

# Nassariidae (Caenogastropoda, Buccinoidea) of the early Miocene Cantaure Formation of Venezuela

BERNARD LANDAU

Centro de Geologia da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal; bernielandau@sapo.pt

This paper gives the first account of the nassariid assemblage found in the early Miocene (Burdigalian) outcrop at Cantaure, Paraguán Peninsula, Venezuela. Six species are recorded, of which three are new, viz. *Nassarius cantauranus* spec. nov., *Psilarius silvai* spec. nov. and *Psilarius obesus* spec. nov. *Nassa corneliana* Olsson, 1914, is a subjective junior synonym of *Nassarius caloosaensis* (Dall, 1890), and *Uzita prista* Gardner, 1944, *Nassarius (Nanarius) parapristus acolus* Woodring, 1964, and *Nassarius (Nanarius) parapristus conarus* Woodring, 1964, are junior subjective synonyms of *Nanarius parapristus* (Gardner, 1944).

Key words: Gastropoda, Nassariidae, *Nassarius*, *Psilarius*, taxonomy, Miocene, Venezuela.

## INTRODUCTION

No species of Nassariidae Iredale, 1916, were mentioned in Jung's (1965) systematic description of the Lower Miocene Cantaure Formation fossil molluscan assemblage on the Paraguán Peninsula, Venezuela. In this paper I rectify this omission and describe and discuss the members of this family found in the Cantaure Formation. The stratigraphy, age and fauna of the Cantaure Formation are described in the first paper in this series (Landau & Vermeij, 2010).

## MATERIAL AND METHODS

The material described here is in the Gibson-Smith collection

housed in the Naturhistorisches Museum Basel, Switzerland, and the Bernard Landau collection, now deposited in the Naturhistorisches Museum Wien, Vienna.

Abbreviations: NMB, Naturhistorisches Museum Basel; NHMW, Naturhistorisches Museum Wien; BL, Bernard Landau collection; dp, diameter of protoconch, hp, height of protoconch; dp/hp, ratio of diameter to height of protoconch; n, diameter of nucleus (initial "cap" of protoconch); dV1, diameter of first protoconch whorl.

## SYSTEMATIC PART

Superfamily Buccinoidea Rafinesque, 1815

Family Nassariidae Iredale, 1916

Subfamily Nassariinae Iredale, 1916

Discussion. — Landau et al. (2009) discussed the difficulty of separating the European nassariid species into well-differentiated supraspecific taxa based on shell characters, and followed Adam & Glibert (1974) in using informal species-groups. Nevertheless, even within the European faunas, certain genera such as *Cyclope* Risso, 1826, and *Demoulia* Gray, 1838, can be distinguished with confidence. I have adopted a similar approach in this work, recognising certain genera whilst still using *Nassarius* Duméril, 1806, in its broadest sense, without proposing species-groups.

Genus *Nassarius* Duméril, 1806

Type species (by subsequent monotypy, Von Froriep 1806: 167): *Buccinum arcularia* Linnaeus, 1758 (Iredale, 1916: 83). Recent, Indo-West Pacific.

*Nassarius cantauranus* spec. nov. (Figs 1, 2, 19, 20)

Type series. — Holotype NHMW 2009z0156/0001, height 10.4 mm (Figs 11-13); paratype 1, NHMW 2009z0156/0002, height 10.7 mm; paratype 2, NHMW 2009z0156/0003, height 8.4 mm (Figs 19, 20), all from Cantaure Formation (early Miocene, Burdigalian), lower shell bed, 1 km SW of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (locality GS12PGNA of Gibson-Smith & Gibson-Smith 1979).

Other material examined. — Maximum height 11.1 mm: 14 specimens, Gibson-Smith collection, NMB collection lot DS 4101, locality NMB 17516; 10 specimens BL.

Etymology. — The species name reflects the type locality.

Diagnosis. — A *Nassarius* species with small, robust shell and conical spire; protoconch multispiral with small nucleus; five almost flat-sided whorls; axial sculpture of 13 rounded ribs; spiral sculpture much reduced, present only on early teleoconch whorls; subsutural collar narrow, weakly constricted; labral varix thick; aperture denticulate within, adapical and mid-aperture denticle more prominent than others; abapical portion of columella denticulate, with parietal denticle.

Description. — Shell small, robust, inflated, bucciniform, with conical spire. Protoconch multispiral, of 2.75 smooth convex whorls, with small nucleus ( $dp = 560 \mu$ ,  $hp = 600 \mu$ ,  $dp/hp = 0.93$ ,  $n = 70 \mu$ ,  $dV1 = 110 \mu$ ). Junction with teleoconch marked only by beginning of spiral sculpture. Teleoconch with five very weakly convex, almost straight-sided whorls, periphery at abapical suture. Suture deeply impressed, weakly undulating. Spiral sculpture of four narrow, rounded spiral cords on first teleoconch whorl, weakening abapically, obsolete on third teleoconch whorl. Axial sculpture of 13 low ribs of rounded section, developing after first quarter teleoconch whorl, each cord equal in width to one interspace; becoming more widely spaced abapically. Slightly constricted, relatively narrow subsutural collar delimited adapically by indistinct spiral groove, indenting axial ribs. Last whorl about 65% of total height, very weakly constricted at base, bearing 1-3 indistinct spiral cords on base. Aperture pyriform, about 35% of total height; outer lip thickened by labial varix, especially adapically; denticulate within. Denticulation rather variable; adapical denticle delimiting anal canal and mid-apertural denticle prominent in all specimens;

abapical denticle delimiting border of siphonal canal well-developed; one or two weaker denticles present between each pair of more prominent denticles. Anal canal represented by well-developed rounded notch; siphonal canal narrow, open. Central portion of columella concave, bearing about five broad denticles abapically; parietal tooth present. Columellar callus narrow, moderately thickened, clearly delimited. Siphonal fasciole flattened, poorly delimited from base, bearing 5-6 flat-topped spiral cords.

Remarks. — *Nassarius cantauranus* spec. nov. is very distinctive in having almost obsolete sculpture on the last whorl, and is completely different from any of its congeners in the tropical American Neogene or Recent Caribbean assemblages. *Nassarius galbanus* Jung, 1969, from the Lower Pliocene Coubaril Beds of Trinidad bears a slight resemblance in having a solid shell, albeit smaller and more elongate, with axial sculpture weakening abapically. However, the spiral sculpture persists around the entire last whorl in *N. galbanus*. In the Recent tropical American Pacific fauna, *N. fontainei* (D'Orbigny, 1841) from Peru also has a subsutural collar and a similar stocky shape, but *N. fontainei* is twice as large as *N. cantauranus* spec. nov., and the axial ribs remain well-developed on the last whorl in *N. fontainei*.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela.

