

***Morum (Oniscidia) domingense* from the Caribbean Neogene vs. the Recent *M. (O.) lindae*: One taxon or two?**

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ABSTRACT. The *Morum chipolanum*-group of *Morum (Oniscidia)* species has a long geologic history in Tropical America, although their specimens are never abundant. Most of the original descriptions were based on very few shells. The lack of information concerning intraspecific variability makes classification sometimes difficult within this group of species with somewhat conservative shell design. This study attempts to distinguish several Caribbean Neogene taxa on the basis of combined shell morphometry and qualitative shell characteristics, paying special attention to the distinction between the shells of *M. (O.) domingense* from the Upper Miocene-Lower Pliocene of the Dominican Republic and those of the Recent *M. (O.) lindae* from the coasts of Colombia and Venezuela, in order to ascertain if they should be assigned to the same or to distinct taxa. The largest number of specimens yet considered is assembled, drawn from adequately illustrated specimens in the literature, collections and high quality digital photographs posted on the Internet. Analysis shows that by morphometry alone these two taxa cannot be reliably distinguished, but when the morphometric data is considered in combination with other observable shell characteristics the two sets of shells are most likely distinct, actually representing two different taxa. This conclusion is further strengthened by palaeobiogeographical data.

INTRODUCTION

The genus *Morum* Röding, 1798, now placed in the family Harpidae Bronn, 1849 (Hughes & Emerson, 1987) superfamily Muricoidea Rafinesque, 1815 (Bouchet & Rocroi, 2005), comprises a small group of species of carnivorous marine gastropods (J. Smith *in* Beesley *et al.*, 1998), occurring in tropical to subtropical seas worldwide. They are found in shallow to fairly deep waters, but are always uncommon to very rare (J. Smith *in* Beesley *et al.*, 1998). The subgenus *Oniscidia* Mörsch, 1852 (= *Cancellomorum* Emerson & Old, 1963, see Vokes, 1998) comprises a group of *Morum* species with a cancellate sculpture; for full discussion on the taxonomic problems regarding the name *Oniscidia* we refer to Beu (1976) and Vokes (1998). In this paper we will only discuss what Vokes (1998) called the *M. chipolanum*-group of species, characterized by an ornamentation of elongated pustules on the parietal shield as opposed to coarse rugae, as seen in *Morum* (“*Oniscidia*”) sp. from the Middle Eocene Gatuncillo Formation (Woodring,

1959) and the Recent Brazilian *M. (O.) matthewsi* Emerson, 1967.

A handful of species belonging to the *M. chipolanum*-group have been described from the Caribbean Neogene and Recent faunas.

The earliest Tropical American records are for the Peruvian *M. peruvianum* Olsson, 1931 from the Eocene Chira Formation (Olsson, 1931) and for *M. (O.) harpula* (Conrad, 1848) from the Lower Oligocene Vicksburg group of Mississippi, USA (MacNeil & Dockery, 1984).

From the Lower Miocene the following species have been reported: *Morum chipolanum* Dall, 1925 from the Chipola Formation of Florida, USA and Baitoa Formation of the Dominican Republic (see Vokes, 1998), and *M. (Oniscidia) jungi* Landau, 1996 from the Cantare Formation of Venezuela (see Landau, 1996). *M. harrisi* Maury, 1925, from the Lower Miocene Pirabas Limestone of Brazil, is based on internal moulds and its apertural features are unknown (Maury, 1925). *Morum (O.) coxi* (Trechmann, 1935) occurs in the lower Middle Miocene (Robinson &

Jung, 1972) Grand Bay Formation of Carriacou (Jung, 1971). In the Upper Miocene and Lower Pliocene assemblages *M. (O.) domingense* (Sowerby, 1850) occurs in the Cercado, Gurabo and Mao Formations of the Dominican Republic (Vokes, 1998).

Morum (O.) meganae Raymond, 1997 was recently described from the Middle Pliocene Pinecrest Beds of Florida and *M. (O.) macgintyi* Smith, 1937 [*M. (O.) obriena* Olsson & Petit, 1964, is almost certainly a junior synonym of *M. (O.) macgintyi* (Emerson, 1967; Vokes, 1998)] occurs in the Upper Pliocene Caloosahatchee Formation of Florida (Petuch, 1994).

