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Southern Caribbean Neogene palaeobiogeography revisited. New data from the Pliocene of Cubagua, Venezuela

Bernard Landau ^{a,b,*}, Geerat Vermeij ^c, Carlos Marques da Silva ^d

^a *Centro de Geologia da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal*

^b *International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal*

^c *Department of Geology, University of California at Davis, One Shields Avenue, Davis, CA 95616, USA*

^d *Departamento e Centro de Geologia da Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal*

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Abstract

Based on new data from the Pliocene gastropod assemblage of Cubagua Island, Venezuela, the palaeobiogeography of the southern Caribbean is reviewed. The data obtained from the southern Caribbean assemblages demonstrate a highly endemic fauna along the northern coasts of South America, distinct from that found in the neighbouring Isthmian region to the west, which has probably been in place since at least the early Neogene. These assemblages are characterised by a relative stability at generic level, but an extremely high turnover rate at specific level. The name Colombian–Venezuelan–Trinidad Subprovince is chosen over Puntagavilanian Subprovince and chorotypes and chronotypes are selected for the Gatunian Province and the Colombian–Venezuelan–Trinidad Subprovince.

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1. Introduction

Numerous Neogene (including Quaternary, according to the latest revision of the chronostratigraphic scale, see [Gradstein et al., 2004](#)) fossiliferous deposits, rich in shallow marine molluscan fossils, crop out along or adjacent to the northern Atlantic coast of Venezuela. The fossil assemblages of the better known deposits, such as the Cantaure and Punta Gavilán Formations, Falcón State,

have been described (e.g., [Rutsch, 1934](#); [Jung, 1965](#)), whilst others remain largely unknown.

The presence of Neogene fossils of molluscs on the Island of Cubagua, Nueva Esparta State ([Fig. 1](#)), situated between the Island of Margarita to the North and the Araya Peninsula to the South, has been known since at least the late 1930s ([Schilder, 1939](#)). However, until now there has been no thorough account of the fossil assemblage.

The data on which this paper is based is the result of extensive collecting carried out in the last five years and an updated systematic revision of the entire Pliocene gastropod assemblage so far found in Cubagua (see Appendices A and B). This revision has enabled us to have a better understanding of the southern Caribbean

* Corresponding author. Centro de Geologia da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.

E-mail addresses: bernielandau@sapo.pt (B. Landau), vermeij@geology.ucdavis.edu (G. Vermeij), Paleo.Carlos@fc.ul.pt (C.M. da Silva).

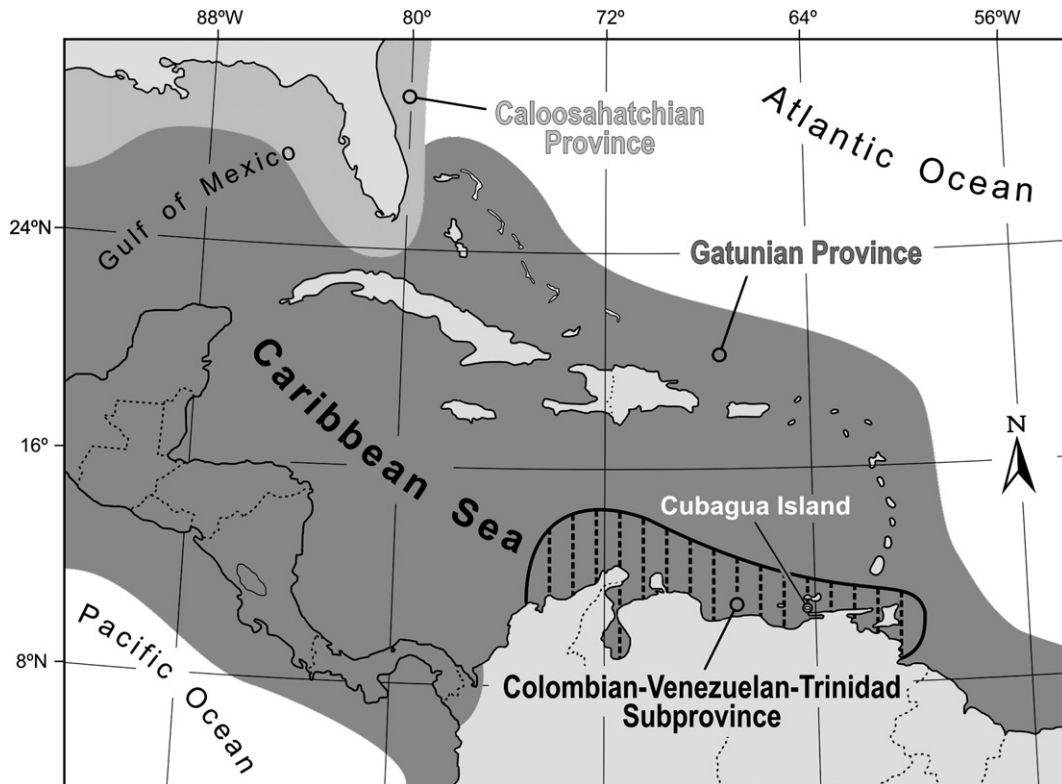


Fig. 1. Geographic location of Cubagua Island and distribution of the Miocene to Early Pleistocene biogeographic provinces and the Colombian–Venezuelan–Trinidad Subprovince.

marine gastropods and their palaeobiogeography in the Pliocene, and to study its relationship to other Caribbean Pliocene gastropod assemblages.

