

The Neogene tropical America fish assemblage and the paleobiogeography of the Caribbean region

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Abstract This first analysis of the marine fish fossil record in the Caribbean region during the Neogene is based on comprehensive new faunal compilation lists at the generic level from basins of nine Central and South American countries during Miocene and Pliocene times. Joint ordination and classification techniques were used to analyze data comprising 236 genera and 346 species. Principal Component Analyses were used to calculate covariance and variance between localities. We identified four subprovinces, representing four different patterns. The subprovince of Venezuela shows distinct and unique features since the Neogene in the diversity of ecosystems represented. The Antillean subprovince has a western orientation and is composed of Jamaica, the Dominican Republic, and the Trinidad islands. The third subprovince combines Panama and Ecuador. It reflects the Pacific faunal influence into the proto-Caribbean and a characteristic benthopelagic fauna. The fourth subprovince is Costarican. Its nektonic fish fauna reflects the overprinting impact over the proto-Caribbean fish fauna mostly due to local paleo-environmental changes (neritic, estuarine and deep water

assemblages), whereby the overall composition of genera is largely not affected (except few lamnids, such as the giant-toothed white sharks and the wide-toothed mako shark). The results of the analyses are concordant with previous ones based on invertebrates and identified regions in need of study (e.g., Colombia, Nicaragua, Honduras, and Brazil).

Keywords Neogene · Caribbean · Gatunian · Province · Teleostean · Elasmobranch

Introduction

The formation of the Caribbean Sea coupled with that of the Panamanian Isthmus during the latest part of the Cenozoic Era resulted in one of the great natural experiments in evolution. The ‘Great American Biotic Interchange’ that took place in the continental communities has been largely addressed by studies of vertebrate animals, most specially mammals (Webb, 2006; Woodburne, 2010). Our understanding of the changes in marine environments is based on investigations of diverse invertebrate groups. Dynamic processes of the ocean currents, physical and chemical water mass conditions, and geographic configurations including Caribbean isolation along the geochronological sequence, produced direct influence over the Neogene Amphi-American marine communities (Corals: Johnson, Sánchez-Villagra, & Aguilera, 2009; Budd, Stemann, & Johnson, 1994, 1996; crustacean decapods: Schweitzer & Iturralde-Vinent, 2005; Collins, Portell, & Donovan, 2009; Aguilera, Rodrigues de Aguilera, Vega, & Sánchez-Villagra, 2010; echinoids: Mihaljević et al., 2010; mollusks: Jackson, Jung, Coates, & Collins, 1993; bryozoans: Cheetham & Jackson, 1996; Cheetham, Jackson, & Sanner,

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2001; O’Dea, Herrera-Cubilla, Fortunato, & Jackson, 2004; O’Dea et al., 2007; O’Dea & Jackson, 2009). These faunal changes are characterized by extinction and turnover in Miocene–Pliocene times.

We address the paleobiogeography in this region and geological time using a rich and complex new database of fossil fish taxa, thus investigating for the first time the marine realm with the most diverse group of vertebrates. The data include almost 100 ‘families’, 236 genera, and 346 species, from 11 Neogene basins in Tropical America. We aim to produce the first qualitative and quantitative analysis of marine fish diversity of the past Caribbean biogeography.

We adopt the term “Gatunian Province” (Landau, Vermeij, & Marques da Silva, 2008) for the geographical area (proto-Caribbean) and the geochronological sequence (Miocene–Pliocene) of interest. This region presents a rich basis for investigation considering the geographic displacement, emersions, and submersions of sedimentary basins, transgression and regression of the sea level, changes in the oceanographic conditions, and species extinction and turnover. There is an ongoing debate over the geographic extension and geochronologic subprovinces involved (Woodring, 1974; Petuch, 1982, 1988, 2004; Landini, Carnevale, & Sorbini, 2002a; Landini et al., 2002b; Porta, 2003; Landau et al., 2008; Harnik, Jablonski, Krug, & Valentine, 2010; Távora, Rodrigues dos Santos, & Neto, 2010). Multiple tectonic and geographical variables were considered in the early model of Caribbean biogeography developed by Rosen (1975) based on living fauna and considering monophyletic clades. Rosen (1975) found for example the influence of the Pacific faunas on the Caribbean and mentioned a ‘track Pacific–Atlantic’. Although not comparable in extent or approach, our work on monophyletic clades of fish in geological time, represents an independent examination of a similar region to that examined by Rosen (1975).

The tectonic context

The geographic configuration of Tropical America during the Cenozoic is the result of the Caribbean plate tectonic interaction with the North American, South American, Nazca, and Cocos plates (e.g. Wadge & Bunke, 1983; Pindell & Barrett, 1990; Pindell et al., 2005; Bachmann, 2001; Iturralde-Vinent, 2004–2005). The tectonic dynamic involved the subduction of western Central America and the eastern Lesser Antilles, the displacement of the Greater and Lesser Antilles and the volcanic island arc coupled with the uplift of the Panama Isthmus (Wadge & Bunke, 1983; Coates & Obando, 1996; Hoernle et al., 2002). These events resulted in the faunal isolation of the Western Central Atlantic and the Eastern Central Pacific at about

3.5 Ma, and the displacement of the multiple sedimentary basins to different geographic locations through time. Prior to the formation of the Panamanian barrier, the trans-isthmus passage was an open seaway permitting a strong inflow of the equatorial Pacific current into the proto-Caribbean, characterized by rich nutrient concentrations to produce high primary productivity (Schneider & Schmittner, 2006; Newkirk & Martin, 2009). The superficial circumtropical current went in western direction through the Panamanian seaway, towards the Pacific Ocean (Iturralde-Vinent & MacPhee, 1999; Schweitzer, Iturralde-Vinent, Hetler, & Velez-Juarbe, 2006).

Methods

Data were obtained from sampling during field trips to Ecuador, Costa Rica, Panama, and Venezuela under the scope of the Panama Paleontology Project (PPP), with identifications and leadership in this portion of the work by the senior author and in co-operation with Werner Schwarzhans (Hamburg) in respect to joint publications in preparation. The local geology and stratigraphical reference follow Coates, Collins, Aubry, and Berggren (2004); (Coates, McNeill, Aubry, Berggren, and Collins, 2005), and Quiróz and Jaramillo (2010). The field trip to Brazil was under the scope of the Museu Emilio Goeldi Paleontology Project; the geological and stratigraphical references follow Rossetti and Góes (2004). Specimens from Trinidad and Dominican Republic were studied based on additional PPP samples and collections at the Museum of Natural History of Belgium, Museum of Natural History of Basel, and Smithsonian Natural History Museum. Data from Cuba, Puerto Rico, Grenadines, Tobago, and Jamaica as well as complementary information from the other countries were taken from published literature (Table 1). Our data were standardized at the generic level, as is common in this kind of study (Foote & Miller, 2007). This procedure served also to diminish distortions caused by preservation and sampling biases, endemic groups and nomenclatural uncertainties.

We grouped basins according to the countries studied, which are deemed good representatives of the Miocene–Pliocene sequence forming the proto-Caribbean Gatunian Province in terms of geographical, paleoenvironmental and geochronological sequence (Table 1). Biases are sometimes attributed to few samples of taxa in certain basins (e.g., Barbados Island) or the absence (lack of preservation or study) of teleosteans or elasmobranchs (e.g., Brazil and Dominican Republic, respectively).

