

A Large New Species of *Lobatus* (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with Notes on the Genus

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Abstract. A very large new stromb is described from the Neogene of the Dominican Republic, *Lobatus vokesae* sp. nov. *Lobatus* is used here as a genus to include the Tropical American clade of species previously placed in the subgenus *Tricornis*. The new species has characters in common with all the various subgenera proposed within the genus, making subgeneric assignment of this early member of the genus *Lobatus* undesirable.

Key Words: Gastropoda, *Lobatus*, new species, systematics, Neogene, Dominican Republic.

INTRODUCTION

The Strombidae are a group of tropical to subtropical gastropods, predominantly inhabiting the intertidal and subtidal zones, feeding on macroalgae and epiphytes (Robertson, 1961; Berg, 1975). Species in this family are conspicuous because of their medium-sized to very large, solid, heavy shells.

The early and late Miocene deposits on the island of Hispaniola, and more specifically the outcrops occurring along the Cibao valley of the Dominican Republic, are well known for their fauna of Strombidae. Sowerby (1850) was the first to describe fossil mollusks from these rich localities and named three species of *Strombus*. Subsequent workers such as Maury (1917) and Pilsbry & Johnson (1917) have brought the number of strombid taxa known from these deposits to nine (Table 1). However, this is far from being a comprehensive list of the strombid taxa occurring in the Dominican Republic. Our own collections (BL) include probably four undescribed species, the most spectacular of which is described in this paper.

SYSTEMATIC DESCRIPTION

Genus *Lobatus* Iredale, 1921

Type species: (by monotypy, Iredale, 1921: 208): - *Strombus bituberculatus* Lamarck, 1822: 690. Junior subjective synonym of *S. raninus* Gmelin, 1791: 3511. Recent, West Indies and Florida.

Remarks: Throughout the Neogene, the Strombidae have formed an important part of tropical American assemblages, especially in the western Atlantic, where they diversified into numerous species and formed several distinct species groups. Classically, Neogene tropical American *Strombus* species have been placed in three genera or subgenera; *Strombus* (s.s.) [type species *S. pugilis* Linnaeus, 1758, by subsequent designation, Recent, western Atlantic], *Lentigo* Jousseaume, 1886 [type species *Strombus lentiginosus* Linnaeus, 1758, by monotypy, Recent, East Africa], and *Tricornis* Jousseaume, 1886 [type species *Strombus tricornis* Lightfoot, 1786, by monotypy, Recent, Indo-Pacific]. The new species described in this paper belongs to the last group.

Table 1

Preliminary list of strombid taxa so far recorded from the Neogene Dominican Republic. Column 1: the original name under which the taxon was described; column 2 the formation in which it occurs (recorded from literature and BL collections); column 3: original references and subsequent references with figures. Sowerby's (1850) type material was illustrated by Pflug (1961).

Taxon	Formation	Reference
<i>Strombus haitensis</i> Sowerby, 1850	Gurabo and Cercado	Sowerby, 1850, p. 48, pl. 9, fig. 7 Pflug, 1961, p. 26–27, pl. 3, figs 1, 2, 3, 5, 6, 8
<i>Strombus proximus</i> Sowerby, 1850	Gurabo and Cercado	Sowerby, 1850, p. 48, pl. 9, fig. 8 Pflug, 1961, p. 24–26, pl. 2, figs 5, 6, 8, 9, 10
<i>Strombus bifrons</i> Sowerby, 1850	Gurabo	Sowerby, 1850, p. 48, pl. 9, fig. 9 Pflug, 1961, p. 27–28, pl. 4, figs 1–4, 7, 8, 10
<i>Strombus ambiguus</i> Sowerby, 1850	Unknown	Sowerby, 1850, p. 48 Pflug, 1961, p. 28–29, pl. 4, figs 5, 6, 9
<i>Strombus pugiloides</i> Guppy, 1866	?Cercado	Maury, 1917, p. 120, pl. 20, fig. 6 Pflug, 1961, p. 23–24, pl. 3, figs 4, 7
<i>Strombus maoensis</i> Maury, 1917	?Mao	Maury, 1917, p. 120, pl. 21, fig. 1
<i>Strombus galliformis</i> Pilsbry, 1917		Pilsbry, 1917, p. 170
<i>Strombus dominator</i> Pilsbry, 1917	Gurabo	Pilsbry & Johnson, 1922, p. 366, pl. 31, figs 1–2 Pilsbry, 1917, p. 170
<i>Strombus (Lentigo) cf. raninus</i> Gmelin, 1791	Gurabo	Pilsbry & Johnson 1922, p. 366, pl. 32, figs 1, 9 Jung & Heintz, 2001, p. 44, fig. 19

