Pliocene Gastropods from the Caribbean Island of Cubagua (Venezuela):
Taxonomy and Palaeobiogeography

Bernard Manuel Landau

Doutoramento em Geologia
(Paleontologia e Estratigrafia)

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A systematic account of the Pliocene (upper Zanclean to lower Piacenzian) gastropod assemblage found on the Island of Cubagua, Venezuela is given. 126 species are recorded belonging to 95 genera. During the course of this work 13 species were described as new to science and numerous new synonymies suggested, published in LANDAU, PETIT & SILVA, (2007) and LANDAU & SILVA (2010).

Patterns of extinction and local disappeance at subgenus and species level are discussed and compared to those seen in other Tropical American Neogene assemblages. The figures suggest a high degree of generic stability within the Caribbean Neogene prior to the total closure of the Central American Seaway (CAS), but a rapid turnover at specific level.

The biogeography of the southern Caribbean Neogene is discussed and previous work updated. Our data again distinguish a biogeographic unit centred on the north coast of Venezuela, including the Colombian Pliocene assemblages. This group of assemblages is distinct from those found in the Isthmian region of Tropical America, and in the central Caribbean. This biogeographic unit seems to have been in place since at least the Early Miocene, and whilst showing dramatic changes in faunal composition at specific level over time, altered little at generic level until the total disappearance of the ‘paciphile taxa’, which occurred in two pulses, the first at the beginning of the Late Pliocene, the second at the end of the Early Pleistocene. The geographic expression of this unit apparently has not altered over time, and does not seem to have been greatly affected by the closure of the CAS responsible for the demise of the Neogene Gatunian Province and the subsequent rise of the Late Pleistocene to Recent Caribbean Province. Although the bioprovinces changed, the subprovince remained unaltered. This suggests that the oceanographic conditions in the region have not changed greatly since Early Miocene times, and seem not to have been significantly affected by the uplift of the Isthmus of Panama. The name Colombian-Venezuelan-Trinidad Subprovince is chosen over Puntagavilian Subprovince and chorotypes and chronotypes discussed for the Gatunian Province and the Colombian-Venezuelan-Trinidad Subprovince.

A key fact in the history of Neogene Caribbean marine molluscs is the disappearance of the “paciphile” taxa that occurred throughout Tropical America during the Miocene and Pliocene, but subsequently suffered a range contraction, and became largely or entirely restricted to the eastern Pacific portion of their original distribution. A detailed revision of the paciphilic gastropods increased the number of known supraspecific taxa from 30 to 67. What forces led to the disappearance of these paciphile taxa in the Atlantic portion of their original distribution is at present unclear, as there seem to be no obvious common environmental factor or ecological requirements uniting this paciphilic assemblage of taxa. It is suggested that for paciphile species the emergence of the isthmus during the Late Pliocene cut off the source populations of the planktonically-dispersing molluscs dependent on Pacific source populations. The sink populations thus became stranded on the Atlantic coast of South America and elsewhere in the Caribbean, where they became unsustainable and eventually disappeared. A reappraisal of all known paciphile species indicates an inferred planktotrophic larval development, which supports this hypothesis.

Paciphiles did not disappear simultaneously, but seem to have suffered a steep decline during the Late Pliocene. A revision of all known gastropod paciphile generic, subgeneric and specific taxa allowed the recognition of three Gatunian Neogene Paciphile Molluscan Units (GNPMU). GNPMU 1 is characterized by the highest number of paciphile taxa. This unit is already in place in the Early Miocene and ends at the beginning of the Late Pliocene. GNPMU 2 is characterized by an impoverished number of paciphilic elements, devoid of the two largest paciphilic groups; the cancellarids and the muricids. This unit ends during the Late Pleistocene Calabrian-Ionian boundary. GNPMU 3 is characterized by the absence of any paciphilic elements in their assemblages, and runs into Recent times.

Based on these paciphile generic, subgeneric and specific taxa, for the Gatunian Province, two pulses of local disappearance from the Atlantic portion of their original distribution can be identified. The first marked by the overall decrease in Atlantic paciphile diversity and the total disappearance of all the paciphilic cancellarids and muricids, roughly corresponding with the timing given for the closure of the CAS. The second marked by the complete disappearance of all paciphiles from the Atlantic roughly coincides with the total closure of all connections between the Atlantic and Pacific.

**KEY WORDS:** Venezuela, Caribbean, Gastropods, Pliocene, Taxonomy, Palaeobiogeography, Ecostratigraphy.
RESUMO


Os padrões de extinção e de desaparecimento local ao nível subgenérico e específico são discutidos e comparados com os registados noutras associações neogénicas tropicais americanas. Os dados obtidos sugerem elevada estabilidade genérica no seio das associações neogénicas das Caraíbas ante-encerramento da Central American Seaway (CAS), mas rápida renovação (turnover) a nível específico.

É discutida a biogeografia do Neogénico do sul das Caraíbas e são actualizados os trabalhos anteriores. Os dados obtidos mostram claramente uma unidade biogeográfica centrada na costa norte da Venezuela, incluindo também as associações pliocénicas colombianas. Este grupo de associações é distinto dos encontrados na região do Istmo do Panamá e no centro das Caraíbas. Esta unidade biogeográfica parece ter-se instalado no início do Miocênico Inferior e, apesar de ter experimentado fortes mudanças faunísticas a nível específico, pouco se alterou a nível genérico até ao desaparecimento dos táxones pacíföricos ocorrido em dois impulsos: o primeiro registado no início do Pliocênico Superior e o segundo nos finais do Plistocênico Inferior. A expressão geográfica desta unidade parece não se ter alterado ao longo do tempo e não ter sido afectada significativamente pelo fecho da CAS, causa do desmembramento da Provincia Gatuniana neogénica e do subsequente advento da actual Provincia das Caraíbas no Plistocênico Superior. Apesar das paleobioprovíncias se terem alterado modificando, a subprovíncia manteve-se inalterada. Isto sugere que as condições oceanoográficas gerais na região não se modificaram significativamente desde o Miocênico Inferior, não tendo sido afectadas decisivamente pela emergência do Istmo do Panamá. Manteve-se o nome Suprovincia Colômbia-Venezuela-Trinidad (CVT) para esta unidade, em vez de Subprovíncia de Puntagavián e foram discutidos os corotipos e cronotipos para a Provincia Gatuniana e a Subprovíncia CVT.

Um facto crucial na história dos moluscos marinhos neogénicos das Caraíbas é o desaparecimento dos táxones neogénicos pacíföricos que ocorreram em toda a América tropical no Mio-Pliocênico, mas que subsequentemente se viram restringidos à porção pacífica da sua distribuição geográfica original. A revisão detalhada destes gastrópodes ampliou o número de táxones supra-específicos pacíföricos de 30 para 67. As causas que levaram ao desaparecimento dos táxones pacíficos nas Caraíbas são ainda motivo de investigação e de controvérsia. Contudo, é sugerido que, a nível específico, a emergência do Istmo do Panamá poderá ter isolado as “sink populations” de gastrópodes plânctontróficos das Caraíbas das respectivas “source populations” pacíficas, das quais dependiam. As populações “sink” nas Caraíbas tornaram-se insustentáveis e acabaram por desaparecer. A revisão de todas as espécies de gastrópodes pacíficos revelou que possuíam desenvolvimento larvar plânctontrófico, o que apoia esta hipótese.

Os gastrópodes pacíficos não desapareceram de um golpe, parecendo ter experimentado declínio abrupto a partir do Pliocênico Superior. A revisão dos táxones pacíficos permitiu a fundamentação de três “Gatunian Neogene Paciphilic Molluscan Units” (GNPMU). GNPMU1 é caracterizada por elevado número de pacíficos, abarcando o Miocênico inferior e o início do Pliocênico Superior. A GNPMU2 é caracterizada por uma associação reduzida de pacíficos, desprovida de Cancellariidae e de Muricidae. Esta unidade estende-se da fronteira Calabriano-Jóniano do Plistocênico Superior à actualidade. É caracterizada pela total ausência de táxones de gastrópodes pacíficos.

Com base nos gastrópodes pacíficos (a nível genérico e subgenérico) da Provincia Gatuniana podem ser caracterizados dois momentos de desaparecimento local de moluscos gastrópodes nas Caraíbas. O primeiro marcado pelo declínio generalizado da diversidade dos pacíficos atlânticos e pelo o desaparecimento total dos Cancellariidae e Muricidae pacíficos, correspondendo, grosso modo, ao período de fecho da CAS. O segundo impulso é marcado pelo desaparecimento de todos os restantes gastrópodes pacíficos das Caraíbas, coincidindo aproximadamente com o fecha total das ligações entre o Atlântico e o pacífico via CAS, já durante o Plistocênico Superior.

PALAVRAS-CHAVE: Venezuela, Caraíbas, Gastrópodes, Pliocênico, Taxonomia, Paleobiogeografia, Ecostratigrafia.
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CHAPTER 1: INTRODUCTION

Numerous Neogene fossiliferous deposits, rich in molluscan fossils, outcrop along or adjacent to the northern Atlantic coast of Venezuela. The fossil assemblage of the better known deposits, such as the Cantaure (Jung, 1965) and Punta Gavilán Formations (Rutsch, 1934, 1942) in Falcón State and those of the Cabo Blanco Group (La Pailas, Playa Grande, Mare and Abisinia Formations) (Weisbord, 1962-1967) have been described, whilst others remain almost unknown.

The presence of fossils of molluscs on the Island of Cubagua, Nueva Esparta State, situated between the Island of Margarita to the North and the Araya Peninsula to the South, is known since at least the 1930s (Schilder, 1939). Ingram (1947b) described two new species of Cypraea, C. grahami and C. rugosa, from the Neogene deposits of the island, Gibson-Smith (1973) described Voluta cubaguaensis, and E. H. Vokes (1990a) a new Haustellum species, H. mimiwilsoni. However, the assemblage outcropping on the island has never been listed nor studied in detail.

The Caribbean area in the Neogene has a turbulent geological and geographical history, which greatly affected the assemblages found in the area, their composition and patterns of appearance and subsequent extinction. Through most of the Neogene, tropical America has been biogeographically divided into two distinct provinces (Petuch, 1982; Vermeij, 2005); the northern Caloosahatchian Province along the North American East coast from North Carolina to northern Mexico, and to the south the Gatunian Province comprising all the Pacific tropical America and, in the Atlantic, including the Caribbean and the tropical East coast of South America, down to central Brazil in the Atlantic and northern Peru in the Pacific (Petuch, 2004), with a transition zone in northern Mexico and the Antilles Arc region. The Mio-Pliocene Cubagua faunas where part of the Atlantic portion of the Neogene Gatunian Province.

The first attempt to define aspects of the fossil fauna of the Caribbean region in terms of zoogeographical patterns was by Woodring (1959a) who described the “Tertiary Caribbean Molluscan Faunal Province” founded on his work on Jamaican (Woodring, 1928) and Panamanian faunas (Woodring, 1957, 1959b). Supported by further publications, including other Caribbean faunas, this was later revised and called the “Middle Miocene Caribbean Faunal Province” (Woodring, 1965) based on the distribution of characteristic molluscan assemblages and genera in the Caribbean and eastern Pacific regions. He further refined his palaeobiogeography in Woodring (1974) when he described the “Miocene Caribbean Faunal Province” with six subprovinces.

Petuch (1982) recognised two distinct faunal provinces in what is now the tropical and subtropical western Atlantic and eastern Pacific, which existed from at least the lower Miocene to the lower Pliocene, and coined the terms “Caloosahatchian Province” for the northern region along the North American East coast from North Carolina to northern Mexico, and replaced Woodring’s (1974) “Miocene Caribbean Faunal Province” with “Gatunian Province”. He argued that Woodring’s term was misleading ‘…in the sense that this area contained a fauna that remained virtually intact, as chronospecies, over a much longer period of time. Considering the more expansive temporal scope of this faunal region, I here propose the term…..’ (Petuch, 1982, p. 280). The terms Caloosahatchian and Gatunian Provinces have since been accepted in the literature (Petuch, 1988, 2004; Vermeij & Petuch 1986; Robinson, 1991; Vermeij, 2005).

Petuch (1988) refined his ideas on the Pliocene provinces and extended the Pacific northern limit of the Gatunian Province to the north of Baja California and the southern limit to at least southern Brazil. He recognized nine subprovinces within the Pliocene Gatunian Province. For our study area he erected the “Puntagavilanian Subprovince”, corresponding roughly to Woodring’s (1974) Miocene ‘Colombian-Venezuelan-Trinidad Subprovince’. This included the faunas represented by the fossil assemblages of the Punta Gavilán Formation, Cubagua Formation and Mare Formation of Venezuela, and Springvale and Talparo Formations of Trinidad. He gave a list he considered characteristic Puntagavilanian genera, species, and species complexes.
INTRODUCTION

PETUCH (2004) further developed his concept of provinciality in the tropical American Neogene, and gave a distinct name for the provinces in each time interval. Each of these newly erected provinces is divided into higher resolution units – subprovinces – than in his previous works.

As far as the study area is concerned, according to PETUCH’S (2004) biogeographic model, the Cainozoic Island of Cubagua, would be part of the Antiguan Province, Bohioan Subprovince in the Oligocene; the Baitoan Province, Cantaurean Subprovince in the Miocene and remained in the Gatunian Province, Puntagavilian Subprovince as previously described in the Pliocene (PETUCH, 1991).

Petuch’s model and concepts of palaeobiogeographical units are too complex and artificial (ALLMON, 2005). This study of the Cubagua fauna will bring new data, which will enable us to reanalyse these concepts of provinciality in the southern Caribbean. The Cubagua fauna, placed centrally within the known southern Caribbean outcrops is well situated to test Petuch’s model.

The aims of this work are
1. A detailed taxonomic study of the fossil gastropod taxa found in the Cerro Negro Member of the Cubagua Formation on Cubagua Island.
2. To review the present knowledge of the Neogene biogeography of the southern Caribbean, and assess whether our data supports present concepts and biogeographic models.
3. To investigate patterns of extinction at differing taxonomic levels and compare them to other Pliocene Atlantic patterns of extinction.
4. To assess whether biostratigraphic faunal units are applicable to Caribbean faunas.

CHAPTER 2: GEOGRAPHICAL AND GEOLOGICAL SETTING

2.1 Geographical setting

The area of research is placed geographically along the northern Caribbean coasts of mainland Venezuela, and Venezuelan Islands situated close to the mainland. The focus of research was based around the Island of Cubagua, which lies between Isla Margarita and the Venezuelan mainland (Text-Figure 1).

Cubagua Island is the smallest and least populated of the three islands constituting the Venezuelan state of Nueva Esparta, after Isla Margarita and Coche. It is located 16 km north of Araya Peninsula, the closest mainland area. The island is 9.2 by 3.6 km in size, an elliptical shape with the longer axis east-west. Its area is 22.438 km². The coast consists of cliffs from five to seven meters high in the south, and from 20 to 24 meters high in the north, with some beaches. The highest elevation of the flat-topped island reaches 32 meters.

Although Cubagua has a rich history, with the first human settlement in the Meso-American period dated at 2325 B.C, and had the first “city” in Venezuela, Nueva Cádiz, in the 16th century, Cubagua is now virtually uninhabited, with no streets or roads, water or electricity, and just a few fishermen’s shacks bordering the beach on the north side, Playa Charagato. It is served by irregular ferries and other boats from Punta de Piedras, the capital of Tubores municipality, located eight kilometers to the northeast, on Isla Margarita. Punta de Piedras is also the location of EDIMAR, the oceanographic institute and part of the La Salle Institute. Without the permission, co-operation and logistic help from EDIMAR this work would not have been possible. EDIMAR runs a small research station on Playa Charagato, which served as a base during the field work.

Cubagua is essentially a barren island with xerophytic vegetation, which became quite dense on our last visit in 2009, following unusually high rainfall. Cacti and a few legumes dominate the island, which is also the home to iguanas, hares and feral goats. There is no fresh water on the island.
**Text-Figure 1.** Geographic location of Cubagua Island and the outcrops sampled.

**Text-Figure 2.** Geographical location of the Araya Peninsula and the outcrops studied.
A second area of research was centered around the town of Araya located on the westernmost extremity of the Araya Peninsula, Sucre State. Araya can be accessed either by land following a poorly maintained road which spans the Araya Peninsula, or more easily by ferry or small boats which leave from Cumaná called “Tapaitos”.

Araya is a small tourist town dominated by the 17th century fort “Castillo de Araya”, constructed by the Spanish to protect the valuable salt flats from British and Dutch raiders. The fossil localities are located close to the fort at Cerro Barrigón (Text-Figure 2). The interior of the peninsula is even more arid than Cubagua Island, with little vegetation apart from scrub bush and cacti.

2.2 Geological setting

The standards for the lithostratigraphy of Venezuela are set in the LÉXICO ESTRATIGRÁFICO DE VENEZUELA (LÉXICO, 1997), published by the Ministerio de Energía y Minas de la República Bolivariana de Venezuela. This publication gives information on the lithological description, stratigraphic position and geographic extension of every Venezuelan Formation, as well as comments on the fossil content and references to further works on each of these lithostratigraphic units.

The most important Northern Venezuelan Neogene Basins are the Falcón Basin, Falcón State, central northern coast of Venezuela including the Paraguaná Peninsula and the Costa Afuera Basin including the Araya Peninsula in Sucre State and Margarita and Cubagua Islands in Nueva Esparta State (LÉXICO, 1997). Rich Pliocene molluscan assemblages, dealt with in this work, are part of both of these basins. The following Text-Figures (3, 4) have been adapted from the Lexico for these two areas. In this overview of the Neogene marine stratigraphy of Northern Venezuela special attention will be given to those formations rich in molluscan fossils.

2.2.1 The Falcón Basin

Many of the most important molluscan fossiliferous assemblages of the northern Venezuelan Neogene occur in the following formations in the Falcón Basin,

Lower Miocene:

The Cantaure Formation (Text-Figure 3) (HUNTER, 1978; GIBSON-SMITH & GIBSON-SMITH, 1979) is exposed in a series of arroyos about 500 m south of an abandoned house known as “Casa Cantaure”, which is 14 km west of Pueblo Nuevo in the Paraguaná Peninsula of Venezuela, with a thickness of about 75 m (JUNG, 1965). JUNG (1965) published a monograph describing many of the mollusc taxa found in the deposits. More recently a trickle of papers has been published describing new and interesting taxa (LANDAU & PETIT, 1996; VERMEIJ, 2001b amongst others). LANDAU & VERMEIJ (2010) gave an overview of all the taxa described from the Cantaure assemblage since JUNG’S (1965) and introduced a series of papers by Landau and co-authors (LANDAU, 2010a, b; LANDAU & GROVES, 2011; LANDAU & VERMEIJ, 2010, in press a, b, c) addressing various gastropod groups. Nevertheless, many undescribed taxa remain.

### Upper Miocene:

The term Caujarao Formation was coined by Wiedenmayer (1937) describing fossiliferous limestones, clayey limestones, sandstones and sands outcropping near Coro. The type section is exposed on the banks of the Coro River, near Caujarao, 3 km south of Coro, Miranda District, Falcon State. Wozniak & Wozniak (1987) placed the basal part of the Caujarao Formation within the *Globorotalia menardii* Zone, uppermost Middle Miocene, with the levels above containing a planktic forams assemblage attributable to the *Globorotalia acostaensis* Zone, followed other assemblages attributable to the *Globorotalia humerosa* Zone, Upper Miocene.

Giffin et al. (1992) assign the Cumarebo limestones from *Globorotalia humerosa* Zone to *Globorotalia margaritae* Zone (Upper Miocene to Lower Pliocene) and calcareous nannoplankton zones NN11-NN12 (Upper Miocene to Lower Pliocene). Hodson (1926), Hodson et al., (1927) and Hodson & Hodson (1931) described some of the molluscan assemblage found in this formation.

Collections of molluscs from these deposits are present in the Gibson-Smith Collection in the Natuurhistorischesmuseum in Basel, Switzerland and a small lot in the B. Landau/NHMW collection. Unfortunately, the most fossiliferous outcrop by the Carrizal cemetery situated 14 km northeast of Santa Ana de Coro, Falcon State, has disappeared under a rubbish dump (BL personal observation, 2002).

### Pliocene:

The Punta Gavilán Formation (Text-Figure 3) outcropping along the northeast coast of Falcón State was first described by Rutsch (1934). Reddish limestones are exposed in the type section at Punta Gavilán, extremely rich in molluscan and echinoid fossils. Díaz de Gamero (1985) considered the eastern

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**Text-Figure 3.** Lithostratigraphic formations of the Falcón Basin (adapted from the LÉXICO, 1997).
part of the formation to span the entire Pliocene, and based on planktic forams fossil assemblages placed in the *Globorotalia margaritae* Zone and *Pulleniatina obliquiloculata* Zone (now known as *Globorotalia miocenica*) and in the western portion he only recognized the upper Pliocene *Pulleniatina obliquiloculata* Zone. **MACHADO et al.** (1996) assigned a Lower Pliocene age for the type section based on calcareous nannoplankton, between NN12 and NN15. **RUTSCH** (1934, 1942) described the gastropod fossil assemblage found in the Punta Gavilán Formation.

### 2.2.2 The Costa Afuera Basin

In this work we discuss the gastropod assemblage found in the Cubagua Group and will discuss in greater detail the lithostratigraphy of this Group. The **LÉXICO** (1997) considered Cubagua Island as part of the Costa-Afuera Basin and the Araya deposits under Araya and Paria (see Text-Figure 4).

**DALTON** (1912) was the first to mention the “Cubagua layers” and designated the type section on Cubagua Island.

**VIGNALI** (1965) in a geological study of the western part of the Araya Peninsula recognized Miocene to Pleistocene deposits. He described a lower member with a type section at the lower part of the Cerro Barrigón locality (near Araya, in the western tip of the Araya Peninsula), Cerro Verde and an upper member, Cerro Negro with type section at Cerro Negro 2km north of Manicure, also Araya Peninsula, Sucre State. He recognized the contact between the two members at Cerro Barrigón. **VIGNALI** (1965) gave a list of fossils found in the Cerro Verde Member and correlated it with La Vela, El Veral, Punta Gavilán and Springvale Formations, dating them as Upper Miocene. The Cerro Negro Member was correlated again with the Punta Gavilán and Springvale Formations, and assigned to the uppermost Upper Miocene (**VIGNALI**, 1965).

**Text-Figure 4.** Lithostratigraphic formations of the Costa Afuera Basin (adapted from the **LÉXICO**, 1997).
MACSOTAY (1965) gave a faunal list of the macrofossils found on the Araya Peninsula and again considered both the Cerro Verde and Cerro Negro Members to be Upper Miocene.

MACSOTAY (1971) considered the Cerro Verde and Cerro Negro Members as formalized and used by VIGNALI (1965), but raised them both in hierarchical position to formation. He reconsidered the stratigraphical position of the Cerro Negro Formation as entirely restricted to the Pliocene.

PADRÓN et al. (1993) reviewed the Neogene-Quaternary of the Araya Peninsula and Margarita and Cubagua Islands. They recognized La Tejita Formation on Margarita Island overlain by a section of Cerro Negro Formation. On Cubagua Island and the Araya Peninsula they considered the sections to belong principally to the Cubagua Formation, and identified VIGNALI’S (1965) ‘Cerro Verde’ and ‘Cerro Negro’ Members. On their stratigraphic section (PADRÓN et al., 1993: figures 3-4), the fossiliferous layers at Cerro Barrigón (Araya Peninsula) and Cañón de las Calderas (Cubagua Island) were placed at the very base of the ‘Cerro Negro’ Member sequence cropping out in the cañón. PADRÓN et al. (1993) considered the Cubagua Formation to range from the Upper Miocene to the Lower Pleistocene.

Text-Figure 5. Stratigraphy of the Cubagua Group (adapted from MACSOTAY et al., 1995). Synonyms: 1. Cerro Verde Member; 2. Carenero Formation; 3. Las Hernandez Formation; 4. Cerro Negro Member.

MACSOTAY et al. (1995) raised the hierarchical rank of the Cubagua sequence from Formation to Group, which consisted of the older predominantly clayey Upper Miocene La Güica Formation, with a conglomeratic-sandy marine marginal component La Tejita Formation (Text-Figure 5). Above lay the...
sandy-limestone Araya Formation, with a psephitic-carbonate Aramina Formation. The terms ‘Cerro Verde’ and ‘Cerro Negro’ Members of the Cubagua Formation coined by VIGNALI (1965) and used by authors such as GIBSON-SMITH & GIBSON-SMITH (1974), JUNG (1989) and PADRÓN et al. (1993) were rejected by MACSOTAY et al. (1995) as they were junior synonyms. VIGNALI’S (1965) ‘Cerro Verde’ Member was considered a synonym of the La Tejita Formation (MARTINEZ, 1950), his ‘Cerro Negro’ Member a synonym of the Aramina Formation of DUSENBURY & WALCOTT (1949) and in the LEXICO ESTRATIGRÁFICO DE VENEZUELA (1956). MACSOTAY et al. (1995) considered the Cubagua Group to have a chronostratigraphical range from lower Upper Miocene to lower Upper Pliocene (Text-Figures 5, 7).

The Araya Formation has a thickness of 164m at the holostratotype (Cerros El Macho y Guamache, Araya Peninsula). The 70m of sediments most completely exposed at Cañón de las Calderas, which was nominated as the hypostratotype for the Araya Formation (MACSOTAY et al., 1995), correspond to the upper 70m of the section given by MACSOTAY et al. (1995).

The Aramina Formation consists of conglomerates at the base passing to limestones and sands. The type section is at Quebrada Aramina, a tributary of the river Tuy, Miranda State. The location designated by VIGNALI (1965) as type section for his ‘Cerro Negro’ Member near Manicuare (Araya Peninsula) was considered a hypostratotype by MACSOTAY et al. (1995). He discussed a Pliocene age for this formation, possible Upper Pliocene and considered the molluscan assemblage found there similar to that found in the Springvale Formation of Trinidad, now considered Lower Pliocene in age. The gastropod material reviewed herein originates from the base of the section at Cañón de las Calderas, Cubagua Island and Cerro Barrigón, Araya Peninsula. The Cerro Barrigón sedimentary sequence corresponds to the Aramina Formation (sensu MACSOTAY, et al. 1995) (Text-Figure 5) and the Cañón de las Calderas sedimentary sequence to the Araya Formation (sensu MACSOTAY, et al. 1995) (Text-Figure 5).

Text-Figure 6. Geological map of Cubagua Island (Obtained from LEXICO ESTRATIGRÁFICO DE VENEZUELA (1956) at http://www.pdvsa.com/lexico/museo/image/cubagua2.gif).
On Cubagua Island, according to MACSOTAY et al. (1995) La Güica Formation crops out on cliffs to the north of Quebrada los Muñecos. The Araya Formation crops out on the back cliffs of Cañón de las Calderas. According to Macsotay (personal communication, 2009) the base of the Cañón de las Calderas containing the fossiliferous horizon reviewed herein belongs to the Aramina Formation. However, in MACSOTAY et al. (1995) these fossiliferous sediments were placed in the Araya Formation (see Text-Figure 7). Until this change in opinion is published we will adhere to formation nomenclature outlined by MACSOTAY et al. (1995), but we consider the Aramina Formation of Cerro Barrigón equivalent to the Araya Formation of Cañón de las Calderas.

AGUILERA & AGUILERA (2001) did not follow the lithostratigraphic nomenclature proposed by MACSOTAY et al. (1995). They continued to consider the Cubagua as a formation with four members; the Cerro Verde Member, exposed on Cubagua Island and westernmost Araya Peninsula; the Cerro Negro Member, exposed along Western Araya Peninsula and Cubagua Island; and the La Tejita and Las Hernandez members, exposed on Margarita Island. The reason for persisting with the former lithostratigraphic model is not clear, although AGUILERA & AGUILERA (2001) may have been unaware of the paper by MACSOTAY et al. (1995), as it is not listed in their bibliography.

LANDAU et al. (2007a) were also unaware of MACSOTAY et al. (1995). After numerous discussions and field trips together with Oliver Macsotay in 2009, the terminology proposed by MACSOTAY et al. (1995) is adopted in this work.

Text-Figure 7. Stratigraphical correlation of the Cumana Area (adapted from MACSOTAY et al., 1995).

On the Island of Cubagua two Lower Pliocene fossiliferous areas were sampled:

Cañón de las Calderas outcrop:

The Cañón de las Calderas outcrop corresponds to the basal bed of the Cañón de las Calderas sedimentary sequence as described by PADRÓN (1993), MACSOTAY (1995) and others (Text-Figure 1, Study site 1). The fossiliferous section consists of about 2 m of poorly consolidated fine sands, just above a
clayey layer apparently devoid of macrofossils at the base of the section, approximately 4-5 m above sea level (Text-Fig. 13). The fossils look abundant, but are probably concentrated on the surface by erosion of the sandy matrix. In several arroyos the sandy fossiliferous bed is exposed vertically and the fossils are sparsely distributed. The fossils are found at the very base of the 70 m section at Cañon de las Calderas. Within the fossiliferous bed the shells occur in poorly defined levels; the lowest is richest in bivalves, the middle level is the thickest and contains the greatest diversity of gastropod species, and the upper level containing an assemblage consisting almost entirely of shells of Turritellidae and Vermetidae. The fossils in all layers are relatively well-preserved, most shells showing some surface erosion, and the early whorls of gastropod shells are almost invariably missing or worn. As seen in the geological map of the island (Text-Figure 6) these outcrops are considered to be part of the Araya Formation.

Cerro Colorado outcrop:

The Cerro Colorado outcrop is situated just inland, on the west side of Punta Colorada, the first point following Playa el Falucho (Text-Figure 1, Study site 2). The fossiliferous section is very similar to that found at the Cañon de las Calderas outcrop, about 3 m of poorly consolidated fine sands, approximately 2-5 m above sea level. To the north of the locality, closer to the beach a narrow band of Pleistocene to Holocene consolidated reef limestone crops out, assigned by Padrón et al. (1993) to the Tortuga Formation and in the map above (Text-Figure 4) shaded as El Manglillo Formation. Our sampling location lies just inland from the area shaded as El Manglillo Formation on the geological map, and according to it should correspond to the Upper Miocene La Güica Formation. The Cerro Colorado outcrop has not been mentioned by any previous workers, but in the geological map illustrated by Padrón et al. (1993; hoc opus Text-Figure 13) the Cerro Colorado outcrop is included in the Cerro Negro Member of the Cubagua Formation.

Unfortunately, the Upper Miocene molluscs of Venezuela are poorly known, but the assemblage of molluscan fossils found here is similar to that at Cañon de las Calderas. Based on the number of paciphilic cancellarids found, the Cerro Colorado molluscan fossil assemblage is not significantly different from that of the Cañon de las Calderas (see Landau et al., 2009). Moreover, the turritellid assemblage (see Macsotay, 1971) is similar in both localities, corresponding to the Turritella guppyi zone of Macsotay (1971), i.e., Lower Pliocene (see Text-Figure 14). Moreover, after Padrón et al. (1993; hoc opus Text-Figure 13), the Cerro Colorado area is attributed to the Cerro Negro Member of the Cubagua Formation, as is the Cañon de las Calderas area.

Cerro Barrigón outcrop:

On mainland Venezuela another outcrop, also belonging within the Cubagua Group, occurs at Cerro Barrigón, about 1 km south of the village of Araya on the westernmost Araya Peninsula (see Padrón et al., 1993, Jung, 1989, this work Text-Figure 2). According to Vignal (1965) the Cubagua Formation at Cerro Barrigón cannot be subdivided into the ‘Cerro Verde’ and ‘Cerro Negro’ members. However, both Gibson-Smith & Gibson-Smith (1974) and Jung (1989) positioned the type locality of Strombina arayana Gibson-Smith & Gibson-Smith, 1974 in the ‘Cerro Negro Member’ (equivalent to the Araya Formation of Macsotay et al., 1995).

We agree with Gibson-Smith & Gibson-Smith (1974) that the ‘Cerro Negro Member’ can be clearly distinguished from the underlying ‘Cerro Verde Member’ (equivalent to the La Güica Formation of Macsotay et al., 1995) at Cerro Barrigón, Araya, where it consists of a lower level of fine, poorly consolidated yellow sands (type bed for Strombina arayana), and an upper level of coarser, more consolidated reddish sands, in which the fossils are less well preserved. Both have a rich fossil molluscan assemblage, very similar to that found at Cañon de las Calderas on Cubagua Island. According to Macsotay (personal communication, 2007, 2009) these beds are within the Araya Formation, stratigraphically slightly higher than those cropping out at Cañon de las Calderas.

The island of Cubagua was declared an ‘Archeological and Palaeontological National Park’ in 2006 by the Instituto del Patrimonio Cultural (IPC) of Venezuela (López, 2007).
Other important fossiliferous molluscan assemblages of the Costa Afuera Basin in Miranda and Distrito Federal States are listed below (for correlation see Text-Figure 4):

**Pliocene:**
Lowest part of the Mare Formation (Macsotay, 2007, personal communication).

**Pleistocene:**
- Mare Formation, excluding lowest part (GIBSON-SMITH & GIBSON-SMITH, 1979; MACSOTAY, 2005).

The Mare Formation, first described by HUMBOLDT (1801), is part of the Cabo Blanco Group, which includes the La Pailas, Playa Grande, Mare and Abisinia Formations. The type section is at Quebrada Mare, north of the original airport at Maiquetía. Unfortunately, the expansion of the airport destroyed the section. The lithology consists of fine gravels at the base, passing to sands, progressively finer-grained towards the top of the section. WEISBORD (1964a, b, 1967) monographed the macrofossils from the Playa Grande, Mare and Abisinia Formations, which was supplemented by GIBSON SMITH (1971).

BERMÚDEZ & FUENMAYOR (1962) studied the foraminifera present in the formation and noted that both in the planktic and benthic foraminifera 100% of species were still extant, and that the assemblage in the Playa Grande and Mare Formations were equivalent, placing them in the *Gr. trunculatinoides* Zone. Contrary to this opinion, WEISBORD (1967) assigned the Mare Formation to the Pliocene. CATI et al. (1968) considered the *Gr. trunculatinoides* Zone Pleistocene. Therefore the Playa Grande and Mare Formations were Pleistocene. Isotope dating of Th/U on the most common mollusc in the overlying Abisinia Formation; *Mazatlanica aciculata* indicated a maximum age of 300 Ky. This would suggest a Middle Pleistocene age, close to the limit with the Upper Pleistocene (LÉXICO, 1997).

According to Macsotay (2007, personal communication) the lowest part of the Mare Formation is Pliocene. WEISBORD (1962) described a few fragments of *Malea* from the Mare Formation. *Malea* is a paciphilic taxon (LANDAU et al., 1009; BEU, 2010; LANDAU 2010a). Judging from the figures given by WEISBORD (1962), many of the fossils of molluscs from the Mare Formation are very worn and represented by few or single fragments. The presence of *Malea* does not fit with an earlier age than Middle Pliocene. It is possible that some of these may be reworked from older sediments. Large mollusc fossil collections from Maiquetía are present in the Gibson-Smith Collection in the Natuurhistorischesmuseum in Basel, Switzerland.

The Cumaná Formation was also first described by HUMBOLDT (1814-1825). The type section is at Cerros de Caiguire, east of the city of Cumaná, Sucre State. They consist of sands and limestones with lenses rich in fossils of molluscs and bryozoans. Oliver Macsotay has prepared a monograph of the macrofossils of the Cumaná Formation, which is unpublished and may be a source of further joint research. The Cumaná Formation belongs within the same sedimentary sequence as the Playa Grande and Abisinia Formations and is also in the *Gr. trunculatinoides* Zone (BOLLI, 1972) and therefore Lower Pleistocene to mid Middle Pleistocene (LÉXICO, 1997). The Cerros de Caiguire locality, southeast of the city of Cumaná, Sucre State, was visited by us together with Oliver Macsotay (2009). Unfortunately the outcrops are much deteriorated, in parts built over and the outcrops with fossils of molluscs very poor. However, enough material is available in the Gibson-Smith Collection in the Natuurhistorischesmuseum in Basel, Switzerland and the Macsotay monograph (manuscript) to review the molluscs taxonomically.

Other Upper Pleistocene formations are:
2.3 Biostratigraphic setting

2.3.1 Neogene biostratigraphy of Northern Venezuela based on planktic foraminifera

At least partially, Palaeontology has developed into an applied science by means of its usefulness in the interpretation of stratigraphy: through biostratigraphy. This palaeontological application is based on two fundamental stratigraphic laws: the superposition of strata, and the regular chronological succession of fossil assemblages.

Most of the Cainozoic zonation based on planktic foraminifera for the Palaeogene and Neogene was originally developed in the study area, on the island of Trinidad, West Indies. These zonations are of the taxon-range type in which the unit is the body of strata representing the known range of stratigraphic and geographic occurrence of specimens of a particular taxon.

CUSHMAN & STAINFORTH (1945) subdivided the Oligocene-Miocene Cipero Formation of the Trinidad into three zones. CUSHMAN & RENZ (1947) and STAINFORTH (1948) proposed further zones for the scheme. GRIMSDALE (1951) offered the first intercontinental correlation by age/stage for 41 Cainozoic planktic foraminiferal species from the Gulf of Mexico and the Caribbean with equivalent species from the Middle East.

Text-Figure 8. Biostratigraphic correlation of some uppermost Middle Miocene to Pliocene formations in Trinidad, coastal northeastern Venezuela (Falcón), Aruba, Jamaica and Java (adapted from BOLLI & BERMÚDEZ, 1965).
BOLLI (1957) and BOLLI & BERMÚDEZ (1965) constructed a Miocene to Pliocene zonation for northeastern and northwestern Trinidad, Venezuela, Jamaica and Java based on sequences of planktic foraminifera, and proposed six zones. Foraminifera are ideally suited for sequence zonation, as from the Cretaceous to Early Miocene a sequence of short-lived species is recognized, within which evolutionary lineages enhance the applicability of these microfossils to stratigraphy. After the Middle Miocene short-ranging forms became scarcer and longer-ranging forms, often using a combination, were used by BOLLI & BERMÚDEZ (1965) to construct the Middle Miocene to Pliocene zonation. We note that BOLLI & BERMÚDEZ (1965) considered the *Globorotalia margaritae* Zone as mid Upper Miocene (Text-Figure 8).

In the same year, VIGNALI (1965), in his study on the sedimentary rocks of the Araya Peninsula recognized a Miocene to Pleistocene sequence (Text-Figure 9). He considered the Cubagua Formation to represent a transgressive cycle of deposition, which consisted of a lower sandy and conglomeritic Cerro Verde Member and an upper clays and limestones Cerro Negro Member, deposited during the Upper Miocene. Above this lay the regressive Cerro Barrigón Formation containing fossils of the bivalve *Lyropecten arnoldii*, which he considered a Lower Pliocene index fossil. For his dating VIGNALI (1965) quotes BOLLI & BERMÚDEZ (1965).

![Text-Figure 9. Stratigraphic sequence for the Araya Peninsula (Nueva Esparta) (adapted from VIGNALI, 1965).](image-url)

In the same issue of Geos, MACSOTAY (1965) gave a list of the macrofossils found in the Cubagua Formation, and based on the character of the fauna and number of extinct taxa gave an Upper Miocene age to the Cerro Verde and Cerro Negro Members of the Cubagua Formation.
### GEOGRAPHICAL AND GEOLOGICAL SETTING

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**Text-Figure 10.** First planktic foraminiferal zones erected in Trinidad (adapted from Bolli & Saunders, 1985).

**Text-Figure 11.** Correlation of the Upper Miocene to Holocene low latitude planktic foraminiferal zonal schemes (adapted from Bolli & Saunders, 1985).
BERNARD M. LANDAU

BANNER & BLOW (1965) proposed a planktic foraminiferal zonal scheme closely matching that of BOLLI (1957) for the Oligocene to Middle Miocene. They defined most zones giving two taxa, thus concurrent-range zones, in which the unit is the body of strata including the overlapping parts of the range zones of two specified taxa. They designated a letter and number to each zone, P for Palaeogene and N. for Neogene and numbered the zones sequentially within each subdivision. Since then this scheme has been considerably refined, especially in the Pliocene and Pleistocene.

BOLLI & SAUNDERS (1985) further refined the Upper Miocene and Pliocene zonal schemes, and compared the schemes proposed by other workers (see Text-Figures 10, 11). Here, the Globorotalia margaritae Zone was placed in the Lower Pliocene. In summary, their scheme divided the Oligocene into five zones. The Miocene was divided into 14 zones. The Pliocene was divided into five zones subzones and finally the Pleistocene into four zones. Planktic faunal zones are particularly applicable to the Upper Neogene, a magnitude of the events of appearance and extinction of low latitude planktic foraminiferal taxa from the latest Miocene and throughout the Pliocene is second only to that at the Cretaceous/Cainozoic boundary (BOLLI & SAUNDERS, 1985).

BOLLI (1970) considered the First Occurrence (FO) of Gr. margaritae to mark the Miocene/Pliocene boundary. CITTA (1973) considered the FO slightly above the boundary in the Mediterranean. BERGGREN et al. (1985) estimated an FO for Gr. margaritae at 5.6 Ma and the Last Occurrence (LO) at 3.2 Ma in the Atlantic. Later BERGGREN et al. (1995) determined the LAD (Last Appearance Datum) of Gr. margaritae at approximately 3.58 Ma.

More recently, BYLINSKAYA et al. (2002) and BYLINSKAYA (2002) have improved the resolution of the Globorotalia margaritae Zone, which they consider spans the entire Lower Pliocene, and divided it into three subzones (Text-Figure 12). Material for microfossils was sampled from the localities under study in 2009 to determine if the resolution could be improved based on the calcareous nannofossils. Results are not yet available.

Text-Figure 12. Zonations that use the Globorotalia crassaformis plexus. Paleomagnetic subchrons: J– Jaramillo; O–Olduvai; K– Kaena; M–Mammoth; C–Cochiti; N–Nunivak; S–Sidufjall; T–Thvera (BYLINSKAYA, 2004).
2.3.2 Biostratigraphy of the Cubagua Group based on planktic foraminifera

**Text-Figure 13.** Stratigraphic section of Cañon de las Calderas and geological map of Neogene-Quaternary outcrops of Cubagua Island (PADRÓN et al., 1993).
PADRÓN et al. (1993) recognized five biostratigraphic zones and three subzones based on planktic foraminifera in the Cubagua Formation. We note that they considered the formation to range from the Upper Miocene to the Holocene, which gave a chronostratigraphical range for the Cubagua Group from the middle of the Upper Miocene to the lower Upper Pliocene, a model rejected by MACSOTAY et al. (1995). According to PADRÓN et al. (1993) all zones from the Globorotalia acostaensis to the Globorotalia crassiformis viola were present. They placed the Cerro Barrigón outcrop in the Globorotalia margaritae - Globorotalia miocenica Zone (PADRÓN et al., 1993; figure 3) and the Cañon de las Calderas outcrop in the Gr. margaritae Zone (PADRÓN et al., 1993; figure 4; hoc opus Text-Figure 13). This zone was recalibrated by IACCARINO (in BOLLI et al., 1989) as middle to upper Zanclean.

It seems, therefore that the Cañon de las Calderas outcrop can be placed in the Globorotalia margaritae Zone, which more recently was recalibrated by IACCARINO (in BOLLI et al., 1989, p. 285, fig. 1) as middle to upper Zanclean. If we follow BERRGREN et al. (1985), the Cañon de las Calderas outcrop is dated between 5.6-3.2 Ma, Zanclean to lower Piacenzian.

PADRÓN et al. (1993) also record an abundant and diversified assemblage of calcareous nannoplankton from Araya and Margarita, which spans from the Discoaster calcaris Zone (NN10) to the limit between the Discoaster surculus and D. pentaradiatus Zones (NN16-NN17). This gives a chronostratigraphical range from lower Middle Miocene to upper Miocene, but no information is given on from which localities these nannoplankton assemblages were recorded and does not help further to stratigraphically position our molluscan fossil assemblages.

2.3.3 Neogene Caribbean biostratigraphy based on turritellid gastropods

![Text-Figure 14. Caribbean Neogene turritellid zones correlated with lithostratigraphic Formations of the Zulia Falcón area (left) and northeastern Venezuela (right) (adapted from MACSOTAY, 1971).](image-url)
The first attempt at biostratigraphic zonation for the Venezuelan Neogene based on molluscan assemblages was attempted by Hoffmeister (1933). Working with drill cores from the Miocene La Rosa and Laguillillas Formations (Zulia State, northwestern Venezuela) he identified two biostratigraphic zones for the La Rosa Formation, a lower *Cadulus* Zone and an upper *Microdrillia* Zone.

### Text-Figure 15

Caribbean Neogene turritellid zones correlated with foraminiferal zones (Macsotay, 1971). UE = Upper Eocene, O = Oligocene; UO = Upper Oligocene, LM = Lower Miocene, MM = Middle Miocene, P = Pliocene, LQ = Lower Quaternary, UQ = Upper Quaternary.

<table>
<thead>
<tr>
<th>Global zonation / planktic Foraminifera</th>
<th>Regional zonation / Mollusca</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1</strong></td>
<td><strong>2</strong></td>
</tr>
<tr>
<td><strong>Age</strong></td>
<td><strong>Zones</strong></td>
</tr>
<tr>
<td>P</td>
<td>Grt. truncatulinoides</td>
</tr>
<tr>
<td></td>
<td>Gbg. altisspa s.s.</td>
</tr>
<tr>
<td></td>
<td>Grt. truncatulinoides</td>
</tr>
<tr>
<td></td>
<td>Gbg. altisspa</td>
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<tr>
<td></td>
<td>Grt. margaritae</td>
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<tr>
<td></td>
<td>Grt. dutertrei</td>
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<tr>
<td>UM</td>
<td>Grt. acostaensis</td>
</tr>
<tr>
<td></td>
<td>Grt. menardii</td>
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<td></td>
<td>Gdes. ruber</td>
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<tr>
<td></td>
<td>Grt. fohsi robusta</td>
</tr>
<tr>
<td>MM</td>
<td>Grt. fohsi s.l.</td>
</tr>
<tr>
<td></td>
<td>Grt. fohsi lobata</td>
</tr>
<tr>
<td>LM</td>
<td>Grt. fohsi fohsi</td>
</tr>
<tr>
<td></td>
<td>Grt. fohsi barisanensis</td>
</tr>
<tr>
<td></td>
<td>Praeorb. glomerosa</td>
</tr>
<tr>
<td></td>
<td>Grt. xinl Facing</td>
</tr>
<tr>
<td>O-LM</td>
<td>Catapsydrax stainforthii</td>
</tr>
<tr>
<td>O</td>
<td>G. dissimilis</td>
</tr>
<tr>
<td></td>
<td>Cras. dissimilis</td>
</tr>
<tr>
<td></td>
<td>Grt. kugleri</td>
</tr>
<tr>
<td>UE</td>
<td>G. ciperoensis s.s.</td>
</tr>
<tr>
<td></td>
<td>G. ciperoensis</td>
</tr>
<tr>
<td></td>
<td>G. opima opima</td>
</tr>
<tr>
<td></td>
<td>G. ampliapertura</td>
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<tr>
<td></td>
<td>Cella. chiplensissm</td>
</tr>
<tr>
<td></td>
<td>Cella. chiplensissm</td>
</tr>
<tr>
<td></td>
<td>Hastigerina micra</td>
</tr>
</tbody>
</table>

On top of this lay the Lagunillas Formation in which he recognized a single biostratigraphic zone; *Lithophaga* Zone. On the basis on the fossil assemblage he correctly concluded that these formations were Lower Miocene and not Oligocene as earlier geologists had suggested.

MACSOTAY (1971) constructed a scheme of biozones for the whole ‘Caribbean-Antillean’ palaeoprovince based on their turritellid assemblages (Text-Figures 14, 15).

These zones where of the ‘Assemblage Zone type’, in which the unit is the body of strata characterized by an assemblage of three or more fossil taxa that, taken together, distinguishes it in biostratigraphic character from adjacent zones. This is a system of biostratigraphic zones based on extinctions of turritellids as opposed to ecostratigraphic zones based on local disappearances within a portion of a biogeographic province (i.e. the Atlantic portion of the Neogene Gatunian Province), directly as a result of the closure of the CAS (LANDAU et al., 2009).

If we consider our outcrops on Cubagua Island, which are Araya Formation (former Cerro Negro Formation of VIGNALI, 1965, rejected by MACSOTAY, 1995), these are within the *T. guppyi* zone. This zone, according to MACSOTAY (1971) is defined by the simultaneous occurrence of the following species; *T. gatunensis caronensis*, *T. domingensis*, *T. lloydsmithi*, *T. guppyi* and *T. poncensis*.

When these turritellid assemblages are correlated with foraminiferal zones, we see that the *T. guppyi* zone coincides exactly with the *Globorotalia margaritae* zone of BOLL & BERMUDEZ (1965) and the upper half of N18 and the whole of N19 of BANNER & BLOW (1965).

According to the scheme of turritellid biozones constructed by MACSOTAY (1971), the Cantaure Formation is placed in the Middle Miocene *Turritella abrupta* zone (Figure 14). However, *T. abrupta* SPIEKER, 1922 does not occur in Cantaure, although there is a record for *T. abrupta* (s.l.) in the Gibson-Smith collection in Basel. If it is present in the Cantaure assemblage, it is certainly not common. A few of the other *Turritella* species associated with the *T. abrupta* zone such as *T. cocoditana* F. HODSON, 1926, *T. gilbertharrisi* F. HODSON, 1926 and *T. paraguamensis* F. HODSON, 1931 do occur in Cantaure, whereas most of the others listed by MACSOTAY (1971) such as *T. chipolana* DALL, 1892, *T. mimetes* BROWN & PILSBRY, 1911, *T. warfieldi* F. HODSON, 1926, *T. praecellens* PILSBRY & BROWN, 1917, *T. caparonis* MAURY, 1925, *T. colinensis* F. HODSON, 1926, *T. hubbardi* F. HODSON, 1926, *T. lorensis* F. HODSON, 1926, *T. quirosana* F. HODSON, 1926, *T. montanitensis* F. HODSON, 1926 and *T. bifastigata* NELSON, 1870 do not.

Most other authors, base on different methods of dating, place the Cantaure Formation in the upper Lower Miocene (HUNTER, 1978; GIBSON-SMITH & GIBSON-SMITH, 1979; REY, 1996). MACSOTAY (1971) also placed the *T. mimetes* biozone in the Middle Miocene, however, he considered the Culebra Formation as the type section for this biozone, now also considered Lower Miocene (JUNG, 1989). As discussed in other parts of this work, the stratigraphic assignment of the various Caribbean Formations by various authors have changed over time, and it is likely that the stratigraphic ranges and the positioning of these Turritella biozones need to be updated. It is also possible that the resolution of these units may not be as high as suggested by MACSOTAY (1971).

### 2.3.4 Biostratigraphy of the Cubagua Group based on turritellid gastropods

According to MACSOTAY (1971) in Canõn de las Calderas the assemblage corresponds to the *T. lloydsmithi* Zone, with the *T. guppyi* Zone in the sandy facies at the top of the section. Following his turritellid zonation this would give a chronostratigraphical positioning for the base of the outcrop at the Miocene/Pliocene boundary (Text-Figure 15). In 1971 MACSOTAY used VIGNAL’s (1965) terms “Cerro Verde” and “Cerro Negro”, which MACSOTAY (1971) identified on the Araya Peninsula.

In the lower part of the section for the “Cerro Verde” (Tejita Formation of MACSOTAY et al., 1995) the fossils corresponded to the *T. caronensis* Zone and he recorded finding *T. vistana* and *T. altilirata praecellens*. MACSOTAY (1971) wrote that because of facies change, the *T. lloydsmithi* Zone could
not be distinguished from the *T. guppyi* zone, except by molluscs other than *Turritella*. MACSOTAY (1971) correlates the *T. caronensis* Zone with NN 17, upper Upper Miocene.

In the type locality for the “Cerro Negro” Formation (Aramina Formation of MACSOTAY et al., 1995) the *T. guppyi* Zone was well represented. MACSOTAY (1971) argued that the upper part ended in a hypersaline environment not suitable to turritellids. Near Maricuare there was a good representation on the *T. carthagenensis* Zone. MACSOTAY (1971) correlates the *T. guppyi* Zone with NN 19, late Lower Pliocene and the *T. carthagenensis* Zone with NN 20, early Middle Pliocene.

### 2.4 Age of Tropical American Assemblages:

The age assessment of almost all the Caribbean Neogene assemblages has changed since their original descriptions. Most of the deposits in which they occur are now considered significantly younger than initially thought. Therefore the ages given for the tropical American formations have changed over time. We have endeavoured to give the most up-to-date chronostratigraphic information, with the source in brackets. Formations situated geographically on the Pacific side of the Central American Isthmus are placed in italic.

Most of the Caribbean Neogene literature distinguishes a Lower (Early), Middle and Upper (Late) Pliocene. In this work we have adopted the recent recommendation of the International Commission on Stratigraphy – accepted by the IUGS on June 30, 2009 – on the redefinition of the Pleistocene (now including the Gelasian Stage/Age as its lowermost unit), and the concomitant formal redefinition of the base of the Quaternary System/Period (and thus the Neogene/Quaternary boundary) as defined by the GSSP of the Gelasian Stage at Monte San Nicola, Sicily, with an age of 2.58 Ma (RICCARDI, 2009).

**Lower Miocene:**


**Panama,** Culebra Formation (JUNG, 1989).

**Dominican Republic,** Baitoa Formation, 17.5-14.5 Ma (SAUNDERS et al., 1986).


**Middle Miocene:**

**Florida,** Shoal River Formation (E. H. VOKES, 1989c; JONES et al., 1993).

**Mexico,** Ferrotepec Formation (PERRILLIAT, 1987).

**Panama,** Valiente Formation, Bocas del Toro, dated 11.5-7.2 Ma (COATES et al., 2005).

**Haiti:** Thomonde Formation, Haiti (E. H. VOKES, 1990).


**Carriacou,** Grand Bay Formation (early Middle Miocene) (ROBINSON & JUNG, 1972; DONOVAN et al., 2003).

**Costa Rica,** Punta Judas (SEYFRIED et al., 1985).

**Peru,** Zorritos Formation, lower Middle Miocene (VEGA et al., 2005).
Upper Miocene:

**Dominican Republic**, Cercado Formation, 7.5-5.7 Ma (SAUNDERS et al., 1986).

**Panama**, Chagres Formation (PPP website: http://www.fiu.edu/~collinsl/companion.canar.fg), Gatun Formation (PPP website: http://www.fiu.edu/~collinsl/companion.canar.fg, note: the Lower Gatun Formation extends into the Middle Miocene, from approx. 12-8.2 Ma); Nancy Point Formation, Bocas del Toro, Panama, dated as 7.2-5.3 Ma (COATES et al., 2005); Chucunaque Formation, Darien (COATES et al., 2004); **Colombia**, Usiacuri Formation (BEU, 2010) [Early Pliocene according to JUNG, 1989].


**Ecuador**, Daule, Bahia Formations (J. E. Whittaker written comm. in JUNG, 1989) and Angostura Formation and Esmeraldas beds, Onozole Formation, planktonic foraminiferal zone N.16 (PITT & PITT, 1992).

**Peru**, Tumbes Formation (OLSSON, 1932; BUSH et al., 1994).

Lower Pliocene:

**Dominican Republic**, Gurabo Formation, 5.6-4.0 Ma (SAUNDERS et al., 1986), Mao Formation, 4.0-3.5 Ma (COTTIN IN COLLINS & COATES, 1999).

**Colombia**, Usiacuri Formation (JUNG, 1989; BEU 2007) according to Macsotay (personal communication, 2005) is Late Pliocene, but with reworked Early Pliocene fossils; Tubarí Formation (HUNTER, 1978).


**Venezuela**, El Veral Formation (originally considered Late Miocene DIAZ DE GAMERO, 1968; BOLLI, 1970) now Early Pliocene in *Globorotalia margaritae* to *Globorotalia miocenica* Zones (GIFFUNI et al., 1992; DIAZ DE GAMERO et al., 1994); Punta Gavilán Formation (BOLLI & PREMOLI SILVA, 1973; HUNTER, 1978; MACHADO et al., 1996), San Gregorio Formation, Falcón, Venezuela (MACSOTAY et al., 1998), lowest part of the Mare Formation (Macsotay, 2007, personal communication).

Lower–Upper Pliocene:

**South Carolina**: Yorktown Formation, South Carolina, 4.0-3.0 Ma (DOWSETT & WIGGS, 1992).

**Florida**, Jackson Bluff Formation, 5-2.8 Ma (COTTIN IN COLLINS & COATES, 1999) (=Choctawhatchee Frm.) *Ecphora* faunizone age equivalent with (probably) lower Pliocene Tamiami Formation in Sarasota (G. Herbert pers. comm.); lower Pinecrest Beds units 10-5 dated as 4.6-3.0 Ma (LYONS, 1991).

**Jamaica**, Bowden Formation included in *Globorotalia margaritae* Zone (BOLLI & BERMUDEZ, 1965) assigned to Early Pliocene (BOLLI & PREMOLI SILVA, 1973), Late Miocene to Early Pliocene (BERGGREN, 1993), early Late Pliocene (calcaceous nanoplankton zone NN16) (AUBRY, 1993), Early Pliocene by JUNG & HEITZ, 2001, 2.8-1.6 Ma (COTTIN IN COLLINS & COATES, 1999), olistotome with reworked ‘middle’ Pliocene fossils (Macsotay, 2007, personal communication).

**Panama**, Cayo Agua Formation dated as 5.0-3.4 Ma (COATES et al., 2005); Shark Hole Point Formation dated as 5.3-3.6 Ma (COATES et al., 2005).

**Ecuador**, Jama Formation (J. E. Whittaker written comm. in JUNG, 1989), Canoa Formation (LANDINI et al., 2002).
GEOGRAPHICAL AND GEOLOGICAL SETTING

Upper Pliocene:


**Costa Rica**, Banano Formation 3.6-2.4 Ma (COTTON in COLLINS & COATES, 1999).

**Panama**, Charco Azul Group, Penita Formation, 3.5-2.2 Ma (COTTON in COLLINS & COATES, 1999).

Lower Pleistocene:

**Florida**, upper Pinecrest units 4-2 dated as 2.5-2.0 Ma (LYONS, 1991); upper Pinecrest and lower Caloosahatchee Formation ages are not distinguishable based on the resolution of the isotopic technique used, but the Pinecrest is almost certainly lower in the section. Also, we refer to the Pinecrest as the Pinecrest beds or the Pinecrest Sand as it is not a formal lithostratigraphic unit. Formally, the Pinecrest sand were considered a biostratigraphic interval within the Tamiami Formation; Caloosahatchee Formation (LYONS, 1991, p. 146) [PETUCH 1994 considers it to straddle the Plio-Pleistocene boundary, we have followed LYONS who used an integrated chronostratigraphic dating technique]; Nashua Formation (PETUCH, 1994, p. 3).

**Panama**, Escudo de Veraguas Formation, Bocas del Toro, 2.2 -1.8 Ma (COTTON in COLLINS & COATES, 1999).

**Costa Rica**, Moin Formation, 1.9-1.5 Ma (COTTON in COLLINS & COATES, 1999); Charco Azul Group, Burica Formation, 1.8 -1.5 Ma (COTTON in COLLINS & COATES, 1999).


Lower-Upper Pleistocene:

**Florida**, Bermont (1.7-1.0 Ma) (HULBERT & MORGAN, 1989; WEBB et al., 1989; LYONS, 1991, p. 159).

**Panama**, Charco Azul Group, Armuelles Formation, 1.7 to1.5-0.5 Ma (COTTON in COLLINS & COATES, 1999).

**Puerto Rico**: Quebradillas Formation, although lowest part is Upper Miocene (MOUSSA et al., 1987).

**Trinidad**, Matura shell bed, Talparo Formation (J. B. Saunders pers comm. in JUNG, 1989).


Upper Pleistocene:

**Florida**, Fort Thompson Formation composed of several transgressive and regressive cycles (0.95-0.22 Ma) (WEBB et al., 1989; LYONS, 1991, p. 160).

**Mexico**, Santa Ines Bay, Baja California Sur (DURHAM, 1950; EMERSON et al., 1981; JUNG, 1989).


**Panama**, Swan Cay Formation (1.8-0.9 Ma: COATES in COLLINS & COATES, 1999: text-fig. 5).

**Dominican Republic**, La Isabella Formation (MARCANO & TAVARES, 1982).

CHAPTER 3: SYSTEMATIC PALAEONTOLOGY

3.1 Material and Methods

The material described herein was collected between 2000 and 2009 on Cubagua Island and in 2006 and 2009 on the Araya Peninsula. Field sampling was conducted with the collaboration and field support of the Estación de Investigaciones Marinas de Margarita (EDIMAR), Fundación La Salle de Ciencias Naturales, Venezuela, which kindly put its facilities at our disposal. This work is the result of an ongoing collaboration between the Fundación La Salle and the Geological Research Center and the Department of Geology of the Faculty of Sciences of Lisbon University for the study of the Pliocene Cubagua Island malacological assemblages.

All the type material is deposited in the Museo de la Estación de Investigaciones Marinas de Margarita, EDIMAR (EDIMAR coll.) and in the Naturhistorische Museum Wien, Vienna (NHMW), Austria, other specimens figured are in the BL collection donated to the NHMW.

Within the systematic section of this work we acknowledge a methodological failure in not comparing our material to type specimens, as it was not feasible to visit institutions in the United States for logistical reasons. However, this failure is greatly compensated when working with Caribbean fossil faunas as the literature is usually more recent than that consulted when working with European faunas, and the type specimens are on the whole adequately described and illustrated.

One of the largest collections of Caribbean Neogene fossils housed at the Naturhistorisches Museum in Basel, Switzerland (NHMB) was visited by one of us (BL, in 2009 and 2010) and our material compared to that deposited there. This museum has a history for nearly a century of oil geologists from this area of Switzerland spending their working careers in tropical America, returning to Basel with large collections that have gradually accumulated there. Collections have been contributed by (among others) Hans Kugler, Rolf Rutsch and Peter Jung, as well as from many oil companies, and recently this has been the repository of the large collections for the Dominican Republic and Panama Paleontology Projects. The enormous, highly diverse collections gathered from Neogene sequences of northern Venezuela by Jack and Win Gibson-Smith have also been incorporated in the Museum’s collection. For Cubagua Island and the Araya Peninsula these collections are, however, not particularly rich, but what is present is recorded in the material studied.

Large collections from the Caribbean have been accumulated the author over the last 25 years and have also been used as comparative material. The Bernard Landau collection (BL coll.) will eventually be annexed to the NHMW collections.

The classification adopted here is according to BOUCHET & ROCROI (2005). For all species a comprehensive synonymy is given both in the fossil and Recent literature in order to determine the distribution of the species over geologic time.

Abbreviations used:

EDIMAR coll.  Museo de la Estación de Investigaciones Marinas de Margarita, Venezuela.
NHMW     Naturhistorische Museum Wien, Vienna.
NMB      Naturhistorisches Museum Basel, Switzerland.
UCMP    University of California, Museum of Paleontology, Berkeley, California.
ZMA     Zoological Museum, University of Amsterdam.
PRI     Paleontological Research Institution, Ithaca, NY, USA.
3.2 Systematics

Superfamily     Trochoidea RAFINEQUE, 1815
Family           Calliostomatidae THIELE, 1924
Subfamily       Calliostomatinae THIELE, 1924
Genus and subgenus  Calliostoma SWAINSON, 1840.

Type species Trochus conulus LINNAEUS, 1758, by subsequent designation, HERRMANNSEN, 1846.

Calliostoma (Calliostoma) calderense LANDAU & SILVA, 2010
Pl. 1, Figs 1-3

2010a    Calliostoma (Calliostoma) calderense LANDAU & SILVA, p. 10, pl. 1, figs 1-3.

Dimensions and type material: Holotype MOBR-M-3872 (Pl. 1, Fig. 1), height 17.0 mm, maximum diameter 16.8 mm (EDIMAR coll., ex BL coll.); paratype 1 NHMW 2010/0038/0001 (Pl. 1, Fig. 2), height, 15.5 mm, maximum diameter 14.5 mm (NHMW coll., ex BL coll.); paratype 2 NHMW 2010/0038/0002 (Pl. 1, Fig. 3), height, 19.6, maximum diameter 16.4 mm (NHMW coll., ex BL coll.); paratype 3 NHMW 2010/0038/0003, height, 23.1 mm, maximum diameter 20.2 mm (NHMW coll., ex BL coll.).

Etymology: Named after the type locality, Cañon de las Calderas.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Stratum typicum: Araya Formation, Cubagua Group, Lower Pliocene.

Additional material: 25 specimens BL coll., Cañon de las Calderas, Cubagua Island; 3 specimens BL coll. (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrígón, Araya Peninsula.

Diagnosis:
A Calliostoma (Calliostoma) species with a medium-sized, regularly conical, imperforate shell, with concave whors above the shoulder, a reticulate sculpture on early teleoconch whors, weakly beaded spiral cords with secondary and tertiary cords in the interspaces on later whors, a depressed base bearing spiral cords, which are not beaded, and a very weakly developed basal columellar tooth.

Original description:
“Shell of average size for genus, solid, with elevated conical spire. Protoconch of 1½ convex whors, surface eroded. Teleoconch of seven whors, concave in profile mid-whorl, with periphery short distance above abapical suture. Suture linear, superficial. Sculpture of first teleoconch whorl of three spiral cords, abapical cord stronger. Axial sculture of narrow, close-set, strongly prosocline ribs, which overrun spiral cords, forming tubercles at intersections on early teleoconch whors. Abapically ribs weaken progressively, beading spiral cords from fourth teleoconch whorl. Secondary spiral cords appear in interspaces between primary cords on fourth teleoconch whorl, abapical primary cord gains in strength, twice as broad as other primary spiral cords, forming the shoulder; two cords below shoulder on later whors. Spiral cords of tertiary strength appear on penultimate whorl. Sculpture on later teleoconch whors of finely beaded, weakly developed cords crossed by very close-set prosocline growth lines. Last whorl concave to carina, carina formed by two stronger cords, relatively sharply angled at base. Base almost flat, imperforate, bearing 10-11 spiral ribs, more widely spaced towards columellar callus. Aperture tangential, sub-quadrangular; outer lip sharp. Columella straight, bearing very weak basal columella tubercle. Columella callus not expanded, slightly thickened, covering umbilicus (LANDAU & SILVA, 2010a, p. 10)”.

Discussion:
Calliostoma (Calliostoma) calderense LANDAU & SILVA, 2010 is similar to Calliostoma (Calliostoma) laticarinatum (GUPPY, 1867) from the Matura Shell Bed, Talparo Formation of Trinidad. These beds were originally considered Lower Pliocene by JUNG (1969), but later assigned to the Pleistocene (JUNG, 1989). I have compared our shells from Cubagua with the specimens illustrated by JUNG (1969) in the Basel collections (NMB H14575). The Cubagua specimens are much larger (between 15.7–23.1 mm in height, as opposed to under 10 mm for the Trinidadian specimens), with a narrower apical angle, the sculpture of spiral cords is coarser, less finely beaded and there are usually two cords below the shoulder on the penultimate whorl as opposed to four in C. (C.) laticarinatum.
Calliostoma (Calliostoma) decipiens (Guppy, 1867), from the Lower Pliocene Melajo Clay Member of the Springvale Formation of Trinidad is similar, but has a weaker angulation on the spire whorls, and the distance between the angulation and the abapical suture is less than in Calliostoma (Calliostoma) laticarinatum (Guppy, 1867). Also, the whorl profile above the angulation is more deeply concave in C. (C.) laticarinatum. Jung (1969) noted that the early whorls were similar in both species and that there were some intermediate forms in his Trinidadian material, suggesting the two might be synonyms. Although not commented on by Jung, the spiral sculpture in his illustrations of C. (C.) decipiens (Jung, 1969, pl. 41, figs 6-12) retain a more strongly beaded appearance on the later teleoconch whorls.

A third closely similar species, Calliostoma (Calliostoma) caronianum Maury, 1925, occurring in the Melajo Clay Member of the Springvale Formation of Trinidad, differs in the whorl profile, having a more strongly rounded angulation, a more concave profile above and a more convex profile below. Jung (1969, p. 419) noted as a difference the smaller apical angle in C. (C.) caronianum, evident in his illustrations. All four species, C. (C.) laticarinatum, C. (C.) decipiens, C. (C.) caronianum and C. (C.) calderense are closely similar species belonging to a Calliostoma group with angulated spire whorls and a closed umbilicus.

Calliostoma (E.) olssonii MAURY, 1925 belongs to a distinct Calliostoma group with broad shells, strong beaded sculpture throughout and a deep, wide umbilicus, not closed by columellar callus. Clench & Turner (1960) erected the subgenus Elmerlinia for this group of species. Some authors have placed this tropical American group of perforate Calliostoma-species in the genus Astele, Swainson, 1855 (Macsotay & Campos, 2001), which is also characterised by having umbilicate shells. However, the type species, Astele subcarinata Swainson, 1855 is antipodean and has quite a different type of radula (Clench & Turner, 1960). According to Clench & Turner (1960) Astele does not occur in the western Atlantic. As pointed out by Hickman & McLean (1990) there is no consensus as to the use of subgenera within the Calliostomatinae Thiele, 1924, and a full review of genera is warranted.

Calliostoma (Elmerlinia) olssonii MAURY, 1925 is characterised by cancellate sculpture on the early teleoconch whorls, a sculpture of irregularly beaded spiral cords on the later whorls, on the penultimate and last whorls the cords are beaded on the adapical half of the shell, smooth near the adapical suture, a depressed weakly convex base bearing concentric cords, beaded near the umbilicus, ridge-like towards the periphery, and a wide, deep umbilicus extending to the apex, delimited by a smooth cord. The number, strength and beading of the

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Type species Calliostoma jujubinum Gmelin, 1791, by original designation.

Calliostoma (Elmerlinia) olssonii MAURY, 1925
Pl. 1, Figs 4-6

1925a Calliostoma (Eutrochus) olssonii MAURY, p. 247, pl. 43, figs 6, 14.
2010a Calliostoma (Elmerlinia) olssonii MAURY, 1925 – Landau & Silva, p. 11, pl. 1, figs 4-6.

Material and dimensions: Maximum height 19.4 mm, width 26.4 mm, 12 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
Calliostoma (Elmerlinia) olssonii, 1925 belongs to a distinct Calliostoma group with broad shells, strong beaded sculpture throughout and a deep, wide umbilicus, not closed by columellar callus. Clench & Turner (1960) erected the subgenus Elmerlinia for this group of species. Some authors have placed this tropical American group of perforate Calliostoma-species in the genus Astele, Swainson, 1855 (Macsotay & Campos, 2001), which is also characterised by having umbilicate shells. However, the type species, Astele subcarinata Swainson, 1855 is antipodean and has quite a different type of radula (Clench & Turner, 1960). According to Clench & Turner (1960) Astele does not occur in the western Atlantic. As pointed out by Hickman & McLean (1990) there is no consensus as to the use of subgenera within the Calliostomatinae Thiele, 1924, and a full review of genera is warranted.
spiral cords on the later teleoconch whorls is quite variable. One of our shells has the protoconch preserved; it consists of 1.45 depressed whorls with a small nucleus. The reticulate sculpture on the first protoconch whorl typical in the genus Calliostoma cannot be seen as the protoconch surface is abraded.

Calliostoma (E.) olssoni was described from the Lower Pliocene Springvale Formation of Trinidad. I have compared the Cubagua material to that present in the Basel collections (NMB H 14582-14584) from the Matura Shell Bed, Talparo Formation of Trinidad. These beds were originally considered Lower Pliocene by JUNG (1969), but later assigned to the Pleistocene (JUNG, 1989). All the specimens from Matura are much smaller and possibly juvenile, but they clearly show the same cancellate sculpture on the early teleoconch whorls. The shells are far more depressed than the adult specimens from Cubagua, but two juvenile shells from the Cañon de las Calderas which are similarly depressed. The sculptural variability on the later teleoconch whorls seen in the Cubagua shells is also seen in the Matura specimens.

Of the living species, Calliostoma (Elmerlinia) bullisi CLENCH & TURNER, 1960 from the coast of Brazil is the most similar in its depressed conical shape, but it differs in details of its spiral sculpture, the cords are more regular and all beaded and the basal cords are also beaded on the entire base as opposed to just the cords immediately bordering the umbilicus as in C. (E.) olssoni. Calliostoma (Elmerlinia) adelae SCHWENGEL, 1951 found off southeast Florida, has a far more elevated shell and again regularly beaded cords on the whorl sides and base.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Melajo Clay Member of Springvale Formation, Coubaril beds of Upper Morne l’Enfer Formation, Trinidad (MAURY, 1925a, JUNG, 1969).

Calliostoma (Elmerlinia) pascaleae LANDAU & SILVA, 2010
Pl. 1, Fig. 7; Pl. 2, Figs 1-3

2010a Calliostoma (Elmerlinia) pascaleae LANDAU & SILVA, p. 12, pl. 2, figs 1-3.

Dimensions and type material: Holotype NHMW 2010/0038/0004 (Pl. 1, Fig. 7; Pl. 2, Fig. 1), height 36.9 mm, maximum diameter 37.4 mm (NHMW coll., ex BL coll.); paratype 1 MOBR-M-3873 (Pl. 2, Fig. 2), height 37.8 mm, maximum diameter 39.1 mm (EDIMAR coll., ex BL coll.); paratype 2 NHMW 2010/0038/0005 (Pl. 2, Fig. 3), height 35.4 mm, maximum diameter 31.1 mm (NHMW coll., ex BL coll.); both from Cerro Colorado, 100m west of research station, Cubagua Island, Nueva Esparta State, Venezuela.

Etymology: For Pascale Paques, partner of the first author and great support in this work.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Stratum typicum: Araya Formation, Cubagua Group, Lower Pliocene.

Additional material: One specimen BL coll., Cañon de las Calderas; 15 specimens BL coll., Araya Formation, Cerro Colorado, Cubagua Island.

Diagnosis:
A large Calliostoma (Elmerlinia) species, with cancellate sculpture on the early teleoconch whorls, sculpture of narrow, elevated, strongly beaded spiral cords on later whorls, a depressed convex base bearing sharp-edged spiral ridges, which are not beaded, and a relatively wide, deep umbilicus delimited by a smooth cord.

Original description:
"Shell large for genus, fragile, broadly trochiform. Protoconch very small, of one whorl with medium-sized nucleus. Junction with teleoconch clearly delimited by scar and beginning of cancellate sculpture. Teleoconch of six whorls, with periphery at abapical suture. Suture clearly defined, linear, impressed. First three teleoconch whorls bearing about 25 narrow, strongly prosocline axial ribs and four narrow spiral cords, forming cancellate sculpture with rounded tubercles developed at intersections. Whorls strongly angled at third spiral cord; whorl profile straight above, concave below immediately adjacent to abapical suture. Axial sculpture weakens and disappears on fourth whorl; spiral cords narrow, elevated, prominently beaded, with secondary beaded cord in interspaces. Abapically, angulation prominent on early
teleoconch whorls, weakening adapically, spiral cords becoming more irregular, with intercalated cords of secondary and tertiary strength. Base depressed, weakly convex, with sharp to sharply-rounded edge; bearing 12 sharp-edged ridges, in some specimens very weakly beaded by axial growth lines. Aperture oblique, subquadrate, with relatively straight, basally truncate columella that meets lip at a distinctly obtuse angle; outer lip not thickened; columella callus very narrow. Umbilicus relatively wide, about 25% of maximum diameter of base, sharply delimited by spiral ridge, relatively deep, but not extending to apex, smooth within (LANDAU & SILVA, 2010a, p. 12)."

Discussion:
Although the best-preserved specimen of this Calliostoma species was found in the Cañon de las Calderas, it is far more common in the Cerro Colorado exposure near the Fundación La Salle research station. It belongs to the same group of Calliostoma species as Calliostoma (Elmerlinia) olssoni MAURY, 1925, with broad shells, strong beaded sculpture throughout and a deep, wide umbilicus, not closed by columellar callus. It differs from C. (E.) olssoni in being much larger, in having a less depressed shell, more prominent spiral beading and the umbilicus is narrower and far shallower, extending apically probably only a quarter of the height of the shell.

The shells of Calliostoma (Elmerlinia) plicomphalus (GUPPY, 1867) from the Pleistocene Matura Shell Bed of Trinidad (NMB H 14578, 14579) also have an open umbilicus. They are much smaller than our Cubagua specimens, but judging from the figures given by MAURY (1925a, pl. 43, figs 11, 13, 15) and JUNG (1969, pl. 41, figs 19, 21) are indistinguishable from C. (E.) pascaleae LANDAU & SILVA, 2010 from the dorsal aspect and sculpture. However, when viewed laterally and ventrally, the umbilicus in the shell of C. (E.) pascaleae is much shallower and is bordered by a smooth cord, whereas the umbilicus in C. (E.) plicomphalus is bordered by a beaded cord, clearly described by MAURY (1925a). Similarly, the rest of the spiral cords in Jung’s figures are more strongly beaded than in the new species.

The shells of Calliostoma (Elmerlinia) eremum WOODRING, 1957 from the Upper Miocene Gatun Formation of Panama are very similar to the ones of our new species, but are smaller. There are only three primary cords on the first teleoconch whorl as opposed to four in C. (E.) pascaleae and the sculpture consists mainly of cords of equal strength rather than of primary to tertiary strength as in the specimens of the new species. The shell illustrated by WOODRING (1957a, pl. 22, figs 3-5) is incomplete, but seems to have a narrower apical angle and the base is less flattened. The shells of Calliostoma (Elmerlinia) mancinella OLSSON, 1922 from the Upper Pliocene Banano Formation of Costa Rica are again smaller and much more depressed. Calliostoma grabaui MAURY, 1917 from the Lower Pliocene Gurabo Formation of the Dominican Republic is again much smaller and higher spired. It does not belong within the subgenus Elmerlinia as the base is its shell is imperforate.

In the Recent faunas several representatives of the subgenus occur in Tropical Eastern American waters (see CLENCH & TURNER, 1960). The most closely similar of these is C. (Elmerlinia) bullisi CLENCH & TURNER, 1960, described from Brazilian waters, but also occurring in the waters around Isla Margarita (MACSOTAY & CAMPOS, 2001). Again it differs from C. (E.) pascaleae in having a beaded cord delimiting the umbilicus and beaded cords on the base. Calliostoma (E.) bullisi is very similar to C. (E.) plicomphalus, but seems to have a more depressed shell, with a wider apical angle, and the base is flatter. Nevertheless, the two are very similar and more material is needed to assess the range of variability of the two taxa.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Calliostoma (Elmerlinia) macsotayi LANDAU & SILVA, 2010
Pl. 2, Fig. 4

2010a Calliostoma (Elmerlinia) macsotayi LANDAU & SILVA, p. 13, pl. 2, fig. 4.

Dimensions and type material: Holotype NHMW 2010/0038/0006 (Pl. 2, Fig. 4), height 16.2 mm, maximum diameter 17.6 mm (NHMW coll., ex BL coll.).

Etymology: Named after Oliver Macsotay, dedicated Venezuelan Geologist and great help in this project.
**Type locality:** Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

**Stratum typicum:** Araya Formation, Cubagua Group, Lower Pliocene.

**Diagnosis:**
A *Calliostoma (Elmerlinia)* species with a small to medium-sized, regularly conical shell, with cancellate sculpture on the early teleoconch whorls, a sculpture of six regularly beaded spiral cords on later whorls, with secondary cords intercalated on last whorl, a depressed weakly convex base bearing smooth spiral cords, and a wide, deep umbilicus extending to apex, delimited by a very weakly beaded cord.

**Original description:**
"Shell small to medium-sized for genus, relatively robust, regularly conical, elevated, trochiform. Protoconch missing. Teleoconch of six flat-sided whorls, with periphery at abapical suture. Suture superficial. First three teleoconch whorls bearing weakly developed, strongly prosocline axial ribs and three narrow spiral cords, forming a cancellate sculpture with rounded tubercles developed at intersections. Axial sculpture weakens and disappears on fourth whorl; spiral cords become more numerous, six on fourth whorl, finely beaded, subsutural cord slightly more strongly developed, cords below subequal in strength. Secondary spiral cords only appear in interspaces on last whorl. Very fine, strongly prosocline growth lines cover entire shell surface. Base depressed, weakly convex, bearing 12 cords, very weakly beaded near umbilicus, ridge-like towards periphery. Aperture oblique, subquadrates, with a relatively straight, basally truncate columella that meets lip at a distinctly obtuse angle; outer lip not thickened; columella callus very narrow. Umbilicus relatively narrow, about 20% of maximum diameter of base, sharply delimited by a concentric ridge, very deep, extending to apex, smooth within (LANDAU & SILVA, 2010a, p. 13)."

**Discussion:**
*Calliostoma (Elmerlinia) macsotayi* LANDAU & SILVA, 2010 is the most elevated shell of all the Araya Formation *Calliostoma (Elmerlinia)* species and cannot be confused with any of its congeners in the Pliocene Venezuelan deposits. It is most similar to *C. (E.) plicomphalus* (GUPPY, 1867) discussed above, but this has an umbilicus with a more acutely angled edge which is delimited by a strongly and coarsely beaded cord. The umbilical edge in *C. (E.) macsotayi* is more rounded and the delimiting cord hardly beaded. *Calliostoma (Elmerlinia) eremum* WOODRING, 1957 from the Upper Miocene middle Gatun Formation of Panama has more convex whorls, a wider umbilicus, a strongly beaded base and the suture is impressed, almost canaliculate. The suture in *C. (E.) macsotayi* is quite difficult to observe. *Calliostoma (Elmerlinia) mancinella* OLSSON, 1922 from the Upper Pliocene Banano Formation of Costa Rica has a more depressed shape, a more rounded last whorl and a less depressed base.

Compared with the living species, *C. (E.) macsotayi* is not unlike *Calliostoma (Elmerlinia) adelae* SCHWENGEL, 1951 found off southeast Florida, but *C. (E.) adelae* has a more acutely angled base and the basal cords are all beaded.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Family Turbinidae RAINEQUE, 1815
Subfamily Turbininae RAINEQUE, 1815
Genus *Turbo* LINNAEUS, 1758.

Type species *Turbo petholatus* LINNAEUS, 1758, by subsequent designation, MONTFORT, 1810.

Subgenus *Senectus* SWAINSON, 1840.

Type species *Turbo spenglerianus* GMELIN, 1791 [= *T. canaliculatus* HERMANN, 1781], by subsequent designation. WILLIAMS (2008) pointed out that there was an earlier type designation for the genus *Senectus* SWAINSON, 1840 than HERRMANNSEN (1848), by GRAY (1847), for *T. spenglerianus* [= *T. canaliculatus* HERMANN, 1781]. However, the type species must remain *T. spenglerianus* and not *T. canaliculatus* as stated by WILLIAMS (2008, p. 10), as the synonymy is subjective.

WILLIAMS et al. (2008) redefined the families Trochidae and Turbinidae, which together with Solariellidae POWELL, 1951, Calliostomatidae THIELE, 1924 and Liotiidae GRAY, 1850 make up the superfamily Trochoidea.
Material and dimensions: Maximum height 51.2 mm; one specimen, Lower Pliocene, Araya Formation
Cañon de las Calderas; two specimens, Lower Pliocene, Araya Formation Cerro Colorado (EDIMAR coll.); two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado Cubagua Island; 10 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:

Gmelin (1791) used the Latin word “castanea” (chestnut) as the specific name T. castanea. “Castanea” is a noun, therefore it should not be declined (castaneus, a, um; derived from chestnut).

The taxonomic status of the ‘Turbo castanea’ group is confused. Abbott (1974) considered T. crenulatus Gmelin, 1791 (sp. 29; p. 3595) junior to T. castanea Gmelin, 1791 (sp. 28; same page). Gmelin (1791, p. 3595) based Turbo castanea on Chemnitz (1781, p. 182, figs. 1807-08) and based T. crenulatus on Chemnitz (1781, p. 182, f. 1811-12) in the same work. Since then T. crenulatus has been regarded as a separate species by some (Cáceres & Flores, 1981; Petuch, 1994); a subspecies of T. castanea (Mansfield, 1930; Nowell-Usticke, 1959) or the two forms synonymised with intergrading forms (Woodring, 1957a; Abbott, 1974; Macsotay & Campos, 2001, Alf & Kriep, 2003). These specimens all appear to fall into the range of variation of T. castanea (Harry Lee pers. comm. 2005). Williams (2008) suggested T. castanea may represent a species group, but that this needed confirmation. In Cubagua both the “castanea” (Pl. 2, Fig. 5) and “crenulatus” (Pl. 2, Fig. 6) morphotypes are found and they are provisionally considered to belong to a single species: Turbo (Senectus) castanea.

Turbo crenulatoides Maury, 1917 (Pl. 2, Fig. 7) from the Upper Miocene Cercado Formation of the Dominican Republic was said to differ from T. crenulatus [= T. castanea] in having strongly squamous sculpture covering the entire surface (Maury, 1917). Woodring (1957a, p. 65) already doubted if this form could be separated from strongly lamellar Recent forms. I have collected strongly squamous ‘T. crenulatoides’ from both the Upper Miocene Cercado and Lower Pliocene Gurabo Formations, Dominican Republic together with the more typical T. castanea, which is also found in the stratigraphically older Lower Miocene Baitoa Formation. There are intermediate forms and I agree that they represent a single species with somewhat variable sculpture, pending resolution of the problems discussed above. The shell described as Turbo (Marmorostoma [sic]) crenulatus venezuelensis by Weisbord (1962, p. 87, pl. 6, figs 8-9; hoc opus Pl. 2, Fig. 8) from the Pleistocene Playa Grande Formation of Venezuela fits perfectly within the range of variability of the “crenulatus” morphotype and is here considered a junior subjective synonym of T. (S.) castanea.

Geological and geographical distribution:

Lower Miocene: Baitoa Formation, Dominican Republic (BL coll.).
Upper Miocene: middle Gatun Formation, Panama (Woodring, 1957a); Cercado Formation, Dominican Republic (Maury, 1917); Mataruca Member of Caujaaro Formation, El Carrizal, Venezuela (NMB 2927/2, 2941).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Cerro Barrigón, Araya Peninsula, Venezuela; Punta Gaviñan Formation, Falcón, Venezuela (Rutsch, 1934); Chagres Limestone, Panama (Woodring, 1957a); Gurabo Formation, Dominican Republic (Maury, 1917).
Upper Pliocene: Pncenest Beds, Florida (as Turbo (Marmorostoma) castaneus ayersi, Olsson, 1967a; Petuch, 1994; Bird Road Quarry Middle Pliocene fide Lyons, 1991, p. 176).
Lower-Upper Pliocene: Bowden Formation, Jamaica (Woodring, 1928 as Turbo (Senectus) species, p. 411).
Lower Pleistocene: Caloosahatchee Formation, Florida (Petuch, 1994); Duplin Marl (Mansfield, 1930); Moin Formation, Puerto Limon, Costa Rica (Robinson, 1991).
Lower-Upper Pleistocene: Bermont Formation, Florida (Petuch, 1994); Maiquetia Member of the Playa Grande Formation, Venezuela (Weisbord, 1962).
Upper Pleistocene: Fort Thompson Formation, Florida (Petuch, 1994).
Recent: Cape Hatteras, North Carolina southwards to Mucuripe, Brazil, Caribbean (Macsotay & Campos, 2001).

Genus Lithopoma Gray, 1850.
Type species Trochus tuber Linnaeus, 1758, by monotypy.
Lithopoma brevispinum (Lamarck, 1822)
Pl. 2, Fig. 9

1822  Trochus brevispinus Lamarck, 1822, p. 12.
1850  Trochus auripigmentum Philippi, p. 147.
1861  Trochus auripigmentum Jonas – Reevé, no. 39, pl. 8, fig. 39.
1922  Astralium brevispinum var. basilis Olsson, p. 162 (334), pl. 15 (18), figs 4-5.
1928  Astraea (Astralium) brevispinus basilis [sic] (Olsson) – Woodring, p. 413, pl. 33, figs 4-6.
1962  Astraea (Lithopoma)? differentia Weisbord, p. 98, pl. 7, figs 3-4.
1973  Astraea brevispinosa – Morris, p. 124, pl. 38, fig. 19.
1973  Astraea brevispinosa Lamarck – Princz, pl. 1, fig. 1.
1991  Astralium brevispinum (Lamarck, 1822) – Robinson, p. 114, pl. 2, fig. 12.
1994  Astraea (Astralium) basilis [sic] (Olsson, 1922) – Petuch, pl. 4, fig. E.
1994  Astraea brevispinosa (Lamarck, 1822) – Díaz & Puyana, p. 121, fig. 385.
2001  Astraea (Astralium) phoebea (Röding, 1798) – Macsotay & Campos, p. 35 (non Röding, 1798).
2010a  Lithopoma brevispinum (Lamarck, 1822) – Landau & Silva, p. 15, pl. 2, fig. 9.

Material and dimensions: Maximum height 34.2 mm, five specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; four specimens BL coll. (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
Williams (2007) and Williams et al. (2008) showed that based on molecular data all Caribbean specific taxa, previously assigned to Astraea or Astralium, should be referred to Lithopoma. Astralium Woodring, 1928 is an exclusively Indo-Pacific genus and Astraea is limited to New Zealand.

The Recent Lithopoma phoebea (Röding, 1798) [= L. longispinum Lamarck, 1822], which occurs in southeast Florida and the West Indies is similar, but L. brevispinum has a blotch of bright orange-red colour around the umbilical region and a distinct geographic distribution (Abbott, 1974). Macsotay & Campos (2001) synonymized L. phoebea with L. brevispinum, however, most authors maintain the two taxa distinct (Abbott, 1974; Jong & Coomans, 1988; Robinson, 1991; Redfern, 2001). Astralium brevispinum var. basilis Olsson, 1922 (holotype Pl. 2, Fig. 10) was based on a fossil specimen from the Plio-Pleistocene of Costa Rica (exact locality unknown), with a somewhat heavier basal sculpture. However, this falls within the range of sculptural variability seen in fossil and Recent specimens. Astraea (Lithopoma)? differentia Weisbord, 1962 (holotype Pl. 2, Fig. 11) was erected based on a small very worn shell from the Lower Pleistocene Mare Formation of Venezuela, which is probably conspecific with L. brevispinum, although it is too abraded to be identified certainly.

Geological and geographical distribution:
Upper Miocene: Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (NMB 2926).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.
Lower-Upper Pliocene: Pinecrest Beds, Florida (as Astraea (Astralium) basilis [sic], unit 7 fide Petuch, 1994); Bowden Formation, Jamaica (Woodring, 1928).
Lower Pleistocene: Moin Formation, Puerto Limon, Costa Rica (Robinson, 1991); Mare Formation, Cabo Blanco, Venezuela (Weisbord, 1962, as Astraea (Lithopoma)? differentia).
Lower Pleistocene: La Isabella Formation, Dominican Republic (BL coll.); Tortuga Formation, Cubagua Island, Venezuela (BL coll.).

Clade     Sorbeoconcha
Superfamily    Cerithioidea Fleming, 1822
**Family** Modulidae P. FISCHER, 1884  
**Genus** Modulus GRAY, 1842.  
**Type species** Trochus modulus LINNAEUS, 1758, by subsequent designation, J. E. GRAY, 1847.

*Modulus vermeiji* LANDAU & SILVA, 2010  
Pl. 3, Figs 1-3

**2010a** Modulus vermeiji LANDAU & SILVA, p. 16, pl. 3, figs 1-3.

**Dimensions and type material:** Holotype NHMW 2010/0038/0007 (Pl. 3, Fig. 1), height 15.5 mm, maximum diameter 14.0 mm (NHMW coll., ex BL coll.).

**Etymology:** After Geerat J. Vermeij for his enormous help preparing this monograph.

**Type locality:** Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

**Stratum typicum:** Araya Formation, Cubagua Group, Lower Pliocene.

**Additional material:** Two specimens NHMW 2010/0038/0179 and NHMW 2010/0038/0180 (Pl. 3, Figs 2-3), Carrizal cemetery, Falcón State, Upper Miocene, Mataruca Member, Caujarao Formation, Venezuela (NHMW coll., ex BL coll.).

**Diagnosis:**

A *Modulus* species with a medium-sized biconical shell, with four spiral cords on spire whorls, the abapical cord far more strongly developed, a canaliculated suture, no axial sculpture apart from weak growth lines, base not depressed, bearing nine spiral cords, and with a sharp, strong columellar tooth.

**Original description:**

“Shell medium-sized for genus, trochiform, biconical. Teleoconch of six straight-sided whorls. Suture impressed, narrowly canaliculate. Protoconch and early teleoconch whorls abraded. Fourth and fifth whorls with four spiral cords, last whorl with five, abapical cord far more strongly developed forming periphery. Fine prosocline growth lines present, cutting slightly into peripheral cord giving it a weakly beaded appearance. Last whorl acutely angled at peripheral cord. Base not particularly depressed, bearing nine spiral cords of subequal strength. Umbilicus almost closed. Aperture subquadrate, outer lip sharp, angled at peripheral cord, strongly and deeply lirate within; anal canal not developed, siphonal canal open, very short, wide. Columella deeply excavated in mid-portion, with strong, sharp, sub-horizontal columellar tooth. Columellar callus hardly developed (LANDAU & SILVA, 2010a, p. 16).”

