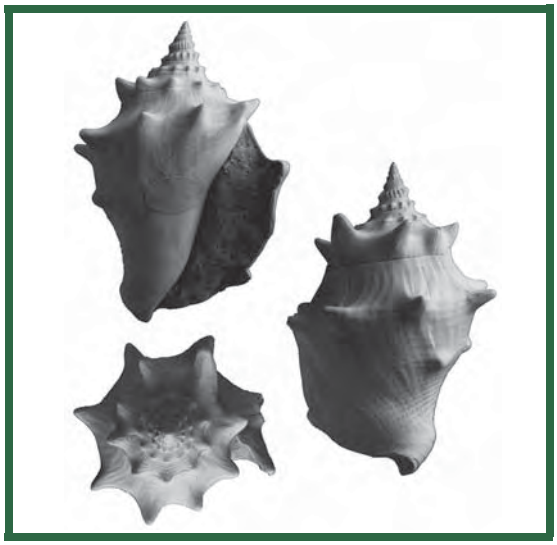

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Bulletins of American Paleontology

Number 376, May 2009

BULLETINS OF AMERICAN PALEONTOLOGY

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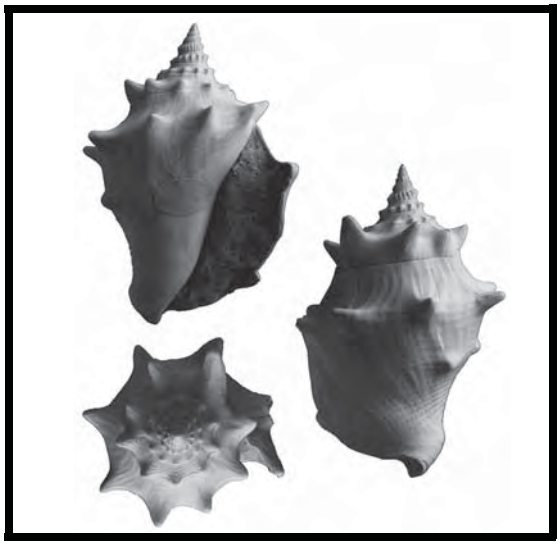

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Number 376, May 2009

ISSN 007-5779
ISBN 978-0-87710-486-5
Library of Congress Catalog Card Number 2009925699
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NEOGENE PALEONTOLOGY OF THE NORTHERN DOMINICAN REPUBLIC. 23. STROMBID GASTROPODS (GENERA *STROMBUS* AND *LOBATUS;* MOLLUSCA: GASTROPODA: STROMBIDAE) OF THE CIBAO VALLEY

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ABSTRACT

Gastropods of the family Strombidae are well-known and important constituents of modern tropical marine communities. The biology of several modern species has been thoroughly investigated due to their economic value as a human food resource. Unlike many gastropods, strombids undergo pseudo-determinate growth; they therefore present intriguing possibilities for investigation of size-related patterns of change. Unfortunately, they also display a wide degree of intraspecific morphologic variation, making reliable determination of species identity difficult.

In this paper, we examine members of this family from the late Miocene and early Pliocene deposits of the Cibao Valley, located in the northwestern portion of the Dominican Republic on the Caribbean island of Hispaniola. After brief descriptions of the general geologic setting of the Cibao Valley and the biology of modern strombids, we delineate the observed geographic and stratigraphic ranges for species of *Strombus* and *Lobatus* in the Cibao Valley. At least 11 species of strombids have been reported from the Dominican Republic. Based on the high degree of intraspecific morphologic variation common in these genera and upon examination of individual specimens, we synonomize several older names and recognize only five species in two genera from the Cibao sequence: *S. bifrons, S. proximus, L. haitensis, L. galliformis,* and *L. dominator*. We describe some aspects of strombid paleoecology and summarize spatiotemporal patterns of distribution. Differences exist between modern strombid populations and our collections of Miocene Dominican ones; strombids of the Cibao Valley are in general smaller and appear to have occupied somewhat different habitats than those of their modern relatives.

RESUMEN

Gastropods del familia Strombidae son un componente conocido e importante de las comunidades modernas marinas tropicales. La biología de varias especies ha sido investigada por su valor económico como comida humana. En contrasto a varios gastropods, los miembros del Strombidae demuestran y determinan su crecimiento, entonces ellos presentan posibilidades para la investigación sobre modalidades de cambio de tamaño. Desafortunadamente también demuestran gran variación morfológica, dificultando la determinacion de la identidad de las especies.

En este trabajo examinamos miembros de las familias de los depósitos Mioceno y Plioceno del Valle Cibao, ubicados en el noroeste de la Dominica Republica en la isla de Hispañola. Después de determinar la geología local del Valle Cibao y la biología de strombidae modernos, observamos el alcance geografico y eststratergico de las especies de los generos *Strombus* y *Lobatus* en el Valle Cibao. Por lo menos 11 especies han sido reportadas de la Republica Dominica. Basado en la cantidad de varaciones morfológicas comunes en esta familia y después de la examinacion de ejemplares individuales, sinonomizamos varios nombres y grupes a solamente cinco especies de este variación: *Strombus bifrons, S. proximus, Lobatus haitensis, L. galliformis,* y *L. dominator*. Describimos varios aspectos de la paleoecología de estas especias y analizamos la modalidad spatiotemporal de distribución. Existen diferencies entre las poblaciones modernas y los del Mioceno Domínico; strombids del Valle Cibao Mioceno aparecen ser más pequeños y ocupan differentes hábitades que sus familiares modernos.

INTRODUCTION

Neogene sediments of the Cibao Valley in the northwestern Dominican Republic contain a rich tropical marine fauna in one of the most continuous and well-exposed sequences of the Caribbean. In 1986, J. Saunders, P. Jung, and B. Biju-Duvall published a survey paper covering the lithology, stratigraphy, and age of exposures in the Cibao Valley. This paper marked the initiation of the Dominican Republic Research Program, an ongoing multidisciplinary attempt to investigate and interpret the paleoenvironments of the northwestern Dominican Republic. The current study is an offshoot of that program.

In this paper, we examine the fossil record of the gastropod genera *Strombus* and *Lobatus* from these deposits. Members of the family Strombidae are abundant and well-studied in the modern Caribbean. After reviewing the biology of this family and examining patterns of morphologic variation in specimens from several collections, we revise the (numerous) species that have been reported from the Dominican Republic and place them into their geographic, biostratigraphic, and paleoecological contexts.

Specimens examined include material from the University of Wisconsin Department of Geology and Geophysics collections under the file number UW1492, as well as specimens borrowed from the Naturhistorisches Museum, Basel, Switzerland, and from Tulane University, New Orleans, Louisiana, USA (Tulane's collections are now housed at the Paleontological Research Institution, Ithaca, New York, USA).

MATERIALS AND METHODS

Specimens evaluated for this study are courtesy of the following: DHG, Geary collections, University of Wisconsin at Madison, Wisconsin, USA, repository number UW1942; JRF, Freiheit collections, University of Wisconsin at Madison, Wisconsin, USA, repository number UW1942; NMB, Naturhistorisches Museum, Basel, Switzerland; TU, Tulane University, New Orleans, Louisiana, USA (collections now at the Paleontological Research Institution, Ithaca, New York).

Abbreviations of repository institutions for type specimens are as follows: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; BMNH, The Natural History Museum [British Museum (Natural History)], London; USNM, National Museum of Natural History (United States National Museum), Washington, DC.

To carry out measurements, digital images (dorsal and ventral) of the individual specimens were created with a Kodak DC260 digital camera. Coordinates of specific locations on each specimen were recorded and distances were calculated from these points. Specific points and distances measured are indicated in Text-fig. 1.

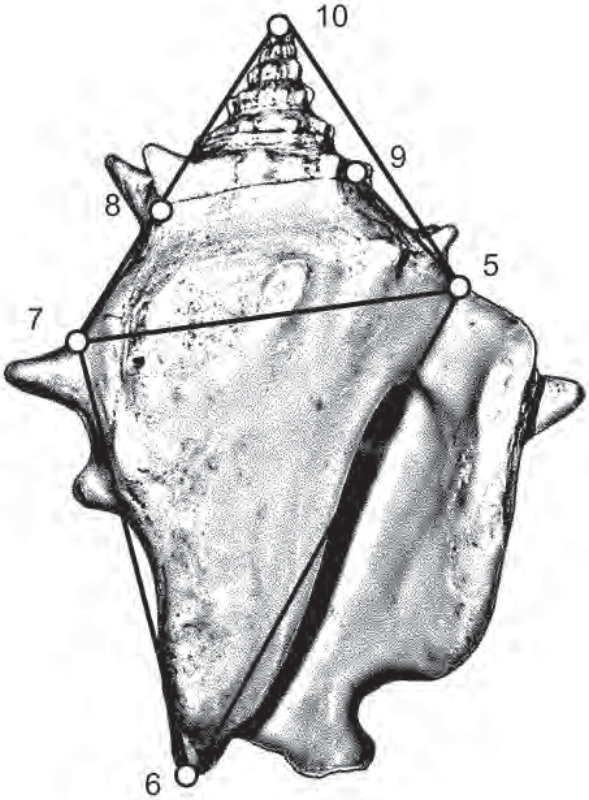
While being photographed, individual specimens were held in place and oriented with modeling clay. Both dorsal and ventral shots were oriented such that the lines corresponding to HEIGHT and MAXWIDTH measurements (see Text-fig. 1) lay in a plane orthogonal to the "line of sight" of the camera. Error analysis was conducted on ten replicate photo sets of the same specimen; measurement error was ± 2.0%.

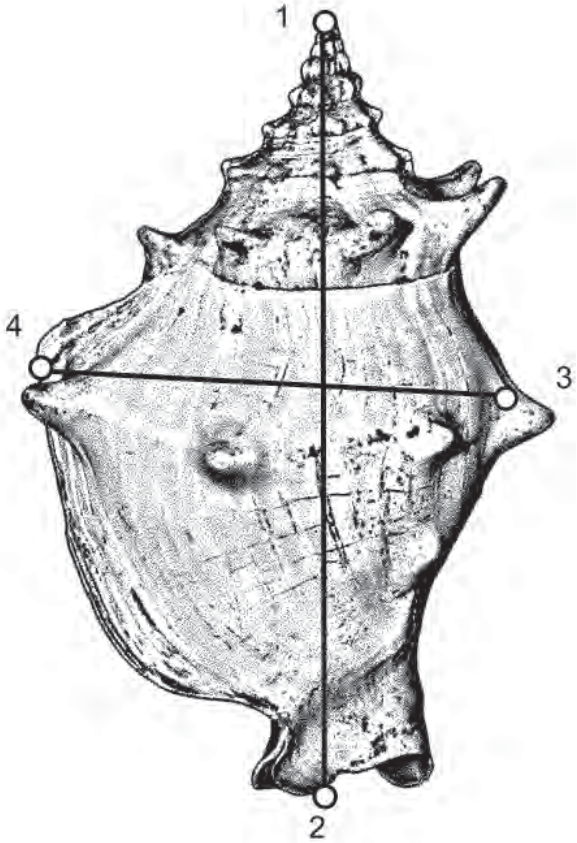
In addition to the measurements noted above, X-Y coordinates of points (ventral view only) were Procrustes transformed with PAST (Hammer et *al.*, 2001, and included references) and used to generate mean shapes (normalized to centroid size) as an aid to visualization of shape change. In cases of minor damage to a specimen (such as the tip of the spire or edge of the lip), the appropriate point was estimated. In cases of more extensive damage, either partial measurements were taken or the specimen was used only for presence/absence data. A total of 1,077 specimens were examined for this study. Of these, 755 were at least tentatively identified to species level and 243 were sufficiently whole to permit all measurements as described in Text-fig. 1.

Image processing and measurement were performed with Adobe Photoshop 5 and the public domain program ImageJ, version 1.33b (Rasband, 2006). Calculations and data analysis were performed with FileMaker Pro 5 database software, Microsoft Excel 97, Minitab 13 statistics software, and the freeware paleontological data analysis program PAST, version 1.68 (Hammer *et al.*, 2001). Text-figures and plates were prepared with the Xara X graphics program.

GENERAL GEOLOGIC SETTING

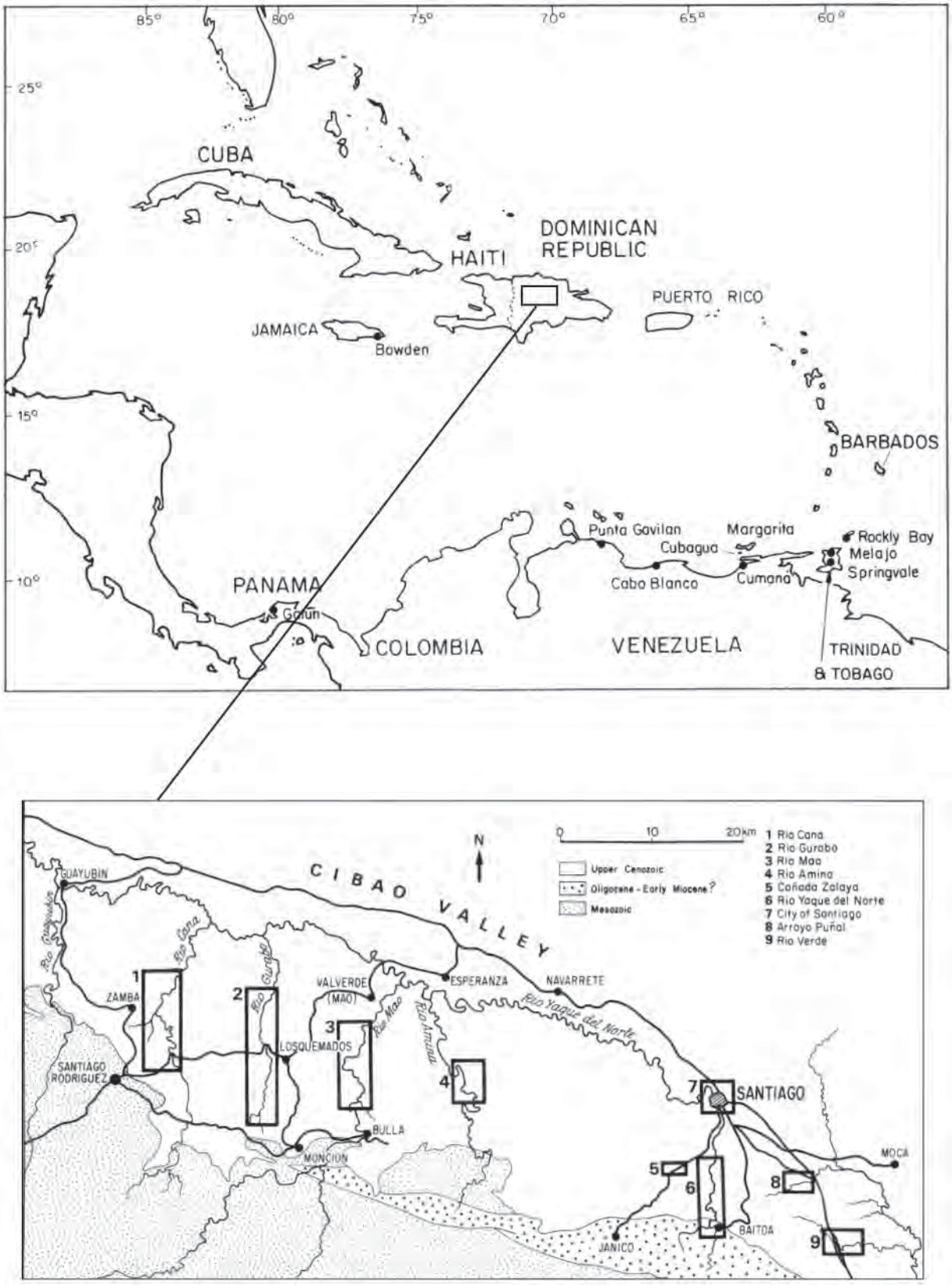
The Cibao Valley lies in the northwestern Dominican Republic on the island of Hispaniola in the Caribbean (Text-fig. 2). It is an east-west trending structural trough, bordered on the north by the Cordillera Septentrional, on the south by the Cordillera Central, and open to the sea at the eastern and western ends. During the Neogene, this was probably a narrow seaway open at both ends; at times it could have been restricted (or even closed) at the western end (Saunders *et al.*, 1986). Siliciclastic and carbonate sediments were shed into the trough from the tectonically driven uplifts to the south and from the shallow marine environments on their flanks. During the Late Miocene and Early Pliocene these environments comprised a prograding and aggrading shelf and slope system. The quantity of clastic input varied, and due to the weathering characteristics of the source rock, tended to be enriched in silts at the expense of sand-sized particles (Evans, 1986). The degrees of uplift and disposition of associated sediments (if any) from the northern side of the trough during this time are





Measurement	First point	Second point
HEIGHT	1 (tip of spire)	2 (maximum anterior extension)
MAXWIDTH	3 (shoulder)	4 (lip at shoulder)
BODWIDTH	5 (aperture at end of suture)	7 (shoulder)
APLENGTH	5 (aperture at end of suture)	6 (tip of siphonal canal)
BODLENGTH	6 (tip of siphonal canal)	7 (shoulder)
APSPIRE	5 (aperture at end of suture)	10 (tip of spire)
APSUTURE	5 (aperture at end of suture)	9 (aperture side suture)
SHOULSPIRE	7 (shoulder)	10 (tip of spire)
SHOULSUTURE	7 (shoulder)	8 (shoulder side suture)

Text-fig. 1. Shell measurements.



Text-fig. 2. Geographic location of the study area. After Saunders *et al.* (1986).

uncertain; the uplift that formed the Cordillera Septentrional probably began at the end of the Miocene (Evans, 1986). Although the tropical environment was theoretically ideal for the growth of coral reefs, the instability of the shelf (due to both continuing tectonism and unconsolidated substratum) and periodic input of siliciclastics prevented extensive framework reef growth. Corals are common but are seldom found *in situ*, typically having been transported and overturned by slumping of the substratum. Nevertheless, well-preserved examples of framework reef development can be seen at a few locations.

A wedge of Neogene sediments, uplifted and tilted but not appreciably deformed, forms the southern wall of the Cibao Valley. The Rio Yaque del Norte runs down the center of the valley; outcrops are primarily determined by the locations of incised river valleys formed by its tributaries. These tributaries run approximately north-south, nearly perpendicular to the strikes of the outcrops that they are exposing. The principle tributaries (west to east) are the Rio Cana, the Rio Gurabo, the Rio Mao, and the Rio Amina. At the eastern end of the Cibao Valley, the headwaters of the Yaque del Norte cut down through the hills in a north-south direction before entering the main valley. The outcrops exposed there represent a somewhat wider span of time than do those farther west (see below). Because of the slight northward dip, travel downstream (north) in any of these valleys leads to progressively younger sediments. Because movement north also entails movement into the trough, downstream travel also means travel through (generally) progressively deeper environments of deposition.

The Late Miocene to Early Pliocene fossiliferous sediments exposed in the tributary valleys are placed in three formations, the Cercado, the Gurabo, and the Mao; together these comprise the Yaque Group. Limited exposures of Middle Miocene sediments at the far eastern end of the Cibao Valley are placed in the Baitoa Formation; this is also a member of the Yaque Group. Due to lateral facies changes and the discontinuous nature of outcrops, correlation between valleys presents a formidable problem that has not yet been entirely solved. The most continuous outcrops are in the Rio Gurabo, where the Mao, Cercado, and Gurabo formations are well established and readily distinguished. Correlation of these formations to the west in the Rio Cana section is possible, although an appreciable element of uncertainty exists. Correlation to the east in the Rio Mao is less certain; farther east than that becomes largely impractical at the formational level.

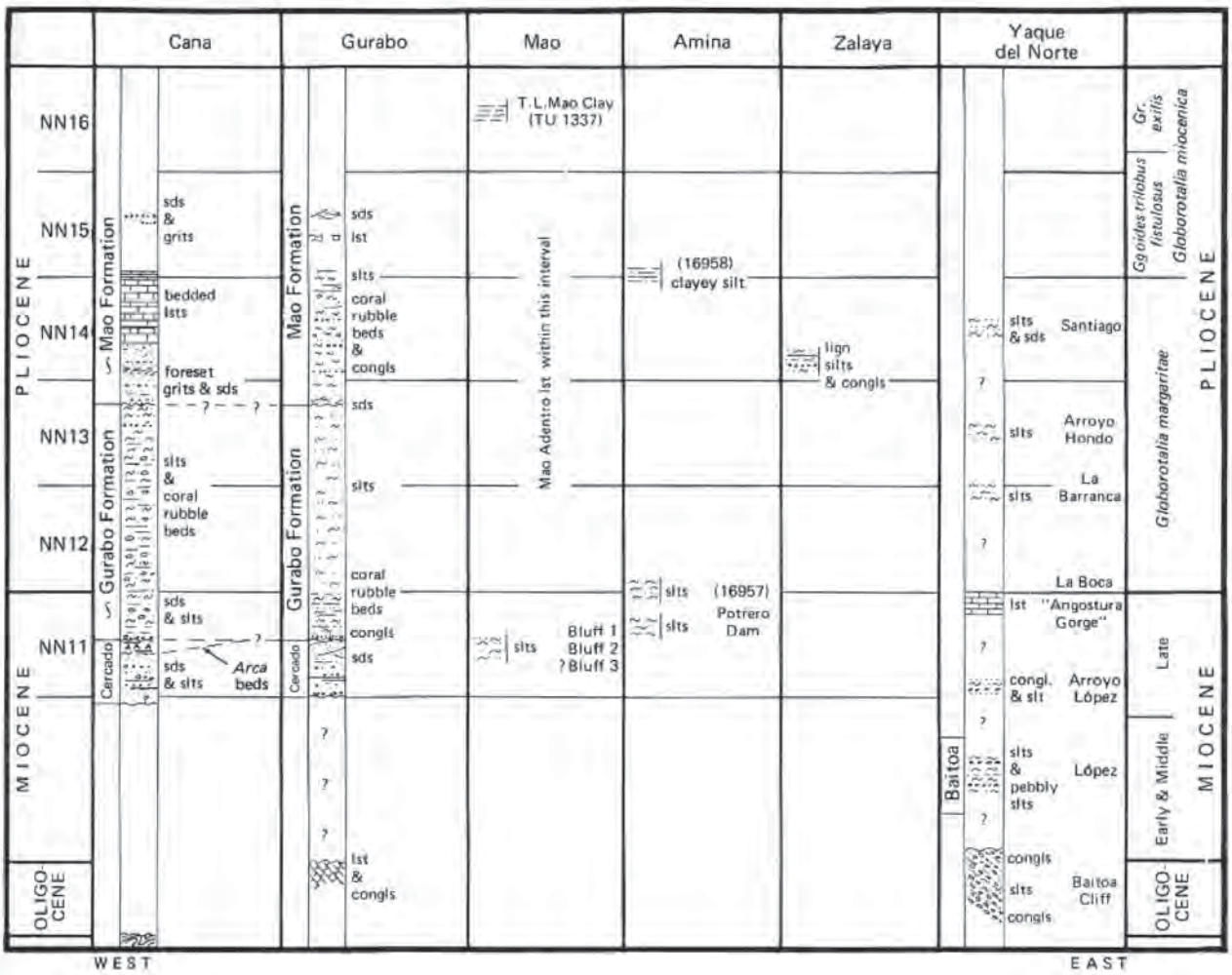
Dating of sediments in the Cibao Valley has been accomplished largely via the use of calcareous nannofossils, planktic foraminiferans, and ostracods. Nannofossil zones can be used to roughly correlate sections between valleys. Text-fig. 3 shows the results of such a correlation. More detailed treatments of this matter can be found in publications by Saunders *et al.* (1986) and Van den Bold (1988).