2. Geological setting

The older geological units outcropping on Cubagua Island belong to the Neogene Cubagua Group. This consists of the lower La Güica and upper Araya formations (Macsotay et al., 1995). The terms Cerro Verde and Cerro Negro Members of the Cubagua Formation coined by Vignali (1965) and used by authors such as Gibson-Smith and Gibson-Smith (1974), Jung (1989), Padrón et al. (1993), Aguilera and de Aguilera (2001) and Landau et al. (2007) were rejected by Macsotay et al. (1995). Therefore, what has until now been referred to in the literature as the Cubagua Formation corresponds now to the Cubagua Group of Macsotay et al. (1995). The Cubagua Group consists of two units: La Güica Formation, the lower unit, and Araya Formation, the upper unit. This latter upper unit corresponds to the Cerro Negro Member of the Cubagua Formation of Vignali (1965).

The Cubagua Group ranges in age from Upper Miocene to Pliocene (Macsotay et al., 1995). The lower La Güica Formation is exposed along the north-central cliffs on Cubagua Island along Quebrada Los Muñecos (Macsotay and Vivas, 1998). These are clayey sediments with horizons of calcareous and dolomitic concretions. The molluscan fossils in this unit show greater decalcification than those found in the overlying Araya Formation.

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

The most fossiliferous locality within the Araya Formation on Cubagua Island is situated on the eastern side of the Cañon de las Calderas. In this locality, 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. The fossils look abundant, but are probably concentrated on the surface by erosion of the sandy matrix. In several arroyos the sandy fossiliferous layer 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.

For more details, geographical location, general geological setting, graphic columnar section of the Cañon de Las Calderas section, positioning of the fossiliferous beds, and additional references see [Padrón et al. \(1993\)](#) and [Macsotay et al. \(1995\)](#).

Within the fossiliferous beds 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 contains an assemblage consisting almost entirely of shells of Turritellidae and Vermetidae. The fossils in all beds are relatively well-preserved, most shells showing some surface erosion, and the early whorls of gastropod shells are almost invariably missing.

The Pliocene gastropod assemblage encountered in the Cañon de las Calderas lower beds indicates a tropical shallow-water, marine environment of normal salinity and with a sandy substrate ([Landau et al., 2007](#)). These conclusions agree with [Aguilera and de Aguilera \(2001, p. 733\)](#): “(...) the sediments of the lower part [of the Cubagua Group, i.e. La Güica Formation] appear to have been deposited in deep water, and the upper part [i.e. Araya Formation] in shallow tropical water.”

3. Biostratigraphic setting

[Bolli and Saunders \(1985\)](#) proposed a planktic foraminiferal low latitude zonal scheme for the Cainozoic, developed mainly in Trinidad but also in Venezuela and the Caribbean. According to the [Bolli and Sanders' \(1985\)](#) zonal scheme, five biostratigraphic zones and three subzones have been recognised in the Cubagua Group. The planktic foraminiferal assemblage present in the Cañon de las Calderas beds indicates placement in the *Globorotalia miocenica* zone ([Castro and Mederos, 1997](#)). This section corresponds to the type section of the *G. miocenica* zone in Venezuela ([Castro and Mederos, 1997](#)).

According to [Bolli and Saunders \(1985\)](#) the *G. miocenica* zone has a middle Pliocene age (3.2–2.4 Ma) - corresponding roughly to the Piacenzian - and is defined as an interval zone, between the LO (last occurrence) of *Globorotalia margaritae evoluta* and the LO of *G. miocenica* or *G. exilis*. After [Berggren et al. \(1995\)](#) the LO of *G. margaritae* occurred at 3.58 Ma and the LO of *G. miocenica* - in the Atlantic - at 2.3 Ma. This range

includes, according to the Pliocene scale of [Berggren et al. \(1995\)](#) and the definition of the Gelasian (lower boundary at 2.58 Ma) by [Rio et al. \(1998\)](#), the entire Piacenzian and the lower part of the Gelasian. According to the biostratigraphic data of [Castro and Mederos \(1997\)](#), this gives a chronostratigraphic range for the Cañon de las Calderas section spanning Piacenzian to lower Gelasian time.

4. Previous works on the Neogene Palaeobiogeography of the southern Caribbean

[Woodring \(1974\)](#) recognised 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 ([Fig. 1](#)).

[Petuch \(1982\)](#) recognized two distinct provinces in the Caribbean Neogene, the Caloosahatchian province to the north and the Gatunian Province to the south.