*Nassarius praeambiguus* (Brown & Pilsbry, 1913) (Figs 3-6, 21-23)

*Nassa* (*Hima*) *praeambigua* Brown & Pilsbry, 1913: 506, pl. 22 figs 6, 7.

*Nassarius* (*Uzita*?) *praeambiguus* (Brown & Pilsbry). Woodring, 1964a: 270, pl. 43 figs 1, 4.

Material and dimensions. — Cantaure, maximum height 8.4 mm: 69 specimens, Gibson-Smith collection, NMB locality 17520; 14 specimens BL. Gatun, maximum height 9.1 mm: 21 specimens, locality PPP 00224 (NMB 17642); 30 specimens, locality PPP 00227 (NMB 17645); 17 specimens, locality PPP 00229 (NMB 17647); 34 specimens, locality PPP 01030 (NMB 18255); 19 specimens, locality PPP 01032 (NMB 18259); 3 specimens, locality PPP 00486 (NMB 17867); 9 specimens, locality PPP 01078 (NMB 18325); 2 specimens, locality PPP 00488 (NMB 17869); 2 specimens, locality PPP 00489 (NMB 17870); 17 specimens, locality PPP 00010 (NMB 18352); 16 specimens, locality PPP 00218 (NMB 17636); 10 specimens, locality PPP 00220 (NMB 17638); 6 specimens, locality PPP 00222

(NMB 17640); 15 specimens, locality PPP 00223 (NMB 17641); 3 specimens, locality PPP 00231 (NMB 17649); 2 specimens, locality PPP 01075 (NMB 18322); 24 specimens BL. Locality data are available on the PPP website, at: <http://www.fiu.edu/~collinsl/compancan.gif>.

Remarks. — *Nassarius praeambiguus* (Brown & Pilsbry, 1913) has a small, inflated shell characterised by its strong sculpture, consisting of broad rounded ribs, each wider than one interspace, crossed by narrow elevated cords, its strongly varicose outer lip, especially adapically where it is almost wing-like (alate), and its relatively small but strongly denticulate aperture. Its protoconch is multispiral, consisting of 2.75 whorls with a small nucleus (dp = 450  $\mu$ , hp = 430  $\mu$ , dp/hp = 1.05, n = 55  $\mu$ , dV1 = 140  $\mu$ ). The specimens from Cantaure (Figs 3, 4) are indistinguishable from those from the middle-late Miocene Gatun Formation of Panama (Figs 5, 6; Woodring, 1964a: pl. 43 figs 1, 4). The protoconch of the specimen from the Gatun Formation illustrated here (Fig. 23) has a similar number of whorls but is larger (dp = 800  $\mu$ , n = 95  $\mu$ , dV1 = 210  $\mu$ ). However, the size of the protoconch can vary intraspecifically in nassariids (Landau et al., 2009).

As pointed out by Woodring (1964a), *N. praeambiguus* does not belong in the same species group as *N. ambiguus* (Pulteney, 1799) [secondary homonym of *Buccinum ambiguum* Solander, 1766], now known as *N. antillarum* (Orbigny, 1842), not *N. albus* (Say, 1826) as stated by Woodring (1964a: 271). *Nassarius antillarum* is a much larger shell with tabulate whorls, finer spiral sculpture and a larger aperture that is not as coarsely denticulate within as *N. praeambiguus*. No Recent species belonging to this group live today in the Caribbean.

Two other species with similar shells occur in the Lower Miocene Chipola Formation of Florida. *Nassarius cinclis* (Gardner, 1944) has a smaller, more elongate shell, the axial ribs are much finer than in *N. praeambiguus*, and of similar strength to the spiral cords, forming a reticulate surface sculpture, and the posterior alation of the outer lip present in *N. praeambiguus* is not as developed. *Nassarius dasynema* (Gardner, 1944) has the same squat shell shape as *N. praeambiguus*, but has finer spiral sculpture, the last whorl is more constricted at the base, the anal notch is wider and again the posterior alation of the outer lip is far less developed than in *N. praeambiguus*. No very similar species are found today in the tropical American Caribbean or

Pacific assemblages.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela; La Boca Formation, Panama (Woodring, 1964a. Dated as 23.07 to 20.62 Ma; Kirby et al., 2007). **Middle to late Miocene:** Lower and Middle Gatun Formation, Panama (Woodring, 1964a) (Lower Gatun Formation extends down into the Middle Miocene, from approx. 12-8.2 Ma; PPP website).

*Nassarius caloosaensis* (Dall, 1890) (Figs 34-42)

*Nassa caloosaensis* Dall, 1890: 134, pl. 9 fig. 7.

*Nassa cornelliana* Olsson, 1914: 7, pl. 4 fig. 11.

*Alectrion cornelliana*. Mansfield, 1930: 76, pl. 4 fig. 11.

*Uzita caloosaensis*. Gardner, 1948: 252, pl. 30 fig. 25.

*Uzita caloosaensis cornelliana*. Gardner, 1948: 252, pl. 30 fig. 24.