Exposures along the eastern portion of the Rio Yaque del Norte (the south-to-north flowing section) include some older outcrops that apparently have no counterpart to the west. At Lopez, richly fossiliferous sediments dating to the middle Miocene lie atop a distinct unconformity with Oligocene conglomerates below. The conglomerates are part of the Tabera Group; the Miocene sediments are placed in the Baitoa Formation, the oldest member of the Yaque Group. A discontinuous series of outcrops farther downstream (north) on the Rio Yaque del Norte extends erratically into the Pliocene. Although these eastern outcrops are apparently contemporaneous with the more western formations (based on evidence from foraminiferans and nannofossils), correlation with them is only practical at the nannofossil-zone level.

Evans (1986) stated that the direction of sea-level change as recorded in the sediments of the Yaque Group corresponds broadly to the Vail *et al.* (1977) sea-level curve, but that local tectonism greatly influenced the magnitude of local changes. In general, the Cercado and Gurabo formations represent aggradational intervals with accommodation space generally increasing faster than sediment supply (except at the boundary between the two formations). Thus these formations each show a deepening trend through time (with a temporary return to shallower conditions at the base of the Gurabo). Northern (upsection) outcrops of these formations therefore represent deeper environments not only because of paleotopography (they are located more troughward) but also because of this trend. The extent of relative sea-level rise is apparently much greater in the Rio Gurabo section than in the Rio Cana, very likely due to differential tectonic effects. The Mao Formation represents a progradational interval and fall of relative sea level, but still consists largely of deep-water deposits. In addition to the depth trends noted above, a west-to-east deepening trend is evident as well.

BIOLOGY OF THE FAMILY STROMBIDAE

Latiolais *et al.* (2006) presented a phylogenetic analysis of 32 species of *Strombus* and 3 species of *Lambis* based on one nuclear and one mitochondrial gene. Their findings suggest that the genus *Strombus* (*sensu* Abbott, 1960) is paraphyletic, with *Lambis* nested within it. In addition, Latiolais *et al.* (2006) found that the subgenus *Tricornis* is polyphyletic and includes a tropical American clade and an Indo-Pacific clade. Kronenberg & Lee (2007) argued that *Lobatus* is the first available name for the group of tropical American strombids previously assigned to the subgenus *Tricornis*. Based on the strong separation of this group in the Latiolais *et al.* (2006) molecular phylogeny, Landau *et al.* (2008) treated *Lobatus* as a full genus. Following their reasoning, the Dominican strombids we discuss here belong to two genera: *Strombus*,



Text-fig. 3. Approximate stratigraphic correlation of sections in the Cibao Valley. After Saunders *et al.* (1986).

for those species previously assigned to *Strombus* (*Strombus*), and *Lobatus*, for those species previously assigned to *Strombus* (*Tricornis*). In general, the generic and subgeneric classification of strombids (as with many other molluscan families) is in need of revision and is in a state of flux as newer molecular datasets are compared with more traditional morphologic data and as new fossil material is described (Kronenberg & Vermeij, 2002; Kronenberg & Lee, 2007; Landau *et al.*, 2008). For these reasons, we restrict ourselves here to using the long-standing *Strombus* and the relatively new but seemingly well-founded *Lobatus*. Subgeneric classifications for these genera will become more clear as work on this family proceeds.

We use the term strombid in this paper to refer to members of *Strombus* and *Lobatus*. A third genus of Strombidae, *Orthaulax* (see Vokes & Vokes, 1968) might occur in these deposits but was not included in our study.

Many strombids are fusiform in shape, whereas others are blocky with a flaring outer lip as adults. Adult height ranges from 0.8 to over 30 cm. Strombid gastropods are commonly known as "conchs" and include the well-known (and commercially important) queen conch, *Lobatus gigas* (Linnaeus, 1758), of the Caribbean (Randall, 1964). Members of the family Strombidae have been found from the Upper Cretaceous but do not become common or diverse until the Eocene (Savazzi, 1991). Modern strombids are restricted to tropical or subtropical regions where they inhabit grass flats, reefs, and lagoons (Abbott, 1960). Estimates of species numbers vary due to the presence of numerous subspecies and varieties; Abbott (1960) listed a total of 50 species worldwide, including seven in the western Atlantic. In spite of the morphological diversity of their shells, strombids are relatively conservative in lifestyle and soft-part morphology; most lead similar lives as juveniles and adults (Savazzi, 1991). Despite numerous earlier reports to the contrary (*e.g.*, Colton, 1905), all modern

strombids are herbivorous or detritivorous (Robertson, 1961). Their depth range is generally limited by the depth at which photosynthesis can take place, and can consequently vary with local conditions, but typically they are found in shallow to very shallow water. Abbott (1960) claimed that strombids can be broadly categorized ecologically by their preference for nutrient-enriched or nutrient-depleted water conditions, but other authors (Pecharde, 1968; Brownell, 1977) have observed assemblages of mixed species with supposedly different preferences. Seagrass beds are mentioned regularly in the literature as ideal environments for many species. No strombids are known from brackish or fresh waters, or from habitats where the water regularly drops below 20°C.

Strombids have planktonic larvae that typically stay in the water column for two to three weeks, although this time can be extended if the veliger is undernourished (Brownell, 1977). Upon metamorphosis, juvenile strombids typically find a habitat with soft substratum in which they can bury themselves; they often congregate together in "herds" in suitable environments (usually a seagrass meadow). Here they begin a period of rapid growth and surreptitious nocturnal gluttony. Experimental and observational evidence each suggest that their principal defenses against predation lie in diurnal burial, congregation in herds, and rapid attainment of large size (Stoner, 1989; Ray & Stoner, 1995). Juvenile strombids are morphologically unspecialized and are generally fairly similar throughout the genus (Savazzi, 1991).

Upon nearing sexual maturity, strombids typically modify the growth of the final whorl to produce a flared and extended outer lip. Once the final whorl has been completed, the adult shell grows no larger, although the animal continues to deposit fresh material on the inside of the shell, especially in the larger species. This can lead to weight differences of over 100% between younger and older adults of similar length (Savazzi, 1991). Mature adults can also actually decrease in length due to abrasion and bioerosion on the exterior surfaces; fresh shell material is deposited only on the interior surfaces. There is no evidence that strombids themselves resorb or dissolve shell material once it has been deposited (Savazzi, 1991).

The locomotion typically used by adult strombids is a "leaping" action rather than the creeping glide employed by most gastropods. Juveniles also practice this behavior, but not as effectively (Berg, 1972). Leaping is accomplished by a violent pushing action of the foot against the substratum, propelling the shell forward (or backward) up to half its length at a time. Several variations on this behavior exist; details were provided by Berg (1974). As the shell gets larger and heavier, leaping becomes a more efficient mode of locomotion than creeping because of the high energetic costs of keeping the shell raised from the substratum during creeping (Savazzi, 1989, 1991). Leaping has been experimentally shown to be effective in confusing scent-oriented invertebrate predators such as starfish and carnivorous snails (Berg, 1974). There is some evidence to suggest a powerful kick from a sharp strombid operculum can deter more motile predators as well (Abbott, 1960; Pecharde, 1970). This vigorous mode of transportation necessitates a shell balanced for such acrobatics (Savazzi, 1991) and a visual system capable of more refined depth perception than that of their more sedentary relatives. The strombid eye is consequently quite well developed and bears a striking resemblance to a vertebrate eye. The shell is modified to accommodate this advanced visual system. It typically displays a notch or embayment near the anterior siphonal canal called the stromboid notch; the left eye stalk protrudes from the siphonal canal, the right from the stromboid notch. The outer lip of the shell is often expanded and flared, helping to stabilize the shell in the dorsal-ventral plane. Many larger strombids have protuberances from their dorsal surfaces that render the shell unstable if turned ventral side up, thus making it easier for the snail to right itself. In others, the spines and protuberances counterbalance the flared lip while the snail is leaping. The lip itself also serves as a protective shield from predators when the snail is grazing or mating.

Most strombids retain at least some of their burrowing habits into adulthood. For a burrowing snail, dorsal protuberances are a liability rather than an advantage, because they stick out when the rest of the shell is buried and reveal the animal's position to potential predators. Deeper burial requires the expenditure of disproportionately greater amounts of energy and becomes an ever-less-attractive option with increasing size. Even though larger strombids still bury themselves, they do not do so as thoroughly or for as long a time period. In addition, larger strombids inhabit a wider range of habitats, including rock bottoms with little or no sediment in which they can bury themselves.

Many large strombids acquire considerable populations of epibionts. Pecharde (1968) observed algal growth approximately two-thirds of a meter in length on individuals of *Strombus* (*Tricornis*) *gigas* (= *Lobatus gigas*) found on rocky substratum. Some of these growths can serve the snail as effective camouflage against visually-oriented predators; other epibionts, such as boring sponges, seriously weaken the shell. Adult strombids of smaller species (*e.g.*, *Strombus pugilis* Linnaeus, 1758) can bury themselves completely for extended periods of time (up to six weeks), especially during the winter months, but do not undergo diurnal burial as the juveniles typically do. The lack of epibionts on most *S. pugilis* individuals (compared to the larger species) can only partially be attributed to their more extensive burial habits; Pecharde (1968) has noted that the periostracum of this species seems particularly effective at warding off settlers.

Over a given portion of theoretically suitable habitat,

the distribution of strombids is typically decidedly non-uniform. Strombid adults are often as gregarious as the juveniles; "herds" of individuals can gather and travel (or bury themselves) together *en masse*, inhabiting only a small portion of the theoretically suitable environment at a time. Groups consisting strictly of adults (both single sex and mixed sex), strictly juveniles, and mixed ages have all been observed (Catterall & Poiner, 1983; Pecharde, 1968). Adults gather in obvious breeding congregations, but can congregate for less apparent reasons as well (Pecharde, 1970). Migrations, either individual or group, can be on a scale of several thousands of meters; modern *Lobatus gigas* individuals have been documented to travel distances of at least 4 km (Hesse, 1979; Hahn, 1989). Frequency of migration is positively correlated with both age and size. Seasonally correlated onshore-offshore migrations have been observed in many species of *Strombus*, with offshore migration coinciding with the winter months. Strombids have also been observed to move to different substrata for different types of activity (D'Asaro, 1965; Hesse, 1979).

Classification of living strombids is based more on soft-part morphology than on shell characteristics (Abbott, 1960; Savazzi, 1991), and Abbott noted that even soft-part characteristics can vary geographically by marine province rather than by assumed phylogenetic relationship. The morphology and size of adult shells are highly variable, and can be influenced by a number of factors. Modern strombids often show some sexual dimorphism, with the female producing a slightly larger and proportionately wider shell. Reed (1993) noted that, in addition, some species (including the modern Caribbean *Strombus pugilis*) show sexual trimorphism, the third form being due to the existence of masculinized females who posses rudimentary male genitals but are still fully functional as females. These individuals bear shells even larger and wider than those of regular females.

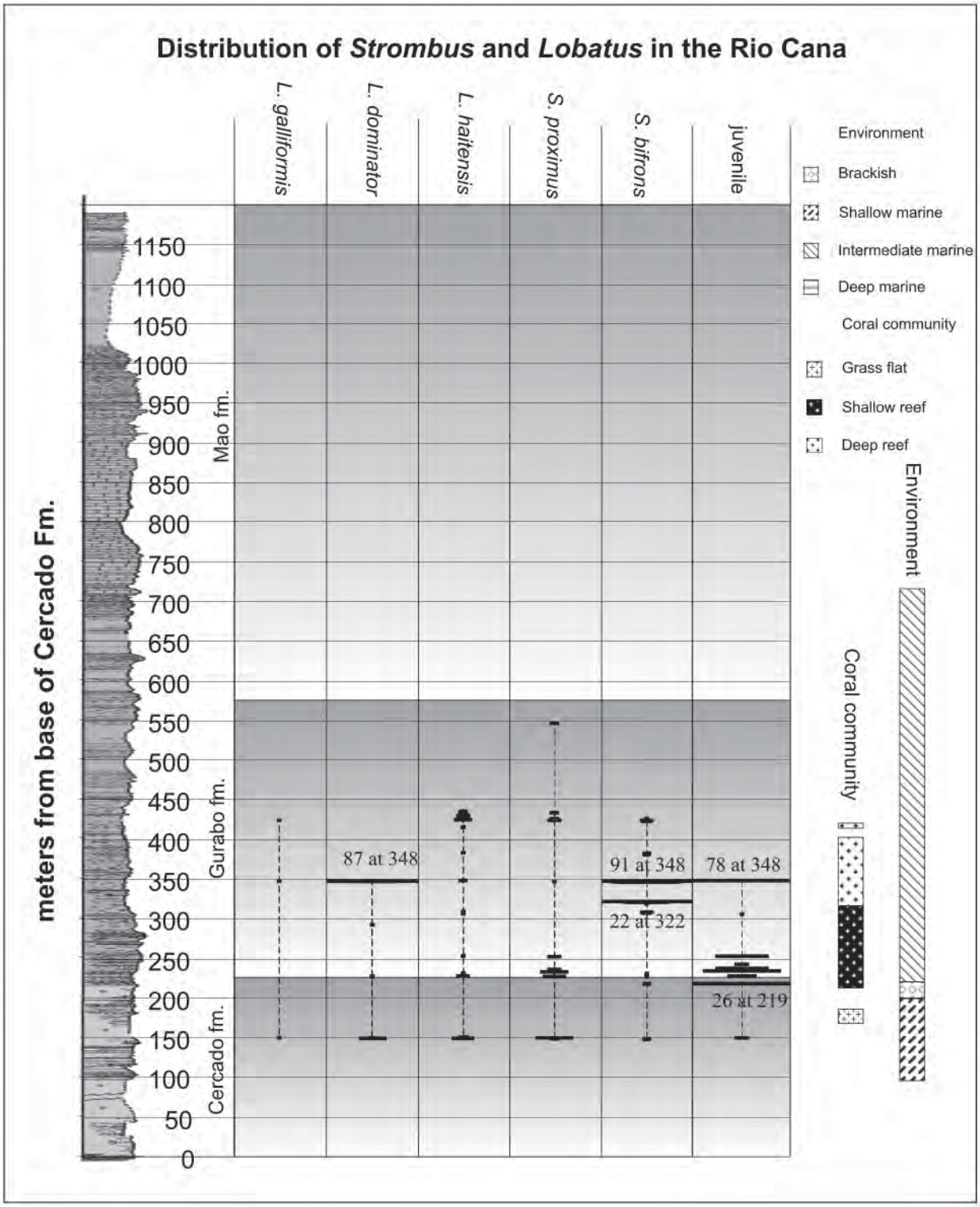
Modern strombids also show a great deal of ecophenotypic variation. Adult size is often positively correlated with increasing depth; individuals from deeper water can be twice the length of their shallow-water conspecifics (Savazzi, 1991). Considering the migratory habits of these mollusks, however, it is possible that this represents an active habitat choice rather than a direct effect of the environment. In a clearer example of environmental effects, Martin-Mora *et al.* (1995) tagged juvenile *Lobatus gigas* and transplanted them to various geographic locations in the Bahamas. They found that the transplants showed morphologic convergence toward pre-existing populations of *L. gigas* at those locations. They did not try to trace these morphologic changes to specific environmental conditions other than to note that high-energy environments tend to result in a more robust morphology. Nor did they attempt to ascertain whether these changes are adaptive in nature. They did, however, note that shell morphology is predictably and allometrically affected by varying growth rates. Specifically, high growth rates result in individuals with elongate spires, medium rates result in a stouter shell with longer spines, and slow rates result in a more slender spire. These changes in growth rate are affected by the availability of preferred food items (at least in *L. gigas*).

Modern strombids also show considerable behavioral potential for producing hybrid forms. In a study that surveyed both wild and captive individuals, Reed (1995a, b) noted that male strombids show remarkably little discrimination in choice of partner and have frequently been observed attempting to mate with other males and females outside their own species. They do, however, show a preference for females that are actually in the process of spawning. Observations of two males (not necessarily of the same species) attempting to mate simultaneously with a single female were "infrequent, but consistent" (Reed, 1995a). Reed (1995a, b) observed frequent interspecific mating between co-occurring species, but only *Strombus pugilis* and *S. alatus* Gmelin, 1791, matings produced fertile eggs (these matings always produced fertile eggs).

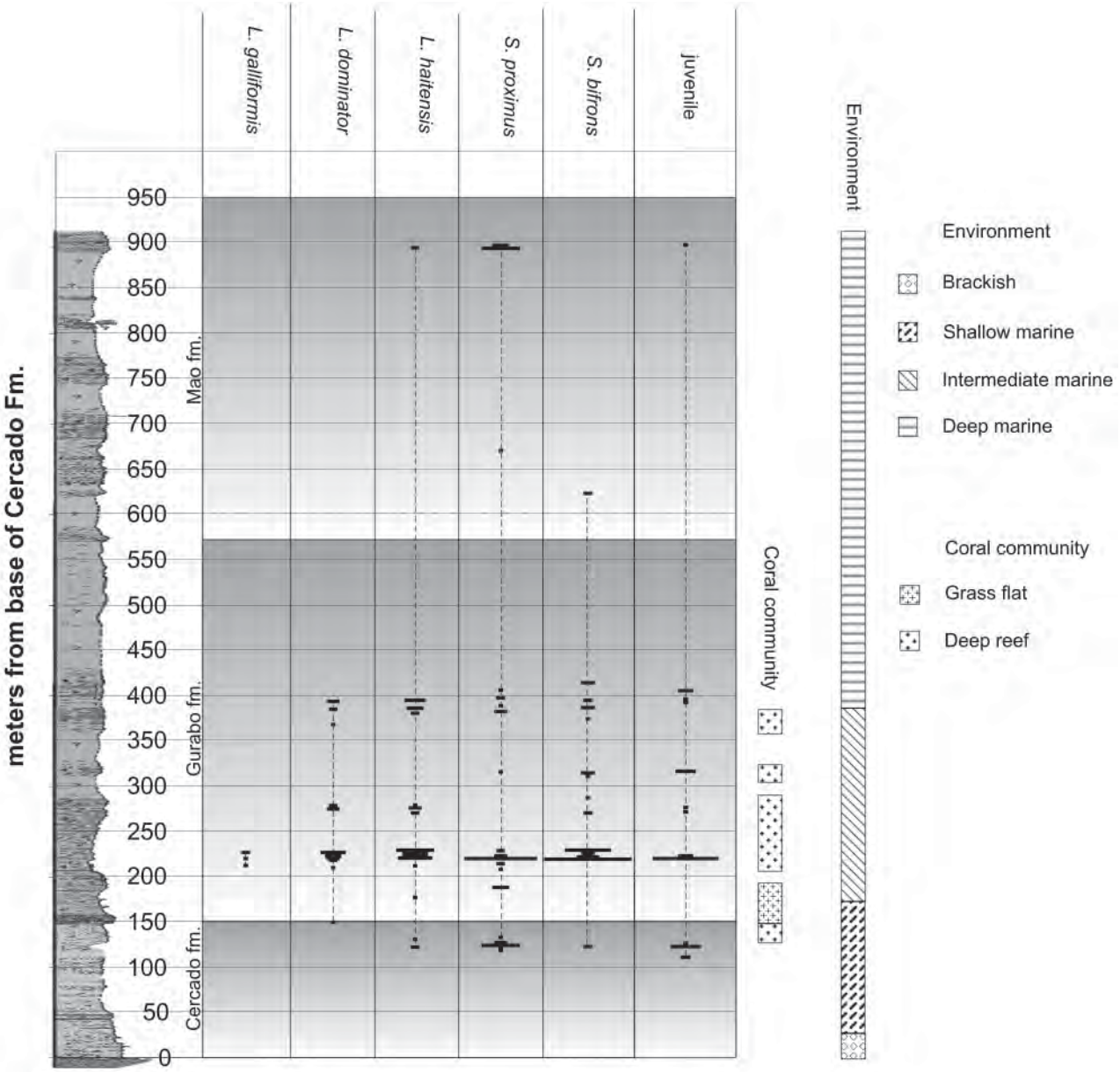
STRATIGRAPHIC DISTRIBUTION

Introduction to the Strombids of the Cibao Valley

Although at least a dozen species of strombids have been reported from the Cibao Valley, we have only found good evidence for the presence of five: *Strombus bifrons* G. B. Sowerby I, 1850, *S. proximus* G. B. Sowerby I, 1850, *Lobatus haitensis* (= *S. haitensis* G. B. Sowerby I, 1850), *L. galliformis* (= *S. galliformis* Pilsbry & Johnson, 1917), and *L. dominator* (= *S. dominator* Pilsbry & Johnson, 1917). Other species reported include *S.* (*S.*) *ambiguus* G. B. Sowerby I, 1850, *S.* (*S.*) *fragilis* Moore, 1863, *S.* (*S.*) *pugiloides* Guppy, 1874, *S.* (*S.*) *pugilis* Linnaeus, 1758, *S.* (*Tricornis*) *bituberculatus* Gabb, 1873 (non Lamarck, 1822), *S.* (*T.*) *maoensis* Maury, 1917, *S.* (*T.*) *gigas* Linnaeus, 1758, *S.* aff. *raninus* Gmelin, 1791 (of Jung & Heitz, 2001), and *L. vokesae* (Landau *et al.*, 2008). We consider *S. ambiguus* and *S. pugiloides* to be synonyms of either *S. bifrons* or *S. proximus* depending on author (see Systematic Paleontology, below). Reports of the presence of *S. pugilis* are ascribed to *S. bifrons* or *S. proximus*; according to Guppy (1873), *S. fragilis* is simply a misprint of *S. pugilis*. *Lobatus maoensis* is considered synonymous with *L. dominator* (small specimens). Although *L. gigas* has been reported from the Cibao Valley, its presence could not be verified; these reports seem likely to have been inspired by the presence of large fragmentary remains of *L. dominator* or *L. vokesae*. Reports of *S.* (*T.*) *bituberculatus* [an obsolete synonym of *S.* (*T.*) *raninus*] or *S.* aff. *raninus* are ascribed to *L. haitensis*.



Text-fig. 4. Distribution of *Strombus* and *Lobatus* in the Rio Cana. Width of bars is proportional to the number of identifiable specimens; the width of each column represents 20 individuals. Locations with more than 20 individuals are noted. Environmental interpretations after Saunders *et al.* (1986); coral communities after Budd *et al.* (1996).