Merging of different time periods for the analysis is justified as there is a well-defined and restricted geological time window represented by the data. Once more precise

Table 1 References of fossil fish records by authors, formations, and age for each country-basin

Country-basin	Reference	Age (formation)
Cuba	Sánchez, 1920	Eocene (Universidad and Consuelo)
	Iturralde-Vinent et al., 1996, 1998	Early Miocene (Husillo)
	Iturralde-Vinent & Case, 1998	Early to Middle Miocene (Cojimar)
	Días-Franco & Rojas-Consuegra, 2009	Middle Miocene (Guines)
Jamaica	Purdy et al., 1996	Late Miocene to Pliocene (Canímar)
	Stringer, 1998	Middle Eocene (Chapelton)
	Donovan & Gunter, 2001	Miocene (Montpelier)
	Ch. Underwood & Mitchell, 2004	Pliocene (Bowden Shell Bed)
Dominican Republic	Nolf & Stringer, 1992	Late Miocene (Cercado)
	Schwarzahns, 1997	Late Miocene to Early Pliocene (Gurabo)
Puerto Rico	Nieves-Rivera, 1999	Early to middle Pliocene (Mao)
	Nieves-Rivera et al., 2003	Middle Miocene (Aymamón)
Venezuela	Casier, 1958	Late Eocene to Early Miocene (Castillo)
	Leriche, 1938	Early Miocene (Cantaure)
	Nolf & Aguilera, 1998	Late Miocene (Socorro, Codore and Urumaco)
	Sánchez-Villagra et al., 2000	Late Miocene to Early Pliocene (Cubagua)
	Aguilera & Rodrigues de Aguilera, 2001, 2004a, b, c	Pliocene (San Gregorio, Paraguaná, Tortuga and Cumaná)
	Aguilera, 2004, 2010	
	Aguilera et al., 2008	
	Aguilera & Lunddberg, 2010	
Costa Rica	Aguilera & Rodrigues de Aguilera, 1999	Late Miocene (Río Banano, Curré and Punta Judas)
	Collins et al., 1999	Late Miocene to Early Pliocene (Uscari)
	Laurito, 1996, 1999, 2004	
	Laurito & Valerio, 2008	
	Laurito et al., 2008	
Panama	Blake, 1862	Early Miocene (Tuira)
	Gillette, 1984	Middle Miocene (Chucunaque and Valiente)
	Aguilera & Rodrigues de Aguilera, 1999	Middle Miocene to Late Miocene (Gatun)
	Collins et al., 1999	Late Miocene (Nancy Point, Chagre and Uscari)
	Pimiento et al., 2010	Late Miocene to Early Pliocene (Shark Hole Point)
Trinidad		Pliocene (Cayo Agua and Escudo de Veraguas)
		Late Pliocene to Pleistocene (Swan Cay)
	Nolf, 1976	Early to Middle Miocene (Brasso)
	Schwarzahns, 1993, 1997	Middle Miocene (Tamana)
Tobago		Late Miocene to Early Pliocene (Morne L'Enfer)
	Donovan et al., 2001	Pliocene (Rockly Bay formation)
Grenada		Early to Middle (Kendeace)
	Portell et al., 2008	Middle Miocene (Grand Bay)
Ecuador		Early Miocene (Viche)
	Landini et al., 1991	Middle Miocene (Angostura)
	Landini et al., 2002a, b	Pliocene (Onzole and Canoa)
	Bianucci et al., 1993, 1997	Early Pleistocene (Jama formation)
Brazil		Early Miocene (Pirabas formation)
	Santos & Travassos, 1960	
	Santos & Salgado, 1971	
	Malabarba, 1991	
	Reis, 2005	
	Oliveira et al., 2008	
	Ramos et al., 2009	
	Costa et al., 2004, 2009	
Távora et al., 2010b		
Costa, 2011		

stratigraphical and temporal information on existing, as well as on new sites becomes available, a new analysis examining changing across the time window examined will be possible.

The binary data matrix includes 236 genera of fossil fishes from nine country-basins; these were analyzed using jointly ordination and classification techniques. Initially, the classification was accomplished using a non-hierarchical K-means algorithm that gathers similar variables in a pre-established number of groups (Legendre & Legendre, 1998). Such groups are geometrically as compact as possible around their respective centroids. The method is particularly efficient when classifying widely distributed variables with many null values without the need for establishing a relative scale of dissimilarity (Legendre, Ellingsen, Bjornbom, & Casgrain, 2002). The best number of groups present in a data set was defined by maximum value of the $C-H$ pseudo- F -statistics (Calinski & Harabasz, 1974) for different partitions (number of groups), where:

$$CH = \left[\frac{R^2}{(K-1)} \right] \cdot \left[\frac{(n-k)}{(1-R^2)} \right]$$

where,

$$R^2 = \frac{(SST - SSE)}{SST},$$

K number of groups and $n = 203$, the number of genera.

SST is the total sum of squared distances to the overall centroid and SSE is the sum of squared distances of the objects to their group's own centroids. The classification was accomplished using the free software K-MEANS2 (Legendre, 2001). In a simulation study involving many stopping rules for cluster analysis, Milligan and Cooper (1985) found that the Calinski–Harabasz criterion was the one that would best recover the correct number of groups.

The principal components analysis (PCA) uses the calculated covariance and variance between localities, for this reason this is a Q-PCA sensu Fasham (1977). The Q-PCA analysis was run using the free software PAST (Hammer, Harper, & Ryan, 2001), and the K-mean for the groups was expressed in the PCAs planes using the concentration ellipse level of 80%. Following Jackson, Somers, and Harvey (1989) the size effect of the linear relationship between the PCA axis 1 and the relative frequency of species occurrence was established with the largest occurrence.

The confidence ellipses of genera groups were formed by computing the three following procedures using PAST software (Hammer et al., 2001) as proposed by Abdi, Dunlop, & Willians (2009): (1) the coordinates of the center of the ellipse of each group in the factorial plane (Axis II and Axis III), (2) the angle between the major axis of the ellipse and the first dimension of the plane, and

(3) the relative size of the minor axis compared to the major axis of the ellipse. To perform these procedures the center of the ellipse must be set at the center of mass of the points. Thereafter, the ratio between the minor axis and the major axis is calculated as done in the ratio of the second to the first eigenvalue. Finally, the angle of rotation is given by the first eigenvector. For a 70% confidence interval, the length of the axes of the ellipse is set to ensure that the ellipse comprehends 70% of the points. It is also important to note that the value of 70% was chosen for visual clarification as to avoid overlapping the ellipses.

