THE GENUS *LEUCOZONIA* (GASTROPODA: FASCIOLARIIDAE) IN THE NEOGENE OF TROPICAL AMERICA

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ABSTRACT

The fasciolariid neogastropod genus *Leucozonia* Gray, 1847, is represented in the Neogene of tropical America by four species: *L. ocellata* (Gmelin, 1791) from the Mare Formation (Late Pliocene) of Venezuela, not treated here; *L. nassa* (Gmelin, 1791), of which *L. caribbeana* Weisbord, 1962, from the Playa Grande Formation (Pleistocene) of Venezuela is a synonym; *L. rhomboidea* (Gabb, 1873) from the Gurabo Formation (Early Pliocene) of the Dominican Republic; and *L. striatula*, n. sp., from the Cercado and lower Gurabo formations (Late Miocene to Early Pliocene) of the Dominican Republic. *Leucozonia rhomboidea* closely resembles the Recent *L. leucozonalis* (Lamarck, 1822) from the northwestern Caribbean and an unnamed Recent species from the Brazilian island of Fernando de Noronha. *Leucozonia striatula* is very similar to the Recent *L. brasiliana* (d'Orbigny, 1841) from the Atlantic coasts of Central and South America.

INTRODUCTION

Species of the fasciolariid neogastropod genus *Leucozonia* are common inhabitants of low rocky intertidal and sublittoral communities in tropical America and the Cape Verde Islands. Despite its ecological prominence, *Leucozonia* is poorly represented in the fossil record. Only two fossil species, *L. rhomboidea* (Gabb, 1873) from the Neogene of the Dominican Republic and *L. caribbeana* Weisbord, 1962, from the Mare Formation (Late Pliocene) of Venezuela have been described. A third species, the Recent *L. ocellata* (Gmelin, 1791), has been recognized in the Mare Formation (Gibson-Smith and Gibson-Smith, 1979), and will not be discussed further here. In this paper, I critically assess the fossil species, and describe *L. striatula*, n. sp., from the Late Miocene and Early Pliocene of the Dominican Republic.

ABBREVIATIONS

ANSP - Academy of Natural Science, Philadelphia, Pennsylvania
NMB - Naturhistorisches Museum, Basel, Switzerland
USNM - United States Museum of Natural History, Washington, D. C.
PRI - Paleontological Research Institute, Ithaca, New York

SYSTEMATICS

Family FASCIOLARIIDAE Gray, 1853
Subfamily PERISTERNIINAE Tryon, 1880
Genus LEUCOZONIA Gray, 1847

Leucozonia GRAY, 1847, Zoological Society of London, Proceedings, v. 15, p. 184.

Type species: *Murex nassa* Gmelin, 1791, by monotypy.

Remarks: Bullock (1974) and Lyons (1991) have pointed out that *Latirus gibbulus* (Linnaeus, 1758), the Indo-West Pacific type species of *Latirus* Montfort, 1810, is very similar in the character of its radula and shell to *Leucozonia*, and that *Leucozonia* may therefore be a junior subjective synonym of *Latirus*. Woodring (1928) recognized that *Latirus* is a heterogeneous group requiring thorough revision, especially among its Indo-West Pacific species. Lyons (1991) referred many fossil and Recent species from the Americas to *Latirus*, but remarked that none of these belong to *Latirus* in the strict sense, as typified by L. *gibbulus*. I have chosen to retain *Leucozonia* as a valid genus, pending a thorough revision of *Latirus* and of such related taxa as *Ascolatirus* Bellardi, 1884; *Dolicholatirus* Bellardi, 1884; *Fractolatirus* Iredale, 1936; *Fusolatirus* Kuroda and Habe *in* Kuroda *et al.*, 1971; *Glaphyrina* Finlay, 1927; *Hemipolygona* Rovereto, 1899 (*Latirus* group 1 of Lyons, 1991); *Hesperisternia* Gardner, 1944; *Latirolagena* Harris, 1897; *Latirulus* Cossmann, 1889; *Neolatirus*

Bellardi, 1884; *Nodopelagia* Hedley, 1915; *Opeatostoma* Berry, 1958; *Peristernia* Mörch, 1852; *Polygona* Schumacher, 1817 (*Latirus* group 2 of Lyons, 1991); *Pseudolatirus* Bellardi, 1884; *Taron* Hutton, 1883; and *Teralatirus* Coomans, 1965.