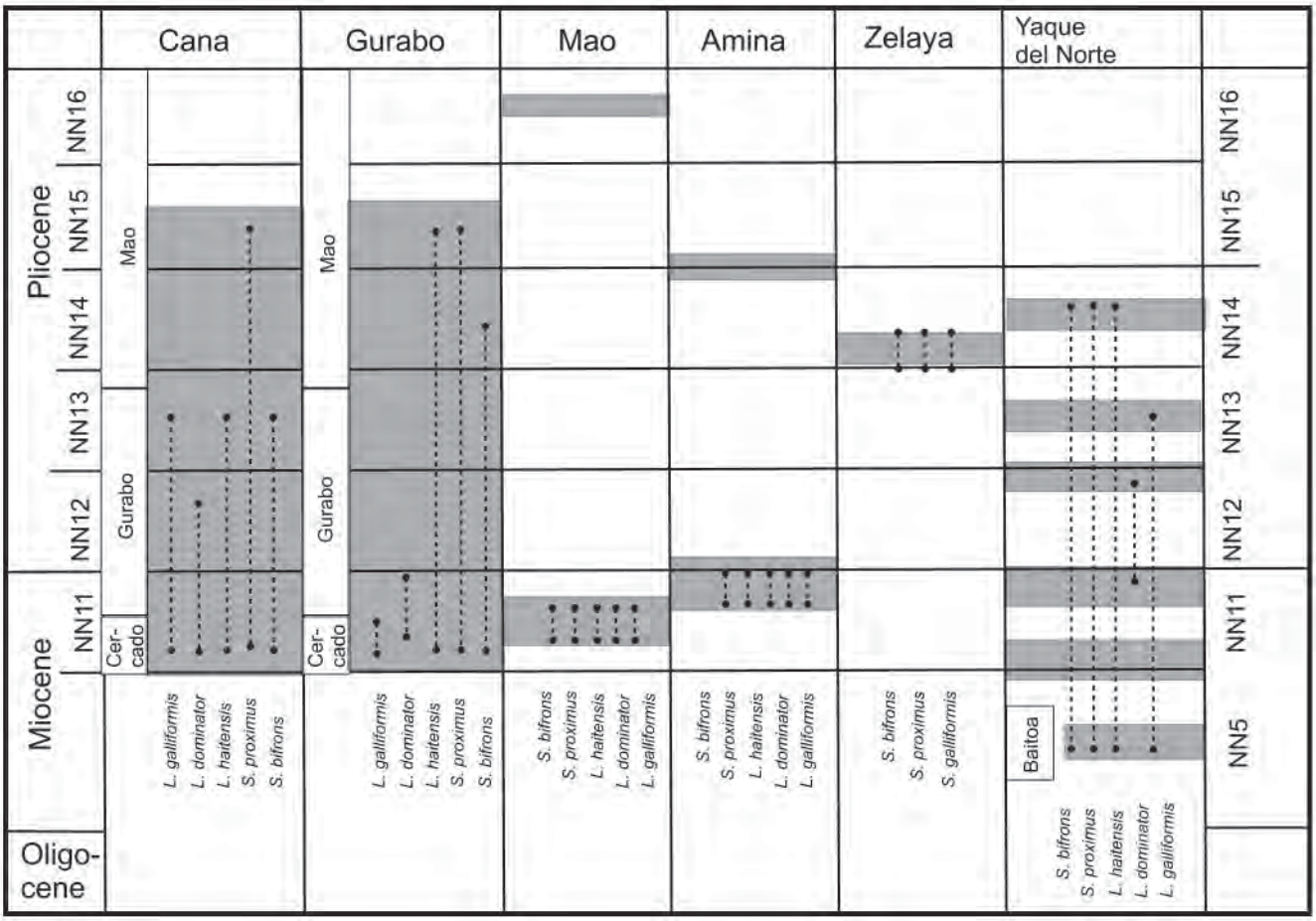


Text-fig. 5. Distribution of *Strombus* and *Lobatus* in the Rio Gurabo. Width of the bars is proportional to the number of identifiable specimens; the width of each column represents 20 individuals. Environmental interpretations after Saunders *et al.* (1986); coral communities after Budd *et al.* (1996).

One large specimen here included in *L. dominator* could well belong to *L. vokesae* (Landau *et al.*, 2008).

Although common in some localities, for the most part, strombids do not make up a major part of fossil assemblages from the Cibao Valley. The most common species, *Strombus bifrons*, has the smallest body size and longest apparent temporal range; *Lobatus dominator* is the largest species and has the shortest observed range. Juvenile shells exhibit fewer distinguishing characteristics than do those of adults, and can be assigned to a given species only with considerable uncertainty. Text-figs 4-5 show strombid locations and ranges plotted against stratigraphic columns for the Rio Cana and Rio Gurabo sections. Text-fig. 6 shows ranges plotted against nannofossil zones for all sections.

As in the modern Caribbean, strombids in the Cibao Valley appear to be restricted to shallow, fully marine environments. Text-figs 4-5 also show strombid distribution in the Rio Cana and Rio Gurabo plotted against two sets of paleoenvironmental



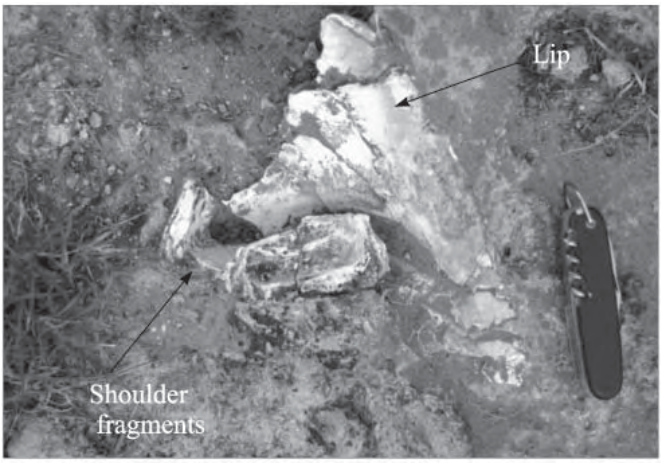
Text-fig. 6. Distribution of strombid gastropods in the Cibao Valley sections. Gray areas indicate the actual presence of outcrops. Modified after Saunders *et al.* (1986). Details on species distributions in Rio Cana and Rio Gurabo are given in Text-figs 4 and 5, respectively.

interpretations. Depth-related paleoenvironments have been derived from Anderson (1996), based originally on Saunders *et al.* (1986) and Van den Bold (1988). Use of these interpretations is somewhat circular, however, because the presence of strombids was used as one criterion for determining shallow marine conditions. Plotted next to these are coral-based paleoenvironmental interpretations as determined by Budd *et al.* (1996). Budd determined her coral communities by cluster analysis of presence/absence data from coral species. Six coral assemblages were distinguishable; these could be grouped into three community types, which she termed seagrass, shallow reef, and deep reef. "Seagrass" environments are characterized by large-polyp solitary corals and can extend to depths of 30 m. "Shallow reefs" are characterized by the presence of hermatypic corals in less than 10 m of water and "deep reefs" by the presence of hermatypic corals in conditions deeper than 10 m. It should be emphasized that none of these community types are exact analogs to modern Caribbean marine communities, most notably the seagrass environments (Budd *et al.*, 1996).

Text-fig. 4 includes specimens from the Arroyo Bellaco and Cañada de Zamba, both of which represent more coral-rich environments than the corresponding location in the Rio Cana proper. The tremendous spike in abundance seen at 348 m on the Rio Cana stratigraphic column represents the Cañada de Zamba specimens, which are not as concentrated in one stratigraphic interval as the figure suggests. Nevertheless, the Zamba location does contain a particularly rich collection of strombid remains; either this was a particularly favorable environment for strombids or their remains have been concentrated here (or both).

RIO CANA

The oldest strombids in the Rio Cana section are found in the Rio Cana proper and its tributary, the Arroyo Bellaco, at approximately stratigraphically equivalent locations. These



Text-fig. 7. Large fragmentary specimen of *Lobatus dominator* (or *L. vokesae*?) from the top of the reef at Arroyo Bellaco, a tributary of the Rio Cana, aproximately 150 m from the base of the Cercado Formation. Knife is 9 cm long. Original shell material present; fragments up to 3 cm thick (UW1942/44).

locations are both interpreted as shallow, clear water, marine environments (Saunders *et al.*, 1986).

The locality at Arroyo Bellaco is the site of a well-preserved framework reef. *Lobatus dominator, Strombus proximus,* and *L. haitensis*, in decreasing order of abundance, have been found here. Although *L. dominator* is typically found in fragmentary form, on the top of the exposed reef these fragments sometimes retain the configuration of the individual specimen; measurements on some of these remains indicate lengths of more than 20 cm (see Text-fig. 7). From this evidence and from the sheer size of some of the fragments (up to 3 cm thick), it is evident that at least one species at this location attained a size approaching the modern *L. gigas* (likely *L. vokesae*). *Strombus proximus* at this location and in the Rio Cana proper show a more gracile form than is typical (see Systematic Paleontology, below, for description of "typical" *S. proximus* morphology). *Strombus bifrons* has not been documented from the Arroyo Bellaco, but a single *S. bifrons* does appear in the Rio Cana at this level.

Following their initial appearances in the middle of the Cercado Formation, strombids are not found again until the top 10 m of the formation, where their reappearance is coincident with a change from a brackish to a normal marine environment. *Strombus proximus* is most abundant here, but *S. bifrons, Lobatus haitensis,* and *L. dominator* are also present. Strombids are again present at the base of the Gurabo Formation. *Strombus bifrons* is the dominant species and *S. proximus* becomes rare; the species composition is otherwise similar. At about 320 m on the column, the coral community changes from shallow-reef to deep-reef assemblages; strombid occurrences are clustered around this transition.

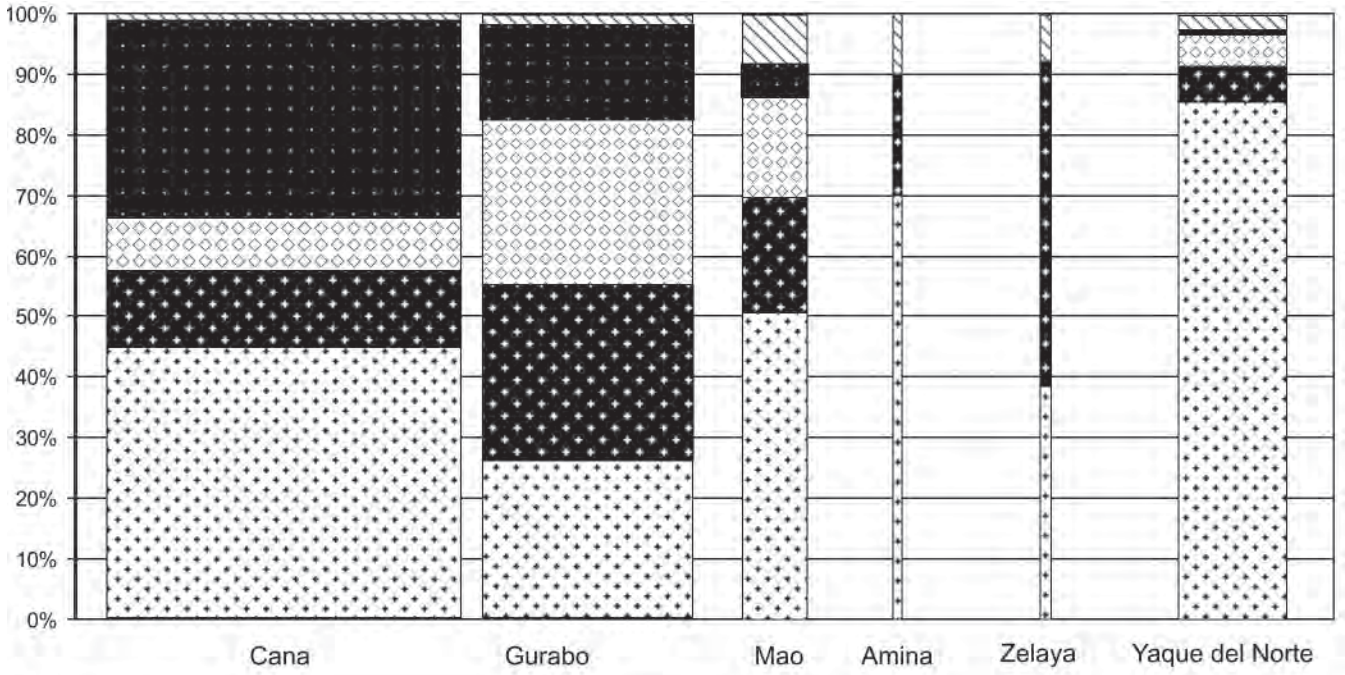
A tributary of the Rio Cana, the Cañada de Zamba, contains outcrops equivalent to roughly 350 m on the stratigraphic column (Saunders *et al.*, 1986). The Cañada de Zamba is home to a rich molluscan fauna and has yielded more strombid specimens than any other single locale. *Strombus bifrons* is the most abundant species and shows a high degree of variability (Pl. 2). *Lobatus dominator* is also common, but no whole (or even measurable) individuals matching the size of the Arroyo Bellaco specimens have been found. Instead, there are many large bioeroded fragments, numerous subadults (well developed enough to be identified as *L. dominator*) and a few smaller measurable adults. Several of the subadult specimens at this location appear to have fallen victim to crabs or other large crustaceans; they show the distinctive pattern of lip damage characteristic of such attacks (Savazzi, 1991). *Lobatus haitensis* is present in the Cañada de Zamba, and it is here that *L. galliformis* makes its sole appearance in the Cana section.

Above the Cañada de Zamba, *Lobatus dominator* is no longer found and *Strombus bifrons* again becomes rare. *Lobatus haitensis* becomes the dominant strombid with *S. proximus* once again relatively common. The distribution of strombids is sparse; a single remaining cluster of occurrences at approximately 425 m coincides with the last occurrence of the deep-reef coral assemblage. Above this there are no strombids until a single last location at 548 m on the column, near the top of the Gurabo. Strombids have not been found above the Gurabo Formation in this section.

Text-fig. 8 shows cumulative population proportions for the Rio Cana and the other rivers in the study area.

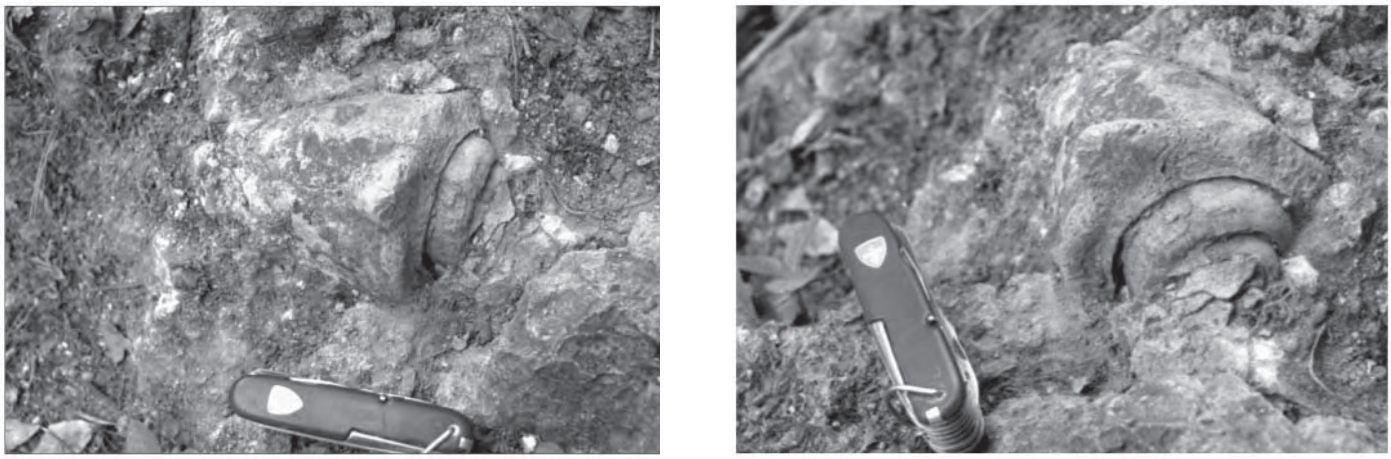
Rio Gurabo

In the Rio Gurabo, the earliest adult strombids are found approximately 117 m from the base of the Cercado Formation, although juveniles have been found down to 90 m. The first identifiable species to appear is *Strombus proximus* (at 117 m), followed by *Lobatus haitensis* and *S. bifrons* at 122 m. A cluster of occurrences is found at this location, coincident with the onset of environmental conditions suitable for reef growth. *Strombus proximus* and *L. haitensis* are found sporadically for the next 25 m of section until the top of the Cercado Formation, which is marked by a coral thicket or patch reef. Casts of large (> 15 cm) strombids have been found at this location that retain enough detail to be identified as *L. dominator* (see Text-fig. 9). Above the reef, in the lower part of the Gurabo Formation, strombid remains are sparse and mostly fragmentary until approximately 220 m. The environment undergoes a change to seagrass conditions at the base of the Gurabo, but by 200 m once again becomes more conducive to reef growth. Shortly after the change to more reef-friendly conditions, strombid occurrences start to rise



	Cana	Gurabo	Mao	Amina	Zelaya	Yaque del Norte
L. galliformis	3	4	6	1	1	3
L. dominator	95	37	4	0	0	1
L. haitensis	25	64	12	0	0	6
S. proximus	37	69	14	2	7	7
S. bifrons	129	61	37	7	5	102

Text-fig. 8. Observed population proportions for strombids by river (east to west) in the Cibao Valley. Width of the column is proportional to the number of specimens evaluated for that river.



Text-fig. 9. Two views of a cast of large specimen of probable *Lobatus dominator* from the "Cercado Reef," Rio Gurabo, at the top of the Cercado Formation. Knife is 9 cm long. Note distinctive sculpture at shoulder. (UW1942/56)

and reach their peak abundance for the Rio Gurabo section at about 220 m. Strombids also reach their highest diversity at 220 m, with all five species present. Above 228 m, there is a hiatus in the presence of strombids for 50 m; then, between 270 and 280 m, there is another cluster of occurrences, primarily *L. haitensis* and *S. proximus*, but with *S. bifrons* and *L. dominator* also present. Above 280 m, strombid occurrences taper off until 322 m at which point there is another 40-m hiatus. Starting at 368 m, strombids start to appear again; at approximately 385 m, another cluster can be found. This cluster is predominantly *L. haitensis* and *L. dominator* with a few *S. proximus* and one or two *S. bifrons*. This location marks the last appearance of *L. dominator*. In this last cluster, strombid occurrences peak at nearly the same horizon as the reef corals disappear (probably due to increasing water depth). From this point strombid occurrences (mostly fragmentary) once again taper off until 414 m where they disappear entirely for over 200 m. At 622 m, a couple of worn *S. bifrons* have been found and at 670 m, a single *S. proximus*; above that there is another 200-m hiatus. At 890 m, there is one last cluster of strombids, this one composed almost entirely of *S. proximus*, with one or two *L. haitensis*.

Rio Mao

Outcrops on the Rio Mao consist of isolated cliffs separated by long stretches of river with no exposures. From youngest to oldest, the three major outcrops are referred to as Maury's Bluffs 1, 2, and 3. A rough correlation with other river sections can be achieved via nannofossil zones. Maury's Bluffs 1 and 2 are in nannofossil zone 11; Bluff 3 has not produced appropriate fossils for placement into a nannofossil zone. Attempts to correlate these outcrops more precisely with the formations in the Cana and Gurabo sections are dubious at best (Saunders *et al.*, 1986).

Strombids are represented at Bluff 3 by only a couple of specimens of *Strombus proximus* and some fragments of *S. bifrons*. This is not the case at Bluffs 1 and 2, where strombids are relatively common and diverse. At Bluffs 1 and 2, *S. bifrons* is the most abundant species followed by *S. proximus*; *Lobatus dominator* and *L. haitensis* are present but not common. The rare *L. galliformis* has been found at a location halfway between Bluffs 1 and 2; it is the only strombid from that location and the only *L. galliformis* known from the Rio Mao section. Text-fig. 8 shows cumulative population proportions for the Rio Mao.

Rio Amina

Only a single location (in nannofossil zone 12) on the Rio Amina has produced strombid specimens. *Strombus bifrons* and *S. proximus* are both present; some fragmentary remains might represent *Lobatus galliformis*. One specimen of *S. proximus* at this location is notable for its well-developed lirations both on the shell exterior and inside the aperture (Pl. 4, Figs 15-17); this specimen strongly suggests a transitional form or hybrid between the other *S. proximus* from this location and the accompanying *S. bifrons*. Text-fig. 8 shows cumulative population proportions for the Rio Amina.

Arroyo Zelaya

In the Arroyo Zelaya (nannofossil zone 14), strombids are represented by a few specimens each of *Strombus bifrons* and *S. proximus*. Fragments of a larger strombid, probably *Lobatus dominator*, have also been found here. All specimens of *S. proximus* from this locality show a peculiar anteriorally displaced body whorl (see Systematic Paleontology, below, under *S. proximus* for more discussion). This morphology occurs elsewhere but is most notable at this locale. In this paper, specimens displaying this morphology are referred to as *S. proximus* "a". The presence of strombids in the Rio Zelaya is noteworthy because Saunders *et al.* (1986) interpreted this environment as deep marine. Anderson (1994), however, noted evidence for transport of shallower sediments into this environment and such transport is the most likely explanation for the presence of strombids.

Rio Yaque del Norte

Outcrops along the eastern end of the Rio Yaque del Norte encompass the greatest time span found in any of the Cibao Valley sections. Unfortunately, the exposures are limited in extent, isolated, and difficult to date.

The oldest outcrops found to contain strombids in the Cibao Valley are located at the Rio Yaque del Norte at Lopez. These outcrops are placed in the Baitoa Formation, which represents a time interval older than those of rivers to the west. A prominent unconformity at this location separates the Baitoa from the late Oligocene conglomerates of the Tabera Group. The outcrops above the unconformity at Lopez have not proven amenable to dating via calcareous nannofossils or planktic forams; Van den Bold (1988), however, used ostracodes to place them in his Aurila amygdala zone, equivalent to nannofossil zones 4-6 (early Middle Miocene).

Strombus bifrons is by far the most common strombid in the Baitoa Formation; *Lobatus haitensis* and *L. galliformis* are present but only represented by a single fragmentary specimen each. *Strombus bifrons* found at this location bear the most resemblance to Woodring's "*bifrons* stout" from the Pliocene Bowden beds in Jamaica (Woodring, 1928).

Strombids next appear in the lower levels of the "Angostura Gorge" section; this particular exposure is noteworthy for the presence of a well-defined framework reef (which unfortunately has been inundated as part of a hydroelectric project). This section has not been dated via foraminiferans or calcareous

nannofossils; other faunal evidence is somewhat contradictory but places this section as no later than nannofossil zone 11 (Saunders *et al.*, 1986). *Lobatus haitensis, Strombus proximus,* and *S. bifrons* are all present here, although none is common; *S. proximus* from this location is noteworthy for its rotundity (Pl. 4, Figs 8-9). The Miocene-Pliocene boundary has been drawn at the southern end of this gorge.

Downstream from the Angostura Gorge section, the next exposures are found at La Barranca. This exposure has been placed in the late early Pliocene, nannofossil zone 12 or 13. *Strombus bifrons* is common here; *S. proximus* and *Lobatus haitensis* are known from a few specimens and *L. dominator* is represented by a single, fragmentary individual. Even farther downstream, in the city of Santiago itself, lie the youngest exposures in this section (nannofossil zone 14). Strombids here are limited to a single specimen each of *S. bifrons, S. proximus,* and *L. haitensis*.

SYSTEMATIC PALEONTOLOGY

Methods and Known Biases

For a number of reasons, the approach taken in this paper has been to use a broad and somewhat flexible set of criteria for determining species membership. The major factors leading to this decision are the inherent morphological variability of strombids, the effects of ecophenotypy, and the potential for gene flow in this region. These reasons are discussed individually in the following paragraphs.

As noted in the section on biology, strombids show a great deal of natural potential for morphological variation. Initial assumptions that the variability observed in modern species can be used to delineate fossil species soon founder on this unavoidable fact. This can be observed both in the collections currently under study and in the literature where references to such things as peculiar morphologies, geographic races, dwarf varieties, and invalid species designations are common (*e.g.*, Dall, 1890; Fluck, 1905; Smith, 1940).

Experiments on modern strombids have shown that many of the more prominent morphological features of the shell can be strongly influenced by the environment. These include such characters as spire length, number and length of spines, shell thickness, and shell shape (Pecharde, 1968; Martin Mora *et al.*, 1995; Ray & Stoner, 1995). Because these characters have been used as the basis for earlier taxonomic distinctions (Abbott, 1960), the approach employed for this paper is to evaluate earlier classifications with caution.