The living *M. (O.) dennisoni* (Reeve, 1842), found from the coasts of Louisiana, USA south to the Caribbean, is immediately distinguished from this group by the larger size of fully adult specimens, by its weaker spiral sculpture, with cords of unequal strength making it difficult often to distinguish cords of primary or secondary strength. This is not the case with any of the other species of the *M. chipolanum*-group in which all the cords are more strongly elevated and of roughly equal strength. The subventral ramp of the last whorl in *M. (O.) dennisoni* is much wider than in any of the other members of the group and there is a marked thickening of the inner aspect of the outer lip mid-height in *M. (O.) dennisoni* not present in the other group members. Finally the pustules tend to be coarser in the shells of *M. (O.) dennisoni*. Rios (1994) suggested *M. (O.) lindae* was a synonym of *M. (O.) dennisoni*. At the time of publication probably only a couple of specimens of the latter were known, and Rios probably considered it a subadult specimen of *M. (O.) dennisoni*. However, as more material of *M. (O.) lindae* has become available it is clear these differences are consistent and not gerontic characters, as the smallest shell of *M. (O.) dennisoni* we have found is within the maximum size range of *M. (O.) lindae* and still shows these consistent differences.

Petuch (1981) assigned a specimen collected from 11 meters depth off the Goajira Peninsula, Colombia to *M. domingense*, noting at the time that the specimens of the species known from the fossil record had 12 axial ridges, whereas the Recent shell had 16. Subsequently, he reassigned the Recent specimen to *Morum (Cancellomorum) lindae* Petuch, 1987 (p. 95, pl. 23, Figs 1-2). He considered *M. domingense* "the direct ancestor" of *M. lindae* and noted that the fossil species: "(...) has fewer axial ribs, is broader and more angled, has a smaller parietal shield, and is far less sculptured and less squamose" (Petuch, 1987, p. 95).

Vokes (1998) accepted the distinction between the fossil and recent taxa, specifying that the number of axial ribs in the fossil shells of *M. (O.) domingense* varied from 10-12 and added that: "(...) the nature of the low stepped spire, with its incised suture and the numerous fine axial lamellae, suggests that *M. lindae* is the linear descendent of the more recently described Cantaure Formation *M. jungi* Landau (1996, p. 53, pl.

1, Figs 1-2) rather than of *M. domingense*." (Vokes, 1998, p. 20).

In all Caribbean assemblages in which *Morum* occurs it is uncommon to very rare and at the time when many of the above taxa were described, they were known from one or two specimens only. As larger numbers of shells have become available and the intraspecific variability better represented, the characteristics separating some of the taxa have become less clear.

This paper started as a discussion over the validity of *M. (O.) lindae* as a distinct taxon from the Mio-Pliocene *M. (O.) domingense*. For each argument put forward supporting their separation, a Recent shell refuting their isolation could be found. Therefore, in the light of the greater amount of material available, we attempt to clarify whether *M. (O.) lindae* and *M. (O.) domingense* are indeed distinct taxa by means of a morphometric comparison. We have added morphometric data on the shells of two further undisputed extinct species; *M. (O.) chipolanum* and *M. (O.) jungi* and the living *M. (O.) dennisoni* in order to investigate the interspecific variability within this group of gastropods with very similar shells. Although the number of shells used in this study is less than that usually used for morphometric studies, we stress that for all species this is the largest number of specimens so far available.

MATERIAL AND METHODS

Data for the fossil shells were obtained from measurements, rib and cord counts as well as observations of shell characteristics of the type material clearly illustrated in Landau (1996) and Vokes (1998) and further specimens in the Bernard Landau collection (*M. (O.) chipolanum*: 10 specimens, 3 from locality TU (Tulane University locality number) 458, 3 from TU 546, 5 from TU 826; *M. (O.) jungi*: 5 specimens from TU 1269; *M. (O.) domingense*: 34 specimens, 2 Cercado Formation from NMB (Naturhistorisches Museum Basel locality number 16832, 32 Gurabo Formation, 2 from TU 1354, 14 from TU 1215, 13 from TU 1219, 3 from TU 1373).

The shells of some *Morum (Oniscidia)* species display a considerable variation in size between fully adult specimens, herein interpreted as shells with a fully expanded parietal shield and thickened outer lip. In *M. chipolanum*, for example, adult shells range from 22.2 mm to 38.8 mm, *M. (O.) domingense* from 20.5 mm to 35.8 mm, adults of *M. (O.) jungi* seem more uniform in size. For the purpose of this study we have not included any adult specimen smaller than 23.5 mm in height.