Leucozonia is characterized by a relatively short, broadly open anterior siphonal canal, by three or four basal columellar folds, a well-marked parietal rib at the adapical end of the inner lip, by having the inner side of the outer lip sculptured by granulated lirae, and usually by having a labral tooth at the outer lip situated at the end of a prominent spiral cord. Below this cord, the last whorl is constricted; that is, it has a concave lateral profile. At least two species, *L. cerata* (Wood, 1828) from the tropical eastern Pacific and *L. ocellata* (Gmelin, 1791) from the tropical western Atlantic, differ from typical *Leucozonia* by having the lirae on the inner side of the outer lip smooth, by having the outer lip planar instead of convex when viewed from the apertural side, and by lacking the labral tooth. The species discussed below all belong to the more typical group of *Leucozonia*.

LEUCOZONIA NASSA (Gmelin, 1791)

Leucozonia caribbeana WEISBORD, 1962, Bulletins of American Paleontology, v. 42, no. 193, p. 361-362, pl. 32, figs. 9, 10.

Remarks: Weisbord (1962) named *Leucozonia caribbeana* from the Maiquetia Member of the Playa Grande Formation of Venezuela. Gibson-Smith and Gibson-Smith (1979) argued that this unit is continuous with, and part of, the Mare Formation, to which they assign a Middle or Late Pliocene age. Gonzalez de Juana *et al.* (1980) regarded the Maiquetia Member as a distinct unit and considered it to be of Pleistocene age. The great majority of species in both the Maiquetia Member and the Mare Formation are still living in Venezuelan waters (Gibson-Smith and Gibson-Smith, 1979). I suspect both units represent the Early Pleistocene.

Weisbord (1962) distinguished *L. caribbeana* from *L. nassa* because the fossil has seven instead of nine shoulder knobs, three instead of four columellar folds, and a wider, more oblique, anterior siphonal canal. The holotype of *L. caribbeana* (PRI 26261) is an immature shell in which the inner side of the outer lip is smooth instead of being ornamented with granulated lirae. Like typical *L. nassa* from the insular Caribbean Recent fauna, *L. caribbeana* has prominent shoulder knobs, three closely spaced spiral cords on the upper part of the last whorl, and a well-developed labral tooth at the end of a fourth primary cord, which is separated from the three upper cords by a spirally threaded sector. Recent *L. nassa* is variable in the number and prominence of shoulder knobs and in the number of columellar folds. The shoulder always forms the widest part of the shell, and bears seven to ten knobs. These knobs are formed where the shoulder cord is crossed by strong axial ribs, whose lower end is marked by the tooth-bearing cord. Recent specimens have three to four (rarely five) columellar folds. I have seen Recent *L. nassa* from Florida, the Bahamas, Saint Maarten, Guadeloupe, Curaçao, and the Brazilian island of Fernando de Noronha. Given the variation observed in Recent *L. nassa*, I see no basis for separating *L. caribbeana*, and I therefore consider *L. caribbeana* as a junior subjective synonym of *L. nassa*.

