotype; Figs 157-158) from the early Pliocene Esmeraldas beds of the Onzole Formation of Ecuador. Later Groves & Nielsen (2003) described *Z. frassinetti* (Figs 159-160) from the early late Miocene, Tortonian of Chile which is here reassigned to the genus *Pseudozonaria*. There is an additional species of *Zonaria* from the Neogene of the Dominican Republic, which awaits publication (BL coll.; unpublished data). The genus has also been recorded from the middle Miocene of the Madeira Archipelago (Lorenz & Groh, 1998).

Figures 96-111

96-99. *Zonaria pingata* n. sp. Holotype NHMW 2010/0036/0018 (NMMW; ex. BL coll.), length 45.8 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **100-103.** *Pseudozonaria praeaequinocialis* n. sp. Holotype NHMW 2010/0036/0019 (NMMW; ex. BL coll.), length 32.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **104-107.** *Pseudozonaria primarobertsii* n. sp. Holotype NMB H18364 (NMB coll.), length 22.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **108-111.** *Pseudozonaria primarobertsii* n. sp. Paratype 1 NMB H18365 (NMB coll.), length 21.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.



The “*Pseudozonaria*” group, which is characterised by its elongate-oval shells with well developed, often sharp cut teeth, densely spotted margins, freckled dorsum and prominent extremities, is closely related. Groves (1997) considered *Pseudozonaria* a subgenus of *Zonaria*; Lorenz & Hubert (2000) used “*Pseudozonaria*” as an informal group within *Zonaria*; Landau & Silva (2010) considered the two separate at full generic rank. *Pseudozonaria* has a fossil record in the tropical American Neogene and is today restricted to the Pacific side of its original wider distribution (i.e. western side of Central America), and is an example of a Paciphile taxon (Woodring, 1966; Landau et al., 2009).

***Zonaria pingata* n. sp.**
Text-figure 8; Figs 96-99

Dimensions and type material. Holotype NHMW 2010/0036/0018, height 45.8 mm (Figs 96-99).

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

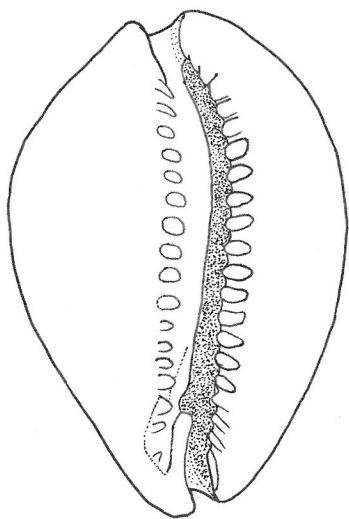
Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Description. Shell medium-sized for genus, solid, ovate-pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire weakly projecting, covered by adapical callus; sides rounded, strongly callused; callus ascending above mid-height, its highest point at the dorsal hump; ventrum flattened, slightly convex in profile; aperture weakly sigmoidal; siphonal canal long, abaxially asymmetrical and recurved, externally surrounded by thick callus collar; exhalant channel weakly bent adaxially, externally surrounded by thick adapical callus; terminal ridge well-developed, tooth-like at its inner extremity; fossula smooth, marked by small depression; three anterior columellar teeth, most anterior thinnest, adapically 14 short, stout, parallel, well-spaced inner teeth, ending abruptly at the basal and columellar planes, not extending onto the ventrum nor the aperture; columella smooth; 20 heavy, regularly-spaced labral teeth; Ventral and marginal zones spotted, marginal callus lighter coloured, dorsum golden-brown with orange watermark-like stains placed in irregular bands.

Shell Formula. 45.8 (67.9 – 58.0) 17: 14

Specimen	collection number	length	width	height	LT	CT
Holotype (Figs 96-99)	NHMW 2010/0036/0018	45.8	31.1	26.1	20	17

Table 9. Dimensions and number of teeth; *Zonaria pingata* n. sp.



Text-figure 8. *Zonaria pingata* n. sp. Holotype NHMW 2010/0036/0018 (NHMW coll.; ex. BL coll.), length 45.8 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Zonaria pingata* n. sp. is described based on a single beautifully preserved specimen and is extremely rare in the Cantaure Formation. The

Cantaure Formation shell differs from the early Pliocene Esmeraldas Formation *Z. pittorum* in being more globose rather than pyriform in shape, the posterior portion of the aperture is more twisted to the left in *Z. pittorum* and the teeth are longer on both sides in *Z. pittorum*. The shell formula of the two is very similar (*Z. pittorum*: 40.1 (68.0 – 52.1) 17: 15).

Zonaria pingata is most similar to *Z. zonaria* (Gmelin, 1791), the type-species of the genus, but has a more ovate shell, the inner lip teeth are shorter and stouter and the siphonal canal is more recurved. The Recent Mediterranean and West African *Zonaria pyrum* (Gmelin, 1791) is similar in shape, but the anterior third of the aperture is expanded, the inner lip teeth are again longer and the margins are uniform orange without spots. The Mediterranean Pliocene *Zonaria porcellus* (Brocchi, 1814) is easily separated by its more elongate-pyriform shape and much finer teeth, which on the inner lip become obsolete adapically.

Etymology. From Latin for stained *Zonaria*.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

***Zonaria pseudotumulus* n. sp.**
Text-figure 9; Figs 132-139

Dimensions and type material. Holotype; NMB H18360, height 27.2 mm (Figs 132-135); paratype 1 NHMW 2010/0036/0022, height, 26.4 mm (Figs 136-137); paratype 2 NHMW 2010/0036/0023, height, 22.2 mm (Figs 138-139).