**Discussion:**

Our single specimen from the Cañon de las Calderas does not fit the description of the numerous *Modulus* species described from the Caribbean Neogene. *Modulus tamenensis* (MAURY, 1925) from the Middle Miocene Brasso Formation of Trinidad probably has the most similar shell. I examined six specimens in the Basel collections (NMB lot 1o434 [sic] from Caparo River) and observed that the shells of this species have a more elevated shell, which is less angular at the periphery, the abapical cord on the spire whorls is not more developed as in *M. vermeiji* LANDAU & SILVA, 2010. Moreover, In *M. tamenensis* there are six cords on the last whorl to the shoulder, the adapical two cords more developed, slightly more widely spaced as opposed to five in *M. vermeiji*.

The specimens of *Modulus willcoxi* DALL, 1892 from the Lower Miocene Chipola Formation of Florida have similar sculpture, but are taller spired, with a broader, less prominent carina. *Modulus basileus* (GUPTY, 1874) from the Pliocene Bowden Formation of Jamaica has similar strong spiral sculpture and the shell seems to display a certain degree of variability (WOODRING, 1928, p. 343), but most specimens have a coarsely tuberculate carina or axial sculpture not seen in *M. vermeiji* and a wider umbilicus. *Modulus basileus sensu* PETUCH, 1994 (non GUPTY, 1874) from the Plio-Pleistocene of Florida is another similar species, but with a smaller shell, with a more depressed spire composed of markedly concave whorls and weaker spiral sculpture.

Two shells of a second *Modulus* species were found by us in the Lower Pliocene Aramina Formation at Cerro Barribón, Araya Peninsula, probably representing a tall-spired form of Recent Caribbean *Modulus modulus* (LINNAEUS, 1758), which has a very variable shell profile, varying from quite
tall-spired to strongly flattened. This morphotype has not been found in the Lower Pliocene Araya Formation of Cubagua.

Compared with the Recent *Modulus carcedonius* (LAMARCK, 1822) from Long Key, Florida (ZMA Moll. 076761) the Recent species is squatter, the peripheral cord is less pronounced, but sharper, the spiral cords are less developed, the cords on the base tend to become narrower and more widely spaced towards the periphery and the last part of the last whorl has a tendency to uncoil. The shell of *M. vermeiji* is more similar in its biconical shape to the tropical American Pacific species *Modulus catenulatus* (PHILIPPI, 1849). However, specimens from the Gulf of California (ZMA Moll. 161863) differ from *M. vermeiji* in having more numerous cords above the abapical cord, which although stronger than the rest, is not as strongly developed as in the Pliocene Venezuelan species. In *M. catenulatus* the base is much more depressed and bears finer cords.

**Geological and geographical distribution:**

Upper Miocene: Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (NMB 2894, 3306 + unnumbered lot).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Family** Potamididae H. & A. ADAMS, 1854

**Genus** Potamides BRONGNIART, 1810

Type species *P. lamarcki* BRONGNIART, 1810, by monotypy.

*Potamides* sp.

Pl. 3, Figs 4-5

2010a *Potamides* sp. – LANDAU & SILVA, p. 17, pl. 3, figs 4-5.

**Material and dimensions:** Maximum height 28.4 mm, five specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:** The five specimens available to us are all broken and abraded shells, suggesting a marked degree of transport prior to burial. The whorls are relatively strongly coronate, with an infrasutural cord bearing ten rounded tubercles, below the infrasutural cord is a relatively broad groove followed by three close set cords bearing much weaker tubercles on early teleoconch whorls, the tubercles weakening abapically. The material available is very poor and these shells have been tentatively assigned to *Potamides* in the widest sense. This is one of a group of brackish water taxa found in Cubagua. All share in common the fact that the shells found in the outcrop are severely abraded and broken, suggesting a somewhat prolonged transport prior to burial, but also that a brackish environment lay nearby.

**Geological and geographical distribution:**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Genus** Terebralia SWAINSON, 1840.

Type species *Strombus palustris* LINNAEUS, 1758, by subsequent designation, SACCO, 1895.

*Terebralia dentilabris* (GABB, 1873)

Pl. 3, Figs 6-10

1873 Cerithium prismaticum GABB, p. 236
1873 Cerithium dentilabre GABB, p. 237.
1922 *Potamides prismaticus* (GABB) – PILSBRY, p. 373, pl. 29, fig. 12.
1922 *Potamides dentilabris* (GABB) – PILSBRY, p. 374, pl. 29, figs 6-7.
1922 *Potamides gastrodon* PILSBRY, p. 374, pl. 32, figs 5-6.
1929 *Potamides* (Pyrazisinus) bolivarenensis WEISBORD, p. 271, pl. 8, fig. 5.
1933 *Terebralia dentilabris* (GABB) – PILSBRY & HARBISON, p. 115.
1959a  *Terebralia dentilabris* (GABB) – WOODRING, p. 178.

2010a  *Terebralia dentilabris* (GABB, 1873) – LANDAU & SILVA, p. 17, pl. 3, figs 6-10.

*non* 1972  *Terebralia dentilabris* (GABB) – HOERLE, p. 20, pl. 1, figs 9-11 [ = *Terebralia harrisi Maury*, 1902].

**Material and dimensions:** One fragment BL coll., 30.5 mm height, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

*Cerithium dentilabre* GABB, 1873 was described from the Dominican Neogene without specifying the locality. Gabb's specimen illustrated by PILSBY (1922, pl. 29, figs 6-7) has an abraded shell, but with surface sculpture clearly preserved, consisting of distinct spiral cords with a slightly stronger and more widely spaced infrasutural cord, a bifid denticle within the outer lip and a single sharp fold on the columella. I have found several specimens just like this in the Lopez Section of the Rio Yaque del Norte (see SAUNDERS et al., p. 24, text-fig. 23), but never a well-preserved shell. GABB (1873) described a second species from the Dominican deposits, *Cerithium prismaticum*, also later figured by PILSBY (1922, pl. 29, fig. 12) distinguished by "having short heavy ribs or nodes, and a deep square-cut groove below the suture" (PILSBY, 1922, p. 373). This is part of the variation of *C. dentilabre* and as first revisers (ICNZ, Art. 24.2), LANDAU & SILVA (2010a) selected the name *Terebralia dentilabris* (GABB, 1873) as the valid one for the species.

Downstream from the Angostura Gorge, however, are deposits of an unnamed Formation, probably of the same age as the Upper Miocene Cercado or Lower Pliocene Gurabo Formations (Emily Vokes pers. comm. 2008), whose assemblage of gastropods suggests a brackish environment. In these deposits a growth series was found, starting with juvenile shells, indistinguishable from those described by Gabb as *C. dentilabre*, to adult shells with a hugely developed outer lip (Pl. 3, Figs 6-8). Figure 7a shows an intermediate growth stage, with the typical early teleoconch whorl sculpture described above and later whorl sculpture changing to broad, elevated, axially elongated tubercles and a weakening of the spiral sculpture, with only the infrasutural cord well developed, as in Gabb's *C. prismaticum*. However, within the aperture the bifid denticle within the outer lip and columella fold can clearly be seen (Fig. 7b). Figure 8 represents a fully adult shell with the outer lip effusely expanded, completely encircling the aperture and leaving the anterior canal as a hole, and a deep sinus on the adapical portion of the outer lip.

One very poorly preserved fragment which LANDAU & SILVA (2010a) ascribed to *Terebralia dentilabris* was found in the Cañon de las Calderas deposits. The shell (Fig. 9) illustrates the typical sculpture seen on the early teleoconch whorls of the Dominican specimens. The back of this shell is missing and a sharp columellar fold is present.

At first sight the ventrolateral varix, enormously expanded lip and closed anterior canal of these specimens recall the shells of *Pyrazisinus* HEILPRIN, 1887, which are most common in the the Miocene to Pleistocene of Florida (PETUCH, 2004) and also occur in the Oligocene to Miocene of Europe (LESPORT & CAHUZAC, 2002). Nevertheless, these features appear to be convergent, because *Pyrazisinus* has recently been transferred to the Batillariidae (OZAWA et al., 2009). A living *Terebralia* having a shell with a similarly expanded aperture and closed canal is *T. sulcata* (BORN, 1778) from the western Pacific. *Terebralia* is characterised by scattered varices on the spire (each with internal teeth), a fold on the columella, and a twisted anterior canal (typical of Potamididae) (PILSBY & HARBISON, 1933; WOODRING, 1959; REID et al., 2008). *Pyrazisinus* has finer spiral sculpture and no varices on the spire, no internal teeth, a straight columella without a fold, and the anterior canal is not twisted (OZAWA et al., 2009). *Terebralia* species were widely distributed in the Cenozoic, but today are confined to the Indo-West Pacific (HOUBRICK, 1991). LANDAU & SILVA (2010a) followed REID et al. (2008, p. 691) in placing *Cerithium dentilabre* in the genus *Terebralia* rather than *Pyrazisinus*.

HOERLE (1972, pl. 1, figs 9-11) illustrated a similar growth series of specimens identified as *T. dentilabris* from the Lower Miocene Chipola Formation of Florida. The sculpture seems different from the Dominican specimens at hand; the axial ribs are less prominent and more close-set, and where the spiral
cords overrun the axial elements stronger tubercles are developed than in our Dominican shells. The difference in the sculpture between the Chipola and Dominican specimens becomes more accentuated as the shell matures, so that on the last whorl in the Dominican specimens the sculpture becomes less distinct and very strong elevated tubercles develop at the periphery (Pl. 3, Fig. 8). In contrast the sculpture on the last whorl in the Chipola shell consists of rows of beads and there are no tubercles at the periphery. Moreover, the Dominican shells attain a larger fully adult size, in excess of 80 mm, whereas the largest Chipola shell illustrated by HOERLE (1972) is 53.7 mm. I have four adult specimens from locality TU547 on the Chipola River (BL coll.), which correspond well with the shells illustrated by HOERLE (1992); maximum size 57.0 mm. The Chipola shells were first described by MAURY (1902) as *Pyrazisinus harrisi* (p. 376, pl. 28, fig. 2), therefore the name *Terebralia harrisi* (MAURY, 1902) is available.

*Potamides (Pyrazisinus) bolivarensis* WEISBORD, 1929 (holotype Pl. 3, Fig. 10) was described based on a single incomplete shell from the ?Miocene of Colombia. The sculpture is identical to that seen in our fragment from Cubagua, and LANDAU & SILVA (2010a) considered this taxon a junior subjective synonym of *T. dentilabris*.

**Geological and geographical distribution:**

?!Lower Miocene: Culebra Formation, Panama (WOODRING, 1959).
?!Middle Miocene: unnamed formation, Colombia (WEISBORD, 1929).

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; unnamed formation, Dominican Republic (PILSBRY, 1922).

**Material and dimensions:** Two fragments BL coll., maximum height 27.2 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
Two fragments consisting of part of the last whorl and two preceding whorls are available. The specimen probably belongs within the genus *Terebralia* SWAINSON, 1840. It has eight strong tubercles midwhorl on the last two whorls, more numerous axial ribs on the preceding whorl. It is possible that these fragments represent the later adult whorls of *Terebralia dentilabris* (GABB, 1873) (see above), but the whorls are more compressed and the tubercles more pointed and restricted to midwhorl rather than elongated as in *T. dentilabris*.

Both of the *Terebralia* species and the ‘Potamides’ species are typical of mangrove or brackish habitat, which may have been present nearby. Although relatively robust shells, all are broken and worn, which suggest a considerable degree of transport.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Family** Turritellidae LOVEN, 1847
**Subfamily** Turritellinae LOVEN, 1847
**Genus** *Turritella* LAMARCK, 1799

Type species *Turbo terebra* LINNAEUS, 1758, by monotypy.

Quantitatively the turritellids form an extremely important part of the Cubagua assemblage. Agglomerations of hundreds of specimens are common in the Cañon de Las Calderas Lower Pliocene outcrops. In the Recent faunas the geographic and seasonal patterns of living turritelline species are associated with coastal upwelling, by reduced shallow-water temperatures and increased abundance of phytoplankton (ALLMON, 1988). Moreover, in the Pleistocene to Recent faunas the presence of turritelline species with large shells with broad whorls is further associated with the intensity of the upwelling. The
increase in the amount of shell material secreted may be explained by increased availability of food associated with stronger upwelling (TEUSCH et al., 2002). Therefore, large quantities of turritellids found in Cubagua, their diversity and the presence of large-shelled species all suggest upwelling in the area in Pliocene times.

Subgenus  
Broderiptella OLSSON, 1964  
Type species Turritella broderipiana D’ORBIGNY, 1840, by original designation.

Turritella (Broderiptella) bifastigata cartagenensis PILSBRY & BROWN, 1917  
Pl. 3, Fig. 12

1917  
Turritella cartagenensis PILSBRY & BROWN, p. 34, pl. 9, figs 1-2.

1925a  
Turritella cartagenensis PILSBRY & BROWN – MAURY, p. 233, pl. 42, fig. 13.

1926  
Turritella bifastigata var. maracaiensis F. HODSON, p. 48, pl. 30, figs 2, 4, 6.

1926  
Turritella bifastigata var. democraciana F. HODSON, p. 50, pl. 30, figs 3, 5.

1929  
Turritella cartagenensis BROWN & PILSBRY [sic] – WEISBORD, p. 266, pl. 8, fig. 1.

1941  
Turritella cf. cartagenensis PILSBRY & BROWN – MERRIAM, p. 207, pl. 38, fig. 9.

1960  
Turritella cartagenensis BROWN & PILSBRY [sic] – BARRIOS, p. 266, pl. 8, fig. 1.

1969  
Turritella (Broderiptella) bifastigata cartagenensis PILSBRY & BROWN – JUNG, p. 436, pl. 44, figs 1-4.

1971  
Turritella bifastigata cartagenensis PILSBRY & BROWN (1917) – MACSOTAY, p. 44, pl. 1, fig. 24.

2010a  
Turritella (Broderiptella) bifastigata cartagenensis PILSBRY & BROWN, 1917 – LANDAU & SILVA, p. 19, pl. 3, fig. 12.

Material and dimensions: Maximum height 113.7 mm, six specimens NMB lot DS 21; one specimen NMB lot DS 34; six specimens EDMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

The early teleoconch whorls of Turritella (Broderiptella) bifastigata NELSON, 1870 have a prominent single carina placed mid-whorl, which disappears on later whorls. OLSSON (1964) based the subgenus Broderiptella on this character, and considered it a wholly American genus represented today in the Caribbean by Turritella (Broderiptella) variegata (LINNAEUS, 1758) and in the western American coasts by Turritella (Broderiptella) broderipiana D’ORBIGNY, 1840 (type species) and Turritella (Broderiptella) gonostoma VALENCIENNES, 1832. The later whorls are sculptured by very fine spiral cords of irregular strength, about 17 per whorl, with a few spiral threads intercalated in some of the interspaces in the last two whorls. There is little intraspecific variation in the specimens at hand. Broderiptella OLSSON, 1964 may not have been strictly tropical American, and may have extended its range into the northwest Pacific during the Lower Miocene (TITOVA, 1983, 1994).

This species group is widespread in the Neogene Caribbean on both sides of the Panamanian Isthmus. Local assemblages have received several names based on relatively minor differences. However, the southern Caribbean Neogene specimens seem to be consistently different from the Pacific shells in having stronger spiral sculpture on the spire whorls, finer sculpture on the base and the whorl profile is less concave. This is clearly illustrated when our shells are compared with the lectotype of T. (B.) bifastigata illustrated by F. HODSON (1926, pl. 30, fig. 1). As pointed out by WOODRING (1957a) Hodson’s Turritella bifastigata var. maracaiensis (Text-Fig. 16, Figs 1-2) and Turritella bifastigata var. democraciana (Text-Fig. 16, Figs 3-4) fall within the variability of T. (B.) bifastigata cartagenensis. This was reaffirmed by morphometric analysis (MACSOTAY & SCHERER, 1972). Our shells from Cubagua are indistinguishable from those illustrated by JUNG (1969, pl. 44, figs 1-4) from coeval beds in Trinidad.

MACSOTAY (1971) suggested a post-Eocene zonation of the Caribbean Neogene on the basis of Turritella species. He considered Turritella bifastigata cartagenensis to be a characteristic subspecies in the southern Caribbean Pliocene assemblages, a position supported by its presence in the Araya Formation at Cubagua.
Text-Figure 16. F. Hodson’s (1926) Turritella types.
Figs 1-2. Turritella bifastigata var. maracaibensis F. Hodson, 1926, holotype PRI 21591, height 60.6 mm, La Vuelta, Falcón, Venezuela, Middle-Upper Miocene. Figs 3-4. Turritella bifastigata var. democraciana F. Hodson, 1926, holotype PRI 21588, height 48.1 mm, Urumaco, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Fig. 5. Turritella guppyi morantensis F. Hodson, 1926, holotype PRI 21565, height 61.1 mm, Bowden, St. Thomas in the East Parish, Jamaica, Bowden Formation, Pliocene. Fig. 6. Turritella guppyi morantensis F. Hodson, 1926, paratype PRI 21580, height 62.3 mm, Bowden, St. Thomas in the East Parish, Jamaica, Bowden Formation, Pliocene. Fig. 7. Turritella robusta fredeai F. Hodson, 1926, holotype PRI 21405, height 107.3 mm, Rio Codore, Urumaco, Venezuela, Upper Miocene. Images courtesy of the Paleontological Research Institution.

Geological and geographical distribution: Atlantic
Upper Miocene: Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (NMB 2940) (F. Hodson, 1926), Urumaco Formation, Venezuela (NMB lot 2253-5); Usiacuri Formation, Colombia (Anderson, 1929; Weibord, 1929; Barrios, 1960); Lower Gatun Formation, Panama (Woodring, 1957a).
Upper Miocene/Lower Pliocene: Cartagena, Colombia (Brown & Pilsbry, 1917).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Melajo Clay Member of Springvale Formation, Coubaril beds of Upper Morne l’Enfer Formation, Trinidad (Maury, 1925a; Jung, 1969); Tuberá Group, northern Colombia (NMB lot 1634/2).

Turritella (Broderiptella) caronensis Mansfield, 1925
Pl. 4, Fig. 1

1925a Turritella gatunensis Conrad – Maury, p. 229, pl. 42, fig. 12 non Conrad, 1857
1925 Turritella gatunensis caronensis Mansfield, p. 51, pl. 8, figs 12-14.
1926 Turritella willistoni F. Hodson, p. 195, pl. 18, figs 2-4, 8.
2010a Turritella (Broderiptella) caronensis Mansfield, 1925 – Landau & Silva, p. 20, pl. 4, fig. 1.

Material and dimensions: Maximum height 50.0 mm, three specimens NMB lot DS 22/1; five specimens NMB lot DS 22/2; 19 specimens BL coll., Lower Pliocene, Araya Formation Canion de las Calderas; one
specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**

The first teleoconch whorl sculpture starts with a medial carina, a character of the subgenus *Broderiptella*, followed a quarter-whorl later by a second cord just above the abapical suture. The two cords are of equal strength by the second teleoconch whorl, after which the abapical cord becomes more prominent, with secondary cords present from the second whorl. The basal carina is prominent from about the third or fourth whorl. Sculpture on intermediate whorls consists of five subequal cords above the carina, one, later two below. The last two whorls are more rounded at the carina, with one or two spiral threads in the interspaces above the carina and three primary cords below. There is a little intraspecific variation in the material present, mainly regarding the strength of the cords above the carina and the presence or absence of spiral threads in the interspaces on the last whorls. The penultimate and last whorls are angular to rounded.

*Turritella (Broderiptella) caronensis* Mansfield, 1925 differs from *Turritella (Broderiptella) gatunensis* Conrad, 1857 from the Middle-Upper Miocene Gatun Formation of Panama in having the early teleoconch whorls less attenuated, but weakly carinate, whereas the later whorls are less strongly carinate than in *T. (B.) gatunensis*. Moreover, the two primary spiral cords on the adult whorls are less strongly developed than in *T. (B.) gatunensis*. *Turritella willistoni* F. Hodson, 1926 was considered a junior subjective synonym of *T. (B.) caronensis* by Macsotay & Scherer (1972). It has one or two spiral cords mid-whorl more strongly developed (clearly illustrated in the original figures F. Hodson, 1926, figs 2-4; fig. 8 has mid-whorl cords of intermediate strength). This strengthening of the cords mid-whorl is not seen in any of the Cubagua shells.

*Turritella lloydsmithi* Pilsbry & Brown, 1917 from the Late Miocene-Early Pliocene of Colombia is a much larger species (five whorls preserved, height 64.6 mm; Pilsbry & Brown, 1917, p. 35), with more crowded spirals separated by narrow grooves. *Turritella (Broderiptella) maiquetiana* Weisbord, 1962 from the Mare Formation of the Cabo Blanco Area of Venezuela has a rounded periphery on the late adult whorls, as opposed to angulated in *T. (B.) caronensis*, and the central carina persists much longer on the early teleoconch whorls (see Weisbord, 1962, pl. 11, figs 13-14).

**Geological and geographical distribution: Atlantic**

Upper Miocene: Urumaco Formation, Venezuela (F. Hodson, 1926; Macsotay & Scherer, 1972). Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; La Vela Formation, Manzanilla Formation, Venezuela (F. Hodson, 1926; Macsotay & Scherer, 1972), Springvale Formation, Trinidad (Maury, 1925a; Mansfield, 1925); Tuberá Group (NMB localities 5227, 5229), northern Colombia.

**Turritella (Broderiptella) planigyrata** Guppy, 1867

Pl. 4, Figs 2-3

1867 *Turritella planigyrata* Guppy, p. 156.
1874 *Turritella planigyrata* Guppy – Guppy, p. 437, pl. 18, fig. 5.
1925a *Turritella planigyrata* Guppy – Maury, p. 232, pl. 42, figs 6-8.
1925 *Turritella planigyrata* Guppy – Mansfield, p. 55, pl. 9, figs 1, 9.
1926 *Turritella planigyrata* Guppy – F. Hodson, p. 29, pl. 19, figs 2, 9.
1942 *Turritella planigyrata* Guppy – Rutsch, p. 131, pl. 8, fig. 5.
1971 *Turritella planigyrata* Guppy (1867) – Macsotay, p. 39, pl. 1, fig. 21.
2010a *Turritella (Broderiptella) planigyrata* Guppy, 1867 – Landau & Silva, p. 20, pl. 4, figs 2-3.

*non* 1917 *Turritella planigyrata* Guppy – Maury, p. 129, pl. 22, fig. 4 [=Turritella mauryae F. Hodson, 1926].

**Material and dimensions:** Height 64.7 mm, 23 specimens EDIMAR coll.; six specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; four specimens BL coll., Lower Pliocene, Araya
Formation Cerro Colorado, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
The first teleoconch whorl sculpture is not preserved in our material. The second teleoconch whorl starts with a prominent median carina and two cords below. On the third teleoconch whorl the abapical cord gains in strength and the central cord weakens. One secondary cord develops in each of the interspaces plus numerous tertiary spiral threads. On the intermediate whorls the carina and abapical cord weaken and the secondary and tertiary cords become crowded and unequal in strength. The last whorls have the carina and suprasutural cord still slightly stronger, two or three cords above the carina gain in strength, and the whole surface is covered by fine tertiary cords of irregular strength. Although the early whorls in all specimens are similar, there is some variability in the loss of the carina on later whorls with it persisting, although weakened in most specimens (Pl. 4, Fig. 2) to almost subobsolete (Pl. 4, Fig. 3).

_Turritella (Broderiptella) planigyrata_ Guppy, 1867 originally was described from Trinidad, where it occurs in the Lower Pliocene Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation (Jung, 1969). It differs from _Turritella (Broderiptella) mimetes_ Brown & Pilsbry, 1911 in having a wider apical angle and different sculpture on the second teleoconch whorl, when a third spiral appears at the lower suture. The median spiral of our Cubagua specimens is not more prominent than the others on the adult whorls, as in the specimens discussed by Jung (1969, p. 439) from the Melajo Clay. _Turritella (Broderiptella) maiquetiana_ Weisbord, 1962 from the Lower Pleistocene Mare Formation of the Cabo Blanco Area of Venezuela has a rounded periphery on the late adult whorls, as opposed to angulated or almost flat in _T. (B.) planigyrata_. The specimens illustrated by Maury (1917, pl. 22, fig. 4) as _Turritella planigyrata_ from the Dominican Republic correspond to a distinct species with weakly beaded spiral sculpture, and were renamed _T. mauryae_ F. Hodson, 1926.

_Geological and geographical distribution:_
Middle Miocene: Manzanilla Formation, Trinidad (Jung, 1969). Upper Miocene: Lagunillas, Mataruca and Taratara Members of the Caujarao Formation, lower part of Aramina Formation, Urumaco Formation, La Pica Formation, Venezuela (Macsotay, 1971). Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula Venezuela; Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (Guppy, 1867, 1874; Maury, 1925a; Mansfield, 1925; H. E. Vokes, 1938; Rutsch, 1942; Jung, 1969).

_Subgenus_ Bactrospira Cossmann, 1912
_Type species Turritella perattenuata_ Heilprin, 1887, by original designation.

_Turritella (Bactrospira) guppyi_ Cossmann, 1909
_Pl. 4, Fig. 4_

1909 _Turritella guppyi_ Cossmann, p. 225.
1926 _Turritella guppyi_ Cossmann – F. Hodson, pl. 27, fig. 1.
1926 _Turritella guppyi morantensis_ F. Hodson, p. 212, pl. 26, figs 3, 5, 6, 8, pl. 28, fig. 4.
1928 _Turritella guppyi_ Cossmann – Woodring, p. 349, pl. 26, figs 7-9.
1971 _Turritella guppyi_ Cossmann (1913 [sic]) – Macsotay, p. 43, pl. 1, fig. 23.
2010a _Turritella (Bactrospira) guppyi_ Cossmann, 1909 – Landau & Silva, p. 21, pl. 4, fig. 4.

_Material and dimensions:_ Maximum height 83.3 mm, nine specimens NMB lot DS 23; five specimens NMB lot DS 24/1, 2; three specimens NMB lot DS 9498/1, 2; seven specimens EDIMAR coll.; 11 specimens BL coll., Lower Pliocene, Araya Formation Cañón de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

_Discussion:_
The first teleoconch whorl is not preserved in our material. The second teleoconch whorl has two cords placed below and above the suture. On the intermediate whorls the cords are slightly beaded, and one
or two fine spiral threads appear in the middle. On the last whorls a secondary cord appears either side of
the adapical primary cord and a further secondary cord appears immediately above the abapical suture.
Further tertiary sculpture occurs between the two primary cords in most specimens. The spiral sculpture is
finely beaded by axial growth lines.

COSSMANN (1912) erected the subgenus Bactrospira as a section of Protoma Baird, 1870 (type
species Turritella cathedalis BROWNART, 1823, Miocene, Europe). However, the two are not related.
Turritella perattenuata HEILPRIN, 1887 from the Pliocene of Florida and the T. altilira-species group form
a Tropical American Neogene clade of closely related species making it preferable to follow OLSON
(1964) and recognise the subgenus Bactrospira rather than include them in the subgenus Torcula Gray,
1847 (type species Turbo exoletus, LINNAeus, 1758, Recent Caribbean) as done by WOODRING (1957a), as
the relationship of Turbo exoletus to T. perattenuata and T. altilira is less obvious.

Turritella (Bactrospira) guppyi is similar to Turritella (Bactrospira) altilira CONRAD, 1857 and its
varieties, which are common and widespread in the Caribbean Neogene, sharing the main sculptural
character of two prominent elevated spiral cords, with a strongly concave section in between, but differs in
having a less solid shell, less strongly beaded spiral cords, and a spiral thread on the infrasutural ramp
absent in T. (B.) altilira. WOODRING (1957a, p. 103) considered T. (B.) guppyi a subspecies of T. (B.)
altilira. The Cubagua material was compared with specimens of T. (B.) altilira from the Middle-Upper
Miocene Gatun Formation of Panama. Apart from the differences mentioned above, in the Cubagua shells
the suture is less deep, the sutural ramp straight to weakly concave rather than strongly concave, and the
adapical major cord is never doubled as is usual for the Gatun species. LANDAU & SILVA (2010a) therefore
maintained them as separate species. The type specimens of Turritella guppyi morantensis F. HODSON,
1926 (Text-Fig. 16, Figs 5-6) from the Pliocene Bowden Formation of Jamaica fall within the range of
variability for T. (B.) guppyi and this name is a junior subjective synonym.

The importance of the sequence of appearance of the primary cords in the classification of
Turritella species has been recognised by numerous authors (MARWICK, 1957a, b; MARTINELL, 1979).
According to WOODRING (1957a) the abapical primary cord appears first, the adapical only on the third
teleoconch whorl. Unfortunately, the apex is missing in all our material from Cubagua. However, in one
almost complete shell which has at least the second teleoconch whorl, both cords are present and of equal
strength. Specimens from the adjacent Caribbean Lower Pliocene Springvale Formation of Trinidad
(MAURY, 1925, as T. altilira var. tornata; MANSFIELD, 1925a, as T. altilira var. chiriquensis) and the
Tuberá Formation of Colombia (ANDERSON, 1929, as T. altilira) all have much stronger beaded cords and
are probably closer to true T. (B.) altilira. A full review of this group is beyond the scope of this work.

Turritella (Bactrospira) perattenuata HEILPRIN, 1887 from the Plio-Pleistocene of Florida is
another member of this group of species, but its shells differ from those of T. (B.) guppyi and the altilira
group in having even more attenuated whorls resulting in an even narrower apical angle. Specimens at hand
from the Lower Pleistocene Caloosahatchee Formation of Florida (BL col.) have an apical angle of about
5°, whereas T. (B.) guppyi from Cubagua has a somewhat wider apical angle of about 9°. The earliest
preserved whorls (probably second teleoconch whorl) in our Floridian shells also have two cords per whorl,
but the whorls are even more attenuated and narrow than in T. (B.) guppyi. Moreover, the carinæ,
especially the adapical carina, are less strongly developed in T. perattenuata. I note that in a statistical
analysis giving the shell characters a numerical description MACSOTAY & SCHERER (1972) considered T.
altilira guppyi a synonym of T. perattenuata. LANDAU & SILVA (2010a) preferred to maintain them as
distinct taxa.

Geological and geographical distribution:
Upper Miocene: Maturaca Member of Caujarao Formation, El Carrizal (NMB 2698), Venezuela.
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela;
Springvale Formation, Trinidad (RUTSCH, 1942); Tuberá Group (NMB lot 1635), northern Colombia.
Lower-Upper Pliocene: Bowden Formation, Jamaica (HODSON, 1926; WOODRING, 1928); Caiguire
Formation, Cumaná Area, Venezuela (F. HODSON, 1926).
**SYSTEMATIC PALAEONTOLOGY**

Subgenus unknown

*Turritella (?) abrupta* SPIEKER, 1922

Pl. 4, Figs 5-7

1899 *Turritella robusta* GRYZBOWSKI, p. 646, pl. 20, fig. 3 (*non T. robusta* GABB, 1864).

1922 *Turritella robusta var. abrupta* SPIEKER, p. 85, pl. 4, fig. 6.

1922 *Turritella charana* SPIEKER, p. 86, pl. 4, fig. 7.

1922 *Turritella robusta* GRYZBOWSKI—Woods in BOSWORTH, p. 110, pl. 18, fig. 4.

1925 *Turritella supraconcaeva* HANNA & ISRAELSKY, p. 59 (new name for *T. robusta* GRYZBOWSKI).

1925a *Turritella trinitaria* MAURY, p. 382, pl. 42, fig. 10.

1926 *Turritella robusta fredeai* F. HODSON, p. 13, pl. 5, figs 1, 3, pl. 6, figs 2, 5, pl. 7, figs 1, 6, 7, pl. 9, fig. 7, pl. 29, fig. 6.

1929 *Turritella fredeai* HODSON—ANDERSON, p. 119, pl. 17, fig. 1.

1929 *Turritella supraconcaeva var. fredeai* HODSON—WEISBORD, p. 262, pl. 9, figs 3-4.

1932 *Turritella abrupta* SPIEKER—LOEL & COREY, pl. 61, fig. 11, pl. 62, figs 2-3.

1938 *Turritella trinitaria* MAURY—H. E. VOKES, p. 26, fig. 29.

1941 *Turritella abrupta* SPIEKER—MERRIAM, p. 48, pl. 29, fig. 4, pl. 30, fig. 6, pl. 31, figs 2-4.

1957a *Turritella abrupta* SPIEKER—WOODRING, p. 106, pl. 23, figs 6, 15, 16.

1964 *Turritella (-) abrupta* SPIEKER—OLSSON, p. 190, pl. 35, fig. 1.

1971 *Turritella abrupta* SPIEKER (1922)—MACSOTAY, p. 36, pl. 1, fig. 20.

1972 *Turritella abrupta* SPIEKER—PERRILLIAT, p. 39, pl. 24, figs 3-5.

1972 *Turritella abrupta* SPIEKER, 1922—MACSOTAY & SCHERER, p. 1728, fig. 5 (1).

1993 *Turritella abrupta* SPIEKER—PITT & PI TT, p. 2, pl. 1, fig. 3.

2010a *Turritella (?) abrupta* SPIEKER, 1922—LANDAU & SILVA, p. 22, pl. 4, figs 5-6.

**Material and dimensions:** Maximum height 165.0 mm; one specimen NMB lot DS 20/1; six specimens NMB lot DS 20/2; six specimens EDIMAR coll.; seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; one specimen BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

This striking large *Turritella* species is found in the Neogene Caribbean on both sides of the Panamanian Isthmus. The oldest record for the species in the Pacific is in the Upper Miocene on both sides of the Isthmus, but so far has been found only on the Caribbean side in the Pliocene. There seems to be no satisfactory subgeneric group to assign this taxon to, and MACSOTAY & SCHERER (1972) in their statistical analysis of shell characteristics suggested that *T. abrupta* was not closely related to any of the other turritellids in the Neogene Caribbean, but may have evolved from *Broderiptella*.

OLSSON (1964, p. 191) commented that the Colombian and Venezuelan specimens had somewhat coarser spiral sculpture than those from the Miocene of Ecuador, and suggested the latter might be given subspecific status. The specimens from Cubagua certainly do have quite prominent spiral sculpture, but as may be seen in Plate 4, Figures 6-7, this can be somewhat variable. One specimen from the Middle-Upper Miocene Gatum Formation of Panama (BL. coll.) has spiral cords of similar strength to that seen in Olsson’s figures. Similarly, the strength of the spiral sculpture is variable in the series of specimens illustrated by F. HODSON (1926) as *Turritella robusta fredeai* (Text-Fig. 16, Fig. 7). WOODRING (1957a, p. 107) considered the specimens from the Lower Pliocene Springvale Formation of Trinidad as belonging to a separate subspecies with a weaker carina. However, the figure in H. E. VOKES (1938, fig. 29) is not significantly different from other Caribbean specimens of *T. abrupta*. Certainly H. E. VOKES (1938) used the name *T. trinitaria* as a synonym and replacement name for *T. robusta* GRYZBOWSKI, preoccupied by *T. robusta* GABB. LANDAU & SILVA (2010a) therefore considered these forms to constitute a single widespread variable species, possibly local assemblages showing some variation.

According to the palaeoprovince for the ‘Caribbean-Antillean’ region based on their turritellid assemblages proposed by MACSOTAY (1971), *T. abrupta*-zone ends at the end of the Lower Pliocene.
However, *T. abrupta* seems to have survived into the Upper Pliocene Agueguexquite Formation of Mexico (PERRILLIAT, 1972).

In the Pacific, this Central American tropical group migrated north as far as California, represented by a very similar species, *Turritella ocoyana* CONRAD, 1855, which differs in the development of the sculpture, the spiral cords developing earlier on the teleoconch whorls than in *T. abrupta* (WOODRING, 1957a).

**Geological and geographical distribution: Atlantic**

Lower Miocene: La Rosa and Socorro Formations, Venezuela (F. HODSON, 1926; MACSOTAY, 1971).

Upper Miocene: Mataruca Member of Caujarao Formation, El Carrizal (NMB 2940), Urumaco Formation (NMB lot 2253/1-4), Venezuela; Usiacuri Formation, Juan de Acosta, Colombia (WEISBORD, 1929); middle Gatun Formation, Panama (WOODRING, 1957a).

Upper Miocene/Lower Pliocene: Cartagena, Colombia (ANDERSON, 1929).

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation (NMB lot DS 5655), Venezuela; Springvale Formation, Trinidad (MAURY, 1925a; H. E. VOKES, 1938); Tuberá Group (NMB lot 1632 1/4), northern Colombia.

Lower Pliocene: Agueguexquite Formation, Mexico (PERRILLIAT, 1972).

**Geological and geographical distribution: Pacific**

Middle Miocene: Cardalitos Formation, Peru (MARKS, 1951); Progreso Formation, Ecuador (OLSSON, 1964), Zorritos Formation, Peru (GRYZBOWSKI, 1899; SPIEKER, 1922).

Upper Miocene: Chucunaque Formation (NMB localities NMB 18514, NMB 18656, NMB 18495, NMB 18541), Darien, Panama.

Subfamily *Vermiculariinae* DALL, 1913

Genus *Vermicularia* LAMARCK, 1799

Type species *Serpula lumbricalis* LINNAEUS, 1758, by monotypy.

*Vermicularia cf. woodringi* OLSSON & HARBISON, 1953

Pl. 4, Fig. 8

2010a *Vermicularia cf. woodringi* OLSSON & HARBISON, 1953 – LANDAU & SILVA, p. 23, pl. 4, fig. 8.

**Material and dimensions:** Height 17.2 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Description:**

Early teleoconch whors turritelliform, later adult whors loosely coiled. Apex missing in examined specimen. Two whors of turritelliform early stage preserved, relatively flat-sided, with spiral sculpture of three narrow elevated cords; adapical cord a short distance below suture, middle cord placed just below mid-whorl, abapical cord at abapical suture. Secondary spiral threads just visible at end of the turritelliform stage. Three later adult whors preserved, irregularly coiled, bearing three prominent spiral cords and numerous spiral threads in interspaces. Axial sculpture of growth lines, becoming more prominent on later whors, giving cords a slightly nodular, irregular aspect. Last whorl strongly angled at abapical cord, base rounded, bearing six very irregular cords with secondary cords or threads in interspaces.

**Discussion:**

The fossil Caribbean *Vermicularia* shells have been assigned to the Recent species *Vermicularia spirata* (PHILIPPI, 1836), or a variety of it. However, the fossil shell from Cubagua is quite different. The importance of the position and placement of the spiral cords on the early adult whors in the Turritellidae was highlighted by MARTINELL (1979) and LANDAU et al. (2004b). The early whors of the Recent Caribbean species (illustrated by REDFERN, 2001, pl. 12, fig. 94) are taller, more convex, with two cords placed above and below mid-whorl, the whorl angular at the abapical cord. In some specimens the adapical cord disappears on the last whorl of the turritelliform stage, so that there is a single carina placed just below
mid-whorl. Specimens from the Lower Pleistocene Moin Formation of Costa Rica are more similar, if not conspecific, with the Recent specimens (see ROBINSON, 1991, pl. 8, figs 5-6). In these Moin Formation shells the abapical cord appears first, followed by the adapical cord one quarter whorl later. A second Recent Caribbean species, *Vermicularia knorrii* (DESHAYES, 1843) differs in small details from *V. spirata* (see REDFERN, 2001), but is quite different again from our Cubagua shell.

The shell illustrated by WOODRING (1928, pl. 26, fig. 5) from the Pliocene Bowden Beds of Jamaica has somewhat more angular whors at the turritelliform stage. He described one to two cords on the early whors, and it seems more likely that this is a species closer to or conspecific with *V. spirata*. MAURY (1925a, p. 380, pl. 41, fig. 6) figured a shell as *Vermicularia spirata* var. *trilineata* GUPPY, with little description, saying it differed from the Recent shell in being a “miniature Pliocene form”. There is insufficient information to be sure what is meant by this record.

As discussed by WOODRING (1928) and JUNG (1969), the type lot of *Vermetus trilineatus* GUPPY, 1864, consisting of six shells, included two species. Four belong to *Vermicularia* (?) *trilineata* illustrated by JUNG (1969). JUNG (1969) discussed the fact that despite additional material from the Pleistocene Matura Shell Bed of Trinidad there was no proof whether this was a *Turritella* or a *Vermicularia*, as all the specimens were juvenile and there was no clear evidence of uncoiling. He went on to say that if it was a *Vermicularia*, it had a long turitelliform stage (largest specimen height 17.7 mm). The turritelliform stage of our shell from Cubagua shows the same sculpture as that illustrated by JUNG (pl. 44, figs 7-8), however, if complete, the turritelliform stage in the Cubagua shell would only be about 7-8 mm in height.

OLSSON & HARBISON (1953, p. 307) described no less than three new *Vermicularia* species from the Plio-Pleistocene of Florida. In their description of *Vermicularia woodringi* the authors clearly discussed “two centrally placed keels nearly equal in size, or with the lower one slightly stronger (…). A third spiral or keel lies in the lower suture (…)”. They distinguished this new species from *V. spirata* by its shorter turritelliform stage and two medially placed keels, and by its more depressed growth habit. They added the shells figured by MAURY (1925a) and WOODRING (1928) to the chresonomy of *V. woodringi*. They believed *Vermetus trilineatus* GUPPY to be a *Turritella*, in which case it would be a junior homonym of *Turritella trilineata* SMITH, 1817 (JUNG, 1969).

Unfortunately, the single shell has a broken apex, and it cannot therefore be said with certainty how long the turritelliform stage is. There is also insufficient material available to know the intraspecific variability within the Cubagua population. Nevertheless, our shell is clearly not conspecific with *V. spirata*. If Guppy’s shells illustrated by JUNG (1969) are conspecific, then the name *Vermicularia trilineata* is available, however, the early stage seems much longer than in our Cubagua shell. If Guppy’s shells are all *Turritella*, then the next available name is *Vermicularia woodringi* OLSSON & HARBISON, 1953, if they are the same species. It is likely that several species are present in the tropical American Neogene, and a revision of these taxa is required taking into account the morphology of the protoconch, the size and number of whors in the turritelliform stage, the number and position of the spiral cords and, importantly, the order in which they appear.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

<table>
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<tr>
<th>Classification</th>
<th>Subdivision</th>
<th>Superfamily</th>
<th>Family</th>
<th>Genus</th>
<th>Type species</th>
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<td>Clade</td>
<td>Littorinimorpha</td>
<td>Calyptraeoidea LAMARCK, 1809</td>
<td>Calyptraeidae LAMARCK, 1809</td>
<td>Calyptraea LAMARCK, 1799</td>
<td><em>Patella chinensis</em> LINNAEUS, 1758, by monotypy.</td>
</tr>
<tr>
<td>Type species</td>
<td><em>Calyptraea centralis</em> (CONRAD, 1841)</td>
<td>Pl. 4, Fig. 9</td>
<td>Infundibulum centralis CONRAD, p. 348.</td>
<td>Infundibulum concentricum H. C. LEA, p. 249, pl. 35, fig. 39.</td>
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</tbody>
</table>
1847  *Calyptrea (Infundibulum) candeanum* D’ORBIGNY, p. 190, pl. 24, figs 26-29.

1850  *Trochita occidentalis* GRAY, p. 84, pl. 130, fig. 2 [sic, 3].

1867  *Trochita candea* D’ORB. – GUPPY, p. 160.

1867b  *Calyptrea Candeeana* D’ORB. – TRYON, p. 121, pl. 34, figs 76-77, 82-83.

1874  *Trochita candea* D’ORB. – GUPPY, p. 440.

1875  *Galerus parvulus* DUNKER, p. 244.

1886b  *Calyptrea Candeana* D’ORB. – TRYON, p. 121, pl. 34, figs 76-77, 82-83.

1874  *Trochita candeana* D’ORB. – GUPPY, p. 440.

1881  *Trochita collinsii* GABB, p. 342, pl. 44, fig. 11.

1910  *Trochita collinsii* GABB – GUPPY, p. 5.

1912  *Calyptrea centralis* CONRAD – MAURY, p. 100, pl. 13, fig. 6.

1925a  *Calyptrea centralis* CONRAD – MAURY, p. 243, pl. 43, fig. 2.

1938  *Calyptrea centralis* (CONRAD) – H. E. VOKES, p. 5.

1940  *Calyptrea centralis* CONRAD – PERRY, p. 120, pl. 24, fig. 171.

1942  *Calyptrea cf. centralis* (CONRAD) – RUTSCH, p. 103.

1947  *Calyptrea centralis* (CONRAD) – GARDNER, p. 562, pl. 56, figs 3-5.

1954  *Calyptrea centralis* CONRAD – ABBOTT, p. 169, pl. 21, fig. o.

1955  *Calyptrea centralis* CONRAD – PERRY & SCHWENGEL, p. 129, pl. 24, fig. 171.

1957a  *Calyptrea centralis* (CONRAD) – WOODRING, p. 80.

1961  *Calyptrea centralis* CONRAD, 1841 – WARMKE & ABBOTT, p. 86, pl. 15, fig. o.


1973  *Calyptrea centralis* CONRAD – MORRIS, p. 163, pl. 45, fig. 3.

1974  *Calyptrea centralis* (CONRAD, 1841) – ABBOTT, p. 139, fig. 1534.

1975  *Calyptrea centralis* (CONRAD, 1841) – RIOS, p. 64, pl. 17, fig. 256.

1975  *Calyptrea centralis* (CONRAD) – REGTEREN ALTENA, p. 29, pl. 6, figs 9-10.

1987  *Calyptrea centralis* (CONRAD) – WARD & BLACKWELDER, p. 171, pl. 37, figs 5-6.

1993  *Calyptrea centralis* (CONRAD, 1841) – CAMPBELL, p. 69, fig. 333.

1994  *Calyptrea centralis* (CONRAD, 1841) – DÍAZ & PUYANA, p. 160, fig. 582.

1994  *Calyptrea centralis* (CONRAD, 1841) – RIOS, p. 71, pl. 24, fig. 274.

2002  *Calyptrea centralis* (CONRAD, 1841) – SIMONE, p. 6, 40, figs 12-14.

2009  *Calyptrea centralis* (CONRAD, 1841) – LEE, p. 76, fig. 357.

2009  *Calyptrea centralis* (CONRAD, 1841) – RIOS, p. 126, fig. 306.

2010a  *Calyptrea centralis* (CONRAD, 1841) – LANDAU & SILVA, p. 24, pl. 4, fig. 9.

**Material and dimensions:** Maximum restored diameter 22.0 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:** As pointed out by several authors (GARDNER, 1947; WOODRING, 1957a; JUNG, 1969), the Recent specimens of this species tend to be smaller than the fossil populations, with the Recent shells rarely surpassing 15 mm diameter (WOODRING, 1957a; DÍAZ & PUYANA, 1994). Our broken shell from Cubagua is no exception; the restored diameter would be at least 22 mm, although the specimen figured only has a maximum dimension of 13.6 mm. However, as discussed by JUNG (1969), small fossil specimens also occur. CAMPBELL (1993, p. 69) also noted that there were at least two ‘ecmorphs’ in the Pliocene Yorktown Formation of North Carolina; the commoner form 5-7 mm diameter, about equal height and width, the other larger, flatter, 15-20 mm diameter. Although he suggested some difference in ecological requirements between the specimens of the two assemblages, it is not clear from the text whether the two are sympatric or occur in distinct geographical areas. Similarly, in the eastern Atlantic, a single widely distributed species, *Calyptrea chinensis* (LINNAEUS, 1758), is present in the North Sea Basin, eastern Atlantic European frontage and North Africa, Mediterranean and Paratethys, ranging stratigraphically from the Middle Miocene to the Recent faunas (LANDAU et al., 2004b).

**Geological and geographical distribution:**

Lower Miocene: Chipola Formation, Florida (GARDNER, 1947).

Middle Miocene: Shoal River Formation, Florida (GARDNER, 1947); lower Gatun Formation, Panama (WOODRING, 1957a).

Upper Miocene: middle Gatun Formation, Panama (WOODRING, 1957a); Mataruca Member of Caujarao
Formation, El Carrizal (NMB 2970), Venezuela.
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1912; H. E. VOKES, 1938; JUNG, 1969); Coubaril beds of Upper Morne l’Enfer Formation (JUNG, 1969).
Lower Pleistocene: Caloosahatchee Formation, Florida (GARDNER, 1947); Mare Formation, Cabo Blanco, Venezuela (NMB coll.); Moin Formation, Puerto Limon, Costa Rica (ROBINSON, 1991).
Lower-Upper Pleistocene: Matura Shell Bed, Talparo Formation, Trinidad (MAURY, 1925a; JUNG, 1969).
Recent: North Carolina and West Indies to Uruguay (DÍAZ & PUYANA, 1994).

**Genus** *Crepidula* LAMARCK, 1799.

**Type species** *Patella fornicata* LINNAEUS, 1758, by monotypy.

*Crepidula maculosa* CONRAD, 1846

**Material and dimensions:** Maximum length 36.0 mm, four specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado Cubagua Island; five specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

The *Crepidula* shells from the Araya Formation vary enormously in shape, from high arched and narrowly elongate to low arched and rounded. One specimen from the upper reddish coarse sandy bed of the Araya Peninsula has a very irregular compressed shape and axial ribbing, which may be caused by growing along the scuptered shell it was adhered to. One of the Recent specimens figured by ABBOTT (1974, fig. 1558, far right) has the same axial ribbing. An oval muscle scar is present on the inside of the shell on the right side just below and in front of the septum. The septum is weakly sinuous is profile, with the concave portion immediately adjacent to the muscle scar. *Crepidula maculosa* CONRAD, 1846 is similar to *Crepidula fornicata* LINNAEUS, 1758, which today has a more northern distribution, but *C. maculosa* lacks an internal muscle scar. The Recent western Atlantic *Crepidula convexa* Say, 1822 also has a single muscle scar, but tends to be smaller-shelled, the edge of the septum is almost straight and it is somewhat more rostrate. Unfortunately the protoconch in our material is abraded, which is an important character in distinguishing species in within the Calyptraeidae (MARSHALL, 2003). *Crepidula convexa* also has a long fossil record extending back to the Miocene in the American eastern Atlantic (HOAGLAND, 1977).
Venezuela of which two, *C. phalaena* and *C. corcovada* have a high-arched dorsum similar to our Cubagua specimens. A revision of these taxa is beyond the scope of this work.

**Geological and geographical distribution:**
Middle Miocene: lower Gatun Formation, Panama (Woodring, 1957a).
Upper Miocene: middle and upper Gatun Formation, Panama (Woodring, 1957a).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (Jung, 1969).
Plio-Pleistocene: Florida (Olsson & Harbison, 1953; Petuch, 1994).
Recent: Both sides of Florida to Mexico (Abbott, 1974).

**Genus** *Crucibulum* Schumacher, 1817.
**Type species** *C. rugosa-costatum* Schumacher, 1817 (= *C. auricula* Gmelin, 1810), by subsequent designation, Burch, 1946.

*Crucibulum (Crucibulum) cubaguaense* Landau & Silva, 2010

**Dimensions and type material:** Holotype NHMW 2010/0038/0008 (Pl. 5, Fig. 1), height 15.2 mm, diameter 27.3 mm (NHMW coll., ex BL coll.); paratype 1 (incomplete) NHMW 2010/0038/0009 (Pl. 5, Fig. 2), height 15.3 mm, diameter 23.5 mm (NHMW coll., ex BL coll.).

**Derivatio nominis:** after Cubagua Island, the type locality.

**Locus typicus:** Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

**Stratum typicum:** Araya Formation, Cubagua Group, Lower Pliocene.

**Diagnosis:**
A *Crucibulum (Crucibulum)* species of small to medium-size, elliptical in ventral plan, antero-posteriorly compressed, with a tall mammillate apex, no surface sculpture, except for commarginal growth ridges.

**Original description:**
“Shell tall, patelliform, of small to medium size, relatively fragile, elliptical in ventral plan, antero-posteriorly compressed. Protoconch abraded. Last whorl steep-sided, anterior wall weakly concave, posterior wall weakly convex. Apex elevated, mammillate, posteriorly recurved, placed midway between centre and posterior border. Surface smooth, sculpture absent, except for commarginal growth ridges. Cup fully detached, except for shell junction along posterior margin, joined at a level above ventral margin of the cup, cup incomplete in all specimens, vertically ovate in cross-section; right anterior border roundly angulated (Landau & Silva, 2010a, p. 26)”.

**Discussion:**
The character of the internal cup, completely detached, places this shell in the subgenus *Crucibulum*. Most unusually for the genus there is no axial sculpture at all, only commarginal growth ridges. The holotype is relatively well preserved and has no trace of even the faintest ribs along the edge. The paratype is slightly incomplete, but has an even taller mammillate apex than the holotype. *Crucibulum (Crucibulum) cubaguaense* Landau & Silva, 2010, with its elevated mammillate apex and absence of sculpture is a very distinctive species. I have not found any fossil or Recent Caribbean or tropical American Pacific species to compare it to.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela
**Crucibulum** *(Crucibulum) subsutum* GUPPY, 1867

Pl. 5, Figs 3-5

1864 *Crucibulum striatum* SAY – GUPPY, p. 15.

1867 *Crucibulum subsutum* GUPPY, p. 160.

1874 *Crucibulum subsutum* GUPPY, p. 441, pl. 18, fig. 4.


2010a *Crucibulum* *(Crucibulum) subsutum* GUPPY, 1867 – LANDAU & SILVA, p. 27, pl. 5, figs 3-5.

**Material and dimensions:** Maximum height 36.0 mm, diameter 53.9 mm, one specimen NMB lot DS 45; 10 specimens EDIMAR coll.; 17 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; eight specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; five specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

*Crucibulum* *(Crucibulum) subsutum* GUPPY, 1867 superficially resembles *Crucibulum* *(Dispotaea)* springvaleense RUTSCH, 1942 from the Lower Pliocene Springvale Formation of Trinidad, but the latter shows the characteristic of the subgenus *C.* *(Dispotaea)*; part of the internal cup is attached to the inner shell wall. The Recent species *Crucibulum* *(Dispotaea) striatum* (SAY, 1822) again differs in the wide attachment area of the cup. *Crucibulum* *(Crucibulum) chipolanum* DALL, 1892, which has been recorded from the Upper Miocene Middle Gatun Formation of Panama (WOODRING, 1957a, p. 82), has a finer sculpture. *Crucibulum* *(Crucibulum) auricula* (GMELIN, 1791) was recorded by WEISBORD (1962, p. 215) from the Lower Pleistocene Mare Formation of Venezuela. The shells illustrated are more depressed with sculpture of less elevated, more irregular radial ribs.

**Crucibulum** *(Crucibulum) subsutum* seems to have been restricted to the Upper Miocene-Lower Pliocene southern Caribbean of Trinidad and Venezuela.

**Geological and geographical distribution:**

Upper Miocene: Matarúca Member of Caujarao Formation (NMB 2712), El Carrizal, Venezuela.

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (BL coll.); Springvale Formation, Trinidad (JUNG, 1969).

Subgenus *Dispotaea* SAY, 1824.

Type species *Calyptrea costata* SAY, 1820, by subsequent designation.

*Crucibulum* *(Dispotaea)* sp.

Pl. 5, Fig. 6

2010a *Crucibulum* *(Dispotaea)* sp. – LANDAU & SILVA, p. 27, pl. 5, fig. 6.

**Material and dimensions:** Maximum height 14.0 mm, six specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

Within the Cubagua material are six small, conical specimens of *Crucibulum* *(Dispotaea)* sp., of variable height, with the internal cap narrowly fused to the interior of the shell, for about one sixth of the cup diameter, up to the cup rim. The fused area is much narrower than that in *C.* *(D.)* springvaleense RUTSCH, 1942 (see WOODRING, 1957a, pl. 19, fig. 9). Our shells are abraded, but show remnants of relatively fine axial sculpture. The sculpture is not unlike that seen in *Crucibulum* *(Dispotaea) marense* WEISBORD, 1962 from the Lower Pleistocene Mare Formation of Venezuela, also with an internal cup with relatively narrow attachment area, but that is a much larger species. *Crucibulum* *(Dispotaea)* venezuelanum WEISBORD, 1962, also from the Mare Formation is quite different, with a much larger umbo, which is loosely coiled and broad axial undulations on the posterior portion of the last whorl, although this character...
might be caused by attachment on another mollusc.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela

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<tr>
<th>Superfamily</th>
<th>Stromboidea RAFFINESQUE, 1815</th>
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<td>Family</td>
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<td>Genus</td>
<td>Strombus LINNAEUS, 1758.</td>
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</table>

Type species *S. pugilis* LINNAEUS, 1758, by subsequent designation; MONTFORT, 1810.

*Strombus arayaensis* LANDAU & SILVA, 2010

Pl. 5, Figs 7-10

2010a *Strombus arayaensis* LANDAU & SILVA, p. 27, pl. 5, figs 7-9.

**Dimensions and type material:**
Holotype MOBR-M-3874 (Pl. 5, Fig. 7), height 70.5 mm, maximum diameter 40.2 mm (EDIMAR coll., ex BL coll.); paratype 1 NHMW 2010/0038/0010 (Pl. 5, Fig. 8), height 74.9 mm, maximum diameter 43.3 mm (NHMW coll., ex BL coll.); paratype 2 NHMW 2010/0038/0011 (Pl. 5, Fig. 9), height 73.7, maximum diameter 43.7 mm (NHMW coll., ex BL coll.); paratype 3 NHMW 2010/0038/0012, height, 69.3 mm, maximum diameter 44.9 mm (NHMW coll., ex BL coll.).

**Etymology:**
Named after the type locality, Araya Peninsula.

**Type locality:**
Upper reddish coarse sandy bed, Cerro Barrigón, Araya Peninsula.

**Stratum typicum:**
Aramina Formation, Cubagua Group, Lower Pliocene.

**Additional material:**
Three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; 11 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Diagnosis:**
A *Strombus* species of medium-size, with a conical pointed spire; early teleoconch whorls sculptured by 11 ribs, abapically becoming rounded knobs at the periphery, expansion rate increases on penultimate whorl exposing the knobs below the shoulder as broad axially elongated ribs; spiral sculpture restricted to one or two infrasutural cords and a few irregular cords on the base; last whorl with shoulder placed high, axial knobs persisting on the last whorl in 70% of the specimens, outer lip not extending beyond penultimate whorl, lirate within; stromboid notch of medium depth, parietal and columellar callus expanded covering most of the venter.

**Original description:**
“Shell medium-sized for genus, relatively broad, with elevated conical pointed spire of seven whors and broad globose last whorl. Protoconch missing in specimens examined. Early and intermediate whors angled at shoulder, with narrow sutural ramp. Suture impressed, following contour of the axial sculpture. Early teleoconch whorl sculpture somewhat eroded, of about 11 axial ribs without varices. Spiral sculpture restricted to single infrasutural cord. Abapically, position of shoulder becomes progressively lower, sutural ramp wider, somewhat concave, axial sculpture weakens on sutural ramp, strengthens at shoulder, forming rounded knobs, position of abapical suture rises, so on fifth whorl suture lies immediately below shoulder knobs. On penultimate whorl expansion rate increases, so whorl is broader, convex, abapical suture again placed lower so axial sculpture below shoulder is exposed, forming axially elongated knobs. Last whorl broad, globose, with narrow, strongly concave sutural ramp, shoulder placed high, acutely rounded, hardly constricted at base. Axial sculpture represented by series of axially elongated knobs at shoulder in 70% of specimens, remainder with knobs subobsolete and rounded ridge at shoulder, spiral sculpture of two very weak cords immediately below suture forming subsutural collar, with up to six irregular cords on the base. Aperture narrow, elongate; outer lip not extending beyond penultimate whorl, flared, lirate within in most specimens; stromboid notch of medium depth. Anal canal represented by narrow groove; siphonal canal open, short, weakly recurved. Columella straight, smooth; columellar and parietal callus expanded covering most of venter, well delimited. No colour pattern preserved (LANDAU & SILVA, 2010a, p. 27)”.
**Discussion:**

These *Strombus* shells found in the Lower Pliocene beds of the Araya Formation at Cañon de las Calderas and the coeval Aramina Formation beds at Cerro Barrigón, Araya Peninsula, are typical of the Floridian Plio-Pleistocene *Strombus alatus* complex. Landau & Silva (2010a) chose Cerro Barrigón as the type locality due to their greater abundance and better preservation in these beds than elsewhere.

**Text-Figure 17:** Shell measurements for Strombidae (adapted from Freiheit & Geary, 2009, text-fig.1).

The first member of this lineage reported in Florida is *Strombus floridanus* Mansfield, 1930 from the Lower Pliocene Jackson Bluff Formation and lower Pinecrest units of Florida. The transformation of *S. floridanus* to *S. alatus* Gmelin, 1791 in the Floridian faunas probably took place over about one million years (Hargreaves, 1995). The number of intermediate forms between *S. floridanus* and *S. alatus* is unclear, and their taxonomy is extremely difficult, as highlighted by Hargreaves (1995). This situation was not helped by the numerous trivial taxa introduced by Petuch (1991, 1994).
Text-Figure 18: Morphometric plots for *Strombus arayaensis* LANDAU & SILVA, 2010 shells from the Lower Pliocene Araya and Aramina Formations of Cubagua and Araya Peninsula (Venezuela) compared with *S. floridanus* MANSFIELD, 1930 and *S. evergladesensis* PETUCH, 1991 from the Plio-Pleistocene of Florida.
Our shells from the Lower Pliocene southern Caribbean of Venezuela are more similar to the early members of the *S. alatus* complex; i.e. *S. floridanus* (*Strombus sarasotaensis* PETUCH 1994 is probably a junior subjective synonym) in having a squat shell, with a shorter spire and the suture is placed just below the shoulder tubercles up to the antepenultimate whorl as opposed to well below, as in *S. alatus*. However, the Venezuelan specimens differ from these early Floridian forms in having less numerous, but more strongly developed tubercles at the shoulder of the spire whorls (10 vs. usually 13-14), which persist as weak tubercles at the shoulder on the dorsum of the last whorl in about 70% of specimens, whereas in both *S. floridensis* and *S. sarasotaensis* the shoulder on the penultimate whorl is smooth in most shells and the last whorl is smooth in all specimens seen. In the smooth specimens of *Strombus arayaensis* LANDAU & SILVA, 2010 the shoulder, although placed in a similar position, is always more prominent than in the Floridian lineage. The strength of the spiral sculpture is extremely variable in all the members of the Plio-Pleistocene *Strombus* lineage, but almost invariably more strongly developed than in *S. arayaensis*.

LANDAU & SILVA (2010a) attempted to distinguish *S. arayaensis*, *S. floridanus* (Pliocene of Florida) and *Strombus evergladesensis* PETUCH, 1991 (the Pleistocene member of the group in Florida) using the morphometric measurements suggested by FREIHEIT & GEARY (2009, text-fig.1), with the exception of the height, which was taken as points 1-2, as the anterior extension of the outer lip is often broken. The following plots (Text-Fig. 18) resulted:

As can be seen from the graphs above, the three species could not be distinguished on these shell morphometrics. There is overlap between all the characters in the three species, although there is a closer grouping of points for *S. floridanus* and *S. arayaensis*, with *S. evergladesensis* more separated.

Compared to the Recent Caribbean *Strombus* species, *Strombus pugilis* (LINNAEUS, 1758) usually has strong spines on the last whorl and the spines are most strongly developed on the penultimate whorl. The outer lip in this species is somewhat alate adapically, whereas the lip in *S. arayaensis* is not alate and sloped abapically. The shells of *Strombus alatus* (GMELIN, 1791) are more slender, also usually spinose on the last whorl and the spines are not usually more strongly developed on the penultimate whorl. Some unusual specimens of *S. alatus* without spines on the last whorl (Gijs Kronenberg coll.) resemble *S. arayaensis* but can be distinguished by their more elongate shell as opposed to the very squat form of the Cubagua species. Most of the specimens of *S. arayaensis* have quite strong and widely spaced growth lines (Pl. 5, Fig. 4), whereas in the Recent species the growth lines are finer and more widely spaced.

Strombs have several defensive mechanisms; “leaping”, the formation of sharp spines, diurnal burial, congregation in herds and the rapid attainment of a large size (STONER, 1989; RAY & STONER, 1995). The development of large defensive spines is a hinderance to burrowing, as they protrude when the rest of the shell is buried and reveal the animal’s position to potential predators (FREIHEIT & GEARY, 2009), and therefore it is assumed that the development of smooth shells should favour a burial defense mechanism.

**Geological and geographical distribution:** Atlantic
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Type species *Strombus granulatus* SWAINSON, 1822, by original designation.

Persististrombus granulatus (SWAINSON, 1822)
Pl. 6, Figs 1-4

1822 *Strombus granulatus* SWAINSON, p. 43.
1823 *Strombus granulatus* – MAWE, p. 127, pl. 25, fig. 3.
1828 *Strombus granulatus* – WOOD, p. 14, pl. 4, fig. 21.
1842 *Strombus granulatus* – SOWERBY; G. B. II, p. 33, pl. 9, fig. 100.
1843 *Strombus granulatus*, SOW. – KIENER, p. 28, pl. 22, fig. 1.
1844 *Strombus granulatus* WOOD – DUCLOS, pl. 11, figs 5-6.
1851 *Strombus granulatus* GRAY – REEVE, pl. 14, fig. 32.
**Material and dimensions:** Maximum height 97.9 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), nine specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

The presence of this group in the Caribbean Neogene faunas was reviewed by Jung & Heitz (2001) under the genus Lentigo. Only four fossil shells identified as Strombus granulatus were available to Jung & Heitz, two from the Pleistocene Armuelles Formation of Panama and two from the Upper Miocene upper Onzole Formation of Ecuador, all from the eastern Pacific. They described a species from the Araya Formation, of Cerro Barrigón, Araya Peninsula, Strombus (Lentigo) barrigonensis Jung & Heitz, 2001, which they distinguished from S. granulatus by having a broader shell, by having a less elevated spire, knobs usually more numerous and less elevated, and the knobs on the spire whorls placed at or just above the suture, whereas in P. granulatus SWAINSON, 1822 the knobs are at mid-whorl. It must be stressed that the material available to Jung & Heitz (2001) was very incomplete. Since then more complete material was found at Cerro Barrigón and the specimens show some degree of variability in all the characters used by Jung & Heitz (2001) to distinguish the two taxa; the height of the spire, shell shape and the number of tubercles on the spire whorls. In the Recent faunas, the shell of Persististrombus granulatus (SWAINSON, 1822) is extremely variable in shape (Kronenberg & Lee, 2005) and the specimens from Cerro Barrigón fit within this variability. Landau & Silva (2010a) therefore considered Strombus (Lentigo) barrigonensis Jung & Heitz, 2001 a junior subjective synonym of Persististrombus granulatus (SWAINSON, 1822).

The subgenus Lentigo Jousseaume, 1886 has usually been used for this genus. Although Persististrombus has a number of characters in common with Lentigo Jousseaume, 1886 (type species by monotypy: Strombus lentiginosus LINNAEUS, 1758), there are conspicuous differences: in Lentigo the adapical part of the outer lip has two notches, resulting in two lobes, of which the most adaxial one is attached to the spire of the shell; species assigned to Lentigo have a more distinct posterior canal, a number of small triangular extensions at the adapical side of the outer lip on the flange between the stromboid notch and the anterior canal, very often rather worn in L. lentiginosus, and a columellar callus which does
not reach the base of the columella, but is thickened at its abapical part, but not forming a distinct pad. Species assigned to Persististrombus also have shells with relatively higher spires than the shells of Lentigo (KRONENBERG & LEE, 2007). This systematic position was supported by molecular studies by LATIOLAIS et al., 2006). Lentigo is here considered to be restricted to the Indo-Pacific. On this subject see also KRONENBERG & VERMEIJ (2002).

The presence of Persististrombus granulatus in Cubagua is interesting. It is the earliest fossil record of the species, placing P. granulatus on the Atlantic side of the Gatunian Neogene paleobiogeographical province before becoming restricted to its modern day eastern Pacific distribution. LOZOUET & MAESTRATI (1986) suggested P. granulatus was a Mesogean relict. Indeed, it belongs to a lineage of strombs, whose shell is morphologically unchanged since the Late Eocene, hence the name Persististrombus (KRONENBERG & LEE, 2007). The earliest tropical American record of the genus is Strombus aldrichi DALL, 1890 from the Lower Miocene Chipola Beds, Florida, eastern USA, whereas the first Panamic record is Upper Pliocene. This westwards spread of the genus agrees with LOZOUET & MAESTRATI (1986). However the paucity of eastern Pacific fossil records probably reflects the rarity of suitable shallow-water facies deposits along the Pacific coast (COLLINS & COATES, 1999, p. 7).

Geological and geographical distribution: Atlantic
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Geological and geographical distribution: Pacific
Upper Miocene to Upper (?) Pliocene: California (POWELL, 1988).
Pleistocene: Armuelles Formation, Panama (JUNG & HEITZ, 2001); Santa Ines Bay, Baja California, Mexico (GRANT & GALE, 1931; DURHAM, 1950; EMERSON & OLD, 1963; SCHNEIDER, 1999, 2004).
Recent: Gulf of California to Ecuador (KREIPL et al., 1999), Galápagos Islands (KRONENBERG & LEE, 2005).

Superfamily: Xenophoroidea TROSCHEL, 1852 (1840)
Family: Xenophoridae TROSCHEL, 1852 (1840)
Genus: Xenophora FISCHER VON WALDHEIM, 1807.

Type species Xenophora laevigata FISCHER VON WALDHEIM, 1807 (= Trochus conchyliophorus BORN, 1780), by subsequent designation, HARRIS, 1897.

Xenophora delecta (GUPPY, 1876)
Pl. 6, Fig. 5

Material and dimensions: One specimen BL coll., height 26.0 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; three specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation, Cerro Barrigón, Araya Peninsula.

Discussion:
The larger of the two fragments found in Cañon de las Calderas clearly shows the relatively wide umbilicus and coarse basal sculpture characteristic of Xenophora delecta (GUPPY, 1876). The shells of the Recent species of Xenophora found on either side of the Isthmus of Panama, Xenophora conchyliophora (BORN, 1780) in the Caribbean, and Xenophora robusta VERRILL, 1870 in the Pacific are very similar and differ from X. delecta in their much smaller umbilicus and smoother sculpture on the base. Indeed some
authors consider *X. robusta* a subspecies of the Caribbean species: *Xenophora conchyliophora robusta* (Woodring, 1957a). Woodring (1957a) suggested that *X. delecta* was not related to any of the Recent tropical American Pacific species, but closer to *Xenophora crispa* (König, 1825) from the European Middle Miocene to Recent faunas and *Xenophora senegalensis*, Fischer, 1873 from the Recent West African coast, which has a similar umbilicus and coarsely sculptured base.

Woodring (1957a) considered the specimen Maury (1917, pl. 23, fig. 7) named as *Xenophora conchyliophora* to be *X. delecta*, but this is unjustified as in the text Maury (1917, p. 133) is very clear on the difference between the two species. Moreover, I have examined two large specimens of *X. conchyliophora* from the Lower Pliocene Gurabo Formation of the Dominican Republic (BL coll.), from the same locality on the Gurabo River as indicated by Maury. The two species seem to have coexisted in the Caribbean at least during the Early Pliocene.

A closely related species occurs in the Lower-Middle Pliocene of Florida; *Xenophora floridana* Mansfield, 1930, which was originally described as a subspecies of *X. delecta* (Mansfield, 1930, p. 121). It differs from *X. delecta* in being higher spired and having a slightly less granulose ornamentation on the base. As already pointed out by Mansfield (1930), *X. floridana* seems to be more profusely loaded with shells and other objects than any specimen of *X. delecta* I have seen from the Dominican Republic.

The shells of *Xenophora textilina* (Dall, 1892) from the Lower Miocene Chipola Formation and Middle Miocene Shool River Formation of Florida are more similar to *X. conchyliophora* than *X. delecta*, but differ from the Recent Caribbean species in larger granulations on the base, but always weaker than those seen in *X. delecta* or *X. floridana*, a wider umbilicus and the area around the umbilicus on the base is distinctly grooved.

**Geological and geographical distribution:**
Upper Miocene: upper Gatun Formation, Panama (Woodring, 1957a); Cercado Formation, Dominican Republic (Maury, 1917).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934).
Lower-Upper Pliocene: Bowden Formation, Jamaica (Woodring, 1928).

Superfamily  
Family  
Subfamily  
Genus  

Type species *P. sculpturatus* H. C. Lea, 1845, by monotypy.

*Petaloconchus sculpturatus alcimus* Mansfield, 1925

Pl. 6, Figs 6-7

1867 *Petaloconchus sculpturatus* LEA – Guppy (partim), p. 156.
1910 *Petaloconchus sculpturatus* LEA – Guppy (partim), p. 5.
1925a *Petaloconchus sculpturatus* var. *domingensis* Sowerby – Maury, p. 226, pl. 41, figs 2, 4, 7.
1925 *Petaloconchus alcimus* Mansfield, p. 51, pl. 9, figs 2-4.
1934 *Vermetus* (*Petaloconchus*) *sculpturatus domingensis* (Sowerby) – Rutsch, p. 45, pl. 1, figs 11, 12, 13.
1942 *Vermetus* (*Petaloconchus*) *sculpturatus* (Lea) – Rutsch, p. 103.
1969 *Petaloconchus sculpturatus alcimus* Mansfield – Jung, p. 444, pl. 43, fig. 32.
2010a *Petaloconchus sculpturatus alcimus* Mansfield, 1925 – Landau & Silva, p. 33, pl. 6, figs 6-7.
Material and dimensions: Maximum height 79.0 mm, four specimens NMB lot 6919/1; one specimen NMB lot 6919/2; 10 specimens EDIMAR coll.; 12 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed); one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion: JUNG (1969) discussed the differences between P. sculpturatus (LEA, 1845) and its subspecies P. sculpturatus alcimus MANSFIELD 1925. Although their sculpture is similar, the shells of the subspecies P. sculpturatus alcimus are much larger and more regularly coiled. I have found the same large specimens in the Lower Pliocene Punta Gavilán Formation of Venezuela. When compared with specimens from the Lower Pliocene Gurabo Formation of the Dominican Republic they are indeed much larger and more regularly coiled. A single specimen (BL coll.) from the Lower Miocene Baitoa Formation of the Dominican Republic is available, which is tightly coiled, but much smaller. Specimens from the Lower Pliocene Tubaré Group (NMB lots B 224, 241, 243, 254, G 430), northern Colombia are all representative of the smaller subspecies P. sculpturatus sculpturatus. Petaloconchus sculpturatus is also common in the Pliocene Pinecrest Beds of Florida, where the shell is also regularly coiled, but again smaller. This large form seems to be restricted to the Lower Pliocene of the southern Caribbean, and LANDAU & SILVA (2010a) therefore accepted Jung’s subgeneric placement.

Geological and geographical distribution:
Upper Miocene: Mataruca Member of Caujarao Formation (NMB 2696), El Carrizal, Venezuela.
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934, as as Vermetus (Petaloconchus) sculpturatus domingensis); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1925a, as Petaloconchus sculpturatus var. domingensis; MANSFIELD, 1925; H. E. VOKES, 1938; RUTSCH, 1942, as Vermetus (Petaloconchus) sculpturatus; JUNG, 1969).

Genus Serpulorbis SASSI, 1827.
Type species S. polyphragma SASSI, 1827 (= Serpula arenaria LINNAEUS, 1758), by monotypy.

Serpulorbis decussatus (GMELIN, 1791)
Pl. 6, Figs 8-9

1791 Serpula decussata GMELIN, p. 3745.
1859 Bivona discussata GMELIN – CHENU, p. 320, fig. 2303.
1862 Thylacodes decussatus var. gamma intermedia MÖRCH, p. 75.
1862 Thylacodes decussatus var. d laevigata MÖRCH, p. 75.
1862 Thylacodes decussatus var. β tenuis MÖRCH, p. 75.
1864 Siphonium decussatum GML. – GUPPY, p. 35.
1867 Siphonium decussatum GML. – GUPPY, p. 156.
1886b Vermetus decussatus GMELIN – TRYON, p. 181, pl. 53, figs 71-72.
1874 Siphonium decussatum GML. – GUPPY, p. 438.
1925a Serpulorbis decussata GMELIN – MAURY, p. 224, pl. 41, fig. 3.
1925 Leminita decussata (GMELIN) – OLSSON & HARBENSON, p. 305, pl. 46, fig. 3.
1961 Serpulorbis decussatus GMELIN, 1791 – WARMKE & ABBOTT, p. 66, pl. 12, fig. d
1869 Serpulorbis decussatus (GMELIN) – JUNG, p. 444, pl. 43, figs 30-31.
1970 Serpulorbis decussatus (GMELIN, 1791) – RIOS, p. 75, pl. 8, lower right fig.
1973 Serpulorbis decussatus (GMELIN, 1791) – MORRIS, p. 145, pl. 41, fig. 8.
1975 Serpulorbis decussata GMELIN 1791 – HUMFREY, p. 83, pl. 6, fig. 2.
1975 Serpulorbis decussatus (GMELIN, 1791) – RIOS, p. 45, pl. 12, fig. 164.
1994 Serpulorbis decussata (GMELIN, 1791) – DIAZ & PUYANA, p. 143, fig. 497.
1994 Serpulorbis decussatus (GMELIN, 1791) – RIOS, p. 67, pl. 22, fig. 259.
2001 Serpulorbis decussatus (GMELIN, 1791) – MACSOTAY & CAMPOS, p. 44.
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2001 Serpulorbis decussatus (GMELIN, 1791) – RIOSS, p. 119, fig. 288.
2009 Serpulorbis decussatus (GMELIN, 1791) – LANDAU & SILVA, p. 33, pl. 6, figs 8-9.

Material and dimensions: Maximum diameter 25.5 mm, five specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion: The shell of Serpulorbis decussatus (GMELIN, 1791) is characterised by its sculpture of thin, relatively strong spiral cords, occasionally made somewhat nodulose by less prominent growth lines, but the nodules are never as numerous or strong as in Serpulorbis papulosus (GUPPY, 1866).

Geological and geographical distribution:
Lower-Upper Pliocene: Bowden Formation, Jamaica (GUPPY, 1866a; WOODRING, 1928).
Plio/Pleistocene: Florida (OLSSON & HARBISON, 1953).
Recent: Western Atlantic, North Carolina, USA to Rio de Janeiro, Brazil, 18-40 m depth (MACSOTAY & CAMPOS, 2001).

Serpulorbis papulosus (GUPPY, 1866)

Pl. 6, Fig. 10

1866a Vermetus papulosus GUPPY, p. 292, pl. 17, fig. 3.
1928 Lemintina papulosa (GUPPY) – WOODRING, p. 436, pl. 26, fig. 6.
1929 Serpulorbis papulosus (GUPPY) – WEISBORD, p. 35, pl. 8, fig. 13.
1929 Serpulorbis papulosa (GUPPY) – ANDERSON, p. 144.
1934 Vermetus (Lemintina) papulosus GUPPY – RUTSCH, p. 46, pl. 1, fig. 14, pl. 2, fig. 1, text-fig. 6.
1947 Lemintina papulosa (GUPPY) – GARDNER, p. 585, pl. 55, fig. 20.
1959a Serpulorbis papulosus (GUPPY) – WOODRING, p. 161, pl. 29, fig. 13.
1961 Serpulorbis papulosus (GUPPY) – PFLUG, p. 22, pl. 2, figs 2-4, 7.
2010a Serpulorbis papulosus (GUPPY, 1866) – LANDAU & SILVA, p. 34, pl. 6, fig. 10.

Material and dimensions: Maximum height 170.0 mm, six specimens NMB lot DS 6925; four specimens EDIMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; one specimen BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion: Serpulorbis papulosus (GUPPY, 1866a) is widely distributed in the Miocene and Pliocene Caribbean region. This species is characterised by its sculpture of widely spaced swollen knobs, which distinguish them from Serpulorbis decussatus (GMELIN, 1791) with its finer sculpture. JUNG (1969) suggested S. papulosus may be the forerunner of S. decussatus, however, this is unlikely as they coexist in the Early Pliocene Caribbean.

Geological and geographical distribution:
Middle Miocene: Shoal River Formation, Florida (GARDNER, 1947); Brasso Formation, Trinidad (WOODRING, 1959).
Upper Miocene: Cercado Formation, Dominican Republic (MAURY, 1917); middle Gatun Formation, Panama (WOODRING, 1959).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavián Formation, Falcón, Venezuela (RUTSCH, 1934); Tuberá Group, northern Colombia (WEISBORD, 1929; ANDERSON, 1929); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1925a; PFLUG, 1961; JUNG, 1969); Gurabo Formation,
Dominican Republic (MAURY, 1917).
Lower-Upper Pliocene: Bowden Formation, Jamaica (WOODRING, 1928).
Upper Pliocene: Banano Formation, Costa Rica (OLSSON, 1922).

Superfamily  Cypraeoidea GRAY, 1824
Family  Cypraeidae GRAY, 1824
Subfamily  Pseudozonariinae LÓPEZ, 2006
Genus  Pseudozonaria SCHILDER, 1927.
Type species  Cypraea arabicula LAMARCK, 1810, original designation.

The Pseudozonaria group is characterised by its elongate-oval shells with well-developed, often sharply cut teeth, densely spotted margins and freckled dorsum and prominent extremities. Today the group is represented by five Tropical American Pacific species: Pseudozonaria aequinoctialis (SCHILDER, 1931), P. annettae (DALL, 1909), P. arabicula (LAMARCK, 1810), P. nigropunctata (GRAY, 1828), P. robertsi (HIDALGO, 1906) (LORENZ & HUBERT, 2000; MEYER, 2003, 2004). Several fossil species belonging to Zonaria JOUSSEAUME, 1884 and Pseudozonaria SCHILDER, 1927 have been described from the Gatunian Neogene. Zonaria and Pseudozonaria are closely related groups, and not all cypraeid specialists agree about their rank or which species belong in which of the two groups. GROVES (1997) considered Pseudozonaria a subgenus of Zonaria; LORENZ & HUBERT (2000) use Pseudozonaria as an informal group within Zonaria. Dirk Fehse (pers. comm. 2009) recommended the two be used as distinct at full generic rank.

LÓPEZ (2006) justified the separation of a new subfamily Pseudozonariinae from the Zonariinae SCHILDER, 1932 based on molecular data (MEYER, 2004), anatomical differences of the mantle and papillae, and some small differences in shell morphology. They also have distinct geographical distributions; Pseudozonariinae are tropical American, today restricted to the western side of Central America; Zonariinae are known since the Eocene in Europe and Recent West African coasts (LORENZ & HUBERT, 2000).

Pseudozonaria fehsei LANDAU & SILVA, 2010
Pl. 6, Fig. 11; Pl. 7, Figs 1-2

2010a  Pseudozonaria fehsei LANDAU & SILVA, p. 35, pl. 6, fig. 11, pl. 7, figs 1-2.

Dimensions and type material: Holotype NHMW 2010/0038/0013 (Pl. 6, Fig. 11), length 26.6 mm, width 16.9 mm (NHMW coll., ex BL coll.); paratype 1 MOBR-M-3875 (Pl. 7, Fig. 1), length 25.4 mm, width 16.1 mm (EDIMAR coll., ex BL coll.); paratype2 NHMW 2010/0038/0014 (Pl. 7, Fig. 2), length 24.1 mm, width 16.0 mm (NHMW coll., ex BL coll.).

Etymology: I have great pleasure in naming this shell for Dirk Fehse, cypraeid expert, who has taught one of us (BL) a lot about these difficult little shells over the years.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Stratum typicum: Araya Formation, Cubagua Group, Lower Pliocene.

Additional material: Maximum length 26.5 mm. 15 specimens (including Paratypes 3-10) BL coll.; Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; nine specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Formula: 24.7 (66-50.6) 18: 16

Original description:

"Shell small, inflated pyriform, anterior terminal rounded, hardly produced, posterior terminal indented, very short, somewhat curved. Spire involute, covered by terminal callus. Dorsum evenly elevated, smooth, margins weakly callused. Venter slightly convex. Aperture almost straight, relatively narrow and slightly curved in posterior portion, widening slightly at anterior end. Labrum very weakly sinuous, moderately thickened in medial portion, slightly internally bevelled and indented at anterior portion, bearing 17-19 sharply-cut, regular labral denticles, not extending onto the lip. Columella peristome angular,
denticulate along entire length, bearing 16-19 sharp, narrow denticles, extending as folds onto the
columella within the aperture, but not onto venter. Terminal fold marginal, bordering siphonal canal, where
it is strengthened and keel-like. Fossula weakly concave, very steep, clearly delimited from rest of the
columella, anterior border formed by the continuation of terminal fold, barely projected at anterior edge of
fossula and with anterior four or five folds developing very weak denticles at inner edge. Anterior margin
of the fossula free, not fused with inside of dorsum. Suggestion of spotted marginal colour pattern present
in one specimen, dorsum decorticated in all shells (LANDAU & SILVA, 2010a, p. 35)

<table>
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<td>16.2</td>
<td>12.5</td>
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<td>18.1</td>
</tr>
</tbody>
</table>

Table 1: Measurements for Pseudozonaria fehsei LANDAU & SILVA, 2010

Discussion:
A small Pseudozonaria species occurs in the Lower Pliocene Araya Formation and is found in
almost all the localities, although never common. In order to help us separate the species included in
Pseudozonaria the shell formula proposed by SCHILDER (1935, p. 327) has been used. This formula is
derived from measurements taken from all available fully mature and normally formed specimens. It
consists of the following elements: [L (W-H) LT: CT], where L = average length in mm, W = average
width/length ratio in %, H = average height/length ratio in %, LT = normalized number of labral teeth, CT
= normalized number of columellar teeth. The normalized number of teeth – in relation to a shell of 25 mm
length – is calculated as follows: T = 7 + [(c-7) x √(L/L)], where T = normalized number of teeth, c =
teeth counted, L = length. The following species are here considered to belong within the genus
Pseudozonaria:

Pseudozonaria telembiensis (OLSSON, 1964) was described from a single specimen from the
Upper Miocene Angostura Formation of Ecuador. A second specimen was illustrated by GROVES (1997).
The Ecuadorian specimens are smaller and relatively broader than P. fehsei LANDAU & SILVA, 2010 The
formula for P. telembiensis is 19.7 (67-52) 16: 15. If compared to that of P. fehsei; 24.7 (66-50.6) 18: 16, it
can be seen that P. telembiensis has a smaller shell, with relatively fewer labral and columellar teeth.

Pseudozonaria cathayae GROVES 1997 described from the Upper Miocene Esmeraldas beds,
Onozole Formation of Ecuador has finer and more numerous apertural teeth, a more prominent basal
marginal callus, and a thicker, more prominent labial lip with incised teeth. It has the formula: 22.3 (71-57)
19: 17. These differences are clearly reflected in the formula.

Pseudozonaria portelli PETUCH, 1990 from the Pleistocene Bermont Formation of Florida has a
similar shell formula; 25 (63.9-51.5) 19: 15, but the teeth are coarser. The columellar teeth are very
strongly developed over the angulation, but they do not extend across the columellar peristome (see
PETUCH, 1990a, fig. 9). P. portelli also has a different shell shape, somewhat humped at mid-shell due to
the strong development of the marginal callus, especially on the columellar side, but there is insufficient
material to be able to tell whether this character seen in the holotype is a constant specific character.
BERNARD M. LANDAU

LANDAU & SILVA (2010a) also considered Zonaria frassinetti GROVES & NIELSEN, 2003 from the lower Upper Miocene, Tortonian of Chile to belong within the Pseudozonaria annettae group. This species is characterised by its shells with a very wide aperture and widely spaced and sharp denticles. This is a different group within Pseudozonaria (see LANDAU & GROVES, in press).

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Subfamily Cypraeinae GRAY, 1824
Genus Muracypraea WOODRING, 1959.
Type species Cypraea mus LINNAEUS, 1758, by original designation.

There is no consensus as to the generic assignment for this group of species. Muracypraea was originally formalized as a subgenus of Cypraea (WOODRING, 1959). LORENZ & HUBERT (2000) considered “Muracypraea” an informal group within Siphocypraea HEILPRIN, 1887. Siphocypraea was proposed as a subgenus within the genus Cypraea for the Siphocypraea problematica complex, with a strongly curled posterior portion. Muracypraea was proposed for a second group of Caribbean Neogene species with a less curled posterior portion, dorsal gibbosity usually well developed and sometimes dorsal tubercles. The distribution of the groups is also distinct; Siphocypraea occurs mainly in the Plio-Pleistocene of Florida, whilst Muracypraea is Caribbean. DONEDDU & MANUNZA (1996) considered Muracypraea a junior synonym of Barycypraea SCHILDER, 1927. They drew attention to the long geological history of the genus with fossil representatives in the Indo-Pacific (see DHARMA, 2005) and the Caribbean Tertiary. DONEDDU & MANUNZA (1996) traced the origins of the Barycypraea mus complex to the Eocene of Colombia; Barycypraea saltoensis (CLARK in CLARK & DURHAM, 1946). KAY (1993) and GROVES (1997) used Muracypraea at full genus rank. Based on mitochondrial molecular data presented by MEYER (2004), the two extant Barycypraea taxa were placed as sister to Zoila JOUSSEAUME, 1884, reaffirming the validity of the subfamilial clade Bernayinae SCHILDER, 1927, whereas Muracypraea mus was placed in the Cypraeinae GRAY, 1824.

The type species of Barycypraea is Cypraea caputviperae MARTIN, 1899 from the Upper Miocene of Java. This group is well represented in the Indonesian Neogene, but did not survive to the present day. The Recent species usually ascribed to Barycypraea: the B. fultoni-group (see LORENZ & HUBERT, 2000) living today off South Africa are not closely related to the M. mus-group in the Caribbean, but more closely related to Zoila (MEYER, 2004). Some of the shells of the Indonesian fossil Barycypraea group are extremely similar to those of Muracypraea in the Tropical American Neogene, however, the dorsum in the Indonesian shells can be very irregular (i.e. Barycypraea zietsmanni LILTVED & LE ROUX, 1998), some member of the group have four tubercles as opposed to only two (i.e. Barycypraea luxuriosa (SCHILDER 1939)), some have a area on the dorsum which is depressed (i.e. Barycypraea caputviperae). Most importantly, the siphonal channel in the Indonesian group does not have a flattened spatulate horizontal expansions on either side produced from the abapical tips of the inner and outer lips. Although the two taxa may well have had a common Tethyan ancestor, the consistent differences, and the geographic separation, justify keeping the groups separate.

Muracypraea grahami (INGRAM, 1947)
Text-Figure 19, figs 1-6; Pl. 7, Figs 3-4, Pl. 8, Figs 1-3; Pl. 9, Fig. 1

1947b Cypraea grahami INGRAM, p. 6, pl. 2, figs 6-7.

1947b Cypraea rugosa INGRAM, p. 7, pl. 2, figs 8-9 (junior homonym of C. rugosa BRODERIP, 1827).

2010a Muracypraea grahami (INGRAM, 1947) – LANDAU & SILVA, p. 36, pl. 7, figs 3-4, pl. 8, figs 1-3, pl. 9, fig. 1.

Material and dimensions: Maximum length 72.9 mm, two specimens EDIMAR coll.; five specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.
Table 2: Measurements for Muracypraea grahami (INGRAM, 1947)

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<tr>
<th>Specimen 1</th>
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</table>

Table: 69.2 (79-56.9) 14: 29

Discussion:
Numerous specific names have been proposed within the Muracypraea henekeni group. WOODRING (1959a) considered them all a single, highly variable species, although he wrote "some of the names in the synonymy may prove to be useful for local populations when adequate samples are available". For discussion on the correct spelling of the trivial name henekeni see WOODRING (1959a, p. 195).

GROVES (1997) suggested that the M. henekeni group may indeed consist of more than one species, and considered the specimens from Panama and Ecuador to differ from those of the Dominican Republic in being smaller, with a more distinctly triangular outline, in having more prominent pairs of dorsal tubercles and in some instances a 'spike-like' dorsal tubercle. He also noted that the colour striping or blotching of dull reddish brown or yellowish orange often seen in the Panama and Ecuador shells is uncommon in the Dominican material. GROVES (1997) suggested a further revision was pending (pers. comm. Groves and Arnold 2005), but this to our knowledge has not been published. If the SCHILDER (1935, p. 327) formula discussed above is applied, the formula for a population of M. henekeni (Pl. 7, Fig. 5) from Upper Miocene Cercado Formation, Rio Gurabo (loc. TU 1378, BL coll.; for Tulane localities see SAUNDERS et al., 1986) is calculated as 57.9 (76-53) 12: 14. When compared with the formula given above for Muracypraea grahami these figures reflect the narrower, less elevated shell of M. henekeni (G. B. SOWERBY I, 1850; for authorship see PETIT, 2009, p. 200) and smaller normalised number of labral teeth and greater number of columellar teeth.