Because of their relatively long time in the plankton as larvae, strombids have a high potential for gene dispersal. In a study of gene frequency in *Lobatus gigas* populations, Mitton *et al.* (1989) calculated that larvae of this species have the potential to be transported throughout the Caribbean and that measured allele frequencies suggest that this is, in fact, the case. They noted, however, that discontinuities in the distribution of certain alleles suggest that certain configurations of currents and geography can isolate subpopulations to a greater or lesser extent, thus preventing Caribbean *L. gigas* from being a single, randomly mating population. The migratory behavior of the adults might play a role in local gene dispersal; they are certainly capable of far wider independent dispersal than other similarly sized adult gastropods. Hesse (1979) documented travels of at least 4 km in adults of *L. gigas*. In addition, she observed migrations through her study area of numerous adults with noticeably different shell characteristics than those of the original population. Finally, the promiscuous mating habits of strombids, although contributing little directly to gene flow between populations, would at least ensure that, no matter how odd, a strombid whose parental population might be some distance away would have few problems finding a mate.

In summary, well-dispersed larval forms and the mobility and reproductive behaviors of adult strombids all contribute to active gene flow among populations. This in turn suggests reduced possibilities for local adaptation and a high potential for hybridization.

Phylum **MOLLUSCA**
Class **GASTROPODA**
Subclass **PROSOBRANCHIA**
Superorder **CAENOGASTROPODA**
Order **SORBEOCONCHA**
Superfamily **STROMBOIDEA**

Shell robust with a relatively large body whorl; narrow aperture with even narrower operculum too small to close aperture.

Family **STROMBIDAE** Rafinesque, 1815

Family characterized by "leaping" mode of locomotion, with operculum, foot, and shell modified to facilitate this method of transport. Visual system well developed, possibly as adaptation to leaping. Juveniles show conservative growth patterns and simple conic shape; specialized shell features produced when adulthood is reached.

Genus ***STROMBUS*** Linnaeus, 1758

Type species.–Strombus pugilis Linnaeus, 1758, by subsequent designation (Montfort, 1810). Recent, West Indies and Florida.

Adult shell generally characterized by extended outer lip and the "strombid notch," an embayment in the siphonal canal that allows protrusion of the right eyestalk.

Strombus bifrons G. B. Sowerby I, 1850
Plates 1-2

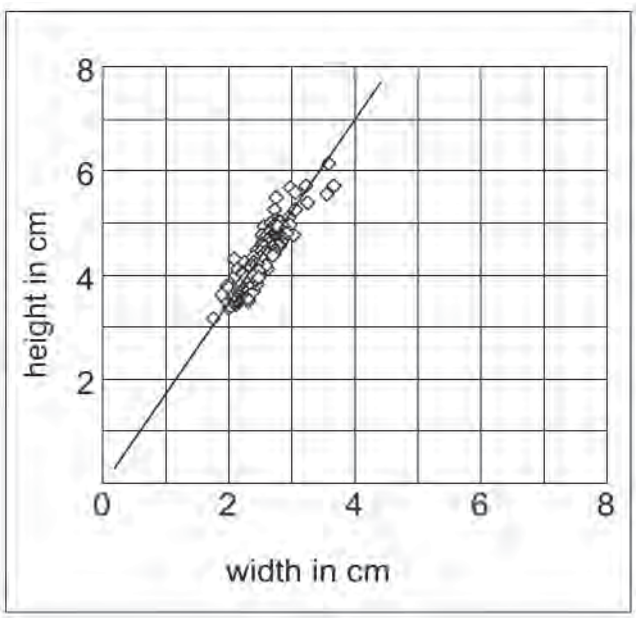
Strombus bifrons G. B. Sowerby I, 1850: 48, pl. 9, fig. 9; Guppy, 1866: 387; 1873: 83; 1874: 438; 1876: 521; Dall, 1903: 1584; Maury, 1917: 283, pl. 46, figs 2-3; 1925: pl. 4, fig. 3; 1925: 373-374, pl. 47, fig. 2; Woodring, 1928: 324, pl. 23, figs 3-4, pl. 24, fig. 1; Woodring, 1959: 190.
Strombus cf. *bifrons* Maury, 1920: 56-57.
Strombus bifrons? Hubbard, 1921: 144.
Strombus pugilis. Gabb, 1873: 233 (in part) (non *pugilis* Linnaeus, 1758).
Strombus ambiguus G. B. Sowerby I, 1850: 48; Guppy, 1874: 438; Dall, 1890: 174, 177; Dall, 1903: 1584; Pilsbry, 1922: 367.
Strombus ambiguus forma *bifrons*. Pilsbry, 1922: 367.
Strombus pugiloides. Perrilliat Montoya, 1972: 65 (non *pugiloides* Guppy, 1874).

Diagnosis.–Shell relatively small (approximately 30-60 mm) and slender, with elevated spire of 8-9 whorls. Shell shape and sculpture highly variable. Lip not extending beyond penultimate whorl; row of knobs (seldom spines) along shoulder. Often with lirate sculpture on body whorl and lips.

Description.–Early spire whorl profiling gently rounded and convex, typically becoming more angular toward penultimate whorl. Anterior canal narrow and moderately to sharply recurved. Stromboid notch varying from shallow and indistinct to well-developed and prominent. Small longitudinal bulge sometimes present behind stromboid notch. Final adult suture ascending to middle or top of knobs on previous whorl; posterior edge of outer lip usually descending from suture. Aperture relatively long and narrow.

Early whorls showing distinct axial ribs with fine spiral threads between them; varices common, often at approximately 180° intervals. At fifth to sixth whorl, ribs gradually becoming slightly angular nodes; occasional varices can still be present but much less common. By body whorl, these typically becoming single row of knobs (or occasionally blunt spines), that can become less distinct toward lip. Spiral threads usually persisting through ontogeny, becoming distinct lirations on later whorls, although in some specimens body and penultimate whorls are smooth. Interior of lip typically lirate along entire length but occasionally smooth. In some specimens, lirations appear to have been covered by deposition of shell material after adult size has been reached; in others they do not appear to have formed in the first place. Columella often displaying anterior and posterior lirae, but can also be smooth.

Type material.–Lectotype, BMNH G83938 (Pl. 1, Figs 1-3).



Text-fig. 10. Height plotted against width for *Strombus bifrons.*

Type locality.–Yaqui valley, Dominican Republic.

Other localities.–*Strombus bifrons* has been found in the following localities (DHG and JRF localities given in their NMB or TU equivalents).

Rio Cana–NMB localities 16817, 16818, 16970, 16966, 16824, 16825, 16828, 16839, 16842, 16862, 16865, 16866, and 17005; TU localities 1230 and 1354.

Rio Gurabo–NMB localities 16154, 15807, 15805, 15837, 16192, 16155, 15909, 16157, 15820, 15821, 15844, 15846, 15860, 15863, 15865, 15866, 15869, 15871, 16808, and 16810; TU localities 1214, 1215, 1231, 1246, 1277, and 1278.

Rio Mao–NMB localities 16910, 16915, 16918, 16919, 16922, 16923, 16924, 16926, 16927, and 17269; TU locality 1293.

Rio Amina–TU locality 1219.

Arroyo Zelaya–NMB localities 17270 and 17271; TU locality 1227.

Rio Yaque del Norte–NMB localities 16935, 16936, 16938, 16943, 17267, 17268, 17273, 17275, 17282, 17283, 17284, 17286, 17287, 17288, 17289, and 17290; TU localities 1206, 1364, 1403, and 1449.

Rio Verde (Rio Yaque del Norte)–TU locality 1250.

Measurements.–Measurements of lectotype: height 49 mm, width 34 mm. Text-fig. 10 shows height plotted against width for measured individuals of this species. Mean height of these

specimens is 42 mm; height ranges from 32-62 mm.

Discussion.–In 1850, Sowerby proposed the specific appelatives *bifrons*, *ambiguus*, and *proximus* for the smaller strombids of the Dominican Republic. Guppy added *pugiloides* in 1873, although in 1876 he synonymized his *Strombus pugiloides* and Sowerby's *S. ambiguus* together under *S. proximus*. The names *S. proximus* and *S. pugiloides* were both chosen to reflect similarity to the modern *S. pugilis*. Gabb (1873) considered all of the small Dominican strombids to be varieties of this modern species. Other early authors (*e.g.*, Pilsbry, 1922) were not so eager to lump all of these together but considerable confusion and inconsistency remained in regard to which features served to distinguish which species. Subsequent authors have generally accepted either two or three of these names as valid. The names *S. bifrons* and *S. proximus* have been the most frequently and consistently applied. We use these terms in this paper, synonymizing the various usages of *S. ambiguus* and *S. pugiloides* with either *S. bifrons* or *S. proximus* as deemed appropriate based on descriptions and illustrations. Although we retain a separate identity for *S. bifrons* and *S. proximus*, a number of transitional forms exist between these two species. It is possible that they are simply end members of a single highly variable species.

The oldest specimens of *Strombus bifrons* in the Cibao Valley (from Baitoa) show features that might be considered transitional between this species and *S. proximus*. As in *S. proximus*, the Baitoa specimens are stouter (greater width-to-height ratio) than Dominican *S. bifrons* as a whole and some have actual spines on the shoulder rather than simply knobs; but as in *S. bifrons*, the body whorls show well-defined lirations and only a moderate degree of lip expansion. Individuals at this location bear the closest resemblance to *S. bifrons* from the Pliocene Bowden beds of Jamaica, figured by Woodring in 1928 (Woodring figured both "stout" and "slender" specimens, but implied that the stout form was the more common of the two).

The Cañada de Zamba also yields interesting "transitional" forms. This location is probably the richest strombid outcrop in the Cibao Valley. It contains no individuals assigned to *Strombus proximus*, but a number of *S. bifrons* specimens from this site resemble *S. proximus* in having a smooth body whorl and shoulder spines (Pl. 2, Figs 4-5). Classification of these specimens is difficult because of the presence of numerous transitional forms between typical *S. proximus* and *S. bifrons*. In addition, a number of other individuals (Pl. 2, Figs 9-10, 14-16) bear an exact resemblance to the figured specimens of *S. pugilis nicaraguensis* Fluck, 1905 (a modern dwarf subspecies of *S. pugilis*) by Clench & Abbott (1941: Pl. 6). Again, intermediates between this form and more typical *S. bifrons* are found at the same location.

Strombus proximus G. B. Sowerby I, 1850
Plates 3-4

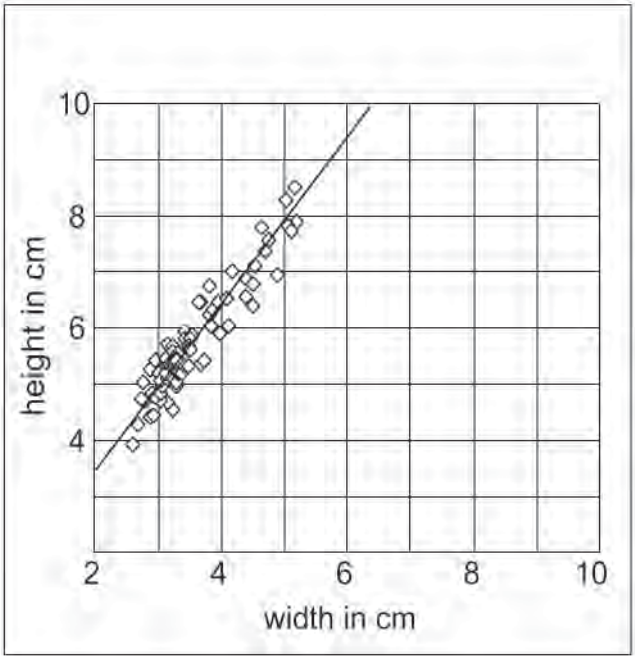
Strombus proximus G. B. Sowerby I, 1850: 48, pl. 9, fig. 8; Guppy, 1866: 157; 1874: 433; 1876: 521.
Strombus fragilis Moore, 1863: 511.
Strombus pugilis Gabb, 1873: 233 (in part).
Strombus pugiloides Guppy, 1874, p. 433
Strombus pugilis var. *proximus*. Dall, 1890: 177.
Strombus proximus. Maury, 1917: 283, pl. 20, figs 4-5.
Strombus pugiloides. Maury, 1917: 284, pl. 20, fig. 6.
Strombus proximus pugiloides. Pilsbry, 1922: 367.
Strombus pugiloides. Olsson, 1922: 314.

Diagnosis.–Shell small to moderate, approximately 40-85 mm. Spire extension variable, with 8-11 whorls. Shell generally stout and robust. Body-whorl suture not extending past shoulder of previous whorl. Spines rather than knobs at shoulder, occasionally with second, weakly developed row along body whorl. Body whorl generally lacking sculpture.

Description.–Early spire whorl profiling gently rounded and convex, typically becoming more angular toward penultimate whorl. Anterior canal slightly to strongly recurved; stromboid notch varying from broad and gentle to strongly indented. In some individuals, suture line and shoulder of body whorl with marked anterior displacement (relative to rates of translation shown by previous whorls), resulting in distinctive morphology (Pl. 4, Figs 4-5, 10-12). Final adult suture never ascending beyond shoulder of preceding whorl; lip usually descending from suture and curving gently outward. Aperture itself relatively broad, except in some mature adults with very thickened, inward-curving lip.

Early whorls with numerous axial ribs and spiral threads. Ribs becoming broader and more widely spaced through ontogeny, becoming nodes for approximately two whorls, then expanding into actual spines on last three whorls. Spines on penultimate whorl often longer than those of body whorl. Body whorl itself typically displaying one well-developed row of spines at shoulder. In some individuals, a second, less well-developed row present lower on the body whorl; this row carrying only two or three nodes and rarely extending to dorsalmost surface. In a few specimens, no spines or nodules in either row extending to dorsalmost surface of body whorl. Spiral threads persisting until penultimate or preceding whorl; in a few specimens, even present on body whorl. Usually body whorl relatively smooth, but often showing faint axial lines apparently marking former growth stages of lip. Columella and interior of lip typically smooth, but lip interior occasionally weakly lirate.

Type material.–Lectotype, BMNH G83936 (Pl. 3, Figs



Text-fig. 11. Height plotted against width for *Strombus proximus.*

8-10); paralectotype, BMNH GG 80354 (Pl. 3, Figs 11-13).

Type locality.–Yaqui Valley, Dominican Republic.

Other localities.–*Strombus proximus* has been found in the following localities (DHG and JRF localities given in their NMB or TU equivalents).

Rio Cana–NMB localities 16838, 16845, 16844, 16842, 16837, 16835, 16866, 16966, 16865, 17005, and 16868; TU localities 1420 and 1422.

Rio Gurabo–NMB localities 15842, 15865, 15833, 15832, 15824, 15814, 15909, 15908, 15903, 15905, 15873, 15878, 15807, 15871, 15904, 16155, 15910, 15909, 16155, and 15805; TU localities 1210, 1212, 1231, 1246, 1278, 1352, 1359, 1211, 1277, and 1296.

Rio Mao–NMB localities 16910, 16913, and 16919; TU localities 1293 and 1379.

Rio Amina–TU localities 1227 and 1453A.

Rio Yaque del Norte–NMB localities 17275 and 17278; TU localities 1206 and 1403.

Rio Verde (Rio Yaque del Norte)–TU locality 1250.

Measurements.–Measurements of lectotype: height 56 mm, width 44 mm. Text-fig. 11shows height plotted against width for individuals of this species measured for this study; mean height of these specimens is 58 mm, range is from 39 -85 mm.

Discussion.–See remarks for *Strombus bifrons*, above. In addition to the web of Caribbean species and subspecies mentioned above, *S. proximus* has also been compared to the eastern Pacific *S. gracilior* G. B. Sowerby I, 1825. Both Sowerby (1850) and Maury (1920) considered *S. proximus* to be closer to *S. gracilior* than to *S. pugilis*.

A number of specimens of *Strombus proximus* show a peculiar, anteriorly displaced body whorl; we have referred to this variant as *S. proximus* "a" (see Pl. 4, Figs 10-12). In many of these specimens, the dorsal spines are reduced or absent; when present, they are displaced anteriorly along with the rest of the body whorl and their protrusion beyond the profile of the body wall is minimized. The profile in general is smooth and rounded. These specimens present a considerably different appearance than the "typical" *S. proximus*, and without a series of intermediate forms, they might be considered a new species.

These features could be adaptive for an infaunal mode of existence. Savazzi (1991) noted that displacement or loss of dorsal protrusions and a general flattening of the dorsal outline (especially the last whorl) are features of modern strombids adapted for such a mode of life. Another possibility (not mutually exclusive) is that the different morphologies result from allometric changes that occur via differential growth rates (see Martin-Mora *et al.,* [1995]). We attempted to test this hypothesis by using oxygen stable isotope ratios to detect seasonal growth intervals (via paleotemperatures) in the strombid shell (Freiheit *et al.*, 2002; see also Geary *et al.*, 1992) and from these to determine growth rates. Results have been inconclusive.

Genus ***LOBATUS*** Iredale, 1921

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

Characterized by medium to very large shell with widely expanding, non-digitate outer lip. Glazed outer edge of rim of outer lip, not bent toward columella at maturity. Typically strong spiral sculpture on the last whorl.

Lobatus haitensis G. B. Sowerby I, 1850
Plates 5-6

Strombus haitensis G. B. Sowerby I, 1850: 48, pl. 9, fig. 7; Guppy, 1867: 157; 1874: 438; 1876: 521; Dall, 1903: 1584; Maury, 1917: 282, pl. 20, fig. 1; Pilsbry, 1922: 366; Woodring, 1928: 325-326; Pflug, 1961: 23-29, pl. 3, figs 1-3, 5-6, 8.

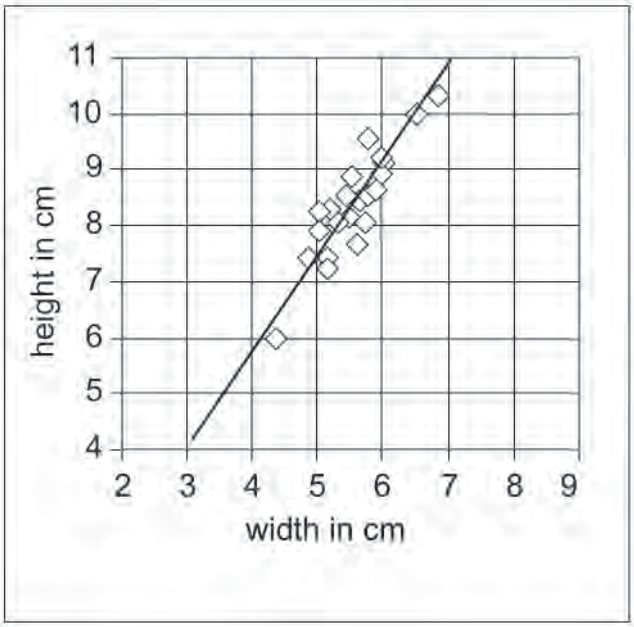
Strombus cf. *haitensis*. Maury, 1920: 55-56.

Strombus bituberculatus. Gabb, 1873: 233 (non *bituberculatus* Lamarck, 1822)

Diagnosis.–Shell medium-sized, approximately 60-100 mm in height. Moderately elevated spire with 9-10 whorls. Shell stout, rugged, often irregular in appearance. Outer lip noticeably thickened, especially at edge. Sculptural elements prominent but irregular. Spiral ribbing usually well developed along body whorl. Row of blunt spines or tubercles along shoulder of body whorl, often with second, less-prominent row midway down whorl.

Description.–First 3-5 whorls displaying convex profile. Succeeding whorls generally weakly concave in profile, when not masked by varices or other sculptural elements. Shoulder rounded rather than sharp, presenting outline more ovate than cone-shaped. Anterior canal weakly to moderately recurved dorsally; a few individuals with minor lirations in this region. Stromboid notch rather shallow. Aperture relatively narrow, especially in specimens with well-developed lip calluses. Columella and inside lip smooth, straight. Outer lip always extending beyond penultimate whorl, usually to point approximately halfway between tip of spire and shoulder, but can extend as far as tip of spire. Edge of lip showing distinctive pattern of thickening, with mature growth strongly reflected away from aperture. Smooth callus often extending around edge of lip and onto dorsal surface of lip for 1-2 mm, creating distinctly raised margin.

First 3-5 whorls showing fine threads (both axial and spiral), regularly spaced axial ribs, and numerous varices. Spiral threads persisting throughout ontogeny, typically coalescing into broader ribs of body whorl; these can, however, maintain independent existence especially in region of anterior canal and posterior lip flare; not uncommonly maintaining some definition even when incorporated into larger ribs. Axial threads becoming broader, fainter, more widely spaced, eventually becoming series of poorly defined axial ridges. At about fifth whorl, axial ribs becoming row of knobs and varices and lessening in frequency, becoming series of irregularly sized and spaced swellings and protrusions, causing suture line to become highly irregular. Between varices, suture line lying across shoulder of previous whorl. In some instances, varices spaced at 180° intervals, occuring at approximately equivalent positions on succeeding whorls creating flattened appearance. Body whorl with broad, irregular spiral ribs with well-defined intercostal intervals of approximately one-quarter width of ribs. More prominent of two rows of tubercles at shoulder, consisting of at least five individual protuberances that occasionally extend into blunt spines, their greatest extension occurring on dorsalmost surface. Abapical row, midway along body whorl, typically with fewer, less prominent knobs, but can be nearly as well developed as adapical. Ventral surface sculptural elements greatly reduced and covered by callus, or absent.



Text-fig. 12. Height plotted against width for *Lobatus haitensis.*

Type material.–Lectotype, BMNH G83927 (Pl. 5, Figs 4-7).

Type locality.–Santo Domingo (Yaqui valley, Dominican Republic).

Other localities.–*Lobatus haitensis* has been found in the following localities (DHG and JRF localities given in their NMB or TU equivalents).

Rio Cana–NMB localities 16817, 16862, 16852, 16839, 16842, 16835, 16828, 16820, 16864, 16867, 16865, and 16868; TU localities 1420 and 1422.

Rio Gurabo–NMB localities 15855, 15863, 15864, 15807, 15811, 15857, 15854, 15909, 15883, 15905, 15869, 15890, 16808, 15807, 15867, 15805, 15865, 15866, 16154, 15861, 16155, and 16157; TU localities 1210, 1211, 1231, 1246, 1277, 1278, and 1296.

Rio Mao–NMB localities 16801, 16910, 16927, and 16931; TU locality 1293.

Rio Yaque del Norte–NMB localities 17275 and 17276; TU locality 1206.

Measurements.–Measurements of lectotype: height 92 mm, width 62 mm. Text-fig. 12 shows height plotted against width for individuals of this species measured for this study. Mean height of these specimens 83 mm; height ranges from 60-103 mm.

Discussion.–The rugged, irregular sculpture of *Lobatus haitensis* makes it one of the more distinguishable Dominican strombids. Nevertheless, occasional specimens can present difficulties when compared to other medium to large Dominican strombids.

Lobatus haitensis can be distinguished from smaller specimens of *L. dominator* by the distinctive recurved pattern of adult outer lip thickening of *L. haitensis* and posterior lip extension only as far as the spire. The outer lip of *L. dominator* typically exhibits posterior extension beyond the spire and when thickened does not create a recurved rim in the aperture. The spiral sculpture of *L. dominator* tends to be less distinct than that of *L. haitensis* and gives *L. dominator* a fluted rather than ribbed appearance. The large exaggerated dorsal spine of *L. dominator* gives the apical profile of most *L. dominator* specimens a more triangular aspect. The sharper shoulder angle of larger *L. dominator* also distinguishes the two species, although the shoulder is less angled in smaller specimens of *L. dominator*.

Lobatus haitensis is far more robust and irregular in appearance than *L. galliformis*. The lip of *L. galliformis* shows posterior extension similar to that of *L. haitensis*, but otherwise resembles the lip of *L. dominator* more closely. The shoulder angle of *L. galliformis* is sharper than that of either *L. haitensis* or smaller individuals of *L. dominator*; the row of knobs on the shoulder of *L. galliformis* is far more regular than similar sculptural elements in *L. haitensis* or *L. dominator*.