The systematics of *Tricornis*, however, require revision. A molecular phylogeny of strombids shows that *Tricornis* is polyphyletic and comprised of separate, distantly related tropical American and Indo-Pacific clades (Latiolais et al., 2006). Kronenberg & Lee (2007) argued that *Lobatus* Iredale, 1921 [type species *Strombus bituberculatus* Lamarck, 1822, by monotypy, Recent Caribbean (junior subjective synonym of *S. raninus* Gmelin, 1791)] is the first available name for the tropical American group previously known as *Tricornis* (sensu Abbott, 1960).

In this paper, we treat *Lobatus* as a full genus, as this clade is separated from all other strombids, including *Strombus* (s.s.), by one of the longest and best-supported branches in the strombid molecular tree. Notably, this conflicts with the tree topology of strombids inferred from anatomical data (Simone, 2005). However, the Latiolais et al. (2006) phylogeny is based on an analysis of nearly three times as many strombid taxa and at least twice the number of phylogenetically informative characters as Simone's (2005) tree, and is less likely to change as more data are added.

Whether and how the *Lobatus* group should be divided into subgenera is not entirely clear with the data at hand. Based on shell features, Petuch (2004) subdivided the tropical American species of *Tricornis* into several subgenera: *Aliger* Thiele, 1929 [type species *Strombus gallus* Linnaeus, 1758, by monotypy, Recent, Caribbean], *Eustrombus* Wenz, 1940 [type species *Strombus gigas* Linnaeus, 1758, by original designation, Recent, Caribbean], *Macrostrombus* Petuch, 2004 [type species *Strom-*

bus costatus Gmelin, 1791, by original designation, Recent, Caribbean] and *Titanostrombus* Petuch, 2004 [type species *Strombus goliath* Schröter, 1805, by original designation, Recent, Brazil]. It should be noted that Petuch (1994) regarded all these as subgenera of *Strombus*, and employed *Lobatus* in the same fashion, viz. a subgenus of *Strombus*. The molecular phylogeny of Latiolais et al. (2006) shows *S. gallus*, *S. gigas* and *S. costatus* to be very closely related.

The genus *Lobatus* Iredale, 1921 was introduced without a description. *Lobatus* is defined here as a clade of medium sized to very large strombs with widely expanding, *non* digitated, outer lips, and a glazed outer edge of the rim of the outer lip, not bent toward the columella when reaching maturity, usually with strong spiral sculpture on the last whorl. This clade is in Recent times restricted to the Caribbean and Panamic faunal Provinces. It is first recorded from the Lower Miocene Chipola Formation of Florida as *Strombus chipolanus* Dall, 1890 (Gardner, 1947; Petuch, 2004) and the Middle Miocene Baitoa Formation of the Dominican Republic by another undescribed species (Bernard Landau unpublished data). *Lobatus* is represented in the Late Miocene to Early Pliocene Dominican Republic assemblages by *S. haitensis*, *S. galliformis*, *S. dominator*, *S. raninus* and *Lobatus vokesae* sp. nov. *Strombus maoensis* Maury, 1917 was based on a single incomplete shell, and despite intensive collecting we have found no further specimens. Maury (1917) compared *S. maoensis* to *S. gallus*, and it probably represents a species of *Lobatus*. *Strombus ambiguus* Sowerby, 1850 is also based on a

juvenile specimen of a *Lobatus* species (lectotype illustrated by Pflug, 1961).

