

Palaeoclimatology of the Pleistocene-Holocene using marine molluscs and hermatypic corals from northern Venezuela

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ABSTRACT. Along the Venezuelan coastline and its islands, 47 outcrops of marine sediments were studied. Their ages, determined by radiometric and palaeontological means, ranged from Middle Pleistocene to Holocene. A total of 234 taxa was identified: Coelenterata 30; Gastropoda, 116 and Bivalvia 88. The Middle Pleistocene sediments are iron-rich sands and clays, only locally with bioclastic limestones. There is barely any coral fauna and the molluscs are small-sized. The assemblages are bivalve-dominated with Atlantic affinities: *Crassostrea patagonica*, *Ostrea puelchana*, *Anomalocardia* spp., *Gemma gemma* and *Macoma venezuelana*. Gastropods include *Cerithidea pliculosa* and *Melongena margaritana* also suggesting temperate-affinity faunas, strongly influenced by heavy rainfalls on coasts and islands.

Late Pleistocene sediments are more calcareous allowing the development of reefal systems with medium biodiversity of corals: *Pocillopora elegans*, *Acropora cervicornis* and *Milleaster* sp. The molluscan assemblages are gastropod-dominated, with smaller sized shells than living Caribbean equivalents: *Astraea*, *Cerithium*, *Conus*, *Murex*, *Chicoreus*, *Oliva*, *Ancilla*, *Persicula*, *Turritella* and *Vasum*. The bivalves are *Crassostrea patagonica*, *Chama ainuosa bermudensis*, *Scapharca couvana*, and these also suggest Atlantic temperate-affinity faunas dominating the coastlines, but not the offshore islands. The rainfall influence is noted in coastal areas in western and eastern Venezuela, while inland and the Llanos became arid.

The Holocene sediments are heterolithic and calcareous, with mangrove-forests on most of Venezuela's coastline. Corals are mostly *Porities* and *Millepora* associations, with small sized *Siderastrea* colonies. Molluscs are very much like living assemblages, where invaders from West Africa appear briefly: *Cerithium guinaicum*, *Cymatium* spp. Climatic conditions are similar, but with higher coastal rainfall that contributed to the proliferation of mangroves. Early and Middle Pleistocene cooling of the surface waters in the southern Caribbean Sea preceded aridity of the Llanos and mountain glaciation of the Late Pleistocene (80 and 15 ka) of the Andean range.

1. INTRODUCTION

There are very few studies concerning the biostratigraphy of the marine Pleistocene-Holocene and the palaeoclimatic interpretation of benthic faunas of tropical countries such as Venezuela. Richards (1943) described fossiliferous terrace deposits with molluscs up to +5 m above sea level from Juan Griego (Margarita Island), which he referred to the Pleistocene. Van Benthem Jutting (1944) reported 20 fossiliferous marine deposits from the northern Venezuelan coastline, including the offshore islands. According to the molluscan faunas studied by P. Wagenaar Hummelinck, these suggested a Pleistocene or even Holocene age, for some of the 'terraces'. Weisbord (1962) attributed the Abisinia Formation to the Pleistocene on the basis of its molluscan fauna, and a radiometric U-Th age of 300 ka.

The study of the planktic foraminiferal

assemblages by Bermudez and Fuenmayor (1962), Bermudez (1966) and Bermudez and Farias (1975) showed that many of the 'Mio-Pliocene' sediments of Venezuela really belonged to the Late Pliocene-Pleistocene (Stainforth, 1969). The first shallow-marine Holocene was identified in northeastern Venezuela by Van Andel (1967) by C-14 dating of mollusc shells.

Macsotay and Moore (1974) added more U-Th ages from Late Pleistocene corals, and C-14 ages from molluscs. Schubert and Szabo (1978) reported Middle and Late Pleistocene U/Th ages from offshore islands of Venezuela, and Rull (2000) added more C-14 ages of Holocene deposits along Venezuelan's coastline.

Based on a study of more than 500 taxa of marine molluscs and about 30 coelenterates, a subdivision of Pleistocene-Holocene time is presented here, valid for the southern Caribbean area. Recent reviews of the living molluscan

fauna of Venezuela's coasts and islands (Princz, 1982; Macsotay and Campos Villaroel, 2001) reveal that a high percentage of fossil species are still living in this area. This fact increased the percentage of recent species in the 'Mio-Pliocene' fossiliferous units, which became increasingly younger as was predicted by Gibson Smith and Gibson Smith (1979), some of them reaching Pleistocene horizons. This coincides with ages derived from planktic foraminifers. This mollusc-coral subdivision scheme is proposed for shelf sediments of the circum- and infralittoral belts, including littoral and paralic palaeoenvironments.

2. PLEISTOCENE SUBDIVISIONS

It is a generally accepted fact, that the *Globorotalia truncatulinoides* total-range zone, is the marine foraminiferal marker of the Quaternary period (Bolli *et al.*, 1985) for the tropical and temperate realms. The subdivision of the Pleistocene proposed on the basis of planktic foraminifers in LEG 15, station 147 (Rogl and Bolli, 1973) is useless in shallow-water facies, as is the case for most of the Pleistocene and Holocene land-based outcrops. Palaeontologically, the Pliocene/Pleistocene boundary seems to be related to the biozone of *Lyropecten arnoldi* (Maloney and Macsotay, 1967) whose range seems to overlap with the *Lopha messor* zone of Hunter (1978), and is already within the *Globorotalia truncatulinoides* biochronozone.

The *Turritella cartagenensis/T. maiquetiana* boundary (Macsotay, 1971) is very near the 1.9 Ma time-line, or the *Globorotalia tosaensis/G. truncatulinoides* boundary, which is the internationally accepted Late Pliocene/Early Pleistocene boundary. Besides the extinction of six species of the genus *Turritella*, it also marks the mass-extinction of over one hundred taxa of pacific affinity gastropods and bivalves (Woodring, 1974).

A change in the composition of reef-crest and reef-buttruss coral assemblages is marked by the appearance of wave-resistant *Acropora palmata* in latest Pliocene or earliest Pleistocene time in the Caribbean Sea. Rapidly growing species of *Acropora* and *Porites* invade and dominate the shallow-water, high-energy habitats of Pleistocene and modern reefs.