Muracypraea specimens from the Miocene Gatun Formation of Panama are again different. All the specimens examined (BL coll.) have an axially striped colour pattern or blotching of dull reddish brown or yellowish orange. Additionally, the marginal callus is extremely thin and poorly delimited, and does not extend onto the dorsum, and the periphery of the Gatun shells feel corrugated, whereas it is smooth in M. henekeni. Two distinct taxa are present within the Gatun assemblages; Muracypraea ishmica (BROWN & PILSBRY, 1911) and Muracypraea woodringi LANDAU & GROVES (in press) (Pl. 7, Fig. 6). The shells of M. ishmica have one broad, smoothly rounded, poorly delimited dorsal gibbosity which is centrally positioned. Muracypraea woodringi has shells with two prominent, widely spaced tubercles, each consisting of several smaller warty tubercles and often a small dorsally placed tubercle mid-dorsum. Muracypraea 'henekeni' of GROVES (1997) from the late Miocene Angostura Formation of Ecuador is conspecific with Muracypraea woodringi (LANDAU & GROVES, in press).

Our specimens from Cubagua are again different from either of the assemblages discussed above. The shells are much larger than seen in M. ishmica, their average size similar to the largest M. henekeni from the Dominican Republic. However, their outline is more triangular than that of M. henekeni and the dorsum is higher. The dorsal tubercles are not symmetrical, subparallel as in M. henekeni, but staggered, the left tubercles placed significantly posteriorly compared to the right, and both placed closer to the midline. The tubercles are on the whole smaller and less distinct than in M. henekeni. The margins are corrugated, as in M. ishmica, but more coarsely so. In the best preserved specimen from Cubagua a suggestion of a striped colour pattern is present, akin to that seen in the Gatun shells. There is no consistent difference in the denticulation between the Cubagua shells and M. henekeni, but there are consistently
fewer denticles than in *M. isthmica*. In our opinion these shells clearly represent a distinct species.

**Text-Figure 19.** *Muracypraea grahami* and *M. rugosa*. 1-3, *Cypraea grahami* Ingram, 1947, Holotype UCMP 33524, Cañon de las Calderas, Cubagua Island, Venezuela. Length 80.0 mm, width, 55.3 mm, height, 41.0 mm. 4-6, *Cypraea rugosa* Ingram, 1947, Holotype UCMP 33525, Cañon de las Calderas, Cubagua Island, Venezuela. Length 72.5 mm, width, 58.0 mm, height, 40.0 mm (photographs courtesy of Lindsey Groves).

Ingram (1947b) described two *Muracypraea* species from the Cubagua assemblage of the Cañon de las Calderas; *Cypraea grahami* (holotype, UCMP 33524, Text-Fig. 19, Figs 1-3) and *Cypraea rugosa* (holotype, UCMP 33525, Text-Fig. 19, Figs 4-6). The holotypes would indeed suggest two distinct taxa, *M. grahami* with a far more rounded posterior outline, the anterior left tubercle placed posteriorly to the dorsal hump, and with relatively few apertural teeth, whereas in *M. rugosa* the anterior tubercle is placed on the apex of the dorsal hump and the dentition is finer. Both these forms are present in our specimens from Cubagua (Pl. 7, Figs 3-4; Pl. 8, Figs 1-3; Pl. 9, Fig. 1) together with intermediate forms. Based on our specimen (Plate 7, Figures 3-4) Landau & Silva (2010a) considered the Cubagua shells conspecific with *Cypraea rugosa* Ingram, 1947. Unfortunately, this is a junior homonym of *C. rugosa* Broderip, 1827, and requires a new name if a larger series truly shows it to be distinct species from *M. grahami*. Rather than suggest another trivial name to add to the confusion of *Muracypraea*, Landau & Silva (2010a) considered them all a single species, using the name *M. grahami* (Ingram, 1947b).

Several taxa have been described from the Lower Pliocene southern Caribbean region. Maury (1925a) noted three taxa from Trinidad. The first, *Cypraea henekeni* (Maury, 1925a, pl. 37, fig. 1) represented by a single specimen with only one tubercle is difficult to assess but is somewhat similar to the Gatun shells. The second, *C. henekeni* var. *lacrimula* Maury, 1925a (pl. 37, fig. 2), is from Machapoorie Quarry, Brasso Formation, Middle Miocene and is also very similar to the Gatun morphotype with the widely spaced dorsal tubercles. Maury (1925a, p. 220) remarked how the tubercles consisted of ‘a cluster of three tear-shaped blisters’. The third, *Cypraea caroniensis* Maury, 1925a (pl. 37, figs 3, 5, 6) from the Lower Pliocene Springvale Formation is described as very large (about 60 mm in length), with a high dorsum and one or two tubercles placed close to the mid-line and staggered, very similar to our Cubagua shells. The type material of *Muracypraea caroniensis* is too poor to characterise the species. Lindsey Groves (pers. comm. 2006) has examined further specimens from UC Berkeley, Paleontological Research
Ingram (1947a) described two species from the Lower Pliocene of Colombia: Cypraea tuberae and Cypraea andersoni, both from Tuberá Hill. The holotypes of both are worn and in poor condition. One complete specimen from the Tuberá Formation of Colombia present in the Basel collections (Lot G. 455) has a relatively small shell, more dorso-ventrally depressed than the Cubagua specimens, less humped dorsally and with a more rounded posterior. The outer lip had 17 denticles and the columella 14. In our opinion these are not conspecific with the Cubagua shells.

*Muracypraea henekeni* seems, therefore to have been restricted to the Dominican Republic late Miocene-Lower Pliocene, Cercado and Gurabo formations. On the Yaque del Norte River, Dominican Republic, just downstream from the López section in beds intermittently exposed when the river is at its lowest, I have found numerous specimens (BL coll.) of a much smaller species within this group of cypraeids with a more globose, rounded shell shape, and more numerous labral and columellar teeth. Although inflated at the posterior part of the dorsum, there is no well-defined gibbosity or tubercles and it has a colour pattern of small orange spots entirely covering the dorsum. This colour pattern was illustrated by Dolin (1991, figs 20b, c). These shells are not juvenile *M. henekeni* as the outer lip is callused, and are probably conspecific with *Loxacypraea chilona* (Dall, 1900). Indeed, Dolin (1991, p. 19) mentioned this species occurred in the Dominican Republic and went on to say it coexisted with *M. henekeni*. These beds on the Yaque del Norte River are probably similar in age to the Cercado Formation (Emily Vokes personal communication). Despite numerous collecting trips to the Dominican Republic I have never found the two species together in the same formation.

In the Lower Miocene Cantaure Formation of Falcón, Venezuela another species occurs that falls within the *Muracypraea* lineage. The shells are smallish (31.5-50 mm), their outline is rounded rather than triangular, and their dorsum is high and rounded, with two small, close-set, subparallel tubercles placed close to the mid-line. The colour pattern is well-preserved and consists of large spots on the margins and smaller spots on the dorsum. In fully adult specimens the labral denticles continue for some distance on the base of the labral callus as distinct folds, whereas the labral denticles are restricted to the inner side of the outer lip in both *M. isthmica* and *M. henekeni*. I believe these to be *Muracypraea hyaena* (Schilder, 1939) (Pl. 8, Fig. 4), the type locality of which is in Falcón State, Lower Miocene (Schilder, 1939) (see Landau & Groves, in press). I do not agree with Dolin (1991) who considered *Siphocypraea hyaena* an altered and truncated specimen of *L. chilona*, although the type is in very poor condition. According to Lindsey Groves (pers. comm. 2006) *Muracypraea quaugga* (Schilder, 1939) from the Upper Miocene Uramacao beds of Venezuela is probably a synonym of *M. isthmica*.

The *Muracypraea* lineage was already present in the southern Caribbean in the Lower Miocene. This group seems to have diversified in the Gatunian biogeographical province into at least six species: *M. hyaena* in the Late Miocene southern Caribbean; *M. isthmica* in the Late Miocene Canal Zone; *M. woodringi* Landau & Groves, 2011 in the Late Miocene Canal Zone and early Pliocene Pacific portion of the bioprovince (Angostura Formation, Ecuador; Olsson, 1964, Groves, 1997); *M. henekeni* in the late Miocene Dominican Republic region (Maury, 1917) and *M. caroniensis* and *M. grahami* in the southern Caribbean Early Pliocene. Woodring (1957b, p. 89) noted that *S. chilona*, *M. henekeni* and *M. mus* were part of the same phylogenetic group, but wrote ‘None of the members of that lineage [of fossil *Muracypraea*] is a likely immediate predecessor of *C. mus*, which is unknown before the Pleistocene (…).’ He did not qualify why he felt the direct relationship between *M. henekeni* and *M. mus* unlikely. Today *M. mus* is found in the southern Caribbean (Lorenz & Hubert, 2000), and it is most likely descended from *M. caroniensis*. 
The shells of the living *Muracypraea mus* (Linnaeus, 1758) differ from those of its fossil congeners in the character of the columellar dentition, obsolete in the central portion, whereas the dentition is always well-developed throughout in all the fossil species. The colour pattern is also different from any of the fossil taxa. In the Recent populations there seem to be tuberculate and non-tuberculate specimens, the significance of which has produced much debate. Doneddu & Manunza (1996) separated the *M. mus* complex into two species and one subspecies; *Muracypraea mus mus*, *Muracypraea mus tristensis* (Petuch, 1987) and *Muracypraea donmoorei* (Petuch, 1979). Lorenz & Hubert (2000) recognized two subspecies, *M. mus mus* (non-tuberculate) and *M. mus bicornis* (G. B. Sowerby III, 1870) (tuberculate) restricted to deeper water. They stated that *M. m. bicornis* was isolated from populations of *M. mus mus*. These populations have been split further into several geographical and ecological variants Petuch (1979, 1987), taxa of dubious taxonomic significance.

The presence of *Muracypraea* in Cubagua is important, as it is one of the typically tropical American Tertiary to Recent taxa, and so detailed comments are included on some of the described forms. However, the taxonomy proposed is clearly provisional as we await the long-promised revision of the group by Groves and Arnold.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (Ingram, 1947b).

**Family** Pediculariidae H. & A. Adams, 1855
**Subfamily** Cypraeidiinae F. A. Schilder, 1925
**Genus** Jenneria Jousseaume, 1884.

*Type species* Cypraea pustulata Lightfoot, 1786, by original designation.

The genus *Jenneria* Jousseaume, 1884 comprises a group of beautiful medium to small cypraeid-like shells covered with wart-like pustules on the dorsum and teeth that extend across the venter. The zoological position of this group is not yet settled; they were placed in the Eocypraeidae Schilder, 1924 by Fehse (2001) and Landau & Fehse (2004), in the Ovuilidae Fleming 1822, subfamily Jennerininae Thiele, 1929 by Bouchet & Rocroi (2005), and more recently transferred to the Pediculariidae H. & A. Adams, 1855, subfamily Cypraeidiinae F. A. Schilder, 1925 by Lorenz & Fehse (2009). Preliminary DNA results support a separation from the Cypraeidae and Ovuilidae and possibly a closer relationship to the Triviidae Troschel, 1863 (Simone, 2004). They are a perfect example of Woodring’s “paciphile” genus, widespread in the Caribbean Neogene, but today found only in the Tropical American Pacific.

**Jenneria loxahatcheensis** (M. Smith, 1936)
Pl. 9, Figs 2-4

<table>
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<th>Year</th>
<th>Citation</th>
</tr>
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<td>1936</td>
<td><em>Cypraea (Pustularia) gabbiana</em> (?) <em>loxahatcheensis</em> M. Smith, p. 137, pl. 9, fig. 3.</td>
</tr>
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<td>1967b</td>
<td><em>Jenneria loxahatcheensis</em> (MAXWELL SMITH) – Olsson, p. 7, pl. 2, fig. 2.</td>
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<td>1994</td>
<td><em>Jenneria loxahatcheensis</em> (M. Smith, 1936) – Petuch, p. 110, pl. 34, figs A-C.</td>
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<td>2010a</td>
<td><em>Jenneria loxahatcheensis</em> (M. Smith, 1936) – Landau &amp; Silva, p. 39, pl. 9, figs 2-4.</td>
</tr>
</tbody>
</table>

**Material and dimensions:** Maximum length 25.8 mm, 11 specimens BL coll., Lower Pliocene, Araya Formation Caño de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; one specimen BL coll., (lower yellow fine sandy bed), one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

The group in tropical America was first monographed by Olsson (1967b), and further taxa were described by Gibson-Smith (1974) and Petuch (1988, 1991). Unfortunately, *Jenneria* specimens are rare in all Caribbean Neogene deposits, and all the previous discussions were based on relatively few individuals. I have managed to amass a relatively good collection of *Jenneria* from the Neogene Caribbean...
(BL coll.), which has allowed us to shed further light on the intraspecific variability and the stratigraphic range of some of these species.

Two quite distinct species occur in the Lower Miocene Caribbean: *Jenneria dominicensis* OLSSON, 1967 (maximum length 20.8 mm) is characterised by its dorsal sculpture of pustules interconnected by a network of fine, interlaced, transverse threads that extend right across the dorsum. I have examined two specimens which vary a little in the size of the pustules, found in the Lower Miocene Baitoa Formation, Rio Yaque del Norte, López section right at the base (BL coll.), a coralline facies exposed only when the river is low. The *Jenneria* specimens were found in cavities in the corals. OLSSON (1967b, p. 7) wrote ‘The types are the two larger of the four specimens in the Gabb collection. Exact locality and horizon in Santo Domingo unknown’. I have not found this species in any of the other Dominican localities. The second species is *Jenneria venezuelana* GIBSON-SMITH, 1974 from the Lower Miocene Cantaure Formation of Venezuela, which is the smallest Caribbean *Jenneria* species (19 lots, maximum length 18.1 mm, although usually much smaller, BL coll.). This species characterised by usually having a well-developed dorsal sulcus, although it is subobsolete in two specimens, by having short anterior and posterior terminal protrusions, which are hardly constricted, and by having the ventral ribs extended onto the dorsal aspect of the terminals. In fact this is a character of the specimens of both these Lower Miocene species, although they can be immediately distinguished by the latticework of threads completely covering the dorsum of *J. dominicensis*.

In the Upper Miocene deposits of the Dominican Republic OLSSON (1967b) recognized two species: *Jenneria gabbiana* (GUPPY, 1876) from the Gurabo Formation and *Jenneria pilsbryi* OLSSON, 1967, locality unknown. I have examined 24 lots of *J. gabbiana* (BL coll.), all from the Gurabo River in coral facies, as before often in ‘pockets’ between or in the corals. They are extremely variable in size, fully adult shells measuring from 14.6-22.7 mm in length (all adults, as *Jenneria* species do not develop their pustular dorsum until fully adult, see OLSSON, 1967b), the dorsal sulcus can be well developed or absent, the pustules variable in strength but relatively small. However, despite these variable characters, the species is distinguished by its relatively elongate cylindrical shape with poorly developed terminals, by its fine, close-set ribs on the dorsum that extend onto the sides as fine radial threads, by its numerous teeth, 27-30 on the labrum, 21-24 on the columella, and by the fine pustular sculpture on the dorsum. I have not found any specimen that can be positively identified as *J. pilsbryi*.

In the Lower Pliocene *Jenneria* has been recorded from a single specimen by ANDERSON (1929) from the Tuberá Formation of Colombia as *Cypraea (Pustularia) gabbiana* Guppy, and by us from the Araya Formation. The shell illustrated by ANDERSON (1929, pl. 15, figs 4-5) is clearly not conspecific with the Dominican *J. gabbiana*; the terminals are much more protruding and it has far fewer and stronger basal ribs. This shell is almost certainly conspecific with the Cubagua specimens, which will be discussed later.

The systematics of the Upper Pliocene-Pleistocene Caribbean assemblages becomes more difficult. OLSSON (1967b) recognized three species in the Floridian fauna. However, PETUCH (1988, 1991) introduced several new taxa from the Floridian deposits differing mainly in details of the dorsal sculpture and outline, but gave no account of the intraspecific variability within his taxa. In order to ascertain how many species exist in the Caribbean Upper Pliocene-Pleistocene deposits we have examined a larger number of specimens (47, BL coll.) all collected from the Lower Pleistocene Moin Formation of Costa Rica. This series of shells shows a tremendous range of variability, so much so that if one had only the extreme forms one would be excused for considering them as belonging to distinct species. This exact observation was made by GIBSON-SMITH (1974) when discussing the variability seen in populations of the Recent tropical American Pacific species *Jenneria pustulata* (LIGHTFOOT, 1786) and is beautifully illustrated for the Recent species by LORENZ & FEHSE (2009). In size the fully adult shells vary from 20.8 to 32.0 mm. The shell profile varies from broad to elongated, the terminals are usually quite strongly produced, somewhat less so in the broader forms, the size and density of pustules is markedly variable, the dorsal sulcus well-developed to obsolete, the junction between the base and dorsum can be smooth to angular and callused, the number of teeth on the labrum 19-22, on the columella 16-19. In fact, the only really constant character is the very narrow aperture, slightly wider abapically, strongly curved inwards adapically, so that in ventral view neither the inner edge of the fossula nor the inside of the shell dorsum are visible.
Having gauged the range of variability within the Costa Rican population we can now try and reassess the Floridian material. If we consider OLSSON’s (1967b) species, Jenneria hepleri OLSSON, 1967 is a very distinct species from the Pliocene Pinecrest Formation quite unlike any of its congeners, the shell is broader and the pustules are far larger and less numerous. Jenneria richardsi OLSSON, 1967 and J. loxahatcheensis (M. SMITH, 1936) are more difficult to distinguish. According to OLSSON (1967b, p. 7) J. loxahatcheensis “(…) differs by its more ovate shape, the two ends not so strongly produced”. Later (1967, p. 8) he adds “From J. loxahatcheensis, this species [J. richardsi] is distinguished by its more elongated form, its weaker dorsal furrow as well as by details of sculpture”. As mentioned above most of these characters are variable at the intraspecific level. However, the width of the aperture was not stressed by Olsson and it can clearly be seen from his figure (OLSSON 1967b, pl. 2, fig. 1a) that the aperture of J. richardsi is much wider so that in vertral view both the fossula and the inside of the shell can be seen. We examined four specimens of J. richardsi (BL coll.) from the Griffin Brothers pit (maximum length 28.8 mm), which corresponds to the Lower Pleistocene Caloosahatchee Formation (fide PETUCH, 1994) and the aperture is consistently wider than the Costa Rican material. Moreover, although the number of teeth on the labrum is not significantly different (21-23), they are fewer and more widely spaced teeth on the columella (14-15). We examined one specimen from the Capeletti Brothers Pit (BL coll.), Upper Pleistocene Bermont Formation (fide PETUCH, 1994) that we identify as J. loxahatcheensis with a narrow aperture, 22 teeth on the labrum and 17 on the columella, which is indistinguishable from the Costa Rican material. Therefore, contrary to what OLSSON (1967b, p. 4) concluded, the Costa Rican shells are J. loxahatcheensis and not J. richardsi. We therefore agree with Olsson’s interpretation of the Floridian faunas. Although we found the two species in distinct formations, no stratigraphic implications are intended due to lack of material.

PETUCH (1988) described a large species, Jenneria lindae, from Mule Pen Quarry, Buckingham formation, equal to the uppermost Pinecrest Beds, Lower Pleistocene (PETUCH, 1994). He compared it to J. gabbiana, but the Floridian shell is much larger than any we have found in the Dominican Republic and has far fewer ribs on the base. Jenneria lindae is far more closely associated with the Floridian group than J. gabbiana. It is very similar to J. richardsi, with a wider aperture than to J. loxahatcheensis, but has more numerous columellar teeth. This may just be a function of its large size. We also noted that in the Costa Rican material, the larger specimens have the greatest number of teeth.

PETUCH (1991) described two new taxa from the Florida fauna; the first is Jenneria keatoneae from the Miami Canal Dig, Lower Pleistocene Caloosahatchee Formation. Inexplicably this species was never illustrated in apertural view, which according to our observations is the most useful. None of the characters discussed by PETUCH (1988) in his comparison with J. richardsi are diagnostic. The description stated “(…) columella with 14 teeth; lip with 19 teeth (…)” (PETUCH, 1991, p. 19). This fits within the variability of J. richardsi, of which it is probably a junior subjective synonym. The second is Jenneria violetae from Petuch Unit 7, Late Pliocene Pinecrest Formation at APAC, Sarasota County. In PETUCH’S (1991) discussion it was compared to J. lindae, another new taxon without even a mention of the two closely similar previously established taxa in the Floridian Pliocene, J. loxahatcheensis and J. richardsi. In the description Petuch stated “(…) 18 teeth on the outer lip; 18 teeth on the columella (…)” (PETUCH, 1991, p. 20). The holotype (PETUCH, 1991, pl. 2, figs 8-9, refigured slightly more clearly in PETUCH, 1994, pl. 34, figs K-L) and a second specimen from the same locality (PETUCH, 1994, pl. 34, figs M-N), only have 15 columellar teeth and a wide aperture similar to that of J. richardsi of which it is undoubtedly a junior synonym. In summary, all the taxa described by PETUCH (1988, 1991) are probably synonyms of J. richardsi.

Comparing the material from Cubagua with the species discussed above, the Venezuelan shells are closest to the Floridian J. richardsi- J. loxahatcheensis group. The Cubagua shells measure 23.3 and 23.5 mm in length, smaller than the average for either of the preceeding species (although some of the Costa Rican shells are smaller), 21-22 labral teeth, 17 columellar teeth and a narrow aperture, again similar to the Costa Rican shells. The dorsal sulcus is subobsolete and the dorsal pustules relatively small. In view of the intraspecific variability encountered within this genus, we consider the Cubagua shells conspecific with those from Costa Rica, J. loxahatcheensis.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela;
Tuberá Group, northern Colombia (Anderson, 1929).
Lower Pleistocene: Caloosahatchee Formation, Florida (Olsson, 1967b); Moin Formation, Puerto Limon, Costa Rica (Robinson, 1991).
Upper Pleistocene: Bermont Formations, Florida (Petuch, 1994).

Superfamily Triviioidea Troschel, 1863
Family Triviidae Troschel, 1863
Subfamily Triviinae Troschel, 1863
Genus Pusula Jousseaume, 1884.

Type species Cypraea radians Lamarck, 1810, by original designation.

As discussed by Fehse & Landau (2003, p. 99), only some members of the genus display all the typical features (see Cate, 1979), and the position of the aperture and the depression of the base are variable. The only constant characters that clearly separate this group from other triviids are the dorsal sulcus, which in most cases is wide and smooth, with the ribs sharply bisected and forming tubercles, spinous in some species, as well as the fewer, coarser ribs. Cypraea pediculus Linnaeus, 1758 is considered to belong within this genus (Fehse, 2002; Fehse & Landau, 2003) and not to Niveria Jousseaume, 1884 (= Salcotrivia Schildner, 1933; see Fehse & Landau, 2003).

Pasula pediculus (s.l.) (Linnaeus, 1758)
Pl. 9, Fig. 5

1758 Cypraea pediculus Linnaeus, p. 724.
1767 Cypraea pediculus forma indica Linnaeus, p. 1180 [name not validly established].
1793 Cypraea oniscus Röding, p. 24.
1793 Cypraea pulex Röding, p. 24 [name not validly established].
1817 Cypraea sulcata Dillwyn, p. 466.
1828 Cypraea Pediculus – Wood, p. 84, pl. 17, fig. 60.
1846 Cypraea pediculus Gray – Reeve, pl. 23, fig. 131.
1859 Cypraea (Trivia) pediculus Linné – Chenu, p. 270, fig. 1733.
1877 Trivia pediculus var. picturata Mörch, p. 49 [name not validly established].
1927 Triviella gamma Mestayer, 188, text-fig. 5.
1928 Trivia (Trivia) pediculus (Linné) – Woodring (partim), p. 319, pl. 22, figs 6-7, 10-11 (non 8-9 = Pasula suffusa jamaicensis Schildner, 1932).
1940 Trivia pediculus Linné – Perry, p. 136, pl. 28, fig. 206.
1953 Trivia (Trivia) pediculus (Linné) – Olsson & HARBISON, p. 265, pl. 60, fig. 1.
1954 Trivia pediculus Linné – Abbott, p. 177, pl. 21, fig. bb.
1955 Trivia pediculus (Linné) – Perry & schwengel, p. 148, pl. 28, fig. 206.
1958 Trivia pediculus (Linné) – Coomans, p. 80, pl. 13, figs left lower and centre.
1961 Trivia pediculus Linné, 1758 – Warmke & Abbott, p. 90, pl. 16, fig. f.
1973 Trivia pediculus (Lin.) – Morris, p. 177, pl. 48, fig. 1.
1974 Trivia (Pusula) pediculus (Linné, 1758) – Abbott, p. 147, fig. 1623, pl. 3, fig. 1623.
1974 Trivia (Pusula) suffusa (Gray, 1832 [sic]) – Abbott, p. 148, fig. 1625 [non Pasula suffusa (Gray, 1827)].
1975 Trivia pediculus Linné 1758 – Humfrey, p. 103, pl. 22, fig. 1.
1975 Trivia (Pusula) pediculus (Linnaeus, 1758) – Rios, p. 71, pl. 20, fig. 289.
1979 Niveria (Niveria) pediculus pediculus (Linnaeus, 1758) – Cate, p. 48, figs 55, 55a.
1979 Triviella gamma Mestayer – Cate, p. 50, pl. 40, fig. 172.
1983 Trivia (Pusula) pediculus (Linnaeus, 1758) – H. E. & E. E. Vokes, p. 21, pl. 7, fig. 10.
1988 Trivia pediculus (L., 1758) – Jong & Coomans, p. 64, pl. 35, fig. 331.
1991 Trivia pediculus (Linnaeus, 1758) – LiPe & Abbott, p. 50, illus.
1994 Niveria pediculus (Linnaeus, 1758) – Petuch, pl. 25, figs I-J.
1994 Niveria permagna bermontiana Petuch, p. 264, pl. 26, fig. E.
1994 Trivia pediculus (Linné, 1758) – Diaz & Puyana, p. 165, fig. 610.
1994 Trivia (Niveria) pediculus (Linnaeus, 1758) – Rios, p. 77, pl. 26, fig. 296.
1998 Pasula pediculus (Linneo, 1758) – Fernández Milera, p. 114, figure.
Material and dimensions: One specimen BL coll., 13.9 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

The *Pusula pediculus* species group has been present in the Caribbean Neogene since at least the Late Miocene. We have examined specimens of a *P. pediculus*-like species from both the Upper Miocene Cercado and Lower Pliocene Gurabo Formations of the Dominican Republic (BL coll.). We have not, however, found it in the Lower or Middle Miocene Venezuelan assemblages. This species group is particularly well represented in the Floridian Plio-Pleistocene, where specimens attain a very large size. This large form has been described as a distinct species, *Pusula permagna* (JOHNSON, 1910). PETUCH (1994) added two further taxa to this species-group in Florida: *Pusula dalli* and *Pusula permagna bermontiana*. *Pusula dalli* differs from the Recent *P. pediculus* in being smaller and having more numerous riblets crossing the outer lip (21-23 vs. 15-18). *P. permagna* is larger, with even more numerous riblets crossing the outer lip (24-25). We see no significant difference between the single Cubagua specimen and shells in the Recent populations, but hesitate to say they are conspecific pending a revision of the tropical American Neogene *Pusula* species (in preparation, Dirk Fehse, pers. comm. 2009).

The Recent Caribbean *Pusula suffusa* (GRAY, 1827) is a similar species differing from *P. pediculus* in having more numerous ribs; the outer lip is crossed by 19-23 (usually 20) riblets whereas *P. pediculus* has 15-18 (usually 17) (ABBOTT, 1974; REDFERN, 2001). The single Cubagua shell has 18 riblets crossing the outer lip. One of the specimens illustrated by WOODRING (1928, pl. 22, figs 8-9) as *Trivia (Trivia) pediculus* from the Bowden Beds of Jamaica was later described as a subspecies of *Niveria suffusa*, *N. suffusa jamaicensis* SCHILDER, 1932.

Geological and geographical distribution:

Upper Miocene: Cercado Formation, Dominican Republic (BL coll.).

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Gurabo Formation, Dominican Republic (BL coll.).

Lower-Upper Pliocene: Bowden Formation, Jamaica (WOODRING, 1928)


Upper Pleistocene: Fort Thompson Formation, Florida (OLSSON & HARBISON, 1953; PETUCH, 1994); La Isabella Formation, Dominican Republic (BL coll.).

Recent: North Carolina to Brazil (ABBOTT, 1974).

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*Pusula orientalis* SCHILDER, 1939
Pl. 9, Figs 6-7

1939 *Pusula (Pusula) radians orientalis* SCHILDER, p. 11, textfigs 2-3.

1969 *Trivia (Pusula) radians orientalis* (SCHILDER) – JUNG, p. 477, pl. 48, figs 3-5 (holotype).

2010a *Pusula orientalis* SCHILDER, 1939 – LANDAU & SILVA, p. 42, pl. 9, figs 6-7.

Material and dimensions: One specimen BL coll., 13.6 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.
Discussion:

Although some members of the genus display all typical shell characters (see CATE, 1979), the position of the aperture and the depression of the base are variable. Unfortunately the dorsum in our single specimen is decorticated, but the rounded base and centrally placed aperture are suggestive of *Pusula*.

*Pusula orientalis* SCHILDER, 1939 (holotype Pl. 9, Fig. 7) was based on a shell fragment from the Pleistocene Matura Shell Bed of Trinidad. According to SCHILDER (1939) it differs from *Pusula radians* (LAMARCK, 1811) in having a slightly greater number of dorsal ribs and denticles, and in having the terminals slightly more produced. The single Cubagua shell has a similar number of ribs on the dorsum and on both the labrum and columella as the holotype (14 and 17 respectively in the holotype; 14 and 18 in our specimen from Cubagua). JUNG (1969; figured specimen holotype NMB H11228) considered the differences described by SCHILDER (1939, p. 11) to fall within the variability of the Recent tropical American Pacific species *P. radians* (LAMARCK, 1811), but in view of the fragmentary material available he did not synonymise the two. Similarly, with our single decorticated specimen, we follow suit. Dirk Fehse (pers. comm. 2009) suggested this species was more like *Pusula solandri* (G. B. SOWERBY I, 1832), and that recent authors had consistently mixed the two. Again, we await his revision of the genus.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.
Pleistocene: Matura Shell Bed, Talparo Formation, Trinidad (JUNG, 1969)

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**Superfamily** Naticoidea GUILDING, 1834  
**Family** Naticidae GUILDING, 1834  
**Subfamily** Naticinae GUILDING, 1834  
**Genus** *Polinices* MONTFORT, 1810.  
Type species *Polinices albus* MONTFORT, 1810, by original designation.

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**Polinices intemeratus** (PHILIPPI, 1851)  
Pl. 9, Fig. 8

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1851 *Natica intemerata* PHILIPPI, p. 129, pl. 18, fig. 10.  
1853 *Natica intemerata* PHILIPPI, p. 233 (text).  
1855 *Natica alabaster* REEVE, pl. 9, fig. 33.  
1855 *Natica rapulum* REEVE, pl. 12, fig. 47.  
1863 *Natica intemerata* PHILIPPI – G. B. SOWERBY II, p. 87, pl. 4, fig. 44.  
1866b *Natica intemerata* PHILIPPI – G. B. SOWERBY II, p. 87, pl. 4, fig. 44.  
1866a *Natica intemerata* PHILIPPI – G. B. SOWERBY II, p. 87, pl. 4, fig. 44.  
1871 *Polinices intemeratus* (PHILIPPI) – PALMER & HERTLEIN, p. 78, pl. 19, fig. 3.  
1955 *Polinices (Polinices) intemeratus* (PHILIPPI, 1853 [sic]) – KEEN, p. 322, fig. 269.  
1958 *Polinices (Polinices) intemeratus* (PHILIPPI, 1853 [sic]) – KEEN, p. 478, fig. 877.  
1971 *Polinices (Polinices) intemeratus* (PHILIPPI, 1853 [sic]) – KEEN, p. 478, fig. 877.  
2010a *Polinices intemeratus* (PHILIPPI, 1851) – LANDAU & SILVA, p. 43, pl. 9, fig. 8.

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**Material and dimensions:** Maximum length 32.0 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

*Polinices intemeratus* (PHILIPPI, 1851) belongs to the tropical American Pacific *Polinices uber* species-group. They are distinguished from other members of the genus by the presence of a riblet within the umbilicus, which runs along the midline of the umbilical channel, expressed on the columella as a low fold. This feature can be clearly seen in the Cubagua specimen (Pl. 7, Fig. 7a) and clearly separates it from all the other Caribbean Neogene *Polinices* species. *Polinices otis* (BRODERIP & G. B. SOWERBY I, 1829) living in the Recent tropical American Pacific (MARINCOCVICH, 1977) and found in the Pacific Upper Miocene of the Esmeraldas beds, Onozole Formation, Ecuador (PITT & PITT, 1992) has a closely similar...
shell, but differs in being more elongate, higher-spired, having a more inflated anterior portion to the last whorl and a wider umbilicus, which is also divided, but lacking a sharp riblet. This is the first record of the species in the Caribbean Neogene, and adds to the small number of paciphilic species found in the Araya Formation deposits.

**Geological and geographical distribution: Atlantic**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela

**Geological and geographical distribution: Pacific**
Upper Miocene: Bahía Formation, Ecuador (Pitt & Pitt, 1992)
Pleistocene: Mexico (Palmer & Hertlein, 1936).
Recent: Western Baja California south to Galapagos Islands and Bahía Independencia, Peru (Marincovich, 1977).

*Polinices stanislasmeunieri* (Maury, 1917)
Text-Figure 20; Pl. 10, Figs 1-3

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<th>Year</th>
<th>Author</th>
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<td>1917</td>
<td>Maury</td>
<td>P. 136, pl. 23, figs 15-16.</td>
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<td>1932</td>
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<td>(Hanna &amp; Israelsky) – Olsson, p. 207, pl. 24, fig. 9.</td>
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<td>1942</td>
<td>Maury – Rutsch</td>
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<td>1942</td>
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<td>p. 40, pl. 37, figs 10, 15, <em>(hoc opus</em> Text-Fig. 20, Fig. 3).</td>
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<td>1951</td>
<td>Maury – Mark</td>
<td>p. 368.</td>
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<td>1957a</td>
<td>Maury – Woodring</td>
<td>p. 90, pl. 21, figs 3-4.</td>
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**Material and dimensions:** Maximum height 56.2 mm, two specimens NMB lot DS 6937; five specimens NMB lot DS 6926/1; three specimens NMB lot DS 6926/2; 11 specimens EDIMAR coll.; nine specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
This species was fully discussed by Pitt & Pitt (1992). According to the authors *Polinices stanislasmeunieri* (Maury, 1917) forms part of the tropical American “white *Polinices* group”, today is represented by more species in the tropical Eastern Pacific than in the Caribbean. Pitt & Pitt (1992) wrote that *P. stanislasmeunieri* probably originated in the Caribbean, although it seems from the distribution below that the Pacific record is older.

*Polinices stanislasmeunieri* is common in the Cubagua assemblage and grows to a much larger size than those from the Middle-Upper Miocene Gatun Formation of Panama. It is extremely variable in almost every aspect: shell thickness, height of the spire and strength of the shoulder on the last whorl. The parietal callus is extremely well developed, more so than the specimens illustrated by Woodring (1957a, pl. 21, figs 11-14) from the Gatun formation, almost filling the umbilicus, similar to the shells figured by...
Jung (1969, pl. 48, figs 16-18; NMB H 15145-7) from the Lower Pliocene Punta Gavilán Formation of Venezuela, although Rutsch (1934, pl. 2, figs 4-5) described Polinices (Polinices?) schombergki based on a single damaged specimen, which may be conspecific with P. stanislasmeunieri.

Polinices coensis Mansfield, 1930 is extremely similar to P. stanislasmeunieri, and contrary to the opinion expressed by Woodring (1957a, p. 91), grows just as large (maximum height 54.2 mm, BL coll.) and shows the same variability in the thickness of the parietal callus as P. stanislasmeunieri. It differs in being lighter-shelled, the spiral sculpture is a little more evident, and the sulcus between the parietal callus and the funicle is usually deeper, although in a few specimens from the Upper Pliocene-Lower Pleistocene Pinecrest Beds at APAC, Sarasota County, Florida, the sulcus is not well developed. Mansfield (1930) erected the genus Dallitesta, with D. coensis as the type species without any discussion or differentiating characters. We assume his character for the genus were distinct spiral sculpture, a narrow umbilicus and weak funicle separated from the parietal callus by a distinct sulcus. This led Kabat (1991) to synonymize Dallitesta with Euspira Agassiz, 1838. However, these characters are not constant within P. coensis, and P. stanislasmeunieri also has weak spiral sculpture. We therefore follow Woodring (1957a) and Pitt & Pitt (1992) in synonymizing Dallitesta with Polinices.

There is still disagreement as to the generic assignment of species in the genera Euspira Agassiz, 1838, Lunatia Gray, 1847 and Polinices, Montfort, 1810.

Text-Figure 20. Some Polinices types synonymised with P. stanislasmeunieri (Maury, 1917). Fig. 1. Polinices caparona Maury, 1925, holotype PRI 1072, height 47.4 mm, Manzanilla Formation, Trinidad, Middle Miocene. Fig. 2. Polinices springvalensis Maury, 1925, holotype PRI 1073, height 40.0 mm, Springvale, Trinidad, Springvale Formation, Lower Pliocene. Fig. 3. Polinices stanislasmeunieri venezuelana F. Hodson, 1927 holotype PRI 22868, height 26.3 mm, Urumaco, Venezuela, Caujarao Formation, Upper Miocene. Images courtesy of the Paleontological Research Institution.

Geological and geographical distribution: Atlantic
Middle Miocene: Lower Gatun Formation, Panama (Woodring, 1957a).
Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917); Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (NMB 2984); Middle and Upper Gatun Formation, Panama (Woodring, 1957a).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; El Veral Formation, Venezuela (Harris in Hodgson et al., 1927, as P. stanislasmeunieri venezuelana); Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934, as P. (P?) schombergki); Tuberá Group, northern Colombia (Anderson, 1929); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad, Trinidad (Maury, 1925a, also as P. caparona and P. springvalensis; H. E. Vokes, 1938; Rutsch, 1942; Jung, 1969).
Upper Pliocene: Banano Formation, Costa Rica (Olsson, 1922).
Geological and geographical distribution: Pacific
Middle Miocene Zorritos Formation, Peru (HANNA & ISRAELSKY, 1925, as N. coronis; Olsson, 1932, as N. coronis).

Genus Mammilla SCHUMACHER, 1817
Type species Mammilla fasciata SCHUMACHER, 1817, by monotypy.

Although usually considered a subgenus of Polinices (i.e. CERNOHORSKY, 1971; MARINCOCVICH, 1977), KABAT et al. (1997) and KABAT (1998; 2000) raised the taxon to full generic rank.

Mammilla arepa LANDAU & SILVA, 2010
Pl. 9, Fig. 9-10

2010a Mammilla arepa LANDAU & SILVA, p. 45, pl. 9, figs 9-10.

Dimensions and type material: Holotype NHMW 2010/0038/0016 (Pl. 9, Fig. 9), length, 31.2 mm, height, 27.0 mm (NHMW coll., ex BL coll.); paratype1 MOBR-M-3876 (EDIMAR coll., ex BL coll.) length 31.5 mm; Paratype 2 NHMW 2010/0038/0015 (Pl. 9, Fig. 10), length 35.8 mm, (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula, Venezuela (NHMW coll., ex BL coll.).

Derivatio nominis: In honour of our staple food, the ‘arepa’, a corn bread, similar in shape to this shell, not particularly tasty, but filling, that kept us going during our field trips to Venezuela. Noun used in in apposition.

Locus typicus: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.
Stratum typicum: Araya Formation, Cubagua Group, Lower Pliocene.
Additional material: Two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; seven specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation, Cerro Barrigón, Araya Peninsula.

Diagnosis:
A medium-sized auriculiform Mammilla species with a large aperture, wide umbilicus, spiral sculpture completely absent, narrow funicule, small, flattened funicular callus, and parietal callus very weakly developed.

Original description:
“Shell medium-sized, relatively fragile, depressed-auriculiform; suture apressed, last whorl greatly expanded. Protoconch of 2.25 smooth, depressed whorls, with small nucleus. Junction with teleoconch not clearly delimited. Teleoconch of three depressed whorls; spire of medium height, whorls weakly concave, last whorl rapidly expanding, with a narrow, weakly concave infrasutural area. Surface sculptured by prominent concentric growth lines. Aperture very large, ovate; outer lip simple, weakly sinuous in profile; columella almost straight. Junction of parietal and columellar callus posterior to centre of aperture. Parietal callus poorly developed for genus, not greatly thickened, narrow, sharply delimited, with a slightly more expanded anterior lobe; transverse groove hardly developed. Umbilicus very wide, open; funicule narrow, elevated; funicular callus flattened, narrow, slightly overhanging funicule medially; anterior channel broad, shallow; posterior sulcus narrow, deep (for terminology see MARINCOCVICH, 1977) (LANDAU & SILVA, 2010a, p. 45)”.

Discussion:
The genus Mammilla SCHUMACHER, 1817 is distinctly tropical, confined largely to the Indo-Pacific region, with a single species present in the Recent eastern Pacific: Mammilla caprae (PHILIPPI, 1850) (MARINCOCVICH, 1977). It is characterised by thin-shelled species with a flattened auriculiform shape, a narrow funicular callus and a thin parietal callus. The genus/subgenus Hypterita WOODRING, 1957, which has almost completely Sinum-shaped shells is similar, but the funicular callus is greatly developed, flattened and expanded covering most of the umbilicus. Mammilla arepa LANDAU & SILVA, 2010 differs
from the Recent eastern Pacific species in being completely devoid of spiral sculpture, whereas *M. caprae* has a spiral sculpture of minute wavey costae. The umbilical width, shape of the funicule and development of the parietal callus is similar in both species. *Mammilla arepa* LANDAU & SILVA, 2010 differs from the numerous Indo-Pacific taxa illustrated by CERNOHORSKY (1971) and HOLLMANN (2008) in details of the funicular shape and absence of spiral sculpture, which is present in many of the Recent species.

The presence of the subgenus *Mammilla* in Cubagua adds a further member to the growing list of WOODRING’s (1966) Paciphile taxa. MARINCOVICH (1977) suggested that *Mammilla* was a Pleistocene migrant from the Indo-Pacific. With this new record of *Mammilla* in the Lower Pliocene Caribbean another possible scenario is that the genus reached the Atlantic from around South Africa as in the case of some tonnoideans (BEU, 2010). *Mammilla arepa* LANDAU & SILVA, 2010 is found in all the Venezuelan Lower Pliocene Araya Formation localities, but is commonest in the coarse reddish sands at Cerro Barrigón.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela

**Genus** *Naticarius* DUMÉRIL, 1805.
**Type species** *Nerita canrena* LINNAEUS, 1758, by monotypy.

*Naticarius canrena canrena* (LINNÉ, 1758)
Pl. 10, Figs 4-5

<table>
<thead>
<tr>
<th>Year</th>
<th>Author</th>
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<tbody>
<tr>
<td>1758</td>
<td>Nerita canrena LINNAEUS</td>
<td>p. 776.</td>
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<td>1855</td>
<td>Natica canrena LINNAEUS – REEVE</td>
<td>pl. 4, fig. 14.</td>
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<td>1867</td>
<td>Natica canrena LINN. – GUPPY</td>
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<td>1886b</td>
<td>Natica canrena LINN. – TRYON</td>
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<td>1925a</td>
<td>Natica canrena (LINNAEUS) MOERCH – MAURY</td>
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<td>Natica canrena (LINNAEUS) – MANSFIELD</td>
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<td>1940</td>
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<td>1942</td>
<td>Natica (Naticarius) canrena LINNÉ – RUTSCH</td>
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<td>1947</td>
<td>Naticarius verae REHDER</td>
<td>p. 19, pl. 1, top figure.</td>
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<td>1954</td>
<td>Natica canrena LINNÉ – ABBOTT</td>
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<td>1958</td>
<td>Natica canrena LINNÉ 1758 – ABBOTT</td>
<td>p. 50, pl. 2, fig. a.</td>
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<td>1960</td>
<td>Natica canrena – PARKER</td>
<td>p. 323, pl. 5, fig. 2.</td>
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<td>1961</td>
<td>Natica canrena LINNÉ, 1758 – WARMEK &amp; ABBOTT</td>
<td>p. 96, pl. 3, fig. D, pl. 17, fig. g.</td>
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<td>1962</td>
<td>Natica (Naticarius) canrena LINNÉ – WEISBORD</td>
<td>p. 244, pl. 23, figs 1-2.</td>
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<td>1975</td>
<td>Natica canrena LINNÉ 1758 – HUMFREY</td>
<td>p. 111, pl. 10, figs 2, 2a, 2b.</td>
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<td>1975</td>
<td>Natica (Naticarius) canrena (L.) – REGTEREN ALTENA</td>
<td>p. 32, pl. 2, figs 1-2.</td>
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<td>1975</td>
<td>Natica (Naticarius) canrena (LINNAEUS, 1758) – RIOS</td>
<td>p. 67, pl. 18, fig. 273.</td>
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<td>1994</td>
<td>Natica canrena (LINNÉ, 1758) – DÍAZ &amp; PUYANA</td>
<td>p. 162, fig. 595.</td>
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<td>1994</td>
<td>Natica (Naticarius) canrena (LINNAEUS, 1758) – RIOS</td>
<td>p. 81, pl. 27, fig. 312.</td>
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<td>1998</td>
<td>Natica canrena (LINNÉO, 1758) – FERNANDEZ MILEA</td>
<td>p. 121, figure.</td>
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<td>2001</td>
<td>Natica (Naticarius) canrena (LINNÉ, 1758) – MACSOTAY &amp; CAMPOS</td>
<td>p. 61, pl. 13, fig. 16.</td>
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Material and dimensions: Maximum height 36.6 mm, one specimen NMB lot 6930; 12 specimens EDIMAR coll.; seven specimens plus one operculum BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

This species is characterized by its inflated last whorl, plicae below the suture on the last whorl and umbilicus shaped like an inverted comma. The protoconch in our Cubagua material is preserved and consists of just over two whorls, similar to that described by Jung (1969) for his material from the Lower Pliocene Springvale Formation of Trinidad. Jung (1964, 1965) discussed the relationship between the shells within the *Naticarius canrena* group in the Caribbean Neogene assemblages. There is no doubt from his works, and our own personal collections, that the Lower Miocene specimens from the Cantaure Formation of mainland Venezuela are different from the Recent ones; the Lower Miocene shells are smaller, with a more elevated spire, a narrower angle between the outer lip and the last whorl adapically and they have a protoconch with a smaller nucleus.

Jung (1964) postulated that there was a gradual increase in the size of the nucleus over time and a decrease in the number of protoconch whorls. Unfortunately, the whorl counts calculated from his figures do not correspond with those given in table 2 (p. 137). Irrespective of the method used for counting, all the figures (except no. 4, Springvale) are within half a whorl of each other, a range of variation acceptable as intraspecific, at least amongst Mediterranean Pliocene *Natica* species (Pedriali & Robba, 2005). Also, the ages of some of the formations studied by Jung (1964) have now changed; the Bowden Formation is now considered Lower-Middle Miocene, not Middle Miocene; the Springvale Formation is Lower Pliocene, not Upper Miocene; the Cantaure Formation Lower Miocene, not Middle Miocene and so on. Nevertheless, like the Springvale shells, the Cubagua shells are large and have a nucleus closer to the modern form. The significance of the slightly smaller protoconch in the absence of other distinguishing characteristics is unclear and we provisionally consider these shells conspecific with the modern form. We consider the Lower-Middle Miocene specimens to belong to a separate ancestral subspecies, *Naticarius canrena antinacca* (Cossmann, 1924).

Both Olsson & Harbison (1953) and Jung (1964) noted some differences in the operculum between the various specific taxa within the species complex. The importance of the operculum in taxonomy, at least in the European naticid faunas, was highlighted by Pedriali & Robba (2005). Jung (1964) figured the operculum of *Naticarius precursor* (Gardner, 1947) from the Lower Miocene Chipola Formation of Florida and showed a very wide central area, followed by about 5-6 commarginal ridges. The operculum of *N. canrena antinacca*, also figured, is similar to that of the modern species, the central area possible a little smaller. Olsson & Harbison (1953) discussed the relationship between *N. canrena* and *Naticarius plicatella* (Conrad, 1863), and concluded that whilst the shells were almost indistinguishable, the operculum of *N. plicatella* had a smaller, somewhat comma-shaped central area, followed by about 11 commarginal ridges, the outer two of which are narrower and sharper, whereas the operculum of *N. canrena* had a wider central area followed by 6-7 commarginal ridges.

We ascribe the single operculum (Pl. 10, Fig. 5) known Araya Formation to *Naticarius canrena* with a little hesitation, as it was not found *in situ*. It has a slightly smaller central area than seen in the operculum of Recent specimens, and 11 commarginal ridges, the outer 4-5 narrower, lower, weaker and more close-set towards the outer edge. We also note that the slight thickening or gibbosity seen in most species mid-length along the inner edge is more accentuated than in any specimens of *N. canrena* we have seen. Therefore this operculum does not match the description of any known species. Unfortunately, as we examined only a single operculum, which was not found *in situ*, we provisionally ascribe the shells to *Naticarius canrena canrena* and draw attention to the differences in the operculum.
SYSTEMATIC PALAEOONTOLOGY

Geological and geographical distribution:
Upper Miocene: Mataruca Member of Caujarao Formation (NMB 2983/1), El Carrizal, Venezuela.
Lower Pliocene: Araya Formation, Cabagua Island, Venezuela; Savaneta Glaucolithic Sandstone Member and Melaño Clay Member of Springvale Formation, Trinidad (MAURY, 1925a; MANSFIELD, 1925; H. E. VOKES, 1938; RUTSCH, 1942; JUNG, 1969); Tuberá Group, northern Colombia (BARRIOS, 1960).
Lower Pleistocene: Mare Formation, Cabo Blanco, Venezuela (NMB coll.).
Upper Pleistocene: La Isabella Formation, Dominican Republic (BL coll.).
Recent: North Carolina to Argentina (MACSOTAY & CAMPOS, 2001).

Genus Stigmaulax MÖRCH, 1852.
Type species Natica sulcata BORN, 1778, by subsequent designation, HARRIS, 1897.

Stigmaulax beaumonti RUTSCH, 1934
Pl. 10, Fig. 6

1934 Natica (Stigmaulax) sulcata beaumonti RUTSCH, p. 50, pl. 2, figs 6-8, pl. 3, fig. 5.
2010a Stigmaulax beaumonti RUTSCH, 1934 – LANDAU & SILVA, p. 47, pl. 10, fig. 6.

Material and dimensions: Maximum height 37.8 mm, two specimens EDIMAR coll.; five specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cabagua Island.

Discussion:
We examined two Cabagua specimens of a large Stigmaulax species, which seems to be conspecific with specimens from the coeval Punta Gavilán Formation of Venezuela. RUTSCH (1934) was absolutely correct to consider this southern Caribbean form a distinct species, but its affinities do not lie with the Caribbean Neogene to Recent Stigmaulax sulcata (BORN, 1778), which has very fine spiral sculpture, but with the group of species without spiral sculpture; the Neogene Caribbean species Stigmaulax guppiana (TOULA, 1909) and the Tropical Eastern Pacific Neogene to Recent species Stigmaulax broderipiana (RECLUZ, 1844). WOODRING (1957a) considered the Punta Gavilán shells a subspecies of S. guppiana, differing in being larger and with the axial grooves continuing from the umbilicus almost to the outer lip.

We have examined specimens of S. guppiana from the Middle-Upper Miocene Gatun Formation of Panama, and found that they differ significantly from our Cabagua shells; when seen in apertural view, the shell of Stigmaulax beaumonti (NMB localities 5222, 5225) is far more elongated horizontally, the last whorl is much more depressed, and the rate of expansion increases towards the outer lip, whereas the last whorl is rounded in S. guppiana, and the rate of expansion is constant throughout the growth of the last whorl. The more elongated shape of S. beaumonti results in a more elongated umbilicus, in which the funicule lies slightly more lower down, resulting in a narrower channel. As WOODRING (1957a) observed, the axial grooves in the Gatun specimens generally end at or above the periphery, whereas in S. beaumonti they extend all the way from the umbilicus almost to the outer lip. The protoconch is preserved in one of the Cabagua specimens and is not significantly different from that of S. guppiana, consisting of just over two smooth whorls. These differences are sufficient in our opinion to consider them specifically distinct.

WOODRING (1957a) mentioned that Stigmaulax guppiana occurred in the Lower Pliocene Gurabo Formation of the Dominican Republic. We examined two specimens from the Gurabo River (Loc. TU 1210; BL coll) which are equal in size to the southern Caribbean Neogene forms and, as in S. beaumonti, the axial grooves extend to the umbilicus. However, the last whorl is inflated and rounded, giving an apertural view profile quite unlike S. beaumonti. The characters of the umbilicus are more like those of S. guppiana, of which it is probably just a local variety. Specimens of this genus have also been figured from the Colombian Lower Pliocene by BARRIOS (1960), however, the figures are too poor to comment on the specific assignation of the shells.

Stigmaulax broderipiana (RECLUZ, 1844) from the Upper Miocene to Recent American Tropical Pacific also has axial grooves which extend to the umbilicus, but is smaller-shelled, the suture is less deeply
impressed and in apertural view the last whorl is less compressed. The protoconchs is similar, consisting of 2.5 smooth whorls.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934); Springvale Formation, Trinidad (RUTSCH, 1942).

Subfamily  Sininae  WOODRING, 1928
Genus  Sinum  RÖDING, 1798.
Type species  Helix haliotidea LINNAEUS, 1758, by subsequent designation, DALL, 1915.

Sinum gabbi (BROWN & PILSBRY, 1913)
Pl. 10, Figs 7-8

1913  Sigaretus (Eunaticina) gabbi BROWN & PILSBRY, p. 509, pl. 22, fig. 13.
1957a  Sinum gabbi (BROWN & PILSBRY) – WOODRING, p. 94, pl. 21, figs 3, 6.
1965  Sinum gabbi (BROWN & PILSBRY) – JUNG, p. 508, pl. 68, figs 3-4.
2010a  Sinum gabbi (BROWN & PILSBRY, 1913) – LANDAU & SILVA, p. 48, pl. 10, figs 7-8.

Material and dimensions: Maximum diameter 26.9 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
A single incomplete specimen of a non-depressed  Sinum  species was found at Cañon de las Calderas. A complete specimen of similar size, with an even less depressed last whorl is in our collections from the contemporaneous Punta Gavilán Formation of mainland Venezuela, which is provisionally considered conspecific. These tall-spired  Sinum  species bear a superficial resemblance to species included in the genus  Eunaticina  FISCHER, 1855, but in these the umbilicus is distinctly open and there is a slender umbilical callus, whereas in  Sinum  the umbilicus is slit-like and there is no umbilical callus.  Eunaticina  is a tropical Pacific genus, represented by a single species on the Pacific side of the central American Seaway (MARINCOVICH, 1977). The presence of the genus  Eunaticina  in the Neogene Atlantic was reported by WOODRING (1928) when he described  E. regia in the Bowden Formation of Jamaica (WOODRING, 1928, p. 387). At the time,  Eunaticina  was not known from the Recent eastern Pacific, but the genus should now be added to the list of paciphile genera.

JUNG (1965) argued that  Sinum quirosanum  F. HODSON (in HODSON, HODSON & HARRIS, 1927, pl. 67, figs 10-12) described from the Miocene of Miranda, Venezuela, was unlikely to be a synonym of  S. gabbi as suggested by WOODRING (1957a). At 4½ whorls it was much smaller than  S. gabbi, but almost twice as high and the aperture was rounder. More specimens of  S. quirosanum  would be needed to endorse this conclusion. The size difference between adult  S. gabbi from Cantaure is quite considerable. However, even the smaller shells have a clearly ovate aperture. We have provisionally excluded  S. quirosanum  from the synonymy.

MAURY (1917) figured and described  Sinum nolani  from the Lower Pliocene Gurabo Formation of the Dominican Republic, with an even more inflated last whorl. We have not found this species in the Dominican Republic, but have collected specimens of a non-depressed  Sinum  species from the Rio Amina beds (BL coll.), Gurabo Formation of the Dominican Republic. Their last whorl is slightly more depressed than that of  S. gabbi and this species is clearly not  S. nolani. We have found specimens of the Recent Caribbean  Sinum maculatum (SAY, 1831) in the Lower Pliocene Arayina Formation of the Araya Peninsula, but not in Cubagua. This species is easily distinguished from  S. gabbi  by its more depressed form and weaker sculpture. We record a single specimen of the very distinctive  Sinum naticoidalis  H. E. VOKES, 1938 from the Lower Pliocene upper reddish coarse sandy bed of the Aramina Formation at Cerro Barrigón, Araya Peninsula.
Geological and geographical distribution:
Lower Miocene Cantaure Formation, Venezuela (JUNG, 1965).
Upper Miocene: middle and upper Gatún Formation, Panama (WOODRING, 1957a).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela;
Punta Gavilán Formation, Falcón, Venezuela (BL coll.).

Superfamily   Tonnoidea SUTER, 1913 (1825)
Family    Tonnidae SUTER, 1913 (1825)
Genus Malea VALENCIENNES, 1832.
Type species Cassis ringens SWAINSON, 1822, by subsequent designation, HERRMANNSEN, 1847

Malea beui LANDAU & SILVA, 2010
Pl. 10, Figs 9-11

Dimensions and type material: Holotype NHMW 2010/0038/0017 (Pl. 10, Fig. 9), height 48.9 mm, width 39.5 mm (NHMW coll., ex BL coll.); paratype 1 MOBR-M-3877 (Pl. 10, Fig. 10), height, 28.0 mm, width 21.6 mm (EDIMAR coll., ex BL coll.); paratype 2 NHMW 2010/0038/0018 (Pl. 10, Fig. 11), height, 55.9 mm (NHMW coll., ex BL coll.).

Etymology: Named after Dr. Alan Beu, tireless worker on Tonnoideans, colleague and friend.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Additional material: Two specimens BL coll., Lower Pliocene, Araya Formation, Cañon de las Calderas, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Diagnosis:
A Malea species with shells of unknown adult size, very wide, subspherical shape, strongly convex last whorl, low spire; numerous narrow, weakly defined spiral cords with convex crests separated by interspaces slightly narrower than the cords.

Original description:
“Shell of unknown adult size (description based on subadult shells), fragile, very wide, subspherical shape, strongly convex last whorl, low spire. Protoconch consists of 3.5 smooth, convex whorls sharply delimited from the teleoconch by a proscoline scar and the beginning of the spiral sculpture. Teleoconch consists of 3.5 convex, weakly shouldered whorls, with a very narrow, shallow sutural ramp, periphery at the abapical suture. Suture impressed and very narrowly canaliculate. First teleoconch whorl bears four primary spiral cords with a single thread in the interspaces. Sharp close-set axial growth lines prominent on the first two whorls, giving the sculpture a finely reticulate appearance. Primary cords increasing in number to six on the penultimate whorl. Two cords on the sutural platform slightly wider spaced. Last whorl greatly inflated, subserical in shape, strongly constricted at the base, bearing 23 close-set narrow spiral cords with convex crests, separated by interspaces slightly narrower than the cords. Aperture elongate, narrow, widening abapically. Outer lip in juvenile unthickened stage, lirate within. Anal canal narrow groove; siphonal canal short, open, wide, strongly abapically recurved. Parietal callus in juvenile unthickened stage. Adapical portion of columella convex, deeply excavated below. Abapical half bears several oblique folds. Siphonal fasciole very short, rounded, abaxially recurved (LANDAU & SILVA, 2010a, p. 49).”

Discussion:
In his monograph of the tropical American Neogene Tonnoideans, Alan Beu hesitated to name these specimens from the Lower Pliocene Araya Formation for lack of complete specimens. In his discussion BEU (2010) considered them a distinct Malea species. On our last field trip to Cubagua Island (2009) no further specimens were collected, but a relatively good, but still incomplete shell was found in the coeval Cerro Barrigón locality on the Araya Peninsula. All the specimens found, although incomplete,
are very characteristic. The full adult size of this species is unknown, but fragments of outer lip found in the deposit suggest a large adult size. In view of the revision of the Cubagua assemblage undertaken herein we consider it justified to describe this taxon based on the scant material available, and we have great pleasure in naming it after BL’s mentor and friend Alan Beu.

“Three specimens from the Cubagua Fm on Cubagua Island represent another unnamed species of Malea. Again, they are the only specimens I [Alan Beu] have examined from this locality and formation in all collections. The smallest, complete specimen (…) has an obviously immature appearance, with a very weakly callused aperture and, in particular, a narrowly out-turned, only weakly ridged outer lip, and only a little callus on the inner lip and columella. A low, smooth callus pad is present on the outer (left) part of the inner lip above the unusually deep columellar embayment, and about 10 high transverse ridges are present on the inner lip in the embayment and on the upper (posterior) part of the anterior siphonal canal, but the transverse ridges are not elevated on raised callous pads. It is also unique among Malea material I have examined in its very wide, subspherical shape, with a wide, strongly convex last whorl and a low spire, even more extremely near-spherical than Recent juvenile material of Malea ringens. The spiral sculpture is also unique, with numerous narrow, rather weakly defined spiral cords with convex crests separated by interspaces each only a little narrower than one cord. On the uncorroded areas on the base and behind the outer lip the spiral cords are seen to be sharply defined, with slightly flatter crests and low but more clearly vertical sides than on the corroded areas of the shell. The numerous narrow cords are similar to those of Malea densecostata, from the nearby Pliocene Punta Gavilán Fm in mainland northern Venezuela, but the cords are lower, wider, and much more closely spaced and the teleoconch is markedly taller and narrower in M. densecostata than in the smallest Cubagua specimen. By this size, juvenile specimens of M. ringens have already developed the deep outer lip fold that permits growth of the wide ventral plate of the outer lip in adults, whereas the Cubagua specimen has only a narrowly thickened aperture. It also has some similarity to the poorly known Malea goliath, and to the Florida Pleistocene species Malea springi. Malea springi is similar in its relatively narrow outer lip and numerous, narrow spiral cords, but again is significantly taller and narrower than the smallest Cubagua specimen. The two larger specimens show that this species is still more nearly similar to M. springi than the low-spired juvenile would suggest, as they are still taller-spired than M. springi, and have a very similar, relatively narrow outer lip and similar relatively narrow, i.e., sharply defined, well-raised callous areas on the inner lip, but differ from M. springi in their fewer, much more widely spaced spiral cords. There is little doubt that the Cubagua Malea is an unnamed species closely related phylogenetically to M. springi” (BEU, 2010, p. 263).

LANDAU et al. (2008) discussed the endemic nature of the Neogene molluscan assemblages found in northern Venezuela, fully justifying the erection of the Colombian-Venezuelan-Trinidad Subprovince of WOODRING (1974), which seems to have been in place since at least the Early Miocene (LANDAU et al., 2008). The genus Malea illustrates this endemism clearly, with four of the nine species recorded by BEU (2010) for Neogene to Recent tropical America endemic to the Colombian-Venezuelan-Trinidad Subprovince (LANDAU, in press). Malea is also an example of a paciphile gastropod (see WOODRING 1966; LANDAU et al., 2009), which according to the fossil record seems to have had its origins in the Atlantic portion of the Neogene Gatunian Province (see VERMEIJ & PETUCH, 1986; VERMEIJ, 2005; LANDAU et al., 2008).

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island (BEU, 2010); Aramina Formation, Araya Peninsula, Venezuela (BL coll.).

**Family** Cassidae LATREILLE, 1825

**Subfamily** Cassinae LATREILLE, 1825

**Genus** Sconsia GRAY, 1847.

Type species Cassidaria striata LAMARCK, 1810, by original designation: Cassidaria striata LAMARCK, 1816 (junior secondary homonym of Sconsia striata (J. SOWERBY, 1812), = Sconsia grayi A. ADAMS, 1855), Pleistocene and Recent, western Atlantic.
Sconsia grayi (A. Adams, 1855)

Pl. 11, Fig. 1


1835a Cassidaria striata Lam. – Kiener, p. 6, pl. 2, fig. 3.

1849 Cassidaria striata Lamarck – Reeve, pl. 1, fig. 2.

1855 Sconsia grayi A. Adams, p. 136, pl. 28, fig. 6.

1857 Cassidaria striata Lam. – Koster, p. 52, pl. 55, figs 1-2.

1859 Cassidaria (Sconsia) striata Lamarck – Chenu, p. 208, fig. 1138.

1866a Cassidaria sublaevigata Guppy, 1866, p. 287, pl. 27, fig. 6.

1874 Cassidaria sublaevigata Guppy – Guppy, p. 439.

1877 Cassidaria (Sconsia) striata Lamarck – Chenu, p. 208, fig. 1138.


1903 Cassidaria sublaevigata Guppy – Dall, p. 1584.


1929 Sconsia laevigata Sowerby – Anderson, p. 142 (non Sconsia laevigata G. B. Sowerby I, 1850).

1934 Sconsia cf. striata (Lamarck) – Rutsch, 1934, p. 53, pl. 11, fig. 11.

1939 Sconsia striata Lamarck – Crench & Abbott, p. 6, pl. 4, figs 1-4.

1948 Sconsia striata Lam. – M. Smith, p. 41, pl. 15, fig. 8.

1959a Sconsia laevigata sublaevigata (Guppy) – Woodring, p. 201, pl. 34, figs 8-9, pl. 35, figs 1-4.

1959 Sconsia barbudensis Higgins & Marrat – Crench, p. 329, pl. 172.

1961 Sconsia striata Lamarck, 1822 – Warming & Abbott, p. 97, pl. 28, fig. g.

1964 Sconsia laevigata gabbi Olsson, p. 169.

1971 Sconsia striata Lamarck, 1816 – Bayer, p. 138, fig. 14, 17A, 20D.

1972 Sconsia striata Lamarck, 1816 – Matthews & Coelho, p. 13, fig. 8.

1973 Sconsia striata (Lam.) – Morris, p. 180, pl. 49, fig. 3.

1974 Sconsia striata Lamarck, 1816 – Abbott, p. 160, pl. 6, fig. 1730.

1975 Sconsia striata Lamarck, 1822 – Humfrey, p. 117, pl. 11, fig. 2.

1975 Sconsia striata (Lamarck, 1816) – Pointier & Lam, p. 13, fig. 309.


1985 Sconsia striata (Lamarck, 1822) – Rios, p. 73, pl. 26, fig. 320.

1987 Sconsia lindae Petuch, 1987, p. 96, pl. 15, figs 7, 8.


1994 Sconsia striata (Lamarck, 1822) – Rios, p. 85, pl. 28, fig. 332.


1997 Sconsia striata (Lamarck, 1816) – Kriegl, p. 30, pl. 10, fig. 28, 28a.

1998 Sconsia striata (Lamarck, 1816) – Pointier & Lam, p. 82, figure.

2001 Sconsia striata (Lamarck, 1816) – Rios, p. 59, pl. 30, fig. 252.


2001 Sconsia sublaevigata (Guppy, 1866) – Beu, p. 712.
2009  *Sconsia striata* (Lamarck, 1816) – Rios, p. 153, fig. 365.
2010  *Sconsia grayi* (A. Adams, 1855) – BEU, p. 232, pl. 66, figs 6-7; pl. 67, figs 1, 3, 5.
2010a  *Sconsia grayi* (A. Adams, 1855) – Landau & Silva, p. 50, pl. 11, fig. 1.

**Material and dimensions:** One specimen BL coll., height 54.2 mm, Lower Pliocene, Araya Formation, Cañon de las Calderas, Cubagua Island.

**Discussion:**

The taxonomy of the Recent Atlantic *Sconsia* species was discussed at length by BEU (2008, 2010), who concluded that *Sconsia lindae* Petuch 1987 was based on tall, elongate specimens with fine spiral threads over most of the adult shell. BEU (2010) examined a large number of specimens collected off the coast of Colombia, and found that the specimens ranged from coarsely sculptured, moderately short-spired ones of the type usually regarded as “typical” *Sconsia grayi* and even more short-spired specimens with a lightly angled shoulder, through to tall and narrow, tall-spired specimens with relatively weak spiral sculpture, of the type named *S. lindae* by Petuch (1987, p. 96, pl. 15, fig. 7, 8), and through to even more extreme, taller specimens than Petuch’s holotype.

In the Caribbean fossil record the genus is represented by *Sconsia laevigata* (G. B. Sowerby I, 1850). *Sconsia laevigata* differs from *S. grayi* in its much wider shape, with a lower spire and a much wider, weakly shouldered last whorl, in retaining low varices all down the spire, in lacking spiral sculpture altogether on the central and peripheral area of large adults, and reduced to fine, low, closely spaced spiral threads on juvenile and half-grown shells, in its more widely flared and thickened outer lip with shorter transverse ridges situated further inside the lip, in the wider, thicker callus area on the base of the lower lip, forming a narrow free margin that extends beyond the margin of the siphonal canal, in having a shorter, wider siphonal canal, and in developing a low, wide swelling, or very low node, on the dorsum of large specimens, so that the whorl becomes weakly Shouldered (BEU, 2010).

*Sconsia grayi* does not intergrade with the Miocene-Lower Pliocene *S. laevigata*, but they are linked through the geological record by an intergrading series of forms (Gabb, 1875; 1881; BEU, 2008, 2010). BEU (2010) re-examined the type material of these intermediate forms and concluded that *Sconsia bocasensis* Olsson, 1922 and *S. laevigata* var. *gabbi* Olsson, 1922 were indistinguishable from the Recent *S. grayi* and therefore junior subjective synonyms. *Sconsia sublaevigata* (Guppy, 1866) was based on a narrow, slightly more weakly sculptured form in Upper Miocene and mid- to Upper Pliocene rocks of Atlantic Panama. BEU (2010) again concluded this also to be merely part of the normal variation of *S. grayi*. Several specimens in both the NMB coll. and BL coll. have faint but obvious, wavy orange axial colour bands, demonstrating that the form identified as *S. sublaevigata* had a similar color pattern to that of Recent specimens of *S. grayi*.

**Geological and geographical distribution: Atlantic**

Upper Miocene: middle and upper Gatun Formation Panama (Toula, 1909; Woodring, 1959); Nancy Point Formation, Bocas del Toro, Panama (BL coll.).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gaviñán Formation, Falcón, Venezuela (Rutsch, 1934; BEU, 2010); Tuberá Group, northern Colombia (Anderson, 1929).
Lower-Upper Pliocene: Bowden Formation, Jamaica (Guppy, 1866a; Woodring, 1928); Cayo Agua Formation, Bocas del Toro, Panama (Olsson, 1922, BEU, 2010).
Lower Pleistocene: Moin Formation, Puerto Limon, Costa Rica (Robinson, 1991); Escudo de Veraguas Formation, Bocas del Toro, Panama (Olsson, 1922, BEU, 2010).
Upper Pleistocene: Swan Cay Formation, Panama (BEU, 2010).
Recent: Throughout the western Atlantic from southern Florida and the Bahamas (Clench & Abbott, 1943) south to Bahia, Brazil (Rios, 1994). However, it seems to be much more common along the coastline of northern South America than elsewhere (BEU, 2010).

**Geological and geographical distribution: Pacific**

Upper Miocene: Angostura Formation, Ecuador (Olsson, 1964)
We follow BEU & CERNOHORSKY (1986) and BEU (2010) in treating *Linatella* as a full genus of Cymatiinae.

*Linatella caudata* (GMELIN, 1791)
Pl. 11, Fig. 2

1791  
*Buccinum caudatum* GMELIN, 3471.
1816  
*Fusus cutaceus* LAMARCK, pl. 427, fig. 4a, b, “Liste des objets”, 6.
1822  
*Cassidaria cingulata* LAMARCK, 1822, p. 216.
1842  
*Triton undosum* KIENER, p. 44, pl. 6, fig. 2 (non *Triton undosum* LAMARCK, 1816, = *Buccinum undosum* LINNAEUS, 1758).
1853  
*Ramularia* (Lagenia) *rostratus* “MARTINI” MÖRCH, p. 110 (adoption of a name now ruled non-binominal).
1853  
*Triton* (Linatella) *poulsenii* MÖRCH, p. 33.
1853  
*Triton* (Linatella) *rostratum* MÖRCH, p. 33.
1883  
*Tritonium* (Cabestana) *verbeeki* BOETTGER, p. 37, pl. 1, fig. 10a, b.
1899  
*Cassis* (Semicassis) *tegalensis* MARTIN, p. 156, pl. 24, fig. 363.
1899  
*Doliom losariense* MARTIN, p. 163, figs 377, 378.
1930  
*Cymatium* (Linatella) *krenkeli* COX, p. 118, pl. 12, figs 20-21b.
1930  
*Cymatium* (Linatella) *floridanum* MANSFIELD, p. 94, pl. 12, fig. 10.
1937  
*Cymatium* (Linatella) *cingulatum peninsulum* M. SMITH, p. 113, pl. 1, fig. 2, pl. 44, fig. 5.
1948  
*Cymatium* (Cymatium) *caudatum* (GMELIN) – M. SMITH, p. 4, pl. 3, fig. 1761.
1957  
*Cymatium* (Linatella) *poulsenii* MÖRCH – CLENCH & TURNER, p. 198, pl. 111, figs 7-8; pl. 113, fig. 2; pl. 115, figs 1-3.
1961  
*Cymatium* (Linatella) *poulsenii* MÖRCH, 1877 – WARMKE & ABBOTT, p. 100, pl. 18, fig. e.
1963  
*Linatella neptunia* GARRARD, p. 43, pl. 7, figs 7-8.
1971  
*Cymatium* (Linatella) *poulsenii* MÖRCH, 1877 – ANDREWS, p. 105, illus.
1973  
*Cymatium* (Linatella) *cingulatum* (LAMARCK) – KILIAS, p.122, fig. 89.
1974  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – ABBOTT, p. 164, pl. 7, fig. 1761.
1975  
*Cymatium* (Linatella) *cingulatum* (MÖRCH) – REGTEREN ALTENA, p. 36, fig. 14.
1975  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – RIOS, p. 80, pl. 22, fig. 325.
1977  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – ABBOTT, p. 132, illus.
1981  
*Cymatium* (Linatella) *poulsenii* MÖRCH, 1877 – COELHO et al., p. 116.
1983  
1983  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – OKUTANI, p. 258, illus.
1984  
1985  
*Linatella* (Linatella) *caudata* (GMELIN, 1791) – BEU, p. 60, fig. 24.
1986  
*Linatella* (Linatella) *caudata* (GMELIN, 1791) – BEU & CERNOHORSKY, p. 244, figs 1, 2, 5-22.
1991  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – LIPE & ABBOTT, p. 12, illus.
1991  
*Neptunea szukouensis* HU & TAO, p. 340, pl. 60, figs 1-2.
1992  
1992  
1992  
*Cymatium* (Linatella) *cingulatum* (LAMARCK, 1822) – HU, p. 763, pl. 125, figs 33, 35.
1993  
*Linatella* (Linatella) *caudata* (GMELIN, 1791) – HENNING & HEMMEN, p. 107, pl. 20, fig. 3.
Material and dimensions: Maximum height 37.8 mm, three specimens BL coll., Lower Pliocene, Araya Formation, Cañon de las Calderas, Cubagua Island.

Discussion:
The shells of *Linatella caudata* are recognisable by their *Tonna*-like shape and sculpture, with a rather low spire, although obviously taller than in *Tonna* species, a short, widely open anterior siphonal canal, lightly shouldered but otherwise strongly and evenly inflated whorls, sculpture of low, wide, rounded, closely spaced spiral cords, and only a weak terminal varix developed on most specimens. Many, but by no means all, specimens have low nodules around the shoulder angle. The prominence of the shoulder angle is highly variable. The width and prominence of the spiral cords is also highly variable, from wide, closely spaced, even cords, to alternating wide and narrow ones, and some specimens have narrow spiral interspaces between the cords, whereas they are equal in width to one cord on most others (BEU, 2010). A geographically widespread species with a long geological history, but never common (for discussion see BEU, 2010). The fossil shells of *L. caudata* could be confused with those of *Monoplex tranquebaricus* (LAMARCK, 1816), as the characteristic generic feature, the operculum, is obviously lost in the fossil state. In *Linatella* species the operculum is oval with the nucleus placed near the centre of the columellar margin, whereas *Monoplex* species have an operculum with an anterior terminal nucleus (BEU, 2010). Nevertheless, the shell of the two species can be distinguished relatively easily, as *M. tranquebaricus* has a shorter last whorl, a more prominent shoulder angulation, coarser to much coarser sculpture, and more prominent transverse ridges on the inner and outer lips than *L. caudata*. *L. caudata* completely lacks obvious axial sculpture, which can be very prominent on some specimens of *M. tranquebaricus*. We have collected numerous specimens of *M. tranquebaricus* from the Upper Pleistocene of the Araya Peninsula, but cannot confirm BEU’S (2010, p. 174) record for the species in the Venezuelan Pliocene.

Geological and geographical distribution: Atlantic
Upper Miocene: Usiacuri Formation, Juan de Acosta, Colombia (BEU, 2010). Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (BEU, 2010); Punta Gavilán Formation, Falcón, Venezuela (BEU, 2010); Melajo Clay Member of Springvale Formation, Trinidad (BEU, 2010); Bocas del Toro, Panama (BEU, 2010). Lower-Upper Pliocene: Choctawhatchee Formation, Florida (MANSFIELD, 1930, as *C. florianum*, BEU, 2010), Cayo Agua Formation, Bocas del Toro, Panama (BEU, 2010). Upper Pliocene: Pinecrest Formation, Florida (PETUCH, 1994, as *C. (L.) florianum*); Banano Formation, Costa Rica (BEU, 2010).
Recent: western Atlantic it occurs from Chincoteague Inlet, Virginia south to Rio de Janeiro, Brazil, eastern Atlantic, off the Canary Islands and Cape Verde Islands (BEU, 2010).

Geological and geographical distribution: Pacific
Upper Miocene: Punta Judas Formation, Costa Rica (BEU, 2010); Java (MARTIN, 1899).
Pliocene: Zanzibar (COX, 1930); Java (MARTIN, 1899).
Pleistocene: Armuelles Formation, Burica Peninsula, Panama (BEU, 2010); New Zealand (BEU, 1976).
Recent: Indo-West Pacific province from East Africa and the Red Sea east to Hawaii and from southern Japan to northern New Zealand (BEU, 2010), Taiwan (HU & TAO, 1991).

Genus  

Monoplex PERRY, 1810
Type species Monoplex australasiae PERRY, 1811 (= Murex parthenopeus SALIS MARSCHLINS, 1793), by subsequent designation by DALL (1904).

We follow BEU (2010) in treating Monoplex as a full genus of Cymatiinae.

Monoplex cercadicus (MAURY, 1917)
Pl. 11, Fig. 3

1917  
Simpulum antillarum variety cercadicum MAURY, p. 270, pl. 17, fig. 2.
1888  
Cymatium (Monoplex) cercadicum (MAURY, 1917) – BEU & KAY, p. 214, figs 83-84.
2010  
Monoplex cercadicus (MAURY, 1917) – BEU, p. 148, pl. 36, figs 6-9, 11; pl. 47, fig. 16.
2010a  
Monoplex cercadicus (MAURY, 1917) – LANDAU & SILVA, p. 53, pl. 11, fig. 3.

Material and dimensions: Maximum height 61.3 mm (incomplete), seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

Monoplex cercadicus (MAURY, 1917) is characterized by having a rather short, strongly inflated last whorl, a moderately short spire, a rapidly contracted neck, and a rather long, narrow, straight anterior siphonal canal, and only the terminal varix developed on almost all specimens. The aperture is very distinctive, both lips are prominently armed with many high, rather widely spaced, transverse ridges, particularly prominent on the narrow inner lip, and grouped into seven pairs of short, very prominent ridges on the outer lip, those of the upper two or three groups subdivided again by a median groove in most specimens.

Monoplex cercadicus is most similar to Monoplex wiegmanni (ANTON, 1839), which differs in having much weaker axial sculpture and in having lower, wider spiral cords and a longer last whorl which, in many specimens, has flatter, less inflated outlines below the shoulder than in C. cercadicus. This suggests that this living eastern Pacific species might have descended from M. cercadicus (BEU, 2010).

Geological and geographical distribution:
Lower Miocene: Baitoa Formation, Dominican Republic (BEU, 2010); Cantaure Formation, Venezuela (BEU, 2010).
Middle Miocene: lower Gatun Formation, Panama (BEU, 2010).
Upper Miocene: Cercado Formation, Dominican Republic (MAURY, 1917; BEU, 2010).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Gurabo Formation, Dominican Republic (MAURY, 1917; BEU, 2010).

Monoplex krebsii (MÖRCH, 1877)
Pl. 11, Figs 4-5

1876  
Triton domingensis GABB – GUPPY, p. 522, pl. 29, fig. 2 (non Triton domingense GABB, 1873).
Material and dimensions: Maximum height 47.9 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion: 
Monoplex krebsii is easily recognised among western Atlantic species by its rather tall spire and long anterior canal, its very prominent, thin varices, the prominent nodules on the intervariceal intervals of most specimens, and its elongate aperture with very prominent, narrow transverse ridges ("teeth") inside the outer lip, and two particularly prominent transverse ridges on the base of the columella, protruding strongly into the aperture (BEU, 2010). The shells from Cubagua are an unusually tall and slender form.

Geological and geographical distribution: Atlantic
Lower Miocene: Chipola Formation, Florida (BEU, 2010); Baitoa Formation, Dominican Republic (BEU, 2010); Cantaure Formation, Venezuela (BEU, 2010).
Middle Miocene: lower Gatun Formation (BEU, 2010).
Upper Miocene: middle and upper Gatun Formation, Panama (BEU, 2010).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (BEU, 2006); Punta Gavilán Formation,
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Falcón, Venezuela (BEU, 2010); Gurabo Formation, Dominican Republic (BEU, 2010).
Middle-Upper Pliocene: Shark Hole Point Formation, Bocas del Toro, Panama (BEU, 2010).
Pliocene (indeterminate): Bowden Formation, Jamaica (BEU, 2010); Plato, Colombia (BEU, 2010).
Lower Pleistocene: Caloosahatchee Formation, Florida (PETUCH, 1994); Moin Formation, Puerto Limon, Costa Rica (ROBINSON, 1991); Escudo de Veraguas Formation, Bocas del Toro, Panama (BEU, 2010); Mare Formation, Cabo Blanco, Venezuela (WEISBORD, 1962).
Lower-Upper Pleistocene: Bermont Formation, Florida (BL coll.).
Upper Pleistocene: Swan Cay Formation, Bocas del Toro, Panama (BEU, 2010); El Manglillo Formation, Araya Peninsula, Venezuela (BEU, 2010).
Holocene: Trinidad (BEU, 2010); Boca Chica, Margarita Island, Venezuela (BEU, 2010).

Genus Turritriton DALL, 1904.
Type species Triton gibbosus BRODERIP, 1833, by original designation.

We follow BEU (2010) in treating Turritriton as a full genus of Cymatiinae.

Turritriton domingensis (GABB, 1873)

Pl. 11, Fig. 6

1873 Tritonium (Ranularia) domingense GABB, p. 212.
1922 Cymatium domingense (GABB) – PILSBRY, p. 356, pl. 29, fig. 2.
1988 Cymatium (Turritriton) domingense (GABB, 1873) – BEU & KNUDSEN, p. 86, figs 31-32.
2010 Turritriton domingensis (GABB, 1873) – BEU, p. 193, pl. 49, figs 1-4, 8.
2010a Turritriton domingensis (GABB, 1873) – LANDAU & SILVA, p. 54, pl. 11, fig. 6.

Material and dimensions: One specimen BL coll., 27.8 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
Turritriton domingensis (GABB, 1873) is the earliest known Turritriton species (BEU & KNUDSEN, 1987). Its shell is taller and narrower than any of the living species, with spiral sculpture more prominent than the Pliocene to Recent tropical western American species Turritriton gibbosus (BRODERIP, 1833), but not as prominent as the strongly sculptured cosmopolitan Pliocene to Recent species Turritriton labiosus (WOOD, 1828). Our single specimen from Cubagua is rather shorter than the typical, very narrow, tall-spired Dominican Republic specimens, and is more or less intermediate between T. domingensis and the squatter-shelled T. gibbosus–T. kobelti species group (which also includes the Miocene species T. grundensis). Unfortunately our single specimen from Cubagua gives us little information on the range of variation in the population.

In the Caribbean Miocene assemblages Monoplex gurabonicus (MAURY, 1917) has a similar size and shape to T. domingensis and has a very similar aperture and similarly low, narrow varices. Monoplex gurabonicus is easily distinguished, however, by having an almost smooth, finely reticulate shell surface, lacking the fasciculate riblet groups and many fine axial riblets of T. domingensis (BEU, 2010).

The only species in Caribbean Miocene-Pliocene assemblages with which it might be confused is Monoplex gurabonicus, which is a similar size and shape to T. domingensis and has a very similar aperture and similarly low, narrow varices. M. gurabonicus easily is distinguished from T. domingensis by having a much more nearly smooth, finely reticulate shell surface, lacking the fasciculate riblet groups and many fine axial costellae of C. domingensis. Rather oddly, MAURY (1917) did not mention this species in her monograph of the Dominican Republic fauna.

Turritriton domingensis is apparently limited to late Early Miocene to Early Pliocene rocks of the Dominican Republic and northern Venezuela, with one record from the Gatun Formation (Late Miocene) of the Atlantic coast of Panama (BEU, 2010).
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**Geological and geographical distribution:**
Lower Miocene: Baitoa Formation, Dominican Republic (BEU, 2010); Cantaure Formation, Venezuela (BL coll.).
Upper Miocene: Gatun Formation, Panama (BEU, 2010); Cercado Formation, Dominican Republic (PILSBRY, 1922; BEU, 2010); Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (BEU, 2010).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Mao Formation, Dominican Republic (BEU, 2010); Gurabo Formation, Dominican Republic (PILSBRY, 1922; BEU, 2010).

<table>
<thead>
<tr>
<th>Family</th>
<th>Personidae Gray, 1854</th>
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<tr>
<td>Genus</td>
<td>Distorsio Röding, 1798.</td>
</tr>
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</table>

Type species *Murex anus* Linnaeus, 1758, by subsequent designation, PILSBRY, 1922.

*Distorsio clathrata* (Lamarck, 1816)

Pl. 11, Figs 7-8

<table>
<thead>
<tr>
<th>Year</th>
<th>Source</th>
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<tr>
<td>1816</td>
<td><em>Triton clathratum</em> Lamarck, pl. 413, fig. 4a, b, “Liste des objets”: 4.</td>
</tr>
<tr>
<td>1842</td>
<td><em>Triton clathratum</em> Lamarck – Kiener, p. 21, pl. 14, fig. 1.</td>
</tr>
<tr>
<td>1844a</td>
<td><em>Triton ridens</em> Reeve (partim) pl. 12, fig. 46.</td>
</tr>
<tr>
<td>1859</td>
<td><em>Persona clathrata</em> Lamarck – Chen, p. 155, fig. 707.</td>
</tr>
<tr>
<td>1866a</td>
<td><em>Persona simillima</em> Sow. – Guppy, p. 288, pl. 17, fig. 13 (non <em>Distorsio simillima</em> G. B. Sowerby I, 1850).</td>
</tr>
<tr>
<td>1867</td>
<td><em>Persona simillima</em> Sow. – Guppy, p. 158 (non <em>D. simillima</em> G. B. Sowerby I, 1850).</td>
</tr>
<tr>
<td>1872</td>
<td><em>Triton ridens</em> Reeve – Küster &amp; Kobelt, p. 202, pl. 58, fig. 4.</td>
</tr>
<tr>
<td>1874</td>
<td><em>Persona simillima</em> Sow. – Guppy, p. 439 (non <em>D. simillima</em> G. B. Sowerby I, 1850).</td>
</tr>
<tr>
<td>1877</td>
<td><em>Distorsio acuta octodentis</em> Mörch, p. 34 (nomen nudum).</td>
</tr>
<tr>
<td>1880b</td>
<td><em>Distorsio cancellinus</em> Roissy – Tryon, p. 35, pl. 17, fig. 17 (non <em>Murex cancellinus</em> de Roissy, 1805, an incorrect usage of <em>Triton cancellinus</em> Lamarck, 1803; Landau et al., 2004a, p. 71, neotype).</td>
</tr>
<tr>
<td>1903</td>
<td><em>Distortrix simillima</em> Sowerby – Dall, p. 1584 (non <em>D. simillima</em> G. B. Sowerby I, 1850).</td>
</tr>
<tr>
<td>1922</td>
<td><em>Distorsio clathrata</em> (Lamarck) – Pillsbury, p. 359.</td>
</tr>
<tr>
<td>1928</td>
<td><em>Distorsio (Distorsio) clathratus gatunensis</em> Toulia – Woodring, p. 300, pl. 19, figs 2-3 (non <em>Distorsio gatunensis</em> Toulia, 1909, = <em>D. decussata</em> Valenciennes, 1832).</td>
</tr>
<tr>
<td>1929</td>
<td><em>Distorsio (Distorsio) clathratus gatunensis</em> Toulia – Weisbord, p. 41, pl. 8, fig. 3 (non <em>Distorsio gatunensis</em> Toulia, 1909, = <em>Distorsio decussata</em> Valenciennes, 1832).</td>
</tr>
<tr>
<td>1930</td>
<td><em>Distorsio clathratus</em> (Lamarck) – Rutsch, p. 607, pl. 17, figs 5-6.</td>
</tr>
<tr>
<td>1934</td>
<td><em>Distorsio clathratus</em> (Lamarck) – Rutsch, p. 28.</td>
</tr>
<tr>
<td>1939</td>
<td><em>Cancellaria (Cancellaria) cossmanni</em> Olsson – Oinomikado, p. 623, pl. 29, fig. 17 (non <em>Cancellaria cossmanni</em> Olsson, 1922).</td>
</tr>
<tr>
<td>1948</td>
<td><em>Distorsio clathratus</em> (Lamarck) – M. Smith, p. 22, pl. 8, figs 6, 12.</td>
</tr>
<tr>
<td>1957</td>
<td><em>Distorsio (Rhysema) clathrata</em> Lamarck – Clench &amp; Turner, p. 236, pl. 131; pl. 132, figs 2-8; pl. 133.</td>
</tr>
<tr>
<td>1960</td>
<td><em>Distorsio clathrata</em> – Parker, p. 323, pl. 4, fig. 21.</td>
</tr>
<tr>
<td>1961</td>
<td><em>Distorsio (Rhysema) clathrata</em> (Lamarck, 1816) – Pflug (partim), p. 41, pl. 9, figs 1-2.</td>
</tr>
<tr>
<td>1961</td>
<td><em>Distorsio clathrata</em> Lamarck, 1816 – Warmke &amp; Abbott, p.102, pl. 18d.</td>
</tr>
<tr>
<td>1962</td>
<td><em>Distorsio (Rhysema) clathrata</em> (Lamarck, 1816) – Weisbord, p. 267, pl. 25, figs 12-16.</td>
</tr>
<tr>
<td>1964</td>
<td><em>Distorsio (Rhysema) clathrata</em> (Lamarck, 1816) – Olsson, p. 174, pl. 30, fig. 1.</td>
</tr>
<tr>
<td>1970</td>
<td><em>Distorsio clathrata</em> (Lamarck, 1816) – Rios, p. 73, pl. 8, lower left fig.</td>
</tr>
<tr>
<td>1971</td>
<td><em>Distorsio (Rhysema) clathrata</em> (Lamarck, 1816) – Andrews, p. 107, Illus.</td>
</tr>
<tr>
<td>1972</td>
<td><em>Distorsio (Rhysema) floridana</em> (Gardner) – Perrilliat, p. 75, pl. 37, figs 6-11 (non <em>Personella floridana</em> Gardner, 1947).</td>
</tr>
<tr>
<td>1973</td>
<td><em>Distorsio clathrata</em> (Lam.) – Morris, p. 185, pl. 50, fig. 9.</td>
</tr>
</tbody>
</table>
1973  
**Distorsio (Rhysema) clathrata** (LAMARCK) – KILIAS, p. 200, fig. 143.

1974  
**Distorsio clathrata** (LAMARCK, 1816) – ABBOTT, p. 165, pl. 7, fig. 1770.

1975  
**Distorsio clathrata** LAMARCK 1816 – HUMFREY, p. 125, pl. 14, figs 1, 1a.

1975  
**Distorsio clathrata** (LAMARCK) – REGTEREN ALTENA, p. 37, pl. 2, figs 6-7.

1975  
**Distorsio clathrata** (LAMARCK, 1816) – ANDREWS, p. 134, illus.

1975  
**Distorsio clathrata** (LAMARCK, 1816) – RIOS, p. 80, pl. 22, fig. 327.

1975  
**Distorsio clathrata** LAMARCK 1816 – HUMFREY, p. 125, pl. 14, figs 1, 1a.

1975  
**Distorsio clathrata** (LAMARCK, 1816) – RIOS, p. 78, pl. 27, fig. 340.

1976  
**Distorsio clathrata** (LAMARCK) – COELHO et al., p. 131, fig. 13.

1977  
**Distorsio (Rhysema) clathrata** (LAMARCK, 1816) – ANDREWS, p. 134, illus.

1981  
**Distorsio clathrata** (LAMARCK, 1816) – OKUTANI, p. 260, illus.

1981  
**Distorsio clathrata** (LAMARCK, 1816) – H. E. & E. H. VOKES, p. 23, pl. 11, fig. 12.

1984  
**Distorsio clathrata** (LAMARCK) – BANDEL, p. 97, fig. 163, pl. 8, fig. 6.