Abbreviations: The following abbreviations are used: NMB = Naturhistorisches Museum Basel localities; TU = Tulane University localities; NHMW = Naturhistorisches Museum in Wien (Austria) collection number; BL coll. = Bernard Landau collection.

SYSTEMATIC DESCRIPTION

Genus *Lobatus* Iredale, 1921

Type species: (by monotypy, Iredale, 1921: 208): - *Strombus bituberculatus* Lamarck, 1822: 690 (junior subjective synonym of *S. raninus* Gmelin, 1791: 3511), Recent, West Indies and Florida.

Lobatus vokesae Landau, Kronenberg and Herbert sp. nov.

(Figures 1–7)

Etymology: We have great pleasure in naming this magnificent shell in honor of Emily Vokes for her enormous contribution to Caribbean Neogene paleontology.

Description: (Based on holotype and paratype) Shell very large, solid, when complete reaching at least 270 mm high. Protoconch not known. Seven teleoconch whorls preserved. Spire broadly conical, weakly coeloconoid in profile, spire whorls depressed in holotype; fifth and penultimate whorls slightly elevated and roundly shouldered in paratype. Sculpture on early teleoconch whorls of small rounded tubercles placed immediately above abapical suture, crossed by numerous fine spiral threads. Abapically tubercles become weaker, subobsolete on fourth whorl, and spiral threads broaden to form relatively narrow, flattened, subequal spiral cords. Suture impressed, crenulated around tubercles on early teleoconch whorls, weakly undulating abapically. Last whorl greatly inflated, bearing three large, roundly pointed tubercles at shoulder, first tubercle placed opposite (to left of) aperture, third on dorsum, second tubercle midway between other two. Dorsal tubercle very strongly developed, first tubercle slightly smaller, intermediate tubercle weakest. Spiral sculpture of broad, flattened, primary spiral cords, only clearly developed on mid-portion of last whorl, where there are 10–13 cords, and numerous irregular flattened secondary cords. Growth lines prominent on portions of last whorl, interrupting secondary cords, giving a somewhat reticulate aspect to parts of dorsum. Outer lip not thickened, greatly expanded, its apical end extended above height of apex (when outer lip complete) and expanded medially to join ventral midline. Outer edge of lip and strombid

notch not preserved. Parietal wall smooth. Base of columella strongly bent backwards. Siphonal canal open, relatively long and broad, bent slightly to right and weakly posteriorly recurved.

Holotype: NHMW 2007z0161/0001

Dimensions of holotype: Length 220 mm; dorso-ventral height (restored) 165 mm; width 190 mm (Figures 1–3).

Type locality: Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15).

Material: Holotype; and 1 Paratype (B. Landau coll.), length 264 mm; dorso-ventral 150 mm; width (incomplete outer lip) 180 mm (Figures 4–7); locality Cañada de Zamba, off Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15).

Remarks: This species is based on two adult specimens from different localities along the Rio Cana, the holotype from beds of late Miocene age, the paratype from basal Pliocene beds. Neither of the specimens is perfect; both are missing the outer part of the outer lip (more complete in the holotype), and the holotype has the top of the dorsal tubercle abraded. The paratype shows signs of damage during life, possibly as a result of attack by a predator, and subsequent repair, with an irregular fracture line running the whole length of the last whorl.

There are some differences between the two specimens; the paratype when complete would have been the larger shell. It has a slightly more elevated spire than the holotype, and the tubercles at the shoulder of the last whorl are even more massive than in the holotype.