The Early/Middle Pleistocene boundary is based on molluscan extinction/appearance horizons (Table 1) studied in Venezuelan and Trinidadian sedimentary rocks. The *Anadara*

patricia biozone, ubiquitous in the hypersaline palaeoenvironments of the Late Pliocene, has its extinction at this boundary. This time must have witnessed important climatic disturbances, as the reef-forming corals disappear completely from the continental shelf area; they only survive on the offshore island shelves. The extinction of many calcitic bivalves, such as *Lyropecten arnoldi*, *Lopha* spp. and *Agerostrea* spp. and the decrease in gastropod biodiversity are associated with this horizon.

The Middle/Late Pleistocene is marked by the increase of gastropods, mostly Atlantic-type genera that replace the Caribbean forms; the coral reefs re-invade the continental shelves, with low diversity and small colony-sizes. Mangrove-related brackish molluscan assemblages become replaced by fresh-water communities. Mollusc shell-size has increased in relation to the Middle Pleistocene, but is still smaller than living representatives.

The Late Pleistocene/Holocene boundary is marked by the disappearance of *Milleaster* and *Pocillopora*, and the temporary invasion of exotic gastropods from West Africa and the withdrawal or disappearance of molluscs from the Atlantic Ocean's temperate fauna. Reef-corals re-invade continental coastlines, and mangrove forests are common all along Venezuelan shores. Palaeontological descriptions and biochrons will be discussed elsewhere.

3. STRATIGRAPHY

3.1. Early Pleistocene (1,750 - 700 ka)

From the molluscan fauna, the following units belong here: Amuay Member of the Paraguana Formation (Hunter and Bartok, 1976), Playa Grande Formation (Gibson Smith and Gibson Smith, 1979) and the Cumana Formation (Macsotay, 1976). The last two units belong to the *Globorotalia truncatulinoides* foraminiferal biozone (Bermudez and Farias, 1975), but their molluscan fauna, suggests restriction to the Early Pleistocene. In Trinidad, the Caparo Member of the Talparo Formation and the Matura Formation, contain the same fauna (Macsotay, 1976). The Cumana Formation has been identified in the subsurface of the Carupano Basin, 300 km northeast of the type locality (Castro and Mederos, 1985).

Sedimentary features. The early Pleistocene marine sediments include a high percentage of conglomeratic horizons, with psammitic matrix. The Cumana and Playa Grande formations expose

Table 1. Biostratigraphical ranges of taxa in the Middle Pleistocene to Recent of the southern Caribbean

	Qr	Qh	PLEISTOCENO		
			S	M	I
CELENERADOS					
<i>Milleaster</i> spp.					
<i>Pocillopora elegans</i>					
<i>Acropora cervicornis</i>					
<i>Acropora palmata</i>					
GASTEROPODA					
<i>Hemitoma multiradiata</i>					
<i>Diodora cayenensis</i>					
<i>Fissurella</i> spp.					
<i>Lucapinella limatula</i>					
<i>Cittarium pica</i>					
<i>Turritella maiquetiana</i>					
<i>Turritella variegata</i>					
<i>Turritella goniostoma</i>					
<i>Planaxis nucleus</i>					
<i>Certhidea piculosa</i>					
<i>Certhium guinaicum</i>					
<i>Bittium caribense</i>					
<i>Alabina cereola</i>					
<i>Trivia pediculus</i>					
<i>Cypraea cinerea</i>					
<i>Cypraea cinerea catiana</i>					
<i>Cymatium nicobaricum</i>					
<i>Chicoreus vokesae</i>					
<i>Chicoreus margaritensis</i>					
<i>Poireria</i> cf. <i>velero</i>					
<i>Purpura patula</i>					
<i>Masatlania cosentini</i>					
<i>Strombina pumilio</i>					
<i>Cantharus tinctus</i>					
<i>Melongena margaritana</i>					
<i>Nassarius polygonatus</i>					
<i>Pallacera uncinata</i>					
<i>Pallacera solidula</i>					
<i>Fusinus closter</i>					
<i>Ancilla</i> spp.					
<i>Olivella venezuelensis</i>					
<i>Olivella salinae</i>					
<i>Vasum pufferi</i>					
<i>Prunum dallianum</i>					
<i>Persicula obesa</i>					
<i>Conus regius</i>					
<i>Conus jaspideus</i>					
BIVALVOS					
<i>Arca zebra abisiniana</i>					
<i>Scapharca couvana</i>					
<i>Scapharca chemitzi</i>					
<i>Scapharca braziliensis</i>					
<i>Brachydontes modiolus</i>					
<i>Perna perna</i>					
<i>Isognomon vulsella</i>					
<i>Chlamys</i> cf. <i>linki</i>					
<i>Aequipecten muscosus</i>					
<i>Argopecten gibbus antecers</i>					
<i>Argopecten imitoides</i>					
<i>Nodipecten arnoldi</i>					
<i>Nodipecten nodosus</i>					
<i>Pecten ziczag caboblanquensis</i>					
<i>Crassostrea rhizophorae</i>					
<i>Crassostrea patagonica</i>					
<i>Ostrea puelchana</i>					
<i>Ostrea libella</i>					
<i>Lucina pensylvanica</i>					
<i>Anodontia alba</i>					
<i>Chama macerophylla</i>					
<i>Chama sinuosa bermudensis</i>					
<i>Trachycardium sanctidavidis</i>					
<i>Tellina strophoidea</i>					
<i>Arcopagia fausta</i>					
<i>Macoma venezuelana</i>					
<i>Asaphis deflorata</i>					
<i>Psephidia</i> cf. <i>cancellata</i>					
<i>Chione mazyckii</i>					
<i>Anomalocardia venezuelana</i>					
<i>Gemma gemma</i>					
<i>Gemma gemma purpurea</i>					
<i>Corbula caribaea pergrata</i>					
POLYCHAETA					
<i>Spirobranchus giganteus</i>					

Qr : Recent
 Qh : Holocene
 PLEISTOCENE
 S : Late
 M : Middle
 I : Early

thick conglomeratic units towards their tops. The Cagiiire and Chiguana formations develop them towards their bases. Most of the conglomerates form lenticular beds, with planar to festooned cross-bedding, and imbrication of clasts towards the base of the bed. Clast size varies from pebble to cobble, and the conglomerates are usually poorly sorted. There are unfossiliferous conglomeratic units of hundreds to thousands of metres thickness, such as the Rio Seep, Coro, Las Pailas and Coche formations. All four overlie well-dated Late Pliocene sediments, and

represent flash flood deposits that otherwise interrupt the dry climatic conditions on the nearby mountains. Some of these alluvial fans overrun the coastal plains, and entered coastal marine environments (Macsotay and Bladier, 1987; Vivas and Macsotay, 1989; Rey, 1990). Poorly-sorted terrigenous components (i.e., silts, sands and grits) dominate these infralittoral units; carbonates are rare. Biodeutral carbonates are mostly restricted to shelves: Amuay Member, Playa Grande and Cerro Gato formations.