[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. He named nine subprovinces within his Pliocene Gatunian Province. [Petuch \(1988\)](#) highlighted the individual nature of the southern Caribbean and erected the “Puntagavilanian Subprovince”, corresponding roughly to [Woodring's \(1974\)](#) Colombian–Venezuelan–Trinidad Subprovince. The Puntagavilanian 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.

[Petuch \(2004\)](#) further developed his palaeobiogeographic model in the tropical American Neogene, and gave distinct names for the provinces over time. 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.

Series	Stage	Biogeographic units (Biochoremas) according to:				
		Woodring (1974)	Petuch (1982)	Petuch (1988)	Petuch (2004)	This paper
Pleistocene	C					
	M					
	L					
Pliocene	Gel					
	Pia					
	Zan					
Miocene	Mes					
	Tor					
	Ser					
	Lan					
	Bur					
	Aqt					

Fig. 2. Comparison of the Miocene to Pleistocene biogeographic models proposed by various workers for the southern Caribbean.

As far as the study area is concerned, according to [Petuch's \(2004\)](#) model, the Cainozoic Island of Cubagua would be part of the Antiguian 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 ([Fig. 2](#)).

5. 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 we

assessed the similarity between the Cubagua Pliocene assemblage and those of other Caribbean Neogene localities (see Appendix A). To do this we have used similarity coefficients. 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)

$$J = C / (n_1 + n_2 - C)$$

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).

$$S = C / n_1$$

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). We have therefore used both methods. The Dice coefficient is most suitable if the two assemblages have similar numbers of individuals, and has therefore not been used.

Table 1

Comparison of the Cubagua assemblage with other Caribbean Pliocene assemblages, at subgenus and species-group level

Formation	#SGA	#SCC	%CTA	Jacc.	Simp.
Punta Gavilán	65	49	56%	2.12	0.75
Springvale	130	63	72%	2.44	0.72
Tuberá	60	45	51%	2.29	0.75
Bocas del Toro	90	42	48%	3.20	0.48
Banano	60	29	33%	4.07	0.48
Agueguexquite	40	24	28%	4.29	0.60
Bowden	220	50	57%	2.94	0.57
Esmeraldas	120	52	59%	3.00	0.59

#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.

Table 2

Comparison of the Cubagua assemblage with other Caribbean Pliocene assemblages at specific level

Formation	#SPA	#SPC	%CTA	Jacc.	Simp.
Punta Gavilán	80	32	27.8%	5.09	0.4
Springvale	220	42	36.5%	6.98	0.36
Tuberá	80	28	24.3%	5.96	0.35
Bocas del Toro	70	10	8.6%	14	0.14
Agueguexquite, Banano, Moin	500	21	18.2%	28.29	0.18
Bowden	420	18	15.7%	28.72	0.16
Esmeraldas	150	8	6.9%	32.13	0.07

#SGA — number of species known from the assemblage; #SCC — number of species in common with the Cubagua assemblage; %CTA — percentage of Cubagua taxa present in the assemblage; Jacc. — Jaccard coefficient; Simp. — Simpson coefficient.

Table 1 gives the results of the comparison of the Cubagua with other Caribbean Pliocene assemblages at subgenus and species-group level (sensu Vermeij and Petuch, 1986). The Jaccard coefficient shows a closer similarity between the Cubagua assemblages and those of Punta Gavilán Formation (Venezuela) and Colombia, i.e. the assemblages on the northern Atlantic coast of South America, than Moin Formation (Costa Rica), Gatun Formation (Panama) and the Dominican Republic, with Pacific Ecuador intermediate. The Simpson coefficient fails to show any obvious similarities between the Cubagua assemblage and any of the others, except the Pacific Ecuadorian assemblage.

The number of subgenera present in each of the Caribbean assemblages discussed is quite dissimilar. Therefore, the Simpson coefficient should be more suitable for analysing this data series. The figures show little difference between the assemblages. At subgeneric level this is probably to be expected, as they all form part of the Gatunian Province. The Jaccard coefficient suggests a greater similarity between the Cubagua assemblage and the other Caribbean assemblages on the northern Atlantic coast of South America, than with the Isthmic, central Caribbean and Pacific Gatunian assemblages.

Table 2 gives the results of the comparison of the Cubagua with other Caribbean Pliocene assemblages at species level. In this data series both the Jaccard and Simpson coefficients clearly show a greater affinity with the other assemblages on the northern Atlantic coast of South America than with the central and Pacific Gatunian ones.

These results suggest that there is no significant difference between the taxonomic compositions of the various Gatunian assemblages at subgeneric level,

although there might be a closer affinity between the assemblages on the northern Atlantic coast of South America than with the rest of the Gatunian Province. At specific level, however, there is a clear association between all assemblages on the northern Atlantic coast of South America. This clearly shows that this group of assemblages, i.e. Colombian, Punta Gavilán, Cubagua and Springvale, form a distinct unit within the Caribbean.