Data for Recent shells of *M. (O.) lindae* were collected from three specimens in the Franck Frydman collection and a further 13 shells illustrated on the Internet (Femorale, 7 specimens; Jaxshells, 3

specimens; worldwideconchology, 1 specimen; mineralislaquila, 1 specimen). *M. (O.) dennisoni* data was collected from the Internet (Femorale 8). Only specimens illustrated with both ventral and dorsal views and with the correct standard orientation were considered. Whilst collecting data from images on the web may not usually be ideal, we suggest that for rare specimens such as this (the type material consists of the holotype alone) it is a useful way to consider the maximum number of specimens known. For this study

internet data was collected from the following sites: Guest Shells (1996), Frank (1998), Coltro (2006); worldwideconchology.com (2006).

Measurements were taken as illustrated in Figure 1. Measurements of Internet photographs were taken with the measuring tool after copying the pictures into Photoshop, thereafter measurements calculated based on the original length given for each specimen. To minimize observer error all measurements were taken by the first author.

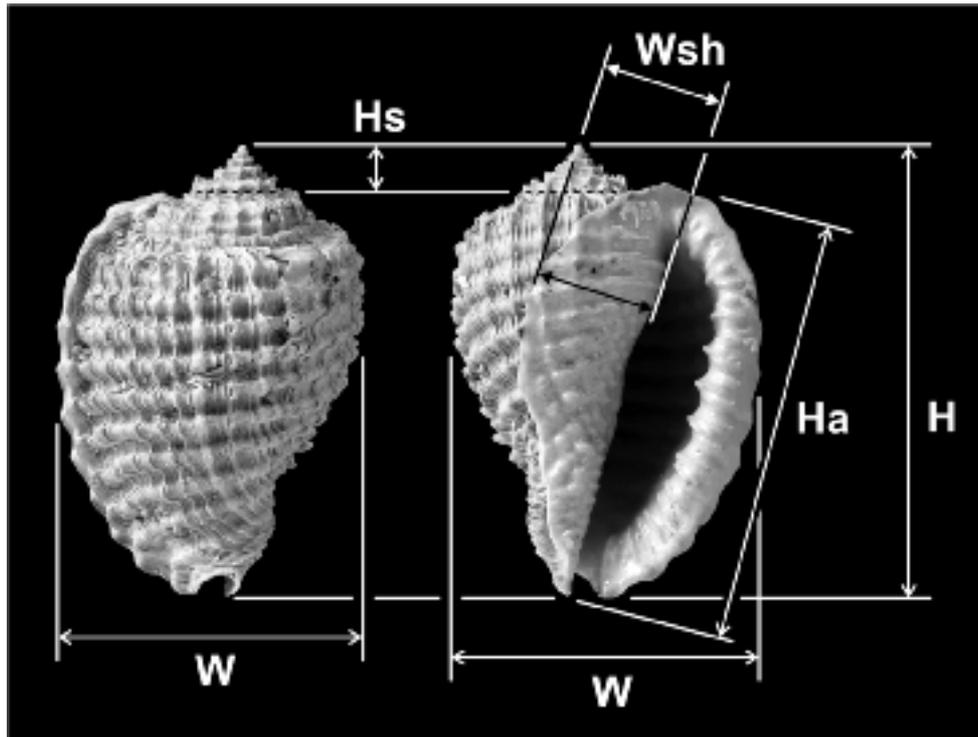


Figure 1. Morphometric measurements taken from a *Morum* shell.

H = total height, W = width of shell, Hs = height of spire, Ha = height of aperture, Wsh = maximum width of parietal shield.

RESULTS

Several specimens of the fossil taxa *M. (O.) domingense* and *M. (O.) chipolanum*, and one Recent shell of *M. (O.) lindae* had their protoconchs well preserved. In all three the protoconch was small, consisting of 1.25-1.5 smooth whorls with a small nucleus. This small paucispiral type of protoconch is highly suggestive of non-planktotrophic larval development. Bouchet (2002) reviewed data on Indo-Pacific *Morum* species and concluded that planktotrophy was the standard method of development in these species. He also noted that all the Caribbean species; *M. lindae*, *M. domingense*, and *M. dennisoni* had paucispiral protoconchs. It therefore seems that unlike the Indo-Pacific species, in the

Caribbean non-planktotrophic development is the norm. This coincides with the type of development observed in the living western Atlantic species *Morum oniscus* (Linnaeus, 1767) (type species of *Morum*), which lays its eggs beneath small slabs of coral at low tide level. The eggs undergo direct development and the gastropods hatch as crawling young (Work, 1969). Protoconch morphology was not, therefore, useful in distinguishing between species within the *M. chipolanum*-group.