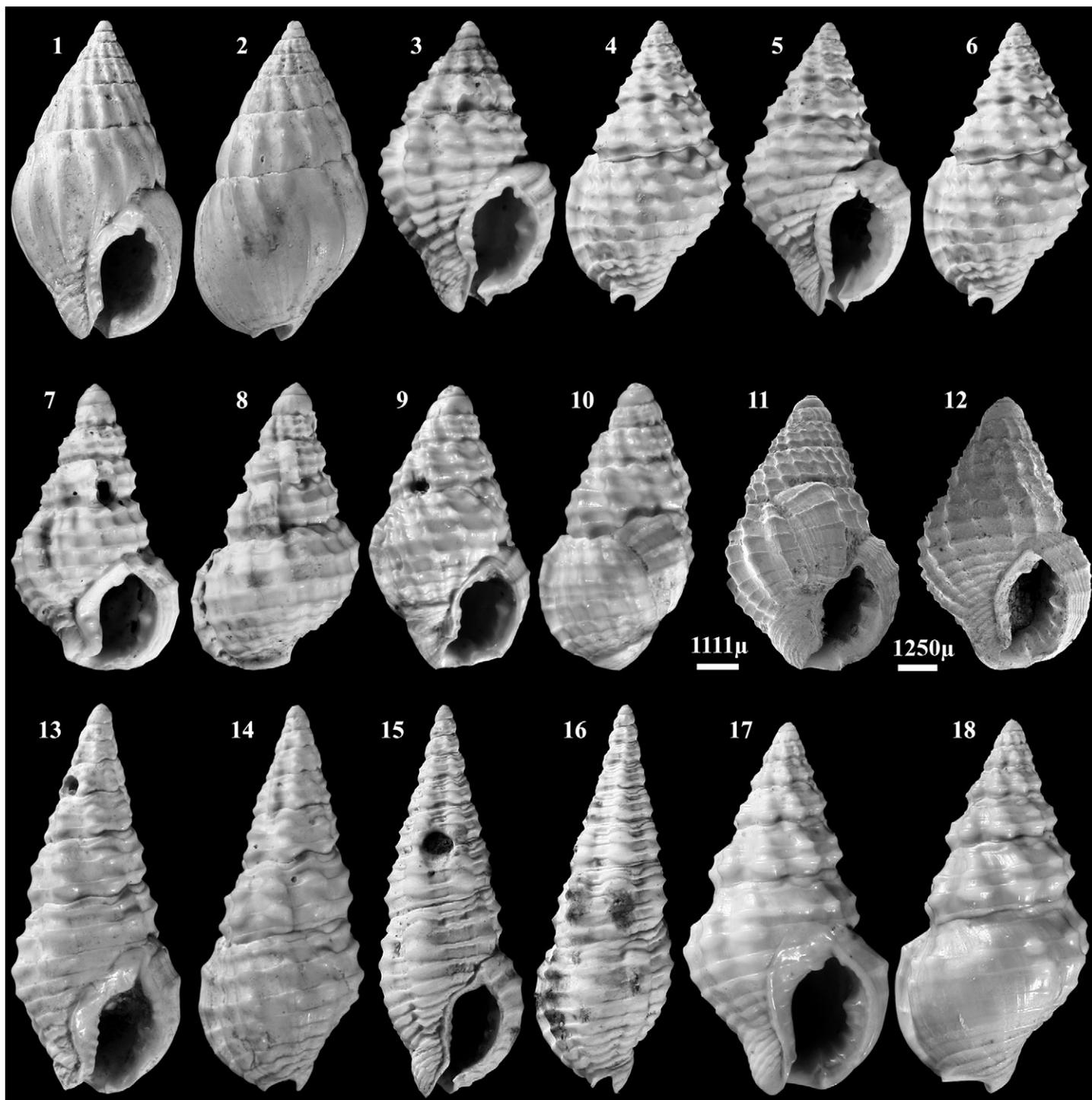
*Nassarius cornelliana* (sic). Ward & Blackwelder, 1987: 176, pl. 40 figs 16-17.

Material and dimensions. — 1 specimen, NHMW 2009z0156/0004, height 3.4 mm (Figs 34-36), Cantaure Formation (early Miocene, Burdigalian).

Remarks. — A single shell is present in my collection from Cantaure representing a minute but very distinctive nassariid, characterised by widely spaced, weakly elevated rounded ribs and spiral sculpture of broad, flattened bands separated by incised spiral grooves; three bands are present on the penultimate whorl and seven on the last whorl. The spiral grooves are irregularly spaced; the adapical groove just below the suture, widely spaced on the mid-whorl, close-set on the base.

I am unable to distinguish this Venezuelan shell from the SE coast American Pliocene to Pleistocene species *Nassarius caloosaensis* (Dall, 1890). The Venezuelan specimen has a slightly squatter form than most USA material, but so do the smaller Floridian specimens. The protoconch is abraded in the single shell from Cantaure (Fig. 35), but is clearly multispiral and of similar dimensions to that of the American specimens. I have numerous shells of *N. caloosaensis* from Florida with the protoconch well preserved and it is also multispiral on these specimens, consisting of 3.5 smooth whorls with a very small nucleus.

American authors have consistently separated the slightly



more elongate, less shouldered specimens as *Nassarius cornellianus* (Olsson, 1914) (Gardner, 1948; Ward & Blackwelder, 1987). However, the specimen illustrated here (Figs 41, 42) from Florida is indistinguishable from that figured by Ward & Blackwelder (1987, pl. 40 figs 16, 17), and was found together with

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Figs 1-18. *Nassarius*, *Nanarius* and *Psilarius* spp. **1-2**, *Nassarius cantauranus* spec. nov., holotype, NHMW 2009z0156/0001 (ex BL), height 10.4 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; **3-4**, *N. praeambiguus* (Brown & Pilsbry, 1913), NHMW 2009z0156/0011 (ex BL), height 7.9 mm, Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; **5-6**, *N. praeambiguus* (Brown & Pilsbry, 1913), NHMW 2009z0156/0012 (ex BL), height 8.4 mm, Lower Gatun Formation (middle Miocene), Loc TU 961, road cuts both sides of Boyd-Roosevelt Highway, E of Cativa (Woodring locality no. 138e), Colón Province, Panama; **7-8**, *Nanarius parapristus* (Gardner, 1944), NHMW 2009z0156/0017 (ex BL), height 8.7 mm, Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; **9-10**, *N. conarus* (Woodring, 1964), NHMW 2009z0156/0019 (ex BL), height 6.2 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; **11**, *N. conarus* (Woodring, 1964), NHMW 2009z0156/0020 (ex BL), height 4.8 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph; **12**, *N. conarus* (Woodring, 1964), NHMW 2009z0156/0021 (ex BL), height 4.7 mm; Lower Gatun Formation (middle Miocene), Loc TU 961, road cuts both sides of Boyd-Roosevelt Highway, E of Cativa (Woodring locality no. 138e), Colón Province, Panama; SEM photograph; **13-14**, *Psilarius silvai* spec. nov., holotype, NHMW 2009z0156/0005 (ex BL), height 10.2 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; **15-16**, *P. leptus* (Woodring, 1964), NHMW 2009z0156/0022 (ex BL), height 11.8 mm; Lower Gatun Formation (middle Miocene), Loc TU 961, road cuts both sides of Boyd-Roosevelt Highway, E of Cativa (Woodring locality no. 138e), Colón Province, Panama; **17-18**, *P. obesus* spec. nov., holotype, NHMW 2009z0156/0008 (ex BL), height 10.7 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela.

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the stockier, more shouldered form (Figs 39, 40). Height of spire and prominence of the shoulder angulation are not good morphological characters for distinguishing nassariid species (Landau et al., 2009) and I consider *Nassa cornelliana* Olsson to be a subjective junior synonym of *Nassarius caloosaensis* (Dall, 1890).

*Nassarius caloosaensis* is quite different from any other fossil or living tropical American Neogene nassariid. Its presence at Cantaure greatly increases both its geographical range, as it is now present in both the Gatunian and Caloosahatchian Palaeobiogeographic Provinces (see Vermeij & Petuch, 1986; Landau et al., 2008) and its stratigraphical range, now early Miocene to Pleistocene.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela. **Pliocene:** Choctawhatchee Formation, *Cancellaria* zone, Florida, USA (Gardner, 1948; for age see Akers, 1972); Yorktown Formation, North Carolina (Ward & Blackwelder, 1987); Pinecrest Beds, Florida, USA (BL). **Early Pleistocene:** Waccamaw Formation, North Carolina (Gardner, 1948); Caloosahatchee Formation, Florida (Gardner, 1948). **Early to Middle Pleistocene:** Bermont Formation, Florida, USA (BL).