Comparisons: *Lobatus vokesae* sp. nov. is similar in size to the Recent *Lobatus gigas*, and both species have a broadly expanded but not thickened outer lip. The character of their spires, however, is quite different, as it is much more elevated in *L. gigas* than in *L. vokesae* n. sp., with all the spire whorls bearing pointed tubercles and a greater number of more pointed tubercles on the shoulder of the last whorl. The first record of *L. gigas* is from the Bowden Formation of Jamaica (Jung, 1971). The Bowden Beds are usually considered late Miocene to early Pliocene (Berggren, 1993) or early Pliocene (Bolli & Bermudez, 1965; Bolli & Premoli Silva, 1973; Jung & Heitz, 2001), although Aubry (1993) placed them in the early late Pliocene (calcareous nannoplankton zone NN16). It has been suggested to us that the Bowden Formation is an olistostrome, which would account for these different ages (Oliver Macsotay, personal communication,



Figures 1–3. *Lobatus vokesae* Landau, Kronenberg and Herbert sp. nov. Holotype, NHMW 2007z0161/0001. Locality: Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15). Length 220 mm; dorso-ventral height (restored) 165 mm; width 190 mm.

2007). *Lobatus gigas* has not been found in the Dominican Republic assemblages.

The Recent *Lobatus goliath* Schröter, 1805 has an even larger shell, also with a non-thickened outer lip, which is even more widely expanded than in the *L. vokesae* sp. nov. or *L. gigas*. The spire of *L. goliath* is similar to that of our new species; depressed, devoid of tubercles (or almost so) and with a coeloconoid profile,

but the tubercles on the last whorl are more numerous and far less strongly developed than in *L. vokesae* sp. nov. We are not aware of any fossil record for *L. goliath*. *Lobatus williamsi* (Olsson & Petit, 1964) from the late Pliocene of Florida, allocated to *Titanostrombus* by Petuch (1994), also lacks the large shoulder tubercles on the last whorl of our new species, but it has some distinct knobs on the shoulder of the



Figures 4–7. *Lobatus vokesae* Landau, Kronenberg and Herbert sp. nov. Paratype, BL coll. Locality: Cañada de Zamba, off Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15). Length 264 mm; dorso-ventral 150 mm; width 180 mm.

penultimate whorl (Petuch, 1994: pl. 20, fig. A) that are not present in *L. vokesae* sp. nov.

The characters of the tubercles and the depressed spire, almost devoid of sculpture, are similar to those of the Recent Florida species *Lobatus costatus* Gmelin, 1791. However, in *L. costatus* the outer lip is not so greatly expanded, especially in the adapical portion, and is very strongly thickened. *L. costatus* is also a smaller species and lacks the complex spiral sculpture of primary and secondary cords present on the last whorl of *L. vokesae*. Petuch (1994) described a subspecies *Strombus (Macrostrombus) costatus griffini* Petuch, 1994 from the Late Pliocene of Florida. The shell illustrated (Petuch, 1994, pl. 19, fig. H) and numerous topotypes in the BL collection all have much weaker tubercles than the Recent shell or *L. vokesae* and we agree that they are not conspecific. However, several other *Strombus (Macrostrombus)* species were described in the same publication, very similar to this subspecies, and a review of these taxa is beyond the scope of this work. *Lobatus costatus* occurs fossil in the Pleistocene Tortuga Formation of Cubagua Island, Venezuela (Bernard Landau unpublished data).

Within the Dominican assemblage, *Lobatus vokesae* sp. nov. is most similar to *L. dominator* in the character of its very prominent dorsal tubercle. However, *L. dominator* has a much smaller shell (less than half the size of *L. vokesae*), the primary spiral cords on the last whorl are more distinct, and the shape of the outer lip is quite different. We (BL coll.) have six specimens of *L. dominator* from the Cercado and Gurabo Formations of the Dominican Republic. These specimens are highly variable, and in the largest the adapical extremity of the outer lip is developed into an open digitation, similar to but not as elongated as that seen in the Recent Caribbean species *L. gallus* (Linnaeus, 1758). *Strombus dominator delabechei* Rutsch, 1931, described from the Bowden Beds of Jamaica, probably falls within the range of variation of Dominican Republic specimens.

The shells of *Lobatus vokesae* sp. nov. demonstrate characters intermediate between those of the subgenera *Eustrombus* (very large, greatly expanded and not thickened outer lip), *Macrostrombus* (ribbed last whorl sculpture, large tubercles at the shoulder) and *Titanostrombus* (very large size, combined with a low, coeloconoid spire) as recognized by Petuch. Therefore, it seems undesirable to assign *L. vokesae*, an early species of *Lobatus*, to any subgenus within the genus *Lobatus*. In the more Recent fossil record fairly well defined lineages can be recognized within *Lobatus*.