Morphometric results on the teleoconch show:

1. In relation to their overall shape, there is overlap between the specimens of four species when comparing width in relation to height, although

M. (O.) domingense tends to have a narrower, more elongated shell compared to the one of *M. (O.) lindae*. *M. (O.) dennisoni* can be separated from the pack having a relatively narrower shell in relation to height (Fig. 2).

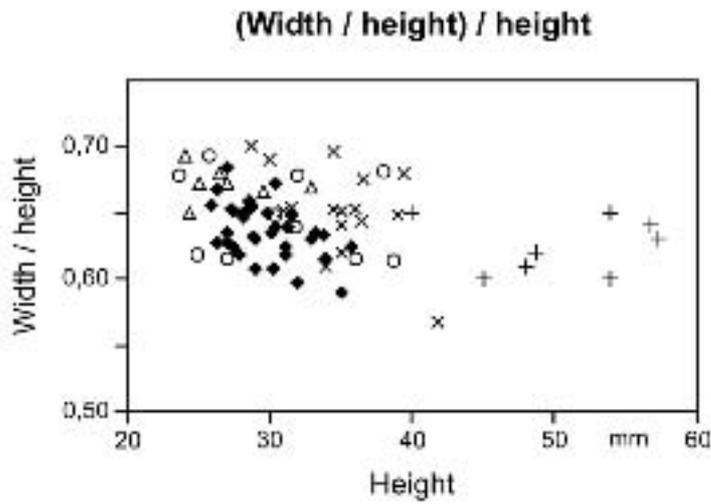


Figure 2. Morphometric plot of (width/height)/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

2. None of the species, except *M. dennisoni*, can be distinguished on the basis of relative spire height or apertural height (Figs 3, 4).

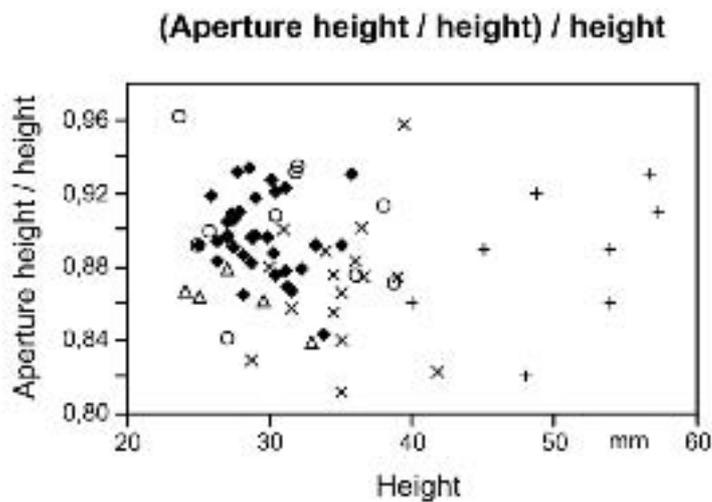


Figure 3. Morphometric plot of (aperture height/height)/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

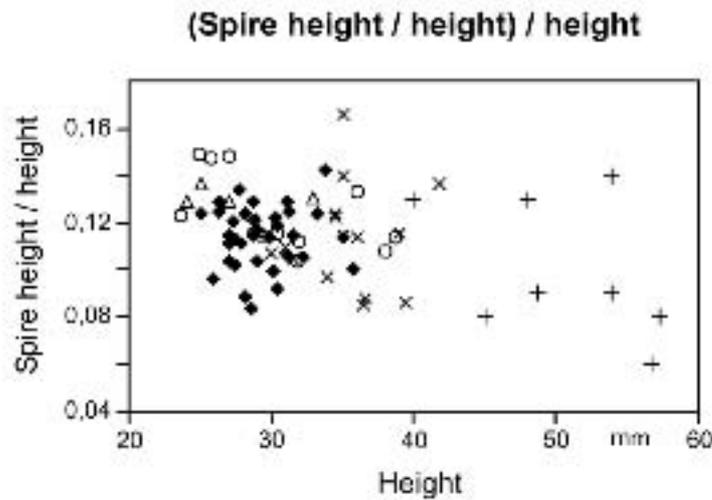


Figure 4. Morphometric plot of (spire height/height)/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

3. *M. (O.) chipolanum* has the broadest parietal shield of the five species, although there is some overlap

with *M. (O.) domingense* and *M. (O.) lindae*, there is no overlap with *M. (O.) jungi* (Fig. 5).