Mineralogical features. A common feature in

the Early Pleistocene marine sediments is the presence of evaporite minerals, such as gypsum, anhydrite and copiapite. They are sulphates, products of evaporation of shallow marine embayments and shoals under a tropical semiarid climatic regime. The Caigüire, Chiguana and Paria formations are typical (Macsotay, 1976).

The continental beds, sandstones and conglomerates frequently develop duricrusts of iron oxides and laterites; these are well exposed in the Coche, Las Pailas and Coro formations, units otherwise with grey tones. They suggest a subhumid tropical climate. Local peat lenses or reworked lignites in the Caigüire, Paria and San Gregorio formations suggest nearby coastal vegetation.

Palaeontological features. Marine shales and siltstones carry frequent pectinids: *Nodipecten*, *Argopecten*, *Leptopecten*, *Pecten* (*Oppenheimipecten*), *Amusium* besides *Plicatula* and *Anomia*, forming oligomictic horizons, suggesting well circulated marine conditions, with high planktic input.

Burrowing detritivore bivalves are common (Table 1). *Crassostrea*-banks (not reefs) occur in most of the marine units. These 'oyster' beds are found in the San Gregorio, Caigüire, Cumana and Paria formations and suggest the presence of estuaries, dependant on rainy seasons.

The scarcity of gastropods and corals, but abundance of rodoliths and stromatolites (never in the same bed) suggest waters with fine sediment in suspension, also related to heavy rainfall along the emerged coasts.

Bivalves, stromatolites and echinoids attained large sizes suggesting relatively low ($21^{\circ}\text{C} \pm 3^{\circ}\text{C}$) temperatures in the water-mass above the shelf. These low average temperatures are not related to Caribbean upwelling, but to cold water-masses entering from the Atlantic Ocean, as was suggested by Macsotay and Vivas (2000) for Oligocene and Miocene times in eastern Venezuela. A good listing of the Early Pleistocene fauna was published by Macsotay (1976). Some large-sized mammal bones observed in the Caigüire Formation remain unstudied, but suggest a humid environment.

3.2. Middle Pleistocene (700 ka - 125 ka)

The units belonging here were identified through radiometric dating and palaeontological evidence. From west to east, we have studied: El Alto sandy conglomerates in Paraguana Peninsula (Hunter and Bartok, 1975; Audemard, 1996a) a beach deposit, very much alike the Abisinia Formation of Vargas State (Weisbord, 1964). The Goaguaza clays (Weisbord, 1962,

1964) along the Carabobo coast are in need of review. The famous Tortuga Formation (Patrick, 1959, emend. Maloney and Macsotay, 1967), found only on offshore islands, is the only coralgal limestone of this time-slice. Finally, La Eminencia Formation (Macsotay and Peraza, in press) is a sandy chalk with basal conglomerates, cropping out in the Cumana and Paraguachoa areas, of eastern Venezuela.

Sedimentary features. The mid-Pleistocene sedimentary units are siliciclastics on the mainland outcrops and carbonates on the offshore islands. The siliciclastic units include fine-grained conglomerates with a sandy matrix, grits, silts and some clays. The Goaguaza clays and silts were intensely bioturbated, suggesting organic-rich muds in the embayments.

The bioclastic and biolithitic carbonates formed when La Tortuga and La Blanquilla were only submarine banks or shoals. They must have preserved the tropical island conditions, with consistently warm temperatures and only occasional rains, since Late Miocene times. Pleistocene times changed the previous oceanographic conditions where hurricanes, originated in the Atlantic Ocean, pushed their anticyclones southward.

The shorelines on the mainland also suggest moderate erosion nearby, and low rates of sedimentation on the shores. The coastlines were dominated by waves, as is suggested by unidirectional cross-bedding. On Margarita Island, a great fresh-water lake developed, behind Juan Griego village. It suggests humid tropical weather over the central mountains (over 1000 m high) of the island. Paraguana also has this phenomenon, but no lacustrine sediments have been found.

Mineralogical features. The mid-Pleistocene age sediments only concentrated iron oxides in the nearshore sediments of the mainland Abisinia and El Alto formations. Their presence is related to the weathering of mafic and ultramafic outcrops nearby. This chemical weathering was related to dry coastal conditions with tropical rains on the mountains. The general absence of peat or lignite suggests dry weather.

The unusual presence in Venezuela of chalky limestone suggests relatively low temperatures in the coastal marine waters in the Cumaná area. The fine-grained quartz sand found in these chalks, seems to be transported by aeolian processes from nearby shorelines.

The advanced recrystallization/replacement observable in all the outcrops of the Tortuga Formation suggests the process had started