The origins of the genus *Lobatus* are unclear at present, but it is likely that it arose from a species which would be allocated to *Persististrombus* Kronenberg & Lee, 2007. Within *Persististrombus* there are some tendencies towards *Lobatus*-like species (Harzhauser & Kronenberg, in prep.).

Geological and environmental setting: The holotype is from the Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15). This is a 50 cm thick bed with closely packed small molluscs in which *Astraea* Röding, 1758 and *Tegula* Lesson, 1835 predominate. Other common gastropods are *Erosaria spurca* (Linnaeus, 1758), *Pachycrommium guppyi* (Gabb, 1873), *Polinices subclausa* (Sowerby, 1850), *Neverita (Hypterita) nereidis* (Maury, 1917) *Semicassis reclusum* (Guppy, 1873) and *Chicoreus cornurectus* (Guppy, 1876). These probably represent shallow inshore conditions.

The paratype is from the Cañada de Zamba locality, a tributary of the Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15). This locality has a rich and varied gastropod fauna with no particular group predominant. Corals are common and represent a reef structure probably less than 30 m in depth (Saunders et al., 1986).

Occurrence: Known only from the late Miocene and early Pliocene Cercado and Gurabo Formations of Rio Cana and its tributary Cañada de Zamba, Dominican Republic.

DISCUSSION

Although the development of a dorsal tubercle is widespread in Recent species of *Lobatus*, the occurrence of this feature in *L. vokesae* is one of the earliest examples within the genus. The function of the dorsal shell protuberance is almost certainly anti-predatory, with a primary role in helping the animal to right its shell after being turned over by predatory fish, crabs, and octopus (Berg, 1975). The large dorsal tubercle forces the overturned shell to lean to either side, which reduces the time and extent to which the animal must extend its soft foot outward and unprotected to right the shell (Savazzi, 1991; see also Carefoot and Donovan, 1995). Selection for a prominent dorsal tubercle should be greatest in larger strombs with a flaring lip, and *L. vokesae* was one of the largest early strombs. Berg (1975) demonstrated that larger strombids are exposed for a longer period of time during righting due, in part, to their own weight and the broad, heavy lip.

Interestingly, the presence or absence of the dorsal tubercle varies interspecifically as well as intraspecifically in strombids, e.g., *Persististrombus granulatus* (Swainson, 1822). An example of the variability of shoulder knobs within a single species of *Lobatus* is illustrated by the case of *L. fetus* (Jung & Heitz, 2001), described from the late Pliocene Escudo de Veraguas Formation, Bocas del Toro area of Panama. In our opinion this is based on a specimen of *L. raninus* in

which the large dorsal shoulder knob is not developed. This variability can also be observed today, albeit uncommonly, in Recent specimens (Gijs Kronenberg, personal observation) and in Pleistocene fossil and Recent *L. costatus* (Gregory Herbert, personal observation). Therefore, a division of *Lobatus* into subgenera based solely on this sculptural element is unwarranted.

The Plio-Pleistocene radiation of *Lobatus* species in Florida resulted in a cohort of species that all had weaker tubercles than the fossil *L. vokesae* and living *L. costatus* or *L. raninus*, or had lost them altogether as in the cases of *Strombus* (*Macrostrombus*) *hertweckorum* Petuch, 1991 and *Strombus* (*Macrostrombus*) *leidy* Heilprin 1886. Whatever changes in predatory patterns led to the loss of tubercles in the Floridian assemblages seem to have affected strombs as a whole, as the genus *Strombus* (s.s.), which is also greatly diversified in the Plio-Pleistocene of Florida, shows a similar pattern, with a radiation of Pliocene species with no tubercles on the last whorl (see Petuch, 1994; Hargreaves, 1995). The actual number of species within this radiation cannot be commented with certainty at present, as the numerous taxa described and illustrated by Petuch (1994) require revision.

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