#### Genus *Nanarius* Woodring, 1964

119

Type species (by original designation): *Uzita paraprista* Gardner, 1944. Neogene, tropical America.

Remarks. — *Nanarius* Woodring, 1964, is considered to be a distinct genus here, based on the characters of its very large protoconch in relation to the teleoconch size and its very short, wide siphonal canal, giving the base of the shell an almost truncated appearance. This seems to be an exclusively Caribbean Neogene genus.

*Nanarius parapristus* (Gardner, 1944) (Figs 7, 8, 24, 25)

*Uzita paraprista* Gardner, 1944: 480, pl. 51, fig. 27.

*Uzita prista* Gardner, 1944: 481, pl. 51 fig. 28.

*Nassarius* (*Nanarius*) *parapristus acolus* Woodring, 1964a: 271, pl. 40 figs 16, 17.

*Nassarius* (*Nanarius*) *parapristus conarus* Woodring, 1964a: 272, pl. 43 figs 3, 8.

Material and dimensions. — Cantaure, maximum height 8.6 mm: 100+, Gibson-Smith collection, NMB locality 17520; 39 specimens BL. Gatun, maximum height 7.5 mm: 9 specimens, locality PPP 00224 (NMB 17642); 39 specimens, locality PPP 00227 (NMB 17645); 5 specimens, locality PPP 00229 (NMB 17647); 5 specimens, locality PPP 01030 (NMB 18255); 16 specimens, locality PPP 01032 (NMB 18259); 12 specimens, locality PPP 00486 (NMB 17867); 10 specimens, locality PPP 01078 (=NMB 18325); 12 specimens, locality PPP 00488 (NMB 17869); 54 specimens, locality PPP 00489 (NMB 17870); 2 specimens, locality PPP 00010 (NMB 18352); 26 specimens, locality PPP 00218 (NMB 17636); 5 specimens, locality PPP 00220 (=NMB 17638); 34 specimens, locality PPP 00222 (NMB 17640); 5 specimens, locality PPP 00223 (NMB 17641); 2 specimens, locality PPP 00231 (NMB 17649); 6 specimens, locality PPP 01075 (NMB 18322); 2 specimens BL. Locality data are available on the PPP website, at: <http://www.fiu.edu/~collinsl/compancan.gif>.

Remarks. — Several nominal taxa have been proposed or ascribed to *Nanarius*. The type species, *Nanarius paraprismus* (Gardner, 1944), was described from the middle Miocene Shoal River Formation of northern Florida (for age see Jones et al., 1993). In the same publication, *Nanarius pristus* (Gardner, 1944) was described from the same deposits. It was said to differ from *N. paraprismus* in being less sharply cancellate and having broader, more widely spaced axial ribs and weaker spiral threads (Gardner, 1944; Woodring, 1964a). Woodring (1964a) described two further taxa from the middle-late Miocene lower and middle Gatun Formation of Panama. *Nanarius paraprismus acolus* was said to differ from the nominate species in being more slender and a little smaller (3.3 mm vs. 3.9 mm), although in his discussion Woodring (1964a: 272) admitted that some specimens are up to 4.0 mm tall. The second form, *Nanarius paraprismus conarus*, was said to be larger, up to 4.7 mm in height, and to have a similar degree of inflation to *Nanarius paraprismus*, but to have a more massive terminal varix and coarser denticles within the aperture than any of the other taxa. All these forms are present in the Cantaure Formation. My largest shell (Figs 7, 8) is 8.6 mm in height and has regularly cancellate sculpture similar to that of *N. paraprismus* and *N. paraprismus acolus*, whereas other specimens (Figs 9-11) have fewer, more strongly prosocline ribs similar to those of *N. pristus* and *N. paraprismus conarus* from Gatun (Fig. 12). The presence, position and strength of the varices are very variable. The protoconchs of all these types have been pho-

tographed and are similar:

*Nanarius paraprismus* morphotype, Cantaure (Figs 24, 25): protoconch multispiral, of 3.75 smooth, convex whorls, with a small nucleus (dp = 1010  $\mu$ , hp = 960  $\mu$ , dp/hp = 1.05, n = approx. 80  $\mu$ , dV1 = approx. 150  $\mu$ ).

*Nanarius paraprismus conarus* morphotype, Cantaure (Figs 26, 27): protoconch multispiral, of 3.25 smooth, convex whorls, with a small nucleus (dp = 840  $\mu$ , hp = 840  $\mu$ , dp/hp = 1, n = approx. 85  $\mu$ , dV1 = approx. 185  $\mu$ ).

*Nanarius paraprismus conarus* morphotype, Gatun (Figs 28, 29): protoconch multispiral, of 3.50 smooth, convex whorls, with a small nucleus (dp = 760  $\mu$ , hp = 751  $\mu$ , dp/hp = 1, n = 70  $\mu$ , dV1 = 130  $\mu$ ).

I therefore consider *Uzita prista* Gardner, 1944, *Nassarius* (*Nanarius*) *paraprismus acolus* Woodring, 1964, and *Nassarius* (*Nanarius*) *paraprismus conarus* Woodring, 1964, to be junior subjective synonyms of *Nanarius paraprismus* (Gardner, 1944). As first reviser (ICZN Article 24.2), I select *Uzita paraprista* Gardner, 1944, as the valid name for the species named both *Uzita paraprista* and *U. prista* by Gardner (1944), as *Uzita paraprista* is the type species of the genus.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela. **Middle Miocene:** Shoal River Formation, northern Florida (Gardner 1944); Lower Gatun Formation, Panama (Woodring 1964a). **Late Miocene:** Upper Gatun Formation, Panama (Woodring 1964a).

#### Genus *Psilarius* Woodring, 1964

Type species (by original designation): *Leptarius leptus* Woodring, 1964a. Neogene, tropical America.

Revised generic description. — Moderately small, very slender to relatively broad, columbellid-like; protoconch multispiral, with small nucleus; sculpture dominated by nodes at intersections of suppressed axial ribs and suppressed spiral threads; nodes absent or reduced on flattened apertural face of last whorl; siphonal fasciole moderately inflated; outer lip varicose, enamel within outer lip slightly erect and everted over labial varix; abapically, small notch present in everted lip margin, reminiscent of the stromboid notch, lip edge slightly flared abapical to notch; denticles within aperture of two types, two

adapical denticles arise from lip edge, fused into a single elongate denticle in some specimens; second group of more prominent denticles lies a short distance within aperture, extending inwards; the most adapical placed just above mid-aperture twice as prominent as the rest in most specimens; columellar lip weakly to strongly denticulate; parietal tooth moderate to strong, bordering anal canal.