Confusion between adult specimens of *Lobatus haitensis* and *Strombus bifrons* or *S. proximus* is unlikely but not inconceivable, especially in the case of fragmentary or highly aberrant individuals of the latter two species. *Lobatus haitensis* typically has a higher degree of irregularity in its sculptural elements, higher irregularity in the spiral sculpture than *S. bifrons*, and higher irregularity in the spines than *S. proximus*. As in all Dominican members of the previously used subgenus *Tricornis*, development of prominent spines or protuberances in *L. haitensis* is largely restricted to the dorsal surface of the body whorl. Spines in *S. proximus* can appear on earlier whorls and are generally present on ventral portions of the shell; if anything, they generally show displacement away from the dorsal surface. The internally angulate lip thickening of *L. haitensis* is also diagnostic.

The thickened outer-lip edge and narrowed aperture of *Lobatus haitensis* are probably defensive adaptations against crabs. Crabs are a major source of predation on modern strombids and probably the most important source of predation on juveniles (Ray & Stoner, 1995). Typically crabs attack the lip of the shell and "peel" it back until they expose the animal inside, leaving a distinctive pattern of breakage at the aperture. Experiments with modern strombid species that display similar thickenings at the margin of the lip have shown that when this structure is removed, the snail becomes far more vulnerable to predation by crabs (Savazzi, 1991). Well-preserved whole fossil crabs have been found in the Cercado Formation of the Rio Gurabo sections where *L. haitensis* is most common.

Lobatus galliformis Pilsbry & Johnson, 1917
Plate 7

Strombus galliformis Pilsbry & Johnson, 1917: 170, pl. 21, figs 1-2; Pilsbry, 1922: 366, pl. 31, figs 1-2; Woodring, 1928: 328, pl. 24, fig. 2.

Strombus haitensis. Dall, 1903: 1584 (in part) (non *haitensis* G. B. Sowerby I, 1850).

Diagnosis.–Shell moderate in size, approximately 50-90 mm. High spired with 9-10 whorls. Shoulder sharply angled. Shell fragile (for a strombid) with relatively thin outer lip. Alate outer lip extending nearly to tip of spire. Sculptural elements pronounced and regular. Row of knobs present along shoulder. Spiral ribbing on body whorl giving distinct fluted appearance.

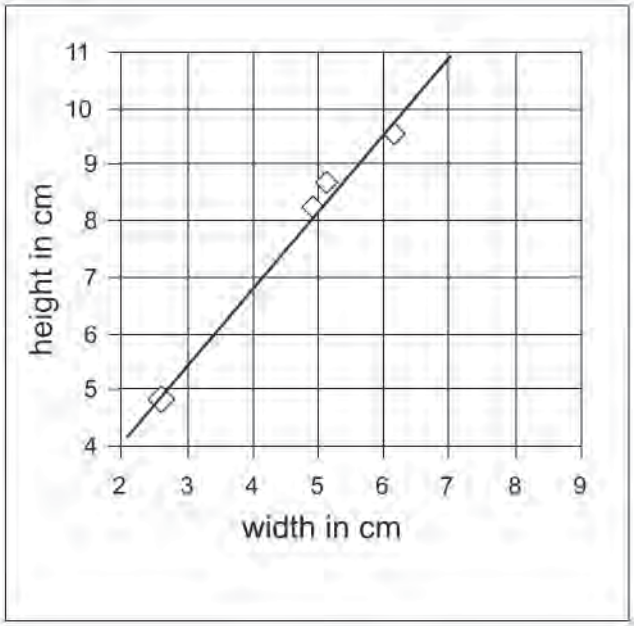
Description.–Early spire whorl profiling angular. Aperture narrow with well-developed stromboid notch, strongly recurved anterior canal. Suture line below shoulder of previous whorl until body whorl, where suture line ascends with lip flare. Outer lip alate with moderate degree of flare; although thickening of lip occurs, edge of lip remains relatively thin and fragile. Lip ascending from point of attachment sometimes to tip of spire.

Early whorls with spiral threads and regularly spaced axial ribs and varices. Ribs giving way relatively abruptly to single row of regularly spaced shoulder knobs; varices can continue for another revolution or two, but are absent by 3-4 whorls from body whorl. Spiral threads becoming well-defined set of ridges, giving body whorl and outer lip distinctly fluted appearance. Faint axial striations present on body whorl; axial ridge and/or depression marking point at which lip begins to flare. Shoulder knobs increasing gradually and regularly in size up to dorsalmost knob on body whorl, which can develop into stout spine. Parietal wall can be smooth or can have plications either restricted to anterior canal or extending along entire length of aperture; outer lip showing similar pattern of variability.

Type material.–Syntype, ANSP 2582 (Pl. 7, Figs 1-3).

Type locality.–Santo Domingo.

Other localities.–*Lobatus galliformis* has been found in the following localities (DHG and JRF localities given in their



Text-fig. 13. Height plotted against width for *Lobatus galliformis.*

NMB or TU equivalents).

Rio Cana–NMB localities 16817 and 16865; TU locality 1422.

Rio Gurabo–NMB locality 16157; TU localities 1278 and 1296.

Rio Mao–NMB locality 16910; TU localities 1293 and 1410.

Rio Amina–TU locality 1219.

Rio Yaque del Norte–NMB locality 17265.

Measurements.–Measurement of syntype: height 100 mm; width 66 mm. Text-fig. 13 shows height plotted against width for measured individuals of this species. Mean height of these specimens 72 mm; height ranges from 48-95 mm.

Discussion.–*Lobatus galliformis* has spiral ribs and axial ridges similar to those of *L. dominator*, but considerably more pronounced, especially on the flared portion of the lip. A single row of knobs is present along the shoulder; these are less variable than the knobs of either *L. dominator* or *L. haitensis*. The sharply angled shoulder resembles that of *L. dominator* and is in marked contrast to the rounded shoulder of *L. haitensis*. The growth pattern of the lip is similar to that of *L. dominator*, but the lip neither extends as far adapically as in most *L. dominator* nor is thickened as much as in a similarly sized *L. dominator*.

Lobatus galliformis is similar to modern *L. gallus* (Linnaeus, 1758) but the modern species has more distinct sculptural elements and much greater posterior and anterior extension of the lip.

Although this is the least common strombid from the Dominican Republic, its observed temporal range (based on presence/absence data) exceeds that of both *Lobatus dominator* and *L. haitensis*. Rarity of *L. galliformis* could result at least partially from taphonomic bias, because it is also the least robust of the Dominican strombids. Two of the four figured specimens had to be held together with clay and glued in order to be photographed or measured.

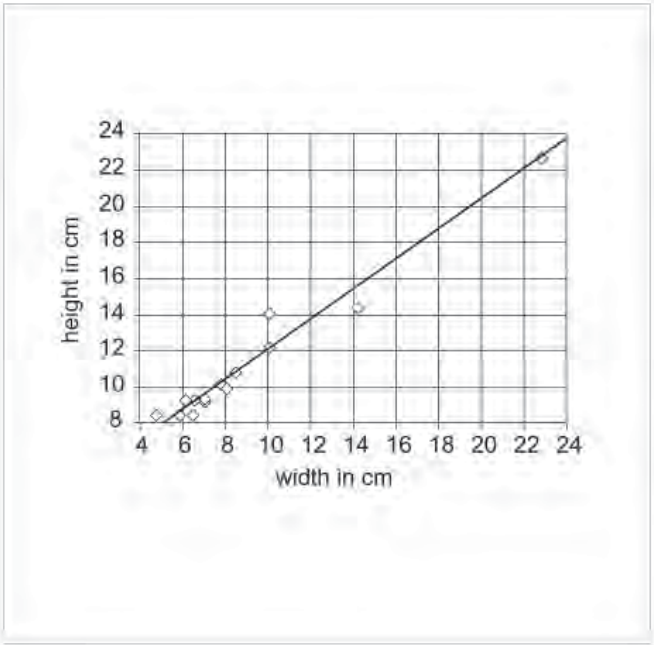
Lobatus dominator Pilsbry & Johnson, 1917
Plates 8-9

Strombus dominator Pilsbry & Johnson, 1917: 171, pl. 32, figs 1, 9; Pilsbry, 1922: 366-367, pl. 32, figs 1, 9.
Strombus dominator delabechi Rutsch, 1931: 254, pl. 12, figs 1-2.
Strombus gigas Lamarck. Gabb, 1873: 234 (in part) (non *gigas* Linnaeus, 1758).
Strombus maoensis Maury, 1917: 284, pl. 21, fig. 1.

Diagnosis.–Shell moderate to very large, approximately 85-230 mm in height. Spire with 8-10 whorls, moderately elevated in smaller specimens, depressed in larger ones. Shell more cone-shaped than ovate, with angled rather than rounded shoulders. Shell robust and very thick in larger specimens. Adults with strongly flared thickened lip and prominent blunt spines at shoulder of body whorl. Lip typically extending posteriorly to tip of spire or beyond.

Description.–Early whorls with convex profile, with suture of each whorl falling well below shoulder of previous whorl. Starting at approximately sixth whorl, suture of each whorl "rising" relative to preceding whorl, typically reaching or even covering preceding whorl's shoulder. This change giving rise to concave rather than convex profile for later whorls. Shoulder sharply angled; larger specimens generally with sharper angles. Juvenile specimens and adults with missing lips extremely cone-like in appearance. Lip strongly flared, showing posterior extension at least as far as spire and usually beyond. Aperture rather narrow; lip flaring at slight angle to aperture, thus enlarging lip without enlarging gape of aperture. In mature specimens, lip can have considerable thickening, 3 cm or more. Anterior canal (and stromboid notch) missing from most specimens; where present, anterior canal with strong dorsal recurvature with moderately well-developed stromboid notch. Columella straight and smooth. Parietal wall and outer lip lacking plications.

Earliest 3-5 whorls with fine spiral threading, with regularly spaced axial ribs and irregularly spaced varices. At approximately sixth whorl, varices rapidly becoming less prominent and less numerous. At same point, ribs changing to row of shoulder knobs and spacing between them increasing.



Text-fig. 14. Height plotted against width for *Lobatus dominator.*

Spiral threads developing into broad, low spiral ridges giving fluted appearance to adult shell. Some faint axial ridging usually present on body whorl. Degree of relief shown by these sculptural features variable, in some cases barely discernible. Single row of stout protuberances along shoulder of body whorl, vestiges of second row present midway down body whorl in few individuals. Typically dorsalmost protuberance extending into blunt spine; others showing considerable variability and can appear as irregular knobs or even coalesce in keel-like structure.

Type material.–Syntype, ANSP 2579 (Pl. 9, Figs 7-9).

Type locality.–Santo Domingo.

Other localities.–*Lobatus dominator* has been found in the following localities (DHG and JRF localities given in their NMB or TU equivalents).

Rio Cana–NMB localities 16817, 16818, 16830, 16852, 16967, and 16879; TU localities 1354 and 1422 (Arroyo Bellaco).

Rio Gurabo–NMB localities 15869, 15867, 15805, 15866, 15865, 16154, 15863, 15807, 15864, 16155, 15868, 15841, 15847, 15848, 15858, 15805, 15870, 15871, and 15877; TU localities 1210, 1231, 1277, and 1296.

Rio Mao–NMB locality 16931; TU localities 1225, 1280, and 1293.

Rio Yaque del Norte–TU locality 1403 (Arroyo Babosico).

Rio Verde (Rio Yaque del Norte)–TU locality 1250,

Measurements.–Measurement of syntype: height 88 mm, width 75 mm. Text-fig. 14 shows height plotted against width for individuals of this species measured in this study. Mean height of these specimens 102.8 mm; height ranges from 84-227 mm.

Discussion.–*Lobatus dominator* is the largest fossil strombid identified from the Dominican Republic. Gabb (1873) reported the presence of *L. gigas* but we were not able to confirm this; some fragmentary remains which might (or might not) be *L. gigas* could not be confidently identified. Smaller specimens of *L. dominator* can resemble either *L. haitensis* or *L. galliformis*. *Lobatus dominator* has been compared to the living *L. gigas, L. costatus* (Gmelin, 1791), and *L. goliath* (Schröter, 1805), all of which are Atlantic species. Morphologically the most similar of these is *L. costatus*. Even more similar morphologically is the eastern Pacific *L. peruvianus* (Swainson, 1823), which differs primarily from *L. dominator* in typically showing lirations in the aperture.

Lobatus dominator can be distinguished from *L. haitensis* by the structure of the lip and by the details of the sculptural elements. In most *L. dominator* individuals, the extreme development of the dorsalmost spine creates an apical profile distinctly more triangular in aspect than that seen in *L. haitensis*. *Lobatus maoensis* was proposed as a species by Maury in 1917, based on a single lipless individual; her figured specimen is nearly identical to some of the smaller examples of *L. dominator* and we have considered it as such in this paper.

This strombid ranges widely in size, with specimens in these collections ranging from 8.4-23 cm in height. Pilsbry & Johnson (1917: 171) noted a similar size range in their original description of the species; the type specimen was "an almost perfect but dwarf specimen" (at 8.8 cm) and "several fragmentary specimens are much larger" up to "perhaps 20 cm."

It is very likely that a strong taphonomic bias exists against larger specimens of *Lobatus*. As noted in the section on strombid biology, large modern strombids typically dwell on the substratum (rather than burrowing into it as many smaller ones do), relying on their size as protection from most predators. As a result, they are vulnerable to the settlement of various endo- and epibionts, especially boring sponges and algae. While the animal is alive, it deters some of these organisms with its periostracum and mitigates the effects of others by reinforcing the interior surfaces of the shell. After death, bioerosion continues unabated and the structural integrity of the shell is greatly reduced. A number of intensely

bored, fragmentary (although massive) remains were found at several locations.

SUMMARY OF STROMBID SPATIOTEMPORAL DISTRIBUTION

Nannofossil zone 5 (middle Miocene)

For nannofossil zone 5, strombids (and outcrops) only appear in the Rio Yaque del Norte, at the eastern end of the study area. Strombids are not common and are mainly represented by a large robust version of *Strombus bifrons.*

Nannofossil zone 11 (late Miocene)

Strombids show the greatest species diversity across the widest area. Most of this diversity is found at the western end of the study area, centered on the Rio Gurabo. Large specimens of *Lobatus dominator* have been found in the Rio Mao and have been documented from fossil reefs at Arroyo Bellaco (a tributary of the Rio Cana) and the Rio Gurabo (the Cercado reef, at about 220 m above the base of the Cercado Formation). The Cercado reef exhibits the most diverse strombid assemblage in the Cibao, with all five species present in a stratigraphic range of two or three meters, four of them represented by more than 20 specimens. Strombids in general are most common near "deep reef" coral assemblages but a large number of juveniles are also found associated with the "shallow reef" assemblage in the Rio Cana. Surprisingly, neither juveniles nor adults are found in "seagrass" assemblages. To the east, the Rio Yaque del Norte deposits harbor a few *Strombus bifrons.*

Nannofossil zone 12 (early Pliocene)

Strombids disappear from the Rio Mao and nearly disappear from the Rio Gurabo. To the west, at the Cañada de Zamba (Rio Cana), the largest concentration of strombids is found: *Lobatus dominator*, *Strombus bifrons,* and juveniles are predominant; a single *S. proximus* and two *L. haitensis* have been found here. Numerous fragments of larger *L. dominator* (and/or possibly *L. vokesae*) are present and appear far more bioeroded and weathered than the smaller whole *L. dominator*. Strombids are more abundant in shell beds (with other mollusks) at the Cañada de Zamba than elsewhere, implying a higher energy environment with more water movement to winnow sediments and concentrate shells. Above the Cañada de Zamba, strombids soon disappear from the Rio Cana as well. To the east, strombids (mostly *S. bifrons*) appear in the Rio Amina and increase in numbers in the Rio Yaque del Norte.

Nannofossil zone 13 (early Pliocene)

Strombids essentially disappear from all localities except the Rio Yaque del Norte in the far east (where only small *Strombus bifrons* were found) and the Rio Cana in the far west (where roughly equal numbers of *S. bifrons, S. proximus,* and *Lobatus haitensis* were found).

Nannofossil zone 14 (middle Pliocene)

Strombid locations are restricted almost exclusively to the two rivers farthest east, the Arroyo Zelaya and the Rio Yaque del Norte. Relatively few strombids are present at either locality. *Strombus proximus* predominates in the Arroyo Zelaya and *S. bifrons* predominates in the Yaque del Norte. Due to uncertainties in dating, it is possible that some specimens assigned to nannofossil zone 13 in the Rio Cana actually belong in this zone.

Nannofossil zone 15 (middle Pliocene)

Strombids are known mostly from the Rio Gurabo where they are represented primarily by a large, robust form of *Strombus proximus.* A single whole *S. proximus* and a few fragmentary specimens appear in the Rio Cana.

ANALYTICAL METHODS

In a study of 1,100 modern *Strombus pugilis*, Goodrich (1944) stressed the high degree of variation in this species but also observed that the basic shape of the shell (when measured without regard to spines or other sculptural elements) remained constant. In light of Goodrich's study and our own observations of sculptural variability, we have chosen a conservative set of measurements, primarily embodying shape, as most appropriate for our analyses. Using measurements as described in Text-fig. 1, we performed two principal components analyses (PCA). The first was on the entire set of all measured whole specimens and was intended to establish a morphospace for strombids as present in the Dominican Republic. The second was performed only on specimens in the genus *Strombus* in an attempt to quantify species relationships. We used the paleontological statistics program PAST (Hammer *et al.*, 2001) to calculate and plot PCAs, employing a variance-covariance matrix. All specimens were assigned to a species before analysis.

As a complement to PCA, we plotted and compared Procrustes-transformed shapes of certain individual specimens and groups, again using the program PAST. Inasmuch as the first PCA axis is often correlated with size whereas Procrustes transformation essentially removes size differences, superimposition of the resulting shapes provides a complementary approach to PCA in visualizing how much variation is described by the remaining axes.

In addition to these analyses of shape, we analyzed temporal and geographic patterns of size variation. Size comparison was based on height measurements. Comparisons based on

composite estimates of body size yielded nearly identical results and are not figured here. Analysis of size variation was carried out via the Kruskal-Wallis test, followed by the Kolmogorov-Smirnov test for pairwise comparisons.

RESULTS AND INTERPRETATION

Morphometrics

PCA (All Species)

Results of the PCA for all species are shown in Text-figs. 15-17. Scatterplots by genus and by species are presented in Text-figs 15 and 16, respectively. Loadings for each PCA axis and examples of individuals scoring high and low on these axes are presented in Text-fig. 17.

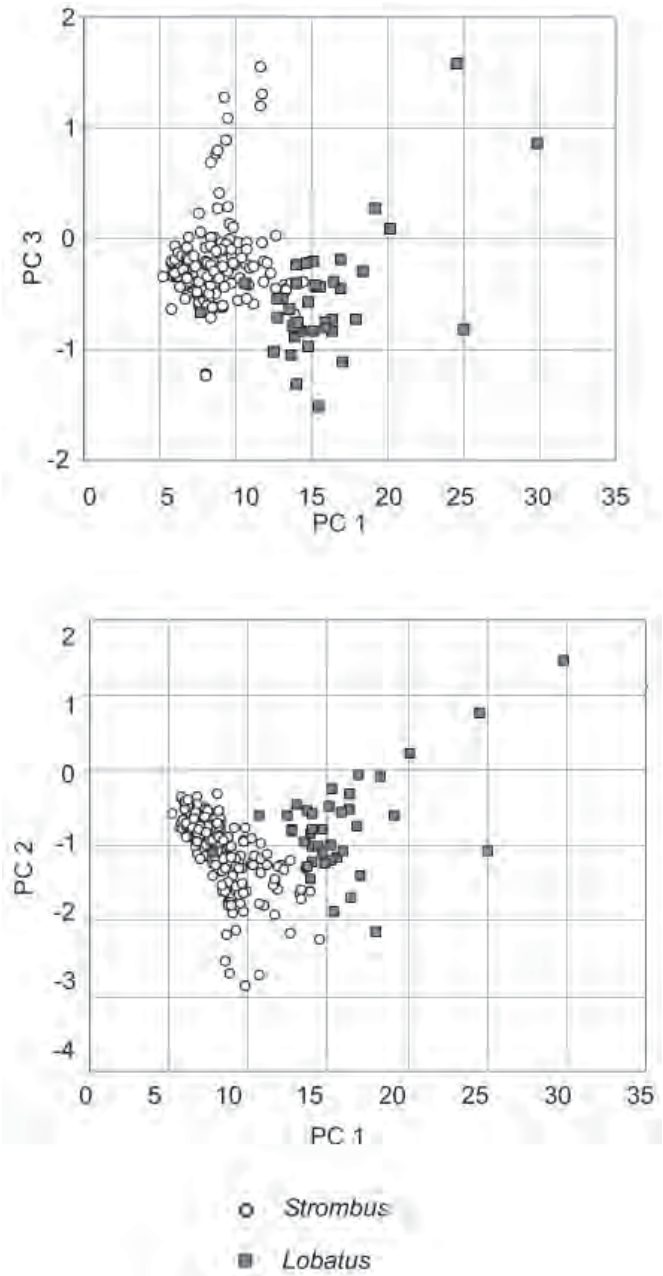
The two genera separate into distinct regions of morphospace. Members of *Lobatus* tended to score higher on PCA 1 than members of *Strombus*; individuals of *Lobatus* that display similar scores to many of *Strombus* on PCA 1 had higher scores on PCA 2 and generally lower scores on PCA 3.

Within genera, species show considerable overlap in the morphospace they occupy. Within *Lobatus*, *L. haitensis* shows some overlap in PCA space with *L. dominator* and nearly complete overlap with *L. galliformis*. For *Strombus*, *S. bifrons* and *S. proximus* appear at the endpoints of a continuum of forms with a large region of overlap in between.

The first three PCs are responsible for 95.7%, 1.9%, and 1.2% of measured variance, respectively. As is commonly the case, the first component (PC 1) relates primarily to size. For PC 2, negative loadings on variables 6 through 9 indicate a higher proportion of the total length of the shell occurs below the shoulder line (the BODWIDTH line in Text-fig. 1). High loadings for MAXWIDTH compared to negative loadings for BODWIDTH on this axis suggest a major contribution to the total width of the shell by the last whorl, probably due to expansion of the lip. Individuals with high scores on PC 2 display relatively low-spired shells with broad lips. PC 3 is more difficult to interpret. High loadings on APSUTURE and SHOULSUTURE without corresponding loadings on APSPIRE and SHOULSPIRE could represent a greater rate of aperture translation during growth or could simply indicate a streamlined, less angular aperture.