LEUCOZONIA STRIATULA, new species
Figures 1, 2

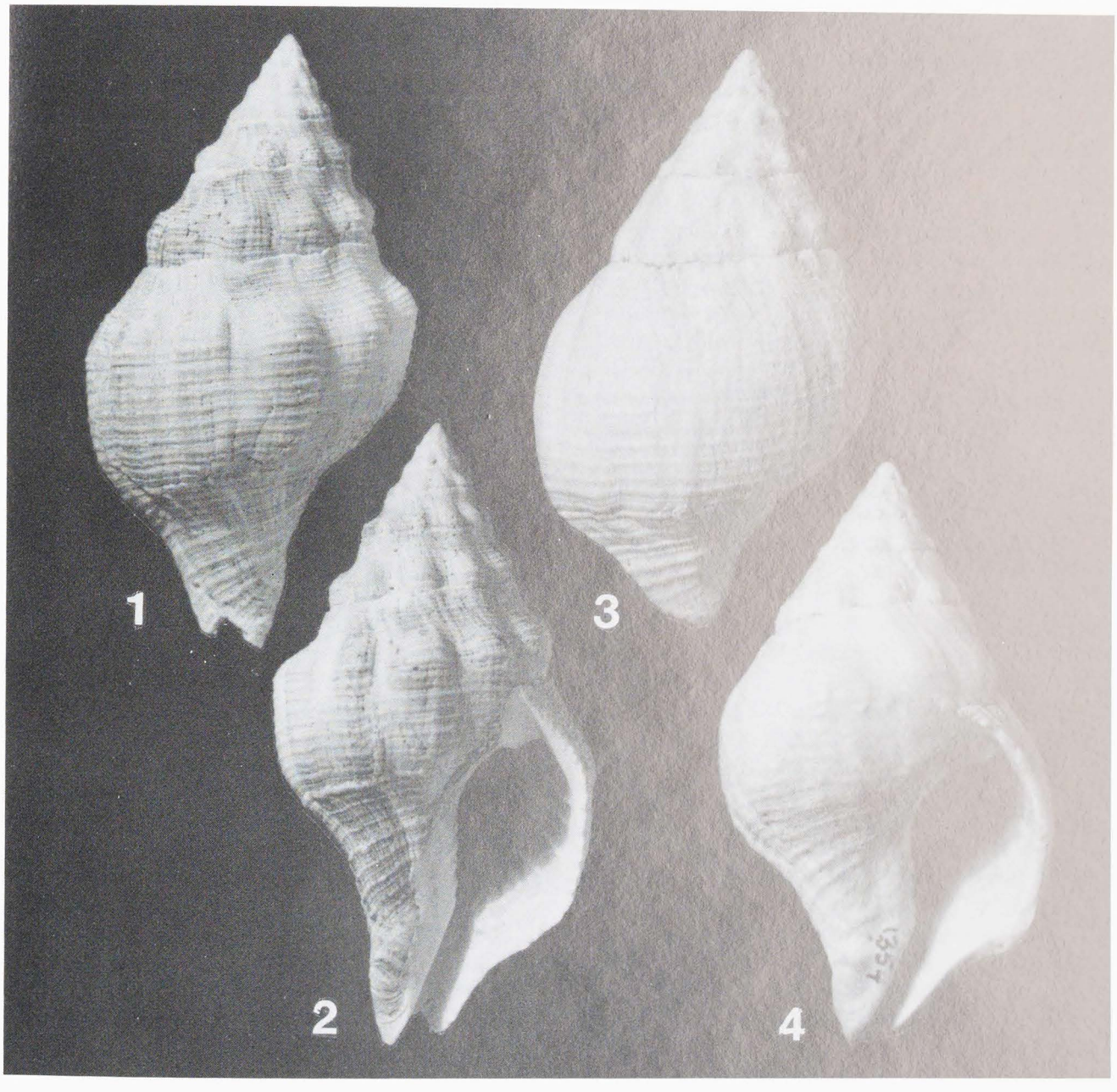
Diagnosis: Leucozonia with well-developed axial ribs, fine spiral threads, a distinct labral tooth, and a long anterior siphonal canal.

Description: Shell moderately large, maximum height 49.1 mm, fusiform, diameter 52-61% of shell height; spire moderately low, last whorl comprising 65-68% of total shell height; protoconch consisting of one smooth whorl; teleoconch consisting of five whorls separated by indistinct, appressed suture; last whorl with angulate shoulder above at widest part of shell, constricted at base; shoulder becoming rounded on last quarter of whorl of large specimens; spiral sculpture of last whorl consisting of ten fine cords on concave subsutural ramp, nine to twelve low cords between shoulder and tooth-bearing cord, and ten to twelve fine cords below tooth-bearing cord; axial sculpture consisting of eight to eleven low, broad, rounded ribs, extend-

ing from suture to suture in spire whorls, and from suture to tooth-bearing cord on last whorl; axial ribs weak and irregular on last quarter whorl of large specimens; outer lip sharp, crenulated at edge, medially convex when viewed from apertural side; sharp labral tooth formed at end of prominent spiral cord at abapical end of convexly rounded sector of last whorl; outer lip forms broad, shallow, concave sinus below labral tooth on abaxial side of siphonal canal; inner side of outer lip with ten deeply recessed lirae; inner lip adherent, with three basal columellar folds; well-developed parietal rib at adapical end of inner lip in large specimens; aperture elongate-ovate, its height:breadth ratio 2.7-2.9; anterior siphonal canal long, 33-40% of total apertural height; siphonal fasciole low, rounded; umbilicus absent.