1984  
**Distorsio clathrata** (LAMARCK) – LAURSEN, p. 27, fig. 42.

1984  
**Distorsio clathrata** (LAMARCK, 1816) – RIOS, p. 78, pl. 27, fig. 340.

1986  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, p. 64, pl. 11, figs 3-4.

1987  

1990  

1990a  

1990b  

1991  
**Distorsio clathrata** (LAMARCK, 1816) – PARTH, p. 11, illus.

1991  
**Distorsio clathrata** (LAMARCK, 1816) – LIPE & ABBOTT, p.14, illus.

1992  
**Distorsio (Distorsio) clathrata** (LAMARCK, 1816) – EMBIT & PUCHEU, p. 110, figs 9-12.

1993  
**Distorsio clathrata** (LAMARCK, 1816) – HENNING & HEMMEN, p. 137, pl. 29, figs 1-3.

1994  
**Distorsio clathrata** (LAMARCK, 1816) – RIOS, p. 91, pl. 30, fig. 358.

1994  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, pl. 39, figs J, N.

1994  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, pl. 39, figs J, N.

1994  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, pl. 39, figs J, N.

1997  
**Distorsio (Rhysema) clathrata** (LAMARCK, 1816) – PETUCH, p. 279, fig. 115A.

1997  
**Distorsio (Rhysema) clathrata** (LAMARCK, 1816) – PETUCH, p. 279, fig. 115A.

1998  
**Distorsio clathrata** (LAMARCK, 1816) – FERNANDEZ MILERA, p. 133, fig. 1.

1998  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, pl. 22, figs 279, 298, 306.

1998  
**Distorsio clathrata** (LAMARCK, 1816) – PETUCH, pl. 22, figs 279, 298, 306.

1999  
**Distorsio clathrata** (LAMARCK, 1816) – LANDAU & SILVA, p. 55, pl. 11, figs 7-8.

**Material and dimensions:** Maximum height 58.1 mm, six specimens NMB lot 12887; one specimen EDIMAR coll.; 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; five specimens BL coll., (lower yellow fine sandy bed), three specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

*Distorsio clathrata* is characterized by its evenly convex shell wall between the varices, and its prominent, narrow, widely spaced spiral cords completely evenly spaced. All other species of *Distorsio* from the study area have markedly humped growth between the varices, an obvious shoulder angle defining a slightly concave suture ramp, and two or more spiral cords more closely spaced than the others and situated on the shoulder angle (BEU, 2010).

*Distorsio clathrata* is widespread in the Caribbean Atlantic fossil record since the Miocene, and is today restricted to the western Atlantic, but in the Early Pliocene it was also present on the west coast of tropical America (OLSSON, 1964; BEU, 2010). It is one of the few examples of a caribophile species.

**Geological and geographical distribution: Atlantic**

Lower Miocene: Kendace Siltstone, Carriacou (BEU, 2010).

Middle Miocene: Carriacou, Grenadine Islands (BEU, 2010); Valiente Formation, Bocas del Toro, Panama (WOODRING, 1957a).
Upper Miocene: Gatun and Chagres Formations, Panama (Woodring, 1957a).

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (BEU, 2010); Punta Gavián Formation, Falcohol, Venezuela (Rutsch, 1930, 1934); Bocas del Toro, Panama (BEU, 2010); Banano Formation, Costa Rica (BEU, 2010); Tuberá Group, northern Colombia (Weisbord, 1929, as D. (D.) clathratus gatunensis; Ohnomikado, 1939 as Cancellaria (Cancellaria) cossmanni; Barrios, 1960, as D. (D.) clathratus gatunensis; BEU, 2010); Gurabo Formation, Dominican Republic (BL coll.).

Lower-Upper Pliocene: Bowden Formation, Jamaica (Guppy, 1866a as Persona simillima; Woodring, 1928 as D. clathratus gatunensis; Pflug, 1961(partim)); Shark Hole Point Formation, Bocas del Toro, Panama (BEU, 2010).

Upper Pliocene: Agueguexquite Formation, Mexico (Perrilliat, 1960, 1972 as Personella floridana).

Lower Pleistocene: Moin Formation, Puerto Limon, Costa Rica (Robinson, 1991); Escudo de Veraguas Formation, Bocas del Toro, Panama (BEU, 2010); Mare Formation, Cabo Blanco, Venezuela (Weisbord, 1962); Maqueta Member of the Playa Grande Formation, Venezuela (Weisbord, 1962).

Lower-Upper Pleistocene: Bermont Formation, Florida (Petuch, 1994).

Late Pleistocene/Holocene: Mississippi delta “mudlumps”, Louisiana, USA (BEU, 2010).

Recent: Western Atlantic, North Carolina and Bermuda south to Sergipe, Brazil (BEU, 2010).

Geological and geographical distribution: Pacific

Upper Miocene: Esmeraldas beds, Onozole Formation, Ecuador (Olsson, 1964; BEU, 2010).

*Distorsio mcgintyi* EMERSON & PUFFER, 1953

Pl. 11, Figs 9-10

1928 *Distorsio* (Distorsio) decussatus simillimus (Sowerby) – Woodring (partim), p. 300, pl. 18, fig. 9, pl. 19, fig. 1.

1951 *Distorsio constricta floridana* OLSSON & MCGINTY, p. 27, pl. 1, figs 5, 6, 9 (junior secondary homonym of Personella floridana Gardner, 1947, transferred to Distorsio by Emerson & Puffer, 1953).


1954 *Distorsio constricta mcgintyi* EMERSON & PUFFER, 1953 – Abbott, p. 197, pl. 25z.

1957 *Distorsio* (Rhysema) mcgintyi EMERSON & PUFFER – CLENCH & TURNER, p. 240, pl. 132, figs 9-10; pl. 134, figs 1-5.

1960 *Distorsio mcgintyi* – Parker, p. 323, pl. 5, fig. 4.

1961 *Distorsio mcgintyi* EMERSON & PUFFER, 1953 – Warmke & Abbott, p. 103, pl. 18, fig. c.

1972 *Distorsio constricta mcgintyi* EMERSON & PUFFER – Lewis, fig. 40.

1973 *Distorsio* (Rhysema) mcgintyi EMERSON & PUFFER – Kilias, p. 204, fig. 146.

1973 *Distorsio mcgintyi* EMERSON & PUFFER – Morris, p. 185, pl. 50, fig. 8.

1974 *Distorsio constricta mcgintyi* EMERSON & PUFFER, 1953 – Abbott, p. 166, fig. 1771.

1975 *Distorsio constricta mcgintyi* EMERSON & PUFFER, 1953 – Rios, p. 80, pl. 22, fig. 328.

1975 *Distorsio mcgintyi* EMERSON & PUFFER – Humphrey, p. 125, pl. 14, fig. 2, 2a.

1981 *Distorsio constricta mcgintyi* EMERSON & PUFFER – Laursen, p. 27, fig. 43.

1981 *Distorsio (Rhysema) constricta mcgintyi* EMERSON & PUFFER – Coelho et al., p. 132, fig. 14.

1985 *Distorsio constricta mcgintyi* EMERSON & PUFFER, 1953 – Rios, p. 78, pl. 28, fig. 341.

1989a *Distorsio constricta mcgintyi* EMERSON & PUFFER, 1953 – Parth, p. 52, centre right fig.

1989b *Distorsio mcgintyi* EMERSON & PUFFER, 1953 – Parth, p. 8, bottom left fig.


Material and dimensions: Maximum height 58.8 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; four specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

Discussion:

Distorsio mcgintyi is easily distinguished from Distorsio clathrata by its more distorted spire, its shorter and wider shape, and its markedly more uneven sculpture. In the tropical western American coasts three similar species occur; Distorsio constricta (Broderip, 1833), Distorsio jenniernestae Emerson & Piech, 1992 and Distorsio minorowohnishii Parth, 1989. For a full discussion see Beu (2010). In the Caribbean fossil assemblages it is most important to distinguish from D. constricta, but D. mcgintyi is characterized by the wide peripheral spiral cord cluster, with three or, in most specimens, four narrow cords, to as many as six on large specimens, on the well raised ridge around the shoulder angle (Beu, 2010).

Geological and geographical distribution:

Lower Miocene: Kendace Siltstone, Carriacou (Beu, 2010); Baitoa Formation, Dominican Republic (Beu, 2010); Cantaure Formation, Venezuela (Beu, 2010).
Middle Miocene: Carriacou, Grenadine Islands (Beu, 2010); Mayo River, Trinidad (Beu, 2010).
Upper Miocene: Cercado Formation, Dominican Republic (Beu, 2010); Gatun Formation, Panama (Beu, 2010); Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (Beu, 2010).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Beu, 2010); Bocas del Toro, Panama (Beu, 2010); Gurabo Formation, Dominican Republic (Beu, 2010).
Lower–Upper Pliocene: Cay Agua and Shark Hole Point Formations, Bocas del Toro, Panama (Beu, 2010); Bowden Formation, Jamaica (Woodring, 1928 (partim), as D. decussatus similimus; Robinson, 1991). Upper Pliocene: Agueguexquite Formation, Mexico (Beu, 2010).
Lower Pleistocene: Moin Formation, Puerto Limon, Costa Rica (Beu, 2010).
Upper Pleistocene: Swan Cay Formation, Bocas del Toro, Panama (Beu, 2010). Recent: Western Atlantic, from Cape Hatteras, North Carolina, Florida and Bermuda to southernmost Brazil, and possibly further south (Beu, 2010).

Family     Bursidae Thiele, 1925
Genus     Marsupina Dall, 1904.
Type species  
Buffo spadiceus Montfort, 1810 (= Murex crassus Dillwyn, 1817, = Murex bufo Bruguière, 1792), by original designation.

Marsupina bufo (Bruguière, 1792)  
Pl. 11, Figs 11-13
Material and dimensions: Maximum height 65.8 mm, seven specimens NMB lot 13339, two specimens NMB lot H 18055; 22 specimens EDIMAR coll.; 50+ specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.
Discussion:

Despite the wide distribution of *Marsupina bufo* (BRUGUIÈRE, 1792) in the Caribbean fossil deposits, it is always rare. Only in the Cubagua assemblage is the species common, where it is one of the most abundant gastropods. Today, specimens are abundant in relatively shallow water along the northern coast of Venezuela, Suriname and Guiana, but associated with areas of upwelling.

Only one specimen has been found on the Panamic coast of the Americas, at Rio Vaca, Puntarenas Province, Costa Rica, which is Plio-Pleistocene, again adding evidence that the Central American seaway was not yet closed by this time (BEU, 2010). The shells in the Cubagua assemblage include many enormous adult specimens showing a marked variability in shape, some more tapered than others, and above all, a wide difference in the size and coarseness of the granular sculpture, as discussed by BEU (2010).

Geological and geographical distribution: Atlantic

Middle Miocene: Shoal River Formation, Florida (E. H. YOKES, 1973, as *Bursa (?Tutufa) amphitrites*).

Upper Miocene: Cercado Formation, Dominican Republic (MAURY, 1917, as *Bursa crassa*); Usiacuri Formation, Juan de Acosta, Colombia (WEISBORD, 1929, as *B. crassa colombiana*; BARRIOS, 1960, as *B. crassa colombiana*; BEU, 2010).

Lower Pliocene: Gurabo and Mao Formations, Dominican Republic (BEU, 2010); Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (BL coll.).

Lower-Upper Pliocene: Bowden Formation, Jamaica (GUPPY, 1866a, as *Ranella crassa*; WOODRING, 1928, as *Bursa (Marsupina) proavus bowdenensis*); Cayo Agua and Shark Hole Point Formations, Bocas del Toro, Panama (BEU, 2010).

Upper Pliocene: Pinecrest Beds, Florida (PETUCH, 1994, as *Bursa (Marsupina) proavus*; Bird Road Quarry Middle Pliocene *fide* LYONS, 1991, p. 176); Banano Formation, Costa Rica (BEU, 2010).

Lower Pleistocene: Moin Formation, Puerto Limon, Costa Rica (ROBINSON, 1991); Maiquitía Member of the Playa Grande Formation, Venezuela (BEU, 2010); Matura Shell Bed, Talparo Formation, Trinidad (JUNG, 1969).

Lower-Upper Pleistocene: Zapato, Colombia (BEU, 2010); Cumaná Formation, Cumaná Hills, Venezuela (BEU, 2010).

Upper Pleistocene:

Recent: Western Atlantic, southeastern Florida (MCINTY, 1940) south to Bahia, Brazil (RIOS, 1994).

Geological and geographical distribution: Pacific

Plio-Pleistocene: Rio Vaca, Puntarenas Province, Costa Rica (BEU, 2010).

Genus *Bursa* RÖDING, 1798.

Type species *Bursa monitata* RÖDING, 1798 (= *Murex bufonius* Gmelin, 1791), by subsequent designation, JOUSSEAUME, 1881.

*Bursa rugosa* (G. B. SOWERBY II, 1835)

Pl. 12, Figs 1-2

1835 *Ranella rugosa* G. B. SOWERBY II, pl. 85, fig. 7

1844b *Ranella rugosa* SOWERBY, Jun. – REEVE, pl. 5, fig. 21a, b.

1934 *Bursa (Marsupina) albofasciata boussingaultii RUTSCH*, p. 58, pl. 3, figs 3-4.

1935 *Bursa [Ranella] sp. – TRECHMAN*, p. 542, pl. 21, fig. 20 (as *Bursa (Ranella) cf. amphitrites* in caption to pl. 21).

1958 *Bursa calicipicta DALL – KEEN* (partim), p. 348, fig. 328 [non *Bursa (Lampadopsis) calicipicta DALL, 1908 = Crossata ventricosa (BRODERIP, 1833)*].

1959a *Bursa (Colubrellina) caelata amphitrites MAURY – WOODRING*, p. 207, pl. 28, figs 1, 2, 7, 8 (non *Bursa amphitrites MAURY, 1917*).

1964 *Bursa (Colubrellina) sp. – OLSSON*, p. 172, pl. 30, fig. 4.

1965 *Bursa (Colubrellina) caelata amphitrites MAURY – JUNG*, p. 513, pl. 68, figs 12-13, pl. 69, fig. 2. (non *Bursa amphitrites MAURY, 1917*).

1971 *Bursa calicipicta DALL, 1908 – KEEN* (partim), p. 508, fig. 965 [non *Bursa (Lampadopsis) calicipicta DALL, 1908 = Crossata ventricosa (BRODERIP, 1833)*].
1971  *Bursa (Colubrellina)* species A. – Jung, p. 189, pl. 11, figs. 5-7.
1972  *Bursa (Colubrellina) caelata amphitrites* Maury – Perrilliat, p. 76, pl. 37, figs 12-15 (non *Bursa amphitrites* Maury, 1917).
1985  *Bursa (Bursa)* rugosa (G. B. Sowerby II, 1835) – Beu, p. 63, fig. 39.
1987  *Bursa (Colubrellina)* sp. – Perrilliat, p. 15, pl. 4, figs 3, 4.
1997  *Bursa (Bursa) rugosa* (G. B. Sowerby II, 1835) – Cossignani, p. 60, illus.
1994  *Bursa amphitrites* Maury, 1917 - Beu, p. 120, pl. 39L, M (not *Bursa amphitrites* Maury, 1917).
1994  *Bursa (Lampasopsis) (sic) amphitrites* Maury, 1917 - Petuch, p. 224, fig. 83J (not *Bursa amphitrites* Maury, 1917).
2001  *Bursa rugosa* (G. B. Sowerby II, 1835) – Beu, p. 711, figs 1.3-1.5.
2010  *Bursa rugosa* (G. B. Sowerby II, 1835) – Beu, p. 59, pl. 5, figs 9, 13-14; pl. 6, figs 1-10.
2010a *Bursa rugosa* (G. B. Sowerby II, 1835) – Landau & Silva, p. 59, pl. 12, figs 1-2.

**Material and dimensions:** Maximum height 55.3 mm, 16 specimens NMB lot II 18050; two specimens NMB lot 12879; nine specimens EDIMAR coll.; 16 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; six specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; seven specimens BL coll., (lower yellow fine sandy bed), 13 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

The shells of *Bursa rugosa* are distinguished from the shells of other, similar *Bursa* species in the study region by its moderately large size (up to c. 70 mm in height); by its very prominent, strongly curved siphonal fasciole, curving to the left of the aperture and then back to the right, to form a deep pseudumbilicus that is covered over in almost all specimens by a wide flare of the inner lip to the left of the lower columellar area; by its equally widely flared outer lip with a weakly digitate outer margin; by its prominent apertural ridges, the inner lip bearing many large, rather closely spaced, weakly anastomosing transverse ridges and the inside of the outer lip bearing five pairs of prominent transverse ridges corresponding to the interspaces between the exterior spiral cords (three ridges are present in a few of these groups, rather than two, in a few specimens); by its short to moderately tall spire with moderately to strongly stepped outlines; by its external sculpture of four major spiral cords, bearing numerous, small to few, large, rounded nodules on at least the upper two cords, forming obvious butteswatches where the cords cross the adapertural and abapertural varicellal hollows, and forming low, rounded but obvious nodules where the cords cross the varices; by its varices being strictly aligned up the opposing sides of the spire until the last whorl or two of large specimens, when they become progressively further offset as the shell grows; by its moderately long semitubular posterior siphonal canals, protruding above the varices on most specimens to produce blunt spines; and by its finely to moderately prominently rugose surface between the major spiral cords (Beu, 2010).

*Bursa rugosa* is particularly interesting for Panamic biogeography as it was widespread and abundant in the Caribbean, Venezuelan and Colombian shallow-water fossil localities of Lower Miocene to Upper Pliocene age, whilst today it occurs only in tropical western America. This is one of the clearest examples of a "Paciphile" tonnoidean species (Beu, 2010).

**Geological and geographical distribution: Atlantic**

Lower Miocene: Cantaure Formation, Venezuela (Jung, 1965, as *Bursa (Colubrellina) caelata amphitrites*).
Middle Miocene: Ferrotepec Formation, Mexico (Perrilliat, 1987 as *Bursa (Colubrellina)* sp.; lower Gatun Formation, Panama (Woodring, 1959, as *Bursa (Colubrellina) caelata amphitrites*; Valiente Formation, Bocas del Toro, Panama (Beu, 2010); Grand Bay Formation, Carriacou (Trechman, 1935, as *Bursa (Ranella)* sp.; Jung, 1971, as *Bursa (Colubrellina)* species A.).
Upper Miocene: Usiacuri Formation, Juan de Acosta, Colombia (Beu, 2010); middle Gatun Formation, Panama (Woodring, 1959, as *Bursa (Colubrellina) caelata amphitrites*; Mataruca Member of Caujarao Formation, El Carrizal, Venezuela (Beu, 2010).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934, as B. (Marsupina) albofasciata boussingaulti).

Lower-Upper Pliocene: Shark Hole Point Formation, Bocas del Toro, Panama (BEU, 2010).

Upper Pliocene: Pinecrest Beds, Florida (PETUCH, 1992, as B. amphitrites, 1994, 1997, as B. (Lampasopsis) amphitrites; Bird Road Quarry Middle Pliocene fide LYONS, 1991, p. 176); Agueguexquite Formation, Mexico (Perrilliat, 1972 as B. (Colubrellina) caelata amphitrites).


Geological and geographical distribution: Pacific

Upper Miocene: Angostura Formation, Ecuador (BEU, 2010); Esmeraldas beds, Onozole Formation, Ecuador (OLSSON, 1964, as Bursa (Colubrellina) sp.).

Pleistocene: Burica Peninsula, Panama (BEU, 2010).

Recent: Eastern Pacific, southern Mexico to at least Paita, Peru (BEU, 2010).

Superfamily Ficoidea MEEK, 1864 (1840)
Family Ficidae MEEK, 1864 (1840)
Genus Ficus RÖDING, 1798.

Type species Ficus variegata RÖDING, 1798, by subsequent designation, DALL, 1906.

Ficus carbasea (GUPPY, 1866)
Pl. 12, Figs 3-4

1866b Ficula carbasea GUPPY, p. 580, pl. 26, fig. 7.
1925a Pyrula trinitaria MAURY, p. 222, pl. 41, figs 9, 12.
1925a Pyrula carbasea GUPPY – MAURY, p. 224, pl. 41, fig. 5.
2010a Ficus carbasea (GUPPY, 1866) – LANDAU & SILVA, p. 60, pl. 12, figs 3-4.

non 1959a Ficus carbasea carbasea (GUPPY) – WOODRING, p. 211, pl. 36, figs 10, 13.
non 1965 Ficus carbasea carbasea (GUPPY) – JUNG, p. 515, pl. 69, figs 3-5.

Material and dimensions: Maximum height 66.1 mm, six specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
Ficus carbasea (GUPPY, 1866) is characterized by having a multispiral protoconch of 2.75 whorls, of which the first 2.5 are smooth, the last 0.25 protoconch whorl bearing a fine reticulate sculpture. Early authors considered almost all the Caribbean Neogene Ficus specimens to belong to this species. The importance of protoconch characteristics in the classification of Caribbean Ficus species was first discussed by B. SMITH (1907) resulting in a much more diverse Neogene ficid fauna than previously thought.

Ficus pilshryi B. SMITH, 1907, from the Pliocene Bowden Shell Beds of Jamaica has a finely sculptured shell with flat spiral interspaces, and a paucispiral protoconch, the first 1.7-1.8 smooth, 0.25-0.3 whorls sculptured (BEU, 2010). The Lower Pliocene specimens recorded by RUTSCH (1934, p. 62, pl. 3, fig. 8) from the Punta Gavilán Formation, Falcón, Venezuela as Ficus aff. ventricosa (SOWERBY) do not correspond to this species, with single secondary cord between each pair of primary spiral cords and a paucispiral protoconch. They may indeed be conspecific with the Bowden material. A further species was described from the Lower Pliocene Tuberaí Group of northern Colombia; Ficus colombiana ANDERSON, 1929. According to the original description it differs from F. carbasea in having a different outline, and four to five secondary cords between each pair of primaries. The specimen figured by WOODRING (1959a) as F. carbasea carbasea is also clearly not this species as the text describes a paucispiral protoconch.

In the Upper Miocene-Lower Pliocene Dominican deposits Ficus gibsonsmithi BEU, 2010 is by far the most common species, and is the species recorded previously by PILSBRY (1922, p. 364) as F. carbasea
BERNARD M. LANDAU

(GUPPY). It differs from all other species in the *F. ventricosa* group by its much narrower, more elongate shape and strongly concave spaces between the primary spiral cords. The protoconch also differs from that of *F. carbasea* in having far fewer whorls, a paucispiral form. A much rarer form in the Dominican deposits is *Ficus bernardi* BEU, 2010, which differs from *F. pilsbryi* and *F. gibsonsmithi* in having a smaller shell, and differing in details of the protoconch whors and teleconch sculpture (see BEU, 2010). An even more elongated species with very fine sculpture occurs in the Dominican Republic; *Ficus lisselonga* BEU, 2010.

The Lower Miocene specimens recorded by JUNG (1965) as *F. carbasea carbasea* from the Cantaure Formation of the Paraguana Peninsula, Venezuela can immediately be distinguished from this species by having a more globose last whorl, more strongly constricted at the base, far more numerous secondary spiral threads between each set of primaries. The protoconch is similar, just over 2.5-2.75 whorls, of which the last quarter whorl is sculptured.

From this discussion it is clear that the Caribbean Neogene *Ficus* species are poorly understood and in urgent need of review. We therefore restrict the distribution of *F. carbasea* to the Lower Pliocene of Trinidad and Cubagua.

**Geological and geographical distribution:**

Upper Miocene: Mataruca Member of Caujarao Formation (NMB 3005/1-2), El Carrizal, Venezuela.

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Springvale Formation, Trinidad (MAURY, 1925a).

Superfamily: Epitonioida BERRY, 1910 (1812)

Family: Epitoniidae BERRY, 1910 (1812)

Genus: *Scalina* CONRAD, 1865.

Type species *Scalina staminea* CONRAD, 1865, by subsequent designation, PALMER, 1937.

*Scalina brunneopicta* (DALL, 1908)

Pl. 12, Fig. 5

1908 *Epitonium (Ferminoscala) brunneopictum* DALL, p. 316, pl. 8, fig. 10.

1941 *Epitonium (Ferminoscala) eleutherium* PILSBRY & OLSSON, p. 38, pl. 2, fig. 7.

1959a *Scalina cf. S. brunneopicta* (DALL) – WOODRING, p. 188, pl. 38, figs 7, 14.


1974 *Amaea (Scalina) brunneopicta* (DALL, 1908) – DUSHANE, p. 53, figs 63, 64, 68.

1979 *Amaea (Scalina) brunneopicta* (DALL, 1908) – DUSHANE, p. 97, figs 3, 4.


2010a *Scalina brunneopicta* (DALL, 1908) – LANDAU & SILVA, p. 61, pl. 12, fig. 5.

**Material and dimensions:** One specimen BL coll., 36.5 mm in height, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

The genus *Scalina* CONRAD, 1865 in the Tropical American Neogene was recently reviewed by DEVRIES (2007b). He placed particular emphasis on the spiral sculpture, arrangement and strength of the spiral cords and the presence or absence of anterior ramping on the primary spiral cords. DEVRIES (2007b) recognised several phylogenetic lineages within *Scalina* in the tropical American Neogene.

In the specimen from Cubagua the spiral cords clearly have anterior ramping. The small spire angle and secondary spiral cords that sometimes are on the verge of becoming as strong as the primary spirals, as well as the relatively few axials that are both extended at the posterior suture and intermittently thickened, are all characters of the Recent tropical American Pacific species *Scalina brunneopicta* (DALL, 1908). This species is also known from the Pacific portion of the Gatunian province, recorded as *Epitonium (Ferminoscala) eleutherium* PILSBRY & OLSSON, 1941, which was synonymised with *Scalina brunneopicta* by DEVRIES (2007b).
This is the first Atlantic record for *S. brunneopicta*, which is added to the small number of specific taxa found in the Cubagua assemblage in the Early Pliocene, but not elsewhere in the Atlantic fossil record, and are today extant in Tropical American Pacific waters.

**Distribution Atlantic:**
Upper Miocene: upper Gatun Formation, Panama (Woodring, 1959).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Distribution Pacific:**
Pliocene: Canoa Formation, Ecuador (Pilsbry & Olsson, 1941).
Recent: Gulf of California and Baja California to Ecuador (Dushane, 1974, 1979).

<table>
<thead>
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<th>Clade</th>
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<tr>
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<td>Subfamily</td>
<td>Muricinae Rafinesque, 1815</td>
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<td>Genus</td>
<td>Chicoreus Montfort, 1810</td>
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<tr>
<td>Type species</td>
<td><em>Murex ramosus</em>, Linnaeus, 1758, by original designation (ICZN Opinion 911, 1970).</td>
</tr>
<tr>
<td>Subgenus</td>
<td><em>Triplex</em> Perry, 1810</td>
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<tr>
<td>Type species</td>
<td><em>Murex foliatus</em> Perry, 1810 (rejected ICZN = <em>T. rosaria</em> Perry, 1810; see Pettit, 2003, p. 47), by monotypy.</td>
</tr>
</tbody>
</table>

George Perry’s molluscan taxa and notes on the editions of his *Conchology* of 1811 including *Triplex foliatus* Perry, 1810 were placed on the Official Index of Rejected and Invalid Specific Names in Zoology in ICZN Opinion 911. The synonym *Triplex rosaria* Perry, 1810 is available for it, although it has usually (but by no means universally) been thought a secondary homonym, and replaced by the much better-known name *T. palmarosae* (Lamarck, 1822) (see Pettit 2003).

The Caribbean Neogene to Recent *Chicoreus* group has usually been placed within the nominate subgenus *Chicoreus* (s.s.) Montfort, 1810 (E. H. Vokes, 1965, 1989a, 1990a). Houart (1992) subdivided the Indo-Pacific species into those members with a labral tooth, which he placed under *Chicoreus* (s.s.) and those without it in the subgenus *Chicoreus* (*Triplex*) Perry, 1810. The labral tooth is absent in all species from the Western Atlantic and they therefore should be included in the subgenus *Chicoreus* (*Triplex*) (pers. comm. Roland Houart, 2007). E. H. Vokes (1990a) argued against this position and placed the Western Atlantic taxa into “species groups”. The presence or absence of a labral tooth is usually taken as a shell character of generic importance (Vermeij, 2001a) and we here adopt the subgenus *Triplex* for these Western Atlantic taxa.

*Chicoreus* (*Triplex*) *cornurectus* (Guppy, 1876)
Pl. 12, Figs 6-7


1876 *Murex cornurectus* Guppy, p. 521, pl. 28, fig. 4.
1917 *Murex* (*Phyllonotus*) *cornurectus* Guppy – Maury, p. 267, pl. 16, figs 9-10.
1925a *Murex brevifrons* Lamark – Maury, p. 138, pl. 6, figs 7, 9 (non *Murex brevifrons* Lamark, 1822).
1959a *Murex* (*Chicoreus*) *brevifrons* Lamark – Woodring (partim), p. 216, pl. 35, fig. 12 only (non *Murex brevifrons* Lamark, 1822).
1965 *Chicoreus* (*Chicoreus*) *cornurectus* (Guppy) – E. H. Vokes (partim), p. 186, pl. 2, fig. 2, text-fig. 2.
1989a Chicoreus (Chicoreus) cornurectus (GUPPY) – E. H. VOKES, p. 31, pl. 2, figs 6-9.
1990a Chicoreus (Chicoreus) cornurectus (GUPPY) – E. H. VOKES, p. 33, pl. 5, fig. 7.
2010a Chicoreus (Triplex) cornurectus (GUPPY, 1876) – LANDAU & SILVA, p. 62, pl. 12, figs 6-7.

non 1922 Murex (Phyllonotus) cornurectus GUPPY – OLSSON, p. 303 (=Chicoreus venezuelanus F. HODSON, 1931).
non 1971 Chicoreus (Chicoreus) cornurectus (GUPPY) – JUNG, p. 192, pl. 10, figs 8-9 (=Chicoreus junki E. H. VOKES, 1990a).

Material and dimensions: Maximum height 46.7 mm, four specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion: Chicoreus (Triplex) cornurectus (GUPPY, 1876) is closely related to the Recent common West Indian species Chicoreus (Triplex) brevifrons (LAMARCK, 1822), from which it differs in having a single elongated varical frond at the shoulder, whereas C. (T.) brevifrons has two large spines with a smaller spinelet between. Furthermore, the shells of C. (T.) cornurectus tend to have two intervarical nodes, whereas C. (T.) brevifrons usually has only one. The protoconch is not preserved in the Cubagua material, but it is morphologically similar in the two species, however, being twice the size in C. (T.) brevifrons (E. H. VOKES, 1989a). The two species must have coexisted for some time in the Neogene Caribbean, as the first confirmed report of C. (T.) brevifrons is from the Middle Miocene of Veracruz, Mexico (E. H. VOKES, 1989a).

Geological and geographical distribution:
Lower Miocene: Cantaure Formation, Paraguana Peninsula, Venezuela (JUNG, 1965 as M. cf. brevifrons; E. H. VOKES, 1989, 1990a); Pirabas Limestone, Brazil (MAURY, 1925b, as M. brevifrons; E. H. VOKES, 1989a, 1990a); Baitoa Formation, Dominican Republic (E. H. VOKES, 1989a).
Lower Pliocene: Quebradillas Formation, Puerto Rico (MAURY, 1920); Araya Formation, Cubagua Island, Venezuela; Melajo Clay Member of Springvale Formation, Trinidad (JUNG, 1969 as M. cf. brevifrons); Gurabo Formation, Dominican Republic (MAURY, 1917; E. H. VOKES, 1989a).

Type species Murex messorius G. B. SOWERBY II, 1841, by original designation.

PETUCH (1994) and HOUART (1999) separated the genus Haustellum sensu PONDER & E. H. VOKES, 1988 into two groups; true Haustellum, with a globose, spineless last teleoconch whorl, rounded varices, large, roundly ovate aperture, broadly expanded columellar lip, spineless siphonal canal, and Vokesimurex PETUCH, 1994, usually smaller-shelled, with an ovately rounded last teleoconch whorl, moderately narrow columellar lip, and varices and siphonal canal often ornamented with prominent spines. This separation was supported by BARCO et al. (2010), based on molecular data. Vokesimurex was originally considered an endemic American genus (PETUCH, 1994), however HOUART (1999) included several Indo-Pacific species within the genus. In the Pliocene both Vokesimurex and Haustellum coexisted in the Gatunian Province. However, Haustellum became extinct in the Americas by the beginning of the Pleistocene.

Vokesimurex messorius (G. B. SOWERBY II, 1841)
Pl. 12, Fig. 8

1841a Murex messorius G. B. SOWERBY II, pl. 194, fig. 93.
1841a Murex nigrescens G. B. SOWERBY II, pl. 198, fig. 113.
1841b Murex messorius G. B. SOWERBY II, p. 137.
1845 Murex funiculatus REEVE, 1845, pl. 19, fig. 74.
1873  *Murex recurvoirostris* BROD. – GABB, p. 201 (non *M. recurvoirostris* BRODERIP, 1833).
1880a  *Murex recurvoirostris* BROD. – TRYON, p. 80, pl. 10, fig. 193, pl. 11, fig. 193, pl. 12, figs 124-128.
1887  *Murex sutilis* WHITE, p. 137, pl. 11, fig. 11.
1911  *Murex messorius* SOWB. – BROWN & PILSBRY, p. 353.
1917  *Murex messorius* SOWERBY – MAURY, p. 265, pl. 16, figs 1-2.
1920  *Murex recurvoirostris* BROD. – PILSBRY, p. 353 (non *M. recurvoirostris* BRODERIP, 1833).
1922  *Murex messorius* SOWERBY – OLSSON, p. 303.
1922  *Murex recurvoirostris* BROD. – PILSBRY, p. 353 (non *M. recurvoirostris* BRODERIP, 1833).
1925a  *Murex messorius* SOWERBY – OLSSON, p. 303.
1935  *Murex (Haustellum) messorius* SOWERBY – TRECHMANN, p. 38, pl. 4, fig. 14.
1945  *Murex (Murex) woodringi* CLENCH & PÉREZ FARFANTE, p. 9, pl. 4, figs 1-3.
1959a  *Murex (Murex) recurvoirostris recurvoirostris* BRODERIP – WOODRING, p. 214, pl. 35, figs 5, 8, pl. 36, figs 11-12 (non *M. recurvoirostris* BRODERIP, 1833).
1960  *Murex messorius* SOWERBY – BARRIOS, p. 279, pl. 9, fig. 8.
1963  *Murex (Murex) messorius* SOWERBY – E. H. VOKES (partim), p. 103, pl. 3, figs 6-7 only.
1967  *Murex (Murex) messorius* SOWERBY – E. H. VOKES, p. 81, pl. 1, figs 1-3, pl. 2, figs 1-8.
1969  *Murex messorius* var. gustaviensis NOWELL-USTICKE, p. 15, pl. 3, fig. 647.
1974  *Murex (Murex) recurvoirostris subsp. recurvoirostris* BRODERIP, 1833 – ABBOTT, p. 172, fig. 1816.
1976  *Murex messorius* SOWERBY, 1841 – RADWIN & D’ATTILIO, p. 68, pl. 11, fig. 7.
1889a  *Murex (Haustellum) messorius* SOWERBY – TRECHMANN, p. 38, pl. 4, fig. 14.
1990a  *Haustellum messorius* (SOWERBY) – E. H. VOKES, p. 16, pl. 4, figs 1-5.
1994  *Murex recurvoirostris* BRODERIP – WEISBORD, p. 278, pl. 26, figs 3-4 [ = *Vokesimurex donmoorei* (BULLIS, 1964)].
2001  *Murex recurvoirostris* BRODERIP – MACSOTAY & CAMPOS, p. 73, pl. 1, figs 5, 9, 11, 14.
2003  *Murex samui* – SUNDERLAND et al., p. 16, unnumbered figure.
2009  *Haustellum messorius* SOWERBY, 1841 – RIOS, p. 201, fig. 495.
2010a  *Vokesimurex messorius* (G. B. SOWERBY II, 1841) – LANDAU & SILVA, p. 63, pl. 12, fig. 8.

*non* 1934 *Murex recurvoirostris* BRODERIP – RUTSCH, p. 64, pl. 4, fig. 1 [ = *Vokesimurex donmoorei* (BULLIS, 1964)].
*non* 1960 *Murex recurvoirostris* BRODERIP – PERILLIAT, p. 21, pl. 3, figs 9-10 [ = *Vokesimurex bellegladeensis* (E. H. VOKES, 1963)].
*non* 1962 *Murex recurvoirostris recurvoirostris* BRODERIP – WEISBORD, p. 278, pl. 26, figs 3-4 [ = *Vokesimurex donmoorei* (BULLIS, 1964)].

**Material and dimensions:** Maximum height 55.9 mm, three specimens EDIMAR coll.; 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
Two closely similar species occur in the Neogene and Recent Venezuelan faunas, *Vokesimurex messorius* (G. B. SOWERBY II, 1841) and *Vokesimurex chrysostoma* (G. B. SOWERBY II, 1841). The latter is generally larger, with fewer intervarical nodules, has a more appressed suture, a more inflated last whorl and a larger aperture with a more expanded parietal shield. However, all these characters may appear in either species with a few shells impossible to identify conclusively (E. H. VOKES, 1989b). Although the
specimens from Cubagua are larger than usual for *V. messorius*, the other shell characters of shape and sculpture conform. We note that in the Holocene Tortuga Formation of Cubagua we have collected only *V. chrysostoma*. *Vokesimurex messorius* has so far only been recorded from the Atlantic side of the Gatunian biogeographical province, whereas *V. chrysostoma* has also been recorded from the Pacific side, present in the Upper Miocene Esmeraldas beds of Ecuador (E. H. Vokes, 1989d).

**Geological and geographical distribution:**
Lower Miocene: Pirabas Limestone, Brazil (Maury, 1925b); Baitoa Formation, Dominican Republic (E. H. Vokes, 1989).
Middle Miocene: Thomonde Formation, Haiti (E. H. Vokes, 1990a).
Upper Miocene: Gatun Formation, Panama (Woodring, 1959, as *M. recurvirostris*); Cercado Formation, Dominican Republic (Maury, 1917; E. H. Vokes, 1989).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Tuberá Group, northern Colombia (Barrós, 1960; E. H. Vokes, 1990a); Gurabo Formation, Dominican Republic (Maury, 1917; E. H. Vokes, 1989).
Lower-Upper Pliocene: Quebradillas Formation, Puerto Rico (Maury, 1920); Bowden Formation, Jamaica (Woodring, 1928, as *M. recurvirostris*).
Upper Pliocene: Banano Formation, Costa Rica (Olsson, 1922).

**Genus** *Haustellum* Schumacher, 1817.
**Type species** *Murex haustellum* Linnaeus, 1758, by tautonymy.

*Haustellum mimiwilsoni* E. H. Vokes, 1990

Text-Figure 21; Pl. 12, Figs 9-11

1990a *Haustellum mimiwilsoni* E. H. Vokes, p. 16, pl. 2, figs 1-2.
2010a *Haustellum mimiwilsoni* E. H. Vokes, 1990 – Landau & Silva, p. 64, pl. 12, figs 9-11, text-fig. 13.

**Material and dimensions:** Maximum height 62.6 mm, four specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**


E. H. Vokes (1990a) attributed a second fragmentary shell from the Upper Pliocene Banano Formation of Costa Rica, which also has a deep sutural gutter, to *H. mimiwilsoni*. This fragment from Costa Rica has the protoconch preserved, consisting of 3.5 smooth whorls. Unfortunately the protoconch is missing in all our Venezuelan specimens we examined. A beautiful specimen from the Pliocene Cayo Agua Formation of Panama (Text-Fig. 21), but also with the protoconch worn, is present in the NMB collections.

As noted by E. H. Vokes (1990a), *H. mimiwilsoni* is remarkably similar to the Recent Australian *Haustellum wilsoni* D’Attilio & Old, 1971, but differs in the size of their protoconch, much larger in *H. wilsoni* and there are no rugae on the inner lip of the Australian species.
Text-Figure 21. 1-5, Haustellum mimiwilsoni E. H. Vokes, 1990, NMB H18102, locality number 17831, Lower Pliocene, Cayo Agua Formation, Panama. Height 73.0 mm.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island (E. H. Vokes, 1990a); Aramina Formation, Araya Peninsula, Venezuela.
Lower-Upper Pliocene: Cayo Agua Formation (NMB H 18102, lot 17831), Panama.

Genus Poirieria Jousseaume, 1880.
Type species Murex zelandicus Quoy & Gaimard, 1833, by original designation.
Subgenus Panamurex Woodring, 1959.
Type species Murex gatunensis Brown & Pilsbry, 1911, by original designation.

Poirieria (Panamurex) eugeniae E. H. Vokes, 1992
Pl. 13, Figs 1-2

1992 Poirieria (Panamurex) eugeniae E. H. Vokes, p. 54, pl. 11, figs 7-8.

Material and dimensions: Maximum height 18.6 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
This is the first fossil record of Poirieria (Panamurex) eugeniae E. H. Vokes, 1992. As discussed by E. H. Vokes (1992) this species forms part of a group of closely related southern Caribbean species; P.
(P.) eugeniae, Poirieria (Panamurex) velero E. H. Vokes, 1970 and Poirieria (Panamurex) recticanalis (Weisbord, 1962). Poirieria (P.) eugeniae differs from the other two in having a slightly larger, more elongate shell, with a higher spire and longer siphonal canal. Five rugae are clearly present on the columella of the Cubagua specimen (Pl. 13, Fig. 1c), which are characteristic of P. (P.) eugeniae, P. (P.) velero E. H. Vokes, 1970 and P. (P.) recticanalis having only four. E. H. Vokes (1992) also discussed differences in the spiral sculpture; both P. (P.) eugeniae and P. (P.) recticanalis have secondary spiral sculpture, whereas P. (P.) velero has only primary cords. One of the shells from Cubagua has no secondary sculpture (Pl. 13, Fig. 2), but neither is it particularly evident in the paratype (E. H. Vokes, 1992, pl. 11, fig. 8), and this may be a somewhat variable character.

The presence of Poirieria (Panamurex) eugeniae in the Lower Pliocene southern Caribbean casts doubts on the lineage suggested by E. H. Vokes (1992), as this is now the oldest member of the group, and therefore unlikely to have evolved from the stratigraphically younger P. (P.) recticanalis. It is more likely that both these species were present in the Pliocene. It is still quite likely that P. (P.) recticanalis was ancestral to P. (P.) velero, as the two species are more closely similar than the others.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.
Recent: Off Santa Marta Colombia, to Golfo de Venezuela, 50 metres depth (Petuch, 1987).

Poirieria (Panamurex) gatunensis (Brown & Pilsbry, 1911)
Pl. 13, Figs 3-4

1911 Murex (Phyllonotus) gatunensis Brown & Pilsbry, p. 354, pl. 26, fig. 2.
1913 Murex (Phyllonotus) gatunensis B. & P. – Brown & Pilsbry, p. 503.
1917 Murex gatunensis B. & P. – Pilsbry & Brown, p. 34.
1959a Paziella (Panamurex) gatunensis (Brown & Pilsbry, 1911) – Woodring, p. 217, pl. 35, figs 6, 7, 9, 10.
1964 Poirieria (Panamurex) gatunensis (Brown & Pilsbry) – E. H. Vokes, p. 18, pl. 2, fig. 32.
1965 Paziella (Panamurex?) cf. gatunensis (Brown & Pilsbry, 1911) – Jung, p. 523, pl. 69, figs 11-12.
1993 Poirieria (Panamurex) gatunensis (Brown & Pilsbry) – Pitt & Pitt, p. 3, pl. 2, fig. 2.
2010a Poirieria (Panamurex) gatunensis (Brown & Pilsbry, 1911) – Landau & Silva, p. 65, pl. 13, figs 3-4.

non 1987 Panamurex gatunensis (Brown & Pilsbry) – Petuch, pl. 15, fig. 8 (= Poirieria (Paziella) petuchi E. H. Vokes, 1992).

Material and dimensions: Maximum height 34.4 mm, 13 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion: As noted by E. H. Vokes (1992), this species is widespread in the Lower Miocene to Pliocene from Panama to Venezuela. Although the Cubagua specimen is poorly preserved, it has a strong spine at the shoulder and no spines encircling the siphonal canal, characteristic of Poirieria (Panamurex) gatunensis.

Geological and geographical distribution:
Lower Miocene: Cantaure Formation, Paraguana Peninsula, Venezuela (Jung, 1965; E. H. Vokes, 1992);
Culebra Formation, Panama (WOODRING, 1959).
Upper Miocene: middle and upper Gatun Formation, Panama (WOODRING, 1959).

Subfamily Typhinae Cossmann, 1903
Genus Typhina Jousseaume, 1880
Type species Typhis belcheri Broderip, 1833, by original designation [synonymised with Talityphis Jousseaume, 1882, Type species Typhis expansus G. B. Sowerby II, 1874, by original designation; Houart, 2002].

Typhina expansa (G. B. Sowerby II, 1874)
Pl. 13, Fig. 5

1874a Typhis expansus G. B. Sowerby II, p. 719, pl. 59, fig 4.
1874b Typhis expansus Sowerby – G. B. Sowerby II, pl. 3, fig 12.
1880 Typhis expansions Sowerby – G. B. Sowerby II, pl. 284b, fig. 24.
1880a Typhis expansions[sic] Sowb. – Tryon, p. 138, pl. 30, fig. 306.
1922 Typhis alatus Sowerby – Olsson, p. 132, pl. 10, fig. 15 [non G. B. Sowerby I, 1850].
1928 Typhis (Talityphis) alatus obesus Gabb – Woodring, p. 294, pl. 18, figs 3-4 [non Gabb, 1873].
1940 Typhis melloleitaoi L. de Morrepes, p. 251, pl. 1, fig. 1-3.
1943 Typhis (Talityphis) expansus Sowerby – Keen, p. 53, pl. 3, fig. 20.
1969 Typhis (Talityphis) obesus Gabb – Gertman (partim), p. 160, pl. 4, fig. 3 only [non Gabb, 1873].
1969 Typhis (Talityphis) expansus Sowerby – Gertman, p. 167, pl. 5, figs 5-6.
1971 Typhis (Talityphis) expansus Sowerby – Bayer, p. 166, figs 35B, 36A, 37, A-C.
1976 Talityphis expansus (Sowerby, 1874) – radwin & D’Attilio, p. 201, fig. 3.
1976 Talityphis perchardei radwin & D’Attilio, p. 236, text-figs. 190-192, pl. 30, fig. 15.
1988 Talityphis expansus (Sowerby, 1874) – D’Attilio & Hertz, p. 59, fig. 73.
1989a Typhis (Talityphis) expansus Sowerby – E. H. Vokes, p. 77, pl. 10, fig. 9, text-fig. 21.
2002 Typhina expansa (Sowerby, 1874) – Houart, fig. 24.
2009 Typhina expansa (Sowerby, 1874) – rins, p. 217, fig. 539.
2010a Typhina expansa (G. B. Sowerby II, 1874) – Landau & Silva, p. 66, pl. 13, fig. 5.

non 1976 Talityphis expansus (Sowerby, 1874) – radwin & D’Attilio, p. 201, pl. 31, fig. 3 [= Typhis (Rugotyphis) puertoricensis Warmke, 1964].

Material and dimensions: Maximum height 30.3 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; one specimen BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
Typhina expansa (G. B. Sowerby II, 1874) has usually been placed in the subgenus Talityphis Jousseaume, 1882, which was synonymised with Typhina Jousseaume, 1880 by Houart (2002). This species is very similar to the fossil Typhina alata (G. B. Sowerby I, 1850) but differs in one constant character: in the shell of T. alata there is a marked swelling anterior to the tubes forming an “intervarical node”. This feature is never present in T. expansa (E. H. Vokes, 1989a). The shells from the Araya Formation of Venezuela, although broken, clearly show no trace of any “intervarical node”. Whilst both occur in the Dominican deposits, E. H. Vokes (1989a) noted that they were not coeval; T. alata occurs in the Lower Pliocene Gurabo Formation whereas T. expansa is found only in the slightly younger Mao
Formation. This seems not to be the case in the southern Caribbean Neogene, as the Gurabo Formation is roughly the same age as the Araya Formation. *Typhina expansa* has also been confused with *Typhina obesa* (GABB, 1873), but this species has quite a different shell shape; much more globose as the name would imply. At the same size the shell of *T. expansa* has a smaller aperture and the shoulder spine is recurved dorsally, rather than turned adapically as in *T. alata*.

**Geological and geographical distribution:**
Upper Miocene: Nancy Point Formation, Bocas del Toro, Panama (OLSSON, 1922).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula; Punta Gavilán Formation, Falcón, Venezuela (BL coll.); Mao Formation, Dominican Republic (E. H. VOKES, 1989a).

**Subfamily** Ocenebrinae COSSMANN, 1903

**Genus** Eupleura H. & A. ADAMS, 1853.

Type species *Ranella caudata* SAY, 1822, by subsequent designation, F. C. BAKER, 1895.

*Eupleura muriciformis* (BRODERIP, 1833)

Pl. 13, Fig. 6

1833 *Ranella muriciformis* BRODERIP, p. 179.

1841a *Ranella muriciformis* BROD. – G. B. SOWERBY II, pl. 88, fig. 11.
1844b *Ranella muriciformis* BRODERIP – REEVE, pl. 7, sp. 34.
1866 *Eupleura muriciformis* (BROD.) – MORRIS, p. 177, pl. 57, fig. 7.
1976 *Eupleura muriciformis* (BRODERIP, 1833) – RADWIN & D’ATTILIO, p. 115, pl. 19, fig. 5.
2010a *Eupleura muriciformis* (BRODERIP, 1833) – LANDAU & SILVA, p. 66, pl. 13, fig. 6.

non 1880b *Eupleura muriciformis* (BRODERIP) – TRYON, pl. 39, fig. 501 [= *Eupleura pectinata* (HINDS, 1844)].
non 1880b *Eupleura muriciformis* (BRODERIP) – TRYON, pl. 39, fig. 504 [= *Eupleura plicata* (REEVE, 1844)].
non 1880b *Eupleura muriciformis* (BRODERIP) – TRYON, pl. 39, fig. 505 [= *Eupleura triquetra* (REEVE, 1844)].
non 1984a *Eupleura muriciformis* (BRODERIP) – E. H. VOKES, pl. 2, fig. 19 [= *Eupleura vokesorum* HERBERT, 2005].

**Material and dimensions:** Maximum height 32.3 mm, 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
HERBERT (2005, p. 305) recorded this species from Cubagua. Although his text reads “Cumana Formation, Island of Cubagua, Venezuela” the attribution to the Cumana formation is a lapsus (Greg Herbert pers. comm., 2006), the specimen is held in the University of California Museum of Paleontology at Berkeley; locality number for the lot is S-122. The exact locality information with the lot is as follows: “About 400 meters SSW of house at Las Calderas, Island of Cubagua, Nueva Esparta, Venezuela. Elevation 12 meters, Araya Formation, Middle Pliocene.” This corresponds to our Cerro Colorado locality.

The specimens figured and discussed herein were collected in Cañon de las Calderas. They are not identical to the Miocene Caribbean specimens of *Eupleura muriciformis* (BRODERIP, 1833) figured by
BERNARD M. LANDAU

Geological and geographical distribution: Atlantic
Upper Miocene: Caújarao Formation, Falcón, Venezuela (HERBERT, 2005).
Lower Pliocene: Araya Formation, Cubagua Island (HERBERT, 2005); Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (HERBERT, 2005); Tuberá Group, northern Colombia (HERBERT, 2005).

Geological and geographical distribution: Pacific
Upper Pliocene: Canoa Formation, Ecuador (HERBERT, 2005).
Recent: Guayamas, Mexico and Bahía Concepcion, Baja California, Mexico south to Peru, intertidal to 30m on mud bottom (HERBERT, 2005).

Subfamily    Rapaninae G RAY, 1853
Genus    Stramonita S CHUMACHER, 1817.
Type species Buccinum haemostoma L INNAEUS, 1767, by subsequent designation, GRAY, 1847.

Stramonita 'biserialis' (BLAINVILLE, 1832)
Pl. 13, Figs 7-8

Material and dimensions: Maximum height 29.9 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
The shells from Cubagua differs from typical specimens of Stramonita rustica (LAMARCK, 1822), a Recent western Atlantic species, ranging from Southern Florida to Brazil (CLENCH, 1947), by having four nodulose spiral cords rather than two and more tubercles in each row on the last whorl. The dentition on the lip is also far more strongly developed in S. 'biserialis' than it is in S. rustica.

VERMEIJ (2001b) in his review of the American species of Stramonita suggested that the taxon S. biserialis (DE BLAINVILLE, 1832) from the Recent fauna of the eastern Pacific, and Stramonita haemastoma haemostoma (L INNAEUS, 1767) may each actually correspond to more than one species. The shells from Cubagua are identical to Recent specimens from Pacific Panama, i.e. the southern form of S. ‘biserialis’. The species was originally named from Mexico and according to VERMEIJ (2001b) the northern specimens
are broader and have a larger number of crenulations on the outer lip (25-30 vs. 21-26) than the southern form. The lip crenulations in the Cubagua shells match those in small individuals of the southern ‘biserialis’ (14-17). In Costa Rica the geographical distribution of the two morphotypes overlap, but the animals live at different shore levels. VERMEIJ (2001b) was unable to find a suitable name for the southern ‘biserialis’, which probably needs a new species designation. However, as pointed out by DeVRIES (2007a), the uncertainty regarding the systematics of *S. biserialis*, *S. haemastoma* and *S. delessertiana* (ORBIGNY, 1841) will probably only be settled when DNA data are available.

*Stramonita ‘biserialis’* belongs to one of two *Stramonita* groups, with shells with long spiral lirae within the outer lip, which in *S. biserialis* and *S. rustica* are accompanied by denticles near the lip’s edge. This group first appears in the Lower Miocene of Cantaure, Venezuela, represented by *S. bifida* VERMEIJ, 2001b. This is the earliest record of any form of *S. biserialis* so far, suggesting that it probably originated in the Caribbean and later migrated into the Pacific and, like other Thaids present in the Caribbean Neogene (i.e. *Acanthais, Neorapana, Tribulus, Vasula* see VERMEIJ, 2001b), now survives only in the Pacific.

**Geological and geographical distribution: Atlantic**

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

**Geological and geographical distribution: Pacific**


**Subfamily Coralliophilinae C HENU, 1859**

**Genus Coralliophila** H. & A. ADAMS, 1853.

Type species *Fusus neritoideus* LAMARCK, 1816, by subsequent designation, IREDALE, 1912.

**Coralliophila sp. aff. C. meyendorffii** (CALCARA, 1845)  
Pl. 13, Fig. 9

2010a  
**Coralliophila sp. aff. C. meyendorffii** (CALCARA, 1845) – LANDAU & SILVA, p. 68, pl. 13, fig. 9.

**Material and dimensions:** One specimen BL coll., 23.3 mm in height, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

A single poorly preserved shell is at hand with a scabrous surface sculpture, typical of Coralliophilinae. The Cubagua shell is characterised by its weak axial sculpture, subobsolete on the second half of the last whorl, weakly carinate spire whors and last whorl rounded at the shoulder rather than carinate, globose last whorl, constricted at the base, relatively large aperture (outer lip incomplete) and long, narrow siphonal canal. The spiral sculpture consists of narrow cords of alternate strength, with the cord at the shoulder slightly more strongly developed.

Numerous species are listed from the western Atlantic faunas on the Western Atlantic Mollusk Database. *Coralliophila abberans* C. B. ADAMS, 1850, which occurs in the Recent faunas from Bermuda to Brazil, also has a globose, rounded last whorl and a large rounded aperture, but has a short, broad siphonal canal (holotype illustrated in KOSUGE & SUZUKI, 1985). It was also recorded from the Pleistocene Moin Formation of Costa Rica by ROBINSON (1991, p. 427, pl. 18, fig. 11), but the illustration shows quite a different species. *Coralliophila aedonia* (WATSON, 1886) from the western Atlantic, from Brazil to Argentina, is a more fusiform species with the last whorl much less inflated than the shell from Cubagua. *Coralliophila caribaea* ABBOTT, 1958, Recent from South Carolina to Brazil, also found in the Pleistocene of Costa Rica (ROBINSON, 1991), has a wider aperture and a more open siphonal canal. *Coralliophila galea* (O’ORBIGNY, 1845) [=*Coralliophila abbreviata* auct. non (LAMARCK, 1816)] and the fossil *Coralliophila miocenica* (GUPPY, 1873) from the Lower Pliocene Gurabo Formation of the Dominican Republic and
Pliocene Bowden Formation of Jamaica are quite different, both having much broader shells with a relatively depressed spire.

The shell from Cubagua is most similar to the Eastern Atlantic and Mediterranean species *Coralliophila meyendorffii* (CALCARA, 1845), which already formed part of the Mediterranean fauna in the Early Pliocene (LANDAU et al., 2007b). If they were conspecific, this would be the only amphiatlantic species in the Cubagua assemblage. Unfortunately there is insufficient material to confirm this hypothesis.

**Geological and geographical distribution:**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Family** Turbinellidae SWAINSON, 1835

**Subfamily** Turbinellinae SWAINSON, 1835

**Genus** Turbinella LAMARCK, 1799.

*Xancus* RÖDING, 1798 (placed on Official Index of Rejected and Invalid Generic Names, ICZN Opinion 489, 1957). Type species *Voluta pyrum* LINNAEUS, 1767, by subsequent designation, DALL, 1906.

*Turbinella trinitatis* (MAURY, 1925)

Pl. 13, Figs 10-12

1866b *Turbinellus ovoideus* KIENER – GUPPY, p. 576.


1925a *Xancus praevioideus* [sic] MAURY – MAURY, p. 207(359), pl. 38(49), fig. 1 *(non MAURY, 1917)*.

1925a *Xancus trinitatis* MAURY, p. 208(360), pl. 39(50), fig. 1.

1931 *Xancus praevioideus riosecanus* H. K. HODSON, p. 12(106), pl. 11(35), fig. 1, pl. 12(36), fig. 1.

1942 *Xancus trinitatis riosecanus* H. K. HODSON – RUTSCH, p. 161, pl. 9, figs 1, 3.


2010a *Turbinella trinitatis* (MAURY, 1925) – LANDAU & SILVA, p. 68, pl. 13, figs 10-12.

? *non* 1942 *Xancus trinitatis* MAURY – RUTSCH, p. 162, pl. 9, figs 2, 4.

**Material and dimensions:** Maximum height 250.0 mm, seven specimens NMB lot DS 6923; 10 specimens EDIMAR coll.; 11 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**

E. H. VOKES (1964, 1998) discussed the presence of two distinct lineages of *Turbinella* in the Caribbean Neogene. The Cubagua species belongs to the smooth "*T. laevigata*" lineage. Part of this lineage is an interesting series of *Turbinella* species from the southern Caribbean Neogene. This series started with *Turbinella falconensis* (H. K. HODSON, 1931) from the Lower Miocene Cantaure Formation of Venezuela, which E. H. VOKES (1964) considered Middle Miocene, followed by *Turbinella trinitatis* (MAURY, 1925) from the Lower Pliocene Springvale Formation of Trinidad, which she considered Upper Miocene, to *Turbinella riosecana* (H. K. HODSON, 1931) from the Middle Miocene Rio Seco Formation of Falcón, Venezuela, which she recorded as Pliocene (Vergel Member of the San Gregorio Formation, Upper Pliocene, see MACSOTAY et al., 1998, 1998), and giving rise to the Recent *Turbinella laevigata* ANTON, 1838, which lives off the coast of Brazil. According to E. H. VOKES (1964), the shells of the various species differed solely in having an increasing degree of inflation of the last whorl, *T. riosecana* being the most inflated of the three fossil forms. There is no question that the shell of *T. falconensis* is not as inflated as the ones of the other two species, but E. H. VOKES (1964, p. 53) admitted the difference in inflation between *T. trinitatis* and *T. riosecana* was small, and that she lacked material to establish the range of variation.
We have not examined any further specimens of *T. trinitatis* (two specimens NMB H 6229 and H 6230 both have broken or depressed apertures so unsuitable for measurement), but we have collected a large enough number of *T. falconensis* from the type locality and of *Turbinella* in Cubagua to evaluate this range of variability (BL coll.). Admittedly, the specimens from Cubagua do not come from the type locality of Río Seco, near Urumaco, District of Democracia, Falcón, Urumaco Formation, Upper Miocene, but they coincide with the illustration of the holotype of *T. riosecana*. We measured 30 specimens of each species; *T. falconensis* has a height/width ratio of 2.68-2.72; *Turbinella* from Cubagua 2.0-2.31. Unfortunately, the illustrated specimens of *T. trinitatis* in MAURY (1925a, pl. 38 (49), fig.1) and RUTSCH (1942, pl. 9, figs 1, 3) are far from well preserved, but the figures show specimens well within the range of variability found in Cubagua (Text-Fig. 22), and the most complete *T. trinitatis* in MAURY (1925a) gives a height/width ratio of 2.14, within the range of *T. riosecana*. We therefore conclude firstly that the shells of *T. falconensis* is clearly distinguished from the other two species by the degree of inflation of the last whorl, and secondly with the new information gleaned from this Cubagua assemblage, there is no justification for separating *T. trinitatis* and *T. riosecana*. Moreover, the chronological series suggested by E. H. VOKES (1964) is now known to be incorrect, as they are now all roughly coeval. *Turbinella riosecana* therefore becomes a junior subjective synonym of *T. trinitatis* (MAURY, 1925).

**Text-Figure 22.** Graph of width vs. height for *Turbinella trinitatis* (MAURY, 1925). The measurements for *T. trinitatis* from Trinidad are an estimate made by MAURY (1925), the measurement for *T. riosecana* is for the holotype, fide E. H. VOKES (1964), incorrectly recorded by Hodson (1931). RUTSCH (1942, pl. 9, figs 2, 4) illustrated a *Turbinella* specimen from the Lower Pliocene Springvale Formation, which although incomplete, is much more elongate. This is the only figured specimen of this form from Trinidad, which may be an abnormal specimen or, as mentioned by E. H. VOKES (1998), there may be a second species present in the Trinidadian Lower Pliocene.

We have examined one juvenile specimen (Pl. 13, Fig. 12) with showing a paucispiral protoconch consisting of just less than two whorls with a big nucleus and bulbous first whorl. This type of protoconch indicates a non-planktrophic mode of development (JABLONSKI & LUTZ, 1980, 1983). This type of protoconch has been described in other Caribbean congeners such as *Turbinella praelaevigata* E. H. VOKES, 1964 (E. H. VOKES, 1998). This Dominican taxon differs from *T. trinitatis* in having a smaller maximum size and a far less inflated last whorl. E. H. VOKES (1998) also commented on the peculiar row of nodules on the inner side of the outer lip extending into the shell, placed in a line anterior to the shoulder. This is also present in the Cubagua specimens, but less strongly developed than in *T. praelaevigata*. In her discussion of *Turbinella praelaevigata* E. H. VOKES (1998) suggested WOODRING’S (1964) Gatun material might correspond to *T. trinitatis*. We have examined several specimens from the Middle-Upper Miocene Gatun Formation at Cativa, which all have a row of weak nodules at the shoulder and do not correspond to *T. trinitatis* as interpreted in this paper.
Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (GUPPY, 1910 ex HARRIS reprint, 1921; MAURY, 1925a; E. H. VOKES, 1938; RUTSCH, 1942; JUNG, 1969).
Upper Pliocene: San Gregorio Formation, Falcón, Venezuela (H. K. HODSON, 1931).

Family Vasinae H. A. ADAMS, 1853 (1840)
Genus Vasum RÖDING, 1798.
Type species Murex turbinellus LINNAEUS, 1758, by subsequent designation, WINKWORTH, 1945.

Vasum haitense (G. B. SOWERBY I, 1850)

Material and dimensions: One specimen BL coll., 96.3 mm in height, Lower Pliocene, Araya Formation, Cañon de las Calderas, Cubagua Island.

Discussion:
Vasum haitense (G. B. SOWERBY I, 1850) is the most common and widespread species of Vasum in the Western Atlantic Miocene, but this is the first record for the Pliocene.

E. H. VOKES (1966, p. 7), in her revision of the genus Vasum in the New World, maintained Vasum quasirosense F. HODSON, 1931 (Pl. 14, Fig. 2) from the lower Lower Miocene La Rosa Formation, Quiróz, State of Falcón, Venezuela distinct from V. haitense, with some hesitation and wrote “The type specimen of this minute form strongly suggests a dwarfed example of the widespread Miocene species V. haitense (…)”. For the present time V. quasirosense will be accepted as a valid species until more material is known. Jung (ibid.) did not cite any species of Vasum from the Paraguaná region.”. We can confirm the presence of V. haitense of the typical form in the Lower Miocene Cantaure Beds of the Paraguaná Peninsula of Venezuela (although rather small; four specimens, maximum height 67.5 mm, BL coll. compared with maximum size of 170.0 mm for Baitoa material BL coll.). It is therefore likely V. quasirosense was based on juvenile material, which we consider a junior synonym of V. haitense.

Geological and geographical distribution:
Lower Miocene Pirabas Limestone, Brazil (MAURY, 1925b, as V. engonatum); Baitoa Formation, Dominican Republic (MAURY, 1917; E. H. VOKES, 1998); Tampa Formation, Florida (DALL, 1903, as V. engonatum); Chipola Formation, Florida (GARDNER, 1944, as Vasum aff. V. engonatum; E. H. VOKES, 1966, 1970b); Cantaure Formation, Paraguaná Peninsula, Venezuela (BL coll.); La Rosa Formation, Quiróz, State of Falcón, Venezuela (F. HODSON, 1931).
Superfamily    Buccinoidea R AFINESQUE, 1815
Family     Buccinidae R AFINESQUE, 1815
Subfamily    Buccininae R AFINESQUE, 1815
Genus    Strombinophos PILSBRY & OLSSON, 1941.
Type species S. loripanus PILSBRY & OLSSON, 1941, by original designation.

Strombinophos perdoctus JUNG, 1969
Pl. 14, Figs 3-4

2010a     Strombinophos perdoctus JUNG – LANDAU & SILVA, p. 70, pl. 14, figs 3-4.

Material and dimensions: Maximum height 32.7 mm, 20 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
One of the two specimens found in Cubagua has the protoconch relatively well preserved, and shows it to consist of about four whorls, as stated in the original description (JUNG, 1969). The Cubagua specimens have nine axial ribs on the penultimate whorl, possibly one more than the holotype judging by the illustration, although JUNG (1969) did not mention the number of ribs in the description. Otherwise our shells match the holotype in the number of spiral cords, in the presence of a secondary cord in the interspaces, in the character of the aperture and the lirate inner aspect of the outer lip. The whorl shape is somewhat variable; rounded (Pl. 14, Fig. 3) to shouldered (Pl. 14, Fig. 4) as in the holotype from Trinidad. The type specimen was not found in the NMB type collection.

The genus Strombinophos is no longer extant, but it was widespread in the Caribbean Neogene. Strombinophos mimicus WOODRING, 1964, from the Middle-Upper Miocene Gatun Formation of Panama is immediately distinguishable by the greater number of axial ribs (12-17 on the penultimate whorl); several species of Strombinophos from the Pliocene of Florida; i.e. Strombinophos floridanus, S. vaughani (MANSFIELD, 1930), S. thayerei (M. SMITH, 1936), S. maxwelli OLSSON & HARBISON, 1953 are all more elongated with a less inflated last whorl. An undescribed species of Strombinophos from the Lower Pliocene Punta Gavilán Formation (BL coll.) differs in having fewer protoconch whorls and more numerous axial ribs (10-11 on the penultimate whorl). Another undescribed species from the Lower Miocene Cantaure Formation (BL coll.) has a shell with a similar number of axial ribs as S. perdoctus, but differs in details of its spiral sculpture.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Melajo Clay Member of Springvale Formation, Trinidad (JUNG, 1969).

Subfamily    Pisaniinae G RAY, 1857
Genus and subgenus    Solenosteira DALL, 1890.
Type species Pyrula anomala REEVE, 1847, by original designation.

Many authors have ascribed to Hanetia JOUSSEAUME, 1880 species that are now included in the genus Solenosteira DALL, 1890 (RUTSCH, 1934; PILSBRY & OLSSON, 1941; OLSSON, 1942, 1964). WOODRING (1964), considered Solenosteira a junior synonym of Hanetia. BERRY (1962), however, noted that the type species of Hanetia, Murex haneti PETIT DE LA SAUSSAYE, 1856, is a Brazilian muricid.

Solenosteira (Solenosteira) magdalenensis WEISBORD, 1929
Pl. 14, Figs 5-6

1929     Solenosteira cochlearis magdalenensis WEISBORD, p. 46, pl. 6, figs 16-17.
1960     Cantharus (Hanetia [sic]) cochlearis magdalenensis WEISBORD – BARRIOS, p. 283, pl. 11, fig. 11.
Material and dimensions: Maximum height 54.0 mm, three specimens NMB lot DS 6918; three specimens EDIMAR coll.; 12 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; 20 specimens BL coll., (lower yellow fine sandy bed), two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion: Three species of Solenosteira (Solenosteira) have been described from the southern Caribbean Lower Pliocene; Solenosteira semiglobosa (Guppy, 1911) [=Solenosteira cochlearis GUPPY, 1911] from the Springvale Formation of Trinidad, Solenosteira cochlearis magdalenensis WEISBORD, 1929 (holotype Pl. 14, Fig. 6) from the Tuberá Group of northern Colombia and Cantharus (Hanetia) gavilanensis RUTSCH, 1934 from the Punta Gavilán Formation of Venezuela. As pointed out by RUTSCH (1942) and JUNG (1969), S. semiglobosa (hypotypes NMB H 6190/1-2) is somewhat variable in the height of the spire and inflation of the last whorl, but in general it is low-spired with a strongly inflated last whorl. It is characterized by the axial ribs, which are usually restricted to the spire whors, about eleven in number, and when present on the last whorl are irregular and poorly developed. Solenosteira gavilanensis (holotype NMB H 1890, paratypes NMB H 1891-2) is higher-spired, the last whorl is less globose, the axial ribs are less numerous, nine in number, and more prominent, well developed on the last whorl, and the spiral cords are finer and sharper. Solenosteira semiglobosa and S. gavilanensis may have coexisted in the Punta Gavilán assemblage (RUTSCH, 1934; JUNG, 1969).

The specimens from Cubagua show intermediate features; the spire is depressed, with about eleven axial ribs, and the last whorl globose as in S. semiglobosa, but the axial ribs are well developed on the last whorl, although not quite as strongly as in S. gavilanensis and the spiral cords are thicker, not as sharp as in S. gavilanensis. Although we have not examined any specimens of Solenosteira magdalenensis from Colombia, the Cubagua shells seem conspecific with the shell described and illustrated by WEISBORD (1929) and BARRIOS (1960). Therefore, in the southern Caribbean Lower Pliocene assemblages, the Cubagua fauna of Solenosteira species shares closer affinities with the Tuberá Formation of Colombia than the geographically closer Springvale or Punta Gavilán Formations.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Tuberá Group, northern Colombia (WEISBORD, 1929; BARRIOS, 1960).

Subgenus Fusinosteira OLSSON, 1932
Type species Purpura fusiformis BLAINVILLE, 1832, by original designation.

Gastropods of the subgenus Fusinosteira OLSSON, 1932 differ from Solenosteira (s.s.) in having a strongly carinate last whorl bearing prominent tubercles. This seems to have been a predominantly tropical American Pacific subgenus even in the Neogene, and is today represented by several taxa in the eastern Pacific (see KEEN, 1971), but none in the Caribbean. It is therefore one of WOODRING’s (1966) paciphile taxa. In the Caribbean Neogene it is represented by Solenosteira (Fusinosteira) falconensis WEISBORD, 1929, Solenosteira (Fusinosteira) santaerosae ANDERSON, 1929 and an undescribed species in the Lower Miocene Cantaure Formation of Venezuela (BL coll.; Bernard Landau unpublished data).

VERMEIJ (2006) synonymised Fusinosteira with Solenosteira and recognised a tropical American Pacific clade of Solenosteira species (including Fusinosteira), which differed from the single living western Atlantic species, Solenosteira cancellaria (CONRAD, 1846). Species of the S. cancellaria group differ from the rest in having rounded rather than shouldered whors, and by exhibiting a tendency for the axial ribs on the last whorl to become very broad and low. The Floridian Plio-Pleistocene species (see PETUCH, 1994) belong to this group and not the tropical American group. Whilst we agree with this conclusion, Olsson’s subgenus is used to refer these species with spines at the periphery.
Solenosteira (Fusinosteira) falconensis WEISBORD, 1929
Pl. 14, Figs 7-9

1929 Solenosteira falconensis WEISBORD, p. 45, pl. 7, fig. 6 (77-8).
1929 Solenosteira hasletti ANDERSON, p. 134, pl. 16, figs 7-A, 8.
1931 Solenosteira falconensis urumacoensis F. HODSON, p. 11, pl. 9, fig. 1.
1932 Solenosteira hasletti ANDERSON – LOEL & COREY, pl. 49, fig. 1.
2010a Solenosteira (Fusinosteira) falconensis WEISBORD, 1929 – LANDAU & SILVA, p. 72, pl. 14, figs 7-9.

Material and dimensions: Maximum height 61.0 mm, seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
Solenosteira (Fusinosteira) falconensis WEISBORD, 1929 is difficult to confuse with any of its congeners, characterized by its very broad infrasutural ramp, by the shoulder placed below mid-whorl on the spire whorls and mid-whorl on the last whorl and by the relatively weak axial sculpture, subobsolete on the last whorl. Solenosteira falconensis WEISBORD has priority over Solenosteira hasletti ANDERSON as Weisbord’s work is dated January 8th, 1929, whereas ANDERSON’S is dated March 29th, 1929. Solenosteira falconensis urumacoensis F. HODSON, 1931 (holotype Pl. 14, Fig. 9) from the Upper Miocene of Rio Codore, Urumaco, mainland Venezuela, is here considered a junior subjective synonym of S. falconensis. The sculpture of the sutural ramp in our specimens from Cubagua is very variable, and the differences noted by WEISBORD (1931) are, in our opinion, insufficient to distinguish a subspecies.

ANDERSON (1929, p. 135, pl. 13, figs 7-10) described a second, rather strange looking, stocky shell ascribed to a species in the Fusinosteira group from the Lower Pliocene Tubera Formation of Venezuela, Solenosteira santaerosae ANDERSON, 1929. Two specimens examined in the NMB collection (lots Br. 243, 252) differ from S. (F.) falconensis in having a broader, convex infrasutural platform and downturned spines at the shoulder. WEISBORD (1929, pl. 7, figs 7-8) also illustrated this form with a shell somewhat intermediate in form between the holotypes of the two species. We examined a single poorly preserved Cubagua shell (Pl. 14, Fig. 8) which is close to the S. (F.) santeirosae morphotype, intermediate between S. (F.) falconensis and S. (F.) santeirosae, but insufficient material exists to conclude whether they are synonymous.

Geological and geographical distribution:
Upper Miocene: Urumaco Formation, Venezuela (F. HODSON, 1931). Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Tubera Group, northern Colombia (WEISBORD, 1929; ANDERSON, 1929; LOEL & COREY, 1932).

Genus Hesperisternia GARDNER, 1944.
Type species H. waltonia GARDNER, 1944, by original designation.

Hesperisternia corrugata (GABB, 1873)
Pl. 14, Figs 10-11

1873 Muricidae corrugata GABB, p. 203.
1873 Nassaria brevis GABB, p. 213.
1922 Nassaria corrugata (GABB) – PILSBRY, p. 348, pl. 22, fig. 15.
2006 Hesperisternia corrugata (GABB, 1873) – VERMEIL, p. 81, figs 20-21.
2010a Hesperisternia corrugata (GABB, 1873) – LANDAU & SILVA, p. 72, pl. 14, figs 10-11.

Material and dimensions: Maximum height 31.3 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.
Discussion:

The genus *Hesperisternia* GARDNER, 1944 was discussed in detail by VERMEIJ (2006). *Hesperisternia corrugata* (GABB, 1873) belongs to a small group of *Hesperisternia* species with a determinate outer lip varix, including the type species *Hesperisternia waltonia* GARDNER, 1944, although the varix is only slightly more strongly developed than the preceding axial rib. It is not uncommon in the Lower Miocene Baitoa Formation of the Dominican Republic in the Lopez Section of the Rio Yaque del Norte and in a coquina bed in the Rio Cana (Upper Miocene, Cercado Formation), but all the shells are small. The specimens from Cubagua are identical to those found in the Dominican assemblages, but of a relatively large size. Only one specimen in the BL collection from the Upper Pliocene Gurabo Formation of the Rio Mao, and the shell illustrated by VERMEIJ (2006, figs 20-21), are of a similar large size.

Geological and geographical distribution:
Lower Miocene Baitoa Formation, Dominican Republic (BL coll.).
Upper Miocene: Cercado Formation, Dominican Republic (GABB, 1873; VERMEIJ, 2006).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

*Hesperisternia tortugera* (OLSSON, 1922)

Pl. 14, Figs 12-13

1922 *Peristernia tortuguera* OLSSON, p. 110, pl. 8, fig. 13.
1991 *Cantharus (Hesperisternia) tortugera* (OLSSON, 1922) – ROBINSON, p. 438, pl. 19, fig. 5.

Material and dimensions: Maximum height 36.4 mm, 11 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

The shells of *Hesperisternia tortugera* (OLSSON, 1922) are closely similar to the Pliocene-Recent Caribbean *Hesperisternia multangulus* (PHILIPPI, 1848), but the shoulder of the whorls is more angular, the spiral sculpture is much stronger and small elongated tubercles are formed by the cords where they override the axial ribs. PETUCH (1994) described and illustrated numerous closely similar shells from the Floridian Plio-Pleistocene, some of which are probably conspecific with *H. multangulus*, whilst others are closely similar to the Cubagua specimens, such as *Hesperisternia miamiensis* PETUCH 1991. A single specimen of *H. miamiensis* from the Upper Pliocene Pinecrest Beds of Sarasota (BL coll.), is even more angular than *H. tortugera*, the spiral cords are sharper and the aperture smaller. Unfortunately the protoconch is not preserved. *Hesperisternia scissus* OLSSON, 1964 from the Upper Miocene Esmeraldas Formation of Ecuador is also closely similar to *H. tortugera*, but differs in having a squatter, even more angular shell, with a wider infrasutural platform bound by a spiral cord bearing short spines rather than elongated tubercles over the axial ribs.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

*Hesperisternia karinae* (NOWELL-USTICKE, 1959)

Pl. 14, Fig. 14

1959 *Cantharus karinae* NOWELL-USTICKE, p. 69, pl. 4, fig. 4.
1969 *Cantharus karinae* USTICKE, 1959 – NOWELL-USTICKE, p. 69, pl. 4, fig. 4.
1991 *Cantharus karinae* NOWELL-USTICKE – LEAL, p. 153, pl. 19, fig. G.
2010a *Hesperisternia karinae* (NOWELL-USTICKE, 1959) – LANDAU & SILVA, p. 73, pl. 14, fig. 14.
Material and dimensions: Maximum height 19.6 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

Vermeij (2006) included Cantharus karinae Nowell-Usticke, 1959 in the genus Hesperisternia, a member of a distinct group within the genus characterised by having shells with strong spiral cords and a narrow, dentate aperture convergent on that of Engina Gray, 1839. However, in the Engina group the inner lip is clearly and strongly denticulate rather than lirate as in the Cantharus group. Hesperisternia karinae is also one of the few Hesperisternia species with a labral varix developed (see under H. corrugata).

We have compared the scant specimens from Cubagua with material from the Lower Pleistocene Moin Formation of Costa Rica (BL coll.) and confirm that they are conspecific. The shell of Hesperisternia karinae (Nowell-Usticke, 1959) is similar to Engina willemsae Jong & Coomans, 1988, but with only two major spiral cords on the penultimate whorl as opposed to four in E. willemsae, the infrasutural ramp is concave in the Cubagua shells, whereas the last whorl in E. willemsae does not have a well-defined infrasutural ramp, the columella is covered in numerous, small, irregular tubercles as opposed to six well defined knobs as described in E. willemsae (Jong & Coomans, 1988). Lastly, the denticles within the outer lip of E. willemsae are well developed as opposed to lirate in H. karinae, a characteristic of the genus Engina.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.
Recent: Oriental part of the Caribbean, from Jamaica and Puerto Rico to Dutch Antilles and Colombia (Diaz & Puyana, 1994).

'Hesperisternia' sp.
Pl. 14, Fig. 15

2010a Hesperisternia' sp. – Landau & Silva, p. 73, pl. 14, fig. 14.

Material and dimensions: One specimen BL coll., 45.7 mm in height, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

A single shell from the Cañon de las Calderas outcrop is remarkably similar to the specimen illustrated by Jung (1969) from Trinidad as Buccinid indet. The last whorl has eight axial ribs as opposed to nine described by Jung (1969, p. 511).

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Tuberá Group, northern Colombia (Anderson, 1929); Coulbaril beds of Upper Morne l’Enfer Formation, Trinidad (Jung, 1969).

Family Columbellidae SWAINSON, 1840
Subfamily Columbellinae SWAINSON, 1840
Genus Strombina MöRch, 1852.
Type species Columbella lanceolata G. B. Sowerby I, 1832, by subsequent designation, BucquoY, Dautzenberg & Dollfus, 1882-1886.

Strombina (Strombina?) cartagenensis PILSBRY & BROWN, 1917
Pl. 15, Fig. 1

1917 Strombina cartagenensis PILSBRY & BROWN, p. 33, pl. 5, fig. 3.
1989 Strombina (Strombina?) cartagenensis PILSBRY & BROWN – Jung, p. 80, fig. 105.
**Strombina (Strombina?) cartagenensis** PILSBRY & BROWN, 1917 – LANDAU & SILVA, p. 74, pl. 15, fig. 1.

**Material and dimensions:** Maximum height 23.5 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

JUNG (1989) lamented the lack of material available for this species, represented only by the holotype from an unknown locality in Colombia. He suggested it was of Miocene age without being more specific. We echo his frustration as the species is again represented by only two specimens from Cañon de las Calderas in a poor state of preservation, with some of the spire decorticated and the apical whorls abraded. Nevertheless, the Cubagua specimens are remarkably similar to the holotype, differing only in the slightly more prominent dorsal gibbosity and the weaker axial sculpture on the second half of the last whorl, where the ribs are obsolete on the Cubagua shells, but developed in the holotype. Both of these features are somewhat variable in *Strombina* species. See series of *Strombina (Strombina) pumilio* (REEVE, 1858) illustrated by JUNG (1989, figs 91-93).

**Geological and geographical distribution:**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; northern Colombia, locality unknown (PILSBRY & BROWN, 1917; JUNG, 1989).

**Family** Nassariidae REDALE, 1916 (1835)

**Subfamily** Nassariinae REDALE, 1916 (1835)

**Genus** Nassarius DUMÉRIL, 1806.

**Type species** Buccinum arcularia LINNAEUS, 1758, by monotypy.

*Nassarius trinitatensis* JUNG, 1969

Pl. 15, Fig. 2

1969 *Nassarius trinitatensis* JUNG, p. 518, pl. 55, figs 6-8.

2010a *Nassarius trinitatensis* JUNG, 1969 – LANDAU & SILVA, p. 74, pl. 15, fig. 2.

**Material and dimensions:** Maximum height 8.0 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**

Although somewhat abraded, the shells from Cubagua match the description given by JUNG (1969). It is a species with a small, stout shell. The specimens we examined have their protoconch preserved, dome-shaped, consisting of three smooth whorls, similar to that seen in the holotype (NMB H 15221). There are 10-12 axial ribs on the last whorl, five spiral cords on the penultimate whorl, with secondary spiral cords in the interspaces; outer lip with 6-7 prominent lirae extending deep within the aperture; inner lip with five rugae in the abapical portion and a prominent parietal denticule. The dentition within the outer lip in the holotype and paratype (NMB H 15222) also consists of six denticles, but they are slightly shorter, so they do not extend as deeply into the aperture as in the Cubagua shells. However, the character of the dentition within a species in nassarids can be highly variable (see LANDAU, SILVA & GILI, 2009).

As discussed by JUNG (1969) *Nassarius trinitatensis* is very similar to *Nassarius cercadensis* (MAURY, 1917) [= *Alectrion brassica* MAURY, 1925; = *Alectrion brassoensis* MANSFIELD, 1925, both from the Middle Miocene Brasso Formation of Trinidad, see WOODRING, 1964], but differs mainly in its larger size. We have compared the Cubagua shells with some specimens of *N. cercadensis* from the Upper Miocene Cercado Formation and Lower Pliocene and Gurabo Formation of the Dominican Republic, and apart from the Dominican shells being smaller and squatter we cannot find any major sculptural difference. We provisionally separate the two species pending further review.
Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Melajo Clay Member of Springvale Formation, Trinidad (JUNG, 1969).

Genus  
**Neoteron PILSBRY & LOWE, 1932**
Type species *N. ariel PILSBRY & LOWE, 1932*, by monotypy.

**Neoteron emilyvokesae LANDAU & SILVA, 2010**
Pl. 15, Figs 3-4

2010a  **Neoteron emilyvokesae LANDAU & SILVA, p. 75, pl. 15, figs 3-4.**

**Dimensions and type material:** Holotype NHMW 2010/0038/0019 (Pl. 15, Fig. 3), height 17.4 mm (NHMW coll., ex BL coll.); paratype 1 NHMW 2010/0038/0020 (Pl. 15, Fig. 4), height 14.3 mm (NHMW coll., ex BL coll.).

**Etymology:** For Emily Vokes, in recognition of her work on the genus.

**Type locality:** Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

**Stratum typicum:** Araya Formation, Cubagua Group, Lower Pliocene.

**Diagnosis:**
A *Neoteron* species with 6-7 broad elevated axial ribs, a weakly canaliculated suture, strongly constricted between base of last whorl and siphonal fasciole, a broad labral varix, less expanded adapically than usual for genus, aperture strongly denticulate with numerous folds and tubercles on columellar callus.

**Original description:**
“Shell relatively large for genus, robust, nassariiform. Protoconch somewhat worn, but probably of about 2-2.5 smooth whorls with a small to medium-sized nucleus. Five teleoconch whorls, roundely angled, with shoulder below mid-whorl. Suture impressed, very narrowly canaliculated. Sculpture on spire whorls severely abraded, but of 6-7 axial ribs, most strongly developed at the shoulder, where they form an axially elongated tubercle; spiral cords narrow, of alternate strength, elevated where they cross axial ribs at shoulder. Axial ribs on last whorl elevated, broadly rounded. Last whorl very strongly constricted at base by a deep trough separating last whorl from siphonal fasciole, axially striate within and partially obscured by overhanging part of last whorl. Aperture ovate, relatively strong, rim slightly raised; outer lip greatly thickened by a broad labral varix, weakly wing-like adapically. Ten denticles of irregular size placed just within outer lip, adapical denticle far more strongly developed than rest. Deeper within the aperture five very strong prominent lirae run deep within aperture. Anal canal represented by deep notch; siphonal canal open, recurved. Columella with three strong oblique folds on abapical portion; adapically, a well developed parietal fold and a further weaker fold below. Columellar callus thickened, clearly delimited, expanded and adherent in parietal portion, erect below. Whole columella and parietal callus surface is covered in irregular plicae and elongated tubercles. Siphonal fasciole broad, flattened, bearing 6-7 cords (LANDAU & SILVA, 2010a, p. 75)”.

**Discussion:**
*Neoteron emilyvokesae* LANDAU & SILVA, 2010 is represented by two, somewhat eroded, but complete shells from the Cañon de las Calderas outcrop. Although the material is scant and the preservation could be better, this peculiar shell deserves attention. The genus *Neoteron* PILSBRY & LOWE, 1932 was, until now, thought to be monotypic, represented by *Neoteron ariel* PILSBRY & LOWE, 1932 from the Recent west coast of Central America. This is the first fossil record for the genus.

*Neoteron* is closely similar to *Trajana* GARDNER, 1948, but differs in the prominently constricted base, very broad, flat, expanded outer lip with strong denticles on the interior edge and the dense spiral sculpture on the dorsal side of the last whorl (CERNOHORSKY, 1981). The genus *Trajana* in the Caribbean Neogene was monographed by VOKES (1969). *Neoteron emilyvokesae* clearly shows this deep basal trough and dense spiral sculpture on the last whorl and fits relatively well within the genus. Being, monotypic, this generic description was based on *N. ariel*; the new taxon does not have the labral varix as strongly developed into a wing-like extension as seen in the shell of *N. ariel*, nevertheless, it does show the same
tendency for the labral varix to become expanded adapically.

*Neoteron* can now be added to the list of paciphilic genera first proposed by Woodring (1966), as this is the earliest record of the genus now restricted to the Pacific side of its original Gatunian distribution.

Interestingly, we have also collected two excellent specimens of *Trajana* from the Lower Pliocene Punta Gavilán Formation of Venezuela (BL coll.). However, they are smaller and clearly represent a distinct species of *Trajana s.s.* (peristome complete, aperture without any denticles, siphonal canal closed). The specimens were examined by Emily Vokes (pers. comm., 1992), and identified as *Trajana pyta* Gardner, 1948, a species previously known from the Pliocene of Jackson Bluff and lower Pincrest units of Florida, thus greatly extending the geographical range of this species in the Pliocene to the southern Caribbean.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

**Subfamily** Bulliinae Allmon, 1990  
**Genus** *Calophos* Woodring, 1964  
**Type species** *C. ectyphus* Woodring, 1964, by original designation.

Woodring (1964) described the genus *Calophos* within the Buccinidae, in a group associated with *Cymatophos* Pilsbry & Olsson, 1941 and *Antillophos* Woodring, 1928, differing from *Cymatophos* Pilsbry & Olsson, 1941 in having shells with finely reticulate sculpture on the early teleoconch whorls, but on later whorls the axial sculpture is weak or absent. He considered it to be an exclusively Miocene genus. However, some of the deposits in which it occurs are now considered Lower Pliocene (i.e. Springvale Formation of Trinidad). Allmon (1990, p. 72) transferred *Calophos* to the Bulliinae.

*Calophos plicatilis* (Böse, 1906)  
Pl. 15, Figs 5-6

<table>
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<th>Year</th>
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<td>1906</td>
<td><em>Cominella plicatilis</em> Böse, p. 39, pl. 5, figs 22-24.</td>
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<td>1990</td>
<td><em>Calophos plicatilis</em> (Böse) – Allmon, p. 74, pl. 12, figs 13-15.</td>
</tr>
<tr>
<td>2010a</td>
<td><em>Calophos plicatilis</em> (Böse, 1906) – Landau &amp; Silva, p. 76, pl. 15, figs 5-6.</td>
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</table>

non 1929 *Dorsanum ? plicatilum* (Böse) – Cooke & Mossom, p. 139, pl. 16, fig. 3 [=*Calophos wilsoni* Allmon, 1990].  
non 1930 *Dorsanum ? plicatilum* (Böse) – Mansfield, p. 73, pl. 17, fig. 3 [=*Calophos wilsoni* Allmon, 1990].  
non 1945 *Dorsanum ? plicatilum* (Böse) – Cooke, p. 184, figs 22-23 [=*Calophos wilsoni* Allmon, 1990].  
non 1964 *Dorsanum ? plicatilum* (Böse) – Olsson & Petit, p. 552, pl. 79, fig. 6 [=*Calophos wilsoni* Allmon, 1990].

**Material and dimensions:** Maximum height 35.2 mm, four specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:** We examined four specimens of a *Calophos* species from Cañon de las Calderas and two from the Araya Peninsula, which seem to be conspecific with a shell from the contemporaneous Punta Gavilán Formation of mainland Venezuela (BL coll.). The strength of the axial ribs is somewhat variable, moderately developed in the illustrated specimen (Pl. 7, Fig. 8), somewhat more strongly developed in two others. Spiral sculpture is present along the entire last whorl in all the specimens at hand. Allmon (1990) discussed the genus *Calophos* Woodring, 1964, and reviewed all the known species. He noted that *Calophos plicatilis* (Böse, 1906) differed most notably from its congener in the persistence of spiral
sculpture across the entire adult last whorl, rather than becoming obsolete in the middle. In this feature it most closely resembles Calophos golfoyaquensis (Maury, 1917), but is larger and the spiral cords are not as sharp (Allmon, 1990). All the Floridian Plio-Pleistocene records of Dorsanum ? plicatilum (Bose) (Cooke & Mossom, 1929; Mansfield, 1930; Cooke, 1945; Olsson & Pettit, 1964) were described as a distinct species, Calophos wilsoni Allmon, 1990, which differed from C. plicatilis in having a larger shell, with a greater variability in the expression of the axial and especially the spiral sculpture. Calophos rohri (Rutsch, 1942) from the contemporaneous Springvale Formation of Trinidad, was based on two immature specimens (holotype NMB H 6187; paratype NMB H 6186) in which the spiral sculpture is present over the entire surface of the last whorl. These shells differ from C. plicatilis in being much more elongate and having no axial sculpture. Jung (1969) interpreted two of his shells from the Melajo Clay Member (NMB H 15215 and H 15216) as undistorted specimens of C. rohri. We (BL) have examined this material in the NMB collection and cannot agree with this conclusion. Jung’s specimens (1969; pl. 54, figs 7-10) are much more like subadult specimens of Gordanops baranoanus (Anderson, 1929).