Results and discussion

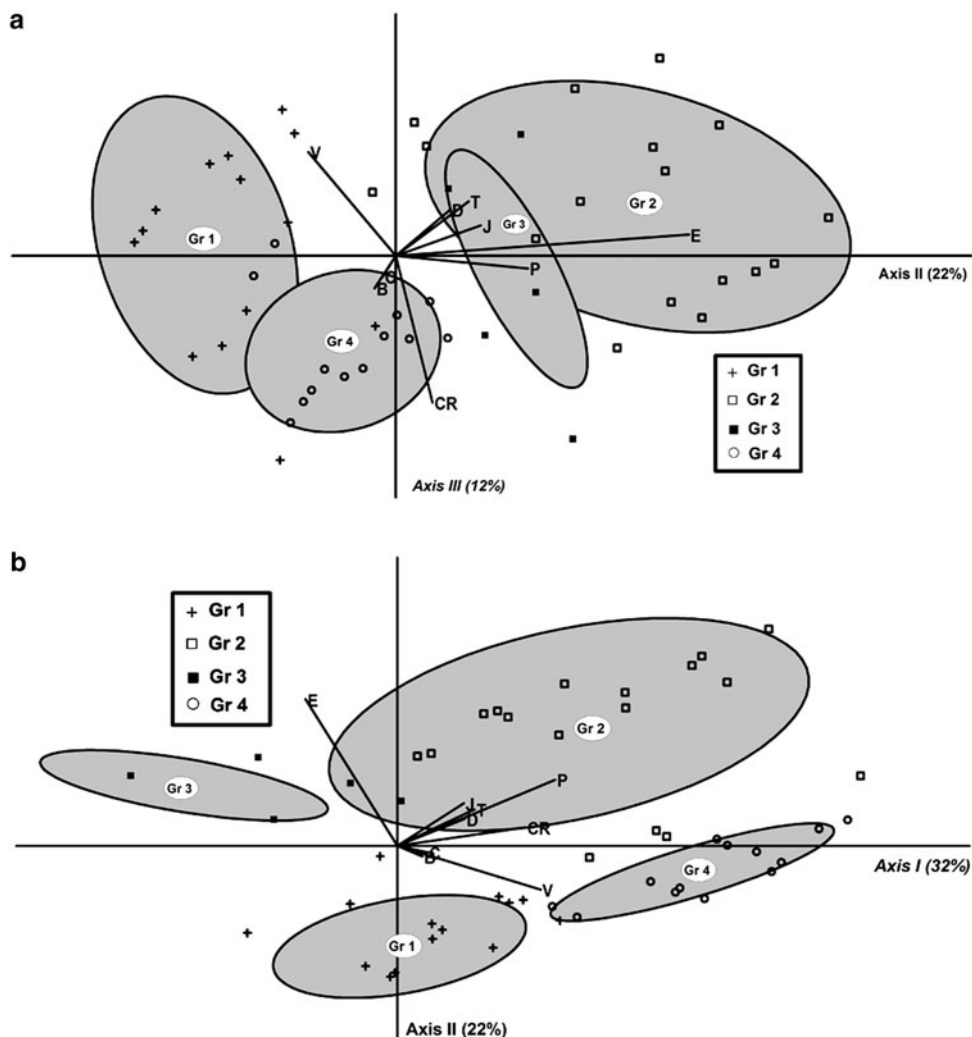
The Miocene–Pliocene fish faunal assemblage established in the Tropical American seaway before the uplift of the Panamanian isthmus is called here the proto-Caribbean fauna, because the Caribbean Sea proper was only formed after the Pacific and Atlantic isolation was complete.

In our assessment the proto-Caribbean fauna is arranged in four different paleobiogeographic patterns of countries/basins and genera assemblages following specific regional paleoenvironments. In terms of faunal composition, age and geographic distribution these four paleobiogeographic patterns can be classified as subprovinces of the Neogene Gatunian bioprovince.

The isolated vector of Venezuela (V) exhibits a pattern of co-occurrence and singularity of fossil fish genera indicated in Fig. 1a (Group 1). Fig. 1b (Group 4) shows Venezuela characterized by a larger frequency of genera of the proto-Caribbean.

Since the Neogene until today, the marine sediment basins of Venezuela represent a faunal subprovince with unique features, which distinguish it from the rest of the Caribbean in diversity of ecosystems represented (estuaries, coastal lagoons, mangrove, rocky bottom, muddy bottom, corals and sea-grasses area, sandy beaches, shallow waters and depth waters, upwelling coastal process, bays and oceanic islands). A similar conclusion was reached by Landau et al. (2008) in their revision of the paleobiogeography of the mollusks of the South Caribbean. Based on their study Landau et al. (2008) recognized a Colombia–Venezuela–Trinidad subprovince. Our analysis though shows large qualitative and quantitative differences between Venezuela and Trinidad (T). An example of the unique composition in the Venezuelan subprovince is the Lower Miocene assemblage of the Cantaure Formation (Nolf & Aguilera, 1998) and that of the Upper Miocene to Lower Pliocene Cubagua Formation (Aguilera & Rodrigues de Aguilera, 2001). The first represents a shallow water environment, and the Cubagua Formation an environment of intense coastal upwelling. The comparisons

Fig. 1 Principal components analysis arranged by genera and country-basin (*B* Brazil, *C* Cuba, *CR* Costa Rica, *D* Dominican Republic, *E* Ecuador, *J* Jamaica, *P* Panamá, *T* Trinidad, *V* Venezuela), and ovoid area of fossil fish assemblage (group species 1, 2, 3 and 4). **a** Axis II versus axis III. **b** Axis I versus axis II



with Trinidad could be expanded in the future with the study of the faunas from the Springvale Formation (Landau et al., 2009). As for Colombia, the available information on Neogene fossil fish is still very preliminary and does not allow conclusions in respect to the suggestion by Landau et al. (2008).

The second subprovince identified by analysis of the fossil fish faunas is the arc of western orientated basins composed of Jamaica (J), Dominican Republic (D) and Trinidad (T) islands. Jamaica and Hispaniola (Haiti and Dominican Republic) moved eastwards along the Eastern Fault in the northern limit of the Caribbean plate during Cenozoic time (Wadge & Bunke, 1983, Pindell et al., 2005). Structural elements affecting Trinidad include a complex mix of contraction, extension, and strike-slip. In the early Cenozoic, deformation and localized uplift of some elements of the passive margin began in the Trinidad region. Through the Oligocene, the leading edge of the Caribbean plate advanced eastward imposing a compressional deformation onto the passive margin of

eastern Venezuela and Trinidad. In the late Miocene, Caribbean-South American relative motion became fundamentally translational (Lingrey, 2007). This subprovince is defined here as the Antillean subprovince and it corresponds in the analysis to the co-occurrence and the exclusivity of the group expressed in Fig. 1a (Group 3); the mean of the species frequency is expressed in Fig. 1b (Group 2).

Given that the angle resulting from the PCA is larger than 45° between Trinidad-Dominican Republic-Jamaica in relation to Panamá-Ecuador, they should best be allocated into two separate subprovinces.

The third subprovince is thus composed of Panama and Ecuador (Fig. 1a; Group 2 and overlap with Group 3). Ecuador has a singular faunal group restricted to the less genera frequency of occurrence pattern (Fig. 1b; Group 3). This pattern reflects the Pacific faunal influence into the proto-Caribbean, because Ecuador, and to some extent also Panama, show species diversity essentially typical for the East Pacific, particularly as to the benthopelagic fauna.

Previous research on Ecuador Pliocene benthonic foraminifera, mollusks, and teleostean fishes (Landini et al., 2002a, b), suggested association within a Panamanian subprovince for this region. Our results for the Miocene–Pliocene are in agreement with the proposition of Landini et al. (2002a, b), extending thus the geochronological range of the subprovince into earlier times equivalent to the proto-Caribbean.

Based on the functional structure of bryozoans and mollusks, O’Dea et al. (2006) hypothesized geochronological abiotic and biotic factors affecting the invertebrate community as consequence of the uplift of the Panamanian isthmus. The change in the water current patterns and the collapse of primary productivity did not lead to synchronous evolutionary responses with immediate extinction and turnover, but rather exhibited a time lag of 2–1 Ma. In contrast to this Pleistocene effect, Johnson et al. (2009) demonstrated that during the Oligocene–Miocene transition a major change occurred in the coral community of the proto-Caribbean with almost 50% of diversity disappearance in the lower Miocene.

The fourth subprovince is here named Costarican and is composed only of Costa Rica (CR) showing the co-occurrence pattern and the singular faunal group expressed in Fig. 1a (Group 4) characterized in the Fig. 1b by high frequency of genera occurrence in this region (Group 2). The absence of fossil fish records in adjacent Nicaragua and Honduras produces regional gaps, to be considered in future studies.

The short vectors of Brazil (B) and Cuba (C) shown by our analysis and the isolated data from Puerto Rico, Tobago, and Grenadine (Table 1) represent preliminary data. However, the associated vertebrate fauna from the lower-middle Miocene Cojimar Formation from Cuba (Iturralde-Vinent, Hubbell, & Rojas, 1996) and the lower Miocene Pirabas Formation from Brazil (Ramos, Santos, Costa, & Toledo, 2009), include similar remains of crocodiles, dugongs (Sirenia), turtles and land mammals (e.g., a rodent). Rosen (1975) had already suggested a close biogeographic link between Cuba and Brazil based on the occurrence of the swamp eel *Ophisternon*.