Remarks. — The genus *Psilarius* Woodring, 1964, comprises a small group of well-defined, slender to moderately inflated, columbellid-like nassariids found only in the Caribbean Neogene and the Plio-Pleistocene of Florida. The genus was originally named *Leptarius*, a homonym of *Leptarius*, Gill, 1864, but Woodring provided the replacement name *Psilarius* in the same year (Woodring, 1964b). Until recently *Psilarius* was considered to be monotypic, but Petuch (1991) described a species from the Pliocene of Florida. Two further species are added here from the early Miocene of Cantaure. Although Woodring (1964a: 272) described the columellar lip as smooth it is clearly denticulate in all shells seen, including those from Gatun. With this additional material a revised generic description is given.

*Psilarius silvai* spec. nov. (Figs 13-16, 30, 31)

Type series and dimensions. — Holotype NHMW 2009z0156/0005, height 11.8 mm (Figs 13, 14); paratype 1 NHMW 2009z0156/0006, height 11.2 mm; paratype 2 NHMW 2009z0156/0007, height 8.7 mm (Figs 30, 31), all from Cantaure Formation (early Miocene, Burdigalian), lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (locality GS12PGNA of Gibson-Smith & Gibson-Smith, 1979).

Other material examined. — 65 specimens, Gibson-Smith collection, NMB locality 17516; 4 specimens Gibson-Smith collection, NMB locality 12842; 7 specimens BL, all from Cantaure Formation, Casa Cantaure, Venezuela.

Etymology. — Named in honour of my great friend, teacher, and co-author of many papers, Dr Carlos Marques da Silva, University of Lisbon, Portugal.

Diagnosis. — A medium-sized, relatively slender *Psilarius* species, with prominent dentition within the aperture, especially on the columella, moderately expanded columellar and

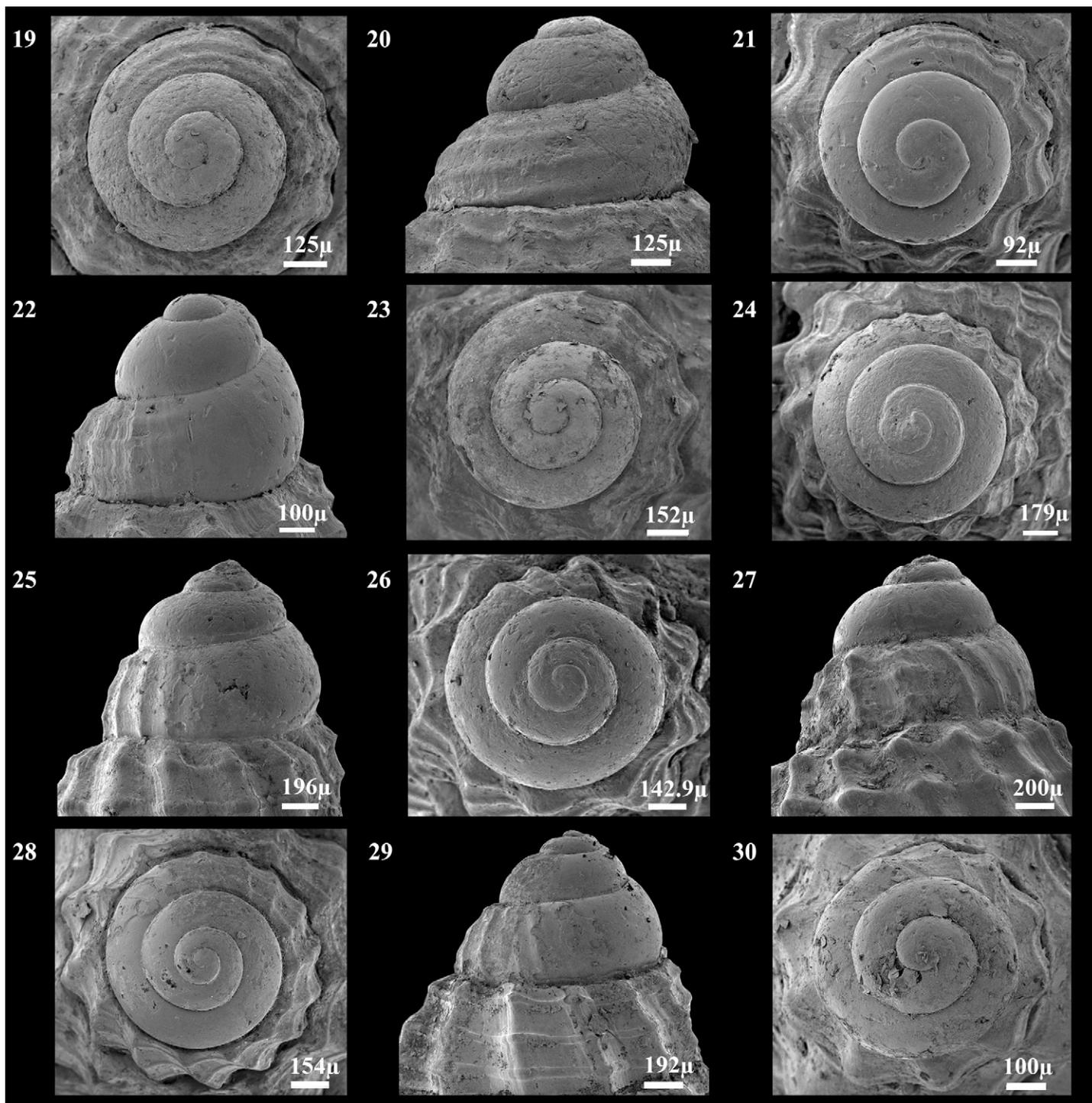
parietal calluses, and a very short siphonal canal.