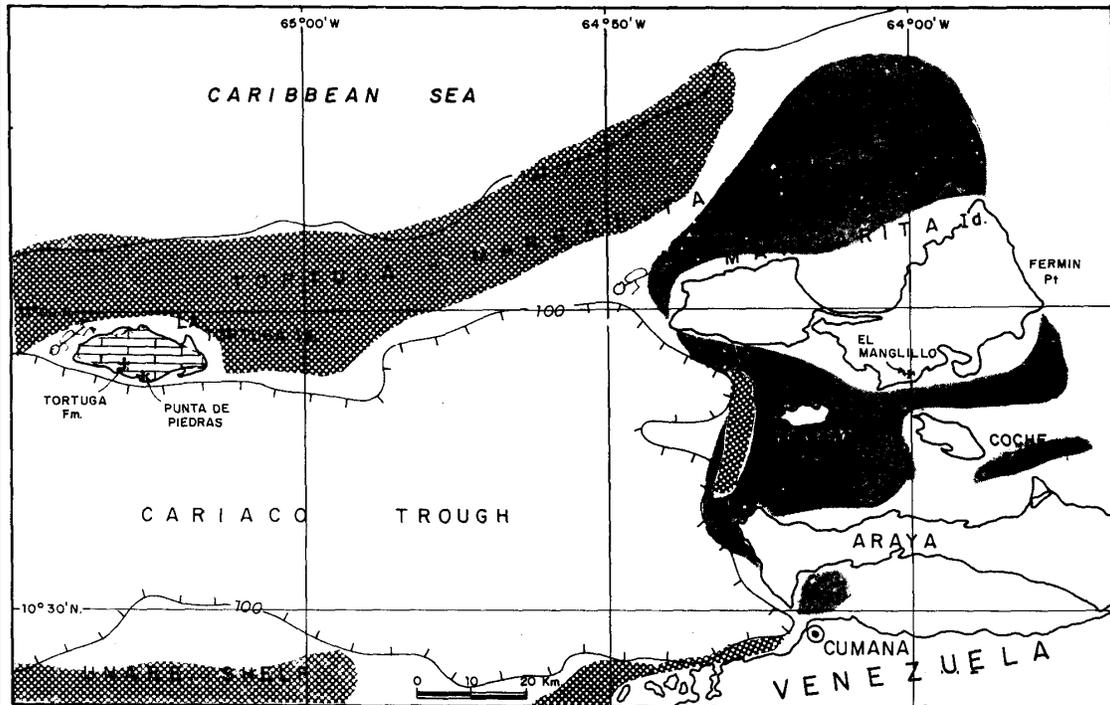


Figure 1. Surface and submarine distribution of Late Pleistocene marine sediments.

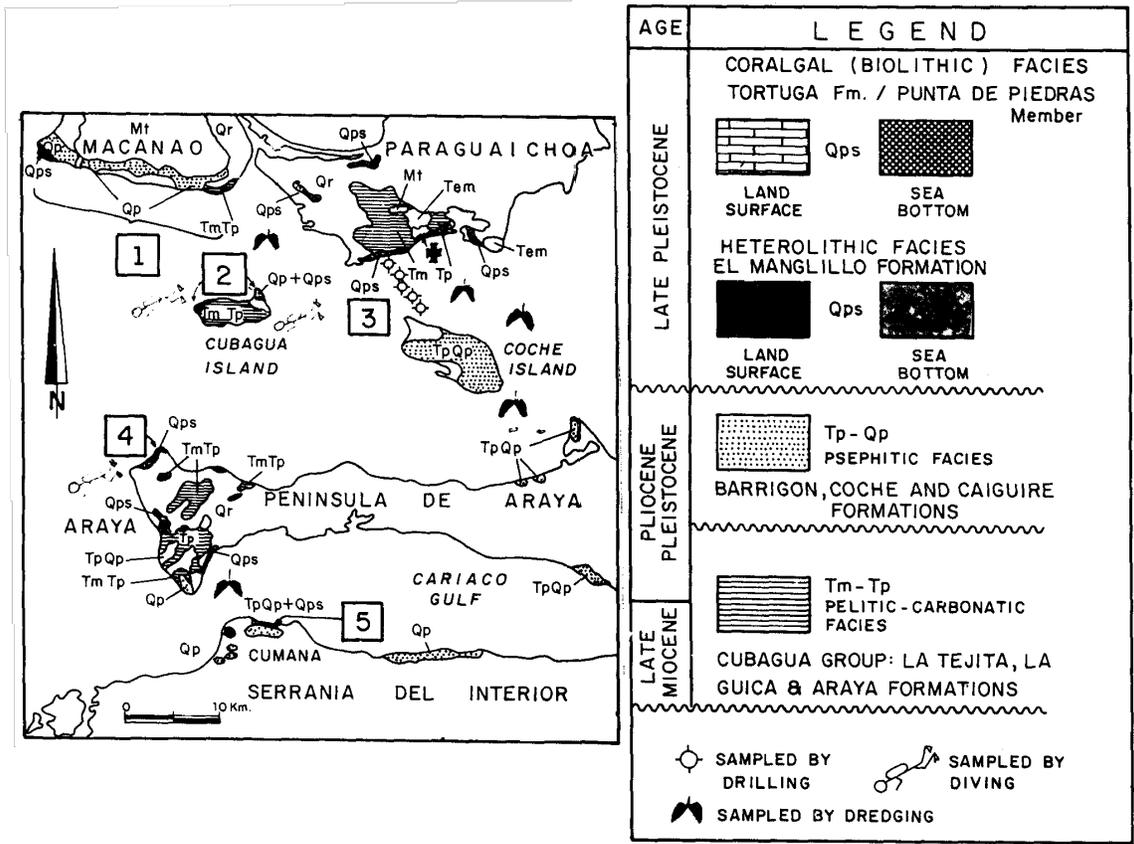


Figure 2. Surface outcrops of Late Miocene to Late Pleistocene marine and continental sediments on Margarita-Araya high.