The fossil sharks and rays’ records from Brazil, Cuba, Puerto Rico, Tobago, and Grenadine are few demersal elasmobranchs widely distributed during the Neogene.

Figure 1a shows the spatial distribution of the genera complexes in four ovoid areas that explain the 70% of the probability of occurrence. The first group is formed by 79 genera and represents the more diverse assemblage in terms of taxa and paleoenvironments (Table 2). This group is characterized mostly by the presence of shallow water demersal fishes, associated with bathypelagic and benthopelagic taxa that reflect productive and environmental stability in this zone. The second group formed by 39

genera is characterized by the presence of shallow water fishes and pelagic planktivores from the neritic zone. The third group formed by 61 genera is characterized by the presence of a large assemblage of fishes that inhabit shallow waters over mud bottom, some of them being associated with brackish environments. This group of fish is indicative for inner platform slope environments and some nocturnal migratory planktivore bathypelagic and carnivore benthopelagic taxa were present. The fourth group is composed of 20 genera, most of them shallow water sharks and rays. Large extinct lamnid sharks, medium sized hemigaleid and carcharinid sharks are present in this group, all of which were widely distributed circumtropically.

The qualitative analysis of the faunal composition based on a comprehensive species list, though preliminary in many aspects (Table 3), shows extinct genera (e.g. *Megaselachus megalodon*), extinct species (e.g. *Hemipristis serra*), and an extremely high turnover rate of species. The list of fossil fishes presented here is the most comprehensive overview and compilation of the Neogene Tropical faunal community, with shallow water (e.g. *Mugil*), brackish (e.g. *Aspistor*), demersal (e.g. *Lepophidium*), bathypelagic (e.g. *Diaphus*), benthopelagic (e.g. *Heptaranchias*), and pelagic (e.g. *Mobula*) faunal elements. Benthic fish representatives exhibit preference for mud bottom (e.g. *Ariosoma*) or sandy bottom (e.g. *Stellifer*). Paleodepth indicators show a range from near shore (e.g. *Equetus*: 0–50 m) to continental slope (*Maurolichus*: 300–500 m depth), and some are known for their diurnal vertical migration (e.g. *Lampadena*).

Summary and conclusions

The fish fossil record in the proto-Caribbean presents identifiable patterns about the pre-isthmus paleobiogeography, denoting the influence of the Pacific current into the Amphi-American fish distribution in the Gatunian Province. We identified the Venezuelan, Antillean, Panamanian, and Costarican subprovinces based on a multivariate analysis of genera. These subprovinces are related to the regional geology and its tectonic dynamics coupled with the oceanographic conditions, paleodepth, and paleoenvironment.

The Caribbean geographic isolation formed as consequence of the Panamanian Isthmus and led to the Plio-Pleistocene extinction and high turnover of the species composition best documented until now in the invertebrate benthic fauna (Aguilera et al., 2010; Budd et al., 1994, 1996; Cheetham & Jackson, 1996; Cheetham et al., 2001; Collins et al., 2009; Jackson et al., 1993, 2009; Mihaljević et al., 2010; O’Dea et al., 2004, 2007; O’Dea & Jackson, 2009; Schweitzer & Iturralde-Vinent, 2005). However, the

Table 2 Functional groups (1–4) organized by genera, trophic preference and habitat

Genera	Family	Trophic	Habitat	G ID	Genera	Family	Trophic	Habitat	G ID
<i>Manta</i>	MYLIOBATIDAE	Planktivore	Pelagic	1	MANT	TRACHICHTHYIDAE	Carnivore	Bathypelagic	1
<i>Acropoma</i>	ACROPOMATIDAE	Carnivore	Demersal	1	ACRO	HOLOCENTRIDAE	Carnivore	Demersal	1
<i>Isacia</i>	HAEMULIDAE	Carnivore	Demersal	1	ISAC	CARANGIDAE	Carnivore	Demersal	1
<i>Diplodus</i>	SPARIDAE	Carnivore	Demersal	1	DIPL	MENIDAE	Carnivore	Demersal	1
<i>Sparus</i>	SPARIDAE	Carnivore	Demersal	1	SPAR	GERREIDAE	Carnivore	Demersal	1
<i>Mokaira</i>	ISTIPHORIDAE	Carnivore	Pelagic	1	MAKA	GERREIDAE	Carnivore	Demersal	1
<i>Ginglymostomus</i>	GINGLYMOSTOMATIDAE	Carnivore	Demersal	1	GING	HAEMULIDAE	Carnivore	Demersal	1
<i>Antennarius</i>	ANTENNARIDAE	Carnivore	Demersal	1	ANTE	SCIAENIDAE	Carnivore	Demersal	1
<i>Lobotes</i>	LOBOTIDAE	Carnivore	Demersal	1	LOBO	SCIAENIDAE	Carnivore	Demersal	1
<i>Sphyraena</i>	SPHYRAENIDAE	Carnivore	Demersal	1	SPHA	PERCOPHIDAE	Carnivore	Demersal	1
<i>Notorhynchus</i>	HEXANCHIDAE	Carnivore	Bathypelagic	1	NOTO	TRICHIURIDAE	Carnivore	Demersal	1
<i>Pseudocarcharias</i>	PSEUDOCARCHARIIDAE	Carnivore	Demersal	1	PSEU	ACHIRIDAE	Carnivore	Demersal	1
<i>Paratodus</i>	LAMNIDAE	Carnivore	Pelagic	1	PARA	DIODONTIDAE	Carnivore	Demersal	1
<i>Galeorhinus</i>	GALEORHINIDAE	Carnivore	Benthopelagic	1	GALE	HEXANCHIDAE	Carnivore	Benthopelagic	1
<i>Etmopterus</i>	DALATIIDAE	Carnivore	Bathypelagic	1	ETMO	ODONTASPIDIDAE	Carnivore	Demersal	1
<i>Trigonognathus</i>	DALATIIDAE	Carnivore	Bathypelagic	1	TRIG	ALOPHIDAE	Carnivore	Benthopelagic	1
<i>Dalatius</i>	DALATIIDAE	Carnivore	Bathypelagic	1	DALA	TRIAXIDAE	Carnivore	Benthopelagic	1
<i>Centrophorus</i>	CENTROPHORIDAE	Carnivore	Bathypelagic	1	CENT	CARCHARINIDAE	Carnivore	Demersal	1
<i>Daenia</i>	CENTROPHORIDAE	Carnivore	Bathypelagic	1	DAEN	SQUALIDAE	Carnivore	Bathypelagic	1
<i>Pristiophorus</i>	PRISTIOPHORIDAE	Carnivore	Demersal	1	PRIS	SQUATINIDAE	Carnivore	Benthopelagic	1
<i>Pteromylaeus</i>	MYLIOBATIDAE	Carnivore	Benthopelagic	1	PTER	RAJIDAE	Carnivore	Benthopelagic	1
<i>Plinthicus</i>	MYLIOBATIDAE	Carnivore	Benthopelagic	1	PLIN	RHINOBATIDAE	Carnivore	Demersal	1
<i>Japonoconger</i>	CONGRIDAE	Carnivore	Demersal	1	JAPO	MYLIOBATIDAE	Planktivore	Plagic	1
<i>Conger</i>	CONGRIDAE	Carnivore	Demersal	1	CONG	MERLUCCIDAE	Carnivore	Benthopelagic	1
<i>Cynopomthicus</i>	MURAENESOCIDAE	Carnivore	Demersal	1	CYNP	ODONTASPIDIDAE	Carnivore	Demersal	1
<i>Harengula</i>	CLUPEIDAE	Planktivore	Pelagic	1	HARE	SCIAENIDAE	Carnivore	Demersal	1
<i>Amphiarus</i>	ARIIDAE	Carnivore	Demersal	1	AMPH	ODONTASPIDIDAE	Carnivore	Demersal	1
<i>Aspistor</i>	ARIIDAE	Carnivore	Demersal	1	ASPI	NARCINIDAE	Carnivore	Demersal	1
<i>Notarius</i>	ARIIDAE	Carnivore	Demersal	1	NOTA	MYLIOBATIDAE	Carnivore	Demersal	1
<i>Bagre</i>	ARIIDAE	Carnivore	Demersal	1	BAGR	ARIIDAE	Carnivore	Demersal	1
<i>Argentina</i>	ARGENTINIDAE	Carnivore	Demersal	1	ARGE	MYCTOPHIDAE	Planktivore	Bathypelagic	1
<i>Scopelosaurus</i>	NOTOSUDIDAE	Planktivore	Bathypelagic	1	SCOP	POLYMIXIDAE	Carnivore	Bathypelagic	1
<i>Neoscopelus</i>	NEOSCOPELIDAE	Planktivore	Bathypelagic	1	NEOS	BATRACHOIDIDAE	Carnivore	Demersal	1
<i>Electrona</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	1	ELEC	LUTJANIDAE	Carnivore	Demersal	1
<i>Physiculus</i>	MORIDAE	Carnivore	Demersal	1	PHYS	SCIAENIDAE	Carnivore	Demersal	1
<i>Snyderidia</i>	CARAPIDAE	Carnivore	Demersal	1	SYND	SCIAENIDAE	Carnivore	Demersal	1
<i>Membras</i>	ATHERINIDAE	Carnivore	Demersal	1	MEMB	ALBULIDAE	Carnivore	Demersal	1

