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Giant-toothed White Sharks and Wide-toothed Mako (Lamnidae) from the Venezuela Neogene: Their Role in the Caribbean, Shallow-water Fish Assemblage

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ABSTRACT.—The role of Neogene giant-toothed lamnid sharks in the Caribbean neritic fish assemblage is discussed based on predator-prey relationships in three different tropical paleoenvironments from the Lower Miocene to Lower Pliocene. New records of extinct giant-toothed white sharks *Carcharodon megalodon* (Agassiz), *Carcharodon subarticulatus* (Agassiz), and wide-toothed mako *Isurus xiphodon* (Agassiz) from coastal shallow waters, coastal upwelling, swampy, coastal lagoon, and sandy littorals of the Venezuela Neogene, suggest these species were large transient piscivores that may have had enough behavioral flexibility to occupy different environments. Giant-tooth shark species, that probably fed mainly on fish, turtles, cetaceans and sirenids, did not exhibit large population sizes. The trophic role that large consumer sharks have carried out represents the higher trophic category, the type of selective pressure, and the control performed in the marine environment. The dynamics of these associations during Neogene is deeply different.

KEYWORDS.—Caribbean, Neogene, sharks, predator

INTRODUCTION

Fossil remains of Neogene lamnid sharks have been the subject of investigations on tooth morphology, taxonomy, phylogeny and distribution as compiled by Purdy et al. (2001). Published literature reflects a tendency to establish a close relationship between cetacean and pinniped abundance, cold and temperate waters and presence of giant-toothed sharks, (e.g., *Carcharodon megalodon*). The scarcity of records of Caribbean lamnids (Kruckow and Thies 1990) and limited records from Barbados and Trinidad (Casier 1958, Flemming and MacFarlane 1998), Costa Rica (Laurito 1999), Jamaica (Donovan and Gunter 2001), Puerto Rico (Nieves-Rivera et al. 2003), Cuba (Iturralde-Vinent et al. 1996), Panama (Gillette 1984), and Venezuela (Leriche 1938; Aguilera and Rodrigues de Aguilera 2001) may be an artifact of sampling; thus, it may be erroneously interpreted as fortuity and scarce giant-toothed shark distributions in the Caribbean sedimentary basin.

Based on the recovery of additional lamnid Neogene specimens and the associated fish fauna in a wide geochronological sedimentary sequence (Lower Miocene to Lower Pliocene) in Venezuela, we interpret the role of giant predators in the Caribbean neritic fish assemblage during the Neogene and provide additional records of the giant-toothed white sharks *Carcharodon megalodon* (Agassiz), *Carcharodon subarticulatus* (Agassiz), and wide-toothed mako *Isurus xiphodon* (Agassiz) from the Venezuela Neogene.

MATERIAL AND METHODS

The study area includes localities in the northwestern and northeastern Venezuela sedimentary basin (Fig. 1). Precise stratigraphy placement of the fossil samples in relation to unit boundaries is unknown. However, studies of the stratigraphy are in progress (A. Coates pers. comm.). We collected samples of shark teeth from surface collections within the scope of the Panama Paleontology Project (Jackson et al. 1999). Shark classification was arranged following