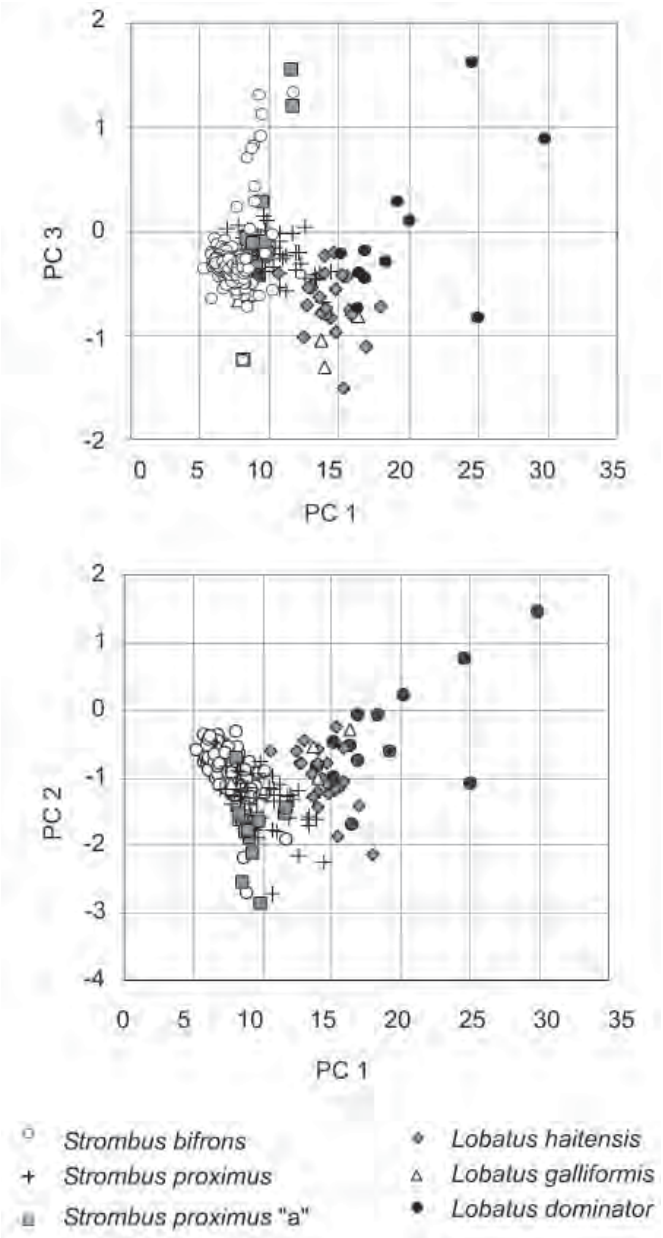
PCA (*Strombus* Only)

Results of the PCA for *Strombus* are shown in Text-figs 18 (scatterplots) and 19 (loadings and examples). The first three PCs are responsible for 90.86%, 3.55%, and 3.38% of measured variance, respectively. Most members of this genus form a tight cluster in morphospace. *Strombus bifrons* and *S. proximus* show very little difference along PCA 2 and PCA 3,

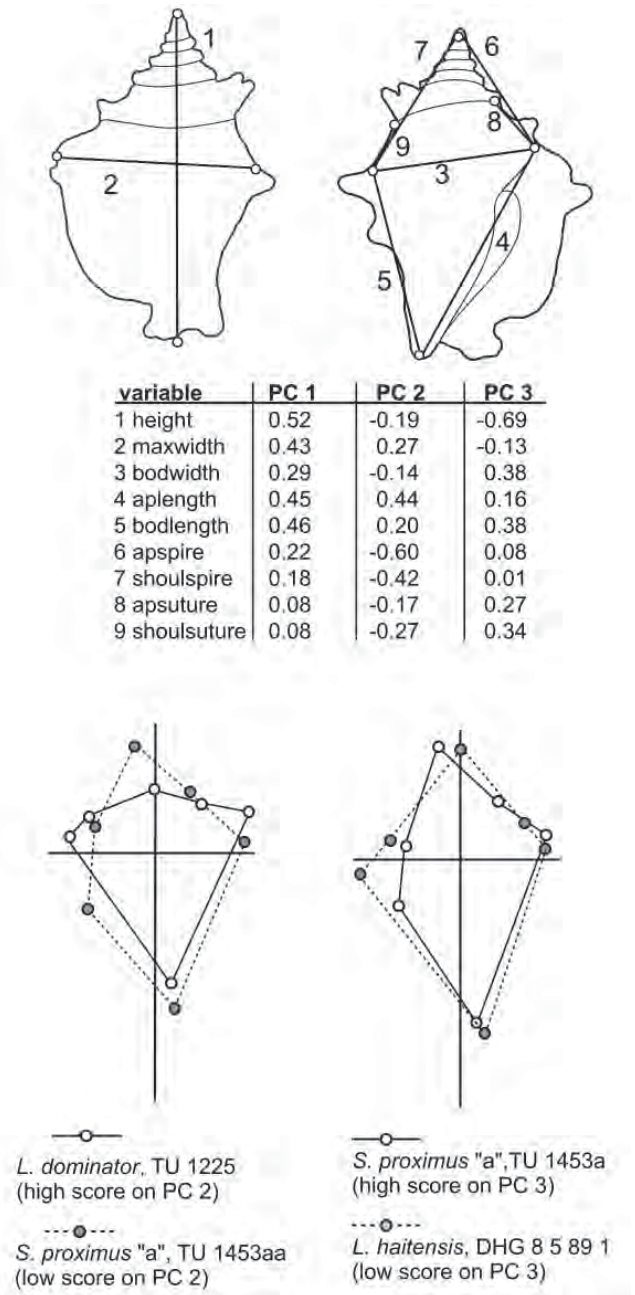


Text-fig. 15. PCA of all measured specimens with data points marked by genus.

and form the endpoints of a range along PCA 1 (the size axis) with a considerable area of overlap. Individuals classified as *Strombus proximus* "a" occur primarily in this "overlap zone" on PC 1; they differ from typical *S. proximus* or *S. bifrons* in their wide range of PC 2 values and in their relatively low values on PC 3. In essence, most of the variation along PC 2 and PC 3 is generated by specimens of *S. proximus* "a". High scores on PC 2 seem to indicate a slightly broader aperture,



Text-fig. 16. PCA of all measured specimens with data points marked by species.



variable	PC 1	PC 2	PC 3
1 height	0.52	-0.19	-0.69
2 maxwidth	0.43	0.27	-0.13
3 bodwidth	0.29	-0.14	0.38
4 aplength	0.45	0.44	0.16
5 bodlength	0.46	0.20	0.38
6 apspire	0.22	-0.60	0.08
7 shoulspire	0.18	-0.42	0.01
8 apsuture	0.08	-0.17	0.27
9 shoulsuture	0.08	-0.27	0.34

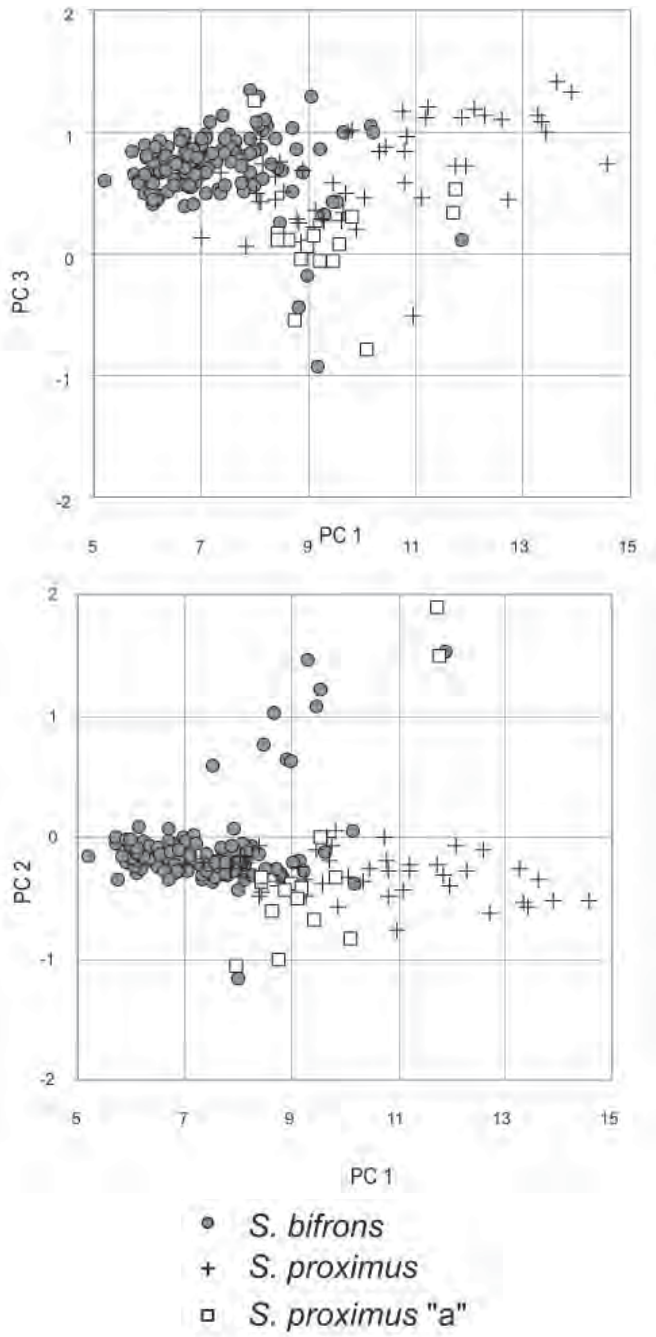
Text-fig. 17. Measurements (variables, at top) used in PCA and associated numerical loadings for each PC axis, and examples (at bottom) of specimens scoring low and high on PCA 2 and 3. The shapes were generated from X-Y coordinates of landmarks on a ventral view of a specimen; coordinates were Procrustes transformed to remove size differences and aligned to the centroid of the resulting shapes (axes cross at centroid).

whereas high scores on PC 3 indicate a slightly more elongate shell and/or aperture.

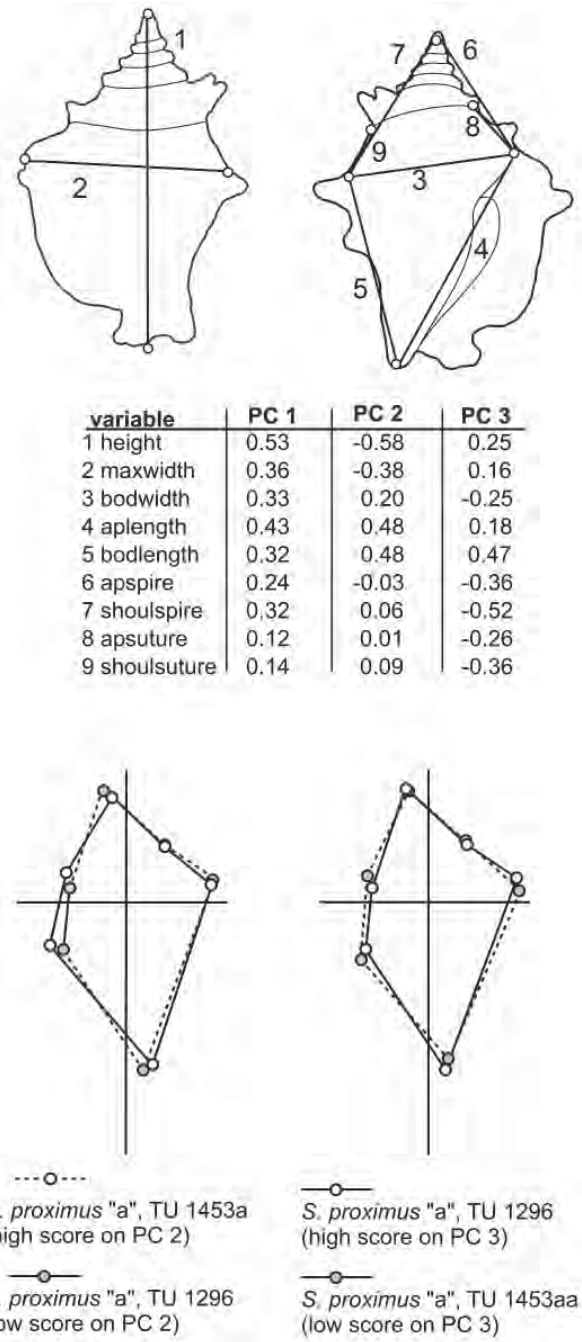
Temporal Variation in Shape

Temporal comparisons of shape change were also performed on *Strombus*; changes in mean shape are shown in Text-fig. 20. Shape change in this genus through time is relatively minor.

Patterns of temporal shape variation could not be

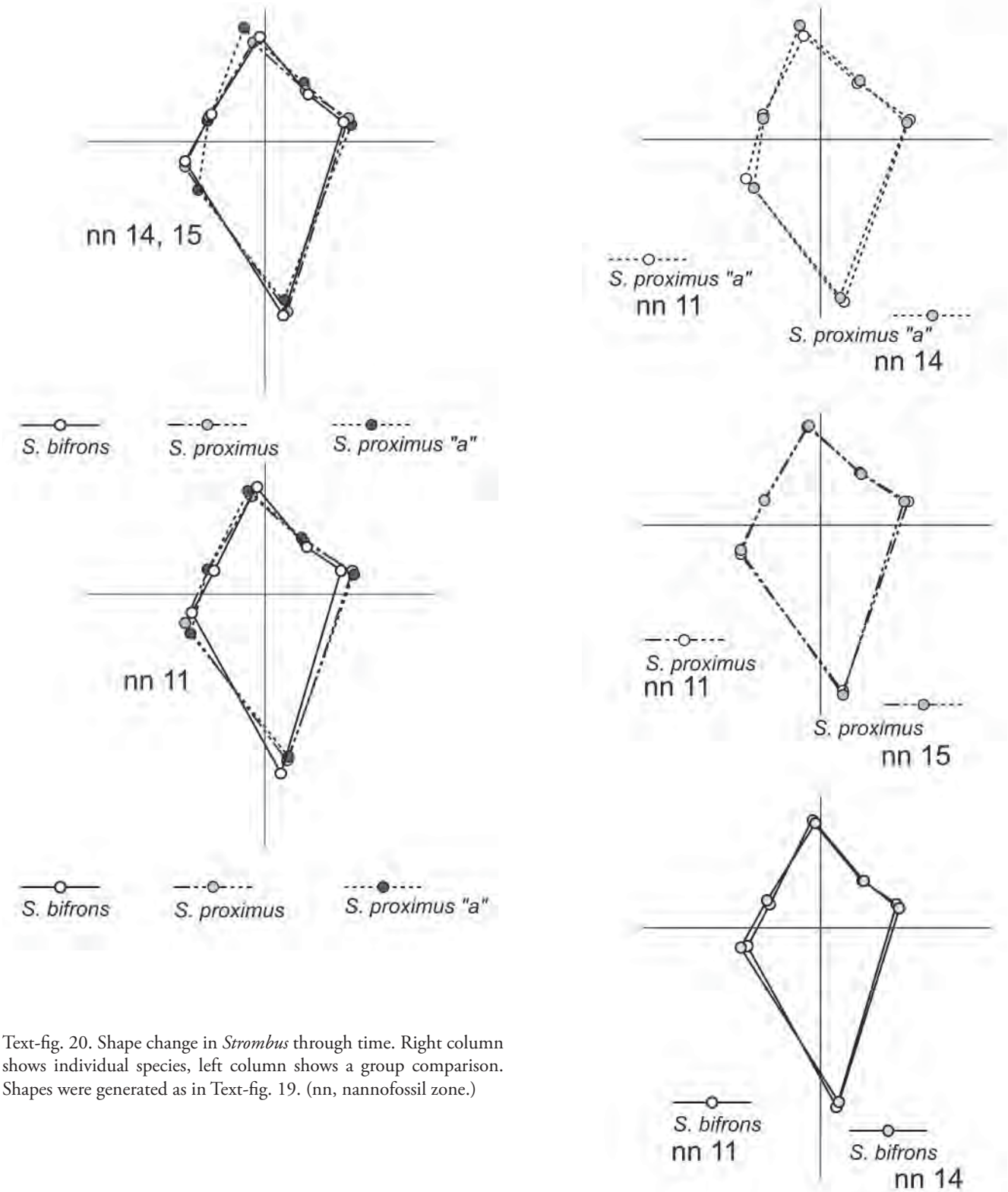


Text-fig. 18. PCA analysis of *Strombus.*

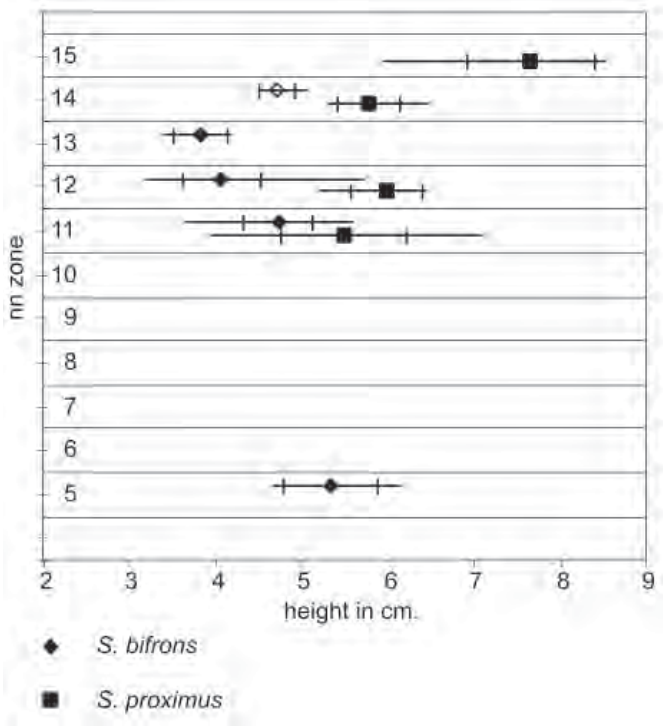


variable	PC 1	PC 2	PC 3
1 height	0.53	-0.58	0.25
2 maxwidth	0.36	-0.38	0.16
3 bodwidth	0.33	0.20	-0.25
4 aplength	0.43	0.48	0.18
5 bodlength	0.32	0.48	0.47
6 apspire	0.24	-0.03	-0.36
7 shoulspire	0.32	0.06	-0.52
8 apsuture	0.12	0.01	-0.26
9 shoulsuture	0.14	0.09	-0.36

Text-fig. 19. Measurements (variables, at top) used in PCA and associated numerical loadings for each PC axis. Examples (at bottom) of specimens scoring low and high on PCA 2 and 3. The shapes were generated from the X-Y coordinates of the landmarks on a ventral view of the specimen; the coordinates were Procrustes transformed to remove size differences and aligned to the centroid of the resulting shapes (axes cross at centroid).



Text-fig. 20. Shape change in *Strombus* through time. Right column shows individual species, left column shows a group comparison. Shapes were generated as in Text-fig. 19. (nn, nannofossil zone.)



Text-fig. 21. Size change in *Strombus bifrons* and *S. proximus* through time. Horizontal bars display total size range; vertical bars show one standard deviation. Although *S. bifrons* in nannofossil zone (nn) 14 is represented by a very small sample size it was displayed (as an unfilled data point) because all individuals differed so much from the previous zone.

Table 1. *Strombus bifrons*: height variation (in cm) across nannofossil zones (nn). Zone 14 was not included in the statistical analyses because of the low number of specimens (n).

nn	mean	maximum	minimum	n
5	5.35	6.16	4.65	8
11	4.73	5.59	3.64	39
12	4.07	5.71	3.18	80
13	3.82	4.2	3.37	13
(14)	4.72	5.07	4.59	4
all	4.32	6.16	3.18	144

Table 2. *Strombus bifrons*: significance of height differences among nannofossil zones (nn). The Kruskal-Wallis test indicates significant differences between the zones ($p < 0.001$). The table shows P values resulting from the Kolmogorov Smirnov test; significant differences are in bold.

nn	5	11	12
11	**0.03**		
12	**< 0.001**	**< 0.001**	
13	**< 0.001**	**< 0.001**	0.22

meaningfully assessed for *Lobatus haitensis, L. galliformis,* or *L. dominator* due to small sample sizes and/or restricted distributions.

Temporal and Geographic Variation in Size

Strombus bifrons

A comparison of *Strombus bifrons* across nannofossil zones shows a size decrease through time, from oldest to youngest (diamonds in Text-fig. 21, Tables 1-2). All differences between zones are significant with the exception of zones 12 and 13, between which sizes do not differ significantly.

Only collections from a single river, the Rio Yaque del Norte, yielded enough specimens to evaluate a within-river pattern. The general pattern of size reduction through time is seen among the Yaque del Norte samples (Table 3); the differences betweeen zone 5 and zones 12 and 13 are significant (Table 4).

Comparisons between rivers can be carried out for two nannofossil zones; in each case two rivers have adequate sample sizes. No significant difference in shell height exists between the Rio Gurabo and Rio Mao zone 11 specimens, or between the Rio Cana and Rio Yaque del Norte specimens (Tables 5-6).

Strombus proximus

The youngest (nannofossil zone 15) sample of *Strombus proximus* consists of significantly larger specimens than examples from earlier zones (black squares in Text-fig. 21, Tables 7-8). Samples of *S. proximus* from just the Rio Gurabo exhibit a similar pattern of size increase in younger specimens (Tables 9-10).

A between-rivers comparison for nannofossil zone 11 revealed that specimens from the Rio Cana and Rio Gurabo sections do not differ significantly but both differ significantly from the Rio Mao section (Tables 11-12).

For the above comparisons, no attempt was made to separate *Strombus proximus* and *S. proximus* "a". It should be noted that nannofossil zone 11 specimens of *S. proximus* "a" show no significant difference in height from nannofossil zone

Table 3. *Strombus bifrons*: height variation (in cm) within the Rio Yaque del Norte. (nn, nannofossil zone.)

nn	mean	maximum	minimum	n
5 (Yaque)	5.35	6.16	4.65	8
12 (Yaque)	3.88	4.67	3.18	31
13 (Yaque)	3.82	4.2	3.37	13

Table 4. *Strombus bifrons*: significance of height variation within the Rio Yaque del Norte. The table shows P values resulting from the Kolmogorov Smirnov test; significant differences are in bold. (nn, nannofossil zone.)

nn	5 (Yaque)	12 (Yaque)
12 (Yaque)	**< 0.001**	
13 (Yaque)	**< 0.001**	0.59

Table 5. *Strombus bifrons*: height variation (in cm) within nannofossil zones (nn) 11 and 12.

nn	mean	maximum	minimum	n
11 (Gurabo)	4.80	5.59	4.31	22
11 (Mao)	4.62	5.4	3.64	12
12 (Yaque)	3.88	4.67	3.18	31
12 (Cana)	4.14	5.67	3.51	46

Table 6. *Strombus bifrons*: significance of height variation within nannofossil zones (nn) 11 and 12. The table shows P values resulting from the Kolmogorov Smirnov test; significant differences are in bold.

nn	11 (Gurabo)	11 (Mao)	12 (Cana)
11 (Mao)	0.63		
12 (Cana)			
12 (Yaque)			0.10

11 *S. proximus* and that all but one or two nannofossil zone 14 specimens are *S. proximus* "a".

Patterns of temporal and geographic variation could not be meaningfully assessed for *Lobatus haitensis*, *L. galliformis*, or *L. dominator* because of small sample sizes and/or restricted distribution.

DISCUSSION

SIZE

Rapid early growth rates are crucial to the survival strategies (and relative success) of modern strombids. Modern strombids suffer high mortality rates as juveniles due to predation. Juvenile survivorship is positively correlated with both individual size (due to size-selective predation) and population density (Ray & Stoner, 1995). Juvenile growth rate, however, is generally negatively correlated with population density (Stoner, 1989). Selective pressures favor individuals that grow rapidly under crowded conditions.

Strombids in the Mio-Pliocene of the Dominican Republic on average do seem to be smaller than those living today in the Caribbean. In *Lobatus*, the apparent size difference could in part be due to a taphonomic bias against larger shells; the lower end of the size range observed in the Neogene is similar to that reported from the modern Caribbean (Clench & Abbott, 1941) and some individual specimens show sizes comparable to modern *Lobatus gigas*. In regards to *Strombus*, however, the upper size limit is unlikely to have been truncated in such a manner. The mean observed length for this genus is 4.79 cm, considerably smaller than the 7-10 cm length quoted by Clench & Abbott (1941) for modern representatives of this genus. Only one Dominican species, *S. proximus*, shows a demonstrable size increase through time.