Rutsch (1942, p. 149, pl. 7, fig. 7) described a second new species of Phos from the Lower Pliocene Springvale Formation of Trinidad; Phos? springvaleensis. The holotype (NMB 6183) has a damaged aperture, but the shell shape and spiral sculpture are similar to C. plicatilis. Rutsch (1942) compared his new taxon with species of Antillophos Woodring, 1928, however, this genus is characterised by shells with strongly reticulate sculpture. It is possible that this shell also corresponds to C. plicatilis, however, we have insufficient material to reach any definitive conclusion.

**Distribution**
Middle Miocene: Tuxtepec, Mexico (Bose, 1906; Allmon, 1990).

**Genus Gordanops Olsson, 1964.**
Type species G. esmeraldensis Olsson, 1964, by original designation.

Olsson (1964) noted that the shells of Phos baranoanus Anderson, 1929 differed from other members of the genus Calophos in having the abapical portion of the outer lip extended upwards forming a long, well-defined anal canal. He erected a new genus Gordanops, in which he included P. baranoanus and Gordanops esmeraldensis Olsson, 1964 from the Esmeraldas beds, Onozole Formation of Ecuador, in which this feature is even more strongly developed. Allmon (1990) synonymised Gordanops with Calophos. However, all the specimens of various species of Calophos we have examined have a small, indistinct anal canal, quite different from that of Gordanops. Moreover, the large, barrel-shaped last whorl is quite different from the shape of the last whorl in other Calophos species. We agree with Olsson (1964) that G. baranoanus and G. esmeraldensis seem to belong to a separate species group, but whether they merit generic or subgeneric status is questionable. Some specimens of Calophos ectyphus Woodring, 1964 (type species of Calophos) from the Upper Miocene Upper Gatun Formation of Panama in which the axial ribs are subobsolete are very similar in sculpture and shell shape, but the anal canal is hardly developed.

Gordanops baranoanus (Anderson, 1929)
Pl. 15, Figs 7-10

<table>
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<th>Year</th>
<th>Description</th>
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<td>1929</td>
<td>Phos baranoanus Anderson, p. 137, pl. 16, figs 4-5.</td>
</tr>
<tr>
<td>1964</td>
<td>Gordanops baranoanus (Anderson) – Olsson, p. 162, pl. 20, fig. 1.</td>
</tr>
<tr>
<td>1990</td>
<td>Calophos baranoanus (Anderson, 1929) – Allmon, p. 76, pl. 11, fig. 16.</td>
</tr>
<tr>
<td>2010a</td>
<td>Gordanops baranoanus (Anderson, 1929) – Landau &amp; Silva, p. 77, pl. 15, figs 7-10.</td>
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</tbody>
</table>

**Material and dimensions:** Maximum height 65.3 mm, two specimens NMB lot DS 29; nine specimens EDIMAR coll.; 11 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation
Cerro Barrigón, Araya Peninsula.

Discussion:
The specimens of *Gordanops baranoanus* (Anderson, 1929) from Cubagua are identical to the shells figured by Anderson (1929) from Colombia, with a greatly inflated, barrel-shaped last whorl and the spiral sculpture obsolete mid-whorl on the last whorl. The strongly developed anal sinus is a very distinctive feature.

Jung (1969) illustrated subadult shells (maximum height 43 mm) from the Lower Pliocene Sringvale Formation of Trinidad under the name of *Calophos rohri* (Rutsch, 1942). As discussed under the previous species, we do not believe the two records represent the same taxon. It is possible that the shells illustrated by Jung are subadult specimens of *G. baranoanus*. In the Cubagua material the ascending portion of the lip forming the anal canal is not formed until the fully adult stage (juvenile: Pl. 15, Fig. 10). More material is required to confirm this.

Geological and geographical distribution:
Upper Miocene: Usiacuri Formation, Juan de Acosta, Colombia (Barrios, 1960).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (Olsson, 1964; Almon, 1990); Tubera Group, northern Colombia (Anderson, 1929); ?Melajo Clay Member of Springvale Formation, Trinidad (Jung, 1969).

Family Melongenidae Gill, 1871 (1854)
Subfamily Melongeninae Gill, 1871 (1854)
Genus *Melongena* Schumacher, 1817.
Type species *M. fasciata* Schumacher, 1817 (= *Murex melongena* Linnaeus, 1758), by monotypy.

*Melongena consors* (G. B. Sowerby I, 1850)
Pl. 15, Figs 11-12

1850 *Pyrula consors* G. B. Sowerby I, p. 49.
1873 *Melongena melongena* L. – Gabb, p. 205.
1876 *Pyrula melongena* (Linn.) – Guppy, p. 523.
1890 *Melongena consors* (Sowerby) – Dall, p. 121.
1917 *Melongena consors* (Sowerby) – Maury, p. 85, pl. 14, fig. 5.
1922 *Melongena consors* (Sowerby) – Olsson, p. 112, pl. 9, fig. 1.
1922 *Melongena consors* (Sowerby) – Pilsbry, p. 347, pl. 31, fig. 5.
1925a *Melongena consors* (Sowerby) – Maury, p. 208, pl. 35, fig. 12.
1929 *Melongena consors* (Sowerby) – Weisbord, p. 44, pl. 7, fig. 5.
1932 *Melongena melongena consors* (Sowerby) – Olsson, p. 176, pl. 19, fig. 4.
1961 *Melongena* (Melongena) *melongena consors* (Sowerby) – Olsson & Richards, p. 10, pl. 2, fig. 5.
1964 *Melongena melongena consors* (Sowerby) – Woodring, p. 273, pl. 44, figs 2, 4, 6, 8.
1994 *Melongena (s.s.) consors taurus* Petuch, p. 302, pl. 56, figs A-B.
2010a *Melongena consors* (G. B. Sowerby I, 1850) – Landau & Silva, p. 77, pl. 15, figs 11-12.

Material and dimensions: Maximum height 155.0 mm, one specimen NMB lot DS 6924; four specimens EDIMAR coll.; five specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
All workers dealing with Caribbean Neogene assemblages have struggled satisfactorily to distinguish the fossil *Melongena consors* (G. B. Sowerby I, 1850) from the Recent western Atlantic species *Melongena melongena* Linnaeus, 1758). Clench & Turner (1956) discussed the tremendous variability within the Recent species, especially in the number of rows of spines, which can be anything from none to four in specimens from a single locality. Many of the characters put forward to distinguish
them such as the shell shape, shape of the spines (G. B. Sowerby I, 1850), surface sculpture (Guppy, 1876), height of the spire and shell thickness (Maury, 1917) are too variable in both forms to be of specific value. As pointed out by Olsson (1932) and Woodring (1964) the most important difference between the two is the suture, which is canaliculated in the Recent species. In the fossil shells the suture is usually appressed, although occasionally slightly excavated, but never canaliculated. Furthermore, we have examined numerous lots of *M. consors* from various Caribbean Neogene deposits (BL coll.), and all, including those from Cubagua, have two, or more often three rows of spines.

Petuch (1994) described a subspecies from the Pliocene Pinecrest Beds (unit 7) of Florida; *Melongena (s.s.) consors taurus*, said to differ from *M. consors* in having larger, more inflated, lower spired shells, with weaker spines and weaker spiral sculpture. We have examined specimens from the type locality, APAC Pit (BL coll.). There are small differences between this Floridian assemblage, which includes the last known occurrence of *M. consors*, and their Caribbean counterparts. As would be expected in a phylogenetic series, these Upper Pliocene specimens have features intermediate between the *M. consors* and *M. melongena*; they are larger (maximum size 215 mm), lighter-shelled than Caribbean *M. consors*, they have a non-canaliculate suture, but they are the only assemblage of *M. consors* with 1-3 rows of spines as opposed to 2-3 seen in all the Caribbean lots. The differences discussed by Petuch (1994) in sculpture are not significant, as we have examined Caribbean specimens from the Upper Miocene Cercado Formation of the Dominican Republic (BL coll.), which have spiral sculpture and others with almost smooth shells. Whether these small differences justify their separation at the subspecific level is debatable. We have included *Melongena (s.s.) consors taurus* in the distribution of *M. consors* as it is probably a junior subjective synonym.

Despite the great variability seen in *M. consors*, several distinct American Neogene species can be recognized. In the Lower Miocene Cantaure Formation of Venezuela the specimens of *Melongena venezuelana* Gibson-Smith & Gibson-Smith, 1983 attain a much larger size (maximum height 200 mm, BL coll.) than the shells of the Caribbean *M. consors*. *Melongena venezuelana* differs in being more strongly shouldered, by never having more than two rows of spines and by usually having spiral sculpture on the infrasutural ramp, although not all specimens show this feature. Gibson-Smith & Gibson-Smith (1983, figs 3-4) illustrated a specimen which they include within the variability of *M. venezuelana* from the Lower Miocene La Candelaria Beds, also on the Paraguaná Peninsula, with much stronger spiral sculpture on the sutural ramp and quite a different shell profile. Gibson-Smith & Gibson-Smith (1983, p. 722) also noted the difference in sculpture and said ‘There are differences in the sculpture of the ramp, discussed later; (…).’ but did not mention it again. We have also collected these shells from the La Candelaria Beds and they are quite different from those of Cantaure. We very much doubt they are conspecific. The shells of *Melongena candelariana* Gibson-Smith & Gibson-Smith, 1983, also from the La Candelaria Beds, are quite different in shape and sculpture. This species belongs within a different clade including *Melongena orthacantha* Pilsbry & Johnson, 1917 from the Lower Miocene Baitoa Formation of the Dominican Republic. The taxon named *Melongena colombiana* Weisbord, 1929 includes again quite different shells and belongs in the genus *Torquifer* Roth, 1981. Neither of the latter two lineages survived into the Recent western Atlantic fauna. Woodring (1964) suggested that the specimen illustrated by Maury (1925a, pl. 35, fig. 12) might correspond not to *M. consors*, but to *M. colombiana*. Unfortunately the specimen is poorly preserved and illustrated only from one side.

We therefore consider *Melongena consors* a separate species from *M. melongena*, the latter well represented in the Pleistocene and Holocene raised terraces of the Tortuga Formation on Cubagua Island, Venezuela (BL coll.). In the Atlantic *M. consors* gave rise to *M. melongena* in the Pleistocene; in the Recent tropical American Pacific it is ancestral to *Melongena patula* (Broderip & Sowerby, 1829), which reaches an even larger size. It differs from *M. consors* in never having more than one row of spines at the shoulder, composed of relatively few spines, and lacking the basal row of spines.

**Geological and geographical distribution: Atlantic**

Lower Miocene: Baitoa Formation, Dominican Republic (Woodring, 1964).

Middle Miocene: lower Gatun Formation, Panama (Woodring, 1964).

Upper Miocene: middle Gatun Formation, Panama (Woodring, 1964); Cercado Formation, Dominican Republic (Maury, 1917; Woodring, 1964); Usiacuri Formation, Juan de Acosta, Colombia (Weisbord,
Family     Fasciolariidae G RAY, 1853
Subfamily    Fasciolariinae G RAY, 1853
Genus     Pleuroploca P. FISCHER, 1884.
Type species     *Murex trapezium* LINNAEUS, 1758, by monotypy.

*Pleuroploca gorgasiana* (BROWN & PILSBRY, 1913)

Pl. 16, Fig. 1

1911    ?*Fasciolaria* sp. undet.  – BROWN & PILSBRY, p. 348.
1913     *Fasciolaria gorgasiana* BROWN & PILSBRY, p. 506, pl. 22, fig. 5.
1922     *Fasciolaria Gorgasiana* BROWN & PILSBRY – OLSSON, p. 105, pl. 8, fig. 9.
1934     *Fasciolaria (Pleuroploca)* cf. *gorgasiana* BROWN & PILSBRY – RUTSCH, p. 74, pl. 5, fig. 3.
1964     *Fasciolaria gorgasiana* BROWN & PILSBRY – WOODRING, p. 275, pl. 43, figs 5, 7, 11, pl. 45, fig. 17.
2010a    *Pleuroploca gorgasiana* (BROWN & PILSBRY, 1913) – LANDAU & SILVA, p. 78, pl. 16, fig. 1.

**Material and dimensions:** Maximum height 155.0 mm, one specimen EDIMAR coll.; two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
This species has been consistently placed within the genus *Fasciolaria* LAMARCK, 1799, but this should be reserved for the tropical American almost-smooth *F. tulipa*-like shells. SNYDER (2003, p. 242) placed *Fasciolaria gorgasiana* BROWN & PILSBRY, 1913 in the genus *Pleuroploca*, a position we follow in this work. In Cubagua this species is represented by three specimens, one is juvenile, the other two are large incomplete adult specimens, but clearly not of maximum size, as the fragment illustrated by WOODRING (1964, pl. 43, fig. 11) must have belonged to a specimen at least 200 mm in height. *Pleuroploca gorgasiana* (BROWN & PILSBRY, 1913) is characterized having a shell with a strongly inflated last whorl and shoulder bearing small blunt spines. The larger Cubagua specimen is similar to that illustrated by WOODRING (1964, pl. 43, figs 5, 7), although the spines are a little more strongly developed.

*Pleuroploca gorgasiana* probably evolved from the Early Miocene *Pleuroploca kempi* (MAURY, 1917) represented in the Lower Miocene Baitoa Formation of the Dominican Republic, which has a smaller shell, with the spire proportionately taller, the last whorl less inflated and the shoulder spines more strongly developed. We examined several specimens of *F. kempi* from the Baitoa Formation (BL coll.), however, we have not found any representatives of this *Pleuroploca* group in the stratigraphically younger Upper Miocene Cercado Formation and Lower Pliocene Gurabo Beds of the Dominican Republic. ANDERSON (1929) recorded, but did not illustrate *P. kempi* from the Lower Pliocene Tubera Group, northern Colombia. According to WOODRING (1964) the Colombian shells probably correspond to *P. gorgasiana*, but are too poorly preserved to be sure. RUTSCH (1934) also recorded *P.* cf. *gorgasiana* from the Lower Pliocene Punta Gavilán Formation of Venezuela. In this specimen the shoulder spines are subobsolete. We also examined a single specimen from these deposits which probably corresponds to *P. gorgasiana* (BL coll.), with a more rounded shoulder and almost no spines. OLSSON (1922, pl. 106, pl. 8, fig. 1) described *Pleuroploca macdonaldi* from the Lower Pliocene Banano Formation of Costa Rica, with a shell bearing stronger spiral sculpture and more horizontally compressed shoulder spines than in *P. gorgasiana*. *Pleuroploca olssoni*

**Geological and geographical distribution: Pacific**
Middle Miocene: Zorritos Formation, Peru (OLSSON, 1932).

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; ?Springvale Formation, Trinidad (MAURY, 1925a); Tubera Group (NMB localities Wheeler 138, 168 and G 452), northern Colombia; Gurabo Formation, Dominican Republic (MAURY, 1917; WOODRING, 1964).
Upper Pliocene: Pinecrest Beds, Florida (PETUCH, 1994, unit 7, as *Melongena (s.s.) consors taurus*); Banano Formation, Costa Rica (OLSSON, 1922).
BERNARD M. LANDAU

ANDERSON, 1929) from the Tuberá Group, northern Colombia is a curious species, with shells displaying prominent rounded shoulder spines, but they develop very late, only on the second half of the last whorl.

Distribution
Middle Miocene: lower Gatun Formation, Panama (WOODRING, 1964).
Upper Miocene: middle Gatun Formation, Panama (WOODRING, 1964).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).
Upper Pliocene: Banano Formation, Costa Rica (OLSSON, 1922).

Subfamily Fusininae W RIGLEY, 1927
Genus Fusinus RAFINESQUE, 1815.
Type species Murex colus LINNAEUS, 1758, by monotypy.

Fusinus vonderschmidti RUTSCH, 1934
Pl. 16, Figs 2-3

1934 Fusinus henikeri vonderschmidti RUTSCH, 1934, p. 77, pl. 6, 5-6, pl. 7, fig. 2.
2010a Fusinus vonderschmidti RUTSCH, 1934 – LANDAU & SILVA, p. 79, pl. 16, figs 2-3.

Material and dimensions: Maximum height 58.0 mm, five specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

Discussion:
Whilst it is clear that the shell ascribed to Fusinus henikeri vonderschmidti by RUTSCH (1934) from the Lower Pliocene Punta Gavilán Formation belongs to the Fusinus henekeni group, the specimen is not conspecific with F. henekeni from the type locality: Lower Pliocene Gurabo Formation of the Dominican Republic. As pointed out by RUTSCH (1934; holotype NMB H 19o1 [sic], paratype H 19o2 [sic]), the Venezuelan shells have fewer axial ribs (seven, rarely eight vs. 9-12), which are much broader and more elevated, and on the last whorl extend almost to the suture, whereas the ribs in F. henekeni shells become subobsolete on the infrasutural ramp. Moreover, in F. vonderschmidti the siphonal canal is broader and shorter than in F. henekeni. Whether all the Dominican shells belong to a single taxon is unclear, three varieties have been recognized: F. henekeni henekeni (G. B. SOWERBY I, 1850), F. henekeni haitensis (G. B. SOWERBY I, 1850) with somewhat carinate shells, and F. henekeni veatchi (MAURY, 1917), in which the axial sculpture does not persist on later adult whorls. WOODRING (1928) clearly considered all three to be separate species. In the Neogene Caribbean material examined by (BL coll.) us there seems to be some gradation between the first two forms, but a full revision of this group is beyond the scope of this work. The material from Cubagua is conspecific with shells from the Lower Pliocene Punta Gavilán Formation (BL coll.). As pointed out by WOODRING (1928) almost every Caribbean Neogene assemblage includes representatives of the F. henekeni group, and therefore the phylogenetic link between F. henekeni and F. vonderschmidti is far from clear. For this reason we prefer to consider them separate at full specific rank.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).

Fusinus springvalensis (MAURY, 1925)
Pl. 16, Figs 4-5

1925a Fusus springvalensis MAURY, p. 206, pl. 35, fig. 11.
1934 Fusinus springvalensis (MAURY) – RUTSCH, p. 75, pl. 5, figs 4-5.
1969 Fusinus sp. JUNG, p. 523, pl. 56, fig. 3.
2010a Fusinus springvalensis (MAURY, 1925) – LANDAU & SILVA, p. 80, pl. 16, figs 4-5.

Material and dimensions: Maximum height 89.3 mm, one specimen EDIMAR coll.; 12 specimens BL
coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

In all the Cubagua shells of Fusinus springvalensis the axial sculpture consists of eight broad flattened ribs, which are strongly developed until the penultimate and last whorl, where the ribs weaken abapically to a varying degree. In the larger shells the ribs are obsolete on the last whorl, but they still persist, albeit weakened, on the smaller specimens. The shell illustrated by JUNG (1969, pl. 56, fig. 3; not found in NMB collection) from the Melajo Clay Member of Lower Pliocene Springvale Formation, Trinidad undoubtedly corresponds to this same species; it is a juvenile (44 mm in height) in which the axial sculpture is prominent. The spiral sculpture in the Cubagua specimens consists of fairly robust cords, triangular in cross-section, with irregularly placed secondary spirals in some of the interspaces.

These Cubagua shells are probably conspecific with Fusinus springvalensis MAURY, 1925 from the Savaneta Glauconitic Sandstone Member of Springvale Formation, Trinidad. Although MAURY (1925a) considered that the most diagnostic character of this species is the absence of axial ribs on the last two whorls of the shell, H. E. VOKES (1938, figs 27-28), who illustrated some better-preserved material, showed the strength and persistence of the axial sculpture to be variable. According to H. E. VOKES (1938, p. 23) the most distinctive feature of F. springvalensis was the presence of ‘(...) interribbing between most, but not all the primary spirals (...).’ The material from Cubagua agrees in most aspects with the shell characters of F. springvalensis, but has a more elongate shape than the shells figured by H. E. VOKES (1938), with much narrower, more convex whorls, producing a deeper suture, more like the type illustrated by MAURY (1925a). The Trinidadian shells illustrated by H. E. VOKES (1938) are larger, up to 126.5 mm in length, and it is possible these represent another closely related, but distinct species. The specimen illustrated by RUTSCH (1934, pl. 5, figs 4-5; hypotype NMB H 1894 and H 1898) is similar to the specimens from Cubagua and is here considered to fall within the range of variability of F. springvalensis.

WOODRING (1964) considered Fusinus magdalenensis ANDERSON, 1929 from the Lower Pliocene Tuberá Group of northern Colombia to be a junior synonym of F. springvalensis. The Colombian shell has the axial sculpture obsolete on the last four whorls and is excluded from the synonymy. Fusinus empleus WOODRING, 1964 from the Upper Miocene Gatun Formation of Panama was described on the basis of a single specimen with an incomplete or subadult aperture. According to WOODRING (1964, p. 276) F. springvalensis has “(...) whorls which are more distinctly constricted in the sutural area, they have also heavier spiral sculpture and wider axial ribs.” We maintain the Gatun species distinct for want of comparative material. Fusinus engonius WOODRING, 1928 from the Pliocene Bowden Formation of Jamaica is similar in size, but has somewhat angular whorls. The Recent Fusinus dilectus (A. Adams, 1856) now living off the north coast of South America from Colombia to Surinam [=Fusinus marensis WEISBORD, 1962 from the Lower Pleistocene Mare Formation (NMB many specimens), see SNYDER, 2003] is also closely related to F. springvalensis, but differs in having shells losing their axial sculpture earlier, so that the last three or four whorls are devoid of ribs, the whorls are rounded, with the periphery placed lower and the siphonal canal is more twisted.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Punta Gavilán Formation, Venezuela (RUTSCH, 1934); Savaneta Glauconitic and Melajo Clay Member of Springvale Formation, Trinidad (H. E. VOKES, 1938; JUNG, 1969).

Superfamily
Family
Subfamily
Tribe
Genus
Type species V. musica LINNAEUS, 1758, by subsequent designation, MONTFORT, 1810.

Voluta cubaguaensis J. GIBSON-SMITH, 1973
Pl. 16, Figs 6-7
1973  \textit{Voluta cubaguaensis} J. GIBSON-SMITH, p. 68, pl. 3, figs 1-3.
2010a \textit{Voluta cubaguaensis} J. GIBSON-SMITH, 1973 – LANDAU & SILVA, p. 80, pl. 16, figs 6-7.

\textbf{Material and dimensions:} Maximum height 108.4 mm, one specimen NMB lot 6928; five specimens EDIMAR coll.; 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

\textbf{Discussion:} \textit{Voluta cubaguaensis} J. GIBSON-SMITH, 1973 is very similar and probably ancestral to the Recent mainly southern Caribbean \textit{Voluta musica} (LINNAEUS, 1758), but differs by having a higher, more pointed spire, with sharper tubercles at the shoulder (rather rounded and blunt in \textit{V. musica}), and by having fewer folds on the columella (5-8 vs. 9-12). J. GIBSON-SMITH (1973) described the holotype as having five columellar folds and three lirations on the parietal area. All the Cubagua specimens have five or six columellar folds, decreasing in strength adapically, but no parietal folds. The sharp tubercles at the shell shoulder described by J. GIBSON-SMITH (1973) do tend to become blunter in larger specimens (Pl. 16, Fig. 4). The protoconch is preserved in several of the specimens and it is similar to that of \textit{V. musica}, smooth mammilate, consisting of about 3.5-4 whorls with a small nucleus (GARCIA, 1988).

\textit{Voluta vautrini} JUNG, 1965 from the Lower Miocene Cantaure Formation of Venezuela is also similar but again has more numerous columellar folds and a paucispiral protoconch. \textit{Voluta cantaurana} J. GIBSON-SMITH, 1973 also from the Cantaure Formation has a more elongated shell in which the ribs do not form prominent tubercles at the shoulder, and the protoconch is again paucispiral.


\begin{tabular}{ll}
Family & Harpidae  \textsc{bron}, 1849  \\
Subfamily & Harpinaceae  \textsc{bron}, 1849  \\
Genus & \textit{Harpa}  \textsc{röd}ing, 1798.  \\
Type species & \textit{Buccinum harpa} LINNAEUS, 1758, by tautonymy.
\end{tabular}

\textit{Harpa crenata} SWAINSON, 1822
Pl. 16, Figs 8-10

\begin{tabular}{ll}
1822 & \textit{Harpa crenata} SWAINSON, p. 5.  \\
1832 & \textit{Harpa scriba} VALENCIENNES, p. 323.  \\
1834 & \textit{Harpa rivoliana} LESSON, pl. 36, figs 1-2.  \\
1835b & \textit{Harpa rosea} KIENER, p. 11, pl. 5, fig. 8 [\textit{non} \textit{H. rosea} LAMARCK, 1816 = \textit{Harpa doris} RÖDING, 1798]  \\
1839 & \textit{Harpa rosea crenata} GRAY, p. 122, pl. 34, fig. 5.  \\
1883 & \textit{Harpa crenata} SWAINSON – TRYON, p. 98, pl. 40, fig. 65.  \\
1948 & \textit{Harpa crenata} SWAINSON – M. SMITH, p. 48, pl. 16, fig. 5.  \\
1958 & \textit{Harpa crenata} SWAINSON, 1822 – KEEN, p. 431, fig. 663.  \\
1964 & \textit{Harpa crenata} SWAINSON – EMERSON, p. 3, fig. 1.  \\
1966 & \textit{Harpa crenata} SWAIN. – MORRIS, p. 194, pl. 59, fig. 16.  \\
1971 & \textit{Harpa crenata} SWAINSON, 1822 – KEEN, p. 620, fig. 1357.  \\
1973 & \textit{Harpa crenata} SWAINSON, 1822 – REIDER, p. 258, pl. 189, figs 1-2, pl. 225.  \\
1980 & \textit{Harpa crenata} SWAINSON, 1822 – WALLS, p. 153, fig. upper left p. 154.  \\
1992 & \textit{Harpa crenata} SWAINSON, 1822 – BERKHOUT, p. 126, pl. 3, fig. 1, text-figs 11-12.  \\
1999 & \textit{Harpa crenata} SWAINSON, 1822 – POPPE et al., p. 14, pl. 13, figs 1-5, pl. 14, figs 1-3.  \\
2004 & \textit{Harpa crenata} SWAINSON, 1822 – OKON, p. 7, figs top left & right.  \\
2010a & \textit{Harpa crenata} SWAINSON, 1822 – LANDAU & SILVA, p. 81, pl. 16, figs 8-10.  \\
\end{tabular}

\textbf{non}1984b \textit{Harpa crenata} SWAINSON – E. H. VOKES, p. 58, fig. 6 (=\textit{Harpa americana} PILSBRY 1922).
**Material and dimensions:** Maximum height 66.2 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula, Venezuela.

**Discussion:**

This well-known Recent Central American Pacific species is represented in both locations on Cubagua Island and in contemporaneous beds at Cerro Barrigón, Araya Peninsula, mainland Venezuela. The presence of this species in the Atlantic portion of the Gatunian biogeographical province in the Early Pliocene is noteworthy, as it is the first Caribbean record for the species. The genus *Harpa* RÖDING, 1798 is also a good example of the group WOODRING (1928) called paciphiles; these are taxa that today are restricted to the Pacific side of their original wider Neogene distribution, and disappeared from the Caribbean side following the uplift of the Central American Isthmus. Five species of *Harpa* RÖDING, 1798 have been described from the Tropical American Neogene. All are extremely rare in their respective assemblages.

The genus is recorded for the first time in the Tropical American Caenozoic in the Lower Oligocene Chira Formation of Peru (OLSSON, 1931) represented by *Harpa myrmia* OLSSON, 1931, characterised by its shell with extremely heavy ribs. The next youngest occurrence is in the Lower Miocene Cantaure Formation of Venezuela. Identified as *H. myrmia* by GIBSON-SMITH & GIBSON SMITH (1982), the Cantaure specimens also have heavy axial ribs, which cross over the suture, forming a series of lamellar flanges across the sutural ramp. The width of the ribs is somewhat variable, some shells illustrated by GIBSON-SMITH & GIBSON SMITH (1982, figs 1-2), and two further specimens (BL coll.) have relatively narrower ribs, whereas the shell in GIBSON-SMITH & GIBSON SMITH (1982, fig. 3) has broad ribs, similar to the Peruvian specimen. As noted by E. H. VOKES (1984b) these shells may or may not be referable to *H. myrmia*.

*Harpa americana* PILSBRY, 1922 from the Upper Miocene of the Dominican Republic (unnamed unit of the same age as Cercado Formation; E. H. VOKES, 1998) is a *Harpa* species with a relatively elongated shell, with low, nodular varices and a non-polished surface. The shells of *Harpa isthmica* E. H. VOKES, 1984 from the Upper Agueguexquite Formation, Middle Pliocene of Mexico (Caribbean) have more numerous and heavier ribs, and a smoother surface. Lastly, the living *Harpa crenata* SWAINSON, 1822 is characterised by having a shell with a more inflated last whorl, fewer axial ribs, with secondary nodes anterior to the shoulder, which become prominent shoulder spines, giving it a “double-shouldered” aspect (E. H. VOKES, 1984b). There are differences also in the protoconch, consisting of 3.5 whorls in *H. crenata* and *H. isthmica* and 4.5 whorls in *H. americana*, although this is somewhat contradictory; the original description gives a protoconch whorl count of three (PILSBRY, 1922, p. 337), whilst E. H. VOKES (1984b, p. 57) states 4.5 whorls.

*Harpa crenata* was also recorded as fossil in the Upper Miocene Esmeraldas beds, Onozole Formation of Ecuador (PITT, 1981; E. H. VOKES, 1984b). The specimen illustrated by E. H. VOKES (1984b, pl. 1, fig. 5) as *H. crenata* with some hesitation is rather elongated for *H. crenata*, and lacks the “double-shouldered” aspect to the shell. The second specimen illustrated by PITT (1981, p. 155, text-fig. 1) is also atypical of *H. crenata*, and although broader, in our opinion both represent specimens of *H. americana*.

E. H. VOKES (1984b) suggested a phylogeny in which *Harpa myrmia* was a distinct lineage on account of having the sutures crossed by extensions of the ribs, not known in any other species. She suggested it derived from the ancestral *Eocithara* line and left no descendants. In the Caribbean E. H. VOKES (1984b) suggested that *H. isthmica* was most similar and possibly ancestral to the Recent West African *H. doris* RÖDING 1798 and *H. americana* gave rise to the Recent West Coast *H. crenata*, and its Early Pliocene relative in Ecuador.

The presence of typical *H. crenata* in the Lower Pliocene of the Araya Formation rather complicates the issue. In our opinion the shells illustrated by PITT (1981) and E. H. VOKES (1984b) from the Esmeraldas beds are more typical of *H. americana*. It is likely that *H. americana* existed on both the Atlantic and Pacific portions of the Gatunian palaeobiogeographic province. *H. crenata* was restricted to the southern part of the province in the Pliocene, and at some stage expanded its range to the Pacific side of.
the palaeobiogeographic province, its distribution subsequently becoming restricted to the Pacific following the closure of the Central American seaway.

The fifth species, *Harpa daisyae* LANDAU et al., (in press) has the smallest shell of all the known Neogene Caribbean *Harpa* species, with elongated shells and finely reticulate surface sculpture. It is most similar to the Recent *Harpa gracilis* BRODERIP & G. B. SOWERBY I, 1829 and possibly was ancestral to it (LANDAU et al., in press).

**Geological and geographical distribution: Atlantic**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

**Geological and geographical distribution: Pacific**
Recent: Baja California, south to Gorgona Island, Colombia (KEEN, 1971).

**Family** Cysticidae S TIMPSON, 1865
**Subfamily** Persiculinae  G.A. & H.K. COOVERT, 1995
**Genus** Persicula SCHAUMACHER, 1817.
*Type species* *P. variabilis* SCHAUMACHER, 1817 (= *Voluta persicula* LINNAEUS, 1758), by monotypy.

1927 *Marginella venezuelana lavelana* F. HODSON in HODSON, HODSON & HARRIS, p. 78, pl. 40, figs 3, 10, 11.
1934 *Persicula (Rabicea) venezuelana lavelana* F. HODSON – RUTSCH, p. 91, pl. 6, figs 9-12.
1962 *Persicula (Rabicea) venezuelana lavelana* (F. HODSON) – WEISBORD, p. 413, pl. 37, figs 15-16, pl. 38, figs 1-4.
1969 *Persicula (Rabicea) cf. interruptolineata* (MEGERLE VON MÜHLFELD) – JUNG, p. 537, pl. 57, figs 11-12.
2010a *Persicula lavelana* (HODSON, 1927) – LANDAU & SILVA, p. 82, text-fig. 13, figs 4-6, pl. 16, fig. 11.

*non* 1965 *Persicula (Rabicea) venezuelana lavelana* (F. HODSON) – JUNG, p. 560, pl. 76, figs 3-4 [*Persicula falconensis* (F. HODSON in HODSON, HODSON & HARRIS, 1927)].

**Material and dimensions:** Maximum height 17.9 mm. 12 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; 11 specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; 18 specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
This group of *Persicula* species were traditionally placed in the subgenus *Rabicea* GRAY, 1857 (type species *Marginella interrupta* LAMARCK, 1822 [= *Marginella interruptolineata* MÜHLFELD, 1818]). COOVERT & COOVERT (1995) synonymised *Rabicea* with *Persicula* based on similar shell, radular and external anatomical characters.

If we were to consider all the records given for *Persicula venezuelana lavelana* (F. HODSON, 1927) to represent a single species, the subspecies would have a relatively long geological history, but a restricted geographic distribution, found only in Venezuela between the Paraguaná Peninsula, Cubagua Island and the Cabo Blanco area of Maiquetía. However, there are small, but significant, differences between at least some of the populations and it more likely that we are dealing with a group of related, but distinct species, probably all characterised by having a colour pattern of spiral bands, similar to that seen in *Persicula interruptolineata* (MÜHLFELD, 1818) today.
Text-Figure 23. Persicula types. Fig. 1. Persicula venezuelana (F. Hodson, 1927), holotype PRI 22887, height 7.6 mm, El Mene de Saladillo, Zulia State, Venezuela, La Rosa Formation, upper Lower Miocene. Fig. 2. Persicula venezuelana (F. Hodson, 1927), paratype PRI 22888, height 8.05 mm, El Mene de Saladillo, Zulia State, Venezuela, La Rosa Formation, upper Lower Miocene. Fig. 3. Persicula falconensis (F. Hodson, 1927), holotype PRI 22882, height 11.0 mm, Cantaure, Falcón, Venezuela, Cantaure Formation, Lower Miocene. Fig. 4. Persicula lavelana (F. Hodson, 1927), holotype PRI 22881, height 11.6 mm, La Vela, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Images courtesy of the Paleontological Research Institution. Figs 5-6. Persicula lavelana (F. Hodson, 1927), paratype PRI 22886, height 11.6 mm, La Vela, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Images courtesy of the Paleontological Research Institution. Fig. 7. Persicula couviana (Maury, 1925), holotype PRI 1035, height 10.9 mm, Trinidad, Springvale Formation, Lower Pliocene. Images courtesy of the Paleontological Research Institution.

Persicula venezuelana F. Hodson, 1927 (Text-Fig. 23, Figs 1-2) is an upper Lower Miocene species from La Rosa Formation Quiróz, State of Zulia, District of Miranda. It has the smallest shell of the species group (7.6-8.2 mm), is somewhat elongate and the outer lip is exteriorly marginate.

The specimens from the Lower Miocene Cantaure Formation of Venezuela illustrated by Jung (1965, pl. 76, figs 3-4) as Persicula (Rubicea) venezuelana lavelana (F. Hodson) are quite different. We have examined numerous specimens (BL coll.); they are larger (11.0-13.0 mm), more inflated, the ventral depression is more strongly developed, the outer lip extends at least to, and usually just above the apex, two or often three relatively broad anterior columellar folds extend horizontally across the base, broader than that figured for Persicula venezuelana by F. Hodson (1927, pl. 40, figs 13-14). Two to four columellar folds are present above these strong horizontal folds, but are very irregular in development and rapidly weaken adapically. Margination on the exterior of the outer lip is seldom present. This assemblage from the Cantaure formation was ascribed to Persicula venezuelana falconensis F. Hodson, 1927 (Text-Fig. 23, Fig. 3), and in our opinion this should be considered a distinct species, Persicula falconensis, and not synonymised with P. venezuelana lavelana as suggested by Jung (1965).

Persicula venezuelana lavelana F. Hodson, 1927 (Text-Fig. 23, Figs 4-6) was based on specimens from several localities from the District of Colina, Falcón, Venezuela. According to the original description they differ from the nominate species in having shells that are much elongate, more globose, and in showing a more prominent longitudinal ridge on the upper part of the inner lip running roughly parallel to the upper part of the aperture, the outer lip is broadened near the middle, somewhat flattened ventrally, and marginate externally. There are more numerous columellar folds adapical to the strong horizontal folds. This description clearly applies to the specimens from various Venezuelan Lower Pliocene localities (i.e. Punta Gavilán Formation, Araya and Aramina Formations; personal observations). There are some differences in size range between the shells of different assemblages (Punta Gavilán 11.4-14.7 mm; Cerro Barrigón 13.1-15.5 mm; Cubagua, Cañón de las Calderas 13.6-14.7 mm; Cubagua, Cerro Colorado 14.5-17.8 mm), and the longitudinal ridge is most prominent in the Punta Gavilán specimens, however, these are calcitic pseudomorphs, which may have changed the shell morphology somewhat. Weisbord (1962) described another species P. hodsoni from the Pleistocene Mare and Abisinia Formations of the Cabo Blanco area, differing mainly in having a thin outer lip. This is usually a juvenile character in marginellids.
and should not be used as a criterion in a taxonomy based on the morphology of adult specimens.

The specimens of *Persicula couviana* (Maury, 1925) [= *Marginella (Persicula) propeobesa* Mansfield, 1925 fide Jung, 1969] (Text-Fig. 23, Fig. 7), found in both the Savaneta Glauconitic Sandstone Member and Melajo Clay Member of the Lower Pliocene Springvale Formation of Trinidad are very similar to *P. lavelana* and seem to differ in being slightly less solid, less inflated, with a thinner parietal callus. Specimens in our collection (BL coll.) from the Savaneta Glauconitic Sandstone Member are smaller and clearly more cylindrical, whereas those illustrated by Jung (1969, pl. 57, figs 13-15) are more inflated. We provisionally separate the two species.

In the Recent faunas this group is represented by *Persicula interruptolineata*, which clearly differs from all its fossil predecessors in having a more elongated shell, which is less globose, the outer lip rises above the apex and is strongly marginate, and there is no clear ventral depression or ridge. Weisbord (1962) described *Persicula (Rabicea) interrupta mareana* from the Pleistocene Mare and Abisinia Formations of the Cabo Blanco area, Venezuela. Weisbord (1962) erected his new taxon as a subspecies of *Marginella interrupta* Lamarck, 1822 erroneously considering Lamarck's name earlier than *Marginella interruptolineata* Mühfeld, 1818. This subspecies is close to, and probably synonymous with, *P. interruptolineata*. If the specimens illustrated by Jung (1969) from the Pleistocene Matura Shell Bed of Trinidad correspond to *P. lavelana*, this suggests that both *P. lavelana* and *P. interruptolineata* (or its predecessor) were both present in the Late Pliocene and Pleistocene, and that the latter is not directly descended from *P. lavelana*. It is more likely that *Persicula obesa* (Redfield, 1848) is descended from *P. lavelana* from which it differs in having smaller, more slender and less globose shells. Weisbord (1962) noted that the specimens he identified as *Persicula (Rabicea) venezuelana lavelana* from the Cabo Blanco area were very similar to *P. obesa*, and Macsotay & Campos (2001) synonymised Weisbord’s record with *P. obesa*. However, the Cabo Blanco shells are larger than any Recent *P. obesa* specimen, and slightly more inflated, although less so than the lower Pliocene fossil shells of *P. lavelana*. The Upper Pliocene and Pleistocene Cabo Blanco species, of which there are hundreds in the NMB collections, may represent an intermediate population. The two shells illustrated by Jung (1969; NMB H 15277, H 15278) from the Pleistocene Matura Shell Bed, Talparo Formation of Trinidad as *Persicula (Rabicea) cf. interruptolineata* are more similar to Weisbord’s Pleistocene specimens of *P. lavelana* from the Cabo Blanco area, and are tentatively included in the synonymy.

We therefore consider there to be at least three distinct species within this species group in the Miocene and Pliocene of Venezuela. Although clearly related, it seems less confusing to consider all three: *Persicula venezuelana*, *P. falconensis* and *P. lavelana*, distinct at full species level. Other modern revisions of fossil marginellid assemblages have also found most species to be geographically restricted and short-lived (Nehm, 2001; Landau et al., 2006), which would be expected from what is known of their larval development mode; as all species are non-planktotrophic (Coover & Coover, 1995; Penchaszaeh & Rincon, 1996).

**Geological and geographical distribution:**

Upper Miocene: State of Falcón, Venezuela (F. Hodson in Hodson et al., 1927).

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934).

Pleistocene: Mare Formation, Cabo Blanco Area, Venezuela (Weisbord, 1962); ?Matura Shell Bed, Talparo Formation, Trinidad (Jung, 1969).

**Persicula sp.**
Pl. 16, Fig. 12.

2010a *Persicula sp.* – Landau & Silva, p. 84, pl. 16, fig. 12.

**Material and dimensions:** Height 8.6 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.
Discussion:

We have examined a single specimen of a *Persicula* species with a smaller, barrel-shaped shell, with a much more cylindrical shell profile than *Persicula lavelana* (F. Hodson, 1927). This specimen is possibly conspecific with *Persicula couviana* (Maury, 1925), but the shell is more solid, the base more strongly callused and the apex more truncated than the holotype of *P. couviana* (Text-Fig. 23, Fig. 7). We have compared the Cubagua shell with specimens of *P. couviana* from the Savaneta Glauconitic Member of the Lower Pliocene Springvale Formation of Trinidad (BL coll.) with a thicker basal callus, with which they compare well, although the apex is more truncated in the Cubagua shell. The shells from the Springvale Formation of Trinidad examined have five columellar folds, as does the holotype and the single specimen from Cubagua. Jüng (1969) synonymised *Marginella (Persicula) propeobesa* Mansfield, 1925 with *P. couviana*, however, the description and holotype of *P. propeobesa* show eight columellar denticles or folds. In his description of the Melajo Clay Member specimens, Jüng (1969) said that the number of folds above the two stronger abapical denticles is variable. The shell shape of Jüng’s (1969) Lower Pliocene Melajo Clay Member specimens is slightly more inflated than those of the Savaneta Glauconitic Member and slightly more truncated apically, like the Cubagua shell. We have insufficient material from Cubagua to be certain whether we are dealing with the same species.

The Recent Caribbean species *Persicula cordorae* de Jong & Coomans, 1998 described from Curaçao is also similar, however, the holotype has a far less prominently developed columellar callus than in the shell from Cubagua, in which the callus envelopes more than half the ventral aspect of the shell.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Family Marginellidae Fleming, 1828  
Subfamily Marginellinae Fleming, 1828  
Tribe Prunini A. & H.K. Coovert, 1995  
Genus *Prunum* Herrmannsen, 1852.  
Type species *Voluta prunum* GMelin, 1791, by monotypy.

In this section we have adopted the shell character nomenclature and shell description style used by Nehm (2001) in his revision of the Neogene Dominican *Prunum* species.

*Prunum carmengutierrezae* LANDAU & SILVA, 2010  
Pl. 17, Figs 1-2

2010a *Prunum carmengutierrezae* LANDAU & SILVA, p. 85, pl. 17, figs 1-2.

Dimensions and type material: Holotype; MOBR-M-3878 (Pl. 17, Fig. 1), length, 27.8 mm (EDIMAR coll., ex BL coll.); paratype 1 NHMW 2010/0038/0021 (Pl. 17, Fig. 2), length 27.5 mm (NHMW coll., ex BL coll.); paratype 2 NHMW 2010/0038/0022, length 27.4 mm (NHMW coll., ex BL coll.).

Derivatio nominis: for Dr. Carmen Gutierrez, Director of the Estación de Investigaciones Marinas de Margarita, EDIMAR, Fundación La Salle de Ciencias Naturales. Venezuela, without whose support this work would not have been possible.

Locus typicus: Cañón de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Stratum typicum: Araya Formation, Cubagua Group, Lower Pliocene.

Additional material: Three specimens NMB lot 25; three specimens NMB lot 26; 17 specimens EDIMAR coll.; 30 specimens BL coll., maximum length 31.2 mm, Lower Pliocene, Araya Formation, Cañón de las Calderas, Cubagua Island.

Diagnosis: A large, cylindrical *Prunum* species, with a short spire, narrow aperture, four equally spaced columellar folds, callus formed on both sides on last whorl, but without forming a callus ring, venter of last whorl completely covered by callus, lip attaching at the same level as spire and without denticles.
Original description:

“Shell large (20-30 mm), cylindrical in shape (height/width > 1.8), with a weakly dome-shape in lateral view. Shell thick (thickness/width > 0.1), weakly shouldered, with a short spire (5-10% of height). Anterior sinus absent. Aperture narrow with anterior lip generally conforming to last whorl. Ventral surface well rounded, lacking flanging or flattening. No colour pattern visible. Four columellar folds present occupying less than half of aperture. Anterior fold not expanded, but uniform in width, forming anterior margin of the aperture. Canal absent posterior to fourth columellar fold. Four columellar folds nearly uniformly spaced. In dorsal view spire callus visible as is lip attachment. Callus band also extending parallel to lip, although not developed into complete callus ring (as in Prunum circumvittatum). Posterior parietal callus process (parietal pad) absent or very weakly developed, apertural callus ridge absent. Callus not filling columellar fold interspaces. Ventral surface of spire partially covered by callus. Ventral surface of last whorl entirely covered by thick callus, sometimes slightly flattened. Outer lip smooth, without denticulations. Thick external varix present. Lip attaching at same level as spire and angling from last whorl at about 80º from columellar axis (LANDAU & SILVA, 2010a, p. 85)”.

Discussion:

*Prunum carmengutierrezae* LANDAU & SILVA, 2010 is one of the most common gastropod species in the Cañon de las Calderas outcrop. The shells are somewhat variable in the height of their spire and the extent of the callus formation, as can be seen in the two specimens figured (Pl 15, Figs 1-2). This new taxon must be distinguished from the numerous other Caribbean Neogene to Recent large shelled *Prunum* species. The shell of the Recent *Prunum prunum* (Gmelin, 1791), which is also represented in Pleistocene and Holocene deposits in mainland Venezuela (i.e. Mare Formation, Cumaná Formation; personal observation) and the Tortuga Formation of Cubagua is about the same size and shape, but is immediately distinguished by its thinner shell, much wider aperture, by the deep anal notch and thinner and less extensive callus formation.

In the Lower Pleistocene Moin Formation of Costa Rica *Prunum limonensis* (Dall, 1896) has a long slender shell, with a very narrow aperture and a somewhat involute spire. It belongs to a separate group of *Prunum* species including *Prunum gibsonsmithorum* NEHM, 2001 and *Prunum willcoxianum* (Dall, 1890).

Of the other Lower Pliocene species, *Prunum springvalensis* (Maury, 1925) from the Springvale Formation of Trinidad (Pl. 17, Fig. 3) has a larger and broader shell, the spire whorls are more convex and the spire less sharp, the aperture is much broader, especially abapically, where the columella is excavated, whereas the columella in the Cubagua specimens of *Prunum carmengutierrezae* is very weakly concave. The external varix in *P. springvalensis* is much more pronounced and the ventral callus much weaker. *Prunum calypsonis* (Maury, 1925) described from the Springvale Formation, but also occurring in the Cubagua fauna, has a slightly smaller shell. Its overall shape and aperture are similar to the Cubagua specimens, but it differs in the character of the external varix, which is again more strongly developed. On the columellar side, the outer edge of the callus is more strongly developed into a projecting rounded ridge, whereas the outer edge of the columellar callus in *P. carmengutierrezae* is clearly delimited, but not particularly thickened. Moreover, the ventral callus in the shell of *P. calypsonis* is strongly thickened and forms a pad on the ventral side of the spire, whereas the callus rapidly thins out adapically in *P. carmengutierrezae*, not forming a thickened pad and barely reaching the apex. *Prunum suteri* (Rutsch, 1934; holotype NMB H 1934, prottype NMB H 1935), from the Lower Pliocene Punta Gavilán Formation of Venezuela is much broader with a shorter spire and a slightly dorsoventrally compressed shell. The external varix and lateral border of the ventral callus are much more strongly thickened and the posterior lip callus extends to the shell apex.

None of the Upper Miocene Dominican Republic species recently revised by Nehm (2001) are particularly similar. *Prunum amina* (Dall, 1896) has a much lower spire and a denticulate outer lip; *Prunum christineladdae* (Maury, 1917) is much lighter-shelled, and almost flat-spired; *P. gibsonsmithorum* has a slender elongated shell as discussed above; *Prunum coniforme* (G. B. Sowerby I, 1850) is smaller with a much shorter spire covered in posterior lip callus. *Prunum gatunense* (Brown & Pilsbry, 1911) from the Gatun Formation of Panama is smaller and squatter, with a denticulate outer lip.
<table>
<thead>
<tr>
<th>Shell size</th>
<th>Dorsal shell shape</th>
<th>Shell shape-lateral</th>
<th>Shell thickness</th>
<th>Shouldering</th>
<th>Morphological feature</th>
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<tr>
<td>Small (1-10mm)</td>
<td>obovate (height/width &lt; 1.8)</td>
<td>weakly domed = 0</td>
<td>thick (thickness/width &gt; 0.1)</td>
<td>strongly shouldered = 1</td>
<td>P. prunum</td>
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<td>thin (thickness/width &lt; 0.1)</td>
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<td>large (20-30mm)</td>
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<tr>
<td>very large (30mm+)</td>
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<td></td>
<td></td>
<td></td>
<td>P. suteri</td>
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</table>

<p>| | | | | | |
|  |  |  |  |  |  |
|  |  |  |  |  | P. carmengutierrezae |
|  |  |  |  |  | P. aminum |
|  |  |  |  |  | P. christineladdae |
|  |  |  |  |  | P. gibsonsmithorum |
|  |  |  |  |  | P. coniforme |
|  |  |  |  |  | P. quirosense |
|  |  |  |  |  | P. latissimum |
|  |  |  |  |  | P. circumvittatum |</p>
<table>
<thead>
<tr>
<th>Morphological feature</th>
<th>Character state</th>
<th>Columnellar position in aperture</th>
<th>Columnellar fold number</th>
<th>Colouration</th>
<th>Ventral surface morphology</th>
<th>Aperture shape</th>
<th>Spire height</th>
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| P. suteri             | 2              | 1                              | 0                       | 0,1         | 0                         | 1             | 1            |
| P. camengutierrezae   | 0              | 0                              | 0                       | 0           | 1                         | 1             | 1            |
| P. aminum             | 0              | 0                              | 0                       | 0           | 1                         | 1             | 1            |
| P. christineladdae    | 1              | 0                              | 0                       | 0           | 0                         | 0             | 0            |
| P. gibsonsmithorum    | 0              | 0                              | 0                       | 0           | 1                         | 0             | 0            |
| P. coniforme          | 1              | 0                              | 0                       | 0           | 1                         | 0             | 0            |
| P. gatunense          | 1              | 1                              | 0                       | 0           | 1                         | 1             | 1            |
| P. quirosense         | 2              | 0                              | 0                       | 0           | 1                         | 1             | 1            |
| P. latissimum         | 1              | 0                              | 1                       | 0           | 1                         | 1             | 1            |
| P. circumvittatum     | 0              | 0                              | 0                       | 1           | 1                         | 1             | 1            |</p>
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<tr>
<th>Morphological feature</th>
<th>Inner apertural callus ridge</th>
<th>Posterior sinus callus</th>
<th>Dorsal callus features</th>
<th>Columellar fold spacing</th>
<th>Posterior fold canal</th>
<th>Anterior fold lip margin expansion</th>
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<td>Crenulations</td>
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<td>Denticulation coverage</td>
<td>Ventral callus area on last whorl</td>
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Lip height in relation to spire above = 0 below = 1 same height = 2

Outer lip angulation <75 degrees = 0 75-90 degrees = 1 >90 degrees = 2

Table 3 (pages 106-110): Characters and character states used for the comparison of some Neogene Caribbean Prunum species (adapted from NEHM, 2001, p. 30-31, table 1).

In the Lower Miocene Cantaure Formation of Venezuela Prunum quirosense (F. Hodson, 1927) is much smaller, taller spired, with a more inflated last whorl and less developed callus. Prunum latissimum (Dall, 1896) from the Lower Miocene Baitoa Formation of the Dominican Republic is a smaller, much squatter shell with denticulations on the outer lip.

In summary, Prunum carmengutierrezae is most similar in size and morphology to coeval Lower Pliocene southern Caribbean species (P. springvalensis, P. calypsonis, P. suteri), and they probably form a phylogenetically related group. Most of the Caribbean Neogene Prunum species are highly endemic, known from a single geographical area. For example, of the Dominican species revised by NEHM (2001), all but two are restricted to the Island of Hispaniola; two are also found in the Bowden Beds of Jamaica, but not further afield. This endemism is not unexpected, as all marginelliform gastropods have paucispiral protoconchs, and those in which the development is known are non-planktotrophic (COOVERT & COOVERT, 1995).

Two further Prunum species occur in the Lower Pliocene of the Araya Formation in the lower bed at Cerro Barrigón, Araya Peninsula, mainland Venezuela. Prunum circumvittatum WEISBORD, 1962, originally described from the Lower Mare Formation of the Cabo Blanco Area, has a very robust shell, characterised by its exaggerated callus formation completely enveloping the venter and encircling the dorsum with a thick, broad, elevated ridge of callus. The second, undescribed species (BL coll.), has a large, cylindrical shell, with a strongly depressed spire.

We have adapted NEHMS (2001) table of character states and expanded it to include more Caribbean Neogene Prunum species (Table 3). Some of his character states have been omitted as they are the same in all Prunum species. For example ‘presence of external varix’ and the ‘absence of an anterior sinus’ are common to all the species. We note that NEHM (2001) in his table recorded the anterior sinus as present, strong = 0, but in the descriptions it is absent in all species. This is probably a lapsus. For the aperture shape we prefer to describe the aperture as either: elongate, widening significantly abapically = 0 or narrow, conforms to last whorl = 1. NEHM’S (2001) description of the aperture of P. christineladdae (MAURY, 1917) as ‘semicircular’ is confusing. We have also removed ‘lip shape in cross section’ as we do
not find this helpful.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

*Prunum calypsonis* (Maury, 1925)
Pl. 17, Fig. 4.

1925a **Marginella calypsonis** MAURY, p. 199, pl. 34, figs 12-13.
1925 **Marginella calypsonis** MAURY – MANSFIELD, p. 39, pl. 6, fig. 11.
1969 **Prunum (Egouena) calypsonis** (MAURY) – JUNG, p. 534, pl. 57, figs 9-10.
2010a **Prunum calypsonis** (MAURY, 1925) – LANDAU & SILVA, p. 88, pl. 17, fig. 4.

**Material and dimensions:** Maximum height 21.6 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; seven specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**
Originally described from the Lower Pliocene Springvale Formation of Trinidad, we figure a syntype for comparison (Pl. 17, Fig. 5). *Prunum calypsonis* (Maury, 1925) differs from *P. carmengutierrezae* in being smaller, with the ventral callus more strongly thickened, especially along the outer edge, which forms a thickened callus ring encircling the dorsum and the spire is slightly shorter with the ventral callus more strongly developed on the ventral side of the spire. In this respect it is most like the shell of *Prunum circumvittatum* Weisbord, 1962 described from the Lower Pleistocene Mare Formation of Venezuela (holotype figured here, Pl. 17, Fig. 6), also found in the Aramina Formation at Cerro Barrigón, Araya Peninsula, but the latter has an obovate shape rather than cylindrical, with the callus ring far more strongly developed. Another Venezuelan species with a strongly developed annular callus is *Prunum colinensis* F. Hodson (1927) from the Upper Miocene Caujarao Formation of Falcón (holotype illustrated here, Pl. 17, Fig. 7). Weisbord (1962) stated that the Miocene species differed from *P. circumvittatum* in being swollen longitudinally along the middle of the dorsum. Judging from the specimens found in the Cerro Barrigón assemblage the shells can be somewhat variable, and the ridge seen in the holotype of *P. colinensis* is not so clear in the paratype (PRI 22993). It is quite possible that *P. circumvittatum* is a synonym of *P. colinensis*, present in the southern Caribbean Neogene from the Upper Miocene to the Lower Pleistocene, but we have insufficient material to be certain.

These large *Prunum* specimens with a heavily callused venter were traditionally placed in the subgenus *Egouena* Joussseaume, 1875, however, the development of the callus was considered to be of specific value only by Coovert & Coovert (1995). For comparison with other congeners see Table 3.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Savaneta Glauconitic Sandstone Member of Springvale Formation, Trinidad (Maury, 1925a; H. E. Vokes, 1938; Rutsch, 1942; Jung, 1969).

Family Mitridae Swainson, 1829
Subfamily Mitrinae Swainson, 1829
Genus *Fusimitra* Conrad, 1855.

**Type species** *Mitra conquista* CONRAD, 1848, by subsequent designation, Grant & Gale, 1931.

We use the genus *Fusimitra* Conrad, 1855 at full genus rank for the tropical American species of the *swainsoni*-group. *Mitra Lamarck, 1798 should be used only for Indo-Pacific shells with a barbed or crenulated outer lip* (Geerat Vermeij personal communication, 2009).

*Fusimitra sanctificrancisci* (Maury, 1925)
Pl. 17, Figs 8-11

1925a **Mitra sancti-francisci** MAURY, p. 204, pl. 35, fig. 13.
Mitra cf. limonensis OLSSON – WEISBORD, p. 48, pl. 6, fig. 13.

1938 Mitra (Tiara) woodringi H. E. VOKES, p. 22, fig. 15.

1942 Mitra (Tiara) sancti-francisci MAURY – RUTSCH, p. 160, pl. 8, fig. 6.

1976 Mitra (Fusimitra) limonensis OLSSON, 1922 – CERNOHORSKY (partim), p. 388, pl. 328, fig. 4 (holotype of Fusimitra sanctifrancisci).

2010a Fusimitra sanctifrancisci (MAURY, 1925) – LANDAU & SILVA, p. 89, pl. 17, figs 8-11.

Material and dimensions: Maximum height 75.8 mm, four specimens EDIMAR coll.; 13 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; 20 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:

Fusimitra sanctifrancisci (MAURY, 1925) was originally described from the Lower Pliocene Springvale Formation of Trinidad. Similar to Fusimitra limonensis (OLSSON, 1922; holotype illustrated here Pl. 17, Fig. 12) from the Upper Pliocene Banano Formation of Costa Rica, it was said to differ in having a shell with only five spiral cords on the penultimate whorl whereas F. limonensis had six, in having a more excavated suture and the last whorl has a marked central constriction (MAURY, 1925a). Later, CERNOHORSKY (1976) synonymized the two.

As can be seen in the growth series illustrated from Cubagua (Pl. 17, Figs 4-7), the shells of this species are somewhat variable, the sculpture can be relatively strong to weak, generally becoming weaker in the central portion of the last whorl with ontogeny. The juvenile forms were well illustrated by H. E. VOKES (1938, fig. 15, height 37.8 mm) as Mitra (Tiara) woodringi, which we consider to be a junior subjective synonym of Fusimitra sanctifrancisci [non Mitra woodringi OLSSON, 1964, which is probably a junior subjective synonym of Fusimitra dunbari (OLSSON, 1932)], and by RUTSCH (1942, pl. 8, fig. 6, height 46.9 mm; NMB H6222). In one of the Cubagua fully adult specimens the siphonal faciole is very strongly developed and rounded forming a narrow pseudumbilicus (Pl. 17, Fig. 9).

Despite the shell variability shown, in our opinion, Fusimitra limonensis is somewhat different from F. sanctifrancisci, as rightly pointed out by MAURY (1925a). All the Cubagua specimens have five spiral cords on the penultimate whorl, whereas the figures for F. limonensis given by OLSSON (1922) for the Banano Formation and WOODRING (1964) for specimens from the Middle-Upper Miocene Gatun Formation of Panama clearly have six cords. The other differences stated by MAURY (1925a) also hold true.

Most authors have treated all these taxa as subspecies of Fusimitra swainsoni BRODERIP, 1836 (CERNOHORSKY, 1976; ROBINSON, 1991), however, their relationship is far from clear. It seems more likely that the Pacific and Atlantic lineages are distinct; in the Pacific the shells of the Recent Fusimitra swainsoni are more similar to ones of the Miocene Fusimitra dunbari (OLSSON, 1932) [=M. woodringi OLSSON, 1964 non H. E. VOKES, 1938] from Ecuador and Peru, without spiral sculpture on the middle of the last whorl; whereas the Recent western Atlantic Fusimitra antillensis is more similar to F. limonensis.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1942); Savaneta Glauconitic Sandstone Member of Springvale Formation, Trinidad (MAURY, 1925a; H. E. VOKES, 1938; RUTSCH, 1942); Tuberá Group, northern Colombia (WEISBORD, 1929).

Subfamily Imbricariinae TROSCHEL, 1867
Genus Subcancilla OLSSON & HARBISON, 1953.
Type species Mitra sulcata SWAINSON in SOWERBY, 1825, by original designation.

CERNOHORSKY (1991) placed many species of mitres with strongly sculptured shells into the M. interlirata-erythrogramma species group, and assigned them to “Ziba” in inverted commas. The genus name Tiara is not applicable to this group as Tiara is a subjective synonym of Vexillum RÖDING, 1758. He stressed that the radula of the type species of Ziba, Mitra carinata SWAINSON, 1824, was not known and the relationship of Ziba to either Cancilla SWAINSON, 1840 or Subcancilla OLSSON & HARBISON, 1953
remained obscure (Cernohorsky, 1991). Salisbury (1991) argued that the genus Ziba had been misinterpreted, and that many of the species therein included should be ascribed to Subcancilla. Cernohorsky (1991) commented that the radula of Mitra sulcata was so different from that of the rest of the M. interlirata-erythrogramma species group that they could not all be included under the genus Subcancilla. Keen (1971) also commented on the problematic taxonomic placement of these tropical American species and concluded that although the genus Cancilla could be used, this was based on an Indo-Pacific species, and that it seemed preferable to adopt Subcancilla, which was based on an eastern Pacific species. This argument seems to have been followed also by Petuch (1994, pl. 80, figs E-L), who placed all the mitres with strongly spirally sculptured shells in the genus Subcancilla, although Schmelz (2001) followed Cernohorsky in using the genus Ziba, this time without inverted commas. To further add to the confusion, Davoli (2000) considered Ziba to be a subgenus of Cancilla.

Radular morphology is important in the generic classification of mitrids (Cernohorsky, 1991), but obviously is never available in the fossil record. Whatever the arguments, in the tropical American Neogene to Recent fauna this group includes mitrids with a small to medium-sized shell sculptured with a presutural carina, spiral grooves or cords and axial lirae in the interspaces. This sculpture is quite different from that of the type species of Ziba. Species of Cancilla have similar sculpture, but without the presutural carina. We therefore follow Keen (1971) and use Subcancilla for this group of Tropical American species until further clarification.

Subcancilla couvensis (Maury, 1925)
Pl. 17, Figs 13-15.

1925a Mitra longa couvensis Maury, p. 355, pl. 35, figs 1, 4.
1991 “Ziba” longa (Gabb, 1873) – Cernohorsky (partim), p. 77, pl. 73, fig. 4 (type figure of M. longa couvensis).
2010a Subcancilla couvensis (Maury, 1925) – Landau & Silva, p. 90, pl. 17, figs 13-15.

Material and dimensions: Maximum height (incomplete) 48.1 mm, one specimen NMB lot DS 6917; three specimens EDIMAR coll.; 11 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
The specimens from Cubagua are identical to those found in the Lower Pliocene Springvale Formation of Trinidad (specimen examined NMB H 6219). Although Subcancilla longa (Gabb, 1873) from the Upper Miocene Cercado and Lower Pliocene Gurabo Formations of the Dominican Republic and the Middle-Upper Miocene Gatun Formation of Panama, and Subcancilla couvensis (Maury, 1925) from the Lower Pliocene Springvale Formation were synonymized by Cernohorsky (1991), we have compared the material from Cubagua with numerous specimens of Subcancilla longa longa (BL coll.) and find the Miocene shells consistently more elongated, the last whorl slightly less inflated, the spire slightly less scalate and the spiral sculpture slightly more delicate than in S. couvensis. Admittedly, these differences are subtle, but constant. No closely related species survive today in the western Atlantic, but the Recent Subcancilla gigantea (Reeve, 1844) from the tropical American Pacific region is closely related.

Subcancilla colombiana (Weisbord, 1929) was described from the Atlantic Miocene (now probably Pliocene) of Colombia. The holotype illustrated here (Pl. 17, Fig. 16) is not well preserved, but seems to represent a distinct species with a more slender, fusiform shell, the shoulder on the last whorl is hardly developed, the primary spiral ribs are sharper and there is no secondary spiral sculpture in the interspaces between the primary cords. The adapical columellar fold is remarkably heavy, far more strongly developed than any of the Cubagua specimens of S. couvensis.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Savaneta Glauconitic Sandstone Member of Springvale Formation, Trinidad (Maury, 1925a).
Family     Costellariidae MACDONALD, 1860
Genus     Conomitra CONRAD, 1865.
Type species Mitra fusoides LEA, 1833, by subsequent designation, FISCHER, 1884.

Conomitra caribbeana WEISBORD, 1929
Text-Figure 24, Fig 6; Pl. 18, Figs 1-3

1929     Conomitra caribbeana WEISBORD, p. 48, pl. 6, figs 14-15.
2010a     Conomitra caribbeana WEISBORD, 1929 – LANDAU & SILVA, p. 90, text-fig. 14, fig 6, pl. 18, figs 1-3.

Material and dimensions: Maximum height 14.8 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:

Text-Figure 24. Type specimens of Conomitra species described by F. HODSON (in HODSON & HODSON, 1931) and WEISBORD (1929), Fig. 1. Conomitra lavelana F. HODSON, 1931, holotype PRI 24117, height 11.2 mm, La Vela del Coro, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Fig. 2. Conomitra lavelana F. HODSON, 1931, paratype PRI 24121, height 15.2 mm, La Vela del Coro, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Fig. 3. Conomitra lavelana F. HODSON, 1931, paratype PRI 24118, height 10.8 mm, La Vela del Coro, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Fig. 4. Conomitra lavelana falconensis F. HODSON, 1931, holotype PRI 24119, height 9.7 mm, La Vela del Coro, Falcón, Venezuela, Caujarao Formation, Upper Miocene. Fig. 5. Conomitra weeksi F. HODSON, 1931, holotype PRI 24120, height 12.2 mm, El Mene de Saladillo, Zulia State, Venezuela, La Rosa Formation, upper Lower Miocene. Fig. 6. Conomitra carribeana WEISBORD, 1929, holotype PRI 22953, height 18.4 mm, Tuberá, Colombia, Tuberá Formation, Lower Pliocene. Images courtesy of the Paleontological Research Institution.

Conomitra carribeana WEISBORD, 1929 is characterised by having biconic shells with a rather short spire and a sharp shoulder, placed high on the last whorl. The specimens from Cubagua have 15-19 axial ribs, slightly fewer than that seen in the Colombian holotype (Text-Fig. 24, Fig. 6), and 14-15 spiral cords on the last whorl. Conomitra lavelana F. HODSON, 1931 from the Upper Miocene Caujarao Formation of Venezuela (Text-Fig. 24, Figs 1-3) has a similar number of sculptural elements (ribs 17-23, cords 15-20; F. HODSON in HODSON & HODSON, 1931), but the shell has a higher spire and the shoulder is more rounded. In the same work F. Hodson (F. HODSON in HODSON & HODSON, 1931) described a subspecies C. lavelana falconensis from the same locality (Text-Fig. 24, Fig. 4). This specimen has quite a different shell profile and fewer ribs and cords, and probably represent a different species. RUTSCH (1934) recorded, but did not figure, both C. lavelana and C. lavelana falconensis from the Lower Pliocene Punta.
Gavilán Formation. We have examined about a dozen specimens from this locality (BL coll.), all belonging to *C. caribbeana*. A further species from the upper Lower Miocene (originally ascribed to the Upper Oligocene) La Rosa Formation of Quiróz, Zulia State, Venezuela was named *Conomitra weeksi* F. Hodson, 1931 (Text-Fig. 24, Fig. 5). This species is slightly larger with somewhat finer spiral sculpture. The original description (Hodson & Hodson, 1931) states ‘27 spiral grooves on the body whorl’. Only 17-20 can be counted on the holotype (Text-Fig. 24, Fig. 5). There are no significant differences between this shell and *C. lavelana*, which we consider a synonym. As first revisers (ICNZ, Art. 24.2), we choose the name *C. lavelana* over *C. weeksi*. Jung (1969) figured an incomplete specimen of *Conomitra* from the Lower Pliocene Melajo Formation of Trinidad. Both the apical angle and sculpture fall within the range of *C. caribbeana*.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (BL coll.); ?Melajo Clay Member of Springvale Formation, Trinidad (Jung, 1969); Tuberá Group, northern Colombia (Weisbord, 1929; NMB lot KA 1015).

**Superfamily** Olivoidea LATREILLE, 1825
**Family** Olividae LATREILLE, 1825
**Subfamily** Olivinae LATREILLE, 1825
**Genus** Oliva BRUGIÈRE, 1789
Type species *Voluta oliva* LINNAEUS, 1758, by monotypy and tautonymy.

The use of subgenera within the genus *Oliva* BRUGIÈRE, 1789 is highly controversial. Petuch & Sargent (1986) recognised 19 subgenera (ten were new and five monospecific). Tursch & Greifeneder (2001, p. 70) argued that ‘(…) in their opinion, most (nearly all) of these subgenera are practically useless and must be considered with great suspicion.’. More recently, Hunon et al. (2009) again used subgenera without any further discussion. We provisionally follow Tursch & Greifeneder (2001) and use *Oliva* in its widest sense.

*Oliva immortua* PILSBRY & BROWN, 1917
Pl. 18, Fig. 4

1917 *Oliva sayana immortua* PILSBRY & BROWN, p. 33, pl. 5, fig. 6.
1922 *Oliva sayana var. immortua* PILSBRY & BROWN – Olsson, p. 89, pl. 7, figs 6-7.
1994 *Oliva (Strephona) immortua* PILSBRY & BROWN, 1917 – Petuch, p. 206, pl. 82, fig. I.
2010a *Oliva immortua* PILSBRY & BROWN, 1917 – Landau & Silva, p. 91, pl. 18, fig. 4.

**Material and dimensions:** Maximum height 47.4 mm, six specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**
The close resemblance of several Neogene Caribbean olive species, and the lack of data on their intraspecific variability, makes their distinction difficult and arbitrary. The classification given here is provisional, based on the literature available and comparisons with *Oliva* from other Caribbean fossil localities. The name *Oliva immortua* PILSBRY & BROWN, 1917, originally created for fossils from the Lower Pliocene of Colombia may be available for these specimens, characterized by their very cylindrical shell, shoulder placed high on the last whorl, short, broad spire and well developed columellar plicae, which are often paired. However, we have not examined any Colombian material to confirm this classification.

The Cubagua specimens differs from *Oliva gatunensis* Toula, 1909, widespread in the Middle-Upper Miocene Gatun Formation of Panama, by having a larger size, a more depressed spire, a more cylindrical last whorl, the shoulder hardly slopes and the periphery is placed high on the last whorl, and by having more strongly developed plicae on the columella. Woodring (1964) synonymised *O. immortua* with *O. gatunensis*. However, the Cubagua and Gatun shells should definitely be ascribed to different species, although the name *O. immortua* may not be appropriate for the Cubagua assemblage as discussed.
above. PETUCH (1994) used the name *Oliva (Strephona) immortua* for a shell from the Upper Pliocene Pinecrest Beds (unit 7) of Florida with similar characteristics. The group is in desperate need of taxonomic revision.

A similar species in the Lower Pliocene Gurabo Formation of the Dominican Republic was illustrated by MAURY (1917, pl. 10, figs 16-17) as *Oliva brevispira* GABB. We have examined numerous specimens from the Gurabo Formation (BL coll.), and they all differ from the Cubagua shells in being smaller, squatter, with a more rounded shoulder, a narrower spire, and a wider aperture, more flared abapically. This is not, however *O. brevispira* of GABB (1873), lectotype figured by PILSBRY (1922, pl. 23, fig. 4), which looks like a somewhat worn shell. Maury’s shells should probably be assigned to *Oliva giraudi* COSSMANN, 1913 (lectotype illustrated by PFLUG, 1961, pl. 15, figs 14-15). Similarly, *Oliva cylindrica* SOWERBY of PILSBRY (1922, pl. 23, figs 2-3) is probably also *O. giraudi*. *Oliva giraudi* was described from Martinique, but COSSMANN (1913) wrote that it was identical to the specimens from the Dominican Republic.

**Geological and geographical distribution:**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Tuberá Group, northern Colombia (PILSBRY & BROWN, 1917).

Upper Pliocene: Pinecrest Beds, Florida (unit 7, PETUCH, 1994); Banano Formation, Costa Rica (OLOSSON, 1922).

*Oliva reticularis s.l.* LAMARCK, 1810

Pl. 18, Fig. 5

<table>
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<tr>
<th>Year</th>
<th>Author</th>
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<tbody>
<tr>
<td>1928</td>
<td>Oliva (Oliva) reticularis trochala WOODRING</td>
<td>p. 226, pl. 13, figs 3-5.</td>
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<td>1934</td>
<td>Oliva (Oliva) cf. reticularis LAMARCK – RUTSCH</td>
<td>p. 79, pl. 5, figs 8-11.</td>
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<td>1964</td>
<td>Oliva (Oliva) reticularis LAMARCK, subspecies – WOODRING</td>
<td>p. 277, pl. 45, fig. 15.</td>
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<tr>
<td>2010a</td>
<td>Oliva reticularis s.l. LAMARCK, 1810 – LANDAU &amp; SILVA</td>
<td>p. 92, pl. 18, fig. 5.</td>
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**Material and dimensions:** Maximum height 47.2 mm, three specimens NMB lot DS 6927/1; 15 specimens NMB lot DS 6933; 12 specimens EDIMAR coll.; 16 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**

*Oliva reticularis* LAMARCK, 1810 is a very variable species. The variability in the Recent fauna throughout its geographical range was discussed in depth by TURSCH & HUART (1990). Remnants of the axial zigzag colour pattern are present on some of the specimens from Cubagua. The shells of *Oliva reticularis trochala* WOODRING, 1928 were said to differ from the nominate species by being stouter and having a smoother outline to the spire. Again, a revision of this group is required before these specimens can be identified with confidence.

**Geological and geographical distribution:**


?Upper-Lower Pliocene: Bowden Formation, Jamaica (WOODRING, 1928); Cayo Agua Formation, Bocas del Toro, Panama (WOODRING, 1964).


Upper Pleistocene: La Isabella Formation, Dominican Republic (BL coll.).

Recent: Western Atlantic, Florida to eastern Brazil and the Caribbean (MACSOTAY & CAMPOS, 2001)

*Oliva aff. reticularis s.l.* LAMARCK, 1810

Pl. 18, Fig. 6

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<th>Year</th>
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<th>Citation</th>
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<td>2010a</td>
<td>Oliva aff. reticularis s.l. LAMARCK, 1810 – LANDAU &amp; SILVA</td>
<td>p. 92, pl. 18, fig. 6.</td>
</tr>
</tbody>
</table>
Material and dimensions: One specimen BL coll., height 47.2 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
The single specimen from the Cañon de las Calderas is slightly more elongated than usual for Oliva reticularis s.l. LAMARCK, 1810, with a slightly higher spire and a strongly twisted pillar. A zig-zag colour pattern is just visible, similar to that seen in O. reticularis, and it is possible that this is just a somewhat unusual specimen of this species.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Oliva couvana MAURY, 1925
Pl. 18, Fig. 7

1925a Oliva couvana MAURY, p. 195, pl. 33, fig. 6.
1942 Oliva plicata couvana MAURY – RUTSCH, p. 157, pl. 8, fig. 4.
1969 Oliva (Oliva) couvana MAURY – JUNG, p. 525, pl. 56, fig. 8.
2010a Oliva couvana MAURY, 1925 – LANDAU & SILVA, p. 93, pl. 18, fig. 7.

Material and dimensions: Maximum height 84.3 mm, one specimen NMB lot DS 6927/2; one specimen EDIMAR coll.; seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; four specimens BL coll., (lower yellow fine sandy bed), 10 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
This large Oliva species from the Cañon de las Calderas deposits is characterised by being only moderately thick-shelled for its size, having a tall spire comprised of elevated, slightly concave whorls separated by a deeply canaliculate suture, the last whorl is weakly shouldered, the pillar is weakly twisted and folds are present along the entire inner lip.

Three large Oliva species are known from the Caribbean Neogene. Oliva tuberaensis ANDERSON, 1929 from the Lower Pliocene Tuberá Formation of Colombia has a very broad and solid shell. According to the original description, and specimens examined (BL) in the NMB collection (NMB lots Br. 251 and Br. 443-244) from Las Perdices Formation, Tuberá Group, the shell bears no folds on the adapical part of the columella. The second species, Oliva cristobalcoloni MAURY, 1917, described from the Upper Miocene Cercado Formation of the Dominican Republic, is based on a juvenile shell of Oliva proavia PILSBRY & JOHNSON in PILSBRY, 1922, which, according to WOODRING (1964) grows to a large size (101 mm). This shell is characterized by its elongated form, tall tapering spire, the sloping shoulder and the periphery placed low on the last whorl. We have examined a single specimen of this rare species (height 57.3 mm; BL coll.) from the Lower Pliocene Gurabo Formation of the Dominican Republic. WOODRING (1964) also recorded it from the Upper Miocene middle Gatun Formation of Panama and the Miocene of Mexico. From the little material we have available, this species differs from the Cubagua specimens in being more elongated, with an even taller spire. The pillar is also less twisted. The third species, O. couvana MAURY, 1925 from the Lower Pliocene Springvale Formation of Trinidad, was considered a subspecies of O. cristobalcoloni by WOODRING (1964). The Trinidadian specimens are also elongated, but the spire is usually shorter (specimen NMB 6208 is relatively tall-spired). According to MAURY (1925) it has about 22 folds above the columnellar plaits. The shells from Cubagua correspond most closely to this species. Until the Caribbean Neogene Oliva species are revised, we consider O. couvana and O. cristobalcoloni to be distinct species.

A large olivid is also present in the Lower Pliocene upper and lower beds at Cerro Barrigón, Araya Peninsula, which may be the same species, but we have provisionally excluded them from the synonymy as they have uniformly lower spired and wider shells.

The ‘Lindoliva radiation of species’ described from the Pleistocene of Florida (PETUCH, 1988) is
interesting. It comprises olivids with elongated shells with a tall spire, sloping shoulder and periphery placed low on the last whorl, very similar in fact to O. cristobalcoloni, and also of similar size. The Floridian material is characterized by a colour pattern of reddish flammules. Unfortunately the examined shell from the Gurabo Formation (BL coll.) does not retain its colour pattern. Petuch (1988) described three species within the genus Lindoliva, all sympatric in the Lower Pleistocene Caloosaahatchee Formation Griffin Brother Pit assemblage. The differences between the three species are based on shell size, width of the last whorl and height of the spire, all within the narrow constraints of the generic description. We have examined a relatively large number of specimens from the Griffin Brother Pit (BL coll.) and in our opinion these three taxa represent different growth stages of a single species. The shell profile has been shown to alter with ontogeny in some olivids, which demonstrates an allometric growth pattern (Tursch, 1997; Tursch & Greifeneder, 2001). In olivid shells the height of the spire and the position and shape of the shoulder can change, and a thickened outer lip cannot be taken as an adult characteristic, as specimens can possess a thick lip long before reaching maximum size (Tursch & Greifeneder, 2001). This allometric growth pattern can even be inconsistent within some species (Tursch et al., 1999). As first revisers (ICNZ, Art. 24.2), we choose the name L. diegelae over L. spengeri and L. griffini as the valid name for this spectacular Florida species.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Savaneta Glauconitic and Melajo Clay Member of Springvale Formation, Trinidad (Maury, 1925a; Rutsch, 1942; Jung, 1969).

Oliva sp.
Pl. 18, Fig. 8

2010a Oliva sp. – Landau & Silva, p. 94, pl. 18, fig. 8.

Material and dimensions: Maximum height 38.7 mm, 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; 4 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
These 14 Oliva specimens are rather small, high-spired, with a relatively short aperture, and the pillar is hardly twisted abapically. In shape they are similar to some species of Olivella, but there is no parietal callus. We cannot match our specimens with any known Recent or fossil species, but bearing in mind the difficulties involved in the taxonomy of Recent tropical American olivid species (see Tursch & Huart, 1990), we are reluctant to go further until the Neogene Oliva species have been revised.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Genus Jaspidella Olsson, 1956
Type species Voluta jaspidea Gmelin, 1791, by original designation.

Olsson (1956) showed this genus to belong within the Olividae rather than the Olivellidae based on radular morphology and lack of callus wash along the parietal wall.

Jaspidella jaspidea (Gmelin, 1791)
Pl. 19, Figs 1-2

1791 Voluta jaspidea Gmelin, p. 3442.
1811 Oliva conoidalis Lamarck, 1811, p. 325.
1835 Oliva conoidalis Lam. – Duclos, pl. 2, figs 17-18.
1850 Oliva jaspidea Gmelin – Reeve, pl. 22, fig. 58.
1852 Oliva (Olivella) exigua Mart. - Mörch, no. 2414, p. 130
1867 Oliva piperita Marrat, 1867, p. 214
1883  Olivella jaspidea Gmelin – Tryon, p. 68, pl. 15, figs 91-94.
1954  Olivella jaspidea Gmelin – Abbott, p. 246, pl. 11, fig. i.
1956  Jaspidea jaspidea (Gmelin) – Olsson, p. 212, pl. 15, fig. 1.
1973  Jaspidea jaspidea (Gmelin) – Morris, p. 223, pl. 61, fig. 9.
1974  Jaspidea jaspidea (Gmelin, 1791) – Abbott, p. 233, color plate 11, fig. 2549.
1975  Jaspidea jaspidea (Gmelin, 1791) – Rios, p. 112, pl. 33, fig. 476.
1983  Jaspidea jaspidea (Gmelin, 1791) – H. E. & E. H. Vokes, p. 27, pl. 17, fig. 4.
1988  Jaspidea jaspidea (Gmelin, 1791) – Jong & Coomans, p. 89, fig. 490.
1994  Jaspidea jaspidea (Gmelin, 1791) – Diaz & Puyana, p. 203, fig. 785.
2003  Jaspidea jaspidea (Gmelin, 1791) – Sterba, p. 120, pl. 47, figs 11-15.
2009  Jaspidea jaspidea (Gmelin, 1791) – Rios, p. 277, fig. 694.
2010a Jaspidea jaspidea (Gmelin, 1791) – Landau & Silva, p. 94, pl. 19, figs 1-2.

Material and dimensions: Maximum height 25.1 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion: The Cubagua shells are somewhat larger than the maximum size of extant Jaspidea jaspidea (max 23.0 mm; Malacolog at http://www.malacolog.org/search.php?nameid=5314), and a little broader, but the character of the spire, fasciolar band, pillar and columellar plaits are similar.

Two further Jaspidea species occur in the Caribbean today: Jaspidea blanesi (Ford, 1898) has a much smaller shell with a deeply excavated columella, and Jaspidea miris Olsson, 1956 also has a smaller shell, which is much stockier, with a shorter spire. We have not been able to find any fossil record for J. jaspidea. Jaspidea sanctidominici (Maury, 1917) from the Lower Pliocene Gurabo Formation of the Dominican Republic is immediately distinguished by its smaller, narrower and more elongate shell with a lower spire comprising fewer whorls. Jung (1969, p. 526, pl. 55, fig. 21) recorded this species from the Lower Pliocene Springvale Formation of Trinidad. We have also compared his illustration with J. sanctidominici from the Dominican Republic (BL coll.) and concur that they are indeed synonymous. Weisbord (1962, p. 17-20) described two new Jaspidea species for the Lower Pleistocene Maria Formation of Venezuela: Jaspidea ? praeopsis and Jaspidea caribbeana. The type material illustrated is so poor it is difficult to pass comment on the validity of these taxa.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.
Recent: Florida, Caribbean (Olsson, 1956) to Brazil (Rios, 1975).

Subfamily Ancillariinae Cossmann, 1899
Genus Eburna Lamarck, 1801
Type species E. flavida Lamarck, 1801 (= Buccinum glabratum Linnaeus, 1758), by monotypy.

Eburna caroniana (Maury, 1925)
Pl. 18, Figs 9-11
Material and dimensions: Maximum height 55.6 mm, three specimens NMB lot 6931; eight specimens EDIMAR coll.; 16 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; two specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:

Eburna caroniana (MAURY, 1925) is similar to the Recent Eburna glabrata (LINNAEUS, 1758), which today inhabits the same geographical area: the Margarita Platform and Aruba (VOSKUIL, 1991), but differs by having a more scalate spire, the whorls separated by a deeper sutural canal, by being higher-spired, with more globose whorls, especially the penultimate one, by having a narrower aperture, a narrower, deeper anal canal, which is strongly angled medially, by being slightly more twisted at the pillar, by having several fine folds on the columellar pillar, and by having a relatively well-developed posterior groove, absent in E. glabrata (for terminology see LANDAU & SILVA, 2006). WOODRING (1964) mentioned the extent of the primary spire callus as another distinguishing character; in E. caroniana the callus stops at the posterior groove, whereas in E. glabrata the callus extends further down to the posterior fasciolar groove. The material from Cubagua is identical to that found in the Lower Pliocene Springvale Formation of Trinidad (compared with hypotypes NMB H 6202/1-2; syntype Pl. 18, Fig. 12) and, as in Trinidad, we have also found the smaller, squatter shells MANSFIELD (1925) assigned to Ancilla caroniana springvalensis (hypotype NMB H 6206) (Pl. 18, Fig. 10).

WOODRING (1964, p. 279, pl. 45, figs 1-2) recorded Eburna pinguis (GABB, 1873) from the middle part of the Middle-Upper Miocene Gatun Formation of Panama and said “A. pinguis is practically a miniature replica of A. caroniana(…)”. However, the specimen illustrated shows completely different apertural characteristics; the pillar is nowhere near as twisted, the columella far less excavated and the anal canal is weakly developed, not narrow and medially bent as in E. caroniana. The species Eburna pinguis was originally erected on the basis of material from Jamaica and the paratype illustrated by WOODRING (1928, pl. 14, figs 6-7) is conspecific with the Panamanian specimens.

VOSKUIL (1991) considered that the American ancillariines all belonged to a single clade, probably beginning with an Amalda-like taxon. He suggested an alternative classification and considered the characters of Amalda tankervillii (SWAINSON, 1825) (tendency to form an umbilicus, glossy, bulbous protoconch, placement of ancillid band and groove and orange colouration) similar to those of Eburna LAMARCK, 1801 and placed Amalda as a subgenus of Eburna. We agree with PASTORINO (2003) that the character of the umbilicus of species included in Eburna warrant full generic status.

We note that some of our specimens have spiral sculpture on the spire. This type of sculpture also occurs in other Caribbean congeners such as Amalda lamellata GUPPY, 1866 (spelling corrected from lamelata by MAURY, 1925) from the Middle Miocene Manzanilla Formation of Trinidad. This type of sculpture appears repeatedly in the Ancillariinae, and is strongly developed in some bullet-shaped Australian species placed within the genus Alocospira COSSMANN, 1899. LOZOUET (1992) also described a single species with spiral sculpture from the Oligocene of Europe, and attributed it to the subgenus Alocospira. These taxa are unlikely to represent a monophyletic group and spiral sculpture on the spire obviously evolved several times.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1925a; MANSFIELD, 1925, also as A. caroniana springvalensis; RUTSCH, 1942, also as A. caroniana springvalensis; JUNG, 1969).

Eburna speciosa RUTSCH, 1934
Pl. 18, Fig. 13

1934 Ancilla (Eburna) glabrata speciosa RUTSCH, 1934, p. 78, pl. 5, figs 6-7.
2010a Eburna speciosa RUTSCH, 1934 – LANDAU & SILVA, p. 95, pl. 18, fig. 13.
Material and dimensions: Maximum height 51.1 mm, four specimens BL coll., Lower Pliocene, Araya Formation Cañón de las Calderas, Cubagua Island.

Discussion: Amongst the *Eburna* material from Cubagua are four shells that are somewhat different from the ones discussed above as *Eburna caroniana*, differing by having a regularly elongate-ovate profile, by having a non-scalate spire, the suture marked only by a slight groove in the primary spire callus, by having a smooth pillar without folds, by having no posterior groove, and by having primary spire callus that extends down to the posterior fasciolar groove. In many of these characters it is more similar to the Recent *Eburna glabrata* (LINNAEUS, 1758) than to *E. caroniana* characters, but in *E. glabrata* the shell profile is less evenly ovate, the spire is shorter and the aperture wider. RUTSCH (1934) described *Ancilla (Eburna) glabrata speciosa* from the Lower Pliocene Punta Gavilán Formation of Venezuela, differing from *E. glabrata* in having a shell with exactly these characters. We have examined the holotype (NMB H 1904, NMB lots DS 5627, DS 5678, DS 5441-2) and two specimens from the Punta Gavilán Formation (BL coll.); the holotype and one of the specimens differ from the Cubagua shells in being more elongated, with a higher spire, whereas the second specimen from Punta Gavilán is broader with a spire height similar to that seen in the Cubagua shells.

It seems, therefore that *E. caroniana* and *E. speciosa* occur together, at least in the Araya Formation and restricted to the southern Caribbean Lower Pliocene. The genus in the Neogene was represented further north by a distinct species, *E. pinguis*. Today the genus is represented in the Caribbean by three species, all of which seem to have a very restricted geographical distribution: *Eburna balteata* (SWAINSON, 1825), endemic to Aruba, *E. glabrata* from the Margarita Platform and Aruba, and *Eburna lienardi* (BERNARDI, 1858) from Aruba and the northeastern coast of Brazil (VOSKUIL, 1991). Although *E. speciosa* is the most similar to *E. glabrata*, and may be ancestral to the Recent species, the shell shape is quite different and we prefer to consider it a distinct species.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).

Superfamily    Cancellarioidea FORBES & HANLEY, 1851
Family     Cancellariidae FORBES & HANLEY, 1851
Subfamily    Cancellariinae FORBES & HANLEY, 1851
Genus    Cancellaria LAMARCK, 1799.
Type species *Voluta reticulata* LINNAEUS, 1767, by original designation.

*Cancellaria (Cancellaria) capeloi* LANDAU, PETIT & SILVA, 2007
Pl. 19, Figs 3-4

Material and dimensions: Maximum height 32.7 mm, holotype; MOBR-M-3359, height, 22.8 mm EDIMAR coll.; paratype 1, height, 30.9 BL coll.; paratype 2, height, 24.6 mm MOBR-M-3360 EDIMAR coll.; paratype 3, height, 20.6 mm BL coll., five further specimens EDIMAR coll.; 17 specimens BL coll., Lower Pliocene, Araya Formation Cañón de las Calderas, Cubagua Island; five specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Original description: “Shell small to medium-sized, solid, ovate, with a medium mesh reticulate sculpture, of which the axial component is slightly stronger. Protoconch missing in all specimens. Teleoconch consists of 4.5-5 weakly convex whorls, with the periphery at the abapical suture. Suture deeply impressed and narrowly canaliculated, giving the spire a somewhat scalate appearance. Sculpture on first teleoconch whorls eroded in all specimens. On the third whorl spiral sculpture consists of five subequal cords, slightly narrower than...
their interspaces. Axial sculpture consists of about 22 strongly prosocline cords, slightly narrower than their interspaces. The spiral sculpture overrides the axial ribs forming tubercles at the intersections, varices absent. Whorl surface covered by fine prosocline growth lines. Last whorl inflated, regularly convex, with twelve spiral cords above the siphonal fasciole, 26-30 axial ribs, and weakly constricted behind the fasciole. Aperture approximately 50% of total height, sub-oval and elongate. Outer lip simple, not thickened by labial varix, weakly prosocline in profile, stromboid notch absent. Lip with a crenulate edge, strongly and deeply lirate within, but the lirae do not extend to the outer edge. Anal canal poorly developed; siphonal canal short, narrow and slightly recurved. Columella bears three non-bifid folds, the adapical fold largest, overlying the siphonal fasciole. Parietal callus thin, adherent onto the ventral aspect of the last whorl, the whorl sculpture visible through the callus. Columella callus thicker, detached forming the medial wall of the umbilical chink. Siphonal fasciole well developed, narrow, rounded and elevated, bearing four or five spiral cords. Umbilical chink relatively wide and deep for genus (Landau et al., 2007a, p. 29)."

**Discussion:**

Although *Cancellaria s.s.* usually has a bifid adapical columellar fold, some species characterized by shells lacking that feature, but possessing the other characters of the nominate subgenus, are considered to be part of the nominate subgenus. Several such species were so treated by Jung & Petit (1990).