Table 2 continued

Genera	Family	Trophic	Habitat	G	ID	Genera	Family	Trophic	Habitat	G	ID
<i>Melamphaes</i>	MELAMPHAIDAE	Planktivore	Bathypelagic	1	MELA	<i>Myctophum</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	1	MYCT
<i>Hyporhamphus</i>	HEMIRHAMPHIDAE	Carnivore	Demersal	1	HYPO	<i>Diaphus</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	2	DIAP
<i>Hildebrandia</i>	CONGRIDAE	Carnivore	Demersal	1	HILDE	<i>Bregmaceros</i>	BREGMACEROTIDAE	Carnivore	Demersal	2	BREG
<i>Epigonus</i>	EPIGONIDAE	Carnivore	Bathydemersal	1	EPIG	<i>Porichthys</i>	BATRACHOIDIDAE	Carnivore	Demersal	2	PORI
<i>Engraulis</i>	ENGRAULIDAE	Planktivore	Pelagic	2	ENGR	<i>Apogon</i>	APOGONIDAE	Carnivore	Demersal	2	APOG
<i>Maurolicus</i>	STERNOPTYCHIDAE	Planktivore	Bathypelagic	2	MAUR	<i>Ariosoma</i>	CONGRIDAE	Carnivore	Demersal	2	ARIO
<i>Saurida</i>	SYNODONTIDAE	Carnivore	Demersal	2	SAUR	<i>Gnathophis</i>	CONGRIDAE	Carnivore	Demersal	3	GNAT
<i>Coelorrhinchus</i>	MACROURIDAE	Carnivore	Benthopelagic	2	COEL	<i>Clupea</i>	CLUPEIDAE	Planktivore	Pelagic	3	CLUP
<i>Ophidion</i>	OPHIDIIDAE	Carnivore	Demersal	2	OPHI	<i>Eutrumus</i>	CLUPEIDAE	Planktivore	Pelagic	3	EURU
<i>Cetengraulis</i>	ENGRAULIDAE	Planktivore	Pelagic	2	CENT	<i>Anchovia</i>	ENGRAULIDAE	Planktivore	Pelagic	3	ANCV
<i>Trachurus</i>	CARANGIDAE	Carnivore	Demersal	2	TRAC	<i>Yarella</i>	NEOSCOPELIDAE	Planktivore	Bathypelagic	3	YARE
<i>Cynoscion</i>	SCIAENIDAE	Carnivore	Demersal	2	CYNO	<i>Ceratoscopelus</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	3	CERA
<i>Equetus</i>	SCIAENIDAE	Carnivore	Demersal	2	EQUE	<i>Lampadena</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	3	LAMP
<i>Larimus</i>	SCIAENIDAE	Carnivore	Demersal	2	LARM	<i>Steindachneria</i>	MERLUCCIIDAE	Carnivore	Bathypelagic	3	STEN
<i>Paralanchurus</i>	SCIAENIDAE	Carnivore	Demersal	2	PARL	<i>Notoscopelus</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	3	NOTO
<i>Syacium</i>	PARALICHTHYIDAE	Carnivore	Demersal	2	SYAC	<i>Paragadus</i>	OPHIDIIDAE	Carnivore	Bathydemersal	3	PARG
<i>Hypophum</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	2	HYGO	<i>Hoplobrotula</i>	OPHIDIIDAE	Carnivore	Benthopelagic	3	HOPL
<i>Ophiidion</i>	OPHIDIIDAE	Carnivore	Demersal	2	OTOP	<i>Genypterus</i>	OPHIDIIDAE	Carnivore	Bathydemersal	3	GENY
<i>Echiodon</i>	CARAPIDAE	Carnivore	Demersal	2	ECHI	<i>Cataetx</i>	BYTHITIDAE	Carnivore	Benthopelagic	3	CATA
<i>Opisthonema</i>	CLUPEIDAE	Planktivore	Pelagic	2	OPIS	<i>Carapus</i>	CARAPIDAE	Carnivore	Demersal	3	CARA
<i>Umbrina</i>	SCIAENIDAE	Carnivore	Demersal	2	UMBR	<i>Antennarius</i>	ANTENNARIDAE	Carnivore	Demersal	3	ANTE
<i>Pythomichtys</i>	HETERENCHELIDAE	Carnivore	Demersal	2	PYTH	<i>Paralabrax</i>	SERRANIDAE	Carnivore	Demersal	3	PARX
<i>Opisthonema</i>	CLUPEIDAE	Planktivore	Pelagic	2	OPIS	<i>Prionodes</i>	SERRANIDAE	Carnivore	Demersal	3	PRIO
<i>Anchoa</i>	ENGRAULIDAE	Planktivore	Pelagic	2	ANCH	<i>Pseudochromis</i>	PSEUDOCROMIDAE	Carnivore	Demersal	3	PSEU
<i>Arius</i>	ARIIDAE	Carnivore	Demersal	2	ARIU	<i>Anisostrema</i>	HAEMULIDAE	Carnivore	Demersal	3	ANIS
<i>Plotosus</i>	PLOTOSIDAE	Carnivore	Demersal	2	PLOT	<i>Brachydeuteres</i>	HAEMULIDAE	Carnivore	Demersal	3	BRAC
<i>Myripristis</i>	HOLOCENTRIDAE	Carnivore	Demersal	2	MYRI	<i>Nemipterus</i>	NEMIPTERIDAE	Carnivore	Demersal	3	NEMI
<i>Citharichthys</i>	PARALICHTHYIDAE	Carnivore	Demersal	2	CITH	<i>Genyonemus</i>	SCIAENIDAE	Carnivore	Demersal	3	GENY
<i>Symphurus</i>	CYNOGLOSSIDAE	Carnivore	Demersal	2	SYMP	<i>Isopisthus</i>	SCIAENIDAE	Carnivore	Demersal	3	ISOP
<i>Paraconger</i>	CONGRIDAE	Carnivore	Demersal	2	PCON	<i>Menticirrhus</i>	SCIAENIDAE	Carnivore	Demersal	3	MENT
<i>Lepophidium</i>	OPHIDIIDAE	Carnivore	Demersal	2	LEPO	<i>Pareques</i>	SCIAENIDAE	Carnivore	Demersal	3	PARQ
<i>Eucinostomus</i>	GERREIDAE	Carnivore	Demersal	2	EUCI	<i>Seriphus</i>	SCIAENIDAE	Carnivore	Demersal	3	SERI
<i>Lactarius</i>	LACTARIIDAE	Carnivore	Bathydemersal	2	LACT	<i>Stellifer</i>	SCIAENIDAE	Carnivore	Demersal	3	STEL
<i>Mugil</i>	MUGILIDAE	Carnivore	Demersal	2	MUGI	<i>Strongylurus</i>	BELONIDAE	Carnivore	Demersal	3	STRO
<i>"Gobiidarum"</i>	GOBIDAE	Carnivore	Demersal	2	GOBI	<i>Hemirhamphus</i>	HEMIRHAMPHIDAE	Carnivore	Demersal	3	HEMIR
<i>Lonchopisthus</i>	OPISTOGNATHIDAE	Carnivore	Demersal	2	LONC	<i>Euleptorhamphus</i>	HEMIRHAMPHIDAE	Carnivore	Demersal	3	EULE
<i>Pristipomoides</i>	LUTJANIDAE	Carnivore	Demersal	2	PRTO	<i>Cymatogaster</i>	EMBLOTIDAE	Carnivore	Demersal	3	CYMA