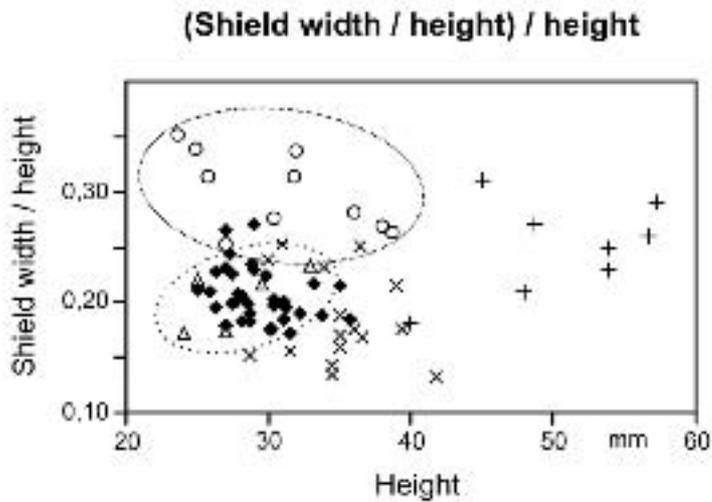


Figure 5. Morphometric plot of (shield width/height)/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

4. *M. (O.) jungi* has consistently fewer axial ribs in relation to height than *M. lindae*. Although there is some overlap, *M. (O.) domingense* also tends to have

fewer ribs than *M. (O.) lindae*. *M. (O.) dennisoni* can also be separated in having fewer ribs in relation to size (Fig. 6).

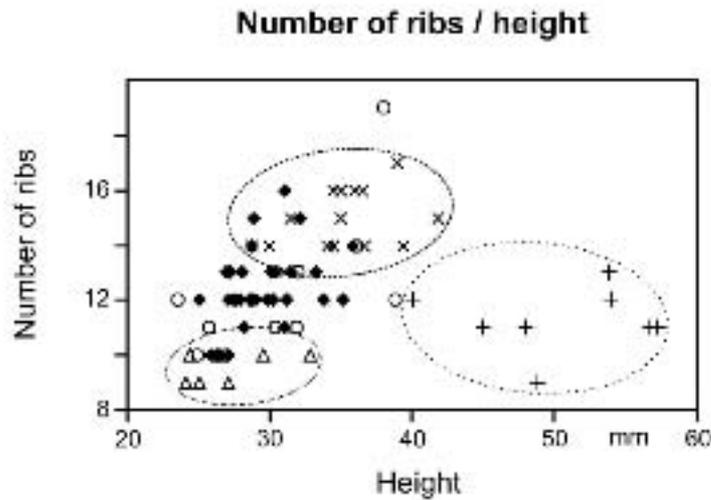


Figure 6. Morphometric plot of number of axial ribs/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

5. *M. (O.) lindae* has consistently fewer spiral cords in relation to height than *M. (O.) chipolanum*. Although there is some overlap, *M. (O.) lindae* also tends to have fewer cords than *M. (O.) domingense* and *M. (O.) jungi* (Fig. 7).

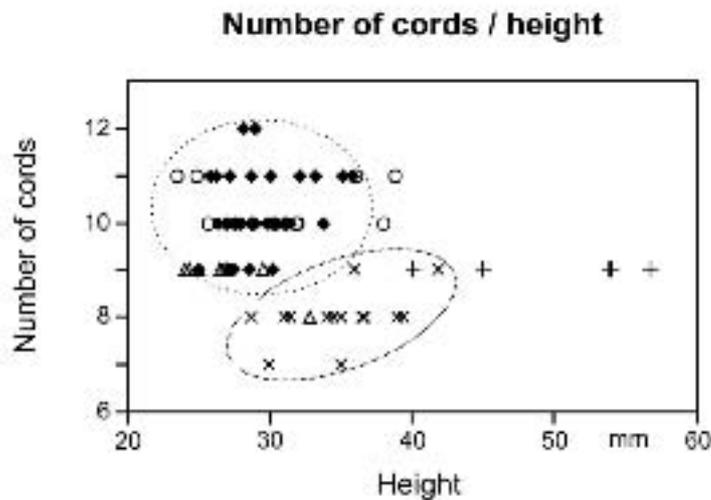


Figure 7. Morphometric plot of number of spiral cords/height. ◆ - *M. domingense*; ○ - *M. chipolanum*; △ - *M. jungi*; × - *M. lindae*; + - *M. dennisoni*.