SHAPE

With respect to shape, *Strombus proximus* "a" is the most extreme of the Dominican strombids. Its morphology becomes more distinct from the strombid norm through time and changes in a manner predicted by functional morphology for more efficient burrowing (see previous discussion in sections on strombid biology and remarks on *S. proximus*). Its morphology is also consistent with allometric changes observed in some modern strombids associated with rapid growth (Martin Mora *et al.*, 1995). In these cases, faster growth is correlated with an abundance of preferred food items and results in longer spired shells. Thus either selective pressure or ecophenotypy (or both) are plausible explanations for the observed shape variation. We attempted to test the hypothesis of shape change due to more rapid growth by using shell profiles of oxygen stable isotope ratios to detect seasonal growth rates (via paleotemperatures) in the strombid shell, and from these to determine growth rates. Results were inconclusive but generally do not appear

Table 7. *Strombus proximus*: height variation (in cm) across nannofossil zones (nn) for all rivers.

nn	mean	maximum	minimum	n
11	5.48	7.11	3.92	54
12	5.98	6.46	5.2	7
14	5.79	6.47	5.3	7
15	7.66	8.52	5.92	8
all	5.78	8.52	3.92	76

Table 8. *Strombus proximus*: significance of height variation. The Kruskal-Wallis test indicates significant differences between the nannofossil zones (nn) ($p < 0.001$). The table shows P values resulting from the Kolmogorov Smirnov test; significant differences are in bold.

nn	11	12	14
12	**0.024**		
14	0.091	0.883	
15	**< 0.001**	**0.002**	**0.002**

Table 9. *Strombus proximus*: height variation within the Rio Gurabo nannofossil zones (nn).

nn	mean	maximum	minimum	n
11 (Gurabo)	5.31	6.76	4.41	31
15 (Gurabo)	7.66	8.52	5.92	8

Table 10. *Strombus proximus*: significance of height variation within Rio Gurabo. The table shows the P value resulting from the Kolmogorov Smirnov test; significant differences are in bold.

nn	11 (Gurabo)
15 (Gurabo)	**< 0.001**

to support this hypothesis (Freiheit *et al.*, 2002). At this time, therefore, selective pressure for more efficient burial seems the better of the two hypotheses.

Paleoecology

Strombids in the Cibao Valley show some notable differences from modern strombids. First, they appear to be less abundant than modern species found in similar environments in the Caribbean. We have no quantitative data to support this idea, but at the least we have found no evidence of accumulations such as one might expect given the tendency of several modern species to "herd" (or see Geary & Allmon, 1990). Second, Dominican fossil strombids are associated with coral communities more closely than are their modern counterparts. *Lobatus dominator* in particular seems to be most abundant near the "deep reef" coral assemblages of Budd *et al.* (1996). Some authors (*e.g.*, Pecharde, 1970) have noted that, in general, the larger strombid species of today prefer a less muddy environment than the smaller ones. The other Dominican species seem to prefer coral communities as well, but are not restricted to them as is *L. dominator*. It is possible that this preference for coral assemblages is a result of lower silt input and/or increased substratum grain size due to autochthonous carbonate production (coral rubble, calcareous algal growth, etc.) in these environments. As noted in the Geologic Setting section, above, clastic input in the Cibao Valley is enriched in silts at the expense of sand-sized particles. It seems likely that increased particle size in the substratum (due to coral and reef-derived debris) is a more important factor in determining strombid distribution than simply the presence of corals.

Savazzi (1991) mentioned extended anterior and/or posterior canals and a "snowshoe" morphology (long spines radiating from the adult lip, as in modern spider conchs and some Cretaceous forms) as possible adaptations for soft substrata. None of the Dominican species has a "snowshoe" morphology. *Lobatus galliformis* possesses an extended posterior lip and recurved anterior canal that might have been advantageous on soft substrata. This interpretation is bolstered by consideration of its presumptive modern descendant, *L. gallus*, which develops an even more exaggerated posterior lip/canal and a strongly recurved anterior canal and lives on soft substrata (Berg, 1975).

Juvenile strombid distributions in the Cibao Valley also

Table 11. *Strombus proximus*: height variation within nannofossil zone (nn) 11.

nn	mean	maximum	minimum	n
11 (Cana)	5.09	6.33	3.92	12
11 (Gurabo)	5.31	6.76	4.41	31
11 (Mao)	6.57	7.11	5.34	9

Table 12. *Strombus proximus*: significance of height variation within nannofossil zone (nn) 11. The table shows P values resulting from the Kolmogorov Smirnov test; significant differences are in bold.

nn	11 (Cana)	11 (Gurabo)
11 (Gurabo)	0.172	
11 (Mao)	**0.002**	**< 0.001**

differ from predictions stemming from modern strombid biology. Modern juvenile strombids not only preferentially inhabit seagrass beds, but also show a far greater tendency to remain in a restricted location than do the adults; thus, one would expect that the distribution of juveniles should be roughly correlated with the location of "grass flat" coral communities. In fact, this is not the case. The single largest concentration of strombid juveniles is found at the Cañada de Zamba; inasmuch as this location displays the single largest concentration of adult strombids (in addition to a rich fauna of other mollusks), the concentration of juveniles is not surprising. In the rest of the Rio Cana section, juveniles are most closely tied to "shallow reef" communities; none have been recorded from "grass flat" locations (see Text-fig. 4). In the Rio Gurabo, juveniles are most closely associated with "deep reef" communities ("shallow reef" communities are not represented in the Gurabo); once again, no juveniles have been recorded from the "grass flat" communities (see Text-fig. 5).

Based on functional considerations alone, *Lobatus dominator* and *L. haitensis* would likely have spent more time on the surface: *L. dominator* by virtue of its size, flared lip, and extended dorsal spines, and *L. haitensis* by virtue of the rough irregularity of its shell (poorly adapted for burrowing but well adapted for resisting crab attacks). As noted in the section on strombid biology, larger strombids tend to live on the substratum rather than in it. They are thereby subject to the attacks of boring organisms (as well as other destructive forces) from which their smaller relatives are spared. While the animal is alive, it can maintain shell integrity against such borers by actively reinforcing the shell from the inside (among other defenses). After the animal is dead, the shell is immediately at the mercy of these organisms. This process could be partly responsible for lack of large specimens of *L. dominator*, even though large fragmentary remains are found. Such fragments invariably show the marks of boring sponges and algae, both postmortem (borings on all surfaces) and premortem (borings restricted to exterior surfaces). In addition, the extended lip and dorsal protuberances of *L. dominator* are more easily broken than similar (although less extended) features displayed by other members of the genus. An additional factor affecting preservation of *L. dominator* could be its preferred habitat. As noted above, *L. dominator* is largely restricted to reef environments; the greater porosity and permeability of reef deposits could have allowed more scope for diagenetic processes to operate.

Those strombids that spend more time living in the substratum might well be more likely to die there and then, having assumed an inanimate state, remain. Certainly most specimens of both *Strombus proximus* and *S. bifrons* show little sign of postmortem colonization by epibionts or borers. Many show little evidence of transport or abrasion of any kind. Furthermore, very few show the distinctive signs of occupation by hermit crabs ("pagurization"; see Walker, 1992). Strombid shells of this size are in high demand by hermit crabs in the modern Carribbean (Berg, 1975). Due to the soft unstable nature of the substrate it is also possible that many of these smaller strombids were caught in slumps or debris flows, thus explaining the observed patterns of distribution and weathering.

CONCLUDING REMARKS

(1) Strombids in the Neogene of the Cibao Valley could have occupied a less prominent position in their communities than do strombids in the modern Carribbean, or at the least appear less abundant.

(2) Strombids in the Cibao Valley appear smaller than their modern Carribbean counterparts. This is particularly notable for *Strombus*.

(3) The two genera of strombids present in the Cibao Valley (*Strombus* and *Lobatus*) show different patterns of

growth in relation to size increase.

(4) The two genera show different probable ecological niches; *Strombus* species were probably more infaunal and commonly buried at death, whereas *Lobatus* species were more adapted for life above the substratum. This idea is supported by consideration of both shell shape and patterns of sculpture and ornamentation on the shell itself.

(5) Neogene Dominican strombids show morphological similarities to both modern Caribbean and modern Pacific forms.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the assistance and support of the following individuals: Peter Jung laid the groundwork; he and Wolfgang Suter also provided photographs used in many of the plates. Nancy Budd, Ross Nehm, Carol Tang, and Laurie Anderson provided expert advice and companionship in the field. We are grateful to Warren Allmon, Peter Roopnarine, and LouElla Saul for careful reviews of the manuscript. Mary Diman helped in preparation of text-figures and plates. Alejandra Guzman prepared the final Spanish abstract. The University of Wisconsin Madison Department of Geology and Geophysics provided research facilities and support. And last, but not least, the friendly people of Mao hosted us in the Dominican Republic.

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PLATES

Plate 1

Figure Page

1-23. *Strombus bifrons* G. B. Sowerby I, 1850. Figs 10-17 courtesy of NMB. Scale bars = 1 cm. 15

1-3. Dorsal, ventral, and apical views; lectotype; BMNH location G83938; Santo Domingo; height 4.75 cm, width 3.30 cm.

4-6. Dorsal, ventral, and apical views; paralectotype; BMNH location GG 20052; Santo Domingo; height 4.44 cm, width 2.62 cm.

7-9. Dorsal, ventral, and apical views; paralectotype; BMNH location GG 20053; Santo Domingo; height 4.51 cm, width 2.70 cm.

10-11. Dorsal and ventral views; NMB location 11110; Bowden Formation, Jamaica; height 5.87 cm, width 3.86 cm.

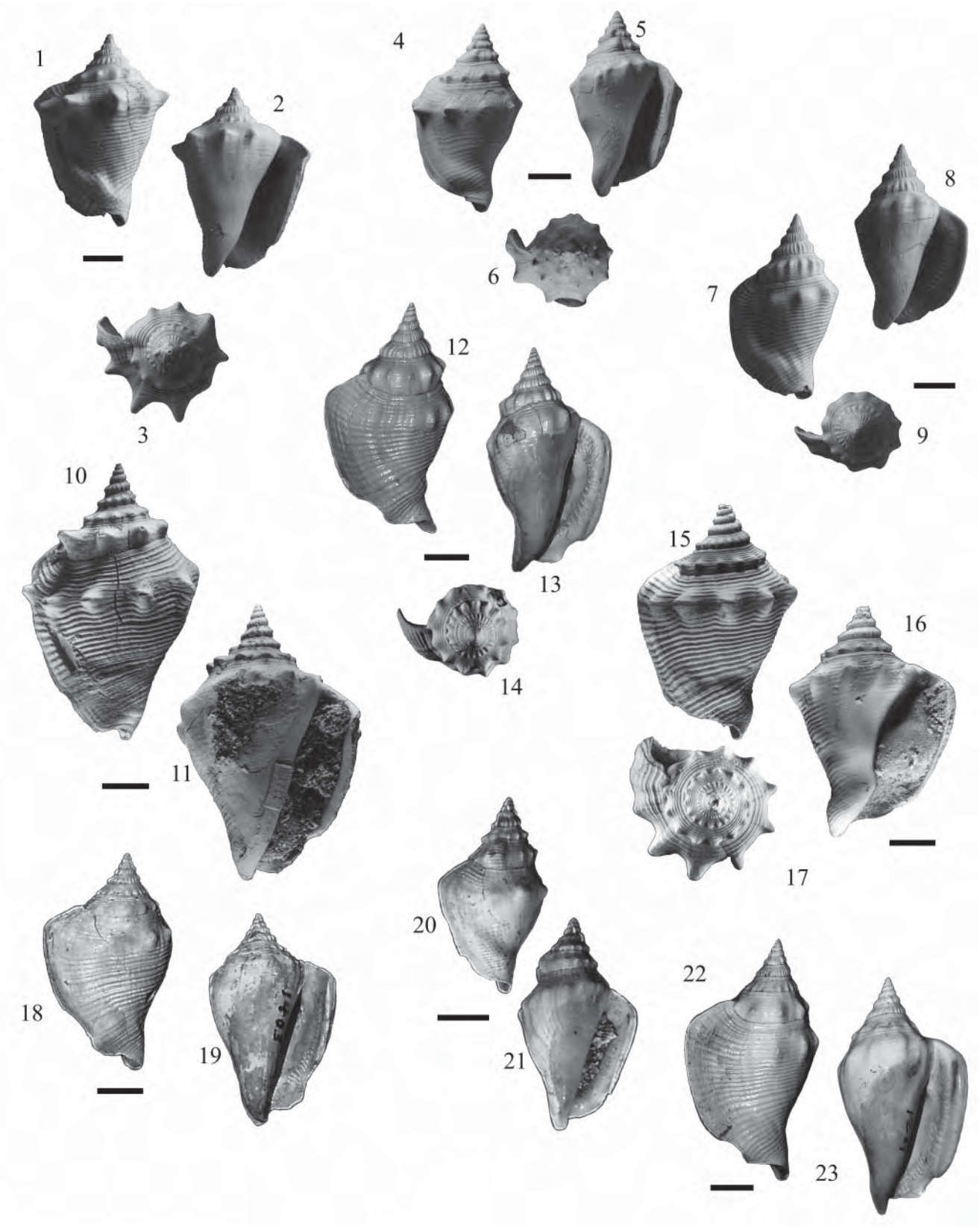
12-14. Dorsal, ventral, and apical views; TU location 1277 (NMB 15871); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 4.82 cm, width 2.66 cm.

15-17. Dorsal, ventral, and apical views; NMB location 16938; Rio Yaque del Norte, nannofossil zone 5; height 4.78 cm, width 3.03 cm.

18-19. Dorsal and ventral views; TU location 1403; Rio Yaque del Norte, nannofossil zone 12; height 4.67 cm, width 2.82 cm.

20-21. Dorsal and ventral views; NMB location 17268; Rio Yaque del Norte, nannofossil zone 13; height 4.16 cm, width 2.28 cm.

22-23. Dorsal and ventral views; TU location 1277 (NMB 15871); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 5.59 cm, width 3.06 cm.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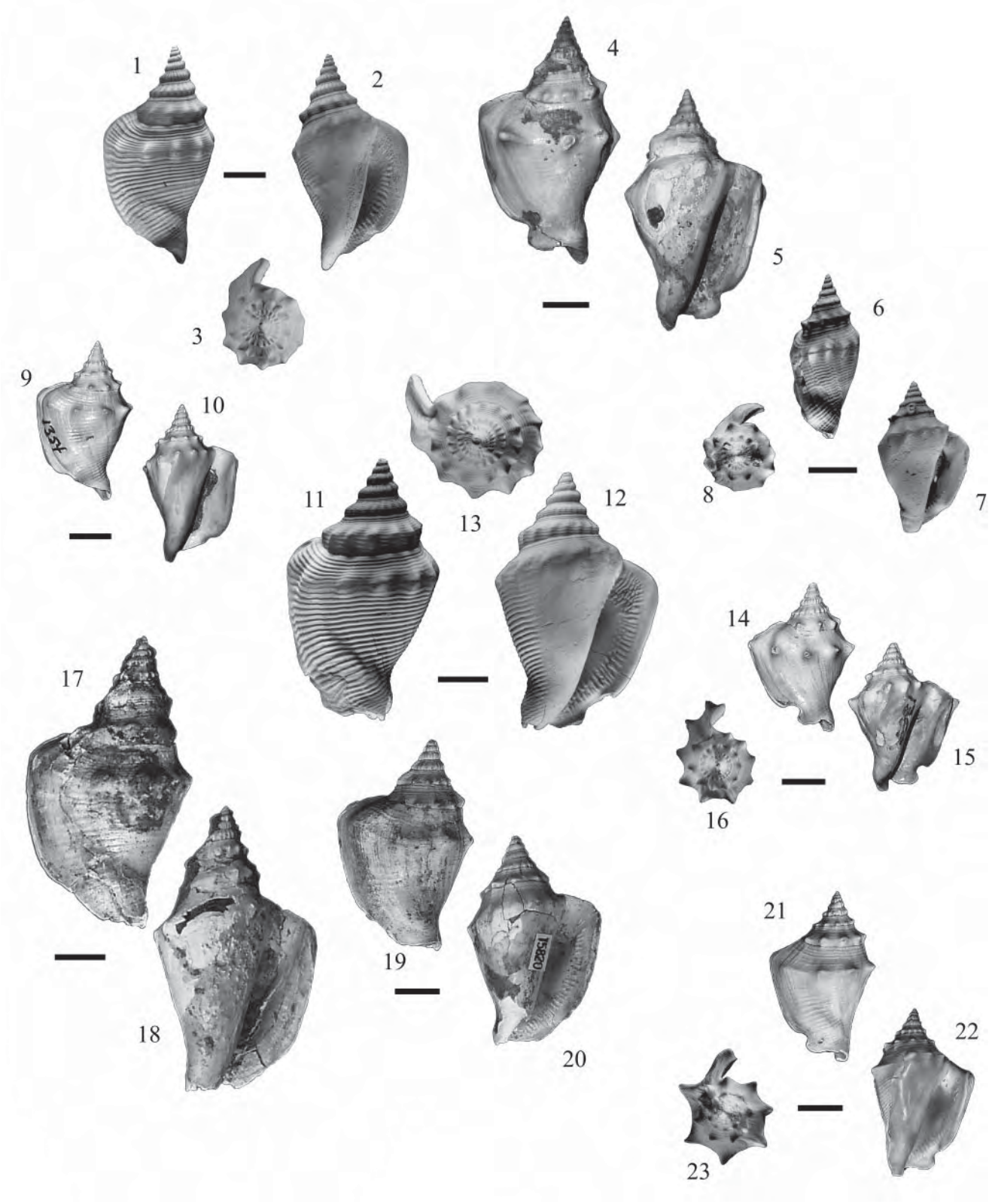
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Plate 2

Figure Page

1-23. *Strombus bifrons* G. B. Sowerby I, 1850. All specimens from the Cañada de Zamba, Rio Cana, Gurabo Formation, nannofossil zone 12, except as noted. Figs 1-3, 6-8, 11-16, and 21-23 courtesy of NMB. Scale bars = 1 cm. 15

1-3. Dorsal, ventral, and apical views; TU 1278; Rio Gurabo, Gurabo Formation; height 5.2 cm, width 2.7 cm.

4-5. Dorsal and ventral views; JRF 60400CdZ008; height 4.83 cm, width 2.63 cm.

6-8. Dorsal, ventral, and apical views; TU location 1354; height 3.12 cm, width 2.11 cm.

9-10. Dorsal and ventral views; TU location 1354; height 3.76 cm, width 2.18 cm.

11-13. Dorsal, ventral, and apical views; TU location 1293; Rio Mao, bluff 1; height 5.14 cm, width 3.12 cm.

14-16. Dorsal, ventral, and apical views; TU location 1354; height 3.51 cm, width 2.30 cm.

17-18. Dorsal and ventral views; DHG 8-3-89-1; height 5.67 cm, width 2.96 cm.

19-20. Dorsal and ventral views; NMB location 15820; Rio Gurabo, Gurabo Formation, nannofossil zone 12; height 4.37 cm, width 2.69 cm.

21-23. Dorsal, ventral, and apical views; NMB location 16825; height 3.75 cm, width 2.20 cm.

Plate 3

Figure Page

1-13. *Strombus proximus* G. B. Sowerby I, 1850. Figs 5-7 courtesy of NMB. Scale bars = 1 cm. 17

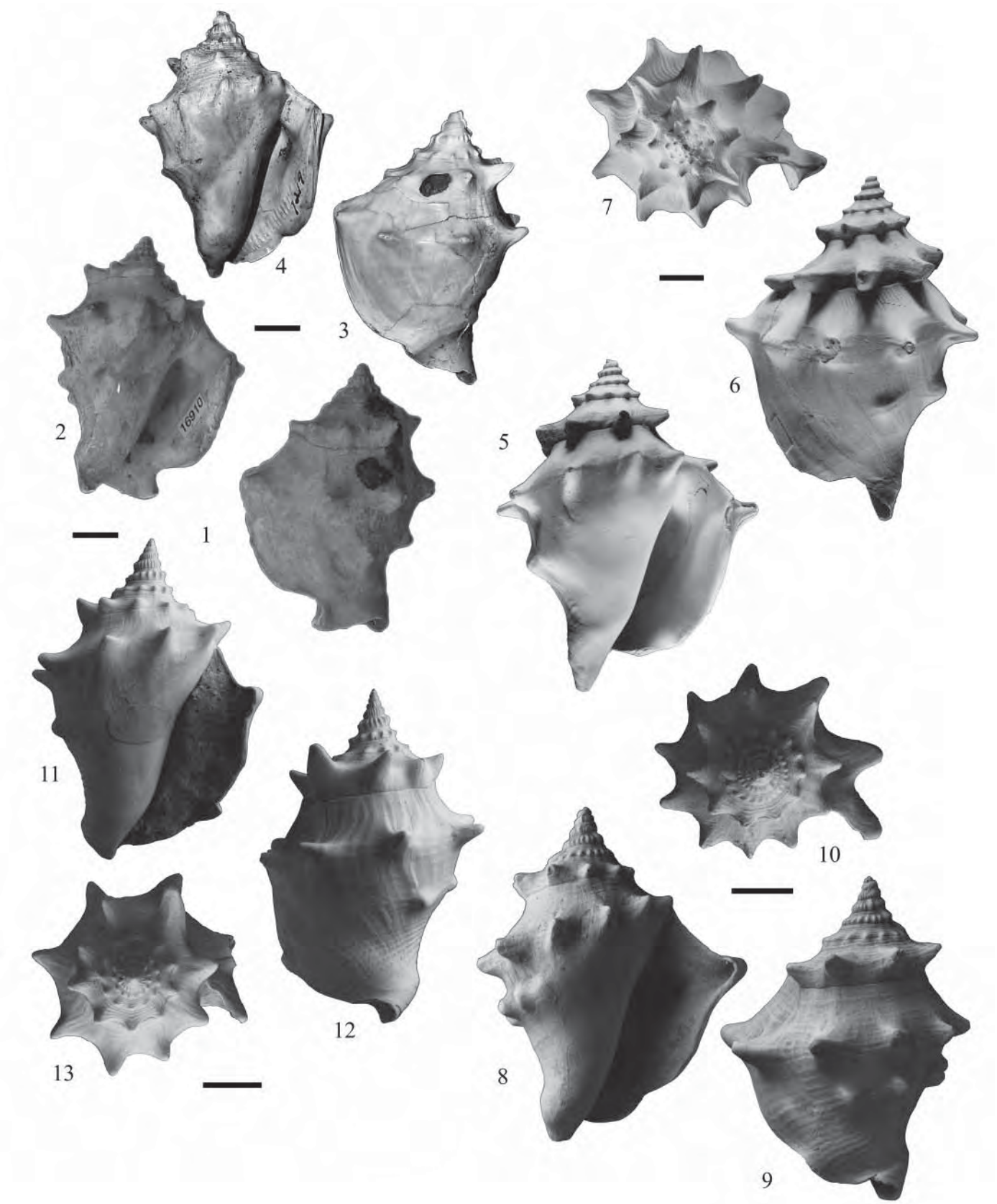
1-2. Dorsal and ventral views; NMB location 16910; Rio Mao, Gurabo Formation, nannofossil zone 11; height 6.05 cm, width 4.12 cm.

3-4. Dorsal and ventral views; TU location 1379; Rio Amina, nannofossil zone 12; height 6.04 cm, width 3.83 cm.

5-7. Ventral, dorsal, and apical views; NMB location 15833; Rio Gurabo, Mao Formation, nannofossil zone 15; height 8.28 cm, width 5.03 cm.

8-10. Ventral, dorsal, and apical views; BMNH G83936; lectotype; Santo Domingo, height 5.5 cm, width 4.3 cm.