6. Discussion of Neogene Southern Caribbean palaeobiogeography in relation to Cubagua

Herein we assess the ‘Colombian–Venezuelan–Trinidad Subprovince’ (Woodring, 1974), or ‘Puntagavilanian Subprovince’ (Petuch, 1988), in relation to the new data available from the study of the Cubagua assemblage.

6.1. 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 and 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).

However, the latest palaeogeographical model proposed by Petuch, especially in his later works (Petuch, 1988, 2004), has been criticized (Allmon, 2005). Here, we will only discuss Petuch’s concepts in relation to the study area.

In order to understand the logic behind Petuch’s model, we must review his definitions of biogeographic units. 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 and Westermann, 2003), there is still no consensus, on the criteria for the definition of biogeographical units or biochoremas. Kauffman (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 Kauffman (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 B 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. In our opinion, 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 and 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 palaeobiogeography 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 and Petuch (1986). It was only later that Petuch (1988) defined the subprovinces based on a list of particular taxa. A critical reevaluation of Petuch's (1988) list of characteristic taxa illustrates Cecca's (2002) point:

6.1.1. Cypraeidae

Erosaria aliena Schilder, 1939: described from the Talparo Formation of Matura, now considered to be of Pleistocene age (Jung, 1989); related to *E. acicularis* (Gmelin, 1791).

Siphocypraea grahami (Ingram, 1947): 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.

6.1.2. 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.

6.1.3. Tonnididae

Malea mareana complex: also occurs in the Floridian Plio-Pleistocene as *Malea densecostata* in Olsson and Petit (1964), Petuch (1989) and Petuch (1994) (not *Malea densecostata* Rutsch, 1934) (Beu, in litteris). However, there are two species of *Malea* endemic to the Puntagavilanian Subprovince: *M. densecostata* Rutsch, 1934 (Punta Gavilán), and *Malea* sp. from Cubagua (Bernard Landau and Alan Beu, unpublished data).

6.1.4. Ranellidae

Charonia weisbordi Gibson-Smith, 1976: = *Charonia lampas* (Linnaeus, 1758) an almost cosmopolitan species (Beu, in litteris).

6.1.5. 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 (1989), 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).

6.1.6. Fasciolaridae

Pleuroploca crassinoda complex: *Pleuroploca 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.

6.1.7. 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 Talparo 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.

6.1.8. Buccinidae

Cymatophos paraguayensis (Hodson and 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.

6.1.9. 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.

6.2. 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 and 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 Puntagavilanian 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 and 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 and de Aguilera, 2001), a general pattern similar to that found in the area today (Carvajal and Capelo, 1993; Macsotay and Campos Villaroel, 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 and 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 *t* significantly different from Woodring's (1974, p. 210, Fig. 1) Miocene Caribbean Province. Therefore it could be argued that the terms Caloosahatchian and Miocene Caribbean Provinces should be used. However, the term Miocene Caribbean Province has since been abandoned, and the terms Caloosahatchian and Gatunian Provinces are now

commonly used in the literature by recent authors (e.g., Vermeij and Petuch, 1986; Robinson, 1991; Vermeij, 2005) and we 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 and Westermann, 2003). In our view this range contraction does not require the erection of a new biogeographic province, and therefore we adhere to Petuch's (1982) definition of the Gatunian Province, and reject the name Baitoan Province.

Petuch's nomenclature of subprovinces is, however, more complicated, and we 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 Puntagavilanian 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 includes in his Limonian Subprovince. As can be seen in Appendix B 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. We therefore reject the name Puntagavilanian Subprovince, a name which to our 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 (Fig. 1).

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 and 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, we suggest a simpler palaeobiogeographic model for the southern Caribbean with a single Colombian–Venezuelan–Trinidad Subprovince (Fig. 1), spanning from the Early Miocene to Recent times (Fig. 2). Even today, the subprovince called Samarian–Venezuelan by Diaz (1995) 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 our data above (Tables 1 and 2). 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.

7. Chorotypes and chronotypes

Westermann (2000) recommended that each biochorema should have a type region (chorotype) and a characteristic stage (chronotype) designated. This has not yet been attempted in Tropical American Neogene palaeobiogeography. We will limit ourselves to designating types for the biogeographic units covered in this paper.

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 and Coates, 1999). We therefore propose 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 and 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, 1989)], *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*, *Dolicholaturus*, *Tiara longa* complex, *Bivetopsis*, *Prunum*, *Ximeniconus* [Florida Plio/Pleistocene (Petuch, 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, 1989)], *Purpurellus* [Gurabo Formation, Dominican Republic (Vokes, 1989); 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 and Vokes, 1997)], *Amalda* [Gatun Formation (Woodring, 1964); Punta Gavilan Formation (Rutsch, 1934); Springvale Formation (Maury, 1925)].

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, we propose 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 and Vivas, 1998), and we propose the Springvale Formation as the chronotype.

8. Implications

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; Petuch, 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.