Several American Neogene Caribbean taxa; *Cancellaria (Cancellaria) barretti* Guppy, 1866, *Cancellaria (Cancellaria) guppyi* Gabb, 1873, *Cancellaria (Cancellaria) petiti* Olsson, 1967, *Cancellaria (Cancellaria) acalypta* Woodring, 1970 are immediately distinguished from *C. (C.) capeloi* Landau, Petit & Silva, 2007 in having a clearly bifurcate adapical columellar fold. The shell of *Cancellaria (C.) harrisi* Maury, 1917, from the Upper Miocene Cercado Formation of the Dominican Republic, which shows a bifid adapical fold, although only slightly so at its terminal portion, is similar in size and shape, but is more elongated and the whorls shouldered close to the suture. *Cancellaria epistomifera sathra* Woodring, 1973 (new name for *C. e. lipara* Woodring, 1970) (Woodring, 1973, p. 481) from the Upper Gatun Formation of Panama is similar to the new species with a scalate spire and slightly umbilicate, these features far more prominent in *C. (C.) capeloi* but differs in having a weakly bifid abapical fold, and being more constricted at the base. We do not consider *C. epistomifera sathra* to be a subspecies of the *C. epistomifera*, widespread in the Dominican Republic Neogene (Jung & Petit, 1990), which is quite different, with a non scalate spire, a far more globose last whorl and flaring outer lip with a deep stromboid notch.

*Cancellaria (Cancellaria) dariena* Toula, 1909 is a *Cancellaria s.s.* with a shell showing a narrow, slightly bifid adapical fold. This species was described from the Gatan area of Panama, and is not particularly similar to *C. (C.) capeloi*, the greatest difference seen at the base, where *C. dariena* is far more constricted with the umbilicus poorly developed, also the posterior fold is much sharper and bifid.

Weisbord (1929, pl. 6, fig. 8) figured a specimen as *Cancellaria dariena* Toula, 1909 from the Tubará Group of Colombia, which is not conspecific with the Gatan taxon. The Colombian specimen seems to have a non-bifurcate adapical fold. Most of the Tubará specimens are stated by Weisbord (1929, p. 282) to have a thickened varix at the outer lip or “about the middle of the body whorl in back,” a feature not seen in *C. (C.) capeloi*. Although the Tubará shell assigned to *C. dariena* is extremely close to *C. (C.) capeloi*, it has slightly fewer axial ribs, less evenly reticulated sculpture and the spire is less scalate.

Of the Lower Miocene species of *Cancellaria s.s.* with a non-bifid adapical fold, *Cancellaria (Cancellaria) rowelli* Dall, 1896 from the Baitoa Formation of the Dominican Republic has a shell with a taller spire, somewhat finer sculpture, the last whorl strongly constricted behind the siphonal fasciole and although the fasciole is also well developed, the umbilicus is narrower than in *C. (C.) capeloi*. *Cancellaria (Cancellaria) hodsonae* Landau & Petit, 1997 from the Cantaure Formation of Venezuela is even more elongate, taller spired, with strong spiral sculpture at the shoulder.

Two further species with non-bifurcate columellar folds occur in the Upper Miocene Cercado Formation of the Dominican Republic; *Cancellaria (Cancellaria) mauryae* Olsson, 1922 and *Cancellaria (Cancellaria) juneta* Jung & Petit, 1990. Both have larger and thinner shells, with a more inflated body
BERNARD M. LANDAU

whorl, a much finer sculpture, a much less elevated the siphonal fasciole, and a very small umbilical chink.

WEISBORD (1962) described Cancellaria torula from the Lower Mare Formation, Middle Pliocene of Venezuela. The type material consisted of a single incomplete and very poorly preserved juvenile specimen. WEISBORD (1962, p. 398) distinguished this mutilated Cancellaria shell from its congeners on the basis of a “strong, irregularly thickened, Distorsio-like ridge on the parietal wall”. GIBSON-SMITH & GIBSON-SMITH (1979) placed C. torula in the synonymy of Cancellaria reticulata (LINNAEUS, 1767) on the basis of the fact that the parietal ridge that WEISBORD (1962) used to differentiate C. torula from C. reticulata and other Cancellaria s.s. was absent in an adult specimen but present in a juvenile collected by the Gibson-Smiths. They declared the ridge to be an “intermittent resting stage in the juveniles but is absent in the adults” (GIBSON-SMITH & GIBSON-SMITH, 1979, p. 26). This ridge is indeed present in juvenile shells of C. reticulata, and a trace of one is present in some adult specimens (Petit pers. obs.). On the basis of the specimen illustrated by WEISBORD (1962), it is impossible to say with any certainty what is meant by C. torula, however, the posterior ridge is finer than that seen in C. capeloi (although Weisbord’s shell is probably juvenile), and the parietal ridge is not present in any of the Cubagua shells, even at the juvenile stage. The GIBSON-SMITH & GIBSON-SMITH (1979) Mare material of Cancellaria (C.) torula is not available but, based on sculpture visible on the type figure of C. torula, the specimen is unlikely to be conspecific with C. reticulata, and possibly closer to C. capeloi. Due to the fact that C. torula has been formalized on a single incomplete and very poorly preserved juvenile specimen, we consider the Weisbord taxon to be a nomen dubium. Moreover, few species are common to both Mare and Cubagua. The supposed conspecificity of C. torula and C. reticulata argues against uniting it with C. capeloi which cannot be confused with C. reticulata.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Cancellaria (Cancellaria) sp.
Pl. 19, Fig. 5

2007a Cancellaria (Cancellaria) ssp. – LANDAU et al., p. 32, figs 7-16.
2010a Cancellaria (Cancellaria) sp. – LANDAU & SILVA, p. 96, pl. 19, fig. 5.

Material and dimensions: Maximum height 47.0 mm, one specimen BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; five specimens BL coll., (lower yellow fine sandy bed), two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
We have eight shells from the Araya Formation tentatively placed in the nominate subgenus; all have a bifurcated posterior columellar fold except for one (LANDAU et al. 2007a; Figs 7-8). One is from Cañon de las Calderas and the other seven from the Aramina Formation of Cerro Barrigón on the Araya Peninsula, five from the ‘lower bed’ (LANDAU et al. 2007a; Figs 7-8, 9-10 and 13-14), two from the ‘upper bed’ (LANDAU et al. 2007a; Fig. 11-12). All five specimens are slightly different, and a short description of each was given by LANDAU et al. (2007a).

Although the sculpture weakens considerably on the last whorl of most of these shells, as seen in the subgenus Pyrula, the posterior columellar fold is bifid in seven of the eight shells and not large and broadly divided, giving the appearance of an additional fold, as in Pyrula (JUNG & PETIT, 1990).

Compared to other Caribbean taxa with fusiform rather than pyriform shells; Cancellaria (Pyrula?) uva JUNG & PETIT, 1990 from the Lower Miocene, Baitoa Formation of the Dominican Republic has closely packed axial cords on the early whorls, similar to specimen 5 (of LANDAU et al. 2007a), but the axial ribs disappear at the end of the penultimate whorl and the spiral sculpture is subobsolete on the last whorl, the shell shape is similar to specimen 1 (of LANDAU et al. 2007a). Cancellaria (Pyrula?) laevescens GUPTY, 1866 is closely similar in shell shape to specimen 1 (of LANDAU et al. 2007a), with a similar number of ribs on the fourth whorl as specimens 2-4 (of LANDAU et
al. 2007a), which persist until the end of the penultimate whorl. All the Pliocene Pacific species from Ecuador; C. (P.?) lacondamini, C. (P.?) picta, C. (P.?) telemba all OLSSON, 1964 have shells with lower-spires and more globose last whors.

Our series of shells is similar to the Recent eastern Pacific group comprising Cancellaria (Cancellaria) obesa SOWERBY, 1832 and Cancellaria (Cancellaria) ovata SOWERBY, 1832, our broader shells with smooth last whors similar to the former, the more fusiform shells with spiral sculpture persisting on the last whorl to the latter. The Pacific Pleistocene Cancellaria (Cancellaria) coronadoensis DURHAM, 1950, which is not consistently different from the Recent Pacific C. (C.) obesa SOWERBY, 1832, is similar to our specimen 1, but the axial sculpture is much finer, and confined to the early teleoconch whors.

With the scant material from the Cubagua Formation available to us we are unable to conclude if we are dealing with a single variable taxon or several distinct sympatric species. Nevertheless, these shells again reflect the strongly paciphile character of the Cubagua cancellarid fauna.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Genus Bivetopsia JOUSSEAUME, 1887.
Type species Cancellaria chrysostoma SOWERBY, 1832, by subsequent designation, COSSMANN, 1888.

LANDAU et al. (2007a) adopted a rather conservative approach in considering many of the cancellarid supra-specific taxa as subgenera of Cancellaria. In this work we elevate their rank to full genus. As discussed by BEU (2009, p. 131), ranking groups as subgenera of another group expresses a phylogenetic hypothesis about their relationship, which, at the moment within cancellarids cannot be proven, and that narrower taxa are more likely to be monophyletic than broader ones.

Bivetopsia pachia (M. SMITH, 1940)
Pl. 19, Fig. 6

1940 Cancellaria chrysostoma SOWERBY, 1832, p. 45, pl. 2, fig. 2.
2007a Cancellaria (Bivetopsia) pachia M. SMITH, 1940 – LANDAU et al., p. 35, figs 20-22.
2010a Bivetopsia pachia (M. SMITH, 1940) – LANDAU & SILVA, p. 97, pl. 19, fig. 6.
non 1994 Bivetopsia pachia (M. SMITH, 1940) – PETUCH, p. 222, pl. 90, fig. C.

Material and dimensions: Maximum height 27.2 mm, one specimen EDIMAR coll.; 14 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; eight specimens BL coll. (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:
The characteristics of the subgenus Bivetopsia JOUSSEAUME, 1887 were discussed by JUNG & PETIT (1990), similar to Bivetiella WENZ, 1943, but usually smaller shelled, without a stromboid notch at the outer lip, and the last whorl strongly constricted behind a well developed siphonal fasciole.

Although JUNG & PETIT (1990) cited Bivetopsia pachia (M. SMITH, 1940) as a subspecies of B. moorei (GUPPY, 1866) they are separate species. Bivetopsia moorei has a shell with a more attenuate profile lacking the strong shoulder and thickened out lip of B. pachia. However, the major and most easily noted difference is the presence of wider spiral cords on the shells of B. pachia, all of which are bifurcated by a deep narrow groove, a feature not prominent in other species. Bivetopsia plecticis (JUNG & PETIT, 1990) has even heavier spiral cords with multiple grooves. The Recent species Bivetopsia rugosa (LAMARCK, 1822), distinguished by its rounded form and low sculpture, also has grooves in the spiral cords but they are neither as pronounced nor prominent as they are in the shells of other species and are sometimes absent on most of the cords. The specimen figured by PETUCH (1994, pl. 90, fig. C) as Bivetopsia pachia does not correspond to that species and cannot be clearly identified from the illustration, but it appears to be a shell of either B. rugosa or of a very closely related unnamed species.
The genus *Bivetopsia* is American, the few known species confined to the Neogene of Florida, the Caribbean and Ecuador, and the Recent fauna of the Caribbean and the Panamic-Pacific provinces. CAHUZAC et al. (2004) suggested *Scalptia spinosa* (GRATELOUP, 1827) from the Lower Miocene of Landes, France, had some features of this taxon, but the shell shape and aperture characteristics are not those of *Bivetopsia*. The group first appeared in the Lower Miocene Cantaure Formation of Venezuela, represented by *Bivetopsia herberti* LANDAU, PETIT & SILVA, 2007, which differs from both *B. pachia* and *B. moorei* in being smaller, squatter, with a more depressed spire, with fewer axial ribs, a similar number of spiral cords, but with a secondary cord in some of the interspaces and the suture is less depressed and not canaliculated. The Cantaure specimen is more similar in shape to the Recent *Bivetopsia chrysostoma* SOWERBY, 1832, type species of *Bivetopsia*, but the umbilicus is wider and the suture again somewhat canaliculated in the Recent species. The presence of *B. pachia* in Cubagua is interesting, making it one of the most long-lived Caribbean Neogene cancellarids, Early Pliocene to Pleistocene, with a wide geographical distribution. Only *Extractrix hoerlei* OLSSON, 1967 has a wider distribution in the Pliocene, reported from the Lower Pliocene of Punta Gavlán, mainland Venezuela (JUNG, 1977) and the Lower-Middle Pliocene of Virginia, USA (CAMPBELL, 1993).

**Geological and geographical distribution:**

**Genus** *Euclia* H. & A. ADAMS, 1853.
**Type species** *Cancellaria cassidiformis* SOWERBY, 1832, by subsequent designation, COSSMANN, 1899.

*Euclia codazzii* (ANDERSON, 1929)
Pl. 19, Fig. 7

1929 *Cancellaria codazzii* – ANDERSON, p. 116, pl. 14, figs 4-7.
1929 *Cancellaria karsteni* – ANDERSON, p. 114, pl. 10, figs 7-9.
1929 *Cancellaria hettneri* – ANDERSON, p. 114, pl. 10, figs 5-6.
1960 *Cancellaria codazzii* ANDERSON – BARRIOS, p. 291, pl. 11, fig. 5.
1969 *Cancellaria* (Euclia) cf. *codazzii* ANDERSON – JUNG, p. 541, pl. 58, fig. 8.
1993 *Cancellaria* (Euclia) *codazzii* ANDERSON – PITT & PITT, p. 6, pl. 2, fig. 10.
2010a *Euclia codazzii* (ANDERSON, 1929) – LANDAU & SILVA, p. 97, pl. 19, fig. 7.

**Material and dimensions:** Maximum height 48.6 mm, one specimen NMB lot 9179; one specimen EDIMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
As discussed by WOODRING (1970), the shells of this species are very variable, with the angulation at the shoulder of the last whorl and the spines more or less developed. WOODRING (1970) considered *Euclia karsteni* (ANDERSON, 1929) and *Euclia hettneri* (ANDERSON, 1929) to be synonyms of *Euclia codazzii*. As first reviser he selected the name *C. codazzii* as the senior synonym, considering the other two nominal species to represent variability extremes. WOODRING (1970) also included in his synonymy *Euclia maldonadoi* OLSSON, 1964 from the Pacific Upper Miocene Angostura Formation of Ecuador. That synonymy was not accepted by JUNG & PETIT (1990) as *E. maldonadoi* has a rounded body whorl whereas the shells of *E. codazzii* have a sharp shoulder with a flat or concave area posterior to the shoulder. Our specimens from Cubagua have a flat or concave shoulder posterior to the angled shoulder and match the type specimen of *E. codazzii*.

The genus *Euclia* H. & A. ADAMS, 1854 is characterized by having swollen axial ribs on the last whorl with a tendency to form nodules at the shoulder. Both *Euclia* and *Pyrucilia* OLSSON, 1932 represent species groups which were present in the Neogene Caribbean but are now restricted to the Pacific. In this
particular case the lineage starts in the Early Miocene with *Euclia werenfelsi* JUNG, 1965 from the Cantaure Formation of Venezuela. This is a species with a relatively small, elongated shell, with fine axial sculpture and relatively well-developed spines at the shoulder. *Euclia codazzi* is then present in both the Atlantic and Pacific in the Late Miocene giving rise to the Pacific Tropical American species of *Euclia* of which *Euclia balboae* PILSBRY, 1931 is the most similar, but differs in having fewer axial ribs on the spire whorls (WOODRING, 1970). The shell of the more common Pacific Pleistocene to Recent *Euclia cassidiformis* SOWERBY, 1832 is larger, more spinose and has angular spire whorls as well on the last whorl.

*Cancellaria epistomifera acuticarinata* WEISBORD, 1929 (holotype Pl. 19, Fig. 8) was based on a small incomplete shell. It is very similar to *Euclia codazzi* (ANDERSON, 1929), and possibly conspecific. If this were the case the name *Euclia acuticarinata* would take priority, as Weisbord’s work is dated January 8th, 1929, whereas Anderson’s is dated March 29th, 1929. Until better-preserved material from Colombia is available we prefer to keep the well-established name *C. (E.) codazzi*.

**Geological and geographical distribution:**

- **Middle Miocene:** lower Gatun Formation, Panama (WOODRING, 1970).
- **Upper Miocene:** middle Gatun Formation, Panama (WOODRING, 1970).
- **Lower Pliocene:** Araya Formation, Cubagua Island, Venezuela (LANDAU et al., 2007a); Tuberá Group, northern Colombia (ANDERSON, 1929; BARRIOS, 1960); Melajo Clay Member of Springvale Formation, Trinidad (JUNG, 1969).

**Euclia leuzingeri** (RUTSCH, 1934)

Pl. 19, Fig. 9

<table>
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<th>Year</th>
<th>Cancellaria species</th>
<th>Reference</th>
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<td>1934</td>
<td>C. reticulata leuzingeri</td>
<td>RUTSCH, p. 89, pl. 7, figs 10-11, pl. 8, figs 1, 2, 5.</td>
</tr>
<tr>
<td>2007a</td>
<td>Cancellaria (Euclia) leuzingeri</td>
<td>RUTSCH, 1934 – LANDAU et al., p. 37, figs 29-31.</td>
</tr>
<tr>
<td>2010a</td>
<td>Euclia leuzingeri</td>
<td>RUTSCH, 1934 – LANDAU &amp; SILVA, p. 97, pl. 19, fig. 9.</td>
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</table>

**Material and dimensions:** Maximum height 55.4 mm, four specimens NMB lot 6921; 14 specimens EDIMAR coll.; 12 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; 14 specimens BL coll., (lower yellow fine sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

*Euclia leuzingeri* (RUTSCH, 1934) is common at both its type locality, at Punta Gavilán, and at Cañón de las Calderas, but has not been found outside of Venezuela. Originally described as a subspecies of *Cancellaria reticulata* (LINNAEUS, 1767), the affinity between the two is superficial. The adapical columellar fold in *C. reticulata* is bifurcate, a character of *Cancellaria s.s.* The form of the columellar folds and the shell outline clearly place *E. leuzingeri* in the genus *Euclia*. The species is very close to the Recent *Euclia laurettae* PETIT & HARASEWYCH, 1998 from bathyal depths in the Golfo de Chiriqui, Panama (Pacific). A characteristic of the shells of most species of the subgenus is the “stretched out” shape of the aperture.

PETIT & HARASEWYCH (1998, p. 113) listed the Cenozoic and Recent species of *Euclia* known from Panamic faunas, as well as Cenozoic species from the Caribbean, where the subgenus no longer occurs (i.e., a paciphile genus). Unfortunately *E. leuzingeri* was omitted from that list.

**Geological and geographical distribution:**

- **Lower Pliocene:** Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (LANDAU et al., 2007a); Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).

**Euclia montserratensis** (MAURY, 1925)

Pl. 19, Fig. 10

<table>
<thead>
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<th>Year</th>
<th>Cancellaria species</th>
<th>Reference</th>
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<td>1925a</td>
<td>Cancellaria montserratensis – MAURY, p. 346, pl. 35, figs 6, 8.</td>
<td></td>
</tr>
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1925a  Cancellaria epistomifera  GUPPY – MAURY, p. 345, pl. 35, fig. 7 (non  C. epistomifera GUPPY, 1876).
1925  Cancellaria springvalensis – MANSFIELD, p. 31, pl. 2, fig. 12.
1938  Cancellaria (Cancellaria) couvana H. E. VOKES, p. 20, fig. 21.
1942  Cancellaria montserratensis MAURY – RUTSCH, p. 163, pl. 9, fig. 7.
1969  Cancellaria (Euclia) montserratensis MAURY – JUNG, p. 539, pl. 58, figs 6-7.
2007a  Cancellaria (Euclia) montserratensis MAURY, 1925 – LANDAU et al., p.37, figs 32-34.
2010a  Euclia montserratensis (MAURY, 1925) – LANDAU & SILVA, p. 97, pl. 19, fig. 10.

**Material and dimensions:** Maximum height 41.8 mm, two specimens NMB lot 9179; 14 specimens EDIMAR coll.; Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; two specimens BL coll., (lower yellow fine sandy bed), 10 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrígón, Araya Peninsula.

**Discussion:**

Euclia montserratensis (MAURY, 1925) is one of the commoner cancellarids found at Cañon de las Calderas. It is easily distinguished from Euclia codazzii (ANDERSON, 1929), which has a shell with a less scalate spire, finer spiral sculpture, less angular whorls, with the shoulder placed further from the suture. MAURY (1925) compared it to Cancellaria harrisi MAURY, 1917, from the Miocene of the Dominican Republic, but this is a much smaller shell with finer sculpture.

**Geological and geographical distribution:**

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (LANDAU et al., 2007a); Tuberá Group, northern Colombia (ANDERSON, 1929; BARRIOS, 1960); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1925; MANSFIELD, 1925; H. E. VOKES, 1938; RUTSCH, 1942; JUNG, 1969).

Genus  Pyruclia OLSSON, 1932.

Type species Cancellaria solida SOWERBY, 1832, by original designation.

**Pyruclia schebei (ANDERSON, 1929)**

Pl. 20, Fig. 1-2

1929  Cancellaria schebei ANDERSON, p. 115, pl. 10, figs 1-4.
2007a  Cancellaria (Pyruclia) schebei ANDERSON, 1929 – LANDAU et al., p.37, figs 35-37.

**Material and dimensions:** Maximum height 77.2 mm, one specimen NMB lot DS 32; three specimens EDIMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; six specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrígón, Araya Peninsula.

**Discussion:**

Pyruclia schebei (ANDERSON, 1929) is not uncommon at Cañon de las Calderas, where the shells reach a large size, but are rarely complete. Although the deep sutural canal is not evident in the figure of the holotype (ANDERSON, 1929, pl. 10, figs 1-2), our specimens match the original description, also having weak axial sculpture confined to the first two to three teleoconch whorls. WOODRING (1970) described a very close species based on a single shell from the upper part of the Gatun Formation of Panama, Pyruclia diadela, said to differ in having a lower spire and a more angular last whorl. The height of the spire and strength and position of the shoulder is rather variable in the Cubagua specimens and, therefore, LANDAU et al. (2007a) consider the latter a junior synonym of P. schebei.

JUNG & PETIT (1990) discussed the characters of the genus Pyruclia, and stressed that only the species with a pyriform shell could be assigned to it with certainty. Pyruclia schebei is somewhat unusual
and can easily be distinguished from its congeners by the extremely wide and deeply channelled sutural canal. The *Pyurclia s.s.* species group seems to have appeared in the Late Miocene simultaneously on both sides of the Central American Seaway, and survived in the Atlantic only into the earliest Pliocene. Today it is represented in the Pacific by two species; *Pyurclia solida* Sowerby, 1832 and *Pyurclia bulbulus* Sowerby, 1832. *Pyurclia solida* is the most similar, but lacks the deep sutural canal.

**Geological and geographical distribution:**
Upper Miocene: upper Gatun Formation, Panama (Woodring, 1970).
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (Landau et al., 2007a); Tuberá Group, northern Colombia (Anderson, 1929).

**Genus** *Massyla* H. & A. Adams, 1854.
Type species *Cancellaria corrugata* Hinds, 1843, by monotypy.

*Massyla cubaguensis* Landau, Petit & Silva, 2007

Pl. 20, Figs 3-4

2007a *Cancellaria (Massyla) cubaguensis* Landau, Petit & Silva, p. 38, figs 38-44

**Material and dimensions:** Maximum height 33.7 mm, holotype; MOBR-M-3363, 25.9 mm EDIMAR coll.; paratype 1, MOBR-M-3364, height, 22.4 mm EDIMAR coll.; one specimens EDIMAR coll.; seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; three specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Original description:**
“Protoconch missing. Teleoconch consists of 5.5 convex whorls, with the periphery at the abapical suture. Sculpture on the first two teleoconch whors worn. Sculpture on the third teleoconch whorl consists of five prominent subequal spiral cords, equal in width to their interspaces, and close-set, strongly prosocline axial lamellae. The number of spiral cords increases abapically, seven on the penultimate whorl, 14–16 on the last whorl, and the axial lamellae become more prominent, about 25 on the last whorl, developing into broad axial folds on the last half whorl. The strength of the axial sculpture is variable, relatively strong in the holotype, giving the last whorl a reticulate appearance, but with the spiral cords predominant, whereas the axial sculpture is much weaker in the paratype. The whole shell surface is covered by very close-set prosocline growth lines. Suture well rounded and deeply impressed. Last whorl strongly inflated, rounded, somewhat barrel-shaped, with the periphery just above mid-whorl, hardly constricted behind the siphonal fasciole. Aperture ovate, outer lip prosocline, thickened by labial varix, strongly and deeply lirate within. Columella straight, with two strong folds, the adapical one much larger, which extends almost to the edge of the thick, well-developed, sharply delimited parietal callus, which is expanded some distance onto the ventral portion on the last whorl, behind which there is a moderately small but deep umbilicus. Siphonal fasciole broad and well developed, bearing six to seven close-set, rounded spiral cords. Siphonal canal extremely short and slightly recurved. The adapical portion of the outer lip bears a strong fold apressed to the body whorl, forming a small anal canal (Landau, Petit & Silva, 2007a, p. 38)”.

**Discussion:**
The Lower Pliocene *Massyla cubaguensis* Landau, Petit & Silva, 2007 is closely related and probably descended from the *Massyla cantaurana* Landau & Petit, 1996 from the Lower Miocene Cantaure Formation of Venezuela, but has a larger shell, the spire is squatter, the axial sculpture weaker, the spiral cords stronger, the parietal callus more strongly developed and the siphonal fasciole broader. *Massyla lopezana* Jung & Petit, 1990 from the Lower Miocene, Baitoa Formation of the Dominican Republic is of similar size and also has a low spire, however it differs from *M. cubaguensis* in having finer, more numerous spiral cords, the parietal callus is less developed, the siphonal canal is narrower and more elevated, the last whorl constricted behind the fasciole, and the siphonal canal much longer. *Massyla*
jadisi OLSSON, 1964 from the Upper Miocene Angostura Formation of northwestern Ecuador is also closely similar, with a low spire and a very short siphonal canal, however it differs mainly in the shape of the last whorl, which is more rounded, the periphery at rather than above mid-whorl and more constricted behind the siphonal fasciole. The holotype of *M. jadisi* has a parietal callus consisting only of a weak wash as contrasted to the heavy and well-defined callus of *M. cubaguaensis*. The Floridian Neogene species, such as *Massyla venusta* (TUOMEY & HOLMES, 1856) and *Massyla propevenusta* (MANSFIELD, 1933) all have shells with much longer siphonal canals.

The genus *Massyla* H. & A. ADAMS, 1854 was well represented and diversified in the Caribbean Neogene, but disappeared from the Atlantic during the Pliocene. Two Recent species occur in fairly shallow water in the southern part of the Panamic-Pacific Province, *Massyla corrugata* HINDS, 1843 and *Massyla obtusa* DESHAYES, 1830. There is a third nominal species, *Massyla cumingiana* (PETIT DE LA SAUSSAYE, 1844) that is probably a synonym of *M. obtusa*.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela (LANDAU et al., 2007a).

**Genus Charcalleria OLSSON, 1942.**
Type species *Cancellaria (Charcalleria) perdiciana* OLSSON, 1942, by original designation.

*Charcalleria terryi* OLSSON, 1942

1942 *Cancellaria (Charcalleria) terryi* OLSSON, p. 62, pl. 8, fig. 1.
1964 *Cancellaria (Charcalleria) sp. – OLSSON, p. 124, pl. 22, fig. 1.
1964 *Cancellaria (Charcalleria) terryi* OLSSON – OLSSON, p. 124, pl. 22, fig. 2.
1965 *Cancellaria (Charcalleria) terryi* OLSSON – JUNG, p. 556, pl. 75, figs. 17-19.
1970 *Cancellaria (Charcalleria) terryi* OLSSON – WOODRING, p. 343, pl. 54, figs 5, 6, 9, 10.
2007a *Cancellaria (Charcalleria) terryi* OLSSON – LANDAU et al., p. 40, figs 45-46.
2010a *Charcalleria terryi* OLSSON, 1942 – LANDAU & SILVA, p. 99, pl. 20, figs 5-6.

**Material and dimensions:** One specimen BL coll., 46.0 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
Our single shell from Cubagua is worn and does not show the axial ribs clearly, but the reticulate sculpture seen in the holotype from the Pacific Charco Azul Group, Penita Formation of Costa Rica (Pl. 20, Fig. 6) is preserved towards the outer lip in the Cubagua specimen. See LANDAU et al. (2007a, p. 40).

**Geological and geographical distribution: Atlantic**
Lower Miocene: Cantaure Formation, Venezuela (JUNG, 1965).
Middle Miocene: lower Gatun Formation, Panama (OLSSON, 1964; WOODRING, 1970).

**Geological and geographical distribution: Pacific**

**Genus Trigonostoma BLAINVILLE, 1827.**
Type species *Delphinula trigonostoma* LAMARCK, 1822, by monotypy.
Subgenus *Ventrilia* JOUSSEAUME, 1887.
Type species *V. ventrilia* JOUSSEAUME, 1887, by monotypy.
Trigonostoma (Ventrilia) rucksorum (Peturuch, 1994)

Pl. 20, Fig. 7

1994 Ventrilia kissimmeensis Petuch, 1994, p. 350, pl. 89, fig. B
1994 Ventrilia rucksorum Petuch, 1994, p. 351, pl. 88, fig. K.
2010a Trigonostoma (Ventrilia) rucksorum (Peturuch, 1994) – Landau & Silva, p. 99, pl. 20, fig. 7.

Material and dimensions: One specimen BL coll., height 36.3 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

A single specimen, in excellent condition, of a Trigonostoma (Ventrilia) shell was collected from the Cañon de las Calderas locality. Although this genus had not been recorded from the Lower Pliocene southern Caribbean, other specimens (BL coll.) collected from coeval deposits at Punta Gavilán, on mainland Venezuela, and in the Springvale Formation of Trinidad are almost certainly conspecific with the one from Cubagua. The shell clearly belongs to the Trigonostoma (Ventrilia) tenerum (Philippi, 1848) species group. The specimen from Cubagua is characterised by its thin shell, weak sculpture and relatively strongly canaliculated infrasutural platform.

Within the tenerum species group Petuch (1994) introduced two new fossil taxa from the Plio-Pleistocene of Florida; Ventrilia kissimmeensis and Ventrilia rucksorum. A single dorsal view of the shell of each of the new species is given, no information on intraspecific variability is presented, and the new taxa are compared only to other new taxa. Neither is compared to T. (V.) tenerum, which also occurs in the Florida fossil record.

Landau et al. (2007a) compared specimens of T. (V.) tenerum from two Upper Pleistocene, Bermont Formation, localities in Florida, and Pleistocene deposits from Lee Creek Mine in North Carolina. They differ from the shell from Cubagua in having slightly stronger sculpture and a flatter infrasutural platform. Six specimens (BL coll.) from the Pliocene Pinestack Beds, from the same locality at the Kissimmee River Canal dig at Okeetantie, Okeechobee County as the shell described by Petuch (1994) as Ventrilia kissimmeensis. They are slightly weaker sculptured than T. (V.) tenerum and the infrasutural platform is more concave similar to our shell from Cubagua. Ventrilia rucksorum described from the Late Pliocene Caloosahatchee Formation is said to differ in having stronger shoulder knobs and having a larger beaded cord around the mid-whorl. If our material from the Kissimmee River is representative of the population, the specimen illustrated as the holotype for V. kissimmeensis is unusually smooth and the shell illustrated as V. rucksorum is more representative of the species. We provisionally accept Trigonostoma (Ventrilia) rucksorum (Peturuch, 1994) as distinct, and possibly the predecessor of T. (V.) tenerum, and as first revisers (ICNZ, Art. 24.2) choose this name over V. kissimmeensis, which we consider an unusually smooth form.

It is not unusual in the Plio/Pleistocene assemblages of Florida to find two congeneric ‘species’, occurring sometimes in the same unit, which are identical except for one consistent difference in sculpture. Vermeij & Vokes (1997) touched on this in their discussion on Pterorhytis (Pterorhytis) fluviana Dall, 1903, and pointed out that specimens found along the Kissimmee River developed elaborately recurved varices (Pterorhytis lindae of Petuch, 1994, pl. 10, fig. 7). A similar situation can be observed with the presence or absence of axial lamellae in Eupleura and Vokesinotus species pairs within the same units (Greg Herbert personal communication 12/07/06 unpublished data). This pattern does not seem to be limited to any specific taxonomic group, and probably reflects environmental differences (e.g. wave energy, depth) rather than actual species differences.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (Landau et al., 2007a); Punta Gavilán Formation, Falcón, Venezuela (BL coll.); Springvale Formation, Trinidad (BL coll.).
Lower Pleistocene: Nashua Formation, Florida (Peturuch, 1994).
Superfamily       Conoidea FLEMING, 1822
Family            Conidae FLEMING, 1822
Subfamily         Coninae FLEMING, 1822
Genus             Conus LINNAEUS, 1758.

Type species *C. marmoreus* LINNAEUS, 1758, by subsequent designation, CHILDREN, 1823.

More than 100 genus-group names have been proposed in the subfamily Coninae (e.g. EMERSON & OLD, 1962; KOHN et al., 1992). These classifications have been based on shell shape, sculpture, colour pattern, radula tooth pattern, and vary widely in their results. These shell characters have not been used in a congruent fashion in previous genus-level classifications (RÖCKEL et al., 1995), and most modern authors recognise a single genus *Conus* (WOODRING, 1970; RÖCKEL et al., 1995; REDFERN, 2001; HENDRICKS, 2009).

Workers on fossil Caribbean assemblages have, however, continued to subdivide *Conus* into numerous subgenera (PETUCH, 1982, 1991, 1994, 2004; VERMEIJ & PETUCH, 1986), and there may be some genetic basis for this, as it seems that distinct sets of *Conus* species inhabited the Indo-Pacific, eastern Pacific and western Atlantic, and eastern Atlantic and former Tethys Realm in the Cainozoic, as less than 1% of fossil species spanned more than one of these regions. However, phylogenetic results also imply that ancestors of modern *Conus* species migrated between regions at least four times, indicating that barriers between these regions have been breached occasionally (DUDA & KOHN, 2005). LANDAU & SILVA (2010a) used subgeneric names to give some idea of the palaeobiogeographic range of the species-groups in a similar way to VERMEIJ & PETUCH (1986), although here they are considered informal group-names until the subgeneric taxa are shown to represent monophyletic groupings.

The shells of *Conus* species show a wide range of intraspecific variability in shape, sculpture and colour patterns, particularly those with a wide geographic range (RÖCKEL et al., 1995). For the fossil cones there is no consensus view on what characters are the most useful for identifying species. LANDAU & SILVA (2010a) agreed wholeheartedly with HENDRICKS’ (2009) approach to fossil cone classification in adopting a conservative morphological species concept (i.e. one that accepts large amounts of intraspecific variation), and have adopted here his methodology, placing importance on the shell characters highlighted by him: shape of the subsutural flexure (for terminology see RÖCKEL et al., 1995; HENDRICKS, 2009, text-fig 2), shell measurements (for terminology see HENDRICKS, 2009, text-fig 3), sculpture, including presence or absence of tubercles on the spire whorls, and colour pattern (under natural and ultraviolet light, see HEDEGAARD et al., 2006). The use of protoconch morphology in the Cubagua specimens is not possible, as the early whorls are invariably poorly preserved. The Caribbean Neogene Conidae is another group in need of revision, and the classification given here should be regarded as provisional.

More recently, a full classification of Recent and fossil conoidean gastropods was published by TUCKER & TENORIO (2009) erecting numerous new genera. LANDAU & SILVA (2010a) did not adopt this classification, as the relationships based upon molecular sequence data are probably premature. Only about 25% of extant species are analyzed, and then their phylogenies are based on only one or two genes. Nevertheless, in many cases the authors have probably identified monophyletic groups and their classifications are included in the chresonymy. LANDAU & SILVA (2010a), however, followed the suprageneric classification suggested by TUCKER & TENORIO (2009), as there seem to be at least two very distinct clades of cones.

*Conus haytensis* G. B. SOWERBY I, 1850

Pl. 20, Fig. 8

1850       *Conus haytensis* G. B. SOWERBY I, p. 44.
1917       *Conus haytensis* SOWERBY – MAURY, p. 35, pl. 5, fig. 1.
1917       *Conus haytensis* var. gurabensis MAURY, p. 35, pl. 4, fig. 9.
1922       *Conus haytensis* SOWERBY – PILSBRY, p. 326, pl. 19, fig. 1.
1961       *Conus (Dendroconus) haytensis* SOW. – PFLUG, p. 60, pl. 16, figs 1-5.
1967a      *Conus druidi* OLSSON, p. 21, pl. 7, fig. 2.
1994       *Conus (Lithoconus) druidi* OLSSON, 1967 – PETUCH, p. 228, pl. 93, figs B-C.
Material and dimensions: One specimen BL coll., height 165.0 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

Conus haytensis G. B. Sowerby I, 1850 is characterised by its very large shell with a sigmoidal outline to the last whorl, low spire with the shoulder forming an adaxial ridge, sutural ramp with raised spiral threads on early teleoconch whorls, symmetrically curved subsutural flexure, and raised spiral threads on the base of the last whorl. The preserved colour pattern consists of three continuous bands, about 30 rows of spiral dots/dashes and axial streaks at the shoulder, and spire with radial streaks.

Landau & Silva (2010a) examined one very large Conus shell from the Cañon de las Calderas deposit in a relatively poor state of preservation which corresponded to this description. The ventral aspect of the shell is broken and severely abraded, but the spire is preserved showing the spiral threads and adaxial ridge on the spire whorls typical of the species.

Conus molis Brown & Pilsbry, 1911 from the Middle-Upper Miocene Gatun Formation of Panama, and recorded from numerous other Caribbean Neogene localities (Olsson, 1922; Anderson, 1929; Weisbord, 1929), was said to differ from C. haytensis in being longer in proportion to width, the early whorls were non-coronate and formed a mucro, the shoulder of the last whorl more acute, below which the side is more convex, more distinctly striate, with the striae at the base more equal and closer, not widely spaced with smaller striae in the intervals as in C. haytensis (Brown & Pilsbry, 1911). Hendricks (2009) suspected that C. molis might be a synonym of C. haytensis, but did not synonymise them due to lack of material. As can be seen from Table 4, C. molis does not seem to be longer in proportion to height than C. haytensis. The convexity of the adapical portion of the last whorl is variable in C. haytensis; the “domingensis” morphotype has a fairly rounded shoulder (see Pfug, 1961, pl. 16, fig. 1). Unfortunately, like Hendricks, I have not seen C. molis from the type locality and cannot comment on the sculptural differences, but concur that the two are probably synonymous.

<table>
<thead>
<tr>
<th>Specimen (only adult specimens)</th>
<th>Height/width</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. molis Holotype Brown &amp; Pilsbry, 1911, pl. 23, fig. 1</td>
<td>1.74</td>
</tr>
<tr>
<td>C. molis Woodring, 1970, pl. 55, fig. 8</td>
<td>1.78</td>
</tr>
<tr>
<td>C. haytensis Pfug, 1961, pl. 16, fig. 1 “domingensis” form</td>
<td>1.76</td>
</tr>
<tr>
<td>C. haytensis Lectotype Pfug, 1961, pl. 16, fig. 2</td>
<td>1.8</td>
</tr>
<tr>
<td>C. haytensis Hendricks, 2009 (mean SL/MD, table 12)</td>
<td>1.78</td>
</tr>
<tr>
<td>C. haytensis “domingensis” form, BL coll. (6 specimens)</td>
<td>1.66 -1.77</td>
</tr>
<tr>
<td>C. haytensis, BL coll. (4 specimens)</td>
<td>1.64 -1.82</td>
</tr>
<tr>
<td>C. druidi Holotype Olsson, 1967a, p. 21, pl. 7, fig. 2</td>
<td>1.79</td>
</tr>
<tr>
<td>C. haytensis this work Pl. 21, Fig. 1</td>
<td>1.75</td>
</tr>
</tbody>
</table>

Table 4: Height/width measurements for C. molis and C. haytensis.

The Conus molis group is one of the Paciphile taxa identified by Woodring (1970). It was placed in the genus Pyruconus Olsson, 1967 by Tucker & Tenorio (2009), who also recognised it as a monophyletic group, present today in the East Pacific, with a fossil record in the western Atlantic.

Geological and geographical distribution:
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Gurabo Formation, Dominican Republic (Maury, 1917, Pilsbry, 1922); Lower-Upper Pliocene: Tamiami Formation, Florida (Petuch, 1994, Hendricks, 2009).
**Conus imitator** BROWN & PILSBRY, 1911
Pl. 20, Fig. 9; Pl. 21, Fig. 1

1911  
**Conus imitator** BROWN & PILSBRY, p. 342, pl. 23, fig. 4.

1911  
**Conus dalli** TOULA, p. 509, pl. 31, fig. 23.

1913  
**Conus (Lithoconus) dalli** TOULA – COSSMANN, p. 41, pl. 3, figs 30-31, pl. 4, figs 7-8.

1917  
**Conus dalli** TOULA – MAURY, p. 48, pl. 7, fig. 15.

1922  
**Conus imitator** BROWN & PILSBRY – OLSSON, p. 45, pl. 2, fig. 6.

1928  
**Conus (Leptoconus) imitator lius** WOODRING (partim), p. 209, pl. 10, fig. 5 (non fig. 6).

1963  
**Conus imitator** BROWN & PILSBRY – PERRILLIAT, p. 27, pl. 6, figs 6-7.

1960  
**Conus imitator** BROWN & PILSBRY – BARRIOS, p. 295, pl. 12, fig. 6.

1970  
**Conus imitator** imitator** BROWN & PILSBRY, 1911 – WOODRING, p. 354, pl. 55, figs 1-2.

2009  
**Gradiconus haytensis** (BROWN & PILSBRY, 1911) – TUCKER & TENORIO, p. 97.

2010a  
**Conus imitator** BROWN & PILSBRY, 1911 – LANDAU & SILVA, p. 101, pl. 20, fig. 9, pl. 21, fig. 1.

**Material and dimensions:** Maximum height 59.5 mm, eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island.

**Discussion:**

**Conus imitator** BROWN & PILSBRY, 1911 is characterised by its medium-sized shell; tall almost smoothly-conical spire; smooth, weakly concave sutural ramp; asymmetrically curved subsutural flexure, sharply angled shoulder on the last whorl and strong spiral sculpture on the base of the last whorl. The preserved colour pattern consists of three continuous bands, about 30 rows of spiral dots/dashes and axial streaks at the shoulder, and spire with radial streaks.

WOODRING (1970, p. 355) discussed the taxonomic significance of the presence or absence of tubercles on the early whorls of **Conus imitator** BROWN & PILSBRY, 1911 and concluded that they could either be present or absent. The presence or absence of tubercles on early post nuclear whors is probably not an intraspecifically variable character. It is possible that some specimens have fewer tuberculate whors and/or that those tubercles have been eroded away (Hendricks personal communication 15-09-09). The shells from Cubagua have the early teleoconch whors poorly preserved, but there is a suggestion of tubercles on the first couple of whors in some of the specimens. TUCKER & TENORIO (2009) placed the species in the genus **Gradiconus** da Motta, 1991, which they consider tropical American, with representatives in both the fossil and Recent faunas in the western Atlantic and eastern Pacific.

I have examined numerous specimens of **C. aff. imitator**, illustrated by JUNG (1965, pl. 78, fig. 12), from the Lower Miocene Cantaure Formation of Venezuela (BL coll.), and agree with WOODRING (1970) that they do not correspond to the same species, although closely related. The Cantaure shells have a far more prominent carina and a strongly flaring outer lip. Moreover, the spire is more depressed, the overlap of the spire whors is such that the suture is at or just below the carina of the preceeding whorl, whereas in **C. imitator** the carina on the shoulder of the preceeding whorl is generally located below the suture, separated by a considerable margin.

**Geological and geographical distribution:**

Middle Miocene: lower Gatun Formation (WOODRING, 1970).
Upper Miocene: middle and upper Gatun Formations (BROWN & PILSBRY, 1911; TOULA, 1911 as **C. dalli**; WOODRING, 1970); Cercado Formation, Dominican Republic (MAURY, 1917, as **C. dalli**; PILSBRY, 1922).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Tuberà Group, northern Colombia (ANDERSON, 1929; BARRIOS 1960); Bocas del Toro, Panama (WOODRING, 1970); Gurabo Formation, Dominican Republic (MAURY, 1917, as **C. dalli**; PILSBRY, 1922).
Lower-Upper Pliocene: Bowden Formation, Jamaica (WOODRING, 1928, as **C. imitator lius**).
Upper Pliocene: Agueguexquite Formation, Isthmus of Tehuantepec, Mexico (PERRILLIAT, 1963); Banano Formation, Costa Rica (OLSSON, 1922).
Conus spurius GMELIN, 1791
Pl. 21, Figs 5-6

1791 Conus spurius GMELIN, p. 3396, no. 67.
1792b Conus proteus HWASS in BRUGUIÈRE, p. 682, pl. 334, figs 1-2.
1792b Conus leoninus HWASS in BRUGUIÈRE, p. 683, pl. 334, pl. 334, fig. 5-6, 9, pl. 335, fig. 5.
1798 Cucullus Ferrugineus RÖDING, p. 41.
1798 Cucullus Quadratus RÖDING, p. 41.
1798 Cucullus Syriacus RÖDING, p. 41.
1798 Cucullus Gualterianus RÖDING, p. 42.
1798 Cucullus leoninus RÖDING, p. 44.
1810 Conus flammeus LAMARCK, p. 279.
1810 Conus ochraceus LAMARCK, p. 275.
1817 Conus Lorenzianus DILLWYN, p. 370.
1844c Conus proteus HWASS – REEVE, pl. 40, fig. 219.
1859 Conus proteus – CHENU, fig. 1553.
1866 Conus leoninus BRUG. – SOWERBY, G. B. II, p. 26, pl. 11, fig. 232.
1872 Conus Bayley JOUSSEAUME, p. 200, pl. 18, fig. 1.
1882 Conus Weinkauffii LÖBBECKE, p. 90, pl. 4, figs 1-3.
1917 Conus proteus HWASS – MAURY, p. 42, pl. 6, fig. 11.
1922 Conus proteus HWASS – OLSSON, p. 43, pl. 2, figs 3-4.
1928 Conus (Lithoconus) proteus HWASS – WOODRING, p. 204, pl. 9, fig. 4.
1937 Conus philogopus TOLMIN, p. 206 [Replacement name for Conus flammeus LAMARCK, 1810, non Cucullus flammeus RÖDING, 1798].
1940 Conus proteus HWASS – PERRY, p. 161, pl. 37, fig. 254.
1942 Conus spurius GMELIN – CLENCH, p. 19, pl. 10, figs 4-5.
1942 Conus spurius atlanticus CLENCH, p. 20, pl. 10, figs 1-3.
1951 Conus spurius aureofasciatus REHDER & ABBOTT, p. 64, pl. 9, figs 3-4.
1955 Conus spurius atlanticus CLENCH – PERRY & SCHWENGEL, p. 178, pl. 37, fig. 254.
1958 Conus spurius GMELIN – COOMANS, p. 100, pl. 15, fig. top right.
1961 Conus spurius GMELIN, 1791 – WARMKE & ABBOTT, p. 130, pl. 24, fig. h.
1964 Conus cherokus OLSSON & PETIT, p. 538, pl. 79, fig. 3.
1966 Conus spurius GMELIN – KÖHN, p. 92, pl. 3, figs 24-25.
1968 Conus proteus HWASS in BRUGUIÈRE – KÖHN, p. 447, pl. 7, fig. 94.
1968 Conus leoninus HWASS in BRUGUIÈRE – KÖHN, p. 463, pl. 5, fig. 57.
1968 Conus spurius arubaensis NOWELL-ÜSTIKE, p. 12, pl. 1, sp. 995.
1970 Conus spurius GMELIN – WOODRING, p. 348, pl. 55, fig. 7.
1973 Conus spurius spurius GMELIN – MORRIS, p. 239, pl. 65, fig. 8.
1973 Conus spurius atlanticus CLENCH – MORRIS, p. 239, pl. 65, fig. 9.
1974 Conus spurius atlanticus CLENCH, 1942 – ABBOTT, p. 254, pl. 14, fig. 2779.
1974 Conus spurius aureofasciatus REHDER & ABBOTT, 1951 – ABBOTT, 255, fig. 2780.
1975 Conus ferugineus (RÖDING) – KÖHN, p. 205.
1975 Conus leoninus (RÖDING) – KÖHN, p. 209, pl. 2, fig. 31.
1975 Conus syriacus (RÖDING) – KÖHN, p. 220.
1975 Conus spurius GMELIN, 1791 – HUMFREY, p. 172, pl. 21, figs 4, 4a.
1979 Conus spurius GMELIN, 1791 – WALLS, p. 861, figs 617.
1983 Conus spurius GMELIN, 1791 – VINK, p. 6, no. 10.
1983 Conus spurius aureofasciatus REHDER & ABBOTT, 1951 – VINK, p. 7, no. 10A.
1985 Conus spurius quadratus (RÖDING), 1798 – VINK, p. 8, no. 10B.
1985 Conus spurius atlanticus CLENCH, 1942 – VINK, p. 10, no. 10C.
1985 Conus spurius lorenzianus DILLWYN, 1817 – VINK, p. 10, fig. 10D.
Conus spurius baylei Jousseaume, 1872 – Vink, p. 11, fig. 10E.

Conus lorenzianus Dillwyn – Kohn, p. 22, fig. 17.

Conus sunderlandi Petuch, p. 75, pl. 12 figs 13-16.

Conus (Lithoconus) spurius Gmelin, 1791 subspecies – Petuch, pl. 23, fig. 1.

Conus spurius Gm., 1791 forma atlanticus Clench, 1942 – Jong & Coomans, p. 102, no. 560.

Conus spurius lorenzianus Dillwyn, 1817 – Diaz, p. 50, fig. 14b.

Conus spurius spurius Gmelin, 1791 – Diaz, p. 49, fig. 14a.


Conus spurius spurius Gmelin, 1791 – Díaz, p. 50, fig. 14b.

Conus spurius lorenzianus Dillwyn, 1817 – Díaz, p. 49, fig. 14a.

Conus lemoni Petuch, p. 103, figs 16-17.

Conus (Lithoconus) spengleri Petuch, p. 103, figs 16-17.

Conus (Leptoconus) spurius quadratus Röding, 1798 – Robinson, p. 536, pl. 25, fig. 1.

Conus (Lithoconus) spengleri Petuch, p. 53, pl. 10, figs 2-3.

Conus spurius Gmelin, 1791 – Díaz, p. 50, fig. 14b.

Conus spurius Gmelin, 1791 – Díaz, p. 50, fig. 14b.

Conus (Lithoconus) cherokus Olsson & Petit, 1964 – Petuch, p. 228, pl. 93, fig. D.

Conus (Lithoconus) spengleri Petuch, p. 103, figs 16-17.

Conus (Lithoconus) spengleri Petuch, p. 228, pl. 93, fig. A.

Conus (Lithoconus) spengleri Petuch, p. 228, pl. 93, fig. A.

Conus (Lithoconus) spengleri Petuch, p. 228, pl. 93, fig. A.

Conus (Lithoconus) cherokus Olsson & Petit, 1964 – Petuch, p. 226, pl. 25, fig. 1.

Conus (Lithoconus) micanopy Petuch, p. 355, pl. 93, fig. G.

Conus (Lithoconus) micanopy Petuch, p. 355, pl. 93, fig. G.

Conus (Lithoconus) spurius Gmelin, 1791 – Petuch, p. 356, pl. 93, fig. E.

Conus (Lithoconus) spurius Gmelin, 1791 – Petuch, p. 226, pl. 25, fig. L.

Conus (Lithoconus) micanopy Petuch, p. 355, pl. 93, fig. G.

Conus (Lithoconus) micanopy Petuch, p. 355, pl. 93, fig. G.

Conus (Lithoconus) spurius Gmelin, 1791 – Petuch, p. 226, pl. 25, fig. L.

Conus (Lithoconus) spurius Gmelin, 1791 – Robinson, p. 226, pl. 25, fig. 1.

Conus (Lithoconus) spengleri Petuch, p. 226, pl. 25, fig. 1.

Conus (Lithoconus) spengleri Petuch, p. 226, pl. 25, fig. 1.

Conus (Dendroconus) patricius Hinds, 1843 – Petuch, p. 226, pl. 93, fig. J-K.

Conus (Dendroconus) patricius Hinds, 1843 – Petuch, p. 226, pl. 93, fig. J-K.

Spuriconus cherokus (Olsson & Petit, 1964) – Petuch, p. 294, pl. 56, fig. C.

Spuriconus cherokus (Olsson & Petit, 1964) – Petuch, p. 294, pl. 56, fig. C.

Spuriconus cherokus (Olsson & Petit, 1964) – Petuch, p. 294, pl. 56, fig. C.

Spuriconus spengleri (Petuch, 1991) – Petuch, p. 294, pl. 86, fig. E.

Spuriconus spengleri (Petuch, 1991) – Petuch, p. 294, pl. 86, fig. E.

Spuriconus spengleri (Petuch, 1991) – Petuch, p. 294, pl. 86, fig. E.

Spuriconus lemoni (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Spuriconus lemoni (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Spuriconus spengleri (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Spuriconus spengleri (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Spuriconus lemoni (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Spuriconus lemoni (Petuch, 1991) – Petuch, p. 294, pl. 90, fig. B.

Material and dimensions: Maximum height 64.4 mm, three specimens NMB lot 6931/1; one specimen NMB lot 6931/2; four specimens EDIMAR coll.; 16 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

Conus spurius Gmelin, 1791 is characterised by its large shell, convex outline of the last whorl, smooth spire whorls, subsutural flexure asymmetrically curved, and raised spiral threads on the base of the last whorl, sometimes extending to the shoulder. The preserved colour pattern consists of about 20 rows of spiral dots, dashes or blotsches, which coalesce to form axial streaks.

Conus spurius is a highly variable species; the shell is more or less broad, the spire can be almost flat to somewhat scalate, the shoulder quite sharp to rounded, and the colour pattern is very variable. Today it is widespread in the Recent Caribbean. Vink (1985) recognized the nominal species and five subspecies within the Caribbean fauna, some differing in the shade of the colour pattern. Landau & Silva (2010a) again adopted the more conservative approach and considered them all a single species. The specimens from Cubagua are relatively broad and flat-spired (although some shells have a scalate spire) with the spiral colour pattern clearly visible, similar to the specimen illustrated by Woodring (1970, pl.
Conus spurius has been ascribed to the subgenus Lithoconus Mörch, 1852, characterised by species with medium to large shells, with a flat or very low spire, almost smooth last whorl with a few spiral ridges abapically, and apertural margins almost parallel. More recently Tucker & Tenorio (2009) suggested the genus Spuriconus Petuch, 2003 was monophyletic, confined to the Recent western Atlantic, with fossil representatives on either side of the Central American Isthmus. Whilst this group is undoubtedly well-represented on the Atlantic side of the Gatunian palaeobiogeographic province, Aguilar & Fischer’s (1986) record for C. proteus (a synonym of C. spurius) for the Late Pleistocene Montezuma Formation of Costa Rica is extremely suspect. This work is full of misidentifications (see Petit, 1997; personal opinion, BL), and our own collecting (BL) has not supported this record.

In Cubagua C. spurius cannot be confused with any of its congeners. In the Florida assemblages the specimens of Conus spuroides Olsson & Harbison, 1953 and Conus evergladesensis Petuch, 1991 are similar but can be distinguished by the height of their spire, breadth of the last whorl, and number or rows of spiral dots (see Hendricks, 2009).

Geological and geographical distribution:
Lower Miocene: Baitoa Formation, Dominican Republic (BL coll.).
Upper Miocene: middle Gatun Formation, Panama (Woodring, 1970); Cercado Formation, Dominican Republic (Maury, 1917, as C. proteus).
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Gurabo Formation, Dominican Republic (Maury, 1917, as C. proteus).
Lower-Upper Pliocene: Tamiami Formation, Florida (Petuch, 1994, Hendricks, 2009); Agua Formation, Bocas del Toro, Panama (Woodring, 1970); Bowden Formation, Jamaica (Woodring, 1928, as C. (Lithoconus) proteus).
Upper Pliocene: Banano Formation, Costa Rica (Olsson, 1922, as C. proteus).
Holocene: Amuay Bay, Paraguana Peninsula, Venezuela (BL coll.).
Recent: Widespread in the Caribbean (Vink, 1985)

Conus sp. aff. C. ultimus Pilsbry & Johnson, 1917
Pl. 21, Figs 7-8

2010a Conus sp. aff. C. ultimus Pilsbry & Johnson, 1917 – Landau & Silva, p. 103, pl. 21, figs 7-8.

Material and dimensions: Maximum height 96.4 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:
The specimens from Cubagua are characterized by their large, very solid shell; elevated, scalate spire; the spire whorls are somewhat worn, but there is a suggestion of tubercles on the early spire whorls; spire whorls roundly shouldered, sutural ramp smooth, sloping; subsutural flexure asymmetrical, curved; and spiral sculpture of widely spaced spiral threads. The subgenus Stephanoconus Mörch, 1852 has been used for this species, although Tucker & Tenorio (2009) placed it in the genus Protoconus da Motta, 1991, a genus with a tropical American distribution in the Recent faunas, found on both sides of the Central American Isthmus.

Conus ultimus Pilsbry & Johnson, 1917 was first described as a subspecies of Conus consobrinus (G. B. Sowerby I, 1850) based on material from the ‘Pliocene’ of Costa Rica (Pilsbry & Johnson, 1917, p. 160; Pilsbry, 1922, p. 330, pl. 20, fig. 8). Tucker & Tenorio (1996, p.114) considered the two taxa synonymous. However, Conus ultimus (interpreted as specimens from the Lower
Pleistocene Moin Formation of Costa Rica, BL coll.) and *C. consobrinus* (as figured by PFLUG, 1961, pl. 17, figs 1-10) are species with quite different shells; the former has the spire whors more strongly carinate and tuberculate than in *C. consobrinus* and the tubercles are present on the entire spire as opposed to just on the early whors as in *C. consobrinus*. The spiral sculpture on the last whorl is entirely different; close-set, weakly tuberculate cords in *C. consobrinus*, smooth cords and rows of tubercles alternating in *Conus ultimus*, and lastly the outer lip profile is strongly rounded and convex in *C. consobrinus*. The two are distinct species. The type material undoubtedly originated from the Lower Pleistocene Moin Formation of Puerto Limon. Specimens of this species have been illustrated by ROBINSON (1991, pl. 25, fig. 10), and I have examined numerous specimens from the Moin Formation (BL coll.). *Conus consobrinus* of Costa Rica differs from the Cubagua shells in being much smaller (maximum height 46.5mm), and in having spiral rows of small tubercles between the spiral threads and well-developed tubercles on the spire whors. The Cubagua shells differ from *C. consobrinus* in being much more massive and in the character of the scalate spire. Interestingly, probably true *C. consobrinus* was found in the Aramina Formation of Cerro Barrigón, but not in Cubagua.

LANDAU & SILVA (2010a) examined specimens of another closely allied species identified as *C. cf. ultimus* from Cañada de Zamba, Lower Pliocene Gurabo Formation of the Dominican Republic (BL coll.). These are far more similar to the Cubagua shells, and in both a pattern of narrow spiral ridges is preserved, weakly tuberculate abapically. However, the Dominican shells are smaller, less robust, far narrower and more elongated than the Cubagua shells. The *Stephanoconus* species-group is well represented in the Neogene deposits of the Dominican Republic, with two further undescribed species represented in the BL collection; one from the Lower Miocene Baitoa Formation represented by specimens with very strong tubercles at the shoulder of the whors, and a second species from the Lower Pliocene Gurabo Formation, represented by specimens with a very tall and slender, more delicate shell, well developed tubercles at the shoulder and a sculpture of very fine weakly tuberculate spiral threads. A full revision of the group in the tropical American Neogene is beyond the scope of this work.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Family: Conilithidae
Subfamily: Conilithinae

*Conus cf. oniscus* WOODRING, 1928
Pl. 21, Figs 2-4

2010a  *Conus cf. oniscus* WOODRING, 1928 – LANDAU & SILVA, p. 104, pl. 21, figs 2-4.

**Material and dimensions:** Maximum height 42.4 mm, one specimen NMB lot 8324; seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; four specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
*Conus cf. oniscus* WOODRING, 1928 is characterised by its medium-sized fusiform shell, spire whors carinate, the sutural ramp concave, subsutural flexure very shallow, U-shaped, incised spiral grooves present on the abapical half of the last whorl, extending sometimes to the shoulder. The colour pattern consists of rows of spiral dots. This species fits well within the American species-group *Ximeniconus* EMERSON & OLD, 1962, characterised by a fusiform shell and a colour pattern of closely placed spiral rows or dots, with or without pustules between rows. The monophylogeny of this group was supported by TUCKER & TENORIO (2009).

The shells from Cubagua are very closely similar to *Conus oniscus* WOODRING, 1928, which occurs in the Plio-Pleistocene of Florida (HENDRICKS, 2009) and Pliocene Bowden Formation of Jamaica (WOODRING, 1928), but differ in two important aspects; the shape of the subsutural flexure, V-shaped in *C. oniscus*, U-shaped in the Cubagua specimens. Although shallow in both species, it is even shallower, almost straight in the Cubagua specimens. Secondly, the sutural ramp in *C. oniscus* develops a mid-ramp
spiral fold on later teleoconch whorls. This is absent in the Cubagua shells and the sutural ramp is more strongly concave. The shell of *Conus marylandicus* Green, 1830, also from the Florida Plio-Pleistocene (Hendricks, 2009) is similar to *C. oniscus*, but differs in having an even shallower, almost flat substural flexure and the sutural ramp on later teleoconch whorls is almost flat to slightly concave and not sigmoidal as in *C. oniscus*, without the raised spiral ridge. The early teleoconch whorls are also different in shape: carinate in *C. oniscus*, angulate in *C. marylandicus*. *Conus marylandicus* is also very similar to the specimens from Cubagua, however, the substural flexure is even shallower, less U-shaped and the sutural ramp more concave in the Cubagua specimens. Unfortunately the early teleoconch whorls are too worn to comment on their shape. According to the size data given by Hendricks (2009, table 7) *C. marylandicus* has a somewhat smaller shell than the Cubagua specimens.

The *Ximeniconus* species group is another example of a paciphile group without representatives in the Recent Caribbean, but with three extant species in the tropical American Pacific: *Conus tornatus* G. B. Sowerby II, 1833, *Conus ximenes* Gray, 1839, and *Conus mahogany* Reeve, 1843.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

*Conus jaspideus* Gmelin, 1791
Pl. 22, Figs 1-2

1791 *Conus jaspideus* Gmelin, p. 3387.
1792b *Conus verrucosus* Hwass in Brungrière, p. 708.
1816 *Conus sulcatus* Mühlfeld, p. 3, pl. 1, fig. 1.
1843 *Conus verrucosus* Hwass – Reeve, pl. 37, fig. 201.
1845 *Conus nodiferus* Kiener, p. 228, pl. 100, fig. 4.
1845 *Conus echinulatus* Kiener, p. 270, pl. 105, fig. 2.
1866 *Conus verrucosus* Brug. – Sowerby, G. B. II, p. 11, pl. 6, figs 125-127.
1869 *Conus stearnsii* Conrad, p. 104, pl. 10, fig. 1.
1870 *Conus corrugatus* G. B. Sowerby III, p. 257, pl. 22, fig. 7.
1816 *Conus trisculptus* Pilbsry & Johnson, p. 160.
1922 *Conus trisculptus* Pilbsry & Johnson – Pilbsry, p. 330, pl. 19, fig. 6.
1925 *Conus multiriratus walli* Mansfield, p. 13, pl. 2, figs 1, 9.
1928 *Conus (Leptoconus) imitator lius* Woodring (partim), p. 209, pl. 10, fig. 6 (non fig. 5).
1930 *Conus pealii* Green, p. 123, pl. 3, fig. 3.
1930 *Conus stearnsii* Conrad – B. Smith, p. 281, figs 3-4.
1936 *Conus verrucosus* Hwass – M. Smith, p. 136, pl. 9, fig. 11.
1940 *Conus stearnsii* Conrad – Perry, p. 162, pl. 37, fig. 256.
1942 *Conus stearnsii* Conrad – Clench, p. 9, pl. 5, figs 1-4.
1942 *Conus jaspideus* Gmelin – Clench, pl. 10, pl. 5, figs 1-4.
1942 *Conus verrucosus* Hwass – Clench, p. 13, pl. 8, figs 1-4.
1944 *Conus verrucosus vanhyningi* Rehder, p. 106.
1953 *Conus jaspideus branhamae* Clench, p. 364, pl. 181, fig. 2.
1953 *Conus (Leptoconus) stearnsii* Conrad – Olsson & Harbison, p. 174, pl. 26, fig. 5.
1954 *Conus stearnsii* Conrad – Abbott, p. 262, pl. 22, fig. y.
1954 *Conus jaspideus* Gmelin – Abbott, p. 262, pl. 14, fig. n, pl. 22, fig. x.
1954 *Conus verrucosus* Hwass – Abbott, p. 262, pl. 22, fig. z.
1955 *Conus stearnsii* Conrad – Perry & Schwengel, p. 180, pl. 37, fig. 256.
1955 *Conus jaspideus* Gmelin – Perry & Schwengel, p. 180, pl. 37, fig. 257.
1958 *Conus jaspideus* Gmelin 1791 – Abbott, p. 88, pl. 3, figs a-j.
1958 *Conus verrucosus* Hwass – Coomans, p. 100, pl. 14, fig. top left.
1958 *Conus jaspideus* Gmelin – Coomans, p. 100, pl. 15, fig. bottom centre.
1961 *Conus jaspideus* Gmelin, 1791 – Warmke & Abbott, p. 130, pl. 24, fig. f.
1961 *Conus verrucosus* Hwass, 1792 – Warmke & Abbott, p. 130, pl. 24, fig. e.
1962 *Conus (Leptoconus) jaspideus caboblanquensis* Weisbord, p. 420, pl. 39, figs 5-16.
1968 *Conus verrucosus* Hwass in Brungrière – Koh, p. 488, pl. 9, fig. 119.
Material and dimensions: Maximum height 30.7 mm, 21 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; Cubagua Island; 11 specimens BL coll., (lower yellow fine sandy bed), four specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.
**Discussion:**

TUCKER & TENORIO (2009) placed this species in the genus *Jaspidiconus* PETUCH, 2003. This genus is well represented in the tropical American Neogene throughout the Gatunian palaeobiogeographic province, but today restricted to the western Atlantic. *Jaspidiconus* should therefore be added to the small number of taxa called Caribphiles (WOODRING, 1966), which became restricted to the Atlantic side of their original wider Gatunian distribution.

*Conus jaspideus* GMELIN, 1791 is characterised by its small shell, with a paucispiral protoconch of less than two whorls with a large nucleus, absence of tubercles on the early postnuclear whorls, smooth sutural ramp, subsutural flexure symmetrically curved, incised spiral grooves extending from the base to at least halfway up the last whorl, the flattened cords between the grooves granulose in some specimens, the granules becoming larger towards the shoulder. The preserved colour pattern consists of about 20 rows of spiral dots and/or dashes, which sometimes merge to form axial streaks and radial blotches on the spire. The number of synonyms listed in the chresonymy is testament to the huge shell variability present in this species. Shells of *C. jaspideus* can have a relatively squat or elevated spire, the last whorl more or less elongated, the spiral grooves restricted to the abapical half of the last whorl or prominent throughout and in specimens in which the spiral sculpture is strongly developed the spiral cords, especially on the adapical half of the shell can bear rows of prominent tubercles. The material from Cubagua shows the same variability seen in the Recent populations in the height of the spire, width and number of spiral cords (15-18), which can be distinctly granular (Pl. 22, Fig. 3) to almost completely smooth (Pl. 22, Fig. 2).

COSTA (1994) reviewed the extant members of the *Conus jaspideus* complex and based on both shell morphology and soft-part anatomy concluded there were only three valid species; *C. jaspideus*, *Conus mindanus* HWASS in BRUGUIÈRE, 1792 and *Conus pusio* HWASS in BRUGUIÈRE, 1792. COSTA (1994) stated that the presence of a carinated shoulder on early teleoconch whorls could be used to distinguish *C. jaspideus* from *C. mindanus* and *C. pusio*, which have an angular and rounded shoulder respectively. Neither of the latter two have a confirmed fossil record.

HENDRICKS (2009) made a good start at wading though the numerous synonyms in the literature concerning the Plio-Pleistocene of Florida. The same task is required for the Caribbean Neogene literature. A full revision of the species in the Caribbean Neogene is not attempted, but a comment on some probable synonyms is made and a comparison with related species is given.

The specimens of *Conus multiliratus* BÖSE, 1906, described from numerous Miocene and Pliocene Caribbean deposits (BÖSE, 1906; BROWN & PILSBRY, 1911; MAURY, 1917; WOODRING, 1928, 1970) can immediately be distinguished by the character of their protoconch, which is multispiral, comprising about three whorls, with a very small nucleus (Middle-Upper Miocene, Gatun Formation, Cativa, Panama, BL coll.). This type of protoconch is typical of an inferred planktotrophic larval development. In contrast the protoconch of *C. jaspideus* is paucispiral with a very large nucleus (HENDRICKS, 2009, pl. 2, figs 12-13), typical of an inferred non-planktotrophic mode of development. This latter type of larval development probably leading to a more limited gene flow might explain the wide variation in shell morphology between populations of *C. jaspideus*. The early teleoconch whorls in *C. multiliratus* are carinate bearing tubercles, whereas those of *C. jaspideus* lack any tubercles. The subsutural flexure is similar in both species, somewhat shallower in *C. multiliratus* and the sutural ramp bears weak to subobsolete cords in *C. multiliratus*, whereas it is smooth in *C. jaspideus*. The last whorl is usually shorter than in *C. jaspideus* with the shoulder proportionally wider. The extent and strength of the cords on the last whorl are variable in both species and the cords can also be granulate in *C. multiliratus*. *Conus gaza* JOHNSON & PILSBRY, 1911 from the Upper Miocene-Lower Pliocene of the Dominican Republic was considered a synonym by WOODRING (1970). Specimens from the Lower Pliocene Gurabo Formation have the same tuberculæate early teleoconch whorls. Unfortunately the protoconch is not preserved in our material.

The specimens described as *Conus walli* MANSFIELD, 1925 from the Lower Pliocene Springvale Formation of Trinidad may correspond to *C. multiliratus* or *C. jaspideus*. The character of the protoconch and presence or absence of tubercles on the early teleoconch whorls is unclear from the original description and further comments on the type lot by WOODRING (1970, p. 326). The smaller specimen illustrated by WOODRING (1928, pl. 10, fig. 6) as *Conus imitator lius* WOODRING, 1928 is very suggestive of *C.
The larger shell (WOODRING, 1928, pl. 10, fig. 5) should be assigned to *C. imitator* BROWN & PILSBRY, 1911. Unfortunately I have not seen the type material to confirm this.

*Conus burckhardti* BÖSE, 1906, also widespread in the Caribbean Neogene assemblages (BÖSE, 1906; BROWN & PILSBRY, 1911; MAURY, 1925; RUTSCH, 1934; WOODRING, 1970) has a multispiral protoconch similar to that of *C. multiliratus* (specimen BL coll. from the Middle-Upper Miocene Gatun Formation, Cativa, Panama), which immediately distinguishes it from *C. jaspideus*. The first teleoconch whorl bears strongly prosocline axial riblets, but abapically the whorls are devoid of tubercles. The character of the subsutural flexure and sutural ramp are similar to that of *C. jaspideus*, but the last whorl is more elongated. Granules can also be present or absent on the cords on the last whorl.

*Conus trisculptus* PILSBRY & JOHNSON, 1917 was described based on material from the Lower Pleistocene Moin Formation of Costa Rica. Numerous specimens from Los Corales, Puerto Limon, Costa Rica (BL coll.) were examined, with a paucispiral protoconch identical to that seen in *C. jaspideus*. About half of the specimens in this assemblage have tubercles on the later teleoconch whorls. This character is also seen in some of the forms considered synonymous with *C. jaspideus* by HENDRICKS (2009, pl. 1, figs 15, 16, 19-22, pl. 2, fig. 1). LANDAU & SILVA (2010a) therefore considered *C. trisculptus* a junior subjective synonym of *C. jaspideus*. None of the shells in the Cubagua assemblage have tuberculate spire whorls.

**Geological and geographical distribution:**

Lower Pliocene: Tamiami Formation, Florida (PETUCH, 1994, HENDRICKS, 2009); Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavián Formation, Falcón, Venezuela (BL coll.); Savaneta Glaucolitic Sandstone Member of Springvale Formation, Trinidad (MANSFIELD, 1925).

Lower-Upper Pliocene: Cayo Agua Formation, Bocas del Toro, Panama (BL coll.).

Lower Pleistocene: Caloosahatchee Formation, Florida (PETUCH, 1994, HENDRICKS, 2009); Moin Formation, Costa Rica (ROBINSON, 1991, as *Conus (Leptoconus) trisculptus*).

Upper Pleistocene: Fort Thompson Formation, Florida (PETUCH, 1994, HENDRICKS, 2009); La Isabella Formation, Dominican Republic (BL coll.).

Recent: Florida, Gulf of Mexico, Caribbean, south to Brazil (COSTA, 1994).

**Family** Turridae H. & A. ADAMS, 1853

The suprageneric classification of the Turridae *sensu lato* is in a similar state of instability and change as seen in the Conidae and Terebridae. TAYLOR *et al.* (1993) reviewed POWELL’s (1966) classic classification of the Turridae, and based on anatomical characters, proposed a scheme with six families within the Conoidea, including Conidae and Terebridae, with some of POWELL’s (1966) classic Turrid subfamilies passing to the Conidae. The initial DNA phylogeny proposed by PULLIANDRE *et al.* (2008, 2009) broadly supports the classification proposed by TAYLOR *et al.* (1993), with a few genera changing families. The molecular phylogeny published to date does not resolve all groups, and more detailed DNA phylogeny for the Conoidea is being prepared in which there may be as many as ten families within the superfamily (Alan Beu, personal communication, 2010). In view of the taxonomic instability present at the moment, LANDAU & SILVA (2010a) chose provisionally to adhere to POWELL’s (1966) more classical classification for the Turridae *sensu lato*.

**Subfamily** Turriculinae POWELL, 1942

**Genus** *Knefastia* DALL, 1919.

Type species *Pleurotoma olivacea* G. B. SOWERBY I, 1833, by original designation.

*Knefastia limonensis* (OLSSON, 1922)

Text-Figure 25; Pl. 22, Figs 3-4

1922 *Turricula lavinoides* OLSSON, p. 55, pl. 4, fig. 6.

1922 *Turricula lavinoides var. limonensis* OLSSON, p. 56, pl. 4, fig. 12.

2006 *Fusiturricula lavinoides* (OLSSON, 1922) – WILLIAMS, no. 2522 (left hand illustration only).

2010a *Knefastia limonensis* (OLSSON, 1922) – LANDAU & SILVA, p. 107, pl. 22, figs 3-4.

**Material and dimensions:** Maximum height 93.1 mm, 10 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; Cubagua Island.

**Discussion:**

*Knefastia limonensis* (OLSSON, 1922) (holotype Pl. 15, Fig. 1) was described from material originating from the Upper Miocene Nancy Point Formation, Toro Cays of Bocas del Toro area, Panama and the Lower Pleistocene Moin Formation of Costa Rica. OLSSON (1922) considered it a variety of *Turricula lavinoides* OLSSON, 1922 (holotype Pl. 15, Fig. 2) from the Upper Pliocene Banano Formation of Costa Rica. The specimens from Cubagua are very large, comparable in size to the specimen figured by OLSSON (1922, pl. 4, fig. 12) from the Toro Cays and those found in the Lower Pleistocene Escudo de Veraguas Formation, Escudo de Veraguas Island, both in the Bocas del Toro area, Panama (BL coll.). The shells from Cubagua show little variability in shape or axial sculpture, although in some specimens secondary spirals are not developed in all the interspaces. There are some small differences between the shells from Cubagua and those from the Bocas area; there is an extra axial rib on the last whorl (9 vs. 8), the spiral cords are slightly stronger and the tubercles formed by the axial sculpture at the shoulder are slightly more pointed in the Bocas material. The specimens from the Moin Formation are again a little different. Numerous specimens from Los Corales, Puerto Limon (BL coll.) were examined, which are never as large (maximum height 52.4 mm) and again the tubercles at the shoulder are sharper. LANDAU & SILVA (2010a) considered these differences trivial, probably representing different ecomorphotypes. The protoconch is preserved in some of the Moin specimens and is paucispiral, of just under two whorls with a large nucleus, suggesting non-planktotrophic type of larval development. *Turricula lavinoides* OLSSON, 1922 again represents the same species with slightly broader ribs and less shouldered whorls. OLSSON (1922) described a similar type of protoconch as that seen in our Moin specimens (protoconch illustrated by JUNG, 1965, pl. 77, fig. 8). As first revisers (ICNZ, Art. 24.2), LANDAU & SILVA (2010a) chose the name *K. limonensis* over *K. lavinoides*.

**Text-Figure 25.** *Turricula lavinoides limonensis* and *Turricula lavinoides*.

Fig. 1. *Turricula lavinoides limonensis* OLSSON, 1922, holotype PRI 20926, height 67.8 mm, Toro Cays, Bocas del Toro, Panama, Nancy Point Formation, Upper Miocene. Fig. 2. *Turricula lavinoides* OLSSON, 1922, holotype PRI 20920, height 54.4 mm, Banano River, Costa Rica, Banano Formation, Upper Pliocene. Images courtesy of the Paleontological Research Institution.

JUNG (1965) illustrated a shell from the Lower Miocene Cantaure Formation of Venezuela as *K. aff. lavinoides*. This specimen is extremely similar to the Cubagua shells, with an analogous type of protoconch, but only about half the size. The Cantaure shells are smaller than the Cubagua and Bocas specimens (maximum height 58.1 mm), with a smaller apical angle. There are some small differences in sculptural details; the axial ribs are narrower, more prosocline, sinuous and more elevated giving the last
whorl a wider shape and the sutural platform is less concave, but the two are very closely related.

*Knefastia* is predominantly or possible exclusively a tropical American genus with a geological range from Oligocene to Recent. Powell (1966) mentioned some unsubstantiated records of *Knefastia* in the Miocene of France and Angola, but I have not encountered these records. They are more likely to refer to the similar western Atlantic genus *Clavatula* Lamarrck, 1801 which differs in having shells with a heavy, nodose infrasutural cord.

Today the genus is still represented in the southern Caribbean by *Knefastia hilli* Petuch, 1990b, which is not particularly similar to *K. limonensis* and as pointed out by Petuch (1990b) is most similar to the Recent Tropical American Pacific species *Knefastia olivacea* (G. B. Sowerby I, 1833). This is probably a separate group of *Knefastia* species. However, the *K. limonensis* group is represented in the Recent tropical American Pacific by *Knefastia funiculata* (Kiener, 1840), which again as a smaller shell, differing in details of the sculpture. The genus was also reported recently from the Pleistocene of Florida, *Knefastia lindae* Petuch, 1994, but again this species is not particularly similar to *K. limonensis*, as it is much squatter with a short spire and siphonal canal.

**Geological and geographical distribution:**
- Upper Miocene: Nancy Point Formation, Bocas del Toro, Panama (Olsson, 1922).
- Upper Pliocene: Banano Formation, Costa Rica (Olsson, 1922, as *Turricula lavionoides*).
- Lower Pleistocene: Moin Formation, Costa Rica (Olsson, 1922; Robinson, 1991); Escudo de Veraguas Formation, Bocas del Toro, Panama (BL coll.).

**Genus Fusiturricula** Woodring, 1928.
Type species *Turris (Surcula) fusinella* Dall, 1908, by original designation.

*Fusiturricula springvaleensis* (Mansfield, 1925)
Pl. 22, Figs 5-8

1925 *Turricula springvaleensis* Mansfield, p. 13, pl. 2, fig. 2.
1934 *Clavatula (Fusiturricula) pagodula* Rutsch, p. 95, pl. 5, fig. 12, pl. 7, fig. 9.
1942 *Clavatula (Fusiturricula) springvaleensis* (Mansfield) – Rutsch, p. 168, pl. 7, fig. 4.
1969 *Fusiturricula (kenfastia) bajanensis* Nowell-Usticke, p. 21, pl. 4, fig. 1047.
2001 *Knefastia alleni* Macsotay & Campos, p. 106, pl. 8, figs 2, 5-7.

**Material and dimensions:** Maximum height 72.8 mm, 13 specimens NMB lot 6932; eight specimens, Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; 10 specimens BL coll., (lower yellow fine sandy bed), two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
Some beautiful complete specimens of *Fusiturricula springvaleensis* (Mansfield, 1925), with intact aperture, were collected at Cerro Colorado, to the SW of the La Salle research station on Cubagua (Pl. 22, Fig. 5). Mansfield (1925) based the species on material from the Lower Pliocene Springvale Formation of Trinidad. The specimen he illustrated is damaged and juvenile (height 44 mm) with the axial sculpture clearly developed on the last whorl, similar to the juvenile specimen illustrated here (Pl. 22, Fig. 8). Rutsch (1942) figured a further, somewhat more adult specimen (hypotype NMB H 6249/1; height 68.6mm) from Breechin Castle Estate, Trinidad. This also has axial sculpture developed on the last whorl.

Rutsch (1934) described a similar species from the coeval Punta Gavilán Formation of Venezuela, *Clavatula (Fusiturricula) pagodula* (holotype NMB H 1942, paratypes H 1943-4, plus lot DS 5553), which differs by having far stronger axial sculpture forming prominent rounded tubercles at the
shoulder, and by having a horizontal rather than sloping sutural ramp. This description was based on fully adult shells.

Fortunately, specimens showing a growth series were found in the Lower Pliocene lower yellow fine sandy bed at Cerro Barrigón, Araya Peninsula (Pl. 22, Figs 6-8), demonstrating that the *F. springvaleensis* morphotype corresponds to juvenile shells, and that the sutural ramp becomes more horizontal with ontogeny. Tubercles at the shoulder can be either present (Pl. 22, Fig. 6) or absent (Pl. 22, Fig. 7) within the same assemblage. The proportion of shells with tubercles on the last whorl changes between assemblages; the shells at Cerro Colorado have mostly a smooth last whorl, whereas those from Punta Gavilán and the upper reddish coarse sandy bed at Cerro Barrigón, Araya Peninsula have tuberculate last whorls. LANDAU & SILVA (2010a) therefore considered *Clavatula (Fusiturricula) pagodula* to be a junior subjective synonym of *Fusiturricula springvaleensis*.

It seems that this large-shelled turrid can still be found living off Venezuela. *Knefastia altenai* MACSOTAY & CAMPOS, 2001, described from the Recent faunas of the Margarita Platform, clearly belongs within the genus *Fusiturricula*. MACSOTAY & CAMPOS (2001, pl. 8, figs 2, 5-7) illustrated two specimens showing exactly the same variability in the presence or absence of tubercles on the last whorl as in *F. springvaleensis*. LANDAU & SILVA (2010a) identified no significant difference between the fossil and Recent specimens and therefore, based on teleoconch morphology, considered *Knefastia altenai* to be a junior subjective synonym of *F. springvaleensis*. Unfortunately no information on the protoconch morphology for this species is available.

*Knefastia paulettae* PRINCZ, 1978, also described from the Recent faunas of the Gulf of Venezuela, also belongs within the genus *Fusiturricula*. The illustration of the holotype differs from *F. springvaleensis* in having axial sculpture that persists to the last whorl and more marked axial growth lines giving the surface a somewhat beaded appearance. Unfortunately, the type material consists of a single specimen (PRINCZ, 1978), so little is known of its intraspecific variability. The shells illustrated by PETUCH (1981, pl. 18, fig. 8), DÍAZ & PUYANA (1994, fig. 863) and RIOS (2009, fig. 811) as *F. jaquensis* (G. B. SOWERBY I, 1850) may be *F. paulettae* (PRINCZ, 1978), and the specimens illustrated by WILLIAMS (2006, no. 2520) as *F. jaquensis* are *Fusiturricula springvaleensis*. It may well be that *F. paulettae* is also a synonym of *F. springvaleensis*. True *Fusiturricula jaquensis* from the Miocene beds of the Dominican Republic has strongly elevated, rounded axial ribs (see MAURY 1917, pl. 8, fig. 1).

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934 as *Clavatula (Fusiturricula) pagodula*); Savaneta Glauconitic Sandstone Member of Springvale Formation, Trinidad (MANSFIELD, 1925; H. E. VOKES, 1938; RUTSCH, 1942).
Recent: Margarita Platform, Venezuela (MACSOTAY & CAMPOS, 2001 as *Knefastia paulettae*).

**Subfamily** Turrinae POWELL, 1942

**Genus** Polystira WOODRING, 1928.
Type species *Pleurotoma albida* PERRY, 1811, by original designation.

*Polystira* sp.
Pl. 22, Fig. 9

2010a *Polystira* sp. – LANDAU & SILVA, p. 110, pl. 22, fig. 9.

**Material and dimensions:** Maximum height 36.2 mm, 15 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:** A relatively slender, medium-sized *Polystira* species occurs in the Cañon de las Calderas assemblage, characterised by spire whorls with three keels, the central keel most strongly developed. A single secondary cord appears in the interspaces on the penultimate whorl. The last whorl is slender, with
the middle keel slightly more strongly developed, and tertiary spiral sculpture in the interspaces; the sinus is deep and U-shaped; the siphonal canal is very long and straight. Unfortunately the protoconch and first teleoconch whors are abraded in all specimens.

At present Jon Todd of the Natural History Museum, London is working on this group. He has kindly examined our shells and is of the opinion that it is one of the many undescribed tropical American Neogene *Polystira* species. It is most similar to the Recent Caribbean species *Polystira albida* (Perry, 1811), but this extant species has more numerous cords, five to seven per whorl as opposed to three in the Cubagua shell. *Polystira barretti* (Guppy, 1866) from the Early Pliocene Bowden Formation of Jamaica has more numerous cords, with a more prominent mid-whorl cord making the spire whors keeled, similar to *Polystira coltrorum* Petuch 1993 from the Recent waters off Brazil. I await this revision for Jon Todd to formally describe the species.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Subfamily **Clavinae** Powell, 1942  
Genus **Hindsiclava** Hertlein & Strong, 1955.  
Type species **Clavatula militaris** Hinds, 1843, by original designation.

**Hindsiclava caroniana** (Maury, 1925)  
Pl. 22, Fig. 10

<table>
<thead>
<tr>
<th>Year</th>
<th>Name</th>
<th>Author</th>
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</thead>
<tbody>
<tr>
<td>1925a</td>
<td><em>Drillia henekeni</em> var. <em>caroniana</em> Maury, p. 189, pl. 32, fig. 12.</td>
<td></td>
</tr>
<tr>
<td>2010a</td>
<td><em>Hindsiclava caroniana</em> (Maury, 1925) – Landau &amp; Silva, p. 110, pl. 22, fig. 10.</td>
<td></td>
</tr>
</tbody>
</table>

**Material and dimensions:** Maximum height 70.9 mm, seven specimens NMB lot DS 30/1; one specimen NMB lot DS 30/2; 22 specimens EDIMAR coll.; 16 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, one specimen BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; nine specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**
As pointed out in the species description (Maury, 1925), *Hindsiclava caroniana* differs from the Lower Pliocene *Hindsiclava henekeni* (G. B. Sowerby I, 1850) from the Gurabo Formation of the Dominican Republic in having more numerous but less prominent axial ribs (11-12 vs. 7-8), which weaken abapically, becoming subobsolete on the last whorl in the largest specimens. Moreover, *H. henekeni* has more angular whors, especially the last whorl, which is rather rounded at the shoulder in *H. caroniana*. The shells from Cubagua are larger than those from the Lower Pliocene Springvale Formation of Trinidad, but otherwise similar. The specimen figured by Jung (1969, pl. 59, fig. 4; NMB H 15316) is incomplete, the sculpture is similar to that seen in the Cubagua material, except that the axial ribs are strong on the adapical portion of the last whorl, whereas they are subobsolescent in the Cubagua shells. *Hindsiclava consors* (G. B. Sowerby I, 1850), also originally described from the Dominican Neogene deposits, but subsequently recorded from numerous other Caribbean Neogene assemblages (Brown & Pilsbry, 1911; Maury, 1920, 1925; Olsson, 1922; Rutsch, 1934; Woodring, 1970) has a smaller shell with more numerous axial and spiral elements forming a reticulate sculpture. These and numerous other related forms that occur in the Tropical American Neogene assemblages await revision.

The genus *Hindsiclava* is well-represented in the Recent faunas on both sides of the Isthmus of Panama. Both *Hindsiclava chazaliei* (Dautzenberg, 1900) and *Hindsiclava tippetti* Petuch, 1987 from the southern Caribbean have finer sculpture than *H. caroniana* and are more closely similar to *H. consors*. It is almost impossible to know what is meant by *Hindsiclava jungi* Macsotay & Campos, 2001 as, due to the poor photographic quality, their figures could represent any *Hindsiclava* species (Macsotay & Campos, 2001, p. 107, cover fig. 2, pl. 8, figs, 12-13, pl. 3, figs 9-12). The description states three spiral
cords on the spire whorls, 13-17 spiral cords and 23-27 axial ribs on the last whorl. *Hindsiclava caroniana* has more numerous spiral elements on the spire whorls and far fewer axial ribs on the last whorl. *Hindsiclava macilenta* (DALL, 1889) from the Recent Caribbean has a much more slender shell with finer sculpture. All the tropical American Pacific *Hindsiclava* species: *Hindsiclava andromeda* (DALL, 1919), *H. hertleini* EMERSON & RADWIN, 1969, *H. militaris* (REEVE, 1843) and *H. resina* (DALL, 1908) have shells with finer sculpture, finer, more acute axial ribs and more angular whorls, again, more similar to *H. consors* than *H. caroniana*.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Savaneta Glauconitic Sandstone Member and ?Melajo Clay Member of Springvale Formation, Trinidad (MAURY, 1925a; H. E. VOKES, 1938; JUNG, 1969).

**Genus Crassispira SWAINSON, 1840.**
Type species *Pleurotoma bottae* VALENCIENNES in KIENER, 1840, by subsequent designation, HERRMANNSEN, 1847.

*Crassispira* cf. *tyloessa* WOODRING, 1970
Pl. 22, Fig. 11


**Material and dimensions:** One specimen BL coll., height 19.6 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
The single Cubagua shell was compared with *Crassispira tyloessa* WOODRING, 1928 from Cativa, Middle-Upper Miocene, Gatun Formation, Panama (BL coll.), which is very similar. The Cubagua shell is slightly larger than any specimen we have seen from Panama (max. height 15.3 mm WOODRING, 1928), broader, with more convex whorls, the first infrasutural cord forms a weaker shoulder, and the base is less constricted. The infrasutural area in *C. tyloessa* bears two weak spiral cords, absent from the Cubagua shell. Although closely related, they are probably distinct species.

Numerous *Crassispira* species occur in the Recent Caribbean faunas with shells differing in sculptural details (see WILLIAMS, 2006, no. 3100-3143). The most similar to the fossil from Cubagua are *Crassispira apicata* (REEVE, 1845) found from Colombia to Brazil, which has a shell with a wider infrasutural collar and more angular whorls, and *Crassispira luctuosa* (ORBIGNY, 1842) again with more angular whorls and a more scalate spire.

**Geological and geographical distribution:** Atlantic
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

*Crassispira* sp.
Pl. 22, Fig. 12

2010a *Crassispira* sp. – LANDAU & SILVA, p. 111, pl. 22, fig. 12.

**Material and dimensions:** One specimen height, height 21.1 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
This species is represented by a single, slightly worn shell, complete except for its protoconch. It is similar to specimens of *Crassispira ponida* WOODRING, 1928 from the Lower Pliocene Bowden Formation of Jamaica, but slightly more elongated. It is similar to the Recent species *Crassispira apicata* (REEVE, 1845) found from Colombia to Brazil, but differs in having a more elongated shell and the axial ribs do not form tubercles at the shoulder as in *C. apicata*. The tubercles give the whorls of *C. apicata* a
somewhat angular appearance.

**Geological and geographical distribution: Atlantic**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Genus *Clathrodrillia* DALL, 1918.

Type species *Pleurotoma gibbosa* BORN, 1778, by original designation.

*Clathrodrillia gatunensis* sensu lato

Pl. 23, Fig. 1

2010a *Clathrodrillia gatunensis* sensu lato – LANDAU & SILVA, p. 111, pl. 23, fig. 1.

**Material and dimensions:** Maximum height 51.7 mm, seven specimens EDIMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, six specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; two specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

WOODRING (1970) discussed the various *Crassipira* species occurring in the Middle-Upper Miocene Gatun Formation of Panama, and concluded that they corresponded to a single variable species: *Clathrodrillia gatunensis* (TOULA, 1909). The fact that he described the protoconch as “(...) 1¾ to 4-whorled, generally 1¾ to 2; (...)” WOODRING (1970, p. 382) strongly suggests that he had at least two species represented in his material. Unfortunately none of the shells from Cubagua bears the protoconch, which is essential in the classification of turrids. LANDAU & SILVA (2010a) therefore consider the Cubagua specimens to be *Clathrodrillia gatunensis* sensu lato and omitted any distribution data until this group is revised.