Holotype: USNM 490523; height 38.5 mm, maximum diameter 22.7 mm, height of aperture plus canal 25.2 mm, breadth of aperture 9.3 mm.

Paratype 1: NMB H 17804, height 49.1 mm, maximum diameter 30.0 mm.



Figures 1, 2: *Leucozonia striatula*, new species. USNM 490523 (holotype), height 38.5 mm; locality TU 1422.
Figures 3, 4: *Leucozonia rhomboidea* (Gabb, 1873). USNM 490550, height 35.4 mm; locality TU 1354.

Paratype 2: ANSP 79634; height 44.0 mm, maximum diameter 24.7 mm.

Paratype 3: PRI 44387; height 41.9 mm, maximum diameter 22.6 mm.

Type locality (holotype and paratypes 1 and 2): locality TU 1422, Arroyo Bellaco, Cercado Formation, Dominican Republic.

Other localities: Paratype 3, locality TU 1215, lower Gurabo Formation, Río Gurabo, bluffs above ford on Los Quemados-Sabaneta Road, Dominican Republic.

Other material examined: Three specimens, locality TU 1422; five specimens, locality TU 1215.

Stratigraphic and geographic distribution: Cercado Formation (Late Miocene) and lower Gurabo Formation (Early Pliocene), Dominican Republic.

Remarks: In several characters, *Leucozonia striatula* represents an intermediate condition between species of *Polygona* (*Latirus* group 2 of Lyons, 1991) and typical *Leucozonia*. Like species of *Polygona*, the new species has a relatively long anterior siphonal canal and fine spiral sculpture. In most species of *Polygona*, spiral sculpture is not as fine as in *L. striatula*, but the number of cords on the last whorl is low as in *L. nassa, L. ocellata*, the deep-water western Atlantic *L. jacarusoi* Petuch, 1987, the eastern Atlantic (Cape Verde Islands) *L. triserialis* (Lamarck, 1822), or the eastern Pacific *L. cerata* (Wood, 1828), *L. rudis* (Reeve, 1846), and *L. tuberculata* (Broderip, 1833). *Leucozonia striatula* differs from tropical American members of the genus *Polygona* by having a distinct labral tooth at the end of a cord, which marks the abapical end of the axial sculpture.

The species most similar to *L. striatula* is the Recent western Atlantic *L. brasiliana* (d'Orbigny, 1841), which is distributed on the coasts of Central and South America, south to southern Brazil. *Leucozonia striatula* differs from *L. brasiliana* by having a slightly lower spire (last whorl comprising 65-68% instead of 63-64% of total shell height), generally fewer axial ribs (eight to eleven as compared to ten to thirteen in *L. brasiliana*), by having the widest part of the shell at the shoulder instead of below the shoulder, and by having finer spiral threads between the shoulder and the suture. *L. brasiliana* was considered to be a synonym of *L. nassa* by Marcus and Marcus (1962). Both *L. brasiliana* and *L. striatula* differ from *L. nassa*, however, in having about ten fine cords between the shoulder and the tooth-bearing cord. In *L. nassa*, there are three large cords at and just below the shoulder, separated from the tooth-bearing cord by fine threads. Most specimens of *L. nassa*, moreover, are less slender than *L. brasiliana* and *L. striatula* (diameter 57-69% as compared to 52-61% of total shell height).

Like *L. rhomboidea* (below), *L. striatula* is found in reef facies (see Saunders *et al.*, 1986). The living *L. brasiliana* occurs in similar habitats.

Leucozonia rhomboidea (Gabb, 1873)
Figures 3, 4

Lagena rhomboidea GABB, 1873, American Philosophical Society, Transactions, new ser., v. 15, p. 218.

Leucozonia rhomboidea (Gabb). PILSBRY, 1922, Proceedings of the Academy of Natural Sciences of Philadelphia, v. 73, p. 345, pl. 21, fig. 9.