Description. — Shell small, solid, slender, columbellid-like. Protoconch multispiral, consisting of 3.0 smooth, convex whorls, with small nucleus ( $dp = 510 \mu$ ,  $hp = 720 \mu$ ,  $dp/hp = 0.7$ ,  $n = 60 \mu$ ,  $dV1 = 140 \mu$ ) Junction with teleoconch delimited clearly by prosocline scar. Teleoconch of 5-6 almost straight-sided whorls with periphery just above abapical suture. Suture linear, undulating. First teleoconch whorl bearing nine prosocline ribs and two narrow spiral cords. Axial ribs broadening and weakening abapically; third spiral cord appearing below adapical suture on second or third whorl. Spiral cords overrid-

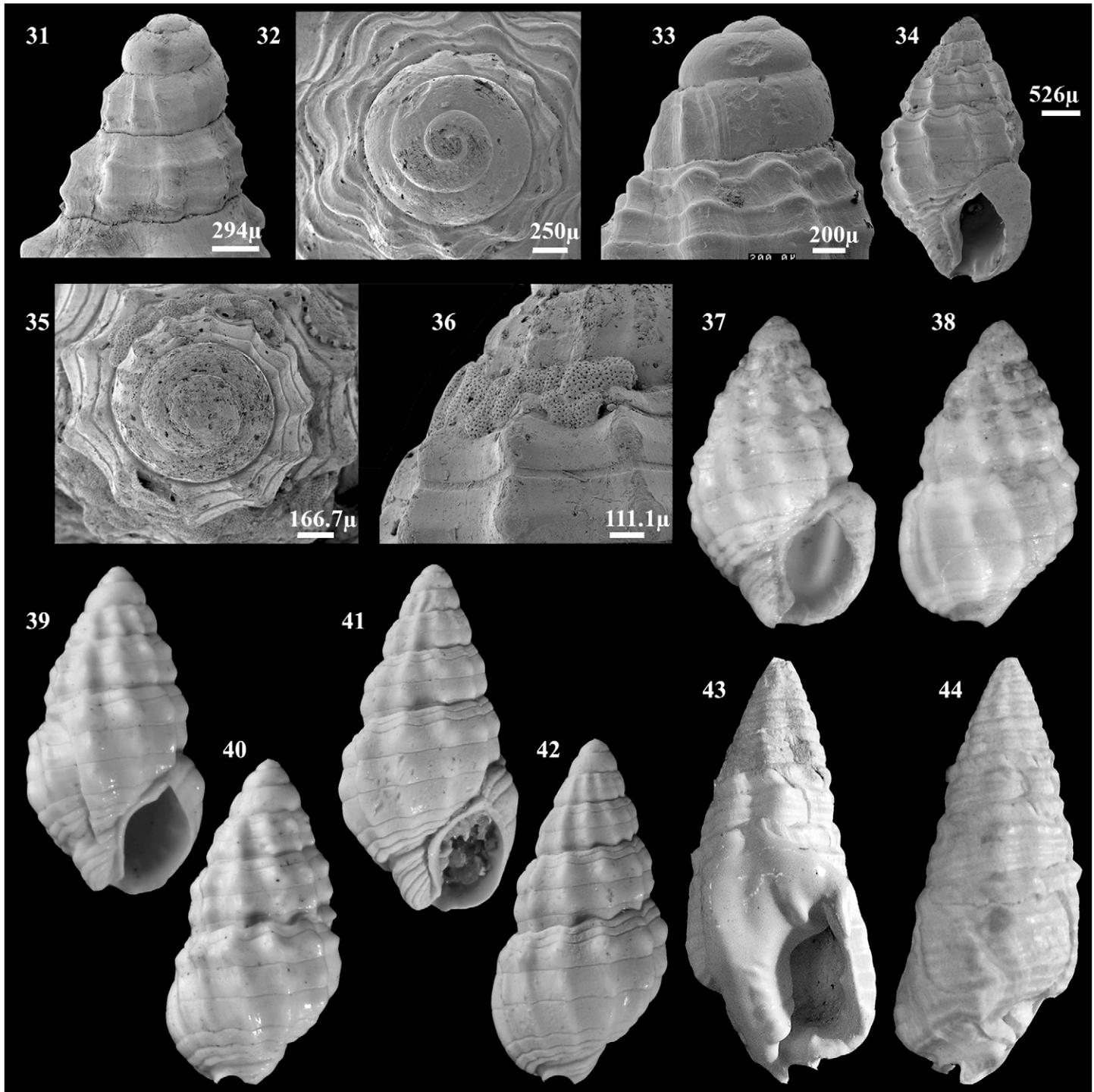
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Figs 19-30. *Nassarius*, *Nanarius* and *Psilarius* spp. 19-20, *Nassarius cantauranus* spec. nov., paratype, NHMW 2009z0156/0003 (ex BL), height 8.4 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch; 21-22, *N. praeambiguus* (Brown & Pilsbry, 1913), NHMW 2009z0156/0013 (ex BL), height 8.0 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch; 23, *N. praeambiguus* (Brown & Pilsbry, 1913). NHMW 2009z0156/0014 (ex BL), height 7.0 mm; Lower Gatun Formation (middle Miocene), Loc TU 961, road cuts both sides of Boyd-Roosevelt Highway, E of Cativa (Woodring locality no. 138e), Colón Province, Panama; SEM photograph, detail of protoconch; 24-25, *Nanarius parapristus* (Gardner, 1944), NHMW 2009z0156/0018 (ex BL), height 6.4 mm; all data as for Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch; 26-27, *N. conarus* (Woodring, 1964), NHMW 2009z0156/0021 (ex BL), height 4.7 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph; 28-29, *N. conarus* (Woodring, 1964), NHMW 2009z0156/0020 (ex BL), height 4.8 mm; Lower Gatun Formation (middle Miocene), Loc TU 961, road cuts both sides of Boyd-Roosevelt Highway, E of Cativa (Woodring locality no. 138e), Colón Province, Panama; SEM photograph, detail of protoconch; 30, *Psilarius silvai* spec. nov., paratype, NHMW 2009z0156/0007 (ex BL), height 8.7 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch.

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ing axial sculpture, swelling at intersections into horizontally elongate nodes. Last whorl flattened ventrally, axial rib above aperture obsolete, next lower one more prominent, varix-like; last whorl somewhat gibbous dorsally, very weakly constricted at base. Aperture small, ovate; outer lip varicose, strongly thickened adapically, denticulate; two denticles at lip margin adapically, delimiting anal canal; four denticles a short distance within aperture, adapical, most prominent one just above mid-aperture, others weakening abapically. Outer lip edge everted, slightly flared anteriorly, with shallow stromboid notch abapically. Anal canal a deep notch; siphonal canal short, open. Inner lip deeply excavated over adapical portion, columella bearing c. five strongly developed, elongate, oblique denticles over abapical portion, one parietal denticle marking medial border of anal canal. Columellar and parietal callus thickened, clearly delimited, moderately expanded, somewhat detached from previous