This species group is still present in the southern Caribbean Sea, represented by *Clathrodrillia gibbosa* (BORN, 1778) [*Clathrodrillia mareana* WEISBORD, 1962, p. 437, pl. 41, figs 16-17 is a junior subjective synonym], which has a shell differing from the Cubagua fossils in having less strongly prosocline axial sculpture and in having the axial and spiral elements of more equal strength, giving the surface a somewhat beaded appearance, whereas the axial sculpture is predominant and the spirals much weaker in the Cubagua shells. I have not been able to find any information on the protoconch morphology in *C. gibbosa* and again stress a revision of the group is needed taking this into account.

**Geological and geographical distribution: Atlantic**

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

*Clathrodrillia* cf. *titra* WOODRING, 1928

Pl. 23, Fig. 2


**Material and dimensions:** One specimen BL coll., height 33.4 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**

The single Cubagua specimen is reasonably well preserved, but, like almost all the Cubagua material, the protoconch is missing. It is closely similar to *Clathrodrillia titra* WOODRING, 1928 from the Lower Pliocene Bowden Formation of Jamaica, and differs mainly in the sculpture of the infrasutural area; according to the original figure flat to concave, bearing narrow rounded cords in *C. titra*, whereas in the Cubagua shell there is a broad rounded infrasutural cord, overlain by finer secondary cords. It is also similar to the Dominican Republic species *Clathrodrillia venusta* (G. B. SOWERBY I, 1850) from the Lower Pliocene Gurabo Formation, but the latter attains a much larger size, the spiral sculpture consists of fine threads rather than overlapping bands, and the Dominican species has an infrasutural area similar to *C.
**SYSTEMATIC PALAEOONTOLOGY**

*tityra. Clathrodillia dautzenbergi* (Tippett, 1995) from the Recent southern Caribbean has a similar-shaped shell, but with more close-set and sharper sculpture.

**Geological and geographical distribution: Atlantic**

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Subfamily Mangeliinae Fischer, 1887

This group is placed in the Conidae rather than the Turridae by Taylor et al. (1993) and Pulliandre et al. (2009).

Genus **Bellaspira** Conrad, 1868.

Type species *Mangelia virginiana* Conrad, 1862, by monotypy.

*Bellaspira niaddrina* (Mansfield, 1925) 
Pl. 23, Fig. 3

1925 *Drillia niaddrina* Mansfield, p. 23, pl. 4, figs 6, 8.

2010a *Bellaspira niaddrina* (Mansfield, 1925) – Landau & Silva, p. 112, pl. 23, fig. 3.

**Material and dimensions:** Maximum height 23.4 mm, 11 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; 5 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

Landau & Silva (2010a) provisionally placed this species in the genus *Bellaspira* Conrad, 1868 (see McClean & Poorman, 1970). None of the Cubagua specimens is complete, all lack the protoconch, and the outer lip is usually broken. It seems that all were inhabited by hermit crabs after death and almost all are incrusted with corals. Our shells are probably conspecific with the shells described by Mansfield (1925) as *Drillia niaddrina* from the Middle Miocene Brasso Formation of Trinidad. The description given by Mansfield (1925) coincides fairly well with our shells from Cubagua, except that he records 14 and 16 axial ribs on his two specimens. Judging from his figures (Mansfield, 1925, pl. 4, figs 6, 8) this must be lapsus, as there cannot be more than 7-8 axials per whorl. The Cubagua shells have 7-8 axials that extend from suture to suture, on some whorls intercalated, others vertically aligned. The spiral sculpture consists of about seven flattened cords of irregular width. *Bellaspira margaritensis* McClean & Poorman, 1970 based on Recent specimens from the southern Caribbean coasts of Colombia and Venezuela (McCLean & Poorman, 1970; Díaz & Puyana, 1994) is very similar, also with seven axial ribs per whorl, a spiral sculpture consisting of fine spiral grooves and a conspicuous parietal tubercle. However, the Recent species has a more slender shape as opposed to the rather squat appearance of the fossils, and *B. margaritensis* has a shell with broader axial ribs.

**Geological and geographical distribution:**

Middle Miocene: Brasso Formation, Trinidad (Mansfield, 1925).

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

Genus **Miraclathurella** Woodring, 1928.

Type species *Miraclathurella vittata* Woodring, 1928, by original designation.

*Miraclathurella sp.*

Pl. 23, Fig. 4

2010a *Miraclathurella sp.* – Landau & Silva, p. 112, pl. 23, fig. 4.

**Material and dimensions:** One specimen BL coll., height 13.7 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.
Discussion:

The single available specimen is poorly preserved, the protoconch and early teleoconch whorls are decorticated. It is characterised by three spiral cords on the spire whorls and about ten on the last whorl. Secondary spiral cords are present in the interspaces on the last whorl, very weak below the suture, gaining in strength abapically, so that at the base the primary and secondary cords are almost of equal strength.

LANDAU & SILVA (2010a) were unable to match the sculpture of the Cubagua specimen with that of any of the described species. In the fossil record the shell of *Miraclathurella ralla* JUNG, 1969, from the Lower Pliocene Melajo Member of the Springvale Formation of Trinidad, is immediately distinguished by the greater number of spiral cords on the spire whorls. *Miraclathurella eucharis* WOODRING, 1970 from the Middle-Upper Miocene Gatun Formation of Panama has a smaller shell, again more numerous cords on the spire whorls, and does not have secondary spiral sculpture on the last whorl. *Miraclathurella vittata* WOODRING, 1928 and *M. entemna* WOODRING, 1928, from the Pliocene Bowden Formation of Jamaica, *M. subconsors* (BOSE, 1910) from the Upper Pliocene Agueguexquite Formation of Mexico and *M. amica* (PILSBRY & JOHNSON, 1917) from the Dominican Neogene all have shells with a finer sculpture with more axial and spiral cords. *Miraclathurella gracilis* (GABB, 1873) has a much more elongated shell shape as well as finer sculpture. In the Recent Caribbean fauna *M. kleinrosa* (USTICKE, 1969) has a much smaller shell and finer sculpture.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Genus *Dolostoma* WOODRING, 1970.

Type species *Dolostoma anorhepes* WOODRING, 1970, by original designation.

*Dolostoma sp.*

Pl. 23, Fig. 5

2010a  *Dolostoma sp.* – LANDAU & SILVA, p. 113, pl. 23, fig. 5.

Material and dimensions: One specimen BL coll., height 15.4 mm, Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

Discussion:

Unusually for the Cubagua material, the protoconch is preserved, albeit somewhat worn. It consists of about three whorls, with a small nucleus. The last protoconch whorl bears prosocline axial riblets similar to those illustrated by WOODRING (1970, pl. 66, fig. 2) for the genus. Our shell is very similar in shape to the shell of *Dolostoma dinota* WOODRING, 1970 from the Middle-Upper Miocene Gatun Formation of Panama, which also has somewhat angular whorls. However, in the Gatun shell the axial ribs are obsolete on the last whorl whereas they are strongly developed in our Venezuelan specimen. *Dolostoma anorhepes* WOODRING, 1970, also from the Gatun Formation has a more elongated shell with less angular whorls.

Geological and geographical distribution:

Lower Pliocene: Araya Formation, Cubagua Island, Venezuela.

Family Terebridae MÖRCH, 1852

Subfamily Terebrinae MÖRCH, 1852

Genus *Terebra* BRUGUIÈRE, 1789.

Type species *Buccinum subalatum* LINNAEUS, 1758, by monotypy.

BRATCHER & CERNOHORSKY (1987) in their revision of the living Terebridae concluded that the shell characters were overlapping, and placed almost all the subgenus and genus-level names previously proposed within the Terebridae in a single genus *Terebra* BRUGUIÈRE, 1789 (he also recognised *Hastula* H. & A. ADAMS, 1853, *Duplicaria* DALL, 1908 and *Terenolla* Iredale, 1939, groups not relevant to the present work). According to the revision by BRATCHER & CERNOHORSKY (1987), the genus *Terebra* includes all
members of the family with shell characters inconsistent with those of the other genera. Most subsequent authors have followed this opinion. Exceptions in the New World literature are PETUCH (1994), who raised *Myurellina* and *Strioterebrum* SACCO, 1891 to full generic status, and some European authors who continue to recognise the genus *Strioterebrum* (CAVALLO & REPETTO, 1991; LOZOUET et al., 2001; SILVA, 2001).

Despite the remarkably homogeneous shell form within the family, the foregut and radular morphology vary widely, reflecting different feeding mechanisms incongruous with the uniformity of shell characters (TAYLOR, 1990). Furthermore, recent DNA work shows that most, if not all, the proposed genera within the Terebridae are polyphyletic (HOLFORD et al., 2009). The current classification is not satisfactory, and unhelpful in palaeobiogeography. We therefore adopt the same approach here as we did with the family *Conus*, and consider *Myurellina* an informal species group. For *Strioterebrum* we follow LOZOUET (2001) and others and consider it a distinct genus.

*Terebra aclinica* OLSSON, 1967

Pl. 23, Figs 6-7

1967a  *Terebra (Myurellina) aclinica* OLSSON, p. 17, pl. 3, fig. 1.

1994  *Myurellina aclinica* (OLSSON, 1967) – PETUCH, pl. 97, fig. B.

2010a  *Terebra aclinica* OLSSON, 1967 – LANDAU & SILVA, p. 113, pl. 23, figs 6-7.

**Material and dimensions:** Maximum height 86.7 mm, two specimens NMB lot 9499; seven specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island; one specimen BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

**Discussion:**

*Terebra aclinica* OLSSON, 1967 forms part of a group of large *Terebra* species that BARSCH (1923) and OLSSON (1967a) placed in the subgenus *Myurellina* BARTSCH, 1923, and is here used as an informal species group. This subgenus was proposed for *Terebra* species with two columellar folds (Pl. 24, Fig 2), a bipartite sculpture separated by a narrow groove, and weak axial sculpture, often obsolete on later adult whorls (see also OLSSON, 1967a). Whilst there may be overlap between the shell characters the subgenus/genus *Myurellina* and other Terebridae that make it impossible to define subgeneric units, it certainly belongs to a group of *Terebra* species that were widespread in the Caribbean Neogene, but today occur only in the tropical American Pacific; i.e. what WOODRING (1928) would define as a Paciphile group. This is the first record of the “*Myurellina* group” in the southern Caribbean Neogene.

The Cubagua material was compared with specimens of *Terebra aclinica* from Late Pliocene Pinecrest Beds, APAC Pit, Sarasota County, Florida (BL coll.) and can find no difference between specimens. Both shells are somewhat variable is the strength of the axial sculpture, but the profile, height of the whorls and comparative width and strengths of the bands are similar. Whilst it seems unlikely that a species until now known only from the Upper Pliocene Pinecrest Formation of Florida should be found in the Lower Pliocene Araya Formation of Venezuela for reasons discussed in the palaeogeographical section, some *Terebra* species of the “*Myurellina* group” are known to have planktotrophic larval development (i.e. *Terebra robusta*, see BRATCHER & CERNOHORSKY), and therefore wider dispersal potential. The only taxa encountered in this work that are present in both the southern Caribbean Lower Pliocene and the Floridian Plio-Pleistocene, are the famously cosmopolitan groups, the Tonnoideans and *Architectonica*, and *Jenneria loxahatcheensis* (M. SMITH, 1934).

**Geological and geographical distribution:** Atlantic

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela.

**Terebra lehneri** RUTSCH, 1942  
Pl. 23, Figs 8-9

1934 *Terebra (Paraterebra) lehneri* RUTSCH, p. 109, pl. 9, fig. 7.  
1967a *Terebra (Paraterebra) inaequalis lehneri* RUTSCH – OLSSON, p. 14, pl. 4, fig. 3.  

**Material and dimensions:** Maximum height (incomplete) 92.7 mm, five specimens NMB lot DS 6935; three specimens EDIMAR coll.; eight specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**  
This species is usually placed in the subgenus *Paraterebra* OLSSON, 1967, characterized by attenuated, slender shells with a tripartite sculpture, in which the sculpture is strong on earlier spire whorls, but obsolete on later ones (OLSSON, 1967a). The strong sculpture on the early whorls is clearly illustrated on Plate 13, Figure 5. All the examined shells from Cañon de las Calderas are incomplete, but the largest specimen (almost complete) would suggest a maximum height of about 105 mm, larger than that recorded by OLSSON (1967a). The holotype NMB H 1975 is also incomplete, a fragment similar in size and stage of growth to the specimen on Plate 13, Figure 5. A preserved colour pattern of large irregular axial blotches is observed on some specimens even without ultra-violet light, similar to that illustrated by OLSSON (1967a, pl. 4, fig. 3b). As mentioned by OLSSON (1967a), the Cubagua shells are more slender than typical *Terebra inaequalis* G. B. SOWERBY I, 1850, with a uniform taper, and LANDAU & SILVA (2010a) therefore considered them to belong to a distinct species. In its tripartite sculpture the shell of *Terebra lehneri* RUTSCH, 1942 is similar to *Terebra isaacpetiti* MAURY (1925), which is widespread in the Caribbean Neogene. However, in this species the sculpture remains strong on later teleoconch whorls (see OLSSON, 1967a, pl. 3, fig. 4; WOODRING, 1970, pl. 61, figs 12-13). The persistence of sculpture on the later whorls characterises OLSSON’S (1967a) *Oreoterebra* species group. The *Paraterebra* species group is still represented in the Caribbean today by *Terebra taurina* (LIGHTFOOT, 1786) (WOODRING, 1970).

**Geological and geographical distribution:**  
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (OLSSON, 1967a); Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).

**Genus Strioterebrum SACCO, 1891.**  
Type species *Terebra basteroti* NYST, 1845, by original designation.

*Strioterebrum meesmanni* RUTSCH, 1934  
Pl. 23, Fig. 10

1934 *Terebra (Strioterebrum) gatunensis meesmanni* RUTSCH, p. 108, pl. 9, figs 14-15.  
2010a *Strioterebrum meesmanni* RUTSCH, 1934 – LANDAU & SILVA, p. 114, pl. 23, fig. 10.

**Material and dimensions:** Maximum height 31.7 mm, two specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**  
Two shells from Cubagua were examined, which are ascribe to *Strioterebrum meesmanni* RUTSCH, 1934. They are characterized by their predominantly axial sculpture, relatively wide subsutural cord followed by a narrow groove and five weak spiral cords (on the penultimate whorl). The columella fold is obscured by matrix in the type material, but in the Cubagua specimens is broad and obscurely bipartite. *Strioterebrum wolfgangi* (TOULA, 1909) from the Middle-Upper Miocene Gatun Formation of the Gatun area and the Pliocene Cayo Agua Formation of the Bocas del Toro area, Panama, is similar, but in this species the spiral cords on the abapical half of the whorl are much thinner. *Strioterebrum laevisascula* (MAURY, 1917) described from the Dominican Neogene, but also recorded from the Lower Pliocene Melajo Member of the Springvale Formation of Trinidad (JUNG, 1969), has stronger tubercles on the subsutural band.
**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934).

**Strioterebrum weisbordi** GIBSON-SMITH & GIBSON SMITH, 1984
Pl. 23, Fig. 11

1962 *Terebra* (Strioterebrum) gatunensis kugleri RUTSCH, 1934 – WEISBORD, p. 428, pl. 40, figs 12-13, pl. 45, figs 24-25 [non *Terebra* (Strioterebrum) gatunensis kugleri RUTSCH, 1934 = Strioterebrum spiriferum (DALL, 1895)].


1981 *Terebra* (Strioterebrum) gatunensis kugleri RUTSCH, 1934 – PETUCH, p. 336, figs 99-100 [non *Terebra* (Strioterebrum) gatunensis kugleri RUTSCH, 1934 = *S. spiriferum* (DALL, 1895)].

1984 *Strioterebrum weisbordi* GIBSON-SMITH & GIBSON SMITH, p. 61, pl. 1, figs 1-2.

2010a *Strioterebrum weisbordi* GIBSON-SMITH & GIBSON SMITH, 1984 – LANDAU & SILVA, p. 115, pl. 23, fig. 11.

**Material and dimensions:** Maximum height 37.0 mm, three specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas, Cubagua Island.

**Discussion:**
*Strioterebrum weisbordi* GIBSON-SMITH & GIBSON SMITH, 1984 is similar to *Strioterebrum spiriferum* (DALL, 1895), which also occurs in the southern Caribbean Lower Pliocene in the Punta Gavilán Formation [Terebra (Strioterebrum) gatunensis kugleri RUTSCH, 1934 = *S. spiriferum* (DALL, 1895), see WOODRING, 1970, p. 409] and Melajo Clay member of the Springvale Formation of Trinidad (WOODRING, 1970). However, it differs from *S. spiriferum* in being smaller, in having less elevated whorls, the spiral groove below the subsutural cord is wider and across it the axial ribs are subobsolete. The columellar fold in *S. weisbordi* is strongly bipartite, whereas in *S. spiriferum* it is broad and low. The base of the whorl is more strongly constricted in *S. weisbordi*, resulting in a shorter more strongly recurved siphonal canal than in *S. spiriferum* (GIBSON-SMITH & GIBSON SMITH, 1984).

The shells from Cubagua are not identical to the type material; the holotype (NMB 17098) has only three spiral cords below the stronger adapical cord on the spire whorls, whereas the Venezuelan shells have four or five. The character of the base, the wide groove below the subsutural cord, and the strongly bipartite columellar fold are similar.

The shell of *Strioterebrum dislocatum* (SAY, 1822) differs from *S. weisbordi* in having fewer axial ribs, the subsutural cord is wider, followed by a narrower spiral groove, and the two columellar folds are fused into a single fold, not strongly bipartite as in *S. weisbordi*. BRATCHER & CERNOHORSKY (1987) synonymised *S. weisbordi* with *Terebra dislocata* (SAY, 1822). However, the Venezuelan material was compared with *S. dislocatum* from the Plio-Pleistocene of Florida, and the differences discussed above found to be consistent. They are therefore considered distinct species.

**Geological and geographical distribution:**
Lower Pliocene: Araya Formation, Cubagua Island, Venezuela; Tuberá Group, northern Colombia (NMB lot 18220).


Recent: North coast of Venezuela from Golfo de Venezuela to Isla Margarita.

Superfamily Architectonicoidea GRAY, 1850
Family Architectonicidae GRAY, 1850
Genus *Architectonica* RÖDING, 1798.
Type species *Trochus perspectivus* LINNAEUS, 1758, by subsequent designation, J. E. GRAY, 1847.
**Architectonica nobilis** RÖDING, 1798
Pl. 23, Fig. 12

1798  
**Architectonica nobilis** RÖDING, p. 78.

1816  
*Solarium granulatum* LAMARCK, pl. 446, fig. 5 [non Solarium granulatum LEA, 1833]
1832  
*Solarium granosum* VALENCIENNES, p. 269.
1844  
*Solarium quadriceps* HINDS, p. 50, pl. 14, figs 7-8.
1849  
*Solarium verrucosum* PHILIPPI, p. 172.
1850  
*Solarium quadriseriatum* G. B. SOWERBY I, p. 51, pl. 10, fig. 8.
1853  
*Solarium verrucosum* PHILIPPI, p. 10, pl. 2, figs 5-6.
1857  
*Architectonica pesspectiva* – TUOMEY & HOLMES, p. 120, pl. 26, fig. 6.
1859  
*Architectonica Valenciennesii* MÖRCH, p. 122.
1863  
*Solarium (Architectonica) nobile* BOLTEN – HANLEY, p. 230, pl. 253, fig. 35.
1863  
*Solarium (Architectonica) granulatum* DESHAYES – HANLEY, p. 231, pl. 250, figs 1-2.
1864  
*Solarium verrucosum* PHILIPPI – REEVE, pl. 2, fig. 8.
1864  
*Solarium granulatum* LAMARCK – REEVE, pl. 2, fig. 7.
1864  
*Solarium granulatum* LAMARCK – REEVE, pl. 2, figs 5-6.
1865  
*Architectonica pespectiva* – TUOMEY & HOLMES, p. 120, pl. 26, fig. 6.
1867  
*Architectonica nobilis* RÖDING, p. 78.
1870  
*Solarium sexlineare* NELSON, p. 11, pl. 6, fig. 11.
1875  
*Solarium (Solarium) granulatum* LAM. – MARSHALL, p. 11, pl. 5, figs 53-54.
1875  
*Solarium (Solarium) verrucosum* PHIL. – MARSHALL, p. 12, pl. 5, figs 53-54.
1887  
*Solarium (Architectonica) granulatum* LAM. – MARSHALL, p. 11, pl. 5, figs 53-54.
1887  
*Solarium (Architectonica) granulatum* LAM. – MARSHALL, p. 11, pl. 5, figs 53-54.
1890  
*Solarium ordinarium* E. A. SMITH, p. 281, pl. 21, fig. 17.
1906  
*Solarium villarelloi* BÖSE, p. 30, pl. 3, figs 4-11.
1909  
*Solarium gatunense* TOULA, p. 692, pl. 25, fig. 3.
1917  
*Solarium quadriseriatum* SOWERBY – MAURY, p. 131, pl. 23, figs 1-2.
1922  
*Architectonica granulata* LAMARCK – OLSSON, p. 154, pl. 13, figs 10-12.
1925a  
*Solarium intraornatum* WHITE – MAURY, p. 59, pl. 2, fig. 1.
1925b  
*Solarium granulatum* LAMARCK – MAURY, p. 61, pl. 2, figs 6-12.
1927  
*Architectonica granulata* LAMARCK – HODSON et al., p. 66, pl. 36, fig. 7.
1928  
*Architectonica (Architectonica) nobilis quadriseriata* (SOWERBY) – WOODRING, p. 354, pl. 27, figs 5-7.
1929  
*Architectonica granulata* LAMARCK – WEISBORD, p. 259, pl. 9, fig. 15.
1930  
*Architectonica granulata* LAMARCK – MANSFIELD, p. 110, pl. 18, figs 1-2.
1932  
*Architectonica (Architectonica) sexlinearis* (NELSON) – OLSSON, p. 213, pl. 21, figs 7, 10.
1932  
*Architectonica sexlinearis* corsica OLSSON, p. 214, pl. 21, figs 5, 8, 9.
1934  
*Architectonica nobilis* (BOLTEN) RÖDING, 1798 – RUTSCH, p. 42, pl. 1, figs 5-7.
1935  
*Solarium gatunense* TOULA – TRECHMANN, p. 549, pl. 21, figs 21-22.
1939  
*Architectonica granulata* LAMARCK – OINOMIKADO, p. 620, pl. 29, fig. 11.
1948  
*Architectonica nobilis* “BOLTEN” RÖDING, 1798 – GARDNER, p. 199, pl. 24, figs 9, 13.
1950  
*Architectonica nobilis* BOLTEN – DURHAM, p. 124, pl. 34, figs 5-7.
1954  
*Architectonica nobilis* RÖDING – ABBOTT, p. 142, pl. 4, fig. m.
1956  
*Architectonica nobilis* RÖDING – PARKER, p. 341, pl. 5, fig. 7.
1958  
*Architectonica nobilis* RÖDING, 1798 – KEEN, p. 292, fig. 191.
1959a  
*Architectonica (Architectonica) nobilis nobilis* RÖDING – WOODRING, p. 165, pl. 19, figs 1-6, 10-12, 14-16.
1960  
*Architectonica (Architectonica) nobilis quadriseriata* (SOWERBY) – PERRILLIAT, p. 18, pl. 3, figs 4-5.
1960  
*Architectonica granulata* LAMARCK – BARRIOS, p. 268, pl. 8, figs 5-6.
1960  
*Architectonica nobilis* – PARKER, p. 321, pl. 4, fig. 1.
1961  
*Architectonica (Architectonica) nobilis nobilis* RÖDING – PFLUG, p. 17, pl. 1, figs 1-7.
1961  
*Architectonica nobilis* RÖDING, 1798 – WARMKE & ABBOTT, p. 65, pl. 11, fig. g
1962  
*Architectonica nobilis* RÖDING – WEISBORD, p. 152, pl. 13, figs 15-16.
1964b  
*Architectonica nobilis* RÖDING – PARKER, p. 345, pl. 4, fig. 1.
Material and dimensions: Maximum diameter 52.5 mm, five specimens NMB lot 6920/1; two specimens NMB lot 6920/2; one specimen NMB lot DS 6941; 10 specimens EDIMAR coll.; 17 specimens BL coll., Lower Pliocene, Araya Formation Cañon de las Calderas; three specimens BL coll., Lower Pliocene, Araya Formation Cerro Colorado, Cubagua Island; 10 specimens BL coll., (upper reddish coarse sandy bed), Lower Pliocene, Aramina Formation Cerro Barrigón, Araya Peninsula.

Discussion:

The Architectonicidae are the only other group apart from the tonnoideans known to have an extended feeding veliger stage enabling larvae to live in the water column for long periods of time and thus to cover great distances passively in ocean currents, ensuring wide distribution ranges (Bieler, 1993). Already Woodring (1959a) recognized that there was a single taxon on both sides of the tropical American Isthmus and synonymised all the earlier nominal taxa under the name *Architectonica (Architectonica) nobilis nobilis* Röding, 1798. Thus *Architectonica nobilis* is probably the longest living and most geographically widespread of all tropical American gastropods.

Woodring (1959a) considered *Architectonica karsteni* Rutsch, 1934, which often coexists with *A. nobilis* in the Caribbean Neogene, as a subspecies, *Architectonica nobilis karsteni* Rutsch, 1934. However, DeVries (1985) and Bieler (1993) gave it full specific status. The shell of Architectonica karsteni differs from *A. nobilis* by not having a distinctly separated proxiumbilical rib on the base, the umbilical crenae forming the only obvious spiral rib around the umbilicus. It has a geological history at least as ancient as that of *A. nobilis*, occurring in the western Atlantic Lower Miocene Cantaure Formation of Venezuela (Jung, 1965) and the eastern Pacific Middle Miocene Daule Formation of Ecuador (Marks, 1969).
1951, as *A. sexlinearis corusca*). *Architectonica karsteni* has not been found in the Cubagua assemblage.

**Geological and geographical distribution: Atlantic**

Lower Miocene: Pirabas Limestone, Brazil (MAURY, 1925b, as *Solarium granulatum*); Baitoa Formation, Dominican Republic (BL coll.); Cantaure Formation, Venezuela (JUNG, 1965).

Middle Miocene: Shoal River Formation, Florida (GARDNER, 1947, as *A. quadriseriata waltonensis*); lower Gatun Formation, Panama (TOULA, 1909, as *Solarium gatunense*; BROWN & PILSBRY, 1911, as *Solarium granulatum gatunense*; WOODRING, 1959).

Upper Miocene: middle and upper Gatun Formation, Panama (TOULA, 1909, as *Solarium gatunense*; BROWN & PILSBRY, 1911, as *Solarium granulatum gatunense*; WOODRING, 1959); Cercado Formation, Dominican Republic (MAURY, 1917, as *Solarium quadriseriatum*; PFLUG, 1960); Usiacuri Formation, Colombia (WEISBORD, 1929, as *A. granulatum*; OINOMIKADO, 1939, as *A. granulata*; BARRIOS, 1960, as *A. granulatum*); Maturaca Member of Caujarao Formation, El Carrizal, Venezuela (NMB unnumbered lot).

Lower Pliocene: Araya Formation, Cubagua Island; Aramina Formation, Araya Peninsula, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (RUTSCH, 1934); Savaneta Glauconitic Sandstone Member and Melajol Clay Member of Springvale Formation, Trinidad (MAURY, 1925a, as *A. granulata*; JUNG, 1969); Gurabo Formation, Dominican Republic (MAURY, 1917, as *Solarium quadriseriatum*; PFLUG, 1960).

Lower-Middle Pliocene: Bowden Formation, Jamaica (WOODRING, 1928 as *A. nobilis quadriseriata*);

Upper Pliocene: Chucatuck Formation, Virginia (TUOMEY & HOLMES, 1857; GARDNER, 1948; CAMPBELL, 1993); Pinecrest Beds, Florida (unit 7, PETUCH, 1994, as *A. catanesei*); Duplin Marl, Florida (MANSFIELD, 1930, as *A. granulata*); Isthmus of Tehuantepec, Mexico (BOSE, 1906, as *Solarium villareloii*; PERRILLIAT, 1960, as *A. nobilis quadriseriata*, 1972); Banano Formation, Costa Rica (OLSSON, 1922, as *A. granulata*).

Lower Pleistocene: Caloosahatchee Formation, Florida (BL coll.); Moin Formation, Puerto Limon, Costa Rica (BL coll.); Maiquetia Member of the Playa Grande Formation, Venezuela (WEISBORD, 1962); Mare Formation, Cabo Blanco, Venezuela (WEISBORD, 1962).

Middle-Upper Pleistocene: Bermont Formation, Florida (PETUCH, 1994); Upper Pleistocene: Fort Thompson Formation, Florida (PETUCH, 1994); La Isabella Formation, Dominican Republic (BL coll.).

Recent: subtropical and tropical eastern and western Atlantic, usually shallow water on sandy substrates, 1-250 m depth (BIELER, 1993; ARDOVINI & COSSIGNANI, 2004).

**Geological and geographical distribution: Pacific**

Middle Miocene Zorritos Formation, Peru (NELSON, 1870, as *Solarium sexlineare*); Las Massas sector, Ecuador (MARKS, 1951).


Lower Pliocene: Jama Formation (PILSBRY & OLSSON, 1941, as *A. sexlinearis*).

Pleistocene: Charco Azul Group, Burica Peninsula, Costa Rica (BL coll.); Montezuma Formation, Nicoloya Peninsula, Costa Rica (BL coll.); Armuelles Formation, Burica Peninsula, Panama (BL coll.); Santa Ines Bay, Baja California, Mexico (DURHAM, 1950).

Recent: Lower California to northern Peru, 1-100 m depth (BIELER, 1993).
CHAPTER 4: PALAEOECOLOGY OF THE LOWER PLIOCENE CAÑON DE LAS CALDERAS MOLLUSCAN ASSEMBLAGE

The Cubagua outcrop contains a relatively abundant and diverse gastropod assemblage, 126 species are recorded belonging to 95 genera and species-group (sensu VERMEIJ & PETUCH, 1982). This diversity is similar to that found in other Caribbean Neogene shallow-water assemblages for the larger gastropod taxa (BL personal observation). Smaller shells are very rarely preserved in the Cubagua assemblage. The most diverse and abundant groups within the assemblage are the turritellids, tonnoideans and cancellarids, with a few species such as Marsupina bufo (BRUGUIÈRE, 1792), Prunum carnegutierrezae nov. sp. and Architectonica nobilis RÖDING, 1798 present in their thousands. Few associated fossils are present in the deposits; a handful of small sharks’ teeth were found and small corals.

The shells found in the Cañon de Las Calderas outcrop are relatively well preserved, although the protoconch and early teleoconch whorls are almost always eroded. As mentioned above, almost no shells under 10 mm in length are preserved. There is little evidence of transport, and in some taxa such as the vermetids and the bivalve genus Panopea MENARD, 1807 shells are preserved in living position.

Most of the genera found in the Lower Pliocene Cubagua assemblage of the Cañon de Las Calderas outcrop are typical of sandy substrates, and are similar to those found in the area today. The sandy lithology of the enclosing beds is in agreement with this interpretation (Text-Fig. 26). Few of the taxa found are typically intertidal, with a single rocky intertidal taxon, Stramonita biserialis (see KEEN, 1971, p. 550) present, although rare. No specimens of patellids or littorinids, typical of rocky intertidal habitats, were found.

Text-Figure 26. Author collecting at the Cubagua outcrop. Scattered mollusks can be seen in the sandy matrix.
The Turritellidae form an important part of the Cubagua assemblage in both diversity and numbers of individuals, especially in the upper layer of the fossiliferous section, in which the oryctocenosis (association of all the fossil elements present in a given fossil locality) is made up almost exclusively of Turritella and Petaloconchus specimens (Text-Fig 27). In the middle fossiliferous layer there are also lenses with large concentrations of turritellids. Elsewhere in the basal fossiliferous sequence of the Cañon de Las Calderas turritellids are found interspersed with other genera. Today representatives of the subgenus Broderiptella still form an important part of the biota on the Margarita platform, where dredgings bring up large numbers of specimens, living in sandy/muddy soft bottoms up to about 90 m depth (Macotay & Campos, 2001). Living as shallow infaunal gastropods, buried just under the surface, most turritellids are ciliary suspension-feeders, although some or all may be deposits feeders or grazers at least part of the time (Allmon, 1988). As can be seen from Table 5, the bathymetric range of most of the extant species represented in the Lower Pliocene Cubagua assemblage is no greater than to 100 m.

Text-Figure 27. Concentration of vermetids. Vermetids and turritellids frequently concentrated in small lenses in the Cubagua outcrop. Centre lower left – Marsupina bufo (Bruguière, 1792), one of the commonest gastropods in the assemblage. In the Recent faunas the geographical and seasonal patterns of living turritelline species are associated with coastal upwelling, with reduced shallow-water temperatures and increased phytoplankton productivity (Allmon, 1988). Moreover, in the Pleistocene to Recent faunas the presence of turritelline species with large shells with broad whorls is further associated with the intensity of the upwelling. The increase in the amount of shell material secreted may be explained by increased availability of food associated with stronger upwelling (Teusch et al., 2002). The large numbers of turritellids found in Cubagua, their diversity and the presence of large-shelled species all suggest the occurrence of upwelling currents in the area in Early Pliocene times.
Table 5: Recent bathymetric ranges of the extant species found in the Lower Pliocene Cubagua assemblage (Cañon de Las Calderas).

A number of taxa are present in the assemblage of which the modern counterparts are large algal browsers in calm areas of sandy-muddy bottoms and marine grasses, such as *Strombus* (REDFERN, 2001), and *Muracyprea*, found in shallow water among seaweed, feeding on algae (LORENZ & HUBERT, 2000). The blades of sea-grass also provide a substrate for microphytic algae such as diatoms, which are important constituents of food for *Modulus* (HOUBRICK, 1980). Other herbivores are *Astralium* and *Turbo*. A relatively high amount of light is required to support these macrobenthic plants, which would suggest a sublittoral zone probably not greater than 30 m depth.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth in meters</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lithopoma brevispinum</td>
<td>0-6</td>
<td>MACSOTAY &amp; CAMPOS (2001)</td>
</tr>
<tr>
<td>Calyptraea centralis</td>
<td>2-95 to 60</td>
<td>MACSOTAY &amp; CAMPOS (2001) DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Crepidula maculosa</td>
<td>to 75</td>
<td>No bathymetric data found</td>
</tr>
<tr>
<td>Pusula pediculus</td>
<td>2-6 to 100</td>
<td>MACSOTAY &amp; CAMPOS (2001) DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Polinices (P.) intermeratus</td>
<td>9-160</td>
<td>MARINCOVICH (1977)</td>
</tr>
<tr>
<td>Naticarius canrena canrena</td>
<td>8-70</td>
<td>MACSOTAY &amp; CAMPOS (2001)</td>
</tr>
<tr>
<td>Sconsia gravi</td>
<td>10-200</td>
<td>BEU (2008)</td>
</tr>
<tr>
<td>Linatella caudata</td>
<td>1-35</td>
<td>MACSOTAY &amp; CAMPOS (2001) as Cymatium (Linatella) poulsenii (MÖRCH, 1877)</td>
</tr>
<tr>
<td>Monoplex krebsii</td>
<td>25-150</td>
<td>DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Marsupina bufo</td>
<td>3-57</td>
<td>MACSOTAY &amp; CAMPOS (2001)</td>
</tr>
<tr>
<td>Bursa rugosa</td>
<td>Rocky intertidal</td>
<td>Alan Beu, personal communication, 2010</td>
</tr>
<tr>
<td>Scalina brunneopicta</td>
<td>10</td>
<td>DE VRIES (2007)</td>
</tr>
<tr>
<td>Vokesimurex messarius</td>
<td>to 30</td>
<td>DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Poirieria (P.) eugeniae</td>
<td>50</td>
<td>E. H. VOKES (1992)</td>
</tr>
<tr>
<td>Eupleura muriciformis</td>
<td>intertidal &amp; offshore</td>
<td>KEEN (1971)</td>
</tr>
<tr>
<td>Stramonita ‘biserialis’</td>
<td>intertidal</td>
<td>KEEN (1971)</td>
</tr>
<tr>
<td>Hesperisterinia karinae</td>
<td>10-50</td>
<td>DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Harpa crenata</td>
<td>no bathymetric data found</td>
<td></td>
</tr>
<tr>
<td>Oliva reticularis</td>
<td>20-128</td>
<td>MACSOTAY &amp; CAMPOS (2001)</td>
</tr>
<tr>
<td>Conus jaspideus</td>
<td>shallow waters</td>
<td>DIAZ &amp; PUYANA (1994)</td>
</tr>
<tr>
<td>Fusiturricula springvaleensis</td>
<td>300</td>
<td>MACSOTAY &amp; CAMPOS (2001) as Knefastia altenai</td>
</tr>
<tr>
<td>Striotrebrum weibordi</td>
<td>to 30</td>
<td>DIAZ &amp; PUYANA (1994)</td>
</tr>
</tbody>
</table>
The genus *Jenneria* is associated with coral reefs. The only remaining extant species, *Jenneria pustulata* (Lightfoot, 1786) lives in the Panamic Province, found as an intertidal and shallow infralittoral organism, living under boulders and in coral reefs. It seems to have a preference for *Pocillopora* (Bertsch, 1984), a scleractinian coral genus particularly abundant in the Caribbean during the Miocene and Pliocene but no longer extant in the western Atlantic, that still survives in abundance in the Recent Tropical American Pacific. The distribution of *Jenneria* probably follows the distribution of this coral. *Poirieria (Panamurex)*, rare in Cubagua, but represented by two distinct species, and *Coralliophila* are genera also associated with coral reefs.

Most of the taxa present indicate normal salinity, however, the presence of *Melongena* is usually taken as indicative of brackish-water conditions associated with mangrove (red mangrove, *Rhizophora mangle* (Linnæus 1753) in the case of Recent *Melongena melongena* Linnæus, 1758, where it feeds on epiphytic bivalves such as *Isognomon* Lightfoot, 1786). Two other genera were found in the Lower Pliocene assemblage of the Cañon de Las Calderas suggesting brackish or mangrove environments: ‘*Potamides*’ and *Terebralia*. However, both of these are represented by incomplete specimens and were probably transported from more or less distant environments.

Feeding upon these herbivores where a variety of carnivorous gastropods. *Pleuroploca* feeds on gastropods, as do *Vokesimurex, Haustellum* and most other muricids. Other voracious carnivores in sand areas are the naticids, preying on bivalves, gastropods, including each other, leaving a distinctive circular boring in the shell of their prey assigned to the ichnogenus *Oichnus* Bromley, 1981 (see Bromley, 1981; Zlotnik & Ceranka, 2005a). Muricids typically bore cylindrical holes; *Oichnus simplex* Bromley, 1981, whilst naticids bore conical holes *O. paraboloides* Bromley, 1981. Both types of predatory holes can be found in our Cubagua material. The Ranellidae and Tonnidae are also important predators, although they are specialized in feeding on echinoderms (Beu in Beesley et al., 1998; Ceranka & Zlotnik, 2003; Zlotnik & Ceranka, 2005b).

The Oliviidae, extremely abundant in the Cubagua assemblage, are active predators of interstitial fauna as well as scavengers. Typically they live as shallow infaunal animals, lying buried just beneath the surface in sandy areas away from sea grass beds by day, and scavenging by night. Similarly, most buccinids inhabit subtidal rubble or sand substrata, and are generalised predators and scavengers (Harasewych in Beesley et al., 1998).

The presence of *Eburna*, an offshoot of *Amalda* in the southern Caribbean, in the Cubagua assemblage is interesting. Today *Amalda* is a temperate genus rather than tropical like *Oliva*. In the Atlantic *Amalda* occurs only off the coasts of northern South America, associated with areas of upwelling of cooler, nutrient-rich waters and off the coast of Mauritania, West Africa, also associated with upwelling. Landau & Silva (2006) suggested it was this upwelling of cooler waters that allowed a temperate genus to survive in a frankly tropical environment. Landau & Silva (2006) described the rich assemblage of *Amalda* species occurring in the Lower Pliocene of the Mediterranean Estepona Basin, southern Spain, but occurring nowhere else in the Mediterranean. Here too the success of the genus was attributed to upwelling, absent in the rest of the Pliocene Mediterranean. The presence of *Eburna* in the Lower Pliocene Cubagua Cañon de las Calderas assemblage is strongly suggestive of upwelling in the area in Early Pliocene times. This conclusion agrees with those of Aguilera & Aguilera (2001) studying the fossil fish assemblages of the Araya Formation, Cubagua Group. *Eburna* is more widespread in the Lower Pliocene Caribbean than it is in the Recent faunas, found in the Panamanian and Jamaican fossil assemblages (but not further north), which would agree with the Neogene Caribbean being more productive than it is today (Keigwin, 1982; Vermeij & Petuch, 1986).

Further evidence for upwelling comes from the presence of *Marsupina bufo* (Bruguère, 1792), rare in all other Caribbean fossil deposits, but in the Cubagua assemblage it is one of the most common gastropod species. Today, specimens are abundant in relatively shallow water along the northern coast of Venezuela, Suriname and Guiana, always associated with areas of upwelling.

Landau & Silva (2010a) therefore concluded that the gastropod assemblage encountered at the Cañon de las Calderas outcrop indicates a tropical shallow marine environment. This is supported by the
abundant presence of well preserved specimens, covering different growth stages, of gastropod taxa known to prefer this specific habitat. These conclusions also agree with AGUILERA & AGUILERA (2001, p. 733) “(...) the sediments of the lower part [of the Cubagua Formation, i.e., Cerro Verde Member] appear to have been deposited in deep water, and the upper part [i.e., Cerro Negro Member, corresponding to the basal Cañon de las Calderas sequence] in shallow tropical water”. The substrate was for the most part sandy or sandy-muddy, with areas of sea grass and patches of coral. Rocky substrate in this particular location was rare or entirely absent. On the whole the assemblage suggests normal salinity, although it is likely that brackish-water conditions associated with mangrove relatively close by. The bathymetric ranges of the taxa present suggest an infralittoral habitat, not deeper than possibly 30-50 m. It is also suggested that this was an area of upwelling or seasonal upwelling from the abundant occurrence of turritellid specimens, namely the presence of large-shelled turritelline species with broad whorls, as well as the presence of *Marsupina bufo* and *Eburna*. These conditions are remarkable similar to those reported by MACSOTAY & CAMPOS (2001) from the marine environments off Cubagua Island today.
CHAPTER 5: PALAEOBIOGEOGRAPHY OF THE SOUTHERN CARIBBEAN NEogene MOLLUSCAN FAUNAS

In the Lower Pliocene Araya Formation of Cubagua 126 species are recorded, representing 95 genera and species-group (sensu VERMEIJ & PETUCH, 1986). Eleven new species are described, bringing the number of endemic species known only from the Araya Formation of Cubagua Island to 14 (including Voluta cubaguaensis J. GIBSON-SMITH, 1973, Cancellaria (Cancellaria) capeloi LANDAU, PETIT & SILVA, 2007 and Cancellaria (Massyla) cubaguaensis LANDAU, PETIT & SILVA, 2007).

Based on the chronostratigraphical range of the species (Appendix 7.1), the deposits are clearly Lower Pliocene, with 47 (37%) of the species extending their range into the Upper Miocene and 37 (29%) into the Upper Pliocene. These figures must be interpreted with caution as the Neogene fossil record is not equally diversified and well-represented throughout Tropical America.

5.1. Extinction and local disappearances in the Pliocene Atlantic portion of the Gatunian Province.

![Text-Figure 28](image)

Text-Figure 28. Geographical location of Cubagua Island and distribution of the Miocene to Early Pleistocene biogeographic provinces and the Colombian–Venezuelan–Trinidad Subprovince (LANDAU et al., 2008).

(a) at subgeneric level.

The Pliocene Tropical American region is divided into two palaeobiogeographical provinces: the Caloosahatchian to the north and the Gatunian to the south (Text-Fig. 28) (PETUCH, 1982; VERMEIJ, 2005; LANDAU et al., 2008). VERMEIJ & PETUCH (1986), working at subgeneric level and with various phylogenetically related species-groups, gave an extinction or local disappearance rate of about 32% for
both the Caloosahatchian province and the Atlantic portion of the Gatunian province, later revised to 27.3% (Vermeij, 2005), and a much lower rate (15%) for the Pacific portion of the Gatunian Province.

In the Araya Formation on Cubagua Island, 95 subgenera and species-groups are represented. 71 (75%) of them still occur in Caribbean waters, 16 (17%) are now restricted to the eastern Pacific and two (2%) are limited to the Indo-West Pacific. This gives an overall extinction and local disappearance rate for the southern Caribbean molluscan faunas since the Early Pliocene of 25%, similar to that recorded by Vermeij (2005) for the Atlantic portion of the Gatunian Province.

About half of the subgeneric taxa represented in the Pliocene Araya Formation of Cubagua, and no longer present in the Recent southern Caribbean, are now restricted to the eastern Pacific, i.e. the western portion of their original distribution (Paciphile taxa, sensu Woodring, 1966). For a complete list of these taxa see Appendix 7.4.

(b) at specific level.

Of a total of 126 species represented in the Lower Pliocene Araya Formation assemblage on Cubagua Island, 31 (24%) species are still extant (Appendix 7.1), 24 (19%) living in the Caribbean Sea, 9 (7%) in the Tropical American Pacific and 2 (1.5%) in both. That gives an 81% extinction and local disappearance rate for the southern Caribbean molluscan faunas since the Early Pliocene. The coeval Punta Gavilán Formation assemblage on mainland Venezuela, when compared with Recent faunas, shows an extinction rate of 85% at species level (B. Landau, unpublished data). This gives an overall extinction and disappearance rate of 81-85% since the Early-Middle Pliocene for the southern Caribbean molluscan faunas of Venezuela.

This brutal extinction and local disappearance rate is far from atypical within Caribbean Neogene faunas. Woodring (1928) gave an 88% rate at specific level for the Pliocene Bowden Formation assemblage of Jamaica and Jung (1969) gave the same figure (88%) for the Pliocene Melajo Formation assemblage of Trinidad.

These extremely high disappearance rates are not just observed when comparing Pliocene and Recent faunas, as only 7 (8%) species found in the Lower Miocene Cantaure Formation of northern Venezuela are present in the Pliocene assemblages of the northern coast of South America. Similarly, if we compare the Araya Formation assemblage to the assemblage from the Mare Formation of Venezuela listed by Weisbord (1962), dated as Pleistocene (Gibson-Smith & Gibson-Smith, 1979), they share only 5 (3.5%) species in common. Moreover, the Mare Formation also contains a very significant number of extinct taxa, although the figure of 75-83% extinction rate given by Weisbord (1962) needs to be revised, as his new taxa were often based on poorly preserved specimens and many are junior subjective synonyms of extant taxa. Nevertheless, these figures clearly show that the Cantaure, Araya and Mare assemblages, and the Recent faunas, share little in common at specific level.

These figures for extinction and local disappearance at subgeneric and specific level suggest a high degree of stability at generic level within the Caribbean Neogene prior to the total closure of the Central American Seaway, but a rapid turnover at specific level. A few species and about half of the subgenera represented in the Pliocene Araya Formation of Cubagua, and no longer present in the Recent southern Caribbean, are now restricted to the eastern Pacific, i.e. the western portion of their original distribution. These taxa are called paciphiles and will be discussed later. Beu (2010) found that even the tonnoideans have relatively few taxa in common in these assemblages, despite their long larval lives.

5.2. Cubagua and the biogeography of the southern Caribbean

5.2.1 Previous Works on the Neogene Palaeobiogeography of the southern Caribbean
WOODRING (1974) recognized that there was a difference between the fossil assemblages of the southern Caribbean, which at the time were all thought to be Miocene in age, and the rest of the Miocene Caribbean Province assemblages. Based on this difference he erected the Colombian–Venezuelan–Trinidad Subprovince (Text-Fig. 29).

**Text-Figure 29.** Biogeographic model proposed by WOODRING (1974) for the Caribbean (adapted from WOODRING, 1974).

PETUCH (1982) recognized two distinct provinces in the Caribbean Neogene, the Caloosahatchian province to the north and the Gatunian Province to the south.

**Text-Figure 30.** Biogeographic model proposed by PETUCH (1982) for the Caribbean.
PETUCH (1988) proposed a divided Miocene Gatunian province, with an Atlantic and Pacific component. According to him, in the Pliocene, the northern limit of the Gatunian Province - in the Pacific sector - was located north of Baja California and the southern limit - in the Atlantic sector - was positioned in southern Brazil (Text-Fig. 31). He named nine subprovinces within his Pliocene Gatunian Province. PETUCH (1988) highlighted the individual nature of the southern Caribbean and erected the “Puntagavilian Subprovince”, corresponding roughly to WOODRING’S (1974) Colombian-Venezuelan-Trinidad Subprovince. The Puntagavilian Subprovince of PETUCH (1988) was based on the faunas represented by the fossil assemblages of the Punta Gavilán Formation, Cubagua Formation and the lower beds of the Mare Formation of Venezuela, and upper beds of the Springvale, Matura, Coubaril and Talparo Formations of Trinidad, but he excluded the assemblages from the Pliocene Atlantic Colombian formations, which he placed in the Limonian Subprovince.

Provinces: C = Caloosahatchian Province; G = Gatunian Province
Subprovinces (Caloosahatchian): 1 = Yorktownian; 2 = Buckinghamian; 3 = Jacksonbluffian
Subprovinces (Gatunian): 4 = Agueguexitean [sic]; 5 = Guraban; 6 = Carriacouan;
7 = Puntagavilian; 8 = Imperialian; 9 = Limonian; 10 = Esmeraldan; 11 = Piraban.

Text-Figure 31. Biogeographic model proposed by PETUCH (1988) for the Caribbean (adapted from PETUCH, 1988; fig. 3).
PETUCH (2004) further developed his palaeobiogeographic model in the tropical American Neogene, and gave distinct names for the provinces over time (Text-Fig. 32). Most importantly, he only recognized the Gatunian and Caloosahatchian Provinces after the late Tortonian, preceded by a single Caribbean Province he named Baitoan, lasting from Late Chattian Oligocene to late Tortonian Miocene. Each of these newly erected provinces was divided into higher-resolution units – subprovinces – than in his previous works.

As far as the study area is concerned, according to PETUCH’S (2004) model, the Cainozoic Island of Cubagua would be part of the Antiguan Province, Bohioan Subprovince in the Oligocene Rupelian to earliest Chattian; the Baitoan Province, Cantaurean Subprovince in the late Chattian to late Tortonian Miocene; the Gatunian Province, Puntagavilanian Subprovince in the late Tortonian Miocene to Calabrian Pleistocene; and finally the Caribbean Province, Venezuelan Subprovince from the early Pleistocene to Recent time.

---

**Table**

<table>
<thead>
<tr>
<th><strong>Rupelian to Earliest Chattian</strong></th>
<th><strong>Late Chattian to Late Tortonian</strong></th>
<th><strong>Late Tortonian to Late Calabrian</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>PT = Proto-Transmarian Province</td>
<td>T = Transmarian Province</td>
<td>C = Caloosahatchian Province</td>
</tr>
<tr>
<td>A = Antiguan Province</td>
<td>T1 = Sankatian Subprovince</td>
<td>C1 = Yorktownian Subprovince</td>
</tr>
<tr>
<td>A1 = Hernandoan Subprovince</td>
<td>T2 = Calvertian Subprovince</td>
<td>C2 = Duplinian Subprovince</td>
</tr>
<tr>
<td>A2 = Vicksburgian Subprovince</td>
<td>T3 = Pungoan Subprovince</td>
<td>C3 = Buckinghamian</td>
</tr>
<tr>
<td>A3 = Alazanian Subprovince</td>
<td>B = Baitoan Province</td>
<td>C4 = Jacksonbluffian Subprov.</td>
</tr>
<tr>
<td>A4 = Guanican Subprovince</td>
<td>B1 = Onlsowian Subprovince</td>
<td>G = Gatunian Province</td>
</tr>
<tr>
<td>A5 = Bohioan Subprovince</td>
<td>B2 = Chipolan Subprovince</td>
<td>G1 = Guraban Subprovince</td>
</tr>
<tr>
<td>A6 = Mancoran Subprovince</td>
<td>B3 = Aqueguexquitean Subprov.</td>
<td>G2 = Veracruzan Subprovince</td>
</tr>
<tr>
<td></td>
<td>B4 = Anguillian Subprovince</td>
<td>G3 = Limonian Subprovince</td>
</tr>
<tr>
<td></td>
<td>B5 = Culebran Subprovince</td>
<td>G4 = Esmeraldan Subprovince</td>
</tr>
<tr>
<td></td>
<td>B6 = Subibajan Subprovince</td>
<td>G5 = Puntagavilian Subprov.</td>
</tr>
<tr>
<td></td>
<td>B7 = Cantaurean Subprovince</td>
<td>G6 = Juraian Subprovince</td>
</tr>
<tr>
<td></td>
<td>B8 = Carriacouan Subprovince</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B9 = Piraban Subprovince</td>
<td></td>
</tr>
</tbody>
</table>

**Text-Figure 32.** Biogeographic model proposed by PETUCH (2004) for the Caribbean (adapted from PETUCH, 2004; figs 9-11 respectively).

---

5.2.2. The Cubagua assemblage and its relationship to other Neogene Caribbean assemblages

In order to test the consistency of the biogeographic units previously defined (WOODRING, 1974; PETUCH, 1988, 2004) for the southern Caribbean during the Pliocene the similarity between the Cubagua
Pliocene assemblage and those of other Caribbean Neogene localities were assessed (see Appendix 7.1). To do this, similarity coefficients were used. All the assemblages examined represent gastropod faunas from shallow marine environments.

In the palaeobiogeographical literature the most widely employed binary similarity coefficients are the Jaccard, Simpson and Dice coefficients (CECCA, 2002). We have used these similarity coefficients to compare the Cubagua assemblage - at both subgeneric and specific levels - with other Neogene Caribbean assemblages. Previously, these tests have been used mostly at the generic level, and HALLAM (1977) argued that at species level they were totally inadequate for taxonomic reasons. HALLAM (1977) was dealing with Jurassic assemblages, which are not composed of fossils preserved in such clear detail as the Neogene ones discussed herein.

Regarding the Neogene southern Caribbean assemblages, we are dealing with well preserved fossils, usually allowing clear and precise identification. Moreover, the taxonomic lists presented here are based on both extensive field sampling and data collected from various bibliographical sources that have been reviewed critically in order to provide an objective account of the composition of the assemblages.

The Jaccard coefficient, $J$, is the ratio of $C$, the number of common taxa of a particular rank between two assemblages (or areas, provinces), and the total number of taxa occurring in both assemblages (CECCA, 2002)

$$J = \frac{C}{n^1 + n^2 - C}$$

where $n^1$ and $n^2$ are the numbers of taxa in the smaller (less diverse) and the larger (more diverse) assemblages respectively.

The Simpson coefficient was devised to minimize the effect of unequal size of the two assemblages being compared, and is expressed by the ratio of the common taxa between two assemblages to the number of taxa present in the smaller (less diverse) one (CECCA, 2002).

$$S = \frac{C}{n^1}$$

<table>
<thead>
<tr>
<th>Assemblage</th>
<th>#SGA</th>
<th>#SCC</th>
<th>%CTA</th>
<th>Jacc.</th>
<th>Simp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araya Peninsula</td>
<td>50</td>
<td>50</td>
<td>100%</td>
<td>0.53</td>
<td>1.0</td>
</tr>
<tr>
<td>Punta Gavilán</td>
<td>65</td>
<td>52</td>
<td>80%</td>
<td>0.48</td>
<td>0.80</td>
</tr>
<tr>
<td>Trinidad (Springvale, Talparo, More, Cipero, Brasso)</td>
<td>130</td>
<td>66</td>
<td>51%</td>
<td>0.42</td>
<td>0.70</td>
</tr>
<tr>
<td>Colombian (Tuberá, Usiacuri)</td>
<td>60</td>
<td>45</td>
<td>75%</td>
<td>0.41</td>
<td>0.75</td>
</tr>
<tr>
<td>Banano/Limón</td>
<td>220</td>
<td>29</td>
<td>13%</td>
<td>0.10</td>
<td>0.31</td>
</tr>
<tr>
<td>Gatunian (Gatun, Bocas del Toro)</td>
<td>200</td>
<td>42</td>
<td>21%</td>
<td>0.17</td>
<td>0.44</td>
</tr>
<tr>
<td>Guraban (Cercado, Gurabo, Mao, Bowden)</td>
<td>220</td>
<td>71</td>
<td>32%</td>
<td>0.29</td>
<td>0.75</td>
</tr>
<tr>
<td>Agueguexquitean (Agueguexquite)</td>
<td>177</td>
<td>24</td>
<td>14%</td>
<td>0.10</td>
<td>0.25</td>
</tr>
<tr>
<td>Esmeraldas</td>
<td>120</td>
<td>63</td>
<td>53%</td>
<td>0.41</td>
<td>0.67</td>
</tr>
</tbody>
</table>

Table 6: Comparison of the Cubagua assemblage with other Caribbean Pliocene assemblages, at subgenus and species-group level based on data presented in Appendix 7.3. #SGA - Number of subgenera known from the assemblage; #SCC - Number of subgenera in common with the Cubagua assemblage; %CTA - Percentage of Cubagua taxa present in the assemblage; Jacc. - Jaccard coefficient; Simp. - Simpson coefficient (LANDAU & SILVA, 2010b).

According to VALENTINE (1973), the Simpson coefficient stresses similarity whereas the Jaccard coefficient emphasizes differences between assemblages because it is more sensitive to differences in diversity. Both these methods have their advantages and drawbacks (CECCA, 2002). Both methods were
therefore used. The Dice coefficient is most suitable if the two assemblages have similar numbers of individuals, and was therefore not used.

Based on preliminary data from the Lower Pliocene gastropod assemblage of Cubagua Island, Venezuela, LANDAU et al. (2008) reviewed the palaeobiogeography of the southern Caribbean. This work did not include data obtained from the 2008 field trip to the Venezuelan Neogene outcrops, and the 2008 data was updated by LANDAU & SILVA (2010b).

Table 6 gives the results of the comparison of the Cubagua with other Caribbean Pliocene assemblages at subgenus and species-group level based on data given in Appendix 7.3 (sensu VERMEIJ & PETUCH, 1986).

Again the Jaccard coefficient shows a very strong correlation between the Araya Peninsula, Punta Gavilán, Trinidadian and Colombian assemblages. The Simpson coefficient again shows a strong correlation between these southern Caribbean assemblages, but also a correlation between them and the Guraban and to a slightly lesser extent the Esmeraldan subprovinces.

<table>
<thead>
<tr>
<th>Assemblage</th>
<th>#SGA</th>
<th>#SCC</th>
<th>%CTA</th>
<th>Jacc.</th>
<th>Simp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araya Peninsula</td>
<td>64</td>
<td>50</td>
<td>78.1%</td>
<td>0.35</td>
<td>0.78</td>
</tr>
<tr>
<td>Punta Gavilán</td>
<td>80</td>
<td>36</td>
<td>45.0%</td>
<td>0.21</td>
<td>0.45</td>
</tr>
<tr>
<td>Trinidad (Springvale, Talpao, Morne, Cipero, Brasso)</td>
<td>220</td>
<td>48</td>
<td>21.8%</td>
<td>0.16</td>
<td>0.38</td>
</tr>
<tr>
<td>Colombian (Tuberá, Usiacuri)</td>
<td>80</td>
<td>31</td>
<td>38.7%</td>
<td>0.25</td>
<td>0.39</td>
</tr>
<tr>
<td>Banano/Limón</td>
<td>500</td>
<td>26</td>
<td>5.2%</td>
<td>0.04</td>
<td>0.21</td>
</tr>
<tr>
<td>Gatunian (Gatun, Bocas del Toro)</td>
<td>400</td>
<td>32</td>
<td>8%</td>
<td>0.07</td>
<td>0.25</td>
</tr>
<tr>
<td>Guraban (Cercado, Gurabo, Mao, Bowden)</td>
<td>420</td>
<td>25</td>
<td>5.9%</td>
<td>0.05</td>
<td>0.20</td>
</tr>
<tr>
<td>Agueguexquitean (Agueguexquite)</td>
<td>264</td>
<td>7</td>
<td>2.7%</td>
<td>0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Esmeraldas</td>
<td>150</td>
<td>13</td>
<td>8.7%</td>
<td>0.05</td>
<td>0.10</td>
</tr>
</tbody>
</table>

Table 7: Comparison of the Cubagua assemblage with other Caribbean Pliocene assemblages at specific level based on data presented in Appendix 7.2. #SPA - Number of species known from the assemblage; #SPC - Number of species in common with the Cubagua assemblage; %CTA - Percentage of Cubagua taxa present in the assemblage; Jacc. - Jaccard coefficient; Simp. - Simpson coefficient (LANDAU & SILVA, 2010b).

Table 7 gives the results of the comparison of the Cubagua with other Caribbean Pliocene assemblages at specific level. Both the Jaccard and Simpson coefficients show a very strong correlation between the Araya Peninsula, Punta Gavilán, Trinidadian and Colombian assemblages, with all the other Gatunian subprovinces far more weakly correlated.

The data presented by LANDAU & SILVA (2010b) did not introduce significant changes and it does not alter the palaeobiogeographic model for the southern Caribbean proposed by LANDAU et al. (2008), updated in LANDAU & SILVA (2010b). In this model a single Colombian–Venezuelan–Trinidad Subprovince, spanning from the Early Miocene to Recent times was proposed (Text-Fig. 33).

5.2.3. Previous biogeographical models

The Recent fauna of the northern Atlantic Coast of South America is different from that of the rest of the Caribbean (PETUCH, 1987; JONG & COOMANS, 1988; DIAZ, 1995). Workers on fossil assemblages have reached similar conclusions (JUNG, 1965, 1969; WOODRING, 1974). These differences have probably been in place since at least the Early Miocene, and the palaeobiogeographical models developed by
different workers for the Neogene southern Caribbean clearly reflect these findings (Woodring, 1974; Petuch, 1982, 1988, 2004).

Text-Figure 33. Miocene to Pleistocene biogeographic models proposed by various workers for the southern Caribbean (Landau & Silva, 2010b).

However, the latest palaeogeographical model proposed by Petuch, especially in his later works (Petuch, 1988, 2004), has been criticized (Allmon, 2005). Here, I will only discuss Petuch’s concepts in relation to the study area.

In order to understand the logic behind Petuch’s model, his definitions of biogeographic units must be reviewed. Whilst stating that biogeographic patterns reflect the interaction of only three parameters: “(…) temperature, salinity and substrate type” (Petuch, 2004: 21), his definition of the units is purely taxonomic. After Petuch (2004: 21): “(…) two adjacent geographical areas can be considered separate molluscan provinces if at least 50% of the species-level taxa are endemic to each area.” For this
“50% Rule”, PETUCH (2004: 21) quotes VALENTINE (1973) and BRIGGS (1974, 1995), and writes: “All provinces are based upon the application of the “50% Rule” to a single large taxonomic group, usually a phylum or a class (…).” PETUCH (2004, p. 21) goes on to say: “Areas within the boundaries of a single province that have at least 30% endemism at the species level are referred to as subprovinces.” Unfortunately he does not give any tables of numbers of taxa that define his biogeographic units. Instead, he gives a list of endemic genera and species complexes for each subprovince, which he considers characteristic.

Despite recent efforts in this direction (WESTERMANN, 2000; CECCA & WESTERMANN, 2003), there is still no consensus, on the criteria for the definition of biogeographical units or biochoremas. KAUFFMANN (1973) proposed a system for differentiation of biogeographic units, based on Cretaceous bivalves, using percentages of endemism, all calculated exclusive of cosmopolitan taxa at generic and subgeneric level: endemic centres 5-10%; subprovinces, 10-15%; provinces, 25-50%; regions 50-75%; and realms >75%.

If one applies both the criteria suggested by VALENTINE (1973) and BRIGGS (1974, 1995) or KAUFFMANN (1973) at the species level, in the same way as PETUCH (1988) apparently did, the Pliocene Puntagavilanian Subprovince (PETUCH 1988, 2004) is sound, as from Appendix 7.2 we see that only 38 (33%) of the species found in Cubagua Formation extend their stratigraphical ranges down into the Miocene. Moreover, only seven (6%) species are common to both the Lower Miocene Cantaure Formation (on which PETUCH, 2004 based his Cantaurean Subprovince) and the Pliocene Araya Formation. Similarly, only 31 species (27%) survived the Pliocene.

There are several problems with PETUCH’S (1988, 2004) model. Firstly he based his biochoremas on selected taxa and not on the overall endemism of the assemblages as suggested by his own ‘50% rule’. Secondly, he based his palaeobiogeographic units not only on the comparison between contemporaneous faunas in different geographical areas, but also on the comparison of assemblages within the same area over time. by LANDAU et al. (2008) argued that palaeobiogeographical units should reflect differences among coeval biota across distinct geographical areas. They should not be based on differences between assemblages of the same area but of different ages. In the Caribbean, with its rapid species turnover, the application of PETUCH’S (1988, 2004) criteria to heterochronous assemblages led to an extremely complex and, what is more, artificial biogeographical model. We agree with WESTERMANN (2000) that the stability of biochorema names should be preserved even when the respective biota change greatly over time.

Whilst CECCA & WESTERMANN (2003) reiterated that the definition of a biogeographical unit or biochorema should be based on the overall endemism of its biota (not particular taxa) within a geographic envelope around a core area, CECCA (2002, p. 90) suggested that almost all palaeobiogeographical of marine fossil invertebrates should be done at generic level because treatment to the species level: “(…) appears to be totally inadequate for taxonomic reasons.”

This is indeed the approach adopted in PETUCH (1982) and VERMEIJ & PETUCH (1986). It was only later that PETUCH (1988) defined the subprovinces based on a list of particular taxa. A critical re-evaluation of PETUCH’S (1988) list of characteristic taxa illustrates CECCA’S (2002) point:

**Cypraeidae**

*Erosaria aliena* SCHILDER, 1939: described from the the Talparo Formation of Matura, now considered to be of Pleistocene age (JUNG, 1989); related to *E. acicularis* (GMELIN, 1791).

*Siphocypraea grahami* (INGRAM, 1947b): the classification of specific taxa within the genus *Muracypraea* is highly complex, and until a revision of all valid taxa is complete phylogenetic associations at specific level are premature.

**Turritellidae**

*Springvaleia secunda* WEISBORD, 1962: the genus seems to be endemic to the ‘Puntagavilanian Subprovince’, although we note that PETUCH (2004) moved the Springvale assemblage to the Cantaurean Subprovince.
Tonnidae
*Malea mareana* complex: also occurs in the Floridian Plio-Pleistocene as *Malea densecostata* in Olsson & Pettit (1964, pl. 79, fig. 5) Petuch, 1989, fig. 4; Petuch, 1994, pl. 35, fig. G (not *Malea densecostata* Rutsch, 1934) (Beu, 2010). However, there are two species of *Malea* endemic to the Puntagavilanian Subprovince: *M. densecostata* Rutsch, 1934 (Punta Gavilán), and *Malea* sp. from Cubagua (Landau, 2010a).

Ranellidae
*Charonia weisbordi* Gibson-Smith, 1976: = *Charonia lampas* (Linnaeus, 1758) an almost cosmopolitan species (Beu, 2010).

Thaididae (now Rapanidae)
*Cymia cocoditana* complex: this occurs in the Lower Miocene Cantaure Formation, included in the Cantaurean Subprovince by Petuch (2004), not in the assemblages from the formations included in the Puntagavilanian Subprovince by Petuch (1988). According to Vokes (1989a), this species is derived from the Peruvian Oligocene species *C. berryi* Olsson, 1931.

*Cymia brightoniana* complex: what is included in these complexes is not specified. The genus *Cymia* also occurs in the Limonian and Guraban Subprovinces (of Petuch 1988, 2004).

Fasciolaridae
*Pleuroplaca crassinoda* complex: *Pleuroplaca turamensis* Jung, 1969, these two species are interesting. We have not found them in Cubagua, but according to Jung (1969) they are most closely related to Recent Eastern Pacific species, they may be characteristic of the Puntagavilanian Subprovince.

Columbellidae
*Parametaria rutschi* complex: *Parametaria* is a paciphile genus represented by *P. dupontii* (Kiener, 1849) in the Recent Panamic Pacific. *P. rutschi* (Jung, 1969) from the Taparo Formation of Matura is now considered to be of Pleistocene age (J. B. Saunders pers. comm. in Jung, 1989). However *P. prototypus* (Guppy, 1876) [= *P. schilderi* (Rutsch, 1942)] is from the Springvale Formation of Trinidad and the subgenus *Parametaria* is also present in the Caloosahatchian province, represented by three species from Florida; *P. lindae*, Petuch, 1986, *P. hertweckorum* and *P. miccosukee* Petuch, 1991. The subgenus *Dominitaria* Jung, 1994, which differs mainly in having sculptured early teleoconch whorls, is present in the Dominican Neogene (Jung, 1994). Interestingly, the *Conus*-like shell shape of *P. rutschi* is very similar to that of *P. (D.) islahispaniolae* Maury, 1917, but its early whorls are smooth.

Buccinidae
*Cymatophos paraguanensis* (Hodson, 1931): *Pallacera urumacoensis* complex, both of these occur in the Lower Miocene Cantaure Formation, not in the assemblages from the formations included in the Puntagavilanian Subprovince by Petuch (1988). Again, both genera are represented in the Limonian and Guraban Subprovinces.

Conidae
*Conus* (*Chelyconus*) *federalis* Weisbord, 1962, *Conus* (*Chelyconus*) planitectum Weisbord, 1962: the holotypes are abraded. To suggest any phylogeny based on this material is pure conjecture.

5.2.4. Colombian-Venezuelan-Trinidad vs. Cantaurean/Puntagavilanian Subprovinces

From a biogeographic standpoint, the Neogene Caribbean before the closure of the Central American Seaway (CAS) was divided into two provinces, the Caloosahatchian to the north and the Gatunian to the south, with its Atlantic and Pacific components (Vermeij & Petuch, 1986; Petuch, 1988). The Atlantic portion of the Gatunian Province gives rise to the Caribbean Province following the total closure of the CAS.
The faunas from the northern coast of South America have probably been different from those of the rest of the Caribbean since at least the Early Miocene (Woodring, 1974; Petuch, 1982, 1988, 2004). This led Woodring (1974) to coin the term Colombian-Venezuelan-Trinidad Subprovince (CVT Subprovince), and Petuch the Pliocene Puntagavilian Subprovince (Petuch, 1988) and the Miocene Cantaurean Subprovince (Petuch, 2004). It is interesting to note that whilst over time species turnover has been intense, the geographical expression of these biogeographic units has not changed, as demonstrated above (Tables 1 and 2). Whilst in the rest of the Caribbean there may well have been important changes in salinity, eustatic changes in sea level (Maier-Reimer et al., 1990), and changes in nutrient supply (Vermeij & Petuch, 1986; Jackson et al., 1993), the southern Caribbean Pliocene assemblages we have encountered suggest normal salinity, soft substrate, relatively shallow waters and seasonal upwelling (Aguilera & Aguilera, 2001), a general pattern similar to that found in the area today (Carvajal & Capejo, 1993; Macsotay & Campos, 2001). This demonstrates that the geographical expression of the biogeographic units discussed above was not fundamentally affected by the closure of the CAS. The oceanographic conditions that made it special before the closure of the CAS must have continued after the closure. What has changed dramatically is the taxonomic composition of the assemblages at species level.

The question of what name to use is somewhat less complicated. Cecca & Westermann (2003, p. 180) suggested that biogeographical unit’s “(...) names are geographic/geologic, not taxonomic. Priority ‘rules’ of synonymy and homonymy should be applied to biochorema names, not rigorously but with common sense.”

The geographical extent of Petuch’s (1982: 286, fig. 2; 1988: 10, fig. 1) Gatunian Province is not significantly different from Woodring’s (1974, p. 210, fig. 1) Miocene Caribbean Province. Therefore it could be argued that the terms Calosahatchian and Miocene Caribbean Provinces should be used. However, the term Miocene Caribbean Province has since been abandoned, and the terms Calosahatchian and Gatunian Provinces are now commonly used in the literature by recent authors (e.g., Vermeij & Petuch, 1986, Robinson, 1991, Vermeij, 2005; Landau et al., 2008; Landau & Silva, 2010), and therefore continue to use them to promote nomenclatural stability.

The geographical range of the Petuch’s (2004) Late Oligocene to Late Miocene Baitoan province includes the whole Caribbean, the Gulf of Mexico, and the coasts of Florida to South Carolina. Therefore, following Petuch’s (2004) model, the Gatunian Province shrank after or during the Late Tortonian Miocene. However, biochoremas are dynamic units which change in range (areal extent) over time (Westermann, 2000; Cecca & Westermann, 2003). Landau et al. (2008) argued that a range contraction did not require the erection of a new biogeographic province, and therefore adhered to Petuch’s (1982) definition of the Gatunian Province, and rejected the name Baitoan Province.

Petuch’s nomenclature of subprovinces is, however, more complicated, and I will only address this question in relation to the study area. When Woodring (1974) suggested the term Colombian-Venezuelan-Trinidad Subprovince, most of the southern Caribbean Lower Pliocene faunas were considered Miocene. Petuch (1988) suggested the term Puntagavilian Subprovince for the Pliocene. In the discussion he states that his new subprovince “(...) corresponds roughly to Woodring’s Colombian-Venezuelan-Trinidad Subprovince.” (Petuch, 1988, p. 97), but then excludes all the assemblages from the Pliocene Colombian Formations, which he included in his Limonian Subprovince. As can be seen in Appendix 7.2 the Colombian assemblages are far more closely related to that of Cubagua and the rest of the northern Atlantic coast of South America than to the Isthmian Pliocene assemblages. Landau et al. (2008) therefore rejected the name Puntagavilian Subprovince, a name which to my knowledge has not been used by any other author, in favour of the Pliocene Colombian-Venezuelan-Trinidad Subprovince of Woodring (1974), which has priority and is more geographically correct.

Furthermore, if all the Pliocene assemblages previously considered Miocene are now removed, the remaining southern Caribbean Miocene assemblages known at this time are insufficient to uphold the higher resolution biogeographic units proposed by Petuch (2004). For example, the Miocene Cantaurean Subprovince (after Petuch, 2004) includes the assemblages of the Springvale Formation of Trinidad, which are now considered Pliocene (Hunter, 1978; Macsotay & Vivas, 1998). At species level there is
very little in common between the Springvale assemblage and that of Cantaure, the type assemblage for the Subprovince.

Based on the existing data, LANDAU et al. (2008) (updated LANDAU & SILVA, 2010) suggest a simpler palaeobiogeographic model for the southern Caribbean with a single Colombian-Venezuelan-Trinidad Subprovince, spanning from the Early Miocene to Recent times (Text-Fig. 33). Even today, the subprovince called Samarian-Venezuelan by DIAZ (1995; Text-Fig. 34) has exactly the same geographical distribution as the Neogene Colombian-Venezuelan-Trinidad Subprovince, although today, according to DIAZ (1995), it seems to be disjunct, separated by a small subprovince called Goajira. Our fossil resolution is insufficient to ascertain if the Goajira subprovince existed in the Mio-Pliocene. DIAZ (1995) also shows a sharp contrast between the fauna of his Samarian-Venezuelan Subprovince and that of his Isthmian Subprovince today, exactly as seen in the data above (Tables 6 and 7). Similarly, the geographical expression of this Recent Isthmian Subprovince is not greatly different from the Atlantic portion of WOODRING’s (1974) Central American-northern South American Subprovince.

Text-Figure 34. Comparison of Pliocene Colombian-Venezuelan-Trinidad Subprovince with Recent provinces according to DIAZ (1995) (adapted from DIAZ, 1995; fig 4).

5.2.5. Chorotypes and chronotypes

WESTERMANN (2000) recommended that each biochorema should have a type region (chorotype) and a characteristic stage (chronotype) designated. This has not been adopted widely in Tropical American Neogene palaeobiogeography. LANDAU et al. (2008) designated types for the biogeographic units covered in the study area.

For the Gatunian Province the best area to choose as characteristic would lie between the Atlantic and Pacific portions of the Neogene Gatunian Province, in the Isthmian area. Here the area around Gatun would be most appropriate, containing assemblages typical for the Gatunian province, with a high number of paciphile taxa and taxa endemic to the Gatunian Province. Such taxa are represented in the assemblages found in the area in the Miocene Gatun Formation (COLLINS & COATES, 1999). LANDAU et al. (2008) therefore proposed the area around Gatun as the chorotype for the Gatunian Province, and the Gatun Formation the chronotype (fide WESTERMANN, 2000).
PETUCH (1982) gave lists of endemic genera and species complexes endemic to the Gatunian and Caloosahatchian provinces (PETUCH’S 1982 use of the term ‘species complex’ is equivalent to the ‘species group’ of VERMEIJ & PETUCH, 1986). These lists, although useful, need to be revised, as several genera endemic to the Caloosahatchian Province according to PETUCH (1982) are also represented in the Gatunian Province assemblages; i.e. Scalina [Gatun Formation, Panama (WOODRING, 1959); Cantaure Formation, Venezuela (JUNG, 1965)], Urosalpinx [Cercado Formation, Dominican Republic (VOKES, 1989a)], Scaphella [Gurabo Formation, Dominican Republic (GABB, 1873; VOKES, 1998)], Trigonostoma tenera complex [Bocas del Toro area (OLSSON, 1922), Araya Formation, Cubagua Group, Venezuela (Landau et al., 2007)], Eratoidea [Gurabo Formation, Dominican Republic (GABB, 1873; MAURY, 1917)]. Similarly, some taxa allegedly endemic to the Gatunian Province are also represented in the Caloosahatchian Province assemblages; i.e. Cyphoma, Pseudocyphoma, Cancellomorum (= Oniscidia fide VOKES, 1998), Marsupina, Calophos, Rhipophos, Eurypyrene, Parametaria, Dolicholatirus, Tiara longa complex, Bivetopsis, Prunum, Ximeniconus [Florida Plio/Pleistocene (PETOUC, 1994)]. There are further generic taxa which, until now, have been found only in the Gatunian Province, which are not included in PETUCH’S (1982) list; i.e. Pterynotus [Gurabo Formation, Dominican Republic (VOKES, 1989a)], Purpurellus [Gurabo Formation, Dominican Republic (VOKES, 1989a); Cantaure Formation, Venezuela (Landau unpublished data): note; not present in Caloosahatchian Province, but present in the Eocene and Oligocene of Florida and North Carolina (PORTELL & VOKES, 1997)], Amalda [Gatun Formation (WOODRING, 1964); Punta Gavilan Formation (Rutsch, 1934); Springvale Formation (MAURY, 1925a)].

WESTERMANN (2000) suggested the designation of chronotypes and chorotypes for each biochorema. This standard had not, as yet, been adopted by palaeobiogeographers. However, if this idea should gain general acceptance, for the study area, LANDAU et al. (2008) proposed as the chorotype of the Colombian-Venezuelan-Trinidad Subprovince the assemblages found on the Island of Trinidad, as they contain genera which are endemic to the subprovince, but have not so far been found in Cubagua, i.e. Springvaleia RUTSCH, 1942 (WOODRING, 1958; JUNG, 1969). These assemblages are part of the Springvale Formation, which is Pliocene in age (HUNTER, 1978; MACSOTAY & VIVAS, 1998), and proposed the Springvale Formation as the chronotype.

5.2.6. Contrasting patterns of extinction and local disappearance: Caribbean and northeastern Atlantic frontage.

In this chapter observations on Neogene to Recent patterns of extinction and local disappearances affecting gastropod faunas in the Caribbean are presented, and compared to patterns observed along the Atlantic European frontage and Western Mediterranean. Although the two assemblages are not directly related, they do share some common elements; both are Lower Pliocene, both tropical, and both were subject to seasonal upwelling (at least the Mondego and Estepona assemblages).

NE Atlantic pattern of extinction and local disappearance

In the North Atlantic, Pliocene times were marked by a series of sharp climatic cooling events, causing pulses of extinction and local disappearance (STANLEY, 1986; STANLEY & RUDDIMAN, 1995; MONEGATTI & RAFFI, 2001). These molluscan Pliocene extinctions and local disappearances were not followed by recovery phases on either side of the Atlantic. As a consequence progressive reduction of thermophilic taxa and general diversity reduction occurred (MONEGATTI & RAFFI, 2001).

Based on the Mediterranean Pliocene assemblages of Italy, MONEGATTI & RAFFI (2001) recognised four Mediterranean Pliocene Molluscan Units (MPMUs). These units are ecobiostatigraphic faunal units based on local disappearance and true extinction events of benthic molluscs. Since the distributions of shallow marine thermophilic benthic molluscs are a proxy for SSTs variations, the boundaries of the MPMUs approximate the major climatic changes (cooling events) of the Northern Hemisphere affecting the Atlanto-Mediterranean region (MONEGATTI & RAFFI, 2001).
The eastern Atlantic component discussed here is centred on the North Sea Basin assemblage from Belgium and the Pliocene molluscan deposits on southern and western Iberian Peninsula; from just within the Mediterranean in the Estepona Basin (Southern Spain), just outside in the Atlantic in the Guadalquivir Basin (SW Spain), and further north in the central West Portugal, the Mondego Basin (Text-Fig. 35).

These assemblages, ranging in age from Zanclean to lower Piacenzian, although not strictly synchronous, fall within the frame of MPMU1 (SILVA, 1995; LANDAU et al., 2003; SILVA & LANDAU, 2007; SILVA et al., 2010). They all precede the mid Pliocene 3.0 Ma cooling event that, after MONEGATTI & RAFFI (2001) triggered the first event of extinction and local disappearance in the Atlanto-Mediterranean region. Therefore, they are eco-biostratigraphically coeval. Both Estepona and Guadalquivir Basins, straddling the Strait of Gibraltar have frankly tropical faunas, typical for MPMU1 as defined for the Mediterranean (SILVA, 1995; MONEGATTI & RAFFI, 2001, LANDAU et al., 2003). The Atlantic Mondego Basin assemblage, although coeval, is not typical of MPMU1 as it is located well outside the Mediterranean, at a more northern latitude than the Guadalquivir Basin, lacks most of the indicators described by MONEGATTI & RAFFI (2001), and has a subtropical character (SILVA, 2001; SILVA et al., 2010).

**Text-Figure 35.** Neogene East Atlantic molluscan biogeographic provinces (adapted from SILVA & LANDAU, 2007). Present day bioprovinces after RAFFI et al. (1985).

MPMUs are valid exclusively within the Mediterranean Basin. The criteria used to define these eco-biostratigraphic units do not apply, directly, to molluscan assemblages outside the Mediterranean, such as the coeval Pliocene Western Iberian Atlantic faunas. On the other hand, once a sound temporal equivalence between Mediterranean and non-Mediterranean assemblages has been established, MPMUs are
a powerful tool for interprovincial palaeoclimatic and palaeoceanographic correlations, as well as for the definition of atlanto-mediterranean palaeobiogeographic boundaries (Silva et al., 2010).

Raffi & Monegatti (1993) and Monegatti & Raffi (2001), based mainly on data from Italian molluscan assemblages, estimated the specific extinction and disappearance rates for Mediterranean Pliocene bivalves marking MPMU boundaries. Until now no detailed figures are available for gastropods for these faunal units.

In order to investigate the extinction rates along the Early Pliocene Atlantic European Frontage and adjacent westmost Mediterranean during MPMU1, we have taken three faunas representing three distinct European Pliocene palaeobiogeographical provinces, which have had their assemblages recently reviewed:

1. The North Sea basin fauna from Belgium in the temperate Boreal Province (Marquet, 1998).
2. The Atlantic fauna of central-west Portugal in the subtropical French-Iberian Province (Silva, 2001).

In the Boreal Province, North Sea Basin, huge geographical changes have occurred since the Miocene. Marquet (1998) listed 132 genera of Gastropods from the Belgian Pliocene, of which 78 are still found at those latitudes, i.e. 41% disappearance (Text-Fig. 36).

In the Mondego Basin, central-west Portugal, Silva (2001) described 116 genera of Gastropods, 76 are still found at those latitudes, i.e. 35% are no longer present at these latitudes, either extinct or experienced a range contraction southwards. In the Estepona basin, we have 337 genera of Gastropods (see references above), 209 still found at those latitudes, i.e. 38% extinct or experienced a range contraction southwards (Text-Fig. 36).

Text-Figure 36. Extinction and local disappearance rates at subgeneric level along the Early Pliocene Atlantic European Frontage and westemmost Mediterranean.
These results suggest a 35-40% generic extinction or local disappearance rate from the Early - mid Pliocene times (corresponding to MPMU1) to Recent faunas in the Atlantic European Frontage and adjacent westernmost Mediterranean.

**Caribbean pattern of extinction and local disappearance at subgeneric level**

As discussed in Chapter 4, the Pliocene Tropical American region is divided into two palaeobiogeographical provinces: the Caloosahatchian to the north and the Gatunian to the south (Text-Fig. 30). VERMEIJ & PETUCH (1986), working at subgeneric level and with various phylogenetically related species-groups, gave an extinction or local disappearance rate of about 32% for both the Caloosahatchian province and the Atlantic portion of the Gatunian province, later revised to 27.3% (VERMEIJ, 2005), and a much lower rate (15%) for the Pacific portion of the Gatunian Province (Text-Fig. 37).

To summarise the findings resented in Section 5.1, 95 subgenera and species-groups are represented in the study area. 71 (75%) of them still occur in Caribbean waters, 16 (17%) are now restricted to the eastern Pacific and two (2%) are limited to the Indo-West Pacific. This gives an overall extinction and local disappearance rate for the southern Caribbean molluscan faunas since the Early Pliocene of 25%, similar to that recorded by VERMEIJ (2005) for the Atlantic portion of the Gatunian Province. About half of the subgenera no longer present in the Recent southern Caribbean are the paciphile taxa.

**Northeastern Atlantic vs. Caribbean patterns of extinction and local disappearance at subgeneric level**

![Text-Figure 37. Extinction and local disappearance rates at subgeneric level in the Caribbean.](image)

The pattern for extinction and local disappearances which emerges along the Atlantic European frontage is one of a stepwise extinction and southwards range contraction of thermophilic molluscan taxa (BRÉBION, 1972, 1981, 1988; SILVA & LANDAU, 2007, SILVA et al., 2010). These extinctions and local disappearances are especially evident at generic/subgeneric level. Relatively few species within genera still
extant in the European coasts became extinct or emigrated southwards. This left in the region an impoverished residual fauna, depleted of the majority of the typically thermophilic elements.

These observations give us a pattern for extinction and local disappearances of gastropods throughout the Neogene at Eastern Atlantic northern latitudes, but what is the situation at more southern latitudes. Unfortunately there are no Neogene shell-bearing marine deposits known at tropical latitudes along the Atlantic African frontage, however, on the other side of the Atlantic, the tropical Caribbean is rich in marine fossiliferous deposits, which might shed light on this subject.

A similar extinction/local disappearance and southward range contraction pattern is observed along the north-eastern coast of North America during the Neogene (STANLEY, 1986; STANLEY & RUDDIMAN, 1995).

However, quite a different pattern is seen in the tropical Caribbean region, with a 25-32% extinction or local disappearance rate, and with at least half of the generic/subgeneric taxa no longer present in the Caribbean now living in the eastern Pacific. Therefore instead of a latitudinal north-south withdrawal we see an east-west longitudinal range contraction of these paciphile taxa following the closure of the CAS. Whereas on both sides of the Northern Atlantic climatic cooling is the main factor driving the southwards range contraction of thermophilic taxa, there is no particular pattern of ecological requirements common to all of these paciphiles.

Northeastern Atlantic pattern of extinction and local disappearance at species level

If we consider the same Pliocene gastropod assemblages along the Atlantic European frontage basins at species level, in the North Sea Basin, of the 236 species taxa listed by MARQUET (1998), 78 are still living. This gives a 66% extinction or local disappearance rate since the early Pliocene. In the Mondego assemblage SILVA (2001) described 165 gastropod species, of which roughly 50% do not occur at central Portuguese latitudes today.

Text-Figure 38. Extinction and local disappearance rates at specific level along the Early Pliocene Atlantic European Frontage and westernmost Mediterranean.
The description of the Estepona Basin assemblage is still in progress, but of the 744 species of gastropods present, 255 are still living in the western Mediterranean, i.e. 66% extinction or local disappearance rate (Text-Fig. 38; Landau unpublished data).

In all three of these assemblages the pattern of disappearance is very clear. In the thermophilic genera almost all the species become extinct, whereas in the more temperature-tolerant genera the specific composition of the genera is often almost unchanged. Therefore, the gastropod extinction and local disappearances, in the Mediterranean and in the adjacent European Atlantic, from Early Pliocene to Recent times runs at around 70-85% for thermophilic species (MARASTI & RAFFI, 1976, 1979; SILVA, 2001).

**Caribbean pattern of extinction and local disappearance at species level**

In the Pliocene Cubagua assemblage 31 (24%) species taxa are still extant, of which only 24 (19%) species are still living in the Caribbean; that gives an 81% disappearance rate for the southern Caribbean. If we were to exclude notoriously cosmopolitan taxa, with geologically long-lived species, such as the Ranellidae and Architectonica, this would give a 90% disappearance rate. This brutal extinction rate is far from atypical within Caribbean Neogene faunas. WOODRING (1928) gave an 88% extinction rate at specific level for the Lower Pliocene Bowden Formation of Jamaica. JUNG (1969) gave the same figure (88%) for the Lower Pliocene Melajo Formation assemblage of Trinidad (Text-Fig. 39). From personal collecting experience similar extinction rates occur in the various Dominican and the Panamanian Gatun Formation assemblages (Landau unpublished data).

Text-Figure 39. Extinction and local disappearance rates at specific level in the Caribbean.

**Discussion**

The figures given above show not only a striking difference in the extinction rates since the Early Pliocene at both generic and species level, but also differing patterns of disappearance.

Along the Atlantic European frontage we see a north-south range contraction, with a 35-40% generic disappearance rate of mainly thermophilic elements within the fauna, and a specific extinction or
local disappearance of 50-66%, of which 70-85% are within the thermophilic genera. The situation in the Caribbean is quite different, where at generic level the fauna remains more stable, with a 25% extinction or local disappearance rate, of which only 8 (8%) are extinct, and 17% are now restricted to the Pacific side of their original Pliocene distribution, following the uplift of the Central American seaway. However, we see a drastic extinction at specific level, with a 75% overall extinction rate and an 82% disappearance rate for the southern Caribbean.

In the Pliocene, the Cubagua region was tropical, based on the molluscan assemblage. Today the region is still tropical and the generic composition of the fauna is little changed, suggesting that temperature change, unlike the pattern seen at higher latitudes, was not a driving force for these extinctions and local disappearances.

These high extinction and local disappearance rates in the Neogene Gatunian Province have been ascribed to shifts in oceanographic conditions after and during the closure of the CAS (MAIER-REIMER et al., 1990); sea level fluctuations and changes in patterns of upwelling and nutrient distribution (VERMEIJ & PETCH, 1986; JACKSON et al., 1993). It does not, at least in stombinids, seem to have been a response to changes in predation (JACKSON et al., 1984).

Unlike the Atlanto-Mediterranean region, where an important diversity decline occurred since early Pliocene times, these Gatunian extinctions and local disappearances are accompanied by high rates of speciation (ALLMON et al., 1993; JACKSON et al., 1993), although some maintain that there has also been a substantial impoverishment in the marine biotas since the Pliocene (VERMEIJ & PETCH, 1986; PETCH, 2004; G. Vermeij, pers. com. 14/12/2005).

Our figures for generic extinction and local disappearance are lower than the global figure given by VERMEIJ & PETCH (1986) for the Gatunian Province. This would suggest that the Cubagua region was more stable than the Gatunian Province as a whole. This could be explained by the Cubagua region being relatively far geographically from the centre of the vicariant event which divided the Gatunian Province in two; the uplift of the Isthmus of Panama. At the specific level, despite this relative generic stability, a drastic extinction (far more significant than the local disappearances) occurred, equal if not higher than that seen in the province as a whole.

5.2.7. Biogeographic implications and conclusions

The Pliocene Araya Formation of the Cubagua Group contains a rich gastropod fossil assemblage, similar in specific composition to other Pliocene assemblages found along the northern coast of South America and Trinidad. This assemblage is similar in generic composition to that of other Caribbean Pliocene faunas, but quite distinct at the species level. Comparison of the assemblages from the northern coast of South America with Miocene and Pleistocene to Recent faunas from the same geographical area shows a very high species turnover.

Since WOODRING (1974) the unique character of these southern Caribbean assemblages has been recognized, and palaeobiogeographic models of varying complexity proposed (WOODRING, 1974, PETCH, 1982, 1988, 2004). Most of these models agree in principal on the biogeographical zonation of Neogene Tropical America into provinces and subprovinces, all highlighting the special character of the north coast of South America. However, despite the general agreement in principal, numerous names have been proposed for the biogeographic units based on different criteria.