Our findings support those of Woodring (1974) and Petuch (1988, 2004) in distinguishing a biogeographic unit centred on the north coast of Venezuela, but contrary to Petuch (1988, 2004), our 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’, which occurred in two pulses, the first at the beginning of the Late Pliocene, the second at the end of the Early Pleistocene (Landau et al., submitted for publication). 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). We find no reason to rename the biochorema and suggest that the name used by Woodring (1974), Colombian–Venezuelan–Trinidad Subprovince, should be retained.

We propose the following type designations for the biochoremas discussed in this paper; the assemblages found in the area around Gatun and the Gatun Form-

ation 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.

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Appendix A. Geographical distribution of gastropods found in the Araya Formation, Cubagua Group, of Cubagua Island

Key to provinces and subprovinces (after Petuch, 1991)

Caloo. Prov.=Caloosahatchian Province

Punt=Puntagavilanian; Lim=Limonian; Gur=Guraban; Esm=Esmeraldan.

Key to formations

Pg=Punta Gavilán Formation (Venezuela); Sp=Springvale Formation (Trinidad); T=Tuberá Formation plus other unnamed Pliocene Colombian Formations; BT=Bocas del Toro Basin (Panama); Ba=Banano Formation (Costa Rica); Ax=Agueguexquite Formation (Mexico); Bo=Bowden Formation (Jamaica); Es=Esmeraldas Formation (Ecuador).

Key to references

A=Petuch (1994); B=Olsson and Harbison (1953); C=Jung (1969); D=Maury (1925); E=Mansfield (1925); F=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, 1959, 1964, 1970, 1973); P=Olsson (1964); R=Woodring (1928); S=Pilsbry and Olsson (1941); T=Olsson (1942); U=Perillat (1960, 1963); V=Alan Beu (in litteris); W=Olsson (1967); X=Jung and Heitz (2001); Y=Vokes (1990); a=Vokes (1992); b=Pitt and Pitt (1992); c=Robinson (1991); d=Jackson et al. (1999); Z=BL collection, unpublished data. The genera recorded do not always correspond to that published by the authors, but have been reviewed critically.

	Caloo. Province	Gatunian Province							
		Punt.		Lim.				Gur	Esm
		Pg	Sp	T	BT	Ba	Ax	Bo	Es
<i>Calliostoma (Calliostoma)</i>	A, B	K	C, E, D	H				R	P, S
<i>Calliostoma (Elmerlinia)</i>			C, D				U		
<i>Turbo (Marmarostoma)</i>	A, B	K						R	
<i>Astralium</i>	A, B		C					R	
<i>Modulus</i>	A, B		D, E					R	
<i>Tympanotonos</i>									
<i>Pyrazisinus</i>	A, B								
<i>Turritella (Broderiptella)</i>	A		C, D, E	H, I, J	M	M			S
<i>Turritella (Bactrospira)</i>	A, B	K	G, D, E	H, I, J	M	M		R	
<i>Turritella (?) abrupta-grp</i>			D, F	H, I					
<i>Vermicularia</i>	A, B		C, D					R	
<i>Calyptraea</i>	A, B		C		d				P
<i>Crepidula</i>	A, B		C, D				U		T
<i>Crucibulum (Crucibulum)</i>	A, B	Z	C, G		d		U		P, S, T
<i>Crucibulum (Dispotaea)</i>	A			H					P, S
<i>Zonaria (Zonaria)</i>		Z						R	
<i>Muracypraea</i>			D	H	M				S
<i>Jenneria</i>	A, W			H					W
<i>Ficus</i>	A, B	K	D	H, J				R	PS
<i>Polinices</i>	A, B	K	C, D, G, b	H, J, b	d	M, b		R, b	P, S, T, b
<i>Naticarius</i>	A, B	K	C, D	I, J	d	d	U	R	P, b
<i>Stigmaulax</i>	B	K	H, J	b	M, d	M, b, d		R	P, S, T
<i>Sinum</i>	A, B	Z	F					R	P, b
<i>Strombus (Strombus)</i>	A, B		D		M, d	M, d		R	
<i>Persististrombus</i>									X
<i>Malea</i>	A	K, V	C, D, F	H, J	M, V	M		R, V	P, S, V
<i>Sconsia</i>	A	K, V		H	M, V, d			R, V	
<i>Cymatium (Linatella)</i>	A	V	V		V				
<i>Cymatium (Monoplex)</i>	A	V	V		V		V	R, V	P, V
<i>Cymatium (Turritriton)</i>	A							V	
<i>Distorsio</i>	A	K, V	D	H, I, J	V	M	U, V	R, V	P, S, T, V
<i>Marsupina</i>	A	K	C, V	I	V			R, V	
<i>Bursa</i>	A	K, V	C, D, V	J	V	M	U, V	V	V, P, S, T
<i>Niveria</i>	A, B							R	
<i>Pusula</i>	A		C						
<i>Petalococonchus</i>	A, B	K	C, D, E	H, I, J	M, d			R	
<i>Serpulorbis</i>	A	K	C, D	I		M		R	P
<i>Scalina</i>			D					R	P, S
<i>Strombinophos</i>	A, B	Z	C						S, T
<i>Solenosteira</i>	A, B	K	C, D, G	H, I, J	M, d	M			S, T
<i>Solenosteira (Fusinosteira)</i>				H					S, T
<i>Hesperisternia</i>	A, B		C		M				P, T
<i>Strombina (Strombina)</i>			N	H, I, J, N		N		N, R	N, T
<i>Fasciolaria gorgasiana grp.</i>		K	C	H	M	M			
<i>Fusinus</i>	A	K	C, D, F	H	M		U	R	P, S
<i>Nassarius</i>	A, B	Z	C, E		d	M, d		R	P, S, T
<i>Trajana (Nerva)</i>									
<i>Gordanops</i>				H, J					P
<i>Calophos</i>	A	Z	C, G				U		
<i>Melongena</i>	A		D	H, I					
<i>Chicoreus (Triplex)</i>	A, B, Y	Y	C, D, Y	Y	M	Y	Y		
<i>Vokesimurex</i>	A, B, Y	K, Y	C	H, J, Y	M, d	M, Y	U	R, Y	Y
<i>Haustellum</i>									
<i>Poirieria (Panamurex)</i>	A, a	a		a			a		a
<i>Eupleura</i>	A, B	L	C, L	L		L			L, S
<i>Stramonita</i>	A		C					R	