DISCUSSION

It is clear from the results above that by this morphometric assessment alone it is not possible to distinguish groups of specimens easily within this assemblage of taxa with highly conservative shell form. Our plots show that *M. (O.) domingense* tends to have a narrower shell than *M. (O.) lindae*, *M. (O.) chipolanum* tends to have the broadest parietal shield, that *M. (O.) jungi* has consistently fewer axial ribs

than *M. (O.) lindae*, and *M. (O.) lindae* has consistently fewer spiral cords than *M. (O.) chipolanum* while tending to have fewer cords than *M. (O.) domingense* and *M. (O.) jungi*. Two further shell features are important in distinguishing the four groups of shells, which are not amenable to morphometric analysis: These are the shape of the parietal shield and the degree of development of secondary scabrous or squamous sculpture formed by the axial growth lines. *Morum*

(*Oniscidia*) *chipolanum* and *M. (O.) jungi* both have a shield which is rounded apically, whereas in *M. (O.) domingense* and *M. (O.) lindae* the shield is somewhat pointed in the area of the posterior canal (see Plate 1). This character does not seem too variable intraspecifically.

The second, the surface scabrosity, is difficult to quantify. There is no doubt that *M. (O.) chipolanum* has the most scabrous surface and *M. (O.) domingense* the least. Whilst some intraspecific variability exists, the most scabrous specimen of *M. (O.) domingense* (Plate 1, Figure 4) is still less scabrous than the smoothest *M. (O.) chipolanum*. *Morum (O.) lindae* usually has a more scabrous surface than *M. (O.) domingense*, although in the occasional specimen (Plate 1, Figure 4) there is little difference between them.

Vokes (1998) discussed a further character, the spire and considered *M. (O.) lindae* to have a more stepped spire than *M. (O.) domingense*. As can be seen from the specimens illustrated (Plate 1) and the plot of (apertural height/height)/height (Figure 3) there is no difference in relative spire height between the three species and only *M. (O.) jungi* has a significantly more stepped spire, i.e. the infrasutural platform is more horizontal.

PALAEOBIOGEOGRAPHIC CONSIDERATIONS

The present Caribbean region in the Miocene and Pliocene was part of the larger palaeobiogeographical Gatunian Province, which straddled the present day region of the Isthmus of Panama and included the modern Caribbean region and Tropical American Pacific (Woodring, 1974; Vermeij, 2005). The closure of the Central American Seaway (CAS) divided the Gatunian Sea, causing a significant change in the faunal composition on the Atlantic side. After the total closure of the CAS the Atlantic portion of the Neogene Gatunian Province gave rise to the Recent Caribbean Province. The Neogene Gatunian Province is characterized by a relative stability of gastropod taxa at generic level, but a very rapid turnover at specific level (Landau *et al.*, in print PPP). These high rates of extinction and local disappearance are accompanied by high rates of speciation (Allmon *et al.*, 1993; Jackson *et al.*, 1993). At species level it is not unusual to have an extinction rate since the Early Pliocene to present times of 80-85% (Woodring, 1928; Jung, 1969, Landau *et al.*, in press), with about half the long-lived taxa belonging to the most notoriously cosmopolitan group of gastropods, the tonnoideans (Beu, in prep).

Within the Gatunian Province, *Morum (Oniscidia) domingensis* is found exclusively in the West Indian Subprovince of Woodring (1974). The northern Caribbean coasts of South America formed the Colombian-Venezuelan-Trinidad Subprovince of Woodring (1974). At specific level, the assemblages

found in the West Indian and Colombian-Venezuelan-Trinidad Subprovince share very few taxa in common. Despite extensive collecting in rich Pliocene sediments in the area, there are no reported occurrences of *M. (O.) domingense* in the fossil record of the Colombian-Venezuelan-Trinidad Subprovince.