Table 2 continued

Genera	Family	Trophic	Habitat	G	ID	Genera	Family	Trophic	Habitat	G	ID
<i>Haemulon</i>	HAEMULIDAE	Carnivore	Demersal	2	HAEM	<i>Hyperprosopon</i>	EMBIOTOCIDAE	Carnivore	Demersal	3	HYPE
<i>Micrometrus</i>	EMBIOTOCIDAE	Carnivore	Demersal	3	MICE	<i>Pristis</i>	PRISTIDAE	Carnivore	Demersal	4	PRST
<i>Abudefduf</i>	POMACENTRIDAE	Carnivore	Demersal	3	ABUD	<i>Rhynchobatus</i>	RHINOBATIDAE	Carnivore	Demersal	4	RHYN
<i>Chromis</i>	POMACENTRIDAE	Carnivore	Demersal	3	CROM	<i>Isurus</i>	LAMNIDAE	Carnivore	Demersal	4	ISUR
" <i>Labridarum</i> "	LABRIDAE	Carnivore	Demersal	3	LABR	<i>Aetobatus</i>	MYLIOBATIDAE	Carnivore	Demersal	4	AETO
" <i>Dactyloscopidarum</i> "	DACTYLOSCOPIIDAE	Carnivore	Demersal	3	DACT	<i>Myliobatis</i>	MYLIOBATIDAE	Carnivore	Demersal	4	MYLI
<i>Eopsetta</i>	PLEURONECTHYDAE	Carnivore	Demersal	3	EOPS	<i>Gadella</i>	MORIDAE	Carnivore	Benthopelagic	4	GADL
<i>Isoopsis</i>	PLEURONECTHYDAE	Carnivore	Demersal	3	ISOP	<i>Neobythites</i>	OPHIIDAE	Carnivore	Demersal	4	NEOB
" <i>Soleidarum</i> "	SOLEIDAE	Carnivore	Demersal	3	SOLE	<i>Parascombrops</i>	ACROPOMATIDAE	Carnivore	Demersal	4	PRAS
<i>Laemonema</i>	MORIDAE	Carnivore	Demersal	3	LAEM	<i>Galeocerdo</i>	CARCHARHINIDAE	Carnivore	Demersal	4	GALO
<i>Rhynchias</i>	CONGRIDAE	Carnivore	Demersal	3	RHEC	<i>Sphyrna</i>	SPHYRNIDAE	Carnivore	Demersal	4	SPHY
<i>Rhynchobatus</i>	RHINOBATIDAE	Carnivore	Demersal	3	RHYN	<i>Megascellachus</i>	OTODONTIDAE	Carnivore	Demersal	4	MEGA
<i>Neoopisthopterus</i>	PRISTIGASTERIDAE	Planktivore	Pelagic	3	NEOP	<i>Carcharhinus</i>	CARCHARHINIDAE	Carnivore	Demersal	4	CARC
<i>Pellona</i>	CLUPEIDAE	Planktivore	Pelagic	3	PELL	<i>Sphyaena</i>	SPHYRAENIDAE	Carnivore	Demersal	4	SPHA
<i>Ctenogaulis</i>	ENGRAULIDAE	Planktivore	Pelagic	3	CETN	<i>Hemipristis</i>	HEMIGALEIDAE	Carnivore	Demersal	4	HEMI
<i>Lampanictus</i>	MYCTOPHIDAE	Planktivore	Bathypelagic	3	LAMI	<i>Dasyatis</i>	DASYATIDAE	Carnivore	Demersal	4	DASY
<i>Merluccius</i>	MERLUCCIIDAE	Carnivore	Demersal	3	MERL	<i>Trichiurus</i>	TRICHIURIDAE	Carnivore	Demersal	4	TRIC
<i>Brotula</i>	OPHIIDAE	Carnivore	Benthopelagic	3	BROT						
<i>Prionotus</i>	TRIGLIDAE	Carnivore	Demersal	3	PRIO						
<i>Epinephelus</i>	SERRANIDAE	Carnivore	Demersal	3	EPIN						
<i>Lutjanus</i>	LUTJANIDAE	Carnivore	Demersal	3	LUTJ						
<i>Orthopristis</i>	HAEMULIDAE	Carnivore	Demersal	3	ORTH						
<i>Pomadasys</i>	HAEMULIDAE	Carnivore	Demersal	3	POMA						
<i>Micropogonias</i>	SCIAENIDAE	Carnivore	Demersal	3	MICR						
<i>Sciaena</i>	SCIAENIDAE	Carnivore	Demersal	3	SCIA						
<i>Sciaenops</i>	SCIAENIDAE	Carnivore	Demersal	3	SCOP						
<i>Peprilus</i>	STROMATIDAE	Carnivore	Demersal	3	PEPR						
<i>Bairdiella</i>	SCIAENIDAE	Carnivore	Demersal	3	BAIR						
<i>Ilisha</i>	PRISTIGASTERIDAE	Planktivore	Pelagic	3	ILIS						
<i>Cetengraulis</i>	ENGRAULIDAE	Planktivore	Pelagic	3	CTEN						
<i>Nebrius</i>	GINGLYMOSTOMATIDAE	Carnivore	Demersal	3	NEBR						
<i>Heterodontus</i>	HETERODONTIDAE	Carnivore	Demersal	4	HETE						
<i>Nebrius</i>	GINGLYMOSTOMATIDAE	Carnivore	Demersal	4	NEBR						
<i>Negaprion</i>	CARCHARHINIDAE	Carnivore	Demersal	4	NEGA						
<i>Rhizoprionodon</i>	CARCHARHINIDAE	Carnivore	Demersal	4	RHIZ						
<i>Isistius</i>	DALATIIDAE	Carnivore	Benthopelagic	4	ISIS						