Appendix A (continued)

	Caloo. Province	Gatunian Province							
		Punt.		Lim.				Gur	Esm
		Pg	Sp	T	BT	Ba	Ax	Bo	Es
<i>Coralliophila</i>	A							R	
<i>Conomitra</i>	A	K	C, G	I					
<i>Persicula</i>	A, B	K	C, D, E			d			
<i>Prunum</i>	A, B	K	C, D, E	H	d	M, d	U	R	P
<i>Mitra</i>		K	D, G	I					S, T
<i>Subcancellaria</i>	A, B	K	D, E, G, F	H, I, J	M, O, d		U	R	P, S
<i>Turbinella</i>	A, B		C, D, G	I	M			R	
<i>Vasum</i>	A								
<i>Voluta</i>					M, d	M, d			
<i>Oliva</i>	A, B	K	C, D, E, G	H, I, J	d	M	U	R	P, S
<i>Eburna</i>		K	C, D, G					R	
<i>Conus (Leptoconus group)</i>									
	A, B	K	C, D, E, F		M, O	M	U	R	T
<i>Conus (Ximeniconus grp)</i>	A, B	K	C, D, E	H	M, O	M	U	R	P
<i>Conus (Lithoconus group)</i>	A, B	K	F	H, I, J	M, O	M		R	
<i>Conus (Stephanoconus grp)</i>							U	R	
<i>Conus (Conasprella grp)</i>	A	K	D, E		M			R	P
<i>Terebra (Myurellina grp)</i>	A	K							T
<i>Terebra (Paraterebra grp)</i>		K	D	H, I, J	O	M	U	R	S
<i>Strioterebrum</i>	A, B	K	C, D, E, G	I, J	M, O, d	M, d	U	R	P, S, T
<i>Polystira</i>	A, B	K	C, D	H, I, J	M, O		U	R	P
<i>Knefastia</i>	A				M, d				T
<i>Fusiturricula</i>		K	G		d		U	R	P, T
<i>Crassispira (Crassispira)</i>	A, B	K	C, D, E, F	I, J	O, d	M	U	R	S
<i>Clathrodrillia</i>	A, B			I, J		M		R	P, S
<i>Cerodrillia</i>	B		E						
<i>Cancellaria (Cancellaria)</i>	A, B	K		H, I, J	M, O, d			M, R	P, S, T
<i>Cancellaria (Bivetopsia)</i>	A							R	T
<i>Cancellaria (Euclia)</i>			C, D, E, F, G	H, I, J					P, S, T
<i>Cancellaria (Massyla)</i>	A, B		C						
<i>Cancellaria (Charcolleria)</i>									P, T
<i>Trigonostoma (Ventrilia)</i>	A, B	Z	Z		M			R	P, S
<i>Architectonica</i>	A	K	C, D	H, I, J	M, d	M	U	R	ST
	67	69		62		50		52	
	67	74		52		50		52	
		49	63	45	42	29	24		

Appendix B. Geological distribution of species found in Cubagua

Key to symbols

● = Atlantic

▲ = Pacific

Species	Miocene			Pliocene	Pleist	Recent
	L	M	U			
<i>Calliostoma (C.) laticarinatum</i> (GUPPY, 1867)				●	●	
<i>Calliostoma (E.) olssoni</i> Maury, 1925				●	●	
<i>Calliostoma (E.)</i> nov. sp.				●		
<i>Turbo (Marmarostoma) castanea</i> Gmelin, 1791	●		●	●	●	●
<i>Astralium brevispina</i> (Lamarck, 1822)				●	●	●
<i>Modulus tamanensis</i> Maury, 1925				●		
<i>Tympanotonos</i> sp.				●		