The data resulting from this work supports the findings of WOODRING (1974) and PETCH (1988, 2004) in distinguishing a biogeographic unit centred on the north coast of Venezuela, but contrary to PETCH (1988, 2004), the data supports the inclusion of the Colombian Pliocene assemblages. This group of assemblages is distinct from those found in the Isthmian region of Tropical America, and in the central Caribbean. This biogeographic unit seems to have been in place since at least the Early Miocene, and whilst showing dramatic changes in faunal composition at specific level over time, altered little at generic level until the total disappearance of the `paciphile taxa'. The geographic expression of this unit apparently has
not altered over time, and does not seem to have been greatly affected by the closure of the CAS responsible for the demise of the Gatunian Province and the subsequent rise of the late Pleistocene to Recent Caribbean Province. Although the bioprovinces changed, the subprovince remained unaltered. This suggests that the oceanographic conditions in the region have not changed greatly since Early Miocene times, and seem not to have been significantly affected by the uplift of the Isthmus of Panama.

Several names have been used for this biogeographic unit; Colombian-Venezuelan-Trinidad Subprovince (WOODRING, 1974); Pliocene Puntagavilanian Subprovince (PETUCH, 1988); and Miocene Cantaurean Subprovince (PETUCH, 2004). I find no reason to rename the biochorema and suggest that the name used by WOODRING (1974), Colombian-Venezuelan-Trinidad Subprovince, should be retained.

LANDAU et al. (2008) proposed the following type designations for the biochoremas discussed in this paper; the assemblages found in the area around Gatun and the Gatun Formation as chorotype and chronotype for the Gatunian Province, and the assemblages occurring on the Island of Trinidad in the Springvale Formation as chorotype and chronotype for the Colombian-Venezuelan-Trinidad Subprovince.
CHAPTER 6: ECOSTRATIGRAPHY OF THE SOUTHERN CARIBBEAN NEogene Molluscan Faunas

6.1 Paciphiles in the Caribbean, background

A key fact in the history of Neogene Caribbean marine molluscs is the disappearance of taxa that occurred throughout tropical America during the Miocene and Pliocene, but subsequently suffered a range contraction, and became largely or entirely restricted to the eastern Pacific portion of their original distribution. WOODRING (1966) coined the term “paciphile” for these marine taxa.

These paciphile elements (see Appendix 7.4) did not disappear from the Neogene Caribbean simultaneously, but seem to have suffered a steep decline during the Late Pliocene. In the biota along the northern coast of South America the percentage of paciphile taxa seems to have remained constant between the Early Miocene and Pliocene, thereafter drastically diminishing in number and practically absent by the Pleistocene.

What forces led to the disappearance of these paciphile taxa in the Atlantic portion of their original distribution is at present unclear. There seems to be no obvious common environmental factor or ecological requirements uniting this paciphilic assemblage of taxa. The assemblage includes taxa with very small to large shells, they are not of any particular bathymetric range, both herbivores and carnivores are represented, and in many cases the paciphilic group disappeared whereas another closely related group persisted. This could be illustrated by the disappearance of the trivid *Pusula* from the Caribbean during the Pleistocene whereas the similar trivid *Niveria* was sympatric with *Pusula* throughout the Neogene, but unlike the latter, persists to Recent times in the Tropical American Atlantic. Similarly, trends in transisthmian evolution of the *Strombina* group (Collumbellidae) were analysed by JACKSON et al. (1996), but whilst they concluded changes in oceanographic condition were obviously important, the mechanisms were still to be elucidated.

There is mounting evidence of the existence of west-east currents from the Pacific into the Caribbean across the CAS since the end of the Oligocene (NESBITT & YOUNG, 1997; SCHNEIDER & SCHMITTNER, 2006; O’DEA et al., 2007). As interoceanic communication became restricted, upwelling and oceanic productivity in the eastern Pacific increased (VERMEIJ, 1997; CHAISSON & RAVELO, 2000; PHILANDER & FEDOROV, 2003; RAVELO et al., 2004; FEDOROV et al., 2006; LAWRENCE et al., 2006), whilst productivity in the Caribbean decreased (COLLINS et al., 1996a, 1996b; TODD et al., 2002; SCHNEIDER & SCHMITTNER, 2006).

It is possible, based on the source-sink population model (PULLIAM, 1988; VERMEIJ & DIETL, 2006), that the emergence of the isthmus during the Late Pliocene might have cut off the source populations of planktonically dispersing paciphile species of molluscs dependent on Pacific source populations. A source population produces enough recruits not only to sustain itself, but to seed other populations. A sink population does not produce enough recruits to maintain itself. The sink populations thus became stranded on the Atlantic coast of South America and elsewhere in the Caribbean, where they became unsustainable and eventually disappeared. In order to support this a more complete search into the inferred larval development of all paciphilic species-level taxa would be useful to test their hypothesis.

The presence of this paciphile cohort of taxa in the Neogene Caribbean is an interesting phenomenon, which could be of use in understanding the dynamics and causes of the biogeographic changes which have occurred in the region in the Neogene. Furthermore, as the disappearance of these paciphiles from the Atlantic portion of their earlier distribution did not happen as a single synchronous event, it may be possible to construct a scale of ecobiostatigraphic faunal units based on the presence of these paciphiles within the assemblages.

6.2 Update to Woodring’s list of Paciphiles, methods
Woodring (1966) gave a complete list of the paciphilic molluscan taxa known at the time. This was later supplemented by Petuch (1981). The gastropod section of these lists has been updated following a comprehensive search of the fossil and Recent literature, visits to museum collections, and supplemented by abundant new fossil material resulting from extensive field work carried out by the author in the Caribbean Neogene in the last 25 years.

The age assignment of most of the Caribbean Neogene formations has changed since their original descriptions. This is largely due to the extensive works of Panama Palaeontology Project (PPP) researchers (e.g., Saunders et al., 1986; Collins & Coates, 1999). Consequently the age assignment of the fossil assemblages from those outcrops has, also, changed significantly since their original description. Therefore, the chronostratigraphical distribution of the taxa in the Caribbean Neogene has been updated (both the occurrences taken from the literature and the new occurrences recorded by our field work) based on the latest stratigraphical information available (e.g., Coates et al., 2003, 2004).

The protoconch types and larval development for the paciphile species discussed is recorded from the literature, with references cited, and the records supplemented and checked when possible against fossil specimens. Protoconch whorls have been counted following the model suggested by Jablonski & Lutz (1980, 1983). Larval development inferred from the protoconch in fossil specimens according to Shuto (1974), Jablonski & Lutz (1980, 1983), Silva (2001).

6.3 Update to Woodring’s list of Paciphiles, results

The systematic update of the paciphile genera, subgenera and species groups in Landau et al. (2009) resulted in a more than doubling of the number of paciphiles from 30, since Woodring (1966), to 64. One subgenus was recorded for the first time; Coralliobia H. & A. Adams, 1853 (Muricidae; Coralliophilinae) and certain taxa classically described as paciphilic, such as Eupyrene Woodring, 1928 (Columbellidae) and Apher a H. & A. Adams, 1854 (Cancellariidae) since found living in Caribbean waters, were removed. This list was further revised by Landau & Silva (2010b), and the number increased to 67 with the addition of Mammilla Schumacher, 1817, Neoteron Pilsbry & Lowe, 1932 and the Conus (Ximeniconus) species group (see Appendix 7.4). The Oocorys elevata species group was removed from the list, as this was a misidentification of a Cantaure shell (Alan Beu, personal communication, 2010).

The Cubagua assemblage is very rich in paciphiles, with 16 paciphilic genera, subgenera and species groups present in the assemblage. Paciphilic species are far less common (see Landau et al., 2009). However, they are relatively well-represented in the Cubagua assemblage by seven species; Persististrombus granulatus (Swainson, 1822), Polinices (Polinices) intermeratus (Philippi, 1851), Bursa rugosa (G. B. Sowerby II, 1835), Scalina brunneopicta (Dall, 1908), Eupleura muriciformis (Broderip, 1833), Stramonita biserialis s. l. (Blainville, 1832) and Harpa crenata Swainson, 1822.

The list includes representatives of numerous distinct gastropod families, with no obvious common environmental or ecological requirements. However, four gastropods families are particularly well represented, comprising between them 48% of all the paciphile higher-level taxa (subgenus and species – group level); the Cancellariidae with 9 (14%), the Muricidae with 8 (12.5%), the Columbellidae with 8 (12.5%), and the Buccinidae with 6 (9%).

Paciphile taxa were present both in the Gatunian biogeographical Province, which straddled the CAS and the Caloosahatchian Province to the north in the Neogene Atlantic (Text Fig 31; for further geographical and chronological range of these provinces as used here, see Vermeij, 2005; Landau et al., 2008).

Although the Gatunian had the greater number of paciphiles in its Neogene faunas, a small number of these survived longer in the Caloosahatchian Province than in the Gatunian Province. Two paciphile taxa, Jenneria Joussaud, 1884 and Malea Valenciennes, 1832 survived into the Bermont Formation in the Florida assemblages (Petuch, 1994), dated as Pleistocene (1.7-1.0 Ma) (Hulbert & Morgan, 1989; Webb et al., 1989; Lyons, 1991).
Landau et al. (2009) recognised that these paciphile elements did not disappear from the Neogene Caribbean simultaneously, but seem to have suffered a steep decline during the Late Pliocene. The number of paciphile taxa seems to have remained high throughout the Miocene (47) and most of the Pliocene (50), with a sharp decline in the number of taxa some time during the Late Pliocene (8). We have not separated the Pliocene faunas, as there are discrepancies in the dating of a number of these assemblages. However, it is clear that in undisputed Late Pliocene assemblages such as the Agueguexquite Formation of Mexico (2.9-2.5 Ma, Cotton in Collins & Coates, 1999) and Caloosahatchee Formation (2.5-2.0 Ma, Lyons, 1991), and Early Pleistocene such as the Moin Formation (1.9-1.5 Ma; Cotton in Collins & Coates, 1999), Ground Creek Unit, Bastimentos Island (1.8 Ma, Coates et al., 2005) and upper part of the Escudo de Veraguas Formation, Bocas del Toro Area, Panama (1.8 Ma, Coates et al., 2005) the number of Paciphiles is significantly reduced (Appendix 7.5).

Appendix 7.6 gives a list of all the paciphile species present in the Caribbean Neogene. All have planktotrophic larval development. One species, Crucibulum (C.) spinosum (Sowerby, 1824), has a paucispiral protoconch with a small nucleus, which according to the criteria herein used to infer larval development from the protoconch in fossil specimens could indicate a non-planktotrophic development (Shuto, 1974; Jablonski & Lutz, 1980, 1983; Silva, 2001), but planktotrophic development has been observed in living specimens (Collin, 2003).

6.4 Paciphiles and faunal units

A system of ecobiostratigraphic units was proposed for the Pliocene Tropical West African-Mediterranean Province by Monegatti & Raffi (2001), which has proved to be of use not only within that biogeographic province, but can also help in the understanding of neighboring biogeographic units (Silva & Landau, 2007).

This led Landau et al. (2009) to investigate the possibility of constructing a similar model for the Neogene American Tropical Atlantic based on these paciphilic taxa. Ecobiostratigraphic units are only valid within the biogeographic unit in which they are constructed (Monegatti & Raffi, 2001; Silva & Landau, 2007). Therefore the Gatunian and Caloosahatchian Provinces will be discussed separately. This

Text-Figure 40. Gatunian Neogene Paciphile Molluscan Units and their chronostratigraphic range. (Adapted from Landau et al., 2008).
series of ecobiostratigraphic units was revised by Landau & Silva (2010b) to take into account the change in the definition of the Pleistocene (Text Fig. 40).

In the Gatunian Province three distinct faunal units can be identified based on the presence/absence of paciphiles (Text Fig. 40). These were called Gatunian Neogene Paciphile Molluscan Units (GNPMU) (Landau et al., 2009). GNPMU 1 is already in place in the Gatunian Early Miocene assemblages such as those of the Cantaure Formation of Venezuela and Baitoa Formation of the Dominican Republic. It is characterized by a high number of paciphile taxa. The faunal unit ends with the disappearance of all the members of the two most prominent group, the paciphilic Cancellariidae and Muricidae. As discussed above, the dating of some of the Pliocene Caribbean assemblages is still disputed, but in undisputed Late Pliocene assemblages such as the Agueguexquite Formation of Mexico (2.9-2.5 Ma, Cotton in Collins & Coates, 1999), and the Banano Formation of Costa Rica (3.6-2.4 Ma, Cotton in Collins & Coates, 1999), the paciphilic cancellarids and muricids are no longer represented in the assemblages. GNPMU 1 therefore ends at about 3.6 Ma, at the beginning or during the Late Pliocene.

GNPMU 1 is stratigraphically a very long lived unit, and includes assemblages such as the Baitoa (17.5-14.5 Ma), Cercado (7.5-5.7 Ma) and Gurabo (5.6-4.0 Ma) formations of the Dominican Republic (Saunders et al., 1986) and Gatan Formation of Panama (12-8.2 Ma, Cotton in Collins & Coates, 1999). It does not seem possible, however, to subdivide it based on its paciphilic elements. Although some paciphile taxa have so far been found only in the Early Miocene, such as Neorapana Cooke, 1918, Acanthais Vermeij & Kool, 1994 and Macron H. & A. Adams, 1853, these are not useful as index taxa as they are neither abundant not common to all the Early Miocene Gatunian assemblages.

GNPMU 2 is characterized by an impoverished number of paciphile elements, devoid of the two main groups discussed above. This second unit ends with the total disappearance of all the paciphile taxa. The most important assemblages within this unit in the Gatunian Province are the ones in the Moin Formation of Costa Rica (1.9-1.5 Ma, Cotton in Collins & Coates, 1999) and in the upper part of the Escudo de Veraguas Formation and the Ground Creek Unit, Bocas del Toro, Panama (both 1.8 Ma, Coates et al., 2005). Stratigraphically this unit Early Pleistocene and ends at the Late Pleistocene Calabrian-Ionian boundary. All the later Pleistocene assemblages within the Caribbean region such as the Isabella Formation of the Dominican Republic (Marcano & Tavares, 1982), Cumaná Formation (Boll, 1972), El Manglillo Formation, Araya Peninsula [= Castillo de Araya beds of Jung, 1989] (Macsotay, 2005a; Macsotay & Hernandez, 2005) and Playa Grande Formation (Jung, 1989) from Venezuela fall within GNPMU 3 and are characterized by the absence of any paciphilic elements in their assemblages, and stratigraphically this unit runs into Recent times.

Similar to the model of Mediterranean Pliocene Molluscan Units (MPMU’s) suggested by Monegatti & Raffi (2001), each GNPMU is defined by the lack of taxa which disappeared in the immediately previous extinction or local disappearance event and by the presence of the particular contingent which disappears in the immediately successive extinction phase.

Within the Caloosahatchian Province the pattern is very similar to that seen in the Gatunian Province, and interestingly the composition of the assemblage of paciphile taxa surviving into the Late Pliocene-Early Pleistocene in these distinct biogeographic provinces is almost identical. Two paciphile taxa, Jenneria and Malea may have survived slightly later in the Florida Pleistocene assemblages. This work is part of an ongoing project dealing with Gatunian assemblages. At present faunal units within the Caloosahatchian Province are not formally named.

6.5 GNPMU’s and other Caribbean Neogene assemblages

Within the Neogene Venezuelan assemblages, excluding the present work, the most thoroughly documented are those of the upper Lower Miocene, Cantaure Formation of the Paraguaná Peninsula, Falcón State (see Section 2.1.1, Text-Figure 3), the Lower Pliocene assemblage of the Punta Gavilán Formation also in Falcón State (see Section 2.1.1, Text-Figure 3) and the Upper Pliocene-Pleistocene localities near Maiquetía, the Mare, Playa Grande and Abisinia Formations (see Section 2.1.2, Text-Figure 4). Unfortunately, the Upper Miocene assemblages of Falcón State are poorly known. If we consider these
assemblages in relation to GNPMU’s, the Cantaure Formation is a splendid example of a GNPMU 1 assemblage, with a high number of paciphilic genera and especially a large number of paciphilic muricids (6) and cancellarids (4) (Table 9). From a palaeoecological point of view the Cantaure Formation is important in having a number of paciphilic taxa associated with rocky substrates not found in other Caribbean Neogene assemblages (VERMEIJ, 2001b; LANDAU & VERMEIJ, 2010).

Table 8: Paciphile genera present in the fossil assemblages of the Cantaure Formation.

<table>
<thead>
<tr>
<th>Rhinoclavus (Ochetoclava)</th>
<th>Hesperisternia panamica group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trochita</td>
<td>Cymatophos</td>
</tr>
<tr>
<td>Pseudadonaria</td>
<td>Macron</td>
</tr>
<tr>
<td>Jenneria</td>
<td>Pleuroloca granosa species group</td>
</tr>
<tr>
<td>Neverita (Glossaulax)</td>
<td>Fusimitra (Mitra (Tiara) longa complex)</td>
</tr>
<tr>
<td>Sinum lacondamini species group</td>
<td>Subcancilla sensu CERNOHORSKY (1991)</td>
</tr>
<tr>
<td>Malea</td>
<td>Strigatella tristis group sensu CERNOHORSKY (1991)</td>
</tr>
<tr>
<td>Ficus ventricosa species group</td>
<td>Harpa</td>
</tr>
<tr>
<td>Purpurellus</td>
<td>Cancellaria (Bivetiella)</td>
</tr>
<tr>
<td>Euplera</td>
<td>Euclia</td>
</tr>
<tr>
<td>Vitularia</td>
<td>Narona</td>
</tr>
<tr>
<td>Cymia</td>
<td>Massyla</td>
</tr>
<tr>
<td>Acanthais</td>
<td>Knefastia</td>
</tr>
<tr>
<td>Neorapana</td>
<td>Curiaturricula</td>
</tr>
<tr>
<td>Sincola (Dorsina)</td>
<td></td>
</tr>
<tr>
<td>Solenosteira, tropical American group (inc. Ficus ventricosa species group)</td>
<td></td>
</tr>
<tr>
<td>Fustinosteira</td>
<td></td>
</tr>
</tbody>
</table>

Table 9: Paciphile genera present in the fossil assemblages of the Punta Gavilán Formation.

The Lower Pliocene Punta Gavilán Formation in Falcón State (see Section 2.1.1) is less well-known. The only collections known are those made by RUTSCH (1930-1942) housed in the NHB (Switzerland) and those in the authors collection. The fossils appear as calcitic pseudomorphs of originally aragonitic shells and are found on the sea cliff face, and often inaccessible except for at lowest tide. Although less speciose, it still contains an important number of paciphiles placing it also within GMPMU1 (Table 9).

Table 10: Paciphile genera present in the fossil assemblages of the Tuberá Group.

The coeval Lower Pliocene Colombian assemblages of the Tuberá Group are known from publications by ANDERSON (1929), WEISBORD (1929) and BARRIOS (1960), and some small collections consulted in the NMB, Switzerland. The assemblage is very similar to that found in Cubagua and contains a significant number of paciphiles, again placing it within GMPMU1 (Table 10).

<table>
<thead>
<tr>
<th>Jenneria</th>
<th>Pleuroloca granosa species group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ficus ventricosa species group</td>
<td>Fusimitra (Mitra (Tiara) longa complex)</td>
</tr>
<tr>
<td>Euplera</td>
<td>Subcancilla sensu CERNOHORSKY (1991)</td>
</tr>
<tr>
<td>Solenosteira, tropical American group (inc. Ficus ventricosa species group)</td>
<td>Euclia</td>
</tr>
<tr>
<td>Fustinosteira</td>
<td></td>
</tr>
<tr>
<td>Cymatophos</td>
<td>Pyruclia</td>
</tr>
</tbody>
</table>

Table 10: Paciphile genera present in the fossil assemblages of the Tuberá Group.
In the Mare Formation, now considered Upper Pliocene-Lower Pleistocene (Macsotay, 2005b), Weibord (1962) described Malea mareana. This is the only paciphile gastropod genus present in the Venezuelan Upper Pliocene-Lower Pleistocene assemblages and places it neatly within GMPMU2. The Upper Pleistocene is well represented along the northern Venezuelan Caribbean coast and outlying islands by several formations: Abisinia Formation, Cumaná Formation, El Manglillo Formation and La Tortuga Formation (see Section 2.4). These assemblages are rich in species and contain no paciphiles, placing them within GMPMU3. Therefore, within the Colombian-Venezuelan-Trinidad Subprovince, the known assemblages can be arranged neatly within the GMPMU ecostratigraphic units.

Elsewhere on the Atlantic Portion of the Mio-Pliocene Gatunian Biogeographical Province, if we consider the assemblages in the neighboring Central American-northern South American Subprovince of Woodring (1974), the most important and richest assemblage occurs in the Middle-Upper Miocene Gatun Formation, which probably has the highest number of paciphiles of any of the Caribbean Neogene assemblages, and is therefore placed within GNPUMU1 (Table 11). The gastropods found in the Gatun Formation were monographed by Woodring (1957-1982), and large collections are present in the NHB, Switzerland and the author’s collection.

Table 11: Paciphile genera present in the fossil assemblages of the Gatun Formation.

<table>
<thead>
<tr>
<th>Teinostoma (Aepystoma)</th>
<th>Pleuroloca granosa species group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solariorbis (Hapalarbis)</td>
<td>Oliva (Strephonella)</td>
</tr>
<tr>
<td>Rhinoclavis (Ochetoclaya)</td>
<td>Fusimitra (Mitrata Tiara) longa complex</td>
</tr>
<tr>
<td>Trochita</td>
<td>Subcancilla sensu Cernohorsky (1991)</td>
</tr>
<tr>
<td>Neverita (Glossaulax)</td>
<td>Strigatella tristis group sensu Cernohorsky (1991)</td>
</tr>
<tr>
<td>Neverita (Hypterita)</td>
<td>Euclia</td>
</tr>
<tr>
<td>Sinum lacoandamin species group</td>
<td>Pyruclia</td>
</tr>
<tr>
<td>Eunaticina</td>
<td>Narona</td>
</tr>
<tr>
<td>Malea</td>
<td>Massyla</td>
</tr>
<tr>
<td>Ficus ventricosa species group</td>
<td>Chelyconus</td>
</tr>
<tr>
<td>Eupleura</td>
<td>Pyruconus</td>
</tr>
<tr>
<td>Solenosteira, tropical American group (inc. Ximenicons)</td>
<td>Cruzituraclua</td>
</tr>
<tr>
<td>Fusinosteira</td>
<td>Glyphostoma (Euglyphostoma)</td>
</tr>
<tr>
<td>Cymatophos</td>
<td>Terebra (Panaterebra)</td>
</tr>
<tr>
<td>Northia</td>
<td>Heliacus (Astronacus) = (Torinista)</td>
</tr>
</tbody>
</table>

Table 11: Paciphile genera present in the fossil assemblages of the Gatun Formation.

The Upper Pliocene Escudo de Veraguas Formation outcropping in the Bocas del Toro area (Caribbean Panama) is well represented in the Panama Paleontology Collection housed in the NMB, Switzerland and in the BL collection. It contains a single paciphile: Knefastia. The Lower Pleistocene Ground Creek Formation on Bastimentos Island (Bocas del Toro Region) was also sampled by the author, and two paciphiles were found: Jenneria and Harpa. Both these assemblages fall within GNPUMU 2. These GNPUMU assignments based on paciphile taxa contents are in agreement with the known stratigraphic positioning of these formations based on other biostratigraphic markers (forams and calcareous nanofossils) and radiometric datings (see Section 2.4). Therefore, the GNPUMU ecostratigraphic units also apply to the Central American-northern South American Subprovince.

In Woodring’s (1974) West Indian Subprovince the gastropod faunas are well represented in the Lower Miocene Baitoa Formation, Upper Miocene Cercado Formation and Lower Pliocene Gurabo Formation of the Dominican Republic. These deposits were monographed by Maury (1917) and Pilsbry (1922), and are being revised in a series of monographs published in theBulletins of American Paleontology. These collections are also housed in the NMB, Switzerland. The author has also undertaken ten field trips to the Dominican Republic, specimens part of the BL collection. All three of these assemblages are rich in paciphiles and are placed in GNPUMU1 (Table 12).
Table 12: Paciphile genera present in the fossil assemblages of the Dominican formations.

Unfortunately, Upper Pliocene-Pleistocene assemblages are scarce in the Dominican Republic. The Upper Pleistocene La Isabella Formation found at La Isabella on the northern Dominican coast has been frequently sampled by the author, and although approximately 88 genera and 106 species of gastropods are represented, there no Paciphiles are present, placing it in GNPMU3. This GNPMU placement is in agreement with the age deduced by MARCANO & TAVARES (1982) (see Section 2.4), and it can be concluded that GNPMUs can be applied to the West Indian Subprovince.

The Agueguexquite Formation, placed geographically on the Isthmus of Tehuantepec, Veracruz, Mexico, was monographed by PERRILLAT (1960-1973). It is important as it is one of the few Neogene Caribbean Upper Pliocene assemblages (see Section 2.4). It has a small number of paciphiles in the fauna and falls within GNPMU2 (Table 13).

Table 13: Paciphile genera present in the fossil assemblages of the Agueguexquite Formation.
It seems, therefore, that the GNPMU biostratigraphic units can be applied throughout the Atlantic portion of the Gatunian Province. However, ecostratigraphic units can only be applied within the biogeographic context or unit in which they were constructed (Silva et al., 2010). When GNPMUs are applied to the Floridian (USA) assemblages in the neighboring northern Caloosahatchian Province, it is clear that paciphiles managed to survive longer here than in the Gatunian Province. It is not easy in the Floridian assemblages to clearly distinguish Upper Pliocene and Lower Pleistocene assemblages and a list is given here of the paciphiles present in the Upper Pliocene: upper Pinecrest Beds units 4-1, Caloosahatchee and Bermont Formations (see Section 2.4). No paciphiles survived into the Upper Pleistocene Fort Thompson Formation (Table 14).

If the disappearance of paciphiles was due to a combination of two key factors: the closure of the CAS and decrease in productivity on the Atlantic side as suggested in this work (see Chapter 7), it is quite possible that paciphiles managed to survive longer in the Caloosahatchian Province if the decrease in productivity was not as severe. Whilst upwelling also decreased along the coasts of Florida (Allmon, 2001; Schneider & Schmittner, 2006), there is some evidence that high productivity in this region persisted due to nutrient input from freshwater runoff (Tao, 2008). Nevertheless, GNPMUs cannot be applied directly to assemblages within the Caloosahatchian Province.

<table>
<thead>
<tr>
<th>Jenneria</th>
<th>Subcancilla sensu Cernohorsky (1991)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pusula, sensu Cate, 1979</td>
<td>Massyla</td>
</tr>
<tr>
<td>Malea</td>
<td>Perplicaria</td>
</tr>
<tr>
<td>Ficus ventricosa species group</td>
<td>Ximeniconus</td>
</tr>
<tr>
<td>Microcithara</td>
<td>Knefastia</td>
</tr>
</tbody>
</table>

Table 14: Paciphile genera present in the fossil assemblages of the Upper Pliocene-Pleistocene formations of Florida. Occurrence data obtained from Petuch (1994).

One important factor limiting the usefulness of GNPMUs to characterize Miocene assemblages, is the very long span of GNPMU1, already in place at the beginning of the Miocene and extending to the Zanclean-Piacenzian boundary. Unfortunately, none of the paciphiles present in the Lower Miocene assemblages alone are common enough to be useful as marker fossils, and the cohort of paciphiles present in the Cantaure assemblage, but not found elsewhere in later deposits, probably reflect palaeoenvironmental change rather than true extinctions and/or disappearances from the Atlantic portion of the Caribbean Gatunian Bioprovince. Following the reasoning given above, if the disappearance of paciphiles was due to a combination of the closure of the CAS and the ensuing decrease in productivity on the Caribbean side, it is likely that further resolution of GNPMU1 is not possible, as extinctions and/or disappearances did not occur until the first major closure event of the CAS, which ultimately gave rise to the decrease in Caribbean productivity (see Section 6.1).

6.6 Paciphiles, their importance in overall extinction following the closure of the CAS

Woodring (1966) first drew attention to the presence of taxa in the Neogene Caribbean, that subsequent, or during, the closure of the CAS became restricted to the Pacific side of their original distribution, and are in the tropical American Pacific faunas today. Petuch (1982) added to the list of 30 or so paciphiles identified by Woodring (1966), but until now the importance of these paciphiles in comparison with the overall extinction seen in the Caribbean subsequent to the closure of the CAS is unknown. Are these paciphiles merely a curious phenomenon, or do they play a major role in understanding the extinction and disappearance of taxa following the uplift of the Isthmus of Panama?

In order to answer this, an attempt was made to see what percentage of the total number of genus/subgenus and species groups disappeared from the Caribbean following the closure of the CAS were paciphiles. The database of living Western Atlantic Marine Mollusca, Malacolog Version 4.1.1 (Rosenberg, 2009; described by Rosenberg, 1993) was used for generic assignments, with a few exceptions where families have been updated (i.e. Tonnoidean genera updated by Beu, 2010). All genera
with species recorded as living exclusively at depths greater than 100m were excluded, as the Caribbean Neogene deposits represent mainly shallow water assemblages. Some groups with mainly very small shells, which are poorly known or poorly represented in fossil assemblages, such as the Rissooidea, Pickworthiidae, Architectibranchia and Cephalaspidea, were also excluded. Records for fossil occurrences were taken from the literature and collections visited during the course of this work and the BL collection.

Appendix 7.7 gives a list of 109 genus/subgenus and species groups identified as being present in the Caribbean portion of the Neogene Gatunian biogeographic province, but no longer present in the Caribbean Province today. Of these, 68 are paciphilic, present today in the tropical American Pacific, 26 are extinct and 15 represent local disappearances, the taxa still found today, but not in the Caribbean.

This suggests that amongst the gastropods, the paciphile were anything but an interesting curiosity, accounting for 60% of the extinctions and disappearances following the closure of the CAS. Moreover the pulses of extinction identified in the paciphile disappearances from the Caribbean discussed above also hold true for extinctions and disappearances as a whole, with the greatest disappearance of genera at the end of the Lower Pliocene and the almost complete disappearance at the end of the Lower Pleistocene, with only one taxon surviving into the Upper Pleistocene, but not present in the Caribbean today.

6.7 Paciphiles and faunal units, implications and conclusions

Based on these paciphile generic, subgeneric and specific taxa, for the Gatunian Province, two pulses of local disappearance from the Atlantic portion of their original distribution can be identified. The first is marked by the overall decrease in Atlantic paciphile diversity and the total disappearance of all the paciphilic cancellariids and muricids, roughly corresponding with the timing given for the closure of the CAS. The second, marked by the complete disappearance of all paciphiles from the Atlantic, roughly coincides with the total closure of all connections between the Atlantic and Pacific.

As we have shown above, the Cubagua assemblage is rich in paciphile taxa, especially in paciphilic Cancellariidae, which all disappeared in the first pulse of local disappearance and extinction at the end of the Zanclean to early Piacenzian. Therefore the Cubagua assemblage lies within GNPMU1. This allows us to suggest an upper chronostratigraphic limit for our Cubagua assemblage no later than upper Zanclean. This is in agreement with the Lower Pliocene age of the deposits discussed in the introduction.

Throughout the Miocene and Pliocene an important and relatively constant number of gastropod taxa were distributed throughout the Neogene Gatunian and Caloosahatchian biogeographical provinces, which following the total closure of the Central American Seaway (CAS) suffered a range contraction, restricting them to the Pacific portion of their original Neogene distribution.

The emergence of the Isthmus of Panama was not a single, short-lived event. COATES et al. (1992) dated the timing of the closure of the CAS at about 3.5 Ma; COATES & OBANDO (1996) at 3.1-2.8 Ma, more recently COLLINS (2003) at about 4 Ma and TIEDEMANN et al. (in COATES et al., 2005) at 2.8 Ma.

After MOLNAR (2008), defining the timing of CAS closing is difficult, if not impossible, until 2.7–2.6 Ma, when the ‘Great American Exchange of vertebrates between North and South America took place. In his critical review, based on the analysis of studies on the evolution of shallow water benthic organisms dwelling on the Atlantic and Pacific sides of Central America, he concluded that if a single date younger than ~ 6 Ma occurs more commonly among the analysed studies than any other that is ~3.5 Ma.

CRONIN & DOWSETT (1996) suggested that whilst the main uplift dated between 3.5-3.1 Ma, a second closing may have occurred between 2.3-2.0 Ma. According to BEU (2001), a seaway (or seaways) still operated, at least intermittently, late in Pliocene time, and at least intermittent marine connections probably continued during Early and perhaps Middle Pleistocene interglacial periods. The presence of paciphiles in the Neogene Atlantic is not significantly different in the Miocene and Pliocene (Text-Fig. 40).
It seems that the presence of paciphiles in the Atlantic was only affected fairly late in the closure of the CAS. Based on these paciphile taxa, two pulses of extinction or local disappearance from the Atlantic portion of their original distribution can be identified. The first is marked by the overall decrease in Atlantic paciphile diversity and the total disappearance of all the paciphilic cancellarids and muricids which occurred at the beginning or during the Late Pliocene, roughly corresponding with the timing given for the closure of the CAS by Coates & Obando (1996). The second is marked by the complete disappearance of all paciphiles from the Atlantic, which again roughly coincides with the total closure of all connections between the Atlantic and Pacific as suggested by Beu (2001).

The evidence from these paciphiles harmonises both these scenarios, but goes against a total closure of the CAS at 4.0-2.8 Ma. There was probably an almost complete closure of the CAS causing the main pulse of disappearance at around 3.6 Ma. Nevertheless, some paciphiles survived in the Caribbean, and continued there whilst, at least intermittently, their populations were supplemented by sporadic influx from the Pacific. Once this Pacific influence stopped completely, these sink population were doomed.

O'Dea et al. (2007) argued that there was a 2 million-year gap between environmental change in Atlantic Central America and subsequent extinction. Our work on the paciphile taxa and southern Caribbean Pliocene gastropod assemblages does not support this view. Firstly, the main pulse of disappearance amongst the paciphiles at the end of GNPMU 1, as shown here, is at about 3.6 Ma. This coincides with the major environmental changes documented by O'Dea et al. (2007). The new data presented here on the total extinction or disappearance of genera/subgenera and species groups from the Caribbean during the Neogene (see Appendix 7.7) further supports the timing of the two major pulses of extinction from the Caribbean seen in the paciphile groups. Secondly, Landau et al. (2008) demonstrated that there had been no significant environmental change between the Miocene and Recent times along the northern coasts of Venezuela, and yet the Pliocene assemblages in the region have an important percentage of paciphile gastropods which disappeared despite no apparent change of environment.

Landau et al. (2009) suggested that paciphilic species vanished in the Caribbean because the west to east current through the increasingly restricted CAS could no longer carry larvae of planktonically dispersing species from source populations in the eastern Pacific to the Caribbean. As a result, Caribbean populations became unsustainable sink populations, and eventually disappeared. Another scenario is that the pre-closure Caribbean high oceanic productivity might have contributed to the maintenance of paciphilic populations in the Caribbean, and that reductions in productivity doomed these local populations (G. S. Herbert, 2008, personal communication). This possibility cannot be eliminated, but if the Caribbean were an important source for populations in the eastern Pacific, there should have been a larger number of so-called caribphiles, species that survived only in the Caribbean after becoming extinct in the eastern Pacific. The number of caribphiles is in fact about one-tenth that of paciphiles.

A review of all known paciphile species (Appendix 7.3) shows all these taxa have an inferred planktotrophic development. The presence of a larval development, enabling the larvae of these paciphile species to easily travel, or be carried, from the Pacific to the Caribbean and maintain the sink populations there viable would support this hypothesis.

There seems to be no obvious common environmental factors or requirements which unite this group and their disappearance from the Atlantic cannot be easily explained by sudden changes in environmental conditions following the closure of the CAS which would single this heterogeneous group of taxa out for disappearance. However, if the Pacific portion of the Gatunian Province were acting as the source population in the late Neogene, the closure of the CAS would have isolated the Atlantic populations from their sources, the sink populations thus becoming stranded on the Atlantic coasts of Tropical America, where they became unsustainable and eventually disappeared.
CHAPTER 7: REMOTE CAUSES OF EXTINCTION AND RESTRICTION IN THE MARINE NEOGENE OF TROPICAL AMERICA: A HYPOTHESIS

One of the world's great geographic events of the last 25 million years is the formation of the Central American land bridge connecting North and South America. This event took place in the Pliocene, 3.5 to 3 Ma, with the land bridge becoming a permanent fixture about 1 Ma during the Early Pleistocene; but it was the culmination of a series of tectonic changes that can be traced back to the Middle Miocene (Coates et al., 2003, 2005; Molnar, 2008). One consequence of the formation of the land bridge was the local or global extinction of a large number of taxa in the Atlantic sector of the American marine tropics during the Pliocene (Woodring, 1966; Vermeij & Petuch, 1986; Almon et al., 1993; Jackson et al., 1993). The causes of this extinction remain matters of investigation and controversy. Based on previously published findings, it is possible to put forward the working hypothesis that the extinctions resulted not merely from environmental changes in the Atlantic sector of tropical America, but also—and perhaps mainly—from the inviability of Caribbean populations, which were cut off from eastern Pacific source populations by the Central American barrier.

7.1 Tropical American Neogene patterns of extinction

During much of the Neogene, marine tropical America was divided into two biogeographic provinces, the Gatunian (comprising the Atlantic sector including the Caribbean region and the north coast of South America, and the Pacific sector from Baja California to Peru), and the Caloosahatchian Province (the continental coast of the southeastern United States to Honduras) (Petuch, 1982; Vermeij, 2005; Landau et al., 2008). In the Gatunian Province, many molluscan clades, as represented by subgenera and species groups, disappeared from the Atlantic sector during and after the Pliocene. Although some of these clades became globally extinct, others survive today in the eastern Pacific (Woodring's 1966 Paciphiles) or in the Indo-West Pacific. The recent compilation published by Landau & Silva, 2010 lists 67 Paciphile gastropod clades (Appendix 7.4). Only four gastropod clades became extinct in the Pacific sector of the Gatunian Province and survive in the Caribbean (Woodring's Caribphiles). These data strongly imply that the tropical eastern Pacific formed a geographic refuge for many Gatunian clades, whereas the Caribbean region as a whole did not (Vermeij, 1986, 1989). There is some evidence for geographic restriction within the western Atlantic, with the mainland coasts of northern South America and Brazil acting as post-Pliocene refuges for a number of previously more widespread molluscan clades such as Eburna (Olividae), Muracypraea (Cypraeidae), the Lobatus goliath group of strombids, and the Turbinella laevigata group of turbinellids (see also Petuch, 1982; Vermeij, 1989).

The magnitude of global or regional extinction in the Atlantic Gatunian Province during the Pliocene was very high. Of 95 subgenera and species groups of gastropods in the Araya Formation (Early Pliocene: late Zanclian) on Cubagua Island, Venezuela, 16 (17%) are Paciphiles, two are found today only in the Indo-West Pacific, and eight (9%) are globally extinct. Hence 81% of Araya species have become regionally or globally extinct. This figure is similar to the 85% magnitude of extinction among gastropods of the coeval Punta Gavilán Formation of Venezuela (Landau, unpublished data) and the 88% extinction calculated by Woodring (1928) for molluscs of the Bowden Formation (Pliocene) of Jamaica. Jung (1969) estimated species-level extinction in the Melao Clay fauna (Pliocene) of Trinidad to be 88%, but Vermeij (2001c) revised this downward to 79% in the light of more recent taxonomic work. Most of these extinctions took place between the end of the Early Pliocene and the Early Pleistocene. Only five species are held in common between the Pliocene Araya Formation and the nearby Early Pleistocene Mare Formation of Venezuela.
Extinction in the eastern Pacific sector of the Gatunian Province was less severe but by no means negligible. Vermeij & Petuch (1986) estimated a magnitude of 15% for molluscan subgenera and species groups, a little more than half the magnitude for Atlantic Gatunian clades; and Vermeij (2001c) calculated a species-level magnitude of molluscan extinction of 72% for the Esmeraldas fauna of the Pliocene Onzole Formation of Ecuador.

Stratigraphic gaps in the Plio-Pleistocene fossil record of northern South America preclude a precise inference of the time of Atlantic Gatunian extinction, but it is clear that almost all Paciphiles had disappeared from the Caribbean between the end of Araya deposition, about 3.5 Ma, and Mare Formation time in the Early Pleistocene (Landau et al., 2009). Disappearance at about 3.5 Ma is close in time to the environmental changes that began a million years earlier, associated with the Central American uplift as documented by O'Dea et al. (2007). A few Paciphiles persisted in the Caribbean region until the Early Pleistocene: the tonnoideans Malea ringens (Swainson, 1822), Bursa rugosa (G. B. Sowerby II, 1835), Distorsio constricta (Broderip, 1833), Monoplex lignarium (Broderip, 1833), and Cypraecassis tenuis (Wood, 1828) (Béu, 2010). The ovulid Paciphilic genus Jenneria Jousseaume, 1884 disappeared from the Caribbean region (Costa Rica and Florida) by the Early Pleistocene, well after its last appearance in the southern Caribbean during the Early Pliocene. The regional extinctions, as represented by the geographic contractions of Paciphiles, were therefore not simultaneous (Landau et al., 2009).

7.2 Extinction and the Source-Sink Hypothesis

Earlier authors ascribed these extinctions to either or both of two factors, a reduction in sea surface temperature and a decrease in Atlantic productivity (Stanley, 1986; Vermeij & Petuch, 1986; Allmon, 1992, 2001). Cooling likely contributed to the more northern Caloosahatchian extinctions, which were concentrated at about 1.7 Ma during the Early Pleistocene, coinciding with the end of deposition of the Caloosahatchee Formation sequence in Florida (Vermeij, 2005); but it is unlikely to have influenced events in the fully tropical southern Caribbean. O’Dea et al. (2007) documented a sharp decline in oceanic productivity on the Atlantic side of Panama and Costa Rica beginning 4.25 Ma (see also Collins et al., 1996a, b; Todd et al., 2002), and suggested that these environmental changes preceded major Atlantic Gatunian extinctions by as much as 2 my (see also O’Dea et al., in press). Reductions in productivity also seem to have occurred during the Pliocene in Florida (Allmon et al., 1996), again before the major end-Caloosahatchee extinctions. In northern South America, however, a regime of high oceanic productivity may have persisted for about 19 Ma from the Early Miocene to the Recent (Landau et al., 2008), though it is always possible that a brief, undocumented interruption could have taken place; yet, as discussed above, the gastropod fauna there suffered a high magnitude of extinction before the Early Pleistocene. A decrease in regional productivity surely affected many taxa directly, and likely accounts for the disappearance of many species endemic to the Atlantic sector of the Gatunian Province; but it may be insufficient to account for the extinction lags in Panama, Costa Rica, and Florida, and it cannot explain events on the north coast of South America or in the productive eastern Pacific.

Could the source-sink hypothesis explain some aspects of marine tropical American extinctions during and after the Pliocene? The general version of this hypothesis was proposed by Pulliam (1988), who pointed out that some populations of a species produce a surplus of individuals and therefore act as sources of recruits for other populations. These other populations would be unsustainable without this subsidy, and therefore act as sinks. Source populations occur in the most productive or optimal areas of the range of a species, whereas sink populations occupy less productive or less advantageous, and often geographically isolated habitats (Vermeij & Dietl, 2006).

For species that lived in both the Atlantic and Pacific sectors of the Gatunian Province, the formation of the Central American land bridge resulted in the isolation of Caribbean populations from those on the Pacific side of tropical America. A reduction in oceanic productivity on the Atlantic side of Central America (O’Dea et al., 2007), together with isolation from highly productive populations in the eastern Pacific, would have rendered many Caribbean populations unsustainable in the long run.
Two predictions follow from this hypothesis. First, currents flowing from west to east through an open CAS should have carried recruits from the productive eastern Pacific to the Caribbean. Second, Paciphiles—those taxa that became restricted to the eastern Pacific following uplift of the land bridge—should be dispersed planktonically. The available evidence, summarized below, supports both predictions.

7.3 Evidence for the Source-Sink Model

The existence of west to east transport across Central America before the land bridge emerged comes from two sources, the origins of some Caribbean species from Pacific ancestors and paleoceanographic models of circulation. Both sources indicate that, whereas Early Neogene water flow was predominantly from east to west, a reversal of direction took place in the Late Miocene.

Data on the geographic and stratigraphic distribution of tropical American taxa indicate that many species with Pliocene or living western Atlantic representatives originated in the eastern Pacific and subsequently expanded into the Atlantic. At least four Paciphile species—Persististrombus granulatus (Swainson, 1822), Scalina brunnneopicta (Dall, 1908), Harpa crenata Swainson, 1822, and Malea ringens (Swainson, 1822)—appeared earlier in the eastern Pacific fossil record than in the western Atlantic (Jung & Heitz, 2001; DeVries, 2007b; Beu, 2010). The same may apply to Stramonita biserialis (Blainville, 1832). All these species, except S. brunnneopicta, have their Caribbean records limited to the Araya Formation (Lower Pliocene) of Venezuela. The following subgenus-level taxa likewise have their earliest stratigraphic appearance in the eastern Pacific and colonized the Atlantic sector in the Lower Pliocene: the buccinoideans Northia Gray, 1847, Nicema Woodring, 1964, and Gemaphos Olsson & Hrabison, 1953 and the cancellarid Hertleinia Marks, 1949 (Woodring, 1964; Jung & Pettit, 1990; Vermeij, 2006). In the ocelenebrine muricid genus Eupleura H. & A. Adams, 1853, the living eastern Pacific E. pectinata (Hinds, 1844) was thought to have spread from the Atlantic to the Pacific (Herbert, 2005), but a more parsimonious interpretation of its fossil record is that the species originated in the eastern Pacific. Its apparent ancestor, E. thompsoni Woodring, 1959, is known from the Upper Miocene Salada Formation of Baja California, Mexico, and from the more or less coeval Gatun Formation of Panama (Herbert, 2005).

Other possible cases of Pacific origin and later spread to the western Atlantic rest on phylogenetic evidence. Among chionine venerid bivalves, the Atlantic Chione palisana group from the Pleistocene Mare Formation of Venezuela is nested in a clade of otherwise Pacific species, as inferred from a morphology-based phylogeny of all living and fossil species in Chione von Mühfeld, 1811 and related genera (Roopnarine, 2001). Similarly, the Recent Caribbean Chione cancellata (Linnaeus, 1767) and C. eros a Dall, 1903 were derived from an eastern Pacific ancestor (Roopnarine, 2001). Molecular phylogenies indicate that the amphili-Atlantic Conus ermineus Born, 1776 is derived from the eastern Pacific C. purpurascens G. B. Sowerby I, 1833 (Duda and Kohn, 2005), and that cowries of the Macrocypraea cervus-zebra group of Atlantic species is derived from the eastern Pacific M. cervinetta (Kiener, 1843) (Meyer, 2003).

Many other taxa, however, have Atlantic origins, or at least earliest occurrences, often dating back to well within the Miocene in the Atlantic; they subsequently spread to the Pacific. This pattern has been documented for the pectinids Leochlamys MacNeil, 1967 ("Flabellitecten" of authors, a Paciphile taxon), Euvola Dall, 1898, Nodipecten Dall, 1898, and Spathochlamys Waller, 1993 (Waller, 2007); the American venerid clade Chioninae and many subclades within this group (Roopnarine, 2001); the strombid Persististrombus Kronenberg & Lee, 2007 (the "Lenigo" of Jung & Heitz, 2001; see Kronenberg & Lee, 2007); the Paciphile muricids Eupleura, Pterorytis Conrad, 1863, Purpurellus Jousseaume, 1880, Neorapana, and the Muricopsis zeteki clade (Vokes, 1989, 1990a; Vermeij & Vokes, 1997; Gibson-Smith et al., 1997; Merle & Houart, 2003; Herbert, 2005); the pseudolivid Macron Adams, 1853 (Gibson-Smith et al., 1997); the Paciphile ovulid Jenneria (Groves, 1997); the Caribphilic cassid Cassis Scopoli, 1777 (Vokes, 1990b; Beu, 2010); pisamine buccinids of the tropical American Cantharus group with Hesperisternia Gardner, 1944 as basal genus (Vermeij, 2006); and the vasiid Vasum Roding, 1798 (Vokes, 1966), among many others. The Paciphile muricid genus Acanthais Vermeij & Kool, 1994 also belongs in this list. The Lower Miocene Stramonita semiplicata Vermeij,
2001 described from the Cantaure Formation of Venezuela (Vermeij, 2001b) and suspected by Vermeij to be ancestral to the living eastern Pacific A. brevidentata (Wood, 1828), is now known to have a labral tooth (based on material in the Landau collection) and therefore indeed belongs to Acanthais. Most of the taxa listed above, together with many others, were already present in the western Atlantic during or before the Miocene. When they spread to the Pacific is not precisely known, but in some cases this could have occurred during or even after the Late Miocene. It thus appears that the east to west expansion of taxa occurred throughout the Neogene, whereas cases of west to east expansion are concentrated in the Late Neogene.

Paleoceanographic evidence and simulations indicate a general east to west circulation through the deep, open CAS during the Oligocene and the first half of the Miocene (Berggren & Hollister, 1977; Kameo & Sato, 2000; Von der Heydt & Dijkstra, 2005, 2006). Currents carried planktonically dispersing larvae from east to west within the Gatunian Province. As the seaway shoaled beginning in the Middle Miocene (Coates et al., 2003, 2005; Molnar, 2008) westward flow may have slowed or perhaps even reversed. Collins et al. (1996a, b) inferred an incursion of cool Pacific water into the Caribbean in the region of the present-day Isthmus of Panama during the latest Miocene (6 Ma). Eastward dispersal of western Pacific recruits to the eastern Pacific began as early as the Late Miocene (Duda & Kohn, 2005) but became particularly prominent during the Pleistocene, with the greatest eastward flow taking place during El Niño years (Lessios et al., 1998; Robertson, 2001). Eastward transport across the Atlantic became common during the Pliocene and Pleistocene (Vermeij & Rosenberg, 1993; Floeter et al., 2008). By the time the CAS was being constricted, therefore, flow in the eastern Pacific and Atlantic sectors of the marine tropics was predominantly eastward, supporting the hypothesis that many western Atlantic populations would have received recruits from the eastern Pacific.

As interoceanic communication became restricted, upwelling and productivity in the eastern Pacific appears to have increased (Vermeij, 1997; Chaisson & Ravelo, 2000; Philander & Fedorov, 2003; Ravelo et al., 2004; Fedorov et al., 2006; Lawrence et al., 2006). If there was eastward flow at this time, as the evidence indicates, the eastern Pacific likely served as a highly productive source for Atlantic populations of planktonically dispersing species. With the emergence of the isthmus during the Late Pliocene, however, this source was cut off. The isthmian region of the Caribbean nearest the last vestiges of the seaway, meanwhile, was experiencing a reduction in oceanic productivity and a corresponding increase in carbonate (as opposed to siliciclastic) sedimentation (Collins et al., 1996a, b; Todd et al., 2002; O'Dea et al., 2007). Planktonically dispersing populations dependent on Pacific source populations thus became stranded on the Atlantic coast of South America, where they became unsustainable and were doomed to extinction.

In support of this scenario, we note that plaktotrophic larval development characterize all the Paciphilic gastropod species known except for the species of Eupleura, which are lecithotrophic (Landau et al., 2009), and therefore have a shorter planktic stage. Moran's (2004) comparisons of six western Atlantic arccoid bivalve species and their six eastern Pacific sister species reveals that, whereas the Atlantic species have maintained consistently large eggs (and therefore presumably short or no planktic stages) from the Miocene onward, Pacific species evolved smaller eggs. Surviving Caribbean species therefore did not directly depend on a high planktic food supply, either locally or in the potential source regions of the eastern Pacific and the Central American land bridge.

Attractive as this scenario is, it probably does not account for all cases of Paciphilic restriction in range. The Paciphile muricid Cymia Mörch, 1860, for example, was represented in Trinidad by the Pliocene C. brightoniana Maury, 1925, which has a paucispiral protoconch of just over one whorl, indicating nonplanktotrophic development (Kool, 1993). Similarly, the species of the columbellid Paciphile genus Parametaria Dall, 1916 in the Caribbean have paucispiral protoconchs (Jung, 1994). Notwithstanding these and perhaps other exceptions, the vulnerability of planktonically dispersing species to local or global extinction in the Pliocene western Atlantic is striking. Moreover, as pointed out above, there were substantial extinctions in the eastern Pacific as well as in the Atlantic. These are not easily reconciled with an increase in oceanic productivity.
We therefore suspect that the extinctions of the Plio-Pleistocene in general reflect a more global signal in conjunction with the workings of more regional factors, including the cut-off from source populations.

7.4 Source-Sink Model, implications

The source-sink perspective presented here could apply to many other episodes of extinction, especially in cases where extinctions are drawn out over time as populations decline at different rates. In most studies of extinction, causal factors are sought in the same environments and regions where species disappear. If, however, the fate of local or regional populations depends on the dynamics of remote source populations and their environments, the causes of at least some extinction may have to be looked for in source regions.

This hypothesis was presented for publication, but was rejected mainly on the grounds that insufficient data was presented at the time covering biogeographic provinces and range charts, first and last occurrence of taxa by location, and rigorous analysis of the data at the time of submission. Some of these criticisms are addressed in this work, with far more data available in the biogeographic section (section 4.2) and in the appendices (section 7.1-7.7). I hope further to address these criticisms with an in-depth analysis of all the gastropod taxa found in the Tropical American deposit. This will become far easier following the recent decision by Dr. Walter Etter and the Naturhistorisches Museum Basel, Switzerland to make the PPP and other Basel Tropical American collections catalogue available on-line (Decision August 2010).
CHAPTER 8: CONCLUSION

This thesis is the culmination of six years work, involving several field trips to the Caribbean and visits to two museum collections. It is also the materialization of the objectives laid out in its inception and the fruit of the patient and passionate investigation of the fossil assemblages not only of Cubagua, but also of numerous other Caribbean Neogene assemblages by the author over the last 25 years.

The systematic portion of this work resulted in a detailed monograph of the gastropod species found in the Lower Pliocene deposits of Cubagua Island (Caribbean Venezuela), collected by the author during four field trips to the island from 2000 to 2009. A total of 126 species were recorded from this previously virtually unknown deposit, belonging to 95 genera. During the course of this work eleven were described as new to science; Calliostoma (Calliostoma) calderense nov. sp., Calliostoma (Elmerlinia) pascaleae nov. sp., Calliostoma (Elmerlinia) macsotayi nov. sp., Modulus vermeiji nov. sp., Crucibulum (Crucibulum) cubaguaense nov. sp., Strombus arayaensis nov. sp., Pseudozonaria fehsei nov. sp., Mammilla arepa nov. sp., Malea beui nov. sp., Neoteron emilyvokesae nov. sp., Prunum carmengutierrezae nov. sp. Several new subjective synonymies were suggested: Turbo crenulatoides Maury, 1917 and Turbo (Marmarastoma) crenulatus venezuelensis Weisbord, 1962 = Turbo (Senectus) castanea Gmelin, 1791; Astralium brevispinum var. basalis Olsson, 1922 = Lithopoma brevispinum (Lamarck, 1822); Cerithium prismaticum Gabb, 1873 = Cerithium dentilabre Gabb, 1873, as first reviser the name Terebralia dentilabris (GABB, 1873) is chosen; Potamides (Pyrazinisus) bolivarenensis Weisbord, 1929 = Cerithium dentilabre GABB, 1873; Pyrazinisus harrisii Maury, 1902 is a distinct species, Terebralia harrisi (Maury, 1902); Cypraea rugosa Ingram, 1947, junior homonym of C. rugosa Broderip, 1827 = Muracyprea grahami (Ingram, 1947), Cypraea caroniensis Maury, 1925 is removed from synonymy of C. henekeni G. B. Sowerby I, 1850; Xancus praevoloides rosaeccanus Hodson, 1931 = Turbinella trinitatis (Maury, 1925); Vaxum quirosense Hodson, 1931 = V. haitense (Sowerby, 1850); Solenosteira basleti Anderson, 1929 and Solenosteira falconensis urumacoensis F. Hodson, 1931 = S. falconensis Weisbord, 1929; Melongena consors taurus Petuch, 1994 = Melongena consors (G. B. Sowerby I, 1850); Marginella venezuelana falconensis F. Hodson, 1927 is removed from the synonymy of Marginella venezuelana lavelana F. Hodson, 1927 and Persicula venezuelana, Persicula falconensis and Persicula lavelana, (F. Hodson in Hodson, Hodson & Harris, 1927) are considered distinct at full specific rank; Mitra (Tira) woodrungi H. E. Vokes, 1938 = Fusimitra sanctifrancisci Maury, 1925; Fusimitra sanctifrancisci and Fusimitra limonensis Olsson, 1922 are considered distinct species; Conomitra weeksi F. Hodson, 1931 = Conomitra lavelana F. Hodson, 1931; Lindoliva spengleri Petuch, 1988 and Lindoliva grifini Petuch, 1988 = Lindoliva diegelae Petuch, 1988; Conus trisculptus Pilsbray & Johnson, 1917 = Conus jaspideus Gmelin, 1791; Clavatula (Fusiturricula) pagoudula Rutsch, 1934 and Knefastia alienai Macsotay & Campos Villarroel, 2001 = Fusiturricula springvalensis (Mansfield, 1925) and Architectonica catanesei Petuch, 1994 = Architectonica nabisli Röding, 1798. These taxonomic findings were published in Landau & Silva (2010). The Cubagua assemblage now becomes the most thoroughly recorded Pliocene gastropod fossil assemblage in Venezuela.

The revision of southern Caribbean Pliocene gastropods resulting from this taxonomic survey allowed a re-evaluation of the biogeographic models proposed for the Neogene Caribbean previously proposed by various workers. The data corroborated preceding observations on the highly endemic nature of the fauna along the northern coasts of South America in the Pliocene, clearly distinct from that found in the neighbouring Isthmian region. Concurrent revisions carried out by the author on Miocene Caribbean assemblages suggests that this biogeographic unit – the so called Colombian-Venezuelan-Trinidad (CVT) Subprovince – seems to have been in place since at least the Early Miocene, and whilst showing dramatic changes in faunal composition at specific level over time, altered little at generic level until the total disappearance of the ‘paciphilic taxa’. It is further suggested that the geographic expression of this unit has not altered greatly over time, and does not seem to have been significantly affected by the closure of the CAS, responsible for the demise of the Gatunian Province and the subsequent rise of the Late Pleistocene to Recent Caribbean Province. Although the major bioprovinces in the Pacific-Caribbean region changed following the closure of the CAS, the CVT Subprovince remained unaltered. This suggests that the local oceanographic conditions along northern South America have not changed greatly since Early Miocene times, and seem not to have been significantly affected by the uplift of the Isthmus of Panama.
CONCLUSION

Woodring’s (1974) name Colombian-Venezuelan-Trinidad Subprovince is chosen over Petuch’s (1988) Puntagavilanian Subprovince, and chorotypes and chronotypes discussed for the Gatunian Province and the Colombian-Venezuelan-Trinidad Subprovince. These findings were published in Landau et al. (2008) and later updated in Landau & Silva (2010b).

Distinctive pattern of extinction were identified in the Neogene Venezuelan assemblages, and within the Caribbean Neogene as a whole. The data suggests a high degree of generic stability within the Caribbean Neogene prior to the total closure of the Central American Seaway (CAS), but a rapid turnover at specific level. Following or during the closure of the CAS, the most important group of taxa to disappear from the Caribbean were the “paciphilic” taxa, accounting for 60% of the extinctions and local disappearances following the closure of the CAS. This pattern is quite different from the pattern of extinction seen at higher latitudes on both the eastern and western Atlantic frontages, where several pulses of southwards retreat of mainly thermophilic taxa is seen during the Neogene, whereas cooler temperature tolerant genera remained, often with the specific composition mostly unaltered. These findings were published in Landau et al. (2008).

As part of this work, a revision of all known gastropod paciphilic genera and subgenera taxa, and their chronostratigraphic ranges in the southern Caribbean, was undertaken based on literature, museum collections and the author’s collections. A total of 67 paciphilic genera and species groups were identified. Their demise in the Atlantic portion of their original distribution occurred in two pulses, which allowed the construction of a system of biostratigraphic units based on the presence/absence of paciphiles, named Gatunian Neogene Paciphile Molluscan Units (GNPMU). GNPMU 1 is characterized by the highest number of paciphile taxa. This unit is already in place in the Early Miocene and ends at the beginning of the Late Pliocene. GNPMU 2 is characterized by an impoverished number of paciphilic elements, devoid of the two largest paciphilic groups; the cancellarids and the muricids. This unit ends during the Late Pleistocene Calabrian-Ionian boundary. GNPMU 3 is characterized by the absence of any paciphilic elements in their assemblages, and runs into Recent times. These findings were published in Landau et al. (2009) and later updated in Landau & Silva (2010c).

The cause of disappearance of paciphilic generic taxa from the Caribbean following the closure of the CAS is unknown. It is suggested, however, that paciphilic species vanished in the Caribbean because after the closure of the CAS the connection between source populations in the Pacific and sink populations in the Caribbean was lost. As a result, the Caribbean sink populations became unsustainable, and eventually disappeared. The fact that there is no evident common ecological trait (trophic type, substrate requirements, habitat, life habit, dimension, thermal requirements, etc.) except that they all have a planktotrophic type of larval development – which could allow longer larval transport from the Pacific into the Caribbean – seems to support this hypothesis. The pre-closure Caribbean high productivity must have contributed to the maintenance of paciphilic sink populations in the Caribbean, and drastic reductions in productivity in the aftermath of the closure of the CAS certainly contributed for the demise of these populations. The decrease in oceanic productivity provides a plausible explanation for the disappearance of the Caribbean populations of Paciphile species, but it does not explain why these species continued to thrive in the Pacific after the closure of the CAS.

Only the combination of these two mechanisms could fully explain the occurrence of Paciphile species: closure of the CAS; demise of sink populations in the Caribbean due to decrease in productivity and separation from source populations in the Pacific; persistence of Paciphile species in the Pacific (i.e., survival of source populations).

Despite a history of almost 150 years of publications covering Caribbean Neogene gastropod assemblages, alpha taxonomy of tropical American Neogene gastropod species is still, if not in its infancy, somewhere in its early teen-age years! Few of the classic monographs covering these Caribbean fossil faunas cover no more than 60-70% of the taxa suspected or known to be present in the assemblage, and most require major revision to update the nomenclature and exclude subjective synonyms. One of the personal triumphs accomplished during this work is to persuade the Naturhistorisches Museum Basel, Switzerland, to make the PPP and other NMB collections openly accessible to all researchers. As a result of discussions with Walter Etter of the Naturhistorisches Museum Basel, Caribbean collection data is now...
CONCLUSION

also openly available on the internet. These collections, when combined with the authors Caribbean
collections, supply a vast amount of material from which further taxonomic studies can be based.
Testament to this are the dozen or so taxonomic papers prepared by myself and co-authors in the wake of
this thesis awaiting publication.

So far, this work has only revised the Colombian-Venezuelan-Trinidad subprovince, its associated
assemblages, related biogeographic models and terminology. This work still needs to be done for the rest of
the Caribbean Neogene, a project the author hopes to embrace once a little more alpha taxonomy is in
place. Ecostratigraphy and GNMPUs are an interesting theme and can, in a very broad sense, be used to
date Caribbean Neogene assemblages. However, the author doubts if a higher resolution is achievable for
reasons outlined in Section 6.5. However, one interesting aspect is that the extinctions/disappearances can
be correlated with the major closures of the CAS, whereas the work of O’DEA et al. (2009) suggests a lag
of about 2 Ma. The methods used are different; we have used extinctions/disappearances of subgenera,
whereas the molluscan part of the O’DEA et al. (2009) data is derived from rarefaction data. Which of these
scenarios is correct, still needs to be tested. This work is being discussed with American colleagues,
including Greg Herbert, to include data from the Caloosahatchian Province. I hope all these various shreds
of information, deduced from the beautiful fossil shells contained in the Neogene American assemblages,
will help me to understand the dynamics of the closure of the CAS, and its influence on molluscan faunas.
One thing is for certain, the end of this chapter I hope will only mark the beginning of many more.
CHAPTER 9: REFERENCES


REFERENCES


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### Chapter 10: Appendices

7.1. Appendix 1, Geological distribution of species found in Cubagua

#### Geological distribution of species found in Cubagua

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7.2. Appendix 2, Geographical distribution of species found in Cubagua compared to adjacent subprovinces

Cubagua and Araya localities: 1 = Cañon de las Calderas, Cubagua Island, 2 = Punta Colorada, Cubagua Island, 3 = Cerro Barrigón, Araya Peninsula.

Pliocene molluscan faunal biogeographical provinces after PETUCH (1988). PG = Puntagavilanian; Pg = Punta Gavilán assemblage (Punta Gavilán Formation), Tr = Trinidad assemblages (Springvale, Talparo, Upper Morne l’Enfer, Cipero and Brasso Formations). LI = Limonian; Co = Colombian assemblages (Tubará and Usiacuri Formations), La = Limón assemblages (Banano and Limón Formations), Ga = Gatunian assemblages (Gatun, Bocas del Toro Formations). GU = Guraban; Guraban assemblages, Dominican assemblages (Cercado, Gurabo and Mao Formations, Bowden Formation). ES = Esmeraldan; Esmeraldan assemblages (Canoa, Zorritos, Tumbes, Daule, Angostura, Esmeralda and Jama Formations). AX = Agueguexitean; Agueguexitean assemblages, Agueguexquite Formation.

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7.3. Appendix 3, Geographical distribution of genera found in Cubagua compared to adjacent Formations in the Pliocene, using PETUCH’s (1991) Subprovinces.

Key to column heads; see Appendix 7.2.

Key to references:
A = PETUCH (1994); B = OLSSON & HARBISON (1953); C = JUNG (1969); D = MAURY (1925); E = MANSFIELD (1925); F = H. E. VOKES (1938); G = RUTSCH (1942); H = ANDERSON (1929); I = WEISBORD (1929); J = BARRIOS (1960); K = RUTSCH (1934); L = HERBERT (2005); M = OLSSON (1922); N = JUNG (1989); O = WOODRING (1957-1973); P = OLSSON (1964); Q = MAURY (1917); R = WOODRING (1928); S = PILSBRY & OLSSON (1941); T = OLSSON (1942); U = PERRILLIAT (1960, 1963, 1972, 1973); V = BEU (2010); W = OLSSON (1967b); X = JUNG & HEITZ (2001); Y = E. H. VOKES (1990); Z = BL collection unpublished data; a = E. H. VOKES (1992); b = PIT & PIT (1992); c = PILSBRY (1922); d = E. H. VOKES (1984b); e = E. H. VOKES (1989d); f = JUNG & PETT (1990); g = ROBINSON (1991); h = E. H. VOKES (1989a); i = OLSSON (1956). The genera recorded do not always correspond to that published by the authors, but have been reviewed critically.

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APPENDICES

7.4. Appendix 4, Preliminary amended list of Paciphilic subgenera and species groups.

Reference to the first author to note the taxon as paciphilic is given. Certain taxa listed as paciphilic, such as *Woodringilla* (WOODRING, 1966), *Eurypyrene*, *Calophos*, *Rhipophos*, *Metaphos*, *Aphera*, *Buridrillia*, *Adelocythara* (PETUCH, 1982) and *Decoriatrivia*, *Oliva* (Porphyria) (PETUCH, 1991) have been removed from the list (updated from LANDAU *et al.*, 2009). For this list we have used the classification according to TUCKER & TENORIO (2009) for the *Conus* species groups.

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7.5. Appendix 5, Stratigraphical distribution of paciphiles within the Atlantic Gatunian (G) and Caloosahatchian (C) provinces (sensu Vermeij, 2005; Landau et al., 2008).

(updated from Landau et al., 2009).

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<td>Planktotrophic-type protoconch (BL pers. obs.)</td>
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#### 7.6. Appendix 6. Preliminary amended list Paciphilic species, with reference to protoconch morphology or larval development.

* Caloosahatchian Province only.

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<th>Reference to development</th>
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### Appendix 7, List of genera/subgenera disappeared from the Caribbean region in Recent times.

† Genus/subgenus = extinct taxon  
Genus/subgenus = paciphile  
Genus/subgenus = extant, but local disappearances, not present in the Recent Caribbean biogeographic province.

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7.7. Appendix 7, List of genera/subgenera disappeared from the Caribbean region in Recent times.
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CHAPTER 11: PLATES

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Fig. 1. *Calliostoma (Calliostoma) calderense Landau & Silva, 2010*. Holotype MOBR-M-3872 (EDIMAR coll., ex BL coll.), Araya Formation, Cañon de las Calderas, Cubagua Island. Height 17.0 mm.

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[Images of various shells labeled from 1 to 11]
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PLATE 3

[Image of various shells labeled from 1a to 12c]
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Fig. 2. *Poirieria (Panamurex) eugeniae* E. H. Vokes, 1992. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 18.5 mm NHMW 2010/0038/0198 (NHMW coll., ex BL coll.).

Fig. 3. *Poirieria (Panamurex) gatunensis* (Brown & Pilsbry, 1911). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 33.0 mm NHMW 2010/0038/0089 (NHMW coll., ex BL coll.).

Fig. 4. *Poirieria (Panamurex) gatunensis* (Brown & Pilsbry, 1911). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 34.5 mm NHMW 2010/0038/0199 (NHMW coll., ex BL coll.).

Fig. 5. *Typhina expansa* (G. B. Sowerby II, 1874). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 26.5 mm NHMW 2010/0038/0090 (NHMW coll., ex BL coll.).

Fig. 6. *Eupleura muriciformis* (Broderip, 1833). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 32.3 mm NHMW 2010/0038/0091 (NHMW coll., ex BL coll.).

Fig. 7. *Stramonita 'biserialis' auct.* (non De Blainville, 1832). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 29.9 mm NHMW 2010/0038/0092 (NHMW coll., ex BL coll.).

Fig. 8. *Stramonita 'biserialis' auct.* (non De Blainville, 1832). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 30.6 mm NHMW 2010/0038/0200 (NHMW coll., ex BL coll.).

Fig. 9. *Coralliophila* sp. aff. *C. meyendorffii* (Calcara, 1845). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 23.3 mm NHMW 2010/0038/0093 (NHMW coll., ex BL coll.).

Fig. 10. *Turbinella trinitatis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 183.0 mm NHMW 2010/0038/0094 (NHMW coll., ex BL coll.).

Fig. 11. *Turbinella trinitatis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 240.0 mm NHMW 2010/0038/0201 (NHMW coll., ex BL coll.).

Fig. 12. *Turbinella trinitatis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Detail of protoconch NHMW 2010/0038/0095 (NHMW coll., ex BL coll.).
Fig. 1. *Vasum haitense* (G. B. Sowerby I, 1850). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 96.3 mm NHMW 2010/0038/0096 (NHMW coll., ex BL coll.).

Fig. 2. *Vasum quirosense* F. Hodson, 1931. Holotype PRI 24115, height 28.3 mm, El Mene de Saladillo, Zulia State, Venezuela, La Rosa Formation, upper Lower Miocene. Image courtesy of the Paleontological Research Institution.

Fig. 3. *Strombinophos perdoctus* Jung, 1969. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 19.2 mm NHMW 2010/0038/0097 (NHMW coll., ex BL coll.).

Fig. 4. *Strombinophos perdoctus* Jung, 1969. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 19.3 mm NHMW 2010/0038/0098 (NHMW coll., ex BL coll.).

Fig. 5. *Solenosteira (Solenosteira) magdalenensis* (Weisbord, 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 45.1 mm NHMW 2010/0038/0099 (NHMW coll., ex BL coll.).

Fig. 6. *Solenosteira cochlearis magdalenensis* Weisbord, 1929. Holotype PRI 22954, height 31.2 mm, Atlantic Department, Colombia, Tuberá Formation, Lower Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 7. *Solenosteira (Fusinosteira) falconensis* Weisbord, 1929. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 57.3 mm NHMW 2010/0038/0100 (NHMW coll., ex BL coll.).

Fig. 8. *Solenosteira (Fusinosteira) falconensis* Weisbord, 1929. Araya Formation, Cañon de las Calderas, Cubagua Island. Morphotype similar to *Solenosteira santaerosae* Anderson, 1929. Height 49.9 mm NHMW 2010/0038/0202 (NHMW coll., ex BL coll.).

Fig. 9. *Solenosteira falconensis urumacoensis* F. Hodson, 1931. Holotype PRI 24144, height 47.7 mm, Rio Codore, mainland Venezuela, Upper Miocene. Image courtesy of the Paleontological Research Institution.

Fig. 10. *Hesperisternia corrugata* (Gabb, 1873). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 29.7 mm NHMW 2010/0038/0101 (NHMW coll., ex BL coll.).

Fig. 11. *Hesperisternia corrugata* (Gabb, 1873). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 31.3 mm NHMW 2010/0038/0203 (NHMW coll., ex BL coll.).

Fig. 12. *Hesperisternia tortugera* (Olsson, 1922). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 27.8 mm NHMW 2010/0038/0102 (NHMW coll., ex BL coll.).

Fig. 13. *Hesperisternia tortugera* (Olsson, 1922). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 27.7 mm NHMW 2010/0038/0204 (NHMW coll., ex BL coll.).

Fig. 14. *Hesperisternia karinae* (Nowell-Usticke, 1959). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 19.6 mm NHMW 2010/0038/0103 (NHMW coll., ex BL coll.).

Fig. 15. ‘*Hesperisternia*’ sp. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 45.4 mm NHMW 2010/0038/0104 (NHMW coll., ex BL coll.).
Fig. 1. *Strombina (Strombina?) cartagenensis* PILSBRY & BROWN, 1917. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 23.5 mm NHMW 2010/0038/0105 (NHMW coll., ex BL coll.).

Fig. 2. *Nassarius trinitatensis* JUNG, 1969. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 8.0 mm NHMW 2010/0038/0106 (NHMW coll., ex BL coll.).

Fig. 3. *Neoteron emilyvokesae* LANDAU & SILVA, 2010. Holotype NHMW 2010/0038/0019 (NHMW coll., ex BL coll.). Araya Formation, Cañon de las Calderas, Cubagua Island. 3c, detail of denticles inside aperture and basal through. Height 17.4 mm.

Fig. 4. *Neoteron emilyvokesae* LANDAU & SILVA, 2010. Paratype NHMW 2010/0038/0020 (NHMW coll., ex BL coll.). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 14.3 mm.

Fig. 5. *Calophos plicatilis* (BÖSE, 1906). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 27.8 mm NHMW 2010/0038/0107 (NHMW coll., ex BL coll.).

Fig. 6. *Calophos plicatilis* (BÖSE, 1906). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 30.0 mm NHMW 2010/0038/0108 (NHMW coll., ex BL coll.).

Fig. 7. *Gordanops baranoanus* (ANDERSON 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 53.7 mm NHMW 2010/0038/0109 (NHMW coll., ex BL coll.).

Fig. 8. *Gordanops baranoanus* (ANDERSON 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 57.8 mm NHMW 2010/0038/0205 (NHMW coll., ex BL coll.).

Fig. 9. *Gordanops baranoanus* (ANDERSON 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 53.8 mm NHMW 2010/0038/0206 (NHMW coll., ex BL coll.).

Fig. 10. *Gordanops baranoanus* (ANDERSON 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Juvenile shell, height 28.9 mm NHMW 2010/0038/0110 (NHMW coll., ex BL coll.).

Fig. 11. *Melongena consors* (G. B. SOWERBY I, 1850). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 132.2 mm NHMW 2010/0038/0111 (NHMW coll., ex BL coll.).

Fig. 12. *Melongena consors* (G. B. SOWERBY I, 1850). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 88.3 mm NHMW 2010/0038/0111 (NHMW coll., ex BL coll.).
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Fig. 1. *Pleuroloca gorgasiana* BROWN & PILSBRY, 1913. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 155.0 mm NHMW 2010/0038/0112 (NHMW coll., ex BL coll.).

Fig. 2. *Fusinus vonderschmidtii* RUTSCH, 1934. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 58.0 mm NHMW 2010/0038/0113 (NHMW coll., ex BL coll.).

Fig. 3. *Fusinus vonderschmidtii* RUTSCH, 1934. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 59.3 mm NHMW 2010/0038/0208 (NHMW coll., ex BL coll.).

Fig. 4. *Fusinus springvalensis* (MAURY, 1925). Araya Formation, Cañón de las Calderas, Cubagua Island. Height 85.3 mm NHMW 2010/0038/0114 (NHMW coll., ex BL coll.).

Fig. 5. *Fusinus springvalensis* (MAURY, 1925). Araya Formation, Cañón de las Calderas, Cubagua Island. Height 79.5 mm NHMW 2010/0038/0209 (NHMW coll., ex BL coll.).

Fig. 6. *Voluta cubaguaensis* GIBSON-SMITH, 1973. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 100.4 mm NHMW 2010/0038/0115 (NHMW coll., ex BL coll.).

Fig. 7. *Voluta cubaguaensis* GIBSON-SMITH, 1973. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 68.6 mm NHMW 2010/0038/0116 (NHMW coll., ex BL coll.).

Fig. 8. *Harpa crenata* SWAINSON, 1822. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 66.2 mm NHMW 2010/0038/0117 (NHMW coll., ex BL coll.).

Fig. 9. *Harpa crenata* SWAINSON, 1822. Upper reddish coarse sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 62.1 mm NHMW 2010/0038/0210 (NHMW coll., ex BL coll.).

Fig. 10. *Harpa crenata* SWAINSON, 1822. Upper reddish coarse sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 62.9 mm NHMW 2010/0038/0211 (NHMW coll., ex BL coll.).

Fig. 11. *Persicula venezuelana* lavelana (HODSON, 1927). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 17.6 mm NHMW 2010/0038/0118 (NHMW coll., ex BL coll.).

Fig. 12. *Persicula sp*. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 8.6 mm NHMW 2010/0038/0119 (NHMW coll., ex BL coll.).
Fig. 1. *Prunum carmengutierrezae* Landau & Silva, 2010. Holotype MOBR-M-3878 (EDIMAR coll., ex BL coll.). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 27.8 mm.

Fig. 2. *Prunum carmengutierrezae* Landau & Silva, 2010. Paratype 1 NHMW 2010/0038/0021 (NHMW coll., ex BL coll.). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 27.5 mm.

Fig. 3. *Prunum springvalensis* (Maury, 1925). Syntype PRI 1034, height 40.0 mm, Trinidad, Springvale Formation, Lower Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 4. *Prunum calypsonis* (Maury, 1925). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 21.6 mm NHMW 2010/0038/0120 (NHMW coll., ex BL coll.).

Fig. 5. *Prunum calypsonis* (Maury, 1925). Syntype PRI 1036, height 20.8 mm, Trinidad, Springvale Formation, Lower Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 6. *Prunum circumvittatus* (Weisbord, 1962). Holotype PRI 26293, height 20.0 mm, Quebrada Mare Abajo, Venezuela, Mare Formation, Lower Pleistocene. Image courtesy of the Paleontological Research Institution.

Fig. 7. *Prunum colinensis* (F. Hodson). Holotype PRI 22889, height 15.0 mm, La Vela, Taratará, Falcón State, Venezuela, Caujarao Formation, Upper Miocene. Image courtesy of the Paleontological Research Institution.

Fig. 8. *Fusimitra sanctifrancisci* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 75.8 mm NHMW 2010/0038/0121 (NHMW coll., ex BL coll.).

Fig. 9. *Fusimitra sanctifrancisci* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 65.1 mm NHMW 2010/0038/0122 (NHMW coll., ex BL coll.).

Fig. 10. *Fusimitra sanctifrancisci* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 43.5 mm NHMW 2010/0038/0123 (NHMW coll., ex BL coll.).

Fig. 11. *Fusimitra sanctifrancisci* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 42.9 mm NHMW 2010/0038/0124 (NHMW coll., ex BL coll.).

Fig. 12. *Fusimitra limonensis* (Olsson, 1922). Holotype PRI 20959, height 75.4 mm, Limon Province, Banano Formation, Upper Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 13. *Subcancilla couvensis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 39.3 mm NHMW 2010/0038/0125 (NHMW coll., ex BL coll.).

Fig. 14. *Subcancilla couvensis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 39.0 mm NHMW 2010/0038/0126 (NHMW coll., ex BL coll.).

Fig. 15. *Subcancilla couvensis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 48.1 mm NHMW 2010/0038/0127 (NHMW coll., ex BL coll.).

Fig. 16. *Subcancilla colombiana* (Weisbord, 1929). Holotype PRI 22951, height 24.3 mm, Atlantic Department, Miocene (probably Pliocene). Image courtesy of the Paleontological Research Institution.
LEGENDS AND PLATES

PLATE 18

Fig. 1. *Conomitra caribbeana* Weisbord, 1929. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 13.8 mm NHMW 2010/0038/0128 (NHMW coll., ex BL coll.).

Fig. 2. *Conomitra caribbeana* Weisbord, 1929. Lower yellow sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 12.9 mm NHMW 2010/0038/0176 (NHMW coll., ex BL coll.).

Fig. 3. *Conomitra caribbeana* Weisbord, 1929. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 14.8 mm NHMW 2010/0038/0177 (NHMW coll., ex BL coll.).

Fig. 4. *Oliva immorta* Pilsbry & Brown, 1917. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 33.9 mm NHMW 2010/0038/0133 (NHMW coll., ex BL coll.).

Fig. 5. *Oliva reticularis* s. l. Lamarck, 1810. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 45.6 mm NHMW 2010/0038/0130 (NHMW coll., ex BL coll.).

Fig. 6. *Oliva aff. reticularis* s. l. Lamarck, 1810. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 47.2 mm NHMW 2010/0038/0131 (NHMW coll., ex BL coll.).

Fig. 7. *Oliva tuberaensis* Anderson, 1929. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 84.3 mm NHMW 2010/0038/0132 (NHMW coll., ex BL coll.).

Fig. 8. *Oliva sp.* Araya Formation, Cañon de las Calderas, Cubagua Island. Height 33.9 mm NHMW 2010/0038/0133 (NHMW coll., ex BL coll.).

Fig. 9. *Eburna caroniana* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 53.5 mm NHMW 2010/0038/0134 (NHMW coll., ex BL coll.).

Fig. 10. *Eburna caroniana* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 26.3 mm NHMW 2010/0038/0135 (NHMW coll., ex BL coll.).

Fig. 11. *Eburna caroniana* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 35.8 mm NHMW 2010/0038/0178 (NHMW coll., ex BL coll.).

Fig. 12. *Eburna caroniana* (Maury, 1925). Syntype PRI 1019, height 50.7 mm, Springvale, Trinidad, Springvale Formation, Lower Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 13. *Eburna speciosa* Rutsch, 1934. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 51.1 mm NHMW 2010/0038/0136 (NHMW coll., ex BL coll.).
PLATE 18
PLATE 19

Fig. 1. *Jaspidella jaspidea* (Gmelin, 1791). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 23.8 mm NHMW 2010/0038/0174 (NHMW coll., ex BL coll.).

Fig. 2. *Jaspidella jaspidea* (Gmelin, 1791). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 25.1 mm NHMW 2010/0038/0175 (NHMW coll., ex BL coll.).

Fig. 3. *Cancellaria (Cancellaria) capeloi* Landau, Petit & Silva, 2007. Holotype; MOBR-M-3359 (EDIMAR coll.) (ex BL coll.), Araya Formation, Cañon de las Calderas, Cubagua Island. Height 22.8 mm.

Fig. 4. *Cancellaria (Cancellaria) capeloi* Landau, Petit & Silva, 2007. Paratype 1; MOBR-M-3359 (EDIMAR coll.) (ex BL coll.), Araya Formation, Cañon de las Calderas, Cubagua Island. Height 30.9 mm.

Fig. 5. *Cancellaria (Cancellaria) sp.* Araya Formation, Cañon de las Calderas, Cubagua Island. Height 46.2 mm NHMW 2010/0038/0137 (NHMW coll., ex BL coll.).

Fig. 6. *Bivetopsia pachia* (M. Smith, 1940). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 24.6 mm NHMW 2010/0038/0138 (NHMW coll., ex BL coll.).

Fig. 7. *Euclia codazzii* (Anderson, 1929). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 41.9 mm NHMW 2010/0038/0139 (NHMW coll., ex BL coll.).

Fig. 8. *Cancellaria epistomifera acuticarinata* Weisbord, 1929. Holotype PRI 22948, height 23.9 mm, Atlantic Department, Miocene (probably Lower Pliocene). Image courtesy of the Paleontological Research Institution.

Fig. 9. *Euclia leuzingeri* (Rutsch, 1934). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 44.2 mm NHMW 2010/0038/0140 (NHMW coll., ex BL coll.).

Fig. 10. *Euclia montserratensis* (Maury, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 37.0 mm NHMW 2010/0038/0141 (NHMW coll., ex BL coll.).
Fig. 1. *Pyruclia schebei* (Anderson, 1929). Araya Formation, Cañón de las Calderas, Cubagua Island. Height 49.9 mm NHMW 2010/0038/0142 (NHMW coll., ex BL coll.).

Fig. 2. *Pyruclia schebei* (Anderson, 1929). Araya Formation, Cañón de las Calderas, Cubagua Island. Height 76.7 mm NHMW 2010/0038/0143 (NHMW coll., ex BL coll.).

Fig. 3. *Massyla cubaguaensis* Landau, Petit & Silva, 2007. Holotype; MOBR-M-3363 (EDIMAR coll.) (ex BL coll.), Araya Formation, Cañón de las Calderas, Cubagua Island. Height 25.9 mm.

Fig. 4. *Massyla cubaguaensis* Landau, Petit & Silva, 2007. Paratype 1; MOBR-M-3363 (EDIMAR coll.) (ex BL coll.), Araya Formation, Cañón de las Calderas, Cubagua Island. Height 22.4 mm.

Fig. 5. *Charcolleria terryi* Olsson, 1942. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 46.0 mm NHMW 2010/0038/0144 (NHMW coll., ex BL coll.).

Fig. 6. *Charcolleria terryi* Olsson, 1942. Holotype PRI 4045, height 40.9 mm, Quebrada Penitas, Puntarenas Province, Costa Rica, Charco Azul Group, Penita Formation, Upper Pliocene. Image courtesy of the Paleontological Research Institution.

Fig. 7. *Trigonostoma (Ventrilia) rucksorum* Petuch, 1994). Araya Formation, Cañón de las Calderas, Cubagua Island. Height 35.9 mm NHMW 2010/0038/0145 (NHMW coll., ex BL coll.).

Fig. 8. *Conus haytensis* G. B. Sowerby II, 1850. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 165.0 mm NHMW 2010/0038/0146 (NHMW coll., ex BL coll.).

Fig. 9. *Conus imitator* Brown & Pilsby, 1911. Araya Formation, Cañón de las Calderas, Cubagua Island. Height 47.2 mm NHMW 2010/0038/0147 (NHMW coll., ex BL coll.).
PLATE 20
PLATE 21

Fig. 1. *Conus imitator* Brown & Pilsbry, 1911. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 59.5 mm NHMW 2010/0038/0212 (NHMW coll., ex BL coll.).

Fig. 2. *Conus cf. oniscus* Woodring, 1928. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 38.3 mm NHMW 2010/0038/0148 (NHMW coll., ex BL coll.).

Fig. 3. *Conus cf. oniscus* Woodring, 1928. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 37.8 mm NHMW 2010/0038/0149 (NHMW coll., ex BL coll.).

Fig. 4. *Conus cf. oniscus* Woodring, 1928. Upper reddish coarse sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 45.8 mm NHMW 2010/0038/0213 (NHMW coll., ex BL coll.).

Fig. 5. *Conus spurius* Gmelin, 1791. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 56.7 mm NHMW 2010/0038/0150 (NHMW coll., ex BL coll.).

Fig. 6. *Conus spurius* Gmelin, 1791. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 48.1 mm NHMW 2010/0038/0214 (NHMW coll., ex BL coll.).

Fig. 7. *Conus sp. aff. an C. ultimus* Pilsbry & Johnson, 1917. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 96.4 mm NHMW 2010/0038/0151 (NHMW coll., ex BL coll.).

Fig. 8. *Conus sp. aff. an C. ultimus* Pilsbry & Johnson, 1917. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 65.2 mm NHMW 2010/0038/0215 (NHMW coll., ex BL coll.).
Fig. 1. *Conus jaspideus* G. MELIN, 1791. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 30.7 mm NHMW 2010/0038/0152 (NHMW coll., ex BL coll.).

Fig. 2. *Conus jaspideus* G. MELIN, 1791. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 24.0 mm NHMW 2010/0038/0153 (NHMW coll., ex BL coll.).

Fig. 3. *Knefastia limonensis* (OLSSON, 1922). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 93.1 mm NHMW 2010/0038/0154 (NHMW coll., ex BL coll.).

Fig. 4. *Knefastia limonensis* (OLSSON, 1922). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 76.4 mm NHMW 2010/0038/0216 (NHMW coll., ex BL coll.).

Fig. 5. *Fusiturricula springvaleensis* (MANSFIELD, 1925). Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 66.3 mm NHMW 2010/0038/0155 (NHMW coll., ex BL coll.).

Fig. 6. *Fusiturricula springvaleensis* (MANSFIELD, 1925). lower yellow fine sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 70.9 mm NHMW 2010/0038/0156 (NHMW coll., ex BL coll.). Specimen with axial sculpture on last whorl.

Fig. 7. *Fusiturricula springvaleensis* (MANSFIELD, 1925). lower yellow fine sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 65.4 mm NHMW 2010/0038/0157 (NHMW coll., ex BL coll.). Specimen without axial sculpture on last whorl.

Fig. 8. *Fusiturricula springvaleensis* (MANSFIELD, 1925). lower yellow fine sandy bed, Aramina Formation, Cerro Barrigón, Araya Peninsula. Height 49.3 mm NHMW 2010/0038/0158 (NHMW coll., ex BL coll.). Juvenile.

Fig. 9. *Polystira* sp. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 35.9 mm NHMW 2010/0038/0159 (NHMW coll., ex BL coll.). 7c, detail of sculpture on penultimate whorl.

Fig. 10. *Crassispira (Crassispira) caroniana* (MAURY, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 70.7 mm NHMW 2010/0038/0160 (NHMW coll., ex BL coll.).

Fig. 11. *Crassispira (Crassispira) cf. tyloessa* WOODING, 1970. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 19.6 mm NHMW 2010/0038/0161 (NHMW coll., ex BL coll.).

Fig. 12. *Crassispira (Crassispira) sp.* Araya Formation, Cañon de las Calderas, Cubagua Island. Height 21.1 mm NHMW 2010/0038/0162 (NHMW coll., ex BL coll.).
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Fig. 1. *Clathrodrillia gatunensis* sensu lato. Araya Formation, Cerro Colorado, Cubagua Island, 100 m north of research station. Height 51.7 mm NHMW 2010/0038/0163 (NHMW coll., ex BL coll.).

Fig. 2. *Clathrodrillia cf. tityra* WOODRING, 1928. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 33.4 mm NHMW 2010/0038/0164 (NHMW coll., ex BL coll.).

Fig. 3. *Cerodrillia niaddrina* (MANSFIELD, 1925). Araya Formation, Cañon de las Calderas, Cubagua Island. Height 23.4 mm NHMW 2010/0038/0165 (NHMW coll., ex BL coll.).

Fig. 4. *Miracloathurella* sp. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 13.7 mm NHMW 2010/0038/0166 (NHMW coll., ex BL coll.).

Fig. 5. *Dolostoma* sp. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 15.4 mm NHMW 2010/0038/0217 (NHMW coll., ex BL coll.).

Fig. 6. *Terebra aclinica* OLSSON, 1967. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 66.4 mm NHMW 2010/0038/0167 (NHMW coll., ex BL coll.).

Fig. 7. *Terebra aclinica* OLSSON, 1967. Araya Formation, Cañon de las Calderas, Cubagua Island NHMW 2010/0038/0168 (NHMW coll., ex BL coll.). Detail of aperture showing two columnellar folds.

Fig. 8. *Terebra lehneri* RUTSCH, 1942. Araya Formation, Cañon de las Calderas, Cubagua Island. Height (incomplete) 71.1 mm NHMW 2010/0038/0169 (NHMW coll., ex BL coll.).

Fig. 9. *Terebra lehneri* RUTSCH, 1942. Araya Formation, Cañon de las Calderas, Cubagua Island. Height (incomplete) 33.9 mm NHMW 2010/0038/0170 (NHMW coll., ex BL coll.). Detail of early teleoconch whorls.

Fig. 10. *Strioterebrum meesmanni* RUTSCH, 1934. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 28.7 mm NHMW 2010/0038/0171 (NHMW coll., ex BL coll.). 5c, detail of sculpture.

Fig. 11. *Strioterebrum weisbordi* GIBSON-SMITH & GIBSON SMITH, 1984. Araya Formation, Cañon de las Calderas, Cubagua Island. Height 37.0 mm NHMW 2010/0038/0172 (NHMW coll., ex BL coll.). 6c, detail of sculpture.

Fig. 12. *Architectonica nobilis* RODING, 1798. Araya Formation, Cañon de las Calderas, Cubagua Island. Diameter 43.1 mm NHMW 2010/0038/0173 (NHMW coll., ex BL coll.).
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Cubagua Island: EDIMAR research station, 2006

EDIMAR students on Cubagua 2006 field trip