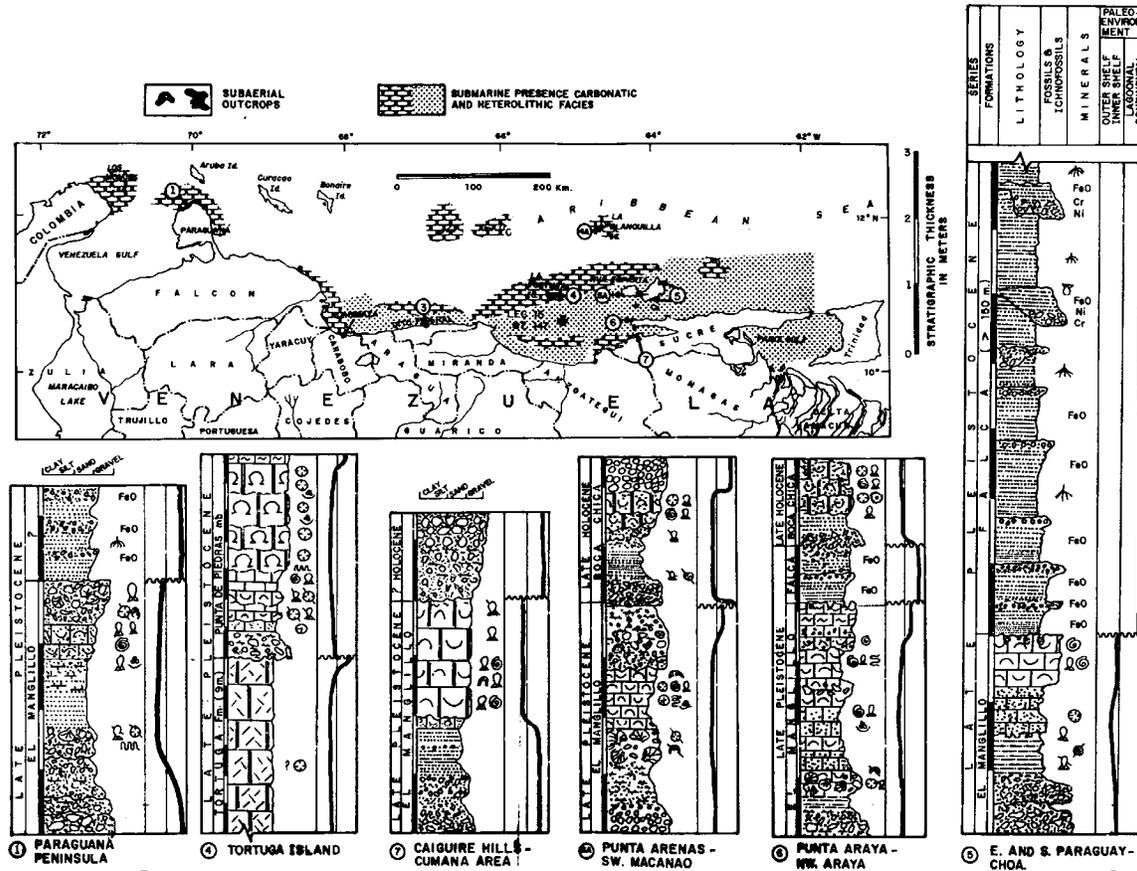


Figure 3. Late Pleistocene to Holocene marine sediments in northern Venezuela and its islands.

already during Middle Pleistocene times. As soon as the uplift of the carbonate banks, which became atolls and later islands, exposed the coralgal reef and lagoon complexes, they must have been subjected to the recrystallization/replacement of aragonite. The offshore islands of Venezuela must have been subjected to heavy rains and tropical hurricanes in this epoch.

Palaeontological features. The most outstanding feature in Middle Pleistocene marine sediments is the small size of the mollusc shells. The El Alto, Abisinia and La Eminencia formations have a molluscan fauna dominated by small bivalves, whereas the gastropods are oligomictic. In these sediments, corals are represented by a few small colonies of *Oculina*, which is an Atlantic genus that can withstand low temperatures (Table 1).

Bivalves with high diversity, including such forms as *Crasspstreia*, *Ostrea* (*Ostrea*), *Gemma*, *Plicatula*, *Glycymeris* and *Anomia* are temperate-affinity taxa which migrated from the Atlantic Ocean and replaced the Pacific fauna of the Miocene-Pliocene (Woodring, 1974). Among the

gastropods, genera (*Tegula*, *Anachis*, *Nitidella*, *Olivella*, *Bulla*) that live on green algae and eel-grass are frequent. Carnivorous genera (*Persicula*, *Conus* and *Cantharus*) are also present. *Melongena margaritana* Richards is more closely related to the floridian *M. corona* (Gmelin), than to the Caribbean *M. melongena*; *Cerithidea pliculosa* lives in the coastal lagoons of the Gulf of Mexico and Yucatan, but not in the southern Caribbean.

On the offshore islands of Venezuela, this is the first horizon that contains extensive colonies of massive *Acropora palmata* (Lamarck) suggesting high-energy wave activity, due to frequent tropical storms.

3.3. Late Pleistocene (125 - 14 ka)

The Late Pleistocene units cited here belong to three facies: two are marine and one is continental. The first is an offshore island facies, consisting almost totally of white, beige and light grey carbonate and divisible into a biohermal (coralgal) fore-reef complex and a back-reef lagoonal (mostly biotrital material with some siliciclastics) complex. This unit, called the Punt

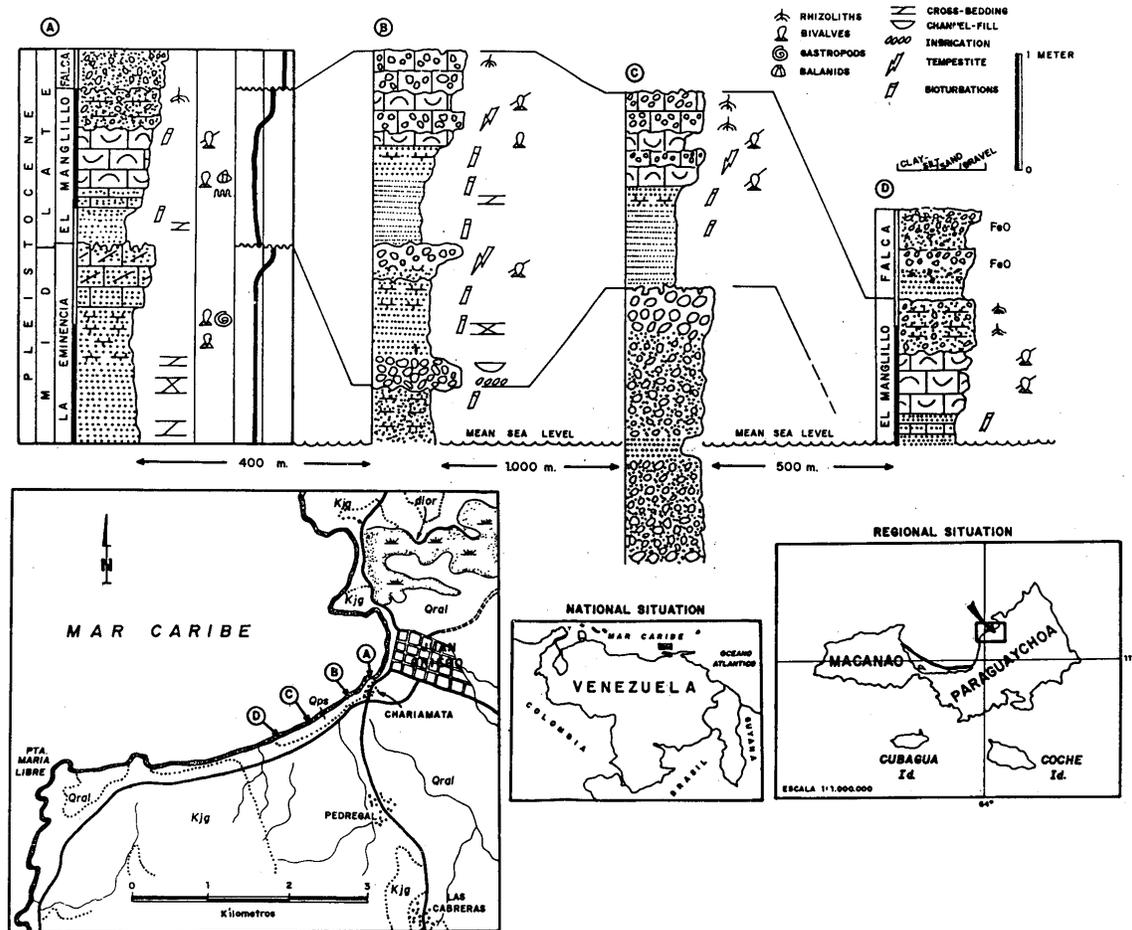


Figure 4. Mid-Late Pleistocene marine sediments near Juan Griego, Paraguaychoa, Venezuela.

a de Piedraa Member, is found on the same offshore islands as the Tortuga Formation *sensu stricto* (Maloney and Macsotay, 1967). The main difference between them is that the Punta de Piedraa Member shows only an initial micritization, whereas the Tortuga Formation is completely recrystallized.