Appendix B (continued)

<i>Pyrazisinus</i> sp.									●
<i>Turritella</i> (<i>Broderiptella</i>) <i>bifastigata cartagenensis</i>			●						●
Pilsbry and Brown, 1917									
<i>Turritella</i> (<i>B.</i>) <i>caronensis</i> Mansfield, 1925									●
<i>Turritella</i> (<i>B.</i>) <i>planigrata</i> Guppy, 1867			?	●					●
<i>Turritella</i> (<i>Bactrospira</i>) <i>guppyi</i> Cossmann, 1909									●
<i>Turritella</i> (?) <i>abrupta</i> Spieker, 1922	▲				●	▲			●
<i>Vermicularia</i> cf. <i>woodringi</i> Olsson and Harb., 1953									●
<i>Calyptraea centralis</i> (Conrad, 1841)	●		●		●			●	●
<i>Crepidula</i> cf. <i>maculosa</i> Conrad, 1834									●
<i>Crucibulum</i> (<i>Crucibulum</i>) nov. sp.									●
<i>Crucibulum</i> (<i>Crucibulum</i>) <i>subsutum</i> Guppy, 1867									●
<i>Crucibulum</i> (<i>Dispotaea</i>) sp.									●
<i>Zonaria</i> (<i>Zonaria</i>) <i>raymondrobertsi</i> (Pilsbry, 1922)					●				●
<i>Zonaria</i> (<i>Zonaria</i>) cf. <i>spurcoides</i> (Gabb, 1873)									●
<i>Muracypraea caroniensis</i> Maury, 1925									●
<i>Jenneria loxahatcheensis</i> (M. Smith, 1936)								●	
<i>Ficus carbacea</i> (Guppy, 1866)									●
<i>Polinices</i> (<i>Polinices</i>) nov. sp.									●
<i>Polinices</i> (<i>P.</i>) <i>stanislasmeunieri</i> (Maury, 1917)	▲				●	▲			●
<i>Naticarius canrena canrena</i> (Linnaeus, 1758)								●	●
<i>Stigmaulax beaumonti</i> Rutsch, 1934									●
<i>Sinum gabbi</i> (Brown and Pilsbry, 1913)	●				●				●
<i>Strombus</i> (<i>S.</i>) sp. aff. <i>S. floridanus</i> Mansfield, 1930									●
<i>Persististrombus granulatus</i> (Swainson, 1822)									▲
<i>Malea</i> nov. sp.									●
<i>Sconsia sublaevigata</i> (Guppy, 1866)					●				●
<i>Cymatium</i> (<i>Linatella</i>) <i>cingulatum</i> (Lamarck, 1822)					●	▲		●	▲
<i>Cymatium</i> (<i>Monoplex</i>) <i>krebsii</i> (MÖRCH, 1877)	●		●		●			●	●
<i>Cymatium</i> (<i>Monoplex</i>) <i>cercadicum</i> (Maury, 1917)	●				●				●
<i>Cymatium</i> (<i>Turritriton</i>) <i>domingense</i> (Gabb, 1873)	●				●				●
<i>Distorsio clathrata</i> (Lamarck, 1816)	●				●			▲	●
<i>Distorsio macgintyi</i> Emerson and Puffer, 1953	●		●		●			●	●
<i>Marsupina bufo</i> (Bruguère, 1792)		●			●			●	●
<i>Bursa rugosa</i> (G. B. Sowerby II, 1835)	●		●		●	▲		●	▲
<i>Niveria pediculus</i> (s.l.) (Linnaeus, 1758)					●			●	●
<i>Pusula radians orientalis</i> Schilder, 1939								●	
<i>Petalococonchus sculpturatus alcimus</i> Mansfield, 1925									●
<i>Serpulorbis decussatus</i> (Gmelin, 1791)								●	●
<i>Serpulorbis papulosus</i> (Guppy, 1866)			●		●				●
<i>Scalina brunneopicta</i> (Dall, 1908)					●			▲	▲
<i>Strombinophos perdoctus</i> Jung, 1969									●
<i>Solenosteira magdalenensis</i> Weisbord, 1929									●
<i>Solenosteira</i> (<i>Fusinosteira</i>) <i>falconensis</i> Weisbord, 1929									●
<i>Hesperisternia corrugata</i> (Gabb, 1873)	●				●				●
<i>Hesperisternia tortugera</i> (Olsson, 1922)								●	
<i>Hesperisternia karinae</i> (Nowell-Usticke, 1959)								●	●
' <i>Hesperisternia</i> ' sp.									●
<i>Strombina</i> (<i>S.</i>) <i>cartagenensis</i> Pilsbry and Brown, 1917									●
<i>Fasciolaria gorgasiana</i> Brown and Pilsbry, 1913					●				●
<i>Fusinus</i> cf. <i>springvalensis</i> (Maury, 1925)									●
<i>Fusinus vonderschmidti</i> Rutsch, 1934									●
<i>Nassarius trinitatensis</i> Jung, 1969									●
<i>Trajana</i> (<i>N.</i>) nov. sp. aff. <i>woodringi</i> Vokes, 1969									●
<i>Gordanops baranoanus</i> (Anderson 1929)					●				●
<i>Calophos</i> sp. aff. <i>Plicatilis</i>									●
<i>Melongena consors</i> (Sowerby, 1850)	●	▲			●				●
<i>Chicoreus</i> (<i>Chicoreus</i>) <i>cornurectus</i> (Guppy, 1876)	●				●				●
<i>Vokesimurex messorius</i> (Sowerby, 1841)	●				●			●	●
<i>Haustellum mimiwilsoni</i> E. Vokes, 1990									●