Table 3 Fossil marine fish species occurrence by country-basin

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID	
ELASMOBRANCHII															
Hexanchiformes	Hexanchidae	<i>Hepranchias perlo</i>	x		x									HEPT	
		<i>Hepranchias tenuidens</i>	x												HEPT
		<i>Notorhynchus</i> sp.	x												NOTO
Heterodontiformes	Chlamydoselachidae	<i>Chlamydoselachus</i> sp.									x			CHLA	
		<i>Heterodontus</i> sp.	x	x	x									HETE	
Orectolobiformes	Ginglymostomatidae	<i>Ginglymostoma delfortriei</i>	x	x	x									GING	
		<i>Ginglymostoma</i> sp.											x	GING	
		<i>Nebrius obliquus</i>										x		NEBR	
Lamniformes	Odontaspidae	<i>Carcharias taurus</i>	x			x								CRIA	
		<i>Odontaspis ferox</i>	x											ODON	
			<i>Odontaspis</i> sp.		x									ODON	
	Pseudocarchariidae	<i>Pseudocarcharias kamoharai</i>	x											PSEU	
	Otodontidae	<i>Megaelachus megalodon</i>	x	x	x	x			x					MEGA	
Lamnidae		<i>Megaelachus subauriculatus</i>	x			x							x	MEGA	
		<i>Cosmopolitodus hastalis</i>	x											COSM	
		<i>Isurus</i> cf. <i>oxyrinchus</i>													ISUR
		<i>Isurus</i> sp.		x	x									x	ISUR
		cf. <i>Paratodus</i> sp.	x												PARA
Alopiidae		<i>Alopias superciliosus</i>	x		x					x				ALOP	
		<i>Alopias vulpinus</i>	x											ALOP	
		<i>Alopias</i> sp.										x		ALOP	
Triakidae		<i>Mustelus</i> sp.	x		x									MUST	
		<i>Galeorhinus</i> sp.	x											GALE	
Hemigaleidae		<i>Hemipristis serra</i>	x	x	x		x	x		x				HEMI	
		<i>Carcharhinus albimarginatus</i>			x										CARC
Carcharhinidae		<i>Carcharhinus egertoni</i>	x	x											CARC
		<i>Carcharhinus falciformes</i>	x		x										CARC
		<i>Carcharhinus limbatus</i>	x												CARC
		<i>Carcharhinus longimanus</i>													CARC
		<i>Carcharhinus macloti</i>												x	CARC
		<i>Carcharhinus</i> cf. <i>obscurus</i>	x					x							CARC
		<i>Carcharhinus</i> cf. <i>perezi</i>	x					x							CARC
		<i>Carcharhinus plumbeus</i>	x												CARC
		<i>Carcharhinus priscus</i>												x	CARC

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad Rico	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		<i>Diaphus aff. splendidus</i>	x									x		DIAP
		<i>Diaphus theta</i>										x		DIAP
		<i>Diaphus spp.</i>	x	x	x	x	x		x			x		DIAP
		<i>Ceratoscopus townsendi</i>										x		CERA
		<i>Electrona risso</i>	x											ELEC
		<i>Hygophum hygomii</i>	x	x						x		x		HYGO
		<i>Hygophum macrochir</i>	x	x										HYGO
		<i>Hygophum reinhardtii</i>										x		HYGO
		<i>Hygophum sp.</i>										x		HYGO
		<i>Lampadena sp.</i>										x		LAMP
		<i>Lampadena jacksoni</i>	x	x										LAMP
		<i>Lampanyctus cupriarius</i>	x	x										LAMI
		<i>Lampanyctus aff. latesulcatus</i>	x											LAMI
		<i>Lampanyctus sp.</i>										x		LAMI
		<i>Lombachia sp.</i>		x										LOMB
		<i>Myctophum cf. punctatum</i>	x						x					MYCT
		<i>Myctophum sp.</i>		x										MYCT
		<i>Notoscopelus sp.</i>											x	NOTO
		<i>Symbolophorus sp.</i>	x	x						x				SYMB
		<i>Stenobranichius sp.</i>										x		STEN
		<i>Triphoturus sp.</i>		x										TRIP
Polymixiiformes	Polymixiidae	<i>Polymixia sp.</i>	x											POLX
Gadiformes	Bregmacerotidae	<i>Bregmaceros sp.</i>	x	x	x	x	x			x		x		BREG
	Macrouridae	<i>Coelorhynchus aff. coelorhynchus</i>	x	x									x	COEL
		<i>Nezumia sp.</i>	x											NEZU
	Moridae	<i>Gadella sp.</i>	x	x	x							x		GADL
		<i>Laemonema sp.</i>												LAEM
	Merlucciidae	<i>Physiculus sp.</i>	x											PHYS
		<i>Merluccius sp.</i>	x										x	MERL
		<i>Merluccius productus</i>											x	MERL
		<i>Steindachneria cf. argentea</i>	x	x										STEI
Ophidiiformes	Ophidiidae	<i>Brotula cf. clarkae</i>											x	BROT
		<i>Brotula sp.</i>										x		BROT
		<i>Dicrolene sp.</i>										x		DICR

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		<i>cf. Genypterus</i> sp.										x		GENY
		<i>Hoplobrotula</i> sp.										x		HOPL
		<i>Lampogranus</i> sp.					x							LAMP
		<i>Lepophidium</i> aff. <i>aporrhox</i>	x										x	LEPO
		<i>Lepophidium</i> cf. <i>cervinum</i>											x	LEPO
		<i>Lepophidium microlepis</i>											x	LEPO
		<i>Lepophidium</i> sp.	x	x	x		x						x	LEPO
		<i>Neobythites</i> aff. <i>unicolor</i>	x											NEOB
		<i>Neobythites</i> sp.		x	x									NEOB
		<i>Ophidion</i> sp.		x									x	OPHI
		<i>Ophidion</i> aff. <i>holbrooki</i>	x											OPHI
		<i>Otophidium</i> sp.									x			OTOP
		<i>Otophidium robinsi</i>	x	x				x						OTOP
		<i>Paragadus</i> sp.									x			PARG
		<i>Paraphidion</i> cf. <i>schmidti</i>												PARO
	Bythidae	<i>Cataetx</i> sp.									x			CATA
		" <i>Dinematichthyinorum</i> " <i>smithvanizi</i>												DINE
		" <i>Dinematichthyinorum</i> " <i>sauli</i>												DINE
	Carapidae	<i>Echiodon</i> sp.	x	x						x				ECHI
		<i>Carapus</i> sp.											x	CARA
		<i>Snyderidia canina</i>	x											SYND
Batrachoidiformes	Batrachoididae	<i>Perulibatrachus</i> sp.										x		PERU
		<i>Porichthys</i> sp.	x	x	x					x				PORI
		<i>Thalassophryne</i> sp.	x											THAL
Lophiiformes	Chaunacidae	<i>Chaunax</i> sp.												CHAU
	Antennariidae	<i>Antennarius</i> sp.											x	ANTE
Atheriniformes	Atherinidae	<i>Atherinops</i> sp.											x	ATHE
		<i>Atherinomorus stipes</i>												ATHM
		<i>Membras</i> sp.												MEMB
Stephanoberyciformes	Melamphaidae	<i>Melamphaes polylepis</i>	x											MELA
		<i>Scopelogadus</i> sp.	x											SCOP
Beryciformes	Trachichthyidae	<i>Hoplostethus mediterraneus</i>	x											HOPL
	Holocentridae	<i>Holocentrus</i> sp.											x	HOLO