A coastal, heterolithic, highly variable sediment consisting of a mixture of siliciclastics and biotrital carbonates, called the El Manglillo Formation, occurs on the northern coasts of Venezuela (Macsotay and Peraza, in press) (Figs 1-4).

Overlying the last facies, are well-sorted ferruginous quartz sandstones, found on the Paraguaná Peninsula and Margarita Island (Fig. 3). The term Faica Formation (Wehrmann and Macsotay, 1995) is available for both localities. Their red, reddish brown and dark brown colours are typical (Fig. 5).

Sedimentary features. The Late Pleistocene marine heterolithic sediments are the coastal expression of a maximum flooding surface. They

start with a basal conglomerate followed by grits, and calcirudites with cross-bedded. Above this horizon, calcarenites with intense bioturbation and tempestites are the most frequent structures. Higher, some hardgrounds allowed the establishment of hermatypic corals up to some tens of metres in size. Locally, stromatolites are established at this horizon. Above, cross-bedded calcarenites and calcirudites, deposited under wave action, are thoroughly traversed by rhizoliths attributed to mangroves (Figs 4-5).

In the calcrites formed at the top of the succession, terrestrial gastropods are frequent, and suggest permanently humid climates on the Araya Peninsula, and Margarita and Cubagua islands – these locations are xerophic today (Fig. 5). This unusual feature was also observed also in the Paraguaná Peninsula (Audemard, 1996b), and Castilletes in the Guajira Peninsula. Macsotay (1965) published a faunal list of both facies from Western Araya under the terms of Castillo de Araya beds (infralittoral) and the ‘authentic Pleistocene’ (gravelly shorelines with

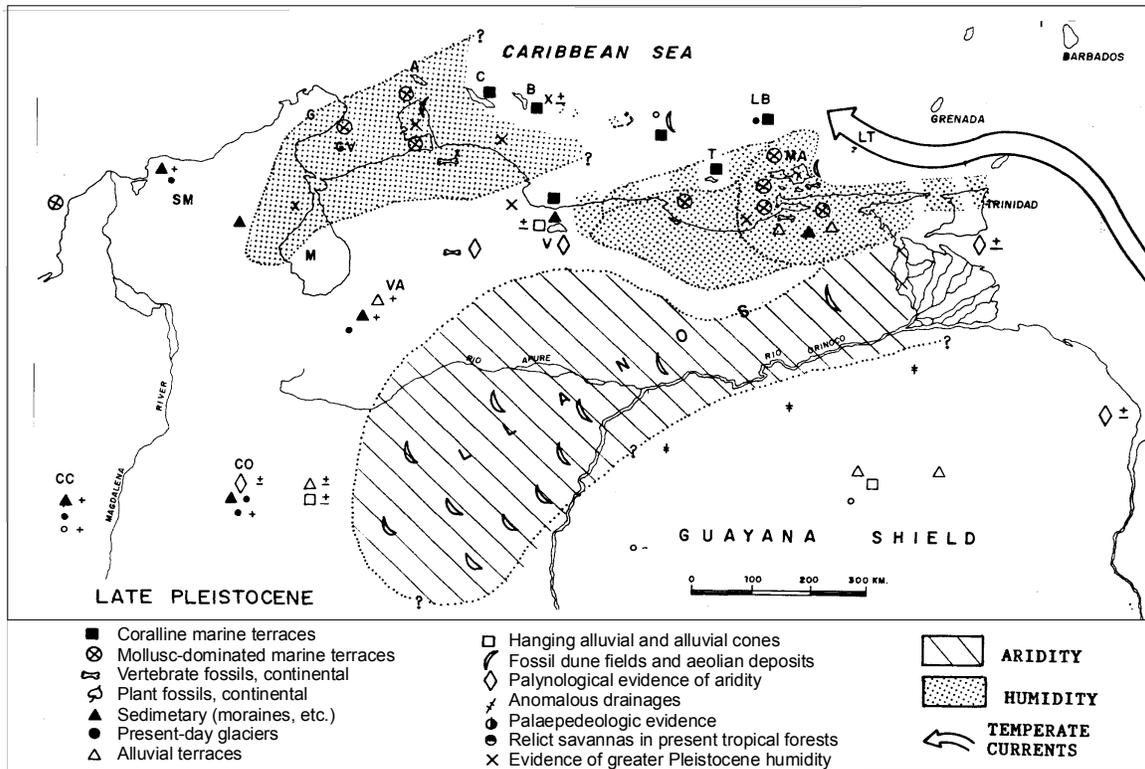


Figure 5. Distribution of palaeoclimatic evidence mainly during the last glacial maximum (Late Pleistocene). Modified from Schubert (1988).

mangroves). This relationship can be observed again in Macanao Peninsula and in the Chiguana area (Macsotay and Caraballo, 1976).

At the top of the calcretes, there is a development of ferruginous quartz sandstones with gravel lenses and small rhizoliths. According to Wehrmann and Macsotay (1995), strong rains eroded the metamorphic rocks and the sands created filled the deep valleys formed during the previous glacial stage. Subsequent dry climates resulted in the development of dune fields that were cemented by iron oxides transported by ephemeral creeks and lagoons (Fig. 6).

The biohermal or fringing reef facies is the classical calcareous unit studied in detail in the Netherland Antilles (Herweijer and Focke, 1978) and Republica Pominicana (Schubert and Cowart, 1980). The outstanding difference with the former is the fact that the reef structure and the lagoon behind it became preserved, with minimal changes, dues to emersion. These calcirudites are composed of biohermal coral and algal assemblages in growth position. The open space between the corals is filled with bioclasts of pebble to boulder size. The lagoonal facies is usually a heterolithic facies in which a basal conglomerate is followed by calcareous sandy

silt intensely bioturbated by *Ophiomorpha*, *Rhizocorallium* and *Thalassinoides*. Some groups of hermatypic corals are found in growth position, others displaced. At the top, mud-cracks are preserved. Almost no calcrete has formed on top of these outcrops.