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Figs 31-44. *Psilarius* and *Nassarius* spp. 31, *P. silvai* spec. nov., paratype, NHMW 2009z0156/0007 (ex BL), height 8.7 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch; 32-33, *P. obesus* spec. nov., paratype, NHMW 2009z0156/0010 (ex BL), height 8.0 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photograph, detail of protoconch; 34-38, *N. caloosaensis* (Dall, 1890), NHMW 2009z0156/0004 (ex BL), height 3.4 mm; Cantaure Formation (Lower Miocene, Burdigalian), lower shell bed, Casa Cantaure, Paraguaná Peninsula, Falcón, Venezuela; SEM photographs; Fig. 35, detail of protoconch; Fig. 36, detail of bryozoan encrustation; Fig. 37, 38, digital photographs, specimen partially coated; 39-40, *N. caloosaensis* (Dall, 1890), NHMW 2009z0156/0015 (ex BL), height 4.0 mm; Bermont Formation (Pleistocene), Palm Beach Rock: 3 miles west of Loxahatchee on Florida highway 441, Palm Beach County, Florida, USA; 41-42, *N. caloosaensis* (Dall, 1890), NHMW 2009z0156/0016 (ex BL), height 4.0 mm; Pinecrest Beds Unit 3 (middle Pliocene), Quality Aggregates Phase 7 quarry, Sarasota, Sarasota County, Florida, USA; 43-44, *P. metae* (Petuch, 1991), holotype, Carnegie Museum of Natural History, CM35656, height 18.0 mm; Pinecrest Beds Unit 7 (middle Pliocene), APAC quarry, Sarasota, Sarasota County, Florida, USA.

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whorl in abapical portion. Siphonal fasciole broad, flattened, bearing c. four spiral cords.

Remarks. — *Psilarius leptus* (Woodring, 1964) was described from the late Miocene Middle Gatun Formation of Panama. It is rare in Panama. Woodring's (1964a) type material consists of three specimens, three specimens are present in the NMB collections (PPP 01075 = NMB18322), and one further specimen from the middle Miocene Lower Gatun Formation at Cativa, Panama is present in the BL collection (Figs 15, 16). *Psilarius metae* (Petuch, 1991) from the Pinecrest Beds, unit 7, at APAC, Florida (middle Pliocene; Lyons, 1991) was said to differ from *P. leptus* in having "a larger shell, with stronger spiral sculpture, and in having a better-developed and larger parietal shield" (Petuch, 1991: 39, pl. 6 fig. 16; apertural view only). Petuch's photograph is severely overexposed, but new photographs of the holotype (Figs 43, 44) reveal further differences between the two taxa. *Psilarius metae* is less slender than *P. leptus*, and the spire whorls have five spiral cords; the subsutural cord is wider and more strongly developed, giving the whorls a weakly coronate appearance; the next cord below is of intermediate strength, and the abapical three cords are weaker and of equal strength. This is in contrast to *P. leptus* and the two new species from Cantaure, in which the infrasutural spiral cord is the weakest. In *P. metae* the outer lip is very strongly flared abapically, a character not seen in its congeners, making the aperture larger and the periphery of the last whorl placed more abapically rather than at mid-whorl as in its congeners; the columellar denticles are less numerous, but more prominent; the parietal denticle is much more prominent and, as rightly pointed out by Petuch (1991), the most striking character is the development of the columellar and parietal callus, covering almost the entire venter of the last whorl. The inner lip callus in all specimens of *P. leptus* I have seen is very modestly developed (Figs 15, 16). Unfortunately, no information on the intraspecific variability can be determined, as *Psilarius metae* was described from a single specimen, and enquiries in the USA have so far failed to uncover further specimens. No specimens are present in the Florida Museum of Natural History (Greg Herbert, personal communication, 2009).

For many years I identified the slender *Psilarius* specimens from Cantaure as conspecific with Gatun specimens. However, close inspection showed that the Cantaure shells are not identi-

cal to those from Gatun. The Venezuelan specimens are slightly less slender, and the denticulation is more prominent, especially on the columella, where the denticles develop into large, elongate denticles as opposed to the small round tubercles present in *P. leptus*. The siphonal canal is slightly shorter, and most importantly the columella and parietal callus is consistently more strongly developed and expanded whereas, as mentioned above, it is narrowly developed in *P. leptus*. Therefore, in slenderness and inner lip callus development *Psilarius silvai* spec. nov. seems to be intermediate in character between *P. leptus* and *P. metae*. However, none of the specimens from Cantaure has the ventral callus expanded as broadly as in *P. metae*, nor do they have it as poorly developed as in *P. leptus*. The protoconch of *P. leptus* from Gatun is similar in shape and size to that of the Cantaure shells.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela.

*Psilarius obesus* spec. nov. (Figs 17, 18, 32, 33)

Type series and dimensions. — Holotype NHMW 2009z0156/0008, height 10.7 mm (Figs 17, 18); paratype 1 NHMW 2009z0156/0009, height 10.0 mm; paratype 2 NHMW 2009z0156/0010, height 8.0 mm (Figs 32, 33); all from Cantaure Formation (early Miocene, Burdigalian), lower shell bed, 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela (locality GS12PGNA of Gibson-Smith & Gibson-Smith 1979).

Other material examined. — All from Casa Cantaure, Venezuela; maximum height 11.6 mm: 14 specimens Gibson-Smith collection, NMB locality 17516; 6 specimens BL.

Etymology. — The species name reflects the rather inflated shape of the last whorl.

Diagnosis. — A *Psilarius* species with a medium-sized shell, a relatively broad multispiral protoconch, angular spire whorls, an inflated last whorl, sculpture subobsolete on the second half of the last whorl, a strongly denticulate aperture, and a thin but widely expanded columella callus.

Description. — Shell small, solid, nassariiform. Protoconch multispiral, dome-shaped, consisting of 2.75-3 smooth, convex whorls, with small nucleus ( $dp = 1210 \mu$ ,  $hp = 830 \mu$ ,  $dp/hp =$

1.46,  $n = 140 \mu$ ,  $dV1 = 310 \mu$ ). Junction with teleoconch delimited clearly by prosocline scar. Teleoconch of 5-6 angular whorls, periphery just below mid-whorl. Suture linear, undulating. First teleoconch whorl bearing ten prosocline ribs and three narrow spiral cords. Axial ribs broadening and weakening abapically; adapical spiral cord placed just below suture, remaining two placed just above and below mid-whorl, abapical one forming periphery. Spiral cords overriding axial sculpture, swelling horizontally at intersections. Last whorl inflated, slightly flattened ventrally: axial rib above aperture obsolete, next lowest more prominent on most specimens; base constricted. Sculpture on second half of last whorl obsolete or almost so, axial sculpture reduced to tubercles at shoulder, spiral sculpture absent around mid-whorl. Aperture roundly ovate; outer lip varicose, particularly thickened adapically, denticulate; two denticles placed at lip margin adapically, in some specimens fused into one elongate denticle, delimiting anal canal; 5-6 denticles a short distance within aperture, of irregular strength, adapical one most prominent, just above mid-aperture height. Outer lip edge everted, with very small stromboid notch abapically, slightly flared anteriorly. Anal canal broad, relatively deep; siphonal canal very short, open. Inner lip roundly excavated, columella bearing irregular denticles or tubercles along its entire length; one parietal ridge marking medial border of anal canal. Columellar and parietal callus weakly thickened, clearly delimited, moderately expanded, somewhat detached from previous whorl over abapical portion. Siphonal fasciole broad, flattened, bearing numerous spiral cords.