Description: Shell medium-sized, maximum height 39.7 mm, fusiform; diameter 62-65% of total shell height; spire moderately low, last whorl comprising 61-65% of total shell height; protoconch consisting of one smooth whorl; teleoconch consisting of six whorls separated by adpressed, indistinct suture; last whorl without shoulder, evenly rounded above, weakly constricted at base; spiral sculpture of penultimate whorl consisting of about sixteen fine threads; spiral sculpture of last whorl consisting of about ten weak basal cords, and of about twenty-three very fine threads on upper part of whorl; axial sculpture consisting of about ten low, rounded ribs on spire whorls, absent on all or least half of last whorl; outer lip medially convex when viewed from apertural side, with labral tooth at end of uppermost spiral cord; inner side of outer lip with eleven lirae; inner lip adherent, with three basal columellar folds; parietal rib situated at adapical end of inner lip in larger specimens; aperture elongate-ovate, its height: breadth ratio 2.5-2.7; anterior siphonal canal 27-31% of total apertural height; siphonal fasciole rounded; umbilicus absent.

Material examined: ANSP 2947 (lectotype),

Cibao region, Dominican Republic; ANSP 79165 (paralectotype), Cibao region, Dominican Republic; NMB locality 16818, Cañada de Zamba, Dominican Republic; USNM 490550, Cañada de Zamba, locality TU 1354, Dominican Republic (figs. 3, 4).

Stratigraphic and geographic distribution: Gurabo Formation (Early Pliocene), Cañada de Zamba, Dominican Republic.

Remarks: Dall (1890, p. 106) thought that Gabb's *Lagena rhomboidea* might be a young specimen belonging to the genus *Mazzalina* Conrad, 1860, but Pilsbry (1922, p. 345) correctly recognized it as a *Leucozonia*. The species closely resembles the Recent *L. leucozonalis* (Lamarck, 1822) from the northwestern Caribbean. Both species reach the same maximum height of about 40 mm. They have a rounded, finely spirally threaded last whorl, and lack a distinct shoulder. *Leucozonia leucozonalis* is generally somewhat more slender (diameter 53-65% of total shell height), lacks the axial sculpture of the upper whorls of *L. rhomboidea*, and has a slightly longer canal (33-36% instead of 27-31% of total apertural height).

An even more similar form is an unnamed Recent species from Fernando de Noronha that previous authors have considered a variety of *L. nassa* (see Smith, 1890; Lopes and Alvarenga, 1955; Matthews and Kempf, 1970; Leal, 1991). This Recent species differs from *L. rhomboidea* by having a somewhat broader shell (diameter 68-74% instead of 62-65% of shell height), a relatively shorter siphonal canal (17-21% instead of 27-31% of apertural length), and in having ten low, rounded, broad, obsolete axial ribs on the last whorl instead of having the last whorl partly or entirely devoid of axial ribs.

The two previously known specimens of *L. rhomboidea* (ANSP 2947 and 79165) are immature shells with a height of about 10 mm. One of these (ANSP 2947, the lectotype) is the only specimen with the protoconch preserved. New material shows that the species attains a height of at least 39.7 mm, a height comparable to that of other species of *Leucozonia*.

Leucozonia rhomboidea has been collected at a single locality, TU 1354 (= locality NMB 16818), in the Early Pliocene part of the Gurabo Formation. The assemblage at this locality represents a coral community of the kind in which *L. leucozonalis* commonly lives today (see Saunders *et al.*, 1986; Vermeij, 1973).

Two of five specimens of *L. rhomboidea* from TU 1354 bear eroded pits evidently excavated by a hipponicid gastropod. I shall report on these pits and their makers in a separate paper.

DISCUSSION

Its Late Miocene occurrence makes *L. striatula* the oldest known member of the genus *Leucozonia*. Further collecting in older deposits will probably reveal even earlier representatives. The available evidence shows that a labral tooth evolved in *Leucozonia* no later than the Late Miocene. Many other gastropods also evolved a labral tooth during the Miocene in tropical America. These include members of the muricid subfamilies Muricinae, Ocenebrinae, and Rapaninae. Species of Pseudolividae and the olivid subfamily Ancillinae inherited the labral tooth from Paleogene ancestors. Oddly enough, the large muricid fauna of the Miocene and Pliocene of the Dominican Republic (Vokes, 1989) is highly unusual among Neogene tropical American muricid assemblages in lacking species with a labral tooth. Pseudolivids and ancillines are also absent from the Late Neogene Dominican fauna. Did the evolution of a labral tooth in *Leucozonia* in the reef environments of the Dominican Republic fill an adaptive gap left vacant by other groups? Further work on the biogeography and phylogeny of gastropods with a labral tooth may shed further light on this interesting possibility.

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