Mineralogical features. No neoformed minerals are present in the biohermal facies, suggesting a very dry climate during and after emersion from the sea. This circumstance allowed the preservation of the aragonite that has been dated by the U/Th method. The heterolithic facies found onshore is marked by strong calcrete formation at the top and dolomitization in the sink-holes, suggesting humid tropical conditions (Fig. 5).

The red ferrolithic sands are a typical case of lateritization of the massive, cross-bedded sandstones. The duricrusts of goethite formed at the base of channels, filled with quartz gravel and heavy minerals, by evaporation of the limited amount of water in the channels.

Palaeontological features. The reestablishment of the hermatypic reef corals along the continental shorelines of Venezuela and the offshore islands is the most striking feature of the Late Pleistocene. On the offshore islands, such as La Tortuga and La Blanquilla (Figs 1, 3), barrier

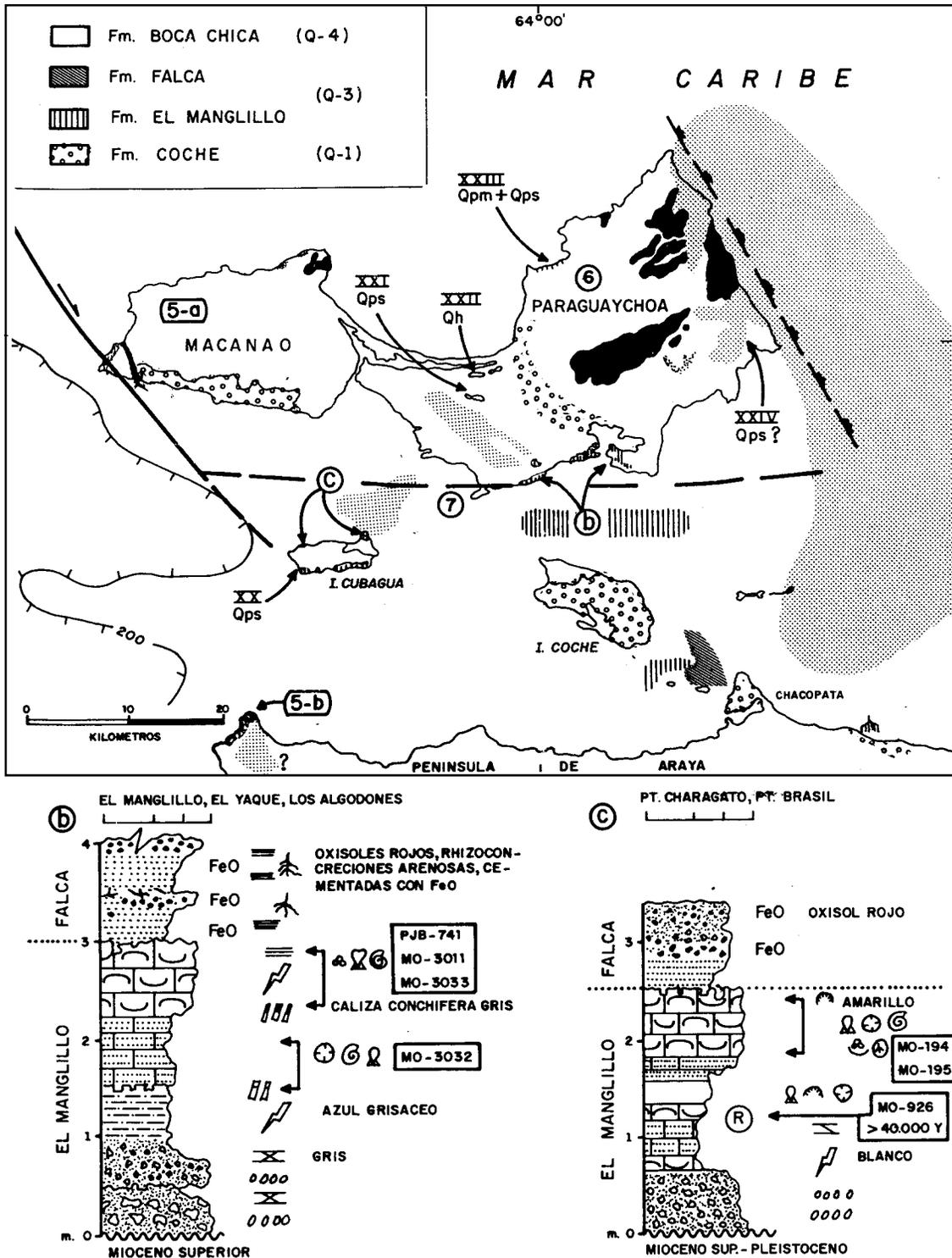


Figure 6. Pleistocene sections.

reefs and lagoonal facies developed in erosional notches cut into sedimentary or igneous substrate (Maloney and Macsoy, 1967). These bioconstructions are integrally preserved, containing most of the species that flourish in the

same areas today. Exceptions include the frequent presence of *Pocillopora elegans* (Dana) in the southern and eastern Caribbean area during the Late Pleistocene (Geister, 1977). This species of hermatypic coral (abundant since Late Miocene

to Recent along the Pacific coasts of Central America) invaded the Caribbean reefs only to briefly disappearing from the area later.

Another common species is *Dendrogyra cylindrus* Ehrenberg, which forms colonial masses up to 3 m high. It is not a living species of the Leeward Antilles or La Blanquilla island (Roos, 1964). The molluscan assemblages in the hermatypic facies are the same genera associated with these carbonates since Miocene times. The gastropods are *Diodora*, *Strombus*, *Cypraea*, *Cyphoma*, *Phalium* (*Tyriocassis*), *Cymatium*, *Charonia*, *Coralliophila*, *Ancilla*, *Voluta* and *Knefastia*; the bivalves, *Barbatia*, *Pinna*, *Pteria*, *Spondylus*, *Lopha*, *Codakia*, *Chama*, *Lyrophora* and *Petricola*. The high biodiversity and abundance of individuals is noteworthy. Tropical genera are dominant, suggesting a palaeotemperature similar to that of the Recent. Among the gastropods, an average smaller size is observed.

The bivalves (especially the calcitic shelled ones) have a larger size than at present (Macsotay and Campos, 2001). We conclude tropical surface temperatures (26°C), with periodical cooling of the bottom waters.