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

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

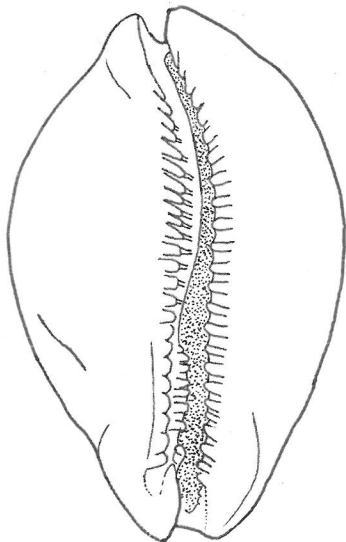
Description. Shell medium-sized, solid, pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, moderately callused, callus ascending to 1/3-1/2 shell height; ventrum weakly convex in profile; margination (sensu Dolin & Lozouet, 2004) prominent, giving the left anterior terminal a pinched appearance; aperture of medium width, anterior portion almost straight,

posteriorly curving to the left, anterior portion very slightly wider; siphonal canal relatively long, narrow, abaxially asymmetrical; exhalant channel moderately produced, limited by parallel lips; columella denticulate along entire length, bearing 22-23 short denticles, which extend as folds a short distance onto the columella peristome and a short distance across the angulation onto the ventrum; anterior portion of angulation swollen and ridge like, overhanging the fossula; anterior columellar teeth more prominent; inner 2/3 of columella peristome smooth; terminal fold oblique (sensu Schilder & Schilder, 1938), separated from the columellar teeth by a deep groove, moderately developed, bordering the siphonal canal, small internal lamina (sensu Dolin & Lozouet, 2004); fossula relatively well developed but poorly delimited, concave, very steep, ridges originating from the anterior columellar teeth run onto the fossula, become obsolete mid-fossula, which is smooth, strengthening again at the inner edge to form inner teeth; 20-27 short labral teeth developed at the lip edge, hardly running onto the labrum. Traces of spotted colour pattern preserved on the dorsum, enhanced under UV light.

Shell Formula. 25.3 (65.1 – 50.1) 23: 22

specimen	collection number	length	Width	height	LT	CT
Holotype (Figs 132-135)	NMB H18360	27.2	17.5	14.1	27	23
Paratype 1 (Figs 136-137)	NHMW 2010/0036/0022	26.4	17.4	12.3	23	22
Paratype 2 (Figs 138-139)	NHMW 2010/0036/0023	22.2	14.5	11.6	20	22

Table 10. Dimensions and number of teeth; *Zonaria pseudotumulus* n. sp.



Text-figure 9. *Zonaria pseudotumulus* n. sp. Holotype NMB H18360 (NMB coll.), length 27.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Zonaria pseudotumulus* n. sp. is closely similar to the early Miocene *Z. tumulus* (Heilprin, 1886) from the Chipola Formation of Florida, but differs in having a less globose shell, the anterior portion of the aperture is less expanded, the outer lip is not sinuous and the fossula is not as wide nor as strongly ridged as in *Z. tumulus*. *Zonaria spurcoides* (Gabb, 1873) (lectotype; Figs 161-164) from the early Miocene Baitoa Formation (Figs 140-143), early Pliocene Gurabo Formation of the Dominican Republic, and early Miocene Chipola Formation of Florida (Dolin, 1991) is even more similar, but differs most notably in the character of the anterior portion of the columella and anterior left terminal; in *Z. pseudotumulus* the anterior portion of the angulation is markedly swollen, overhanging the fossula, the strong anterior teeth extend a short distance over the fossula and are obsolete mid-fossula in the paratypes, in the holotype the anterior two ridges run right across the fossula, although weakened. In *Z. spurcoides* the anterior portion of the angulation is not as swollen, the columellar teeth are wider spaced and continuous across the fossula as narrow ridges joining the columellar teeth at the angulation with the teeth at the inner edge of the fossula. In *Z. pseudotumulus* the anterior left terminal has a pinched and somewhat

twisted appearance, constricted between the groove between the anterior terminal and first columellar tooth on the ventral side and the indented margination on the dorsum. This feature is not seen in *Z. spurcoides*. The fossula is also flatter in *Z. pseudotumulus*.

Etymology. Named reflecting similarity to *Cypraea tumulus* from the early Miocene Chipola Formation of Florida.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

Subfamily **PSEUDOZONARIINAE**

Genus *Pseudozonaria* Schilder, 1927.

Type species *Cypraea arabicula* Lamarck, 1810, original designation.

The “*Pseudozonaria*” group is characterised by its elongate-oval shells with well developed, often sharp cut teeth, densely spotted margins and freckled dorsum and prominent extremities. Today the group is represented by five tropical American Pacific species; *P. aequinotialis* (Schilder, 1931), *P. annettae* (Dall, 1909), *P. arabicula* (Lamarck, 1810), *P. nigropunctata* (Gray, 1828), and *P. robertsi* (Hidalgo, 1906) (Lorenz & Hubert, 2000; Meyer, 2003, 2004). Several fossil species belonging to *Zonaria* Jousseume, 1884 and *Pseudozonaria* Schilder, 1927 have been described from the Gatunian Neogene. *Zonaria* and *Pseudozonaria* are closely related groups, and not all cypraeid specialists are in agreement as to their rank or which species belong in which of the two groups. Groves (1997) considered *Pseudozonaria* a subgenus of *Zonaria*; Lorenz & Hubert (2000) use “*Pseudozonaria*” as an informal group within *Zonaria*, and Landau & Silva (2010) considered both valid genera.

López Soriano (2006) justified the separation of a new subfamily Pseudozonariinae from the Zonariinae Schilder, 1932 based on molecular data (Meyer, 2004), anatomical differences of the mantle and papillae, and some small differences in shell morphology. They also have distinct geographical distributions; Pseudozonariinae are tropical American, today restricted to the western side of Central

America; Zonariinae are known since the Miocene in Europe and Recent of West Africa (Lorenz & Hubert, 2000).

Pseudozonaria praeaequinotialis n. sp.

Text-figure 10; Figs 100-103

Dimensions and type material. Holotype; NHMW 2010/0036/0019, height 32.3 mm (Figs 100-103).