Appendix B (continued)

<i>Poirieria (Panamurex) eugeniae</i> Vokes, 1992				●		●
<i>Poirieria (P.) gatunensis</i> (Brown and Pilsbry, 1911)	●		●	●		
<i>Eupleura muriciformis</i> (Broderip, 1833)		●		●▲	▲	▲
<i>Stramonita 'biserialis'</i>				●		▲
<i>Coralliophila</i> sp. aff. <i>C. meyerdorffii</i>				●		
<i>Conomitra lavelana</i> F. Hodson in Hod. and Hod., 1931			●	●		
<i>Persicula lavelana</i> (Hodson, 1927)			●	●	●	
<i>Persicula</i> sp.				●		
<i>Prunum</i> nov. sp.				●		
<i>Prunum calypsonis</i> (Maury, 1925)				●		
<i>Mitra sanctifrancisci</i> Maury, 1925				●		
<i>Subcancilla longa couvensis</i> (Maury, 1925)				●		
<i>Turbinella trinitatis</i> (Maury, 1925)				●		
<i>Vasum haitense</i> (Sowerby, 1850)	●		●	●		
<i>Voluta cubaguaensis</i> J. Gibson-Smith, 1973				●		
<i>Oliva immortua</i> Pilsbry and Brown, 1917				●		
<i>Oliva reticularis</i> s.l. Lamarck, 1810				●	●	●
<i>Oliva tubaraensis</i> Anderson, 1929			●	●		
<i>Oliva</i> sp. 1				●		
<i>Eburna caroniana</i> (Maury, 1925)				●		
<i>Eburna speciosa</i> Rutsch, 1934				●		
<i>Conus imitator</i> s.l. Brown and Pilsbry, 1911		●	●	●		
<i>Conus oniscus</i> Woodring, 1928				●		
<i>Conus spurius</i> s.l. Gmelin, 1791	●		●	●	●	●
<i>Conus</i> cf. <i>ultimus</i> Pilsbry and Johnson, 1917				●		
<i>Conus walli</i> Mansfield, 1925				●		
<i>Terebra acinica</i> Olsson, 1967				●		
<i>Terebra lehneri</i> Rutsch, 1942				●		
<i>Strioterebrum weisbordi</i> Gibson-Smith and G. S., 1984				●		●
<i>Polystira</i> sp.				●		
<i>Knefastia</i> nov. sp.				●		
<i>Fusiturricula springvaleensis</i> (Mansfield, 1925)				●		
<i>Crassispira (Crassispira) caroniana</i> (Maury, 1925)				●		
<i>Crassispira (C.)</i> cf. <i>tyloessa</i> Woodring, 1928				●		
<i>Crassispira (Crassispira)</i> sp.1				●		
<i>Clathrodrillia gatunensis sensu lato</i> (Toula, 1909)				●		
<i>Clathrodrillia</i> cf. <i>tityra</i> Woodring, 1970				●		
<i>Cerodrillia niadrina</i> (Mansfield, 1925)				●		
<i>Cancellaria (C.) capeloi</i> Landau, Petit and Silva, 2007				●		
<i>Cancellaria (Cancellaria)</i> sp.				●		
<i>Cancellaria (Bivetopsia) pachia</i> M. Smith, 1940				●	●	
<i>Cancellaria (Euclia) codazzii</i> Anderson, 1929			●	●		
<i>Cancellaria (Euclia) leuzingeri</i> Rutsch, 1934				●		
<i>Cancellaria (Euclia) montserratensis</i> Maury, 1925				●		
<i>Cancellaria (Pyruculia) scheibei</i> Anderson, 1929			●	●		
<i>Cancellaria (M.) cubaguaensis</i> Landau et al., 2007				●		
<i>Cancellaria (Charcolleria) terryi</i> Olsson, 1942	●		●	●		
<i>Trigonostoma (Ventrilia) rucksorum</i> (Petuch, 1994)				●	●	
<i>Architectonica nobilis</i> Röding, 1798	●▲	●	●▲	●▲	●▲	●▲
Total	20	10	36	115	25	23
Atlantic only	16	10	31	110	20	16
Pacific only	2	0	0		1	5
Atlantic and Pacific	2	0	5	5	4	2

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