Morum (O.) lindae occurs exclusively off the Caribbean coast of Colombia and Venezuela. As in the Neogene, the fauna of the northern coasts of South America contains a high number of endemic elements (Petuch, 1987; Diaz, 1995). Indeed, Landau *et al.* (in print PPP) argued that the Colombian-Venezuelan-Trinidad Subprovince was probably in place since at least the Early Miocene and has continued as a distinct palaeobiogeographical unit to the present day. Although Petuch (1982) argued that this area had acted as a refugium for Gatunian species unchanged since the Pliocene (a primary relict pocket, according to his nomenclature), this does not stand up to taxonomic scrutiny. Petuch (1988) later considered it a secondary relict pocket, i.e. containing species which closely resemble their Pliocene ancestors. There is no fossil record of *M. (O.) lindae* in the southern Caribbean assemblages. Only one single fragment of *Morum (Oniscidia)* sp. from the Lower Pliocene Punta Gavilán Formation, Falcón Province, mainland Venezuela, is known (BL collection), and it is too incomplete to identify specifically.

CONCLUSIONS

Using a combination of quantitative shell parameters and qualitative shell characters of shield shape and scabrous surface one can conclude that *M. (O.) chipolanum* is most clearly distinguished from its congeners by the round shape of its shield and strongly scabrous surface. *Morum (O.) jungi* is characterized again by its abapically rounded shield, although less expansive than in the previous species and in having consistently fewer axial ribs than its congeners. *Morum (O.) domingense* and *M. (O.) lindae* are less easily distinguished; *M. (O.) domingense* tends to have a more elongated shell, fewer axial ribs as well as a greater number of primary spiral cords and also tends to have a smoother surface although there is some overlap with all these features between the two taxa. Apertural height, spire height and shield width are not useful to distinguish the shells of the two species.

On the basis of protoconch morphology all members of the *M. chipolanum*-group, in which the protoconch is known, have a small paucispiral protoconch, which strongly suggests a non planktotrophic larval development. This type of development is commonly associated with species having a shorter geological longevity and a more restricted geographical distribution (Jablonski & Lutz, 1980; Scheltema, 1989; Gili & Martinell, 1994), which might support the separation of the two taxa. However, this does not seem to be universally true across all gastropod

groups, as Jackson *et al.* (1996) found no correlation between species longevity and inferred developmental modes in Neogene Tropical American strombinids.

Whilst *M. (O.) domingense* and *M. (O.) lindae* show very similar shells, on the basis of our present knowledge of the Caribbean faunal turnover and the biogeography of the Neogene Atlantic Gatunian faunas it would be very unlikely for an exclusively Upper Miocene-Lower Pliocene Gatunian West Indian species to occur today within the Colombian-Venezuelan-Trinidad Subprovince.

Taking all the above arguments into consideration it is most likely that *M. (O.) domingense* and *M. (O.) lindae* actually represent two distinct taxa. There is insufficient evidence to suggest a direct lineage between the two based on their shell morphology and palaeobiogeographic distribution. Further information on the *Morum (Oniscidia)* species present in the Lower Pliocene Punta Gavilán Formation of Venezuela might help to clarify the relationship between these members of the *M. chipolanum*-group in the southern Caribbean.

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Figures 8-23

8-9. *Morum (Oniscidia) chipolanum* Dall, 1925. Loc. TU 546. Chipola River, Calhoun County, Florida, USA, Lower Miocene, Chipola Formation. Height 38.6 mm (B. L. coll).

10-11. *Morum (Oniscidia) domingense* (Sowerby, 1850). Loc. TU 1219. Amina River, Dominican Republic, Lower Miocene, Chipola Formation. Height 34.9 mm (B. L. coll).

12-13. *Morum (Oniscidia) domingense* (Sowerby, 1850). Loc. TU 1215. Gurabo River, Dominican Republic, Lower Miocene, Chipola Formation. Height 35.6 mm (B. L. coll).