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

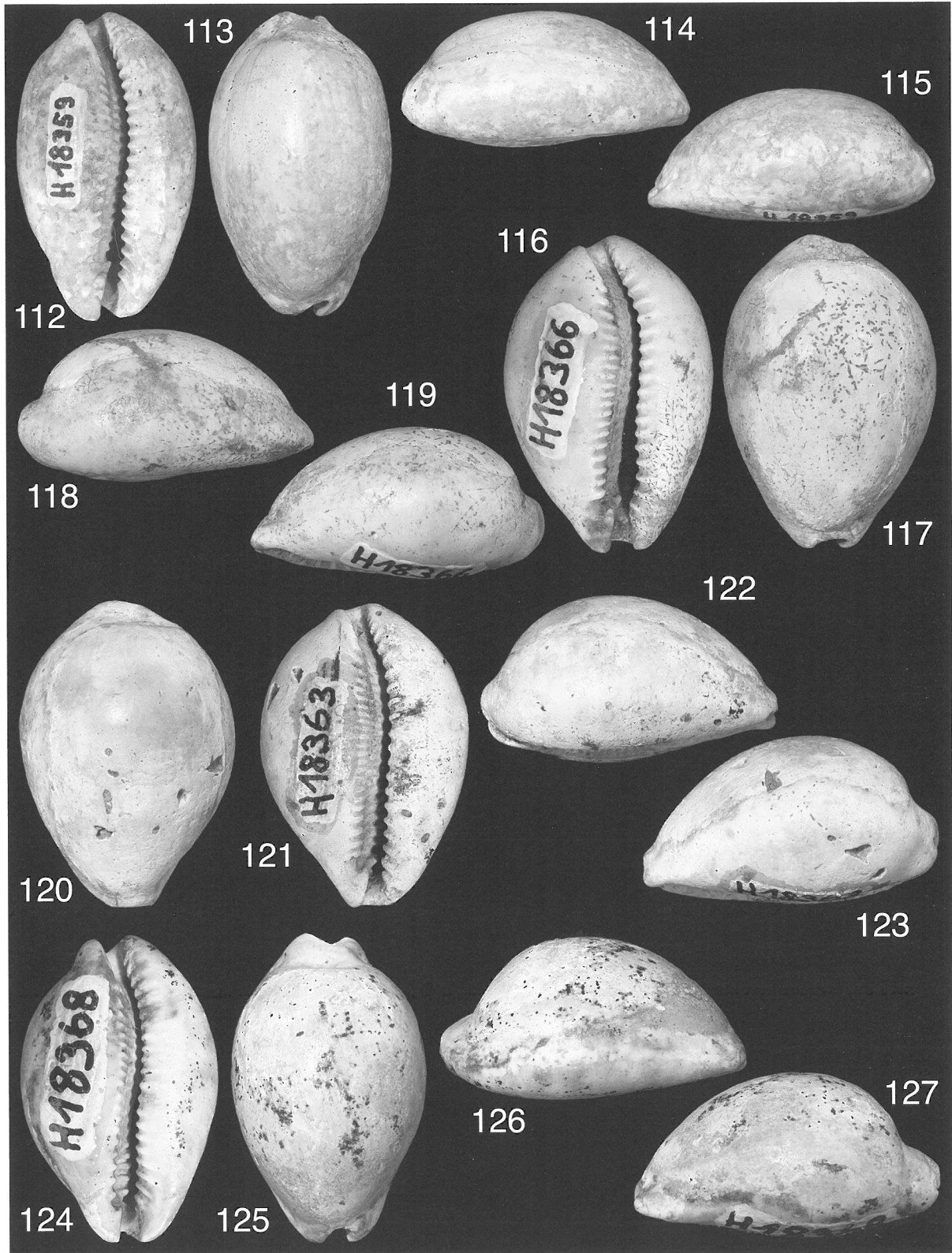
Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Description. Shell of medium size and thickness for genus, inflated pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire weakly projecting, covered by adapical callus; sides rounded, moderately callused; ventrum flattened, convex in profile; aperture relatively wide and straight, posteriorly curving to the left, anterior portion much wider; siphonal canal narrow, abaxially asymmetrical; exhalant channel hardly produced, limited by parallel lips; Columella denticulate along entire length, bearing 19 sharp, narrow denticles, which extend as folds onto the columella peristome within the aperture, but not onto the ventrum with the exception of the three adapical denticles, which extend a short distance over the angulation onto the ventrum; terminal fold marginal, bordering the siphonal canal, where it is strengthened and keel-like, separated from the columellar teeth by a deep groove; fossula small, weakly concave, very steep, poorly delimited from the rest of the columella, bearing ridges which do not extend to the smooth inner edge; 20 very short, sharp labral teeth, developed at the inner edge, but not extending onto the labrum; labrum moderately thickened in the medial portion. A suggestion of a spotted marginal colour pattern and dorsal banding is preserved, this pattern enhanced under UV light.

Shell Formula. 32.3 (65.9 – 51.3) 18: 18

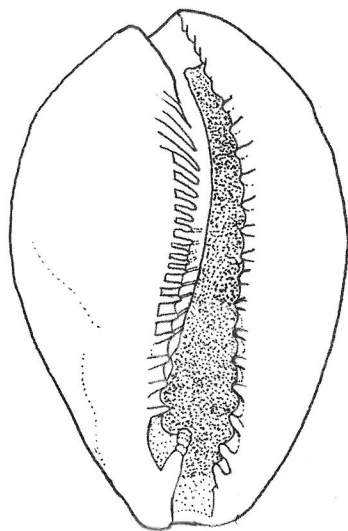
Figures 112-127

112-115. *Pseudozonaria primarobertsi* n. sp. Paratype 3 NMB H18359 (NMB coll.), length 28.9 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **116-119.** *Pseudozonaria primarobertsi* n. sp. Paratype 6 NMB H18366 (NMB coll.), length 24.8 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **120-123.** *Pseudozonaria primarobertsi* n. sp. Paratype 5 NMB H18363 (NMB coll.), length 25.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **124-127.** *Pseudozonaria falconensis* n. sp. Holotype NMB H18368 (NMB coll.), length 16.5 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, State Venezuela.



Specimen	collection number	length	width	height	LT	CT
Holotype (Figs 100-103)	NHMW 2010/0036/0019	32.3	21.3	16.6	20	19

Table 11. Dimensions and number of teeth; *Pseudozonaria praeaequinoctialis* n. sp.



Text-figure 10. *Pseudozonaria praeaequinoctialis* n. sp. Holotype NHMW 2010/0036/0019 (NHMW coll.; ex. BL coll.), length 32.3 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. *Pseudozonaria praeaequinoctialis* n. sp. is clearly the predecessor of the *Pseudozonaria annettae*-group now living in the tropical American Pacific. This group is characterised by their very short teeth and wide apertures. In the Recent faunas two species/subspecies are recognised, which we prefer to recognise at full species level, a northern form, *P. annettae* (Dall, 1909) found along the Pacific coast of Mexico, and a southern form *P. aequinoctialis* (Schilder, 1933) from Panama to Ecuador. The northern form is easily separated from *P. praeaequinoctialis* having a much more elongated-pyriform shell shape. The southern form differs from the northern form in having a heavier, broader shell with slightly coarser teeth, and therefore is closer to the fossil species. *Pseudozonaria praeaequinoctialis* differs from *P. aequinoctialis* in having an even broader shell (width/height 59.1 vs 65.9 in *P. praeaequinoctialis*) and in having considerably fewer columellar denticles (CT = 14 vs. 18 in *P. praeaequinoctialis*).

Zonaria frassinetti Groves & Nielsen, 2003 from the early late Miocene, Tortonian of Chile is here reassigned to the *Pseudozonaria annettae*-group characterised by its very wide aperture and widely spaced and sharp denticles. In *Pseudozonaria frassinetti* these features are exaggerated, so that it has

the widest aperture of any of the group and the least number of teeth, especially on the columellar side where they are obsolete on the posterior portion of the columella (shell formula for *Z. frassinetti*; 28.1 (62.2 – 44.5) 13: 4).

Etymology. Combination of before = ‘prae’ and equinoctial = ‘aequinoctialis’ [Latin].

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

***Pseudozonaria primarobertsi* n. sp.**

Text-figure 11; Figs 104-123

Dimensions and type material. Holotype; NMB H18364, length 22.7 mm (Figs 104-107); paratype 1 NMB H18365, length, 21.3 mm (Figs 108-111); paratype 2 NMB H18367, length, 24.7 mm; paratype 3 NMB H18359, length, 28.9 mm (Figs 112-115); paratype 4 NMB H18361, length, 24.4 mm; paratype 5 NMB H18363, length, 25.3 mm (Figs 120-123); paratype 6 NMB H18366, length, 24.8 mm (Figs 116-119).

Other material. 20 specimens BL coll.

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

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

Description. Shell small, solid, oval-depressed to cylindrical-pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, strongly to moderately callused, callus ascending to 1/3-1/2 shell height; ventrum flattened, very weakly convex at the extremities; aperture of medium width, parasigmoidal, posteriorly strongly curving to the left, anterior portion very slightly wider; siphonal canal narrow, abaxially asymmetrical; exhalant channel weakly produced, deep, limited by parallel lips; columella denticulate along entire length, bearing 16-22 coarse, elevated denticles, which extend as folds onto the columella peristome and a very short distance over the angulation onto the ventrum, anterior two columellar teeth larger and often fused or partially so; terminal fold strongly developed and elevated,

bordering the siphonal canal, where it is strengthened and keel-like with a prominent, elevated internal lamina (sensu Dolin & Lozouet, 2004), separated from the columellar teeth by a deep groove; fossula hardly developed and poorly delimited from the rest of the columella, very steep, bearing ridges which extend to the inner edge, ending in a denticle; 20-24 coarse labral teeth, outer lip bevelled inwards, with teeth

extending across the bevelled inner portion and a short distance onto the labrum. A suggestion of a fine, messy spotted marginal colour pattern is preserved in some specimen, enhanced under UV light.

Shell Formula. 'cylindrical-pyriform morphotype'; 23.0 (65.8 – 51.7) 22: 18

Specimen	collection number	length	width	height	LT	CT
holotype (Figs 104-107)	NMB H18364	22,7	15,3	11,7	20	16
paratype 1 (Figs 108-111)	NMB H18365	21,3	13,9	11,1	21	19
paratype 2	NMB H18367	24,7	15,8	12,6	21	18
paratype 3 (Figs 112-115)	NMB H18359	28,9	17,7	13,1	22	18
BL coll. 1		29,2	18,5	14,3	23	17
BL coll. 2		20,7	14,4	11,4	21	19
BL coll. 3		25,1	16,3	13,1	20	18
BL coll. 4		18,8	12,3	9,8	22	18
BL coll. 5		21,4	14,1	11,2	20	16
BL coll. 6		21,7	13,9	10,9	21	18
BL coll. 7		22,6	15,2	11,9	23	18
BL coll. 8		20,1	14,5	11,5	22	18
BL coll. 9		21,9	15,6	12,1	20	18
BL coll. 10		22,7	14,4	11,8	21	16
BL coll. 11		23,3	15,2	11,9	20	17

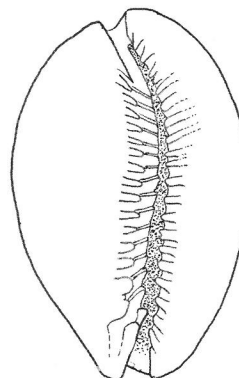
Table 12a. Dimensions and number of teeth; *Pseudozonaria primarobertsii* n. sp., 'cylindrical-pyriform morphotype'.

Shell Formula. 'oval-depressed morphotype'; 23.8 (71.1 – 54.0) 22: 20

Specimen	collection number	length	width	height	LT	CT
paratype 4	NMB H18361	24,4	18	13,4	23	20
paratype 5 (Figs 120-123)	NMB H18363	25,3	18	14,2	21	22
paratype 6 (Figs 116-119)	NMB H18366	24,8	17,1	12,6	22	20
BL coll. 1		27,3	20,7	15,2	22	21
BL coll. 2		23,1	16,3	11,7	24	21
BL coll. 3		22,2	15,3	11,4	22	20
BL coll. 4		22,9	16,6	12,1	20	21
BL coll. 5		24,8	17,3	14	23	19
BL coll. 6		27	18,8	14,4	20	18
BL coll. 7		23	15,9	12,5	22	18
BL coll. 8		19,8	14,3	10,8	21	18
BL coll. 9		21,4	14,8	12	20	22

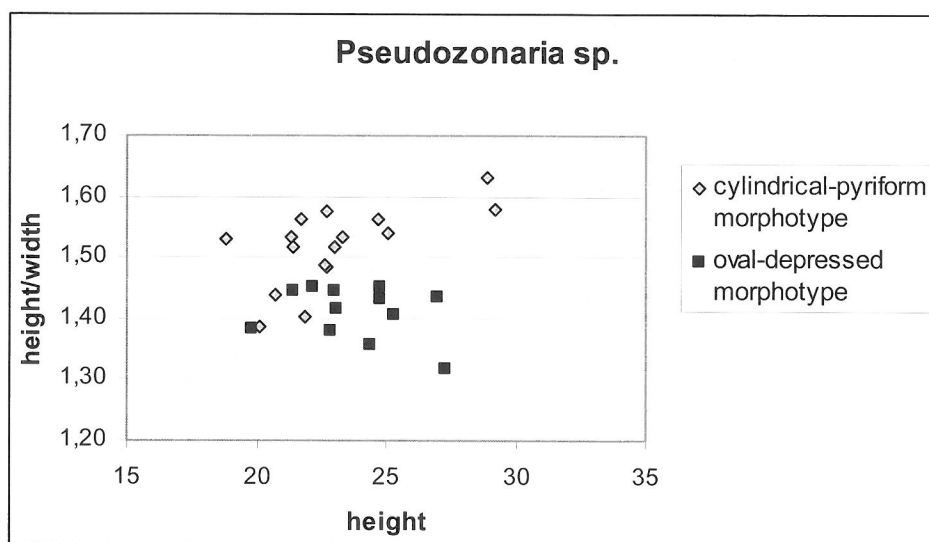
Table 12b. Dimensions and number of teeth; *Pseudozonaria primarobertsii* n. sp., 'oval-depressed morphotype'.

Text-figure 11 (opposite). *Pseudozonaria primarobertsii* n. sp.. Paratype 1 NMB H18365 (NMB coll.), length 21.3 mm. lower shell bed, 1 km southwest of Casa Cantare, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.



Discussion. *Pseudozonaria primaroberti* n. sp. is the most common cypraeid in the Cantare Formation. Two morphotypes occur; a 'cylindrical-pyriform morphotype' and an 'oval-depressed morphotype'. Apart from the difference in shell shape the 'oval-depressed morphotype' tends to have one or two more columellar teeth than the 'cylindrical-pyriform morphotype' and the teeth in general tend to be

somewhat less coarse and elevated in the 'oval-depressed morphotype', however, the character of the strong terminal ridge, very weakly developed fossula and ridged columellar peristome is the same in both morphotypes. Moreover, a fair number of specimens could not be clearly ascribed to one or other morphotypes. The differences seen in the two morphotypes could indicate sexual dimorphism.



Text-figure 12. Height against height/width; *Pseudozonaria primaroberti* n. sp.

Pseudozonaria primaroberti n. sp. is clearly closely similar in size, shape and character of the teeth to the Recent tropical American *P. robertsi* (Hidalgo, 1906). As seen in our fossil taxon, the development of the

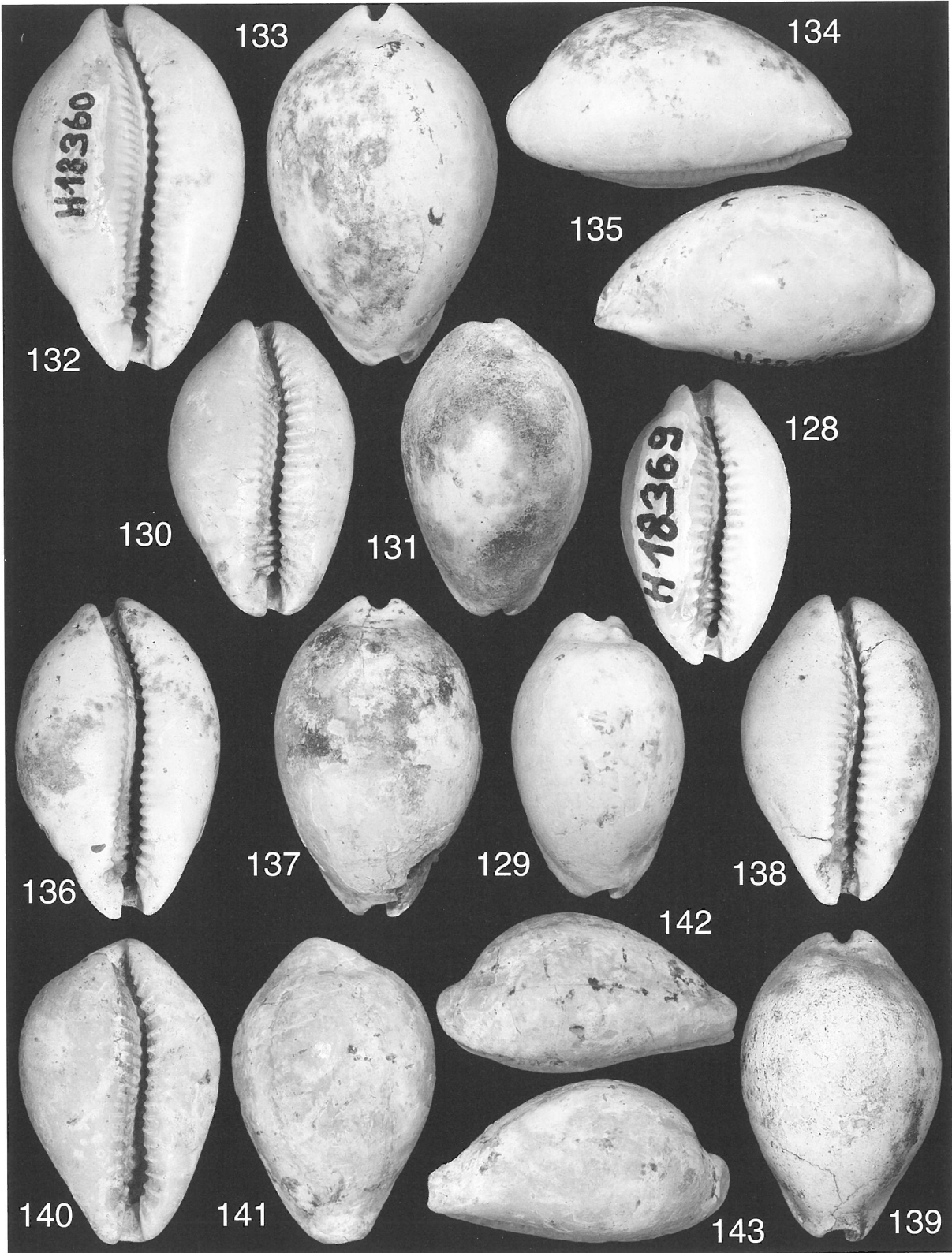
marginal callus in *P. robertsi* is also somewhat variable. The main difference between the two taxa is that the Recent species has fewer columellar teeth (CT = 12 vs 18-20 in *P. primaroberti*).

Figures 128-143

128-129. *Pseudozonaria falconensis* n. sp. Paratype 1 NMB H18369 (NMB coll.), length 14.4 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **130-131.** *Pseudozonaria falconensis* n. sp. Paratype 2 NHMW 2010/0036/0020 (NMMW; ex. BL coll.), length 16.7 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela; **132-135.** *Zonaria pseudotumulus* n. sp. Holotype NMB H18360 (NMB coll.), length 27.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela;

136-137. *Zonaria pseudotumulus* n. sp. Paratype 1 NHMW 2010/0036/0022 (NMMW; ex. BL coll.), length 26.4 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela. **138-139.** *Zonaria pseudotumulus* n. sp. Paratype 2 NHMW 2010/0036/0023 (NMMW; ex. BL coll.), length 22.2 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela;

140-143. *Zonaria spurcoides* (Gabb, 1873) NHMW 2010/0036/0031 (NMMW; ex. BL coll.), length 28.3 mm. Baitoa Formation, early Miocene, Arroyo Hondo, Yaque del Norte River, Dominican Republic.



In the Neogene several species have been described with shells closely similar to those of *P. robertsi*. Olsson (1964) described *P. telembiensis* from the Pacific portion of the Neogene Gatunian Province, from a single specimen from the late Miocene Angostura Formation of Ecuador. Groves (1997) re-illustrated the holotype. This Ecuadorian species is extremely similar in shape to *P. primaroberti*, differing only in the less crowded nature of the teeth (shell formula for *P. telembiensis*; 19.7 (67-52) 16: 15). Groves (1997) described *Zonaria cathyae* from the early Pliocene Esmeraldas beds of the Onzole Formation of Ecuador. Now considered a *Pseudozonaria*, it is extremely similar to the 'oval-depressed morphotype' of *P. primaroberti*, and indeed, apart from slightly fewer teeth in *P. cathyae*, their shell formulae are very similar (shell formula for *P. telembiensis*; 22.3 (71-57) 19: 17). The main difference between the two taxa is in the apertural characteristics of the anterior portion. In all members of the *P. robertsi*-group, including *P. primaroberti*, *P. portelli* Petuch, 1990, *P. raymondoberti* (Pilsbry, 1922) (holotype; Figs 169-172), *P. telembiensis* and *P. fehsei* Landau & Silva, 2010 (holotype; Figs 165-168) the terminal ridge is strong and keel-like followed by a deep groove separating the most anterior columellar tooth, which is usually more strongly developed. *Pseudozonaria cathyae* does not belong to this group, having the anterior third of the aperture dilated by a small hemispherical expansion, and there is no deep groove separating a weaker terminal ridge from the relatively fine columellar teeth.

Pseudozonaria raymondoberti, from the early Pliocene Gurabo Formation of the Dominican

Republic and early Pliocene Bowden Formation of Jamaica, can be easily separated by the consistently well developed and angular marginal callus giving the shell a very broad, depressed shape. *Pseudozonaria raymondoberti* differs from the rest of the *P. robertsi*-group in usually having the terminal ridge less strongly developed, the groove between the terminal ridge and first columellar tooth shallower (although it is quite prominent in the holotype Figs 104-107) and in having fewer, finer, longer teeth (shell formula for *P. raymondoberti*; 28.2 (70.5-51.1) 16: 14: ten specimens from Arroyo Zamba, Dominican Republic, BL coll.).

Pseudozonaria fehsei from the early Pliocene Cubagua Formation of Cubagua Island, Venezuela also has a similar shell shape, but differs in the nature of the aperture, which is a little wider in the anterior portion in *P. fehsei* and the teeth are a little longer and, especially on the labial side, are a little more widely spaced (shell formula for *P. fehsei*; 24.7 (66-50.6) 18: 16). *Pseudozonaria portelli* from the Pleistocene Bermont Formation of Florida has very coarse denticles (shell formula for *P. portelli*; 25 (63.9-51.5) 19: 15), similar in number to *P. fehsei* and *P. telembiensis*, but differs in that the columellar denticles do not extend over the columellar peristome (see Petuch, 1990, fig. 9).

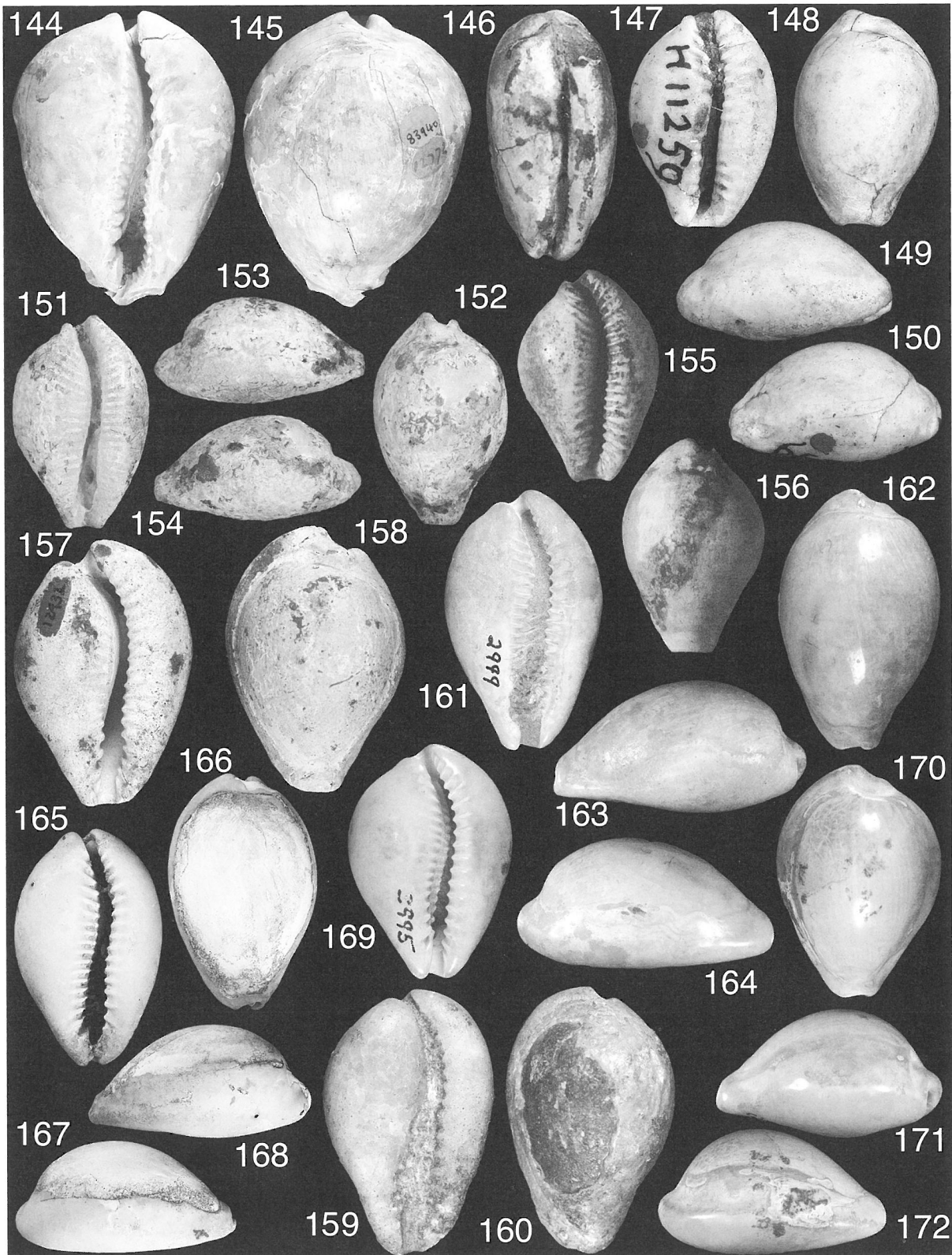
Etymology. Reflecting the earliest species in the *P. robertsi* species-group known.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

Figures 144-172 (type specimens of some tropical American Neogene Cypraeidae).

144-145. *Muracypraea henekeni* (G. B. Sowerby I, 1850) Lectotype BMNH G83940, length, 58 mm, Miocene, Yaque River, St. Domingo. Colld. Col. T.S. Heneken, ('J.S. Heniker'), c. 1848; **146.** *Luria patrespatriae* (Maury, 1917) Holotype PRI 28780 (ex Gabb collection), length 27.9 mm. Bluff 1, Cercado de Mao, Santo Domingo (specimen figured by Maury, 1917, pl. 19, fig. 10; adapical portion of outer lip seems to have been damaged since the original figure was taken). Image courtesy of the Paleontological Research Institution; **147-150.** *Pustularia (Pustularia) americana* Schilder, 1939 Holotype NMB H 11259, length 11.2 mm, width 7.8 mm, height 6.2 mm, Lower Miocene?: Cauto Fluss, road from Alto Cedro to Palma Soriano, Cuba; **151-154.** *Propustularia caribaea* (Schilder, 1939) Holotype NMB H11260, length 13.6 mm, width 9.0 mm, height 6.8 mm, early Middle Miocene Grand Bay Formation, Carriacou; **155-156.** *Propustularia bartschi* (Ingram, 1939) Holotype USNM 559684, length 25.8 mm, width, 17 mm, height 12.8 mm, Lower Pleistocene, Moin Formation, Limon, Costa Rica; **157-158.** *Zonaria pittorum* Groves, 1997 Holotype LACMIP 12432, length 40.1 mm, width 20.9 mm, height 12.8 mm, Lower Pliocene, TU locality 1399, roadcut on west side of village of Camarones, 20 km east of bridge over Rio Esmeraldas, Esmeraldas Beds, Onzole Formation, Ecuador; **159-160.** *Pseudozonaria frassinetti* (Groves & Nielsen, 2003) Hypotype LACMIP 13720, length 23.1 mm, width, 14.8 mm, height, 11.2 mm, early Upper Miocene, Tortonian, Navidad Formation, tidal platform approximately 1 km north of Matanzas, Cardenal Caro Province, central Chile; **161-164.** *Zonaria spurcoides* (Gabb, 1873) Lectotype ANSP 2999, length 32.5 mm, 20.5 mm, height, 16.5 mm, Miocene, Santo Domingo; **165-168.** *Pseudozonaria fehsei* Landau & Silva, 2010 Holotype NHMW 2010/0038/0013 (NHMW coll., ex BL coll.), Lower Pliocene, Araya Formation, Cañon de las Calderas, Cubagua Island. Length 26.6 mm, width 16.9 mm; **169-172.** *Pseudozonaria raymondoberti* (Pilsbry, 1922) Holotype ANSP 3995, length 275 mm, 19 mm, height, 15 mm, Miocene, Santo Domingo.



Pseudozonaria falconensis n. sp.

Text-figure 13; Figs 124-131

Dimensions and type material. Holotype; NMB H18368, height 16.5 mm (Figs 124-127); paratype 1 NMB H18369, height 14.4 mm (Figs 128-129); paratype 2 NHMW 2010/0036/0020, height, 16.7 mm (Figs 130-131); paratype 3 NHMW 2010/0036/0021, height, 14.9 mm.

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

Type stratum. Cantaure Formation (early Miocene: Burdigalian).

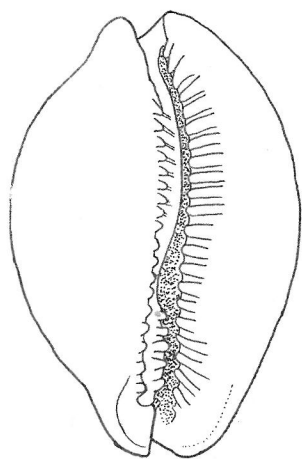
Description. Shell very small, solid, cylindrical-pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute to very weakly projecting, covered by adapical callus; sides rounded, moderately callused, callus ascending to $\frac{1}{3}$ - $\frac{1}{2}$ shell height; ventrum weakly convex in profile; aperture of medium width, almost straight, posteriorly weakly curving to the left,

anterior portion very slightly wider; siphonal canal narrow, abaxially asymmetrical; exhalant channel moderately produced, widening slightly adapically; columella denticulate along entire length, bearing 15-21 short, coarse denticles, which extend as folds a short distance onto the columella peristome, but not across the angulation onto the ventrum, anterior columellar teeth slightly more prominent; inner $\frac{2}{3}$ of columella peristome smooth; terminal fold strongly developed and elevated, bordering the siphonal canal, where it is strengthened and keel-like with a prominent, elevated internal lamina (sensu Dolin & Lozouet, 2004), separated from the columellar teeth by a groove; fossula relatively well developed, concave, but poorly delimited from the rest of the columella, very steep, bearing five ridges of variable strength extending from the anterior columellar teeth to the inner edge of the fossula, where they form relatively long, extremely large, rounded inner teeth; 19-24 coarse labral teeth, anterior third of labral teeth stretched out on slightly constricted, depressed, hemicircular area; outer lip bevelled inwards, with teeth extending across the bevelled inner portion and a variable distance onto the labrum, at most just short of mid-labrum. No colour pattern preserved.

Shell Formula. 14.3 (64.5 – 52.2) 26: 20

specimen	collection number	length	width	height	LT	CT
holotype (Figs 124-127)	NMB H18368	16,5	10,5	8,6	21	19
paratype 1 (Figs 128-129)	NMB H18369	14,4	8,9	7,3	21	15
paratype 2 (Figs 130-131)	NHMW 2010/0036/0020	16,7	10,7	8,5	24	21
paratype 3	NHMW 2010/0036/0021	14,9	9,7	7,9	21	18
BL coll. 3		11,2	7,6	6,2	19	13

Table 13. Dimensions and number of teeth; *Pseudozonaria falconensis* n. sp.



Text-figure 13. *Pseudozonaria falconensis* n. sp. Holotype NMB H18368 (NMB coll.), length 16.5 mm. lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

Discussion. This is the smallest *Pseudozonaria* species in the Cantaure Formation, and easily

recognised by its rather produced posterior extremity and relatively well developed fossula, which is smooth in the middle, but with enormous teeth developed at the inner edge of the fossula. We have not found any congener with this feature similarly strongly developed.

Etymology. Named for Falcón State, Venezuela.

Geological and geographical distribution.

Lower Miocene: Cantaure Formation, Venezuela.

BIOGEOGRAPHIC IMPLICATIONS

The southern Caribbean early Miocene had a rich and varied cypraeid assemblage, with thirteen species here recorded from the early Miocene, Burdigalian assemblage of Cantaure, ten of which are described as new. The presence of an equally rich cypraeid assemblage in the early Miocene of the Chipola Formation, northern Florida, was described by Dolin (1991). As mentioned in the introduction, cypraeids are a difficult group to work with, and both the specific and supraspecific classification varies

enormously between researchers. In order for us to compare the faunas on either side of the Caribbean early Neogene we must first review the classification offered by Dolin (1991). Table 14 presents a generic

revision of Dolin's (1991) taxa. This is not a species-level revision, which is beyond the scope of this work, and some of the taxa may well be junior subjective synonyms (see Fehse, 2004).

Classification fide Dolin (1991)	Current taxonomy
<i>Cypraeorbis emilyae</i> n.sp.	<i>Cypraeorbis emilyae</i> (Dolin, 1991)
<i>Cypraeorbis hertleini</i> (Ingram, 1948)	<i>Cypraeorbis willcoxi willcoxi</i> (Dall, 1890)
<i>Cypraeorbis ballista</i> (Dall, 1915)	<i>Cypraeorbis willcoxi ballista</i> (Dall, 1915)
<i>Zoila willcoxi</i> (Dall, 1890)	<i>Cypraeorbis willcoxi willcoxi</i> (Dall, 1890)
<i>Zoila arlettae</i> n.sp.	<i>Cypraeorbis arlettae</i> (Dolin, 1991)
<i>Siphocypraea chilona</i> (Dall, 1900)	<i>Cypraeorbis chilona</i> (Dall, 1900)
<i>Trona leporina calhounensis</i> n.ssp.	<i>Trona calhounensis</i> Dolin, 1991
<i>Talparia dominicensis</i> (Gabb, 1873) [of Dolin, 1991]	<i>Luria dominicensis</i> (Gabb, 1873) [of Dolin, 1991] = <i>L. dockeryi</i> (Dolin & Lozouet, 2004)
<i>Talparia mariaelisabethae</i> n.sp.	<i>Luria mariaelisabethae</i> (Dolin, 1991)
<i>Mauritia campbelliana</i> (Pilsbry, 1922)	<i>Luria campbelliana</i> (Pilsbry, 1922)
<i>Lyncina theresae</i> n.sp.	<i>Zonaria theresae</i> (Dolin, 1991) [?= <i>Z. mariaelisabethae</i> (Dolin, 1991)]
<i>Erronea (Adusta) tumulus</i> (Heilprin, 1886)	<i>Zonaria tumulus</i> (Heilprin, 1886)
<i>Erronea (Adusta) heilprinii</i> (Dall, 1890)	<i>Zonaria heilprinii</i> (Dall, 1890)
<i>Erronea (Adusta) spurcoides</i> (Gabb, 1873)	<i>Zonaria spurcoides</i> (Gabb, 1873)
<i>Erronea (Adusta) shirleyae</i> n.sp.	<i>Zonaria shirleyae</i> (Dolin, 1991)
<i>Bistolida praelator</i> n.sp.	<i>Zonaria praelator</i> (Dolin, 1991)

Table 14. Cypraeid assemblage present in the early Miocene Chipola Formation of northern Florida; classification of Dolin (1991) vs. current taxonomy.

From a palaeobiogeographic perspective the Cantare Formation assemblage is chronologically the oldest Neogene deposit, situated geographically on the southernmost part of the Gatunian palaeobiogeographic province (Vermeij & Petuch, 1986; Vermeij, 2005; Landau et al., 2008). The Chipola Formation assemblage is situated geographically within the neighbouring northern Caloosahatchian Province, which was already a distinct palaeobiogeographic province by the early Miocene (Vermeij, 2005). In the present work we identify two genera, *Muracypraea* and *Propustularia*, which seem to be endemic to the Gatunian Province. *Pseudozonaria* has not been found in the Caloosahatchian Province during the Miocene or Pliocene, but is represented by a single, extremely rare species in the Pleistocene, *P. portelli* (Petuch, 1990). Conversely, *Cypraeorbis* Conrad, 1865 has not so far been recorded in the Neogene Gatunian Province.

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