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		<i>Rhombopites</i> sp.		x										RHOM
	Lobotidae	<i>cf. Lobotes</i> sp.										x		LOBO
	Gerreidae	<i>Diapteris</i> sp.	x											DIAT
		<i>Eucinostomus</i> sp.	x	x	x				x					EUCI
		<i>Gerres</i> sp.	x											GERR
		<i>Moharra</i> sp.		x										MOHA
	Haemulidae	<i>Anisotremus</i> sp.										x		ANIS
		<i>Brachydeuteres</i> sp.										x		BRAC
		<i>Conodon aoreaxi</i>				x								CONO
		<i>Haemulon</i> aff. <i>aurolineatum</i>	x											HAEM
		<i>Haemulon</i> sp.	x	x	x	x		x						HAEM
		<i>Haemulopsis</i> sp.	x											HAML
		gen., sp. ind.										x		HRUM
		<i>Isacia</i> sp.			x									ISAC
		<i>Orthopristis</i> sp.										x		ORTH
		<i>Orthopristis</i> aff. <i>ruber</i>	x											ORTH
		<i>Pomadasys</i> aff. <i>panamensis</i>	x										x	POMA
		<i>Pomadasys</i> sp.						x						POMA
Nemipteridae		<i>Nemipterus</i> sp.										x		NEMI
Sciaenidae		<i>Aplodinotus hofmani</i>	x											APLO
		<i>Aplodinotus longicaudatus</i>	x											APLO
		<i>Bairdiella icistia</i>												BAIR
		<i>Bairdiella</i> aff. <i>ronchus</i>										x		BAIR
		<i>Bairdiella</i> sp.	x		x									BAIR
		<i>Ctenosciaena</i> aff. <i>gracilicirrhus</i>	x					x						CTEN
		<i>Ctenosciaena</i> sp.										x		CTEN
		<i>Cynoscion</i> aff. <i>arenarius</i>						x						CYNO
		<i>Cynoscion</i> aff. <i>microlepidotus</i>	x	x										CYNO
		<i>Cynoscion nothus</i>						x						CYNO
		<i>Cynoscion</i> aff. <i>jamaicensis</i>		x										CYNO
		<i>Cynoscion</i> spp.	x	x			x							CYNO
		<i>Equetus davidandrewi</i>	x	x								x		EQUE
		<i>Equetus</i> sp.	x	x									x	EQUE

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		<i>Genyonemus</i> sp.										x		GENY
		<i>Isopisthus</i> sp.	x	x				x				x		ISOP
		<i>Larimus</i> aff. <i>fasciatus</i>	x	x										LARI
		<i>Larimus gatunensis</i>	x	x				x						LARI
		<i>Larimus henrii</i>	x											LARI
		<i>Larimus</i> aff. <i>pacificus</i>	x											LARI
		<i>Larimus steurbauti</i>	x											LARI
		<i>Larimus</i> spp.		x	x							x		LARI
		<i>Leiostomus</i> sp.		x										LEJO
		<i>Lonchurus</i> sp.						x						LOCH
		<i>Menticirrhus</i> sp.		x								x		MENT
		<i>Micropogonias ectenes</i>										x		MICR
		<i>Micropogonias coatesi</i>	x											MICR
		<i>Micropogonias furnieri</i>	x											MICR
		<i>Micropogonias</i> sp.			x									MICR
		<i>Nebris</i> aff. <i>occidentalis</i>	x					x					x	NEBR
		<i>Nebris</i> sp.		x	x			x						NEBR
		<i>Nector</i> sp.						x						NECT
		<i>Odontoscion dentex</i>	x	x										ODON
		<i>Ophioscion lundbergi</i>	x	x				x						OPHS
		<i>Pachypops fitchi</i>						x						PACH
		<i>Pachypops</i> sp.						x						PACH
		<i>Pachyurus junki</i>	x											PACK
		<i>Paralonchurus schwarzhansi</i>	x	x										PARL
		<i>Paralonchurus</i> sp.										x		PARL
		<i>Pareques</i> sp.										x		PARQ
		<i>Plagioscion marinus</i>	x											PLAG
		<i>Plagioscion urumacoensis</i>	x					x						PLAG
		<i>Polylemus dumerilli</i>												POLC
		<i>Polylemus trinidadensis</i>		x	x									POLC
		<i>Protoscaena neriticus</i>	x										x	PROT
		<i>Protoscaena</i> sp.												PROT
		<i>Seriphus</i> sp.											x	SERI
		<i>Sciaena bathytatos</i>												SCIA
		<i>Sciaena</i> sp.											x	SCIA

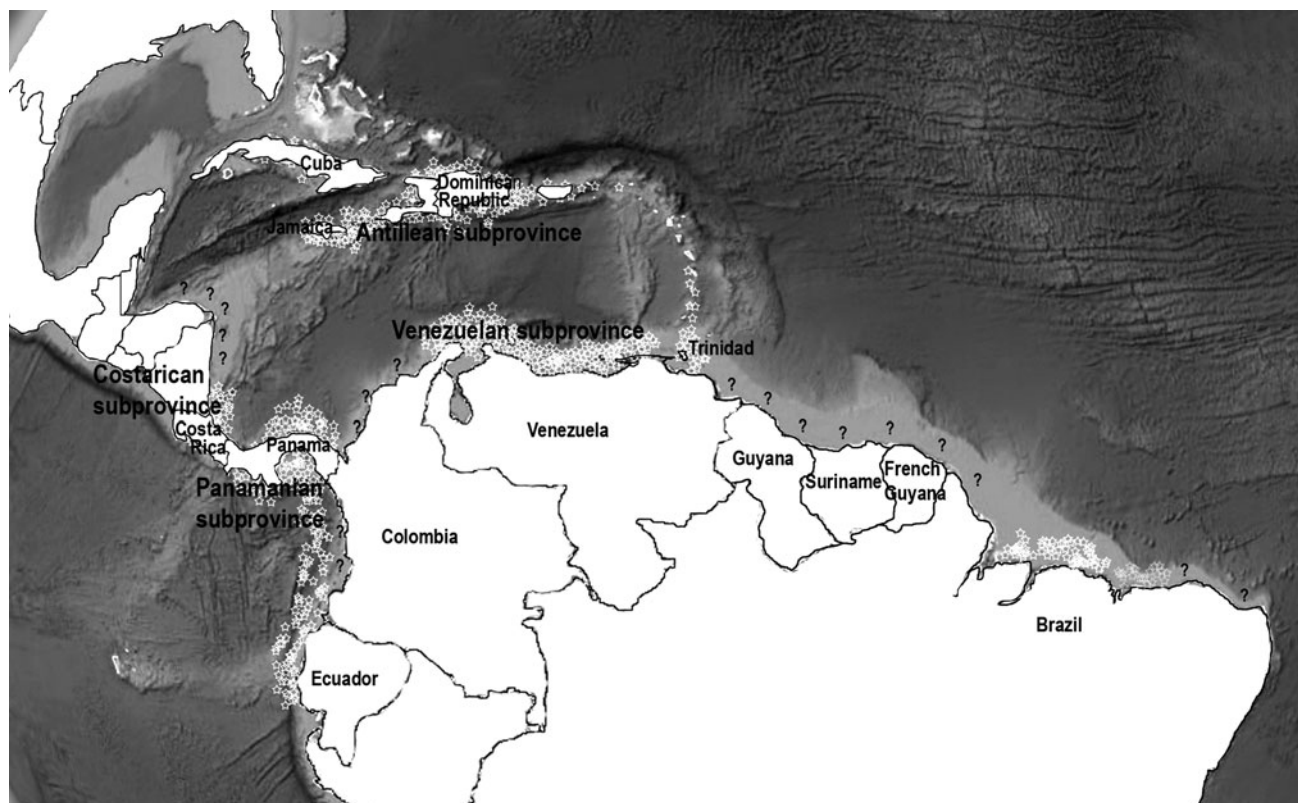


Fig. 2 The proto-Caribbean subprovinces recognized in this work (map modified from Google map). *Question marks* denote unknown fossil fish record and *star symbols* denote sedimentary deposits with potential for fossil fish occurrences

nektonic fish fauna reflects the impact of the proto-Caribbean fish fauna at the generic level in local paleoenvironment community changes in neritic, estuarine and deep water assemblages. The overall diversity remains largely the same, except for a few lamnids, such as the giant-toothed white shark and the wide-toothed mako shark.

The concept of a Gatunian Province is a valid concept in terms of the geographical and geochronological relationship with the proto-Caribbean paleofauna of invertebrate groups studied so far. In addition, we propose the Venezuelan, Antillean, Panamanian, and Costarican subprovinces as clearly recognizable assemblages of marine fishes (Fig. 2).

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