11-13. Ventral, dorsal, and apical views; BMNH GG 80354; paralectotype; Santo Domingo, height 5.57 cm, width 3.7 cm.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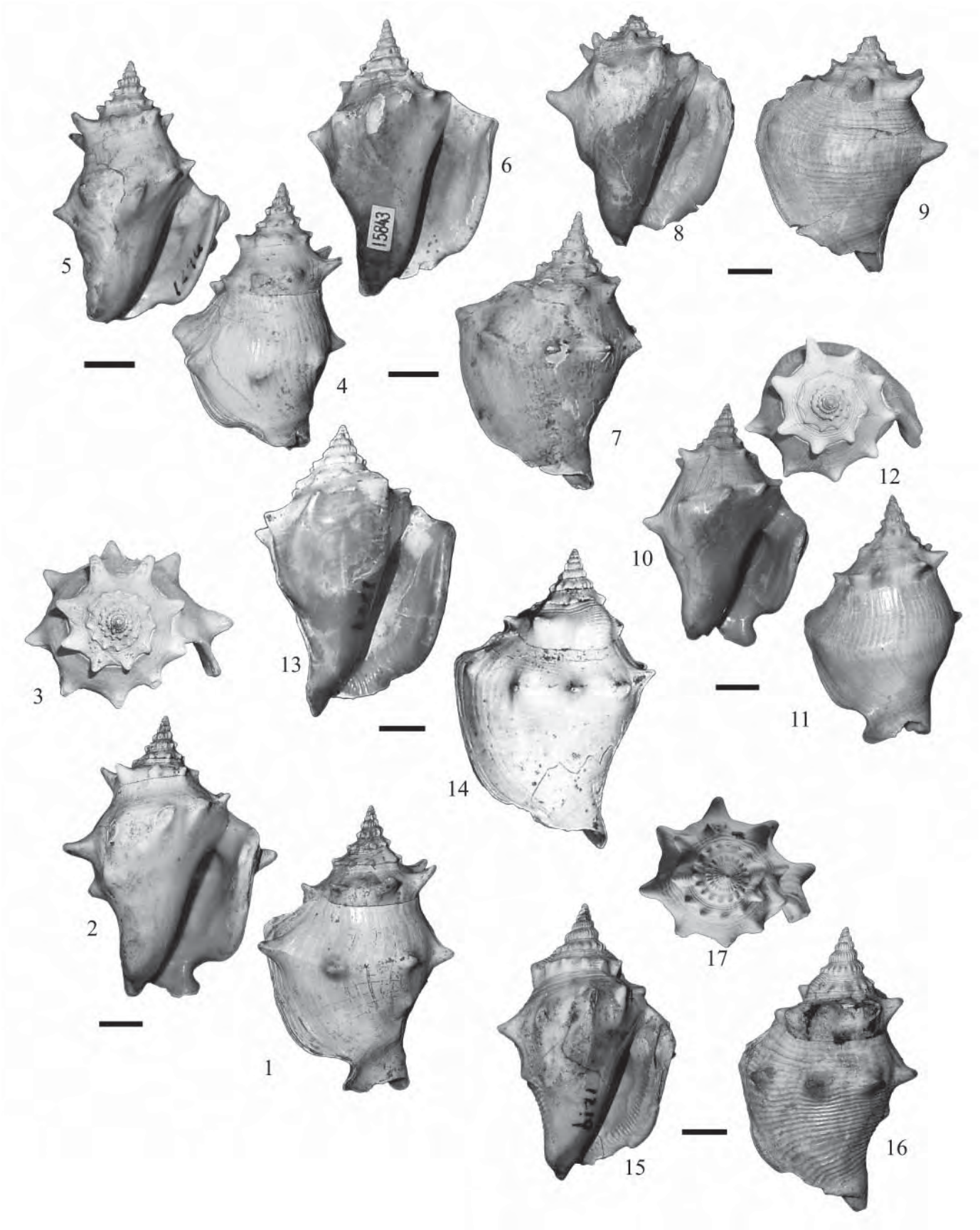
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Plate 4

Figure Page

1-17. *Strombus proximus* G. B. Sowerby I, 1850. Figs 15-17 courtesy of NMB. Scale bars = 1 cm. 17

1-3. Dorsal, vental, and apical views; DHG 8-2-89-5 (NMB 15865); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 5.39 cm, width 3.26 cm.

4-5. Dorsal and vental views; TU location 1296 (NMB 15877); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 5.33 cm, width 3.25 cm.

6-7. Ventral and dorsal views; NMB location 15843; Rio Gurabo, Gurabo Formation, nannofossil zone 12; height 5.20 cm, width 3.33 cm.

8-9. Ventral and dorsal views; NMB location 17278; Rio Yaque del Norte, nannofossil zone 11; height 5.43 cm, width 3.74 cm.

10-12. Ventral, dorsal, and apical views; JRF 60900RG006 (NMB 15863); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 5.10 cm, width 3.16 cm.

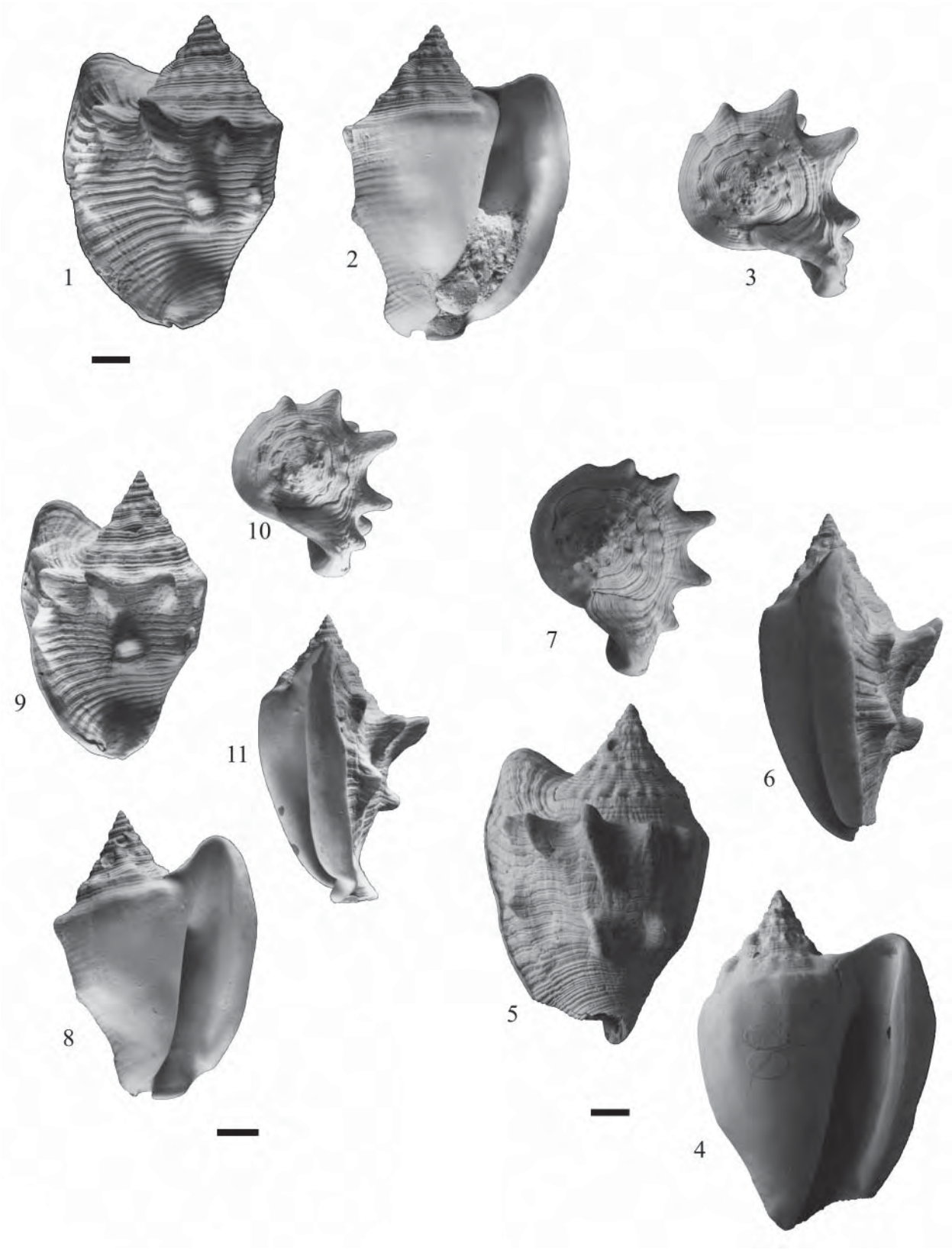
13-14. Ventral and dorsal views; TU location 1379; Rio Mao, nannofossil zone 11; height 6.51 cm, width 4.10 cm.

15-17. Ventral, dorsal, and apical views; TU location 1379; Rio Amina, nannofossil zone 12; height 6.46 cm, width 3.66 cm.

Plate 5

Figure Page

1-11. *Lobatus haitensis* G. B. Sowerby I, 1850. Figs 1-7 courtesy of NMB. Scale bars = 1 cm. 18
1-3. Dorsal, vental, and apical views; TU location 1210 (NMB 15808); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 8.12 cm, width 5.69 cm.
4-7. Ventral, dorsal, dextral, and apical views; lectotype; BMNH G82937; Santo Domingo; height 9.2 cm, width 6.24 cm.
8-11. Ventral, dorsal, apical, and dextral views; DHG 8-2-89-3 (NMB 15863); Rio Gurabo, lower Gurabo Formation, nannofossil zone 11; height 7.21 cm, width 5.14 cm.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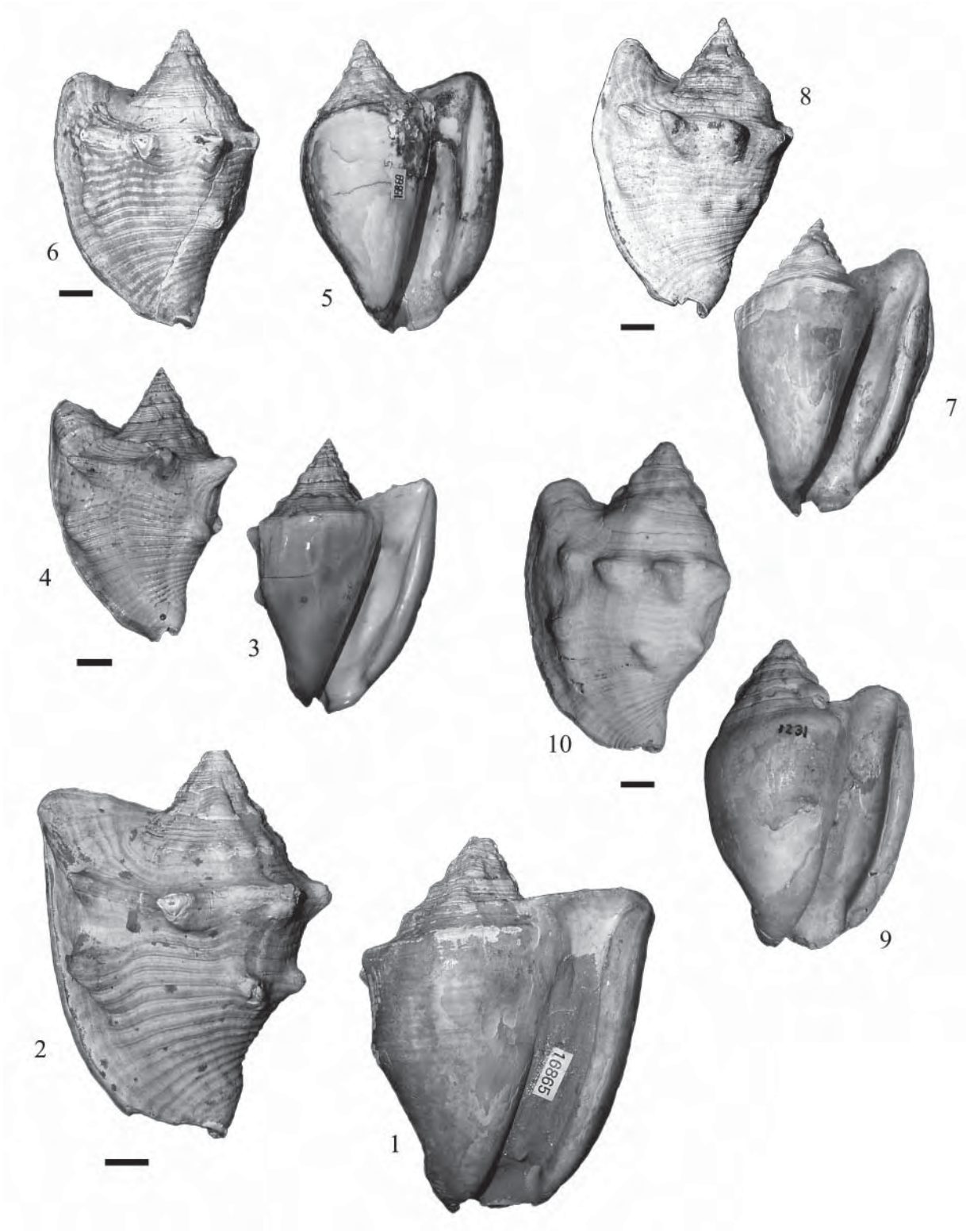
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Plate 6

Figure Page

1-10. *Lobatus haitensis* G. B. Sowerby I, 1850. Scale bars = 1 cm. 18

1-2. Ventral and dorsal views; NMB location 15865; Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 8.65 cm, width 5.86 cm.

3-4. Ventral and dorsal views; DHG 8-5-89-2 (NMB 16154); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 7.89 cm, width 5.02 cm.

5-6. Ventral and dorsal views; NMB location 15869; Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 8.92 cm, width 5.96 cm.

7-8. Ventral and dorsal views; TU location 1293; Rio Mao, nannofossil zone 11; height 9.12 cm, width 5.99 cm.

9-10. Ventral and dorsal views; TU location 1231 (NMB 15870); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 9.21 cm, width 5.96 cm.

Plate 7

Figure Page

1-14. *Lobatus galliformis* Pilsbry & Johnson, 1917. Figs 1-4 courtesy of NMB. Scale bars = 1 cm. 20

1-3. Apical, dorsal, and ventral views; syntype; ANSP 2582, Santo Domingo; height 10.0 cm, width 66 cm.

4-5. Dorsal and ventral views; syntype; ANSP 2582, Santo Domingo; height 74.4 cm, width 46.5 cm.

6-7. Dorsal and ventral views; NMB location 17265; Rio Yaque del Norte, nannofossil zone 5; height 4.80 cm, width 2.60 cm.

8-9. Dorsal and ventral views; TU location 1410; Rio Mao, nannofossil zone 11; height 8.66 cm, width 5.12 cm.

10-12. Dorsal, ventral, and apical views; NMB location 15871; Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 9.54 cm, width 6.14 cm.

13-14. Dorsal and ventral views; JRF 60500RG004 (NMB 16157); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 8.26 cm, width 4.92 cm.

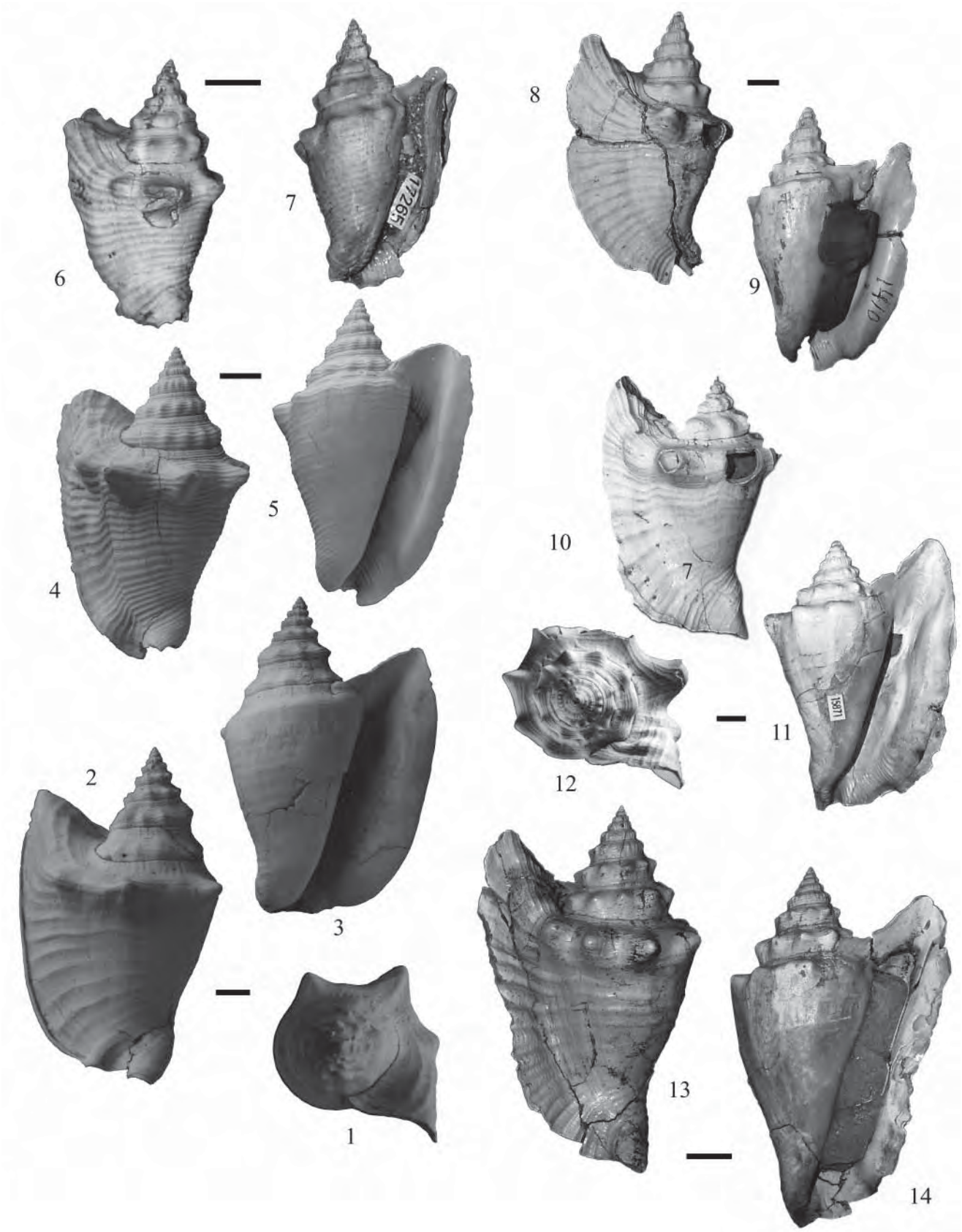
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Plate 8

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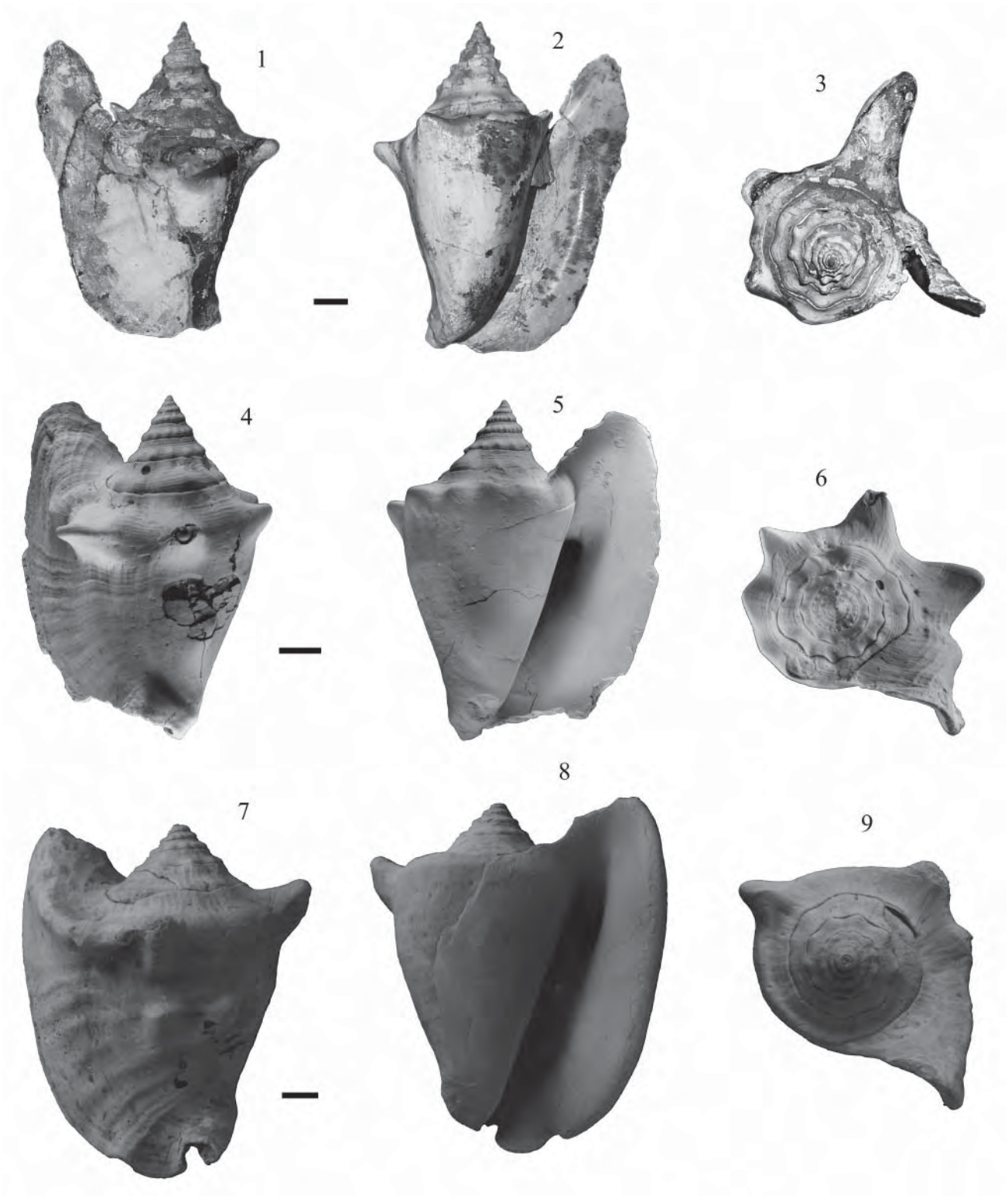
1-12. *Lobatus dominator* Pilsbry & Johnson, 1917. Figs 3-4 and 7-8 courtesy of NMB. Scale bars = 1 cm. . . 21
1-4. Ventral, dorsal, apical, and dextral views; DHG 8-3-89-1 (NMB 16817); Rio Cana, Gurabo Formation, nannofossil zone 12; height 9.16 cm, width 7.06 cm.
5-8. Ventral, dorsal, apical, and dextral views; TU location 1280; Rio Mao, nannofossil zone 11; height 12.18 cm, width 10.09 cm.
9-10. Ventral and dorsal views; TU location 1354 (NMB 16817); Rio Cana, Gurabo Formation, nannofossil zone 12; height 3.76 cm, width 2.18 cm.
11-12. Ventral and dorsal views; collected for DHG, location uncertain, probably Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 22.67 cm, width 22.28 cm.

Plate 9

Figure Page

1-9. *Lobatus dominator* Pilsbry & Johnson, 1917. Figs 4-6 courtesy of NMB. Scale bars = 1 cm. . . . 21
1-3. Dorsal, ventral, and apical views; DHG 8-1-89-2 (NMB 15869); Rio Gurabo, Gurabo Formation, nannofossil zone 11; height 9.23 cm, width 6.18 cm.
4-6. Dorsal, ventral, and apical views; TU 1293; Rio Mao, "bluff one"; height 12.16 cm, width 9.59 cm.
7-9. Dorsal, ventral, and apical views; syntype; ANSP location 2579; Santo Domingo; height 9.1 cm, width 7.64 cm.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PALEONTOLOGICAL
RESEARCH INSTITUTION
1259 Trumansburg Road
Ithaca, New York 14850 U. S. A.

ISSN 007-5779

ISBN: 978-0-87710-486-5
54000
9 780877 104865
US $40.00