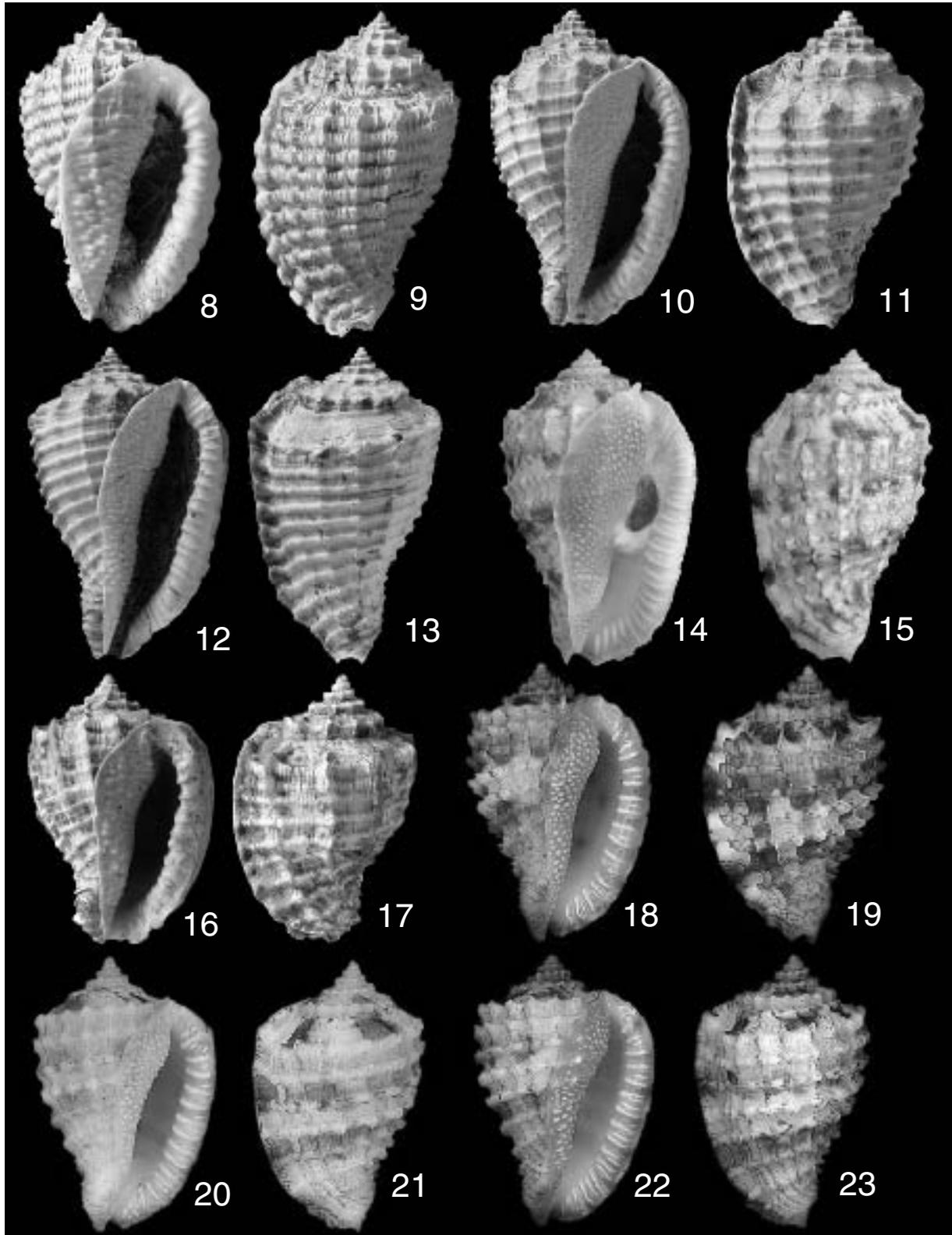
14-15. *Morum (Oniscidia) dennisoni* (Reeve, 1842). Vitoria, Espirito Santo State, Brasil, Recent. Height 48.8 mm (photo: Femorale).

16-17. *Morum (Oniscidia) jungi* Landau, 1996. Loc. TU 1269. Casa Cantaure, Paraganá Peninsula, Falcón State, Venezuela, Lower Miocene, Cantaure Formation. Height 25.0 mm (B. L. coll).

18-19. *Morum (Oniscidia) lindae* Petuch, 1988. Cabo de la Vela, Colombia, Recent. Height 36.0 mm (photo: Femorale).

20-21. *Morum (Oniscidia) lindae* Petuch, 1988. Cabo de la Vela, Colombia, Recent. Height 31.5 mm (photo: Femorale).

22-23. *Morum (Oniscidia) lindae* Petuch, 1988. Cabo de la Vela, Colombia, Recent. Height 39.4 mm (photo: Femorale).



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