No truly brackish water genera are found, suggesting relatively dry climates. The heterolithic facies also has some unusual coral species, such as *Madracis decaetis* (Lyman), *Oculina diffusa* Lamarck and *O. valenciennesi* Milne-Edwards and Haime, which are branching corals of boreal and austral distribution in the Atlantic Ocean. The hydrozoan *Hilleaster* sp., a boreal taxon of the Mio-Pliocene that becomes extinct during the Late Pleistocene, is also frequent. Decimetric size stromatolites are common in the outcrops of northeastern Paraguana (Audemard, 1996b). All the evidence suggests surface temperatures at least 4 or 5 °C below the Caribbean average.

The molluscan assemblages in the heterolithic facies are dominated by the following taxa – gastropods: *Hemitoma*, *Tegula*, *Astraea*, *Modulus*, *Batillaria*, *Cerithium*, *Natica*, *Purpura*, *Columbella*, *Strombina*, *Melongena*, *Nassanus*, *Vasum* and *Bulla*; bivalves: *Noetia* (*Eontia*), *Glycymeris*, *Atrina*, *Isognomon*, *Crassostrea*, *Trachycardium*, *Macrocallista*, *Gemma*, *Anomarcardia* and *Protothaca*. This molluscan fauna contains many brackish-water species suggesting a tropical humid climate. The dominant taxa are invaders from the Atlantic Ocean, such as *Chama sinuosa barbadensis* and *Scapharca couvana*, and survivors of invaders that arrived during Early Pleistocene times [*Crassostrea patagpnensis* (d'Orbigny)].

3.4. Holocene (14 ka - Present)

The only formally published Holocene unit is the Boca Chica Formation (Macsotay and Moore, 1974). It is a heterolithic unit which at first sight is quite like the El Manglillo Formation of the Late Pleistocene. It is exposed in erosional benches, mostly in eastern Venezuela, due to neotectonic uplift. It consists of silty sand with mollusc shells, and layers or fragments of peat. Rhizoliths are commonly observed with the original root turned peat.

Palaeontological features. The hermatypic corals flourished, not only in offshore islands, but also along the continental shores. The average size of colonies is larger than those in the Late Pleistocene outcrops. In the extensive erosional benches cut into the sedimentary rocks, dense populations of *Porites* spp., *Siderastrea siderea* Ellis and Solander, *Diploria strigosa* (Dana) and *Manicina areolata* (Linné) are present (Macsotay and Moore, 1974).

The molluscs have a high biodiversity, with faunal compositions and average individual sizes similar to the living fauna in the same area of the Venezuelan shelf (Macsotay and Campos, 2001). Some extinctions are observed: *Turritella maiquetiana* Weisbord is replaced by *T. variegata* (Linné) and *Crassostrea patagonica* (d'Orbigny) is replaced by *C. rhizophorae*. *Cerithium guinaicum* Philippi and *Arca zebra abisiniana* Weisbord are immigrants from west African coasts that did not survive the Holocene.

The climatic inferences are warm tropical weather, with more rain influence, not only on the mainland, but also on the nearby islands. Offshore islands remained arid.

4. DISCUSSION

Early Pleistocene times brought climatic changes in the southern Caribbean marine area. Mollusc and coral species, whose larvae were transported to the area, rapidly took over the ecological niches of the Pacific-related taxa, which perished after the disappearance of the Panama-Costa Rica seaway. These molluscs and corals came by the following paths:

1. An Early Pleistocene invasion, mostly from Brazil, Uruguay and Argentina's shelf areas. It is explained by the activity of the Antarctic Intermediate Current, which during Early Pleistocene times occupied a shallower position, even upon the shelves. This current introduced low temperature, mineral-rich waters that helped the proliferation of temperate and austral faunas along the shorelines and islands of the southern Caribbean.

2. A Middle Pleistocene invasion, this time from the southeastern coast of North America, bringing temperate-affinity corals and molluscs into the already mixed faunas of the southern Caribbean. The temperature along the southern shores of the Caribbean dropped drastically; plankton-poor surface waters developed together with a benthic population of small-sized molluscs. Hermatypic corals virtually disappeared. The whole northern coast of Venezuela represents a humid tropical environment, even on Paraguaná island, which was still isolated on the shelf (Audemard, 1996b).

The Late Pleistocene presents an increase in molluscan biodiversity and average size, and the re-establishment of some biohermal corals along the coasts of the mainland (Macsotay and Moore, 1974). Humid weather affected an area in northwestern Venezuela (Schubert, 1988) and another in the northeast (Fig. 5) including the nearshore islands. Contemporaneously, a wide area in the Venezuelan and Colombian Llanos, became arid. The Margarita area also shows an alternation (Wehrmann and Macsotay, 1995) of humid and dry weather conditions (Fig. 6). In Cumaná and Juan Griego, extensive freshwater lakes were formed at sea level as a result of the humid weather conditions. Their periodic communication with the sea is attributed to disruption of coastal sand-bars by storms. No such lakes have been documented in eastern Venezuela since Early Pleistocene times (Macsotay and Caraballo, 1976).

During Holocene time, the warming of the surface waters offshore and nearshore is registered by the molluscan and coral faunas. More temperate affinity species disappear and the warm-water taxa re-occupy the ecological niches from biological refuges.

The Margarita area and the Araya Peninsula show a gradual drying of the climate, while humidity seems to displace to the Orinoco delta and the Gulf of Paria (Macsotay and Moore, 1974). In western Venezuela, aridity extended to Falcón State, despite the tropical rains on the San Luis Mountains, and a tombolo with dune systems developed joining Paraguaná to the mainland (Audemard, 1996a).

The Llanos became a savanna-type plain, dissected by many rivers, draining the mountain ranges.

5. CONCLUSIONS

The survival of most of the Late Pliocene and Early Pleistocene coral faunas in the Caribbean

Sea to the present confirms the existence of Quaternary biological 'refuges'. Although denied by Schubert (1988) from mainland evidence, these refuges existed on the islands away from the routes of oceanic currents from the Atlantic Ocean that contoured the continental margins. The molluscs attest to intense climatic changes in the Quaternary, confirming drops in marine surface water temperatures of the southern Caribbean. This event preceded climatic anomalies including aridification on the Llanos and glaciation on the Venezuelan Andes (VA on Fig. 5) by over a million years.

The cooling must have been of 4 to 5°C according to the molluscs and hermatypic corals, not the 2°C stated by CLIMAP Project Members (1981). During the Holocene, a general warming of surface waters is observed along the entire Venezuelan coast, except for the Cariaco trough and gulf, where relict species of temperate affinity still survive.

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