Remarks. — *Psilarius obesus* spec. nov. is quite unlike any of its congeners discussed above and is the least columbellid-like member of the genus. It differs from all of its congeners in having a wider shell with angular rather than almost flat-sided whorls, the last whorl is inflated and constricted at the base, the sculpture on the second half of the last whorl is subobsolete, the aperture is larger, and the number of denticles on both the inner and outer is greater. The protoconch of *P. obesus* spec. nov. is the same height as that of *P. leptus* and *P. silvai* spec. nov., but twice the width. Despite these differences, the distinctive characters of the genus are clearly evident.

Distribution. — **Early Miocene:** Cantaure Formation, Venezuela.

DISCUSSION

In the Cantaure assemblage of Nassariidae, only three species (50%) are endemic. The very small number of taxa makes it difficult to draw firm conclusions, but this figure seems high compared with European assemblages. All the Cantaure nassariids have a multispiral protoconch with a small nucleus, implying planktotrophic development, which would favour wider geographical distribution and, consequently, lower endemism. Moreover, two species (33%) are also found in the Caloosahatchian Palaeobiogeographic Province, whereas nassariid species have been found to be very provincial in Europe (Marquet, 1997; Harzhauser & Kowalke, 2004; Landau et al., 2009). *Nassarius caloosaensis* not only has a very wide geographical range, but is also very long-lived for a nassariid, although not unique (Landau et al., 2009).

Nassariids are a relatively thermophilic group of gastropods, which today attain their greatest diversity in the tropical Indo-West Pacific. However, during the Miocene and Pliocene they reached their height of speciation in the tropical and subtropical European assemblages (Cernohorsky, 1984; Landau et al., 2009). The thermophilic character of the family is illustrated by the steep decline in numbers of both genera and species within the family with increasing latitude along the northwestern Atlantic frontage during the Neogene (Landau et al., 2009).

The rich Cantaure assemblage is frankly tropical in nature and yet there are relatively few species of nassariids. There are probably about 300 species of gastropods in the assemblage, but only six species of Nassariidae, representing three genera. Compared to, e.g., the tropical and subtropical early Pliocene Iberian assemblages where there are 60 species and six genera (17 if species groups are considered, as many of them probably represent distinct genera), nassariids are certainly poorly represented at Cantaure. This is, however, not unusual for the Gatunian Caribbean Neogene. Woodring (1928) recorded two species of Nassariidae in a single genus from the Bowden Formation of Jamaica; Jung (1969) recorded four species in a single genus from the Pliocene of Trinidad; Woodring (1964a) recorded four species and three genera from the Gatun Formation of Panama; Perrilliat (1972) illustrated six species in one genus from the Agueguexquite Formation of Mexico; and there are possibly up to five species in one genus in the Dominican Republic assemblages and three species in one genus in the Moin Formation of Costa

Rica (BL, unpublished data). Nassariids are rather better represented, at least at species level, in the Caloosahatchian Caribbean. Gardner (1944) described 30 species from the early and middle Miocene of Florida, although several of these are synonyms, but she included them in only one genus; Olsson & Harbison (1952) and Petuch (1994) recorded 27 species and possibly up to six genera from the Plio-Pleistocene of Florida; and Campbell (1993) recorded 11 species in two genera from the Yorktown and Chowan River Formations (Pliocene) of Virginia.

In the Pacific Gatunian province, nassariids fared no better. Pitt & Pitt (1997) recorded six species from the Neogene of northwestern Ecuador, all in *Nassarius* (sensu lato) as used here. However, this is almost certainly an underestimate of the true number of nassariid taxa present due to the paucity of Neogene Pacific outcrops, as today 37 species are present in the tropical American Pacific (see below). As in the Western Atlantic, the family was better represented at higher latitudes; Addicott (1965) described 27 species representing at least two genera from the Neogene of California.

Today the Caribbean continues to have a depauperate fauna with 13 species listed by Cernohorsky (1984), all in *Nassarius* (sensu lato). The tropical American Pacific fares slightly better; 33 species were recorded by Keen (1971), revised to 37 by Cernohorsky (1975). These figures do not compare well with the 53 species and six genera of nassariids present in the Recent fauna of eastern Atlantic tropical waters (Landau et al., 2009). Nassariids today attain their greatest diversity in tropical Indo-West Pacific waters (Cernohorsky, 1984). Water temperature alone cannot, therefore, explain the relative paucity of nassariid taxa in the tropical American Neogene and Recent assemblages. A further striking difference between the tropical American Neogene and Recent nassariids and those of the tropical Western Atlantic and Mediterranean Neogene and the Recent tropical Western Atlantic is that they never attained a large size in the Caribbean. Most species are less than 15 mm in height, whereas in the European Neogene assemblages and West Africa today large nassariids such as members of the *Nassarius mutabilis* (Linnaeus, 1758) species group (height up to 43 mm), the *Nassarius turritus* (Borson, 1820) species group (height up to 40 mm) and the genus *Demoulia* Gray, 1838 (height up to 38 mm; Landau et al., 2009) are diverse and abundant. A third difference is that specimens of nassariids are relatively uncommon in all the Neogene tropical

American assemblages sampled by me, as well as low in species diversity. Most species are represented in the author's collection by no more than a couple of dozen specimens, whereas in most European Neogene assemblages it is not uncommon to find upwards of 30 specimens per kilogram of sieved matrix.

One can only conclude that despite the tropical temperatures in the Neogene to Recent Caribbean, conditions were sub-optimal for the family. Nassariids are most suited to muddy shallow-water environments. These sites are uncommon in the Caribbean, but when present nassariids can be locally abundant, but not diverse. In the Indo-West Pacific province nassariids are very common and diverse on mud-flats, near mangroves, and in adjacent sand flats consisting of extensive fine sand. However, in Guam and the Marshall Islands, where mud is rare and not extensive, as in the Caribbean, nassariids are also uncommon (Geerat Vermeij, personal communication 14.x.2009). It is likely that part of the explanation for the failure of nassariids to diversify in the Caribbean as successfully as they did in Europe and the Indo-West Pacific was the lack of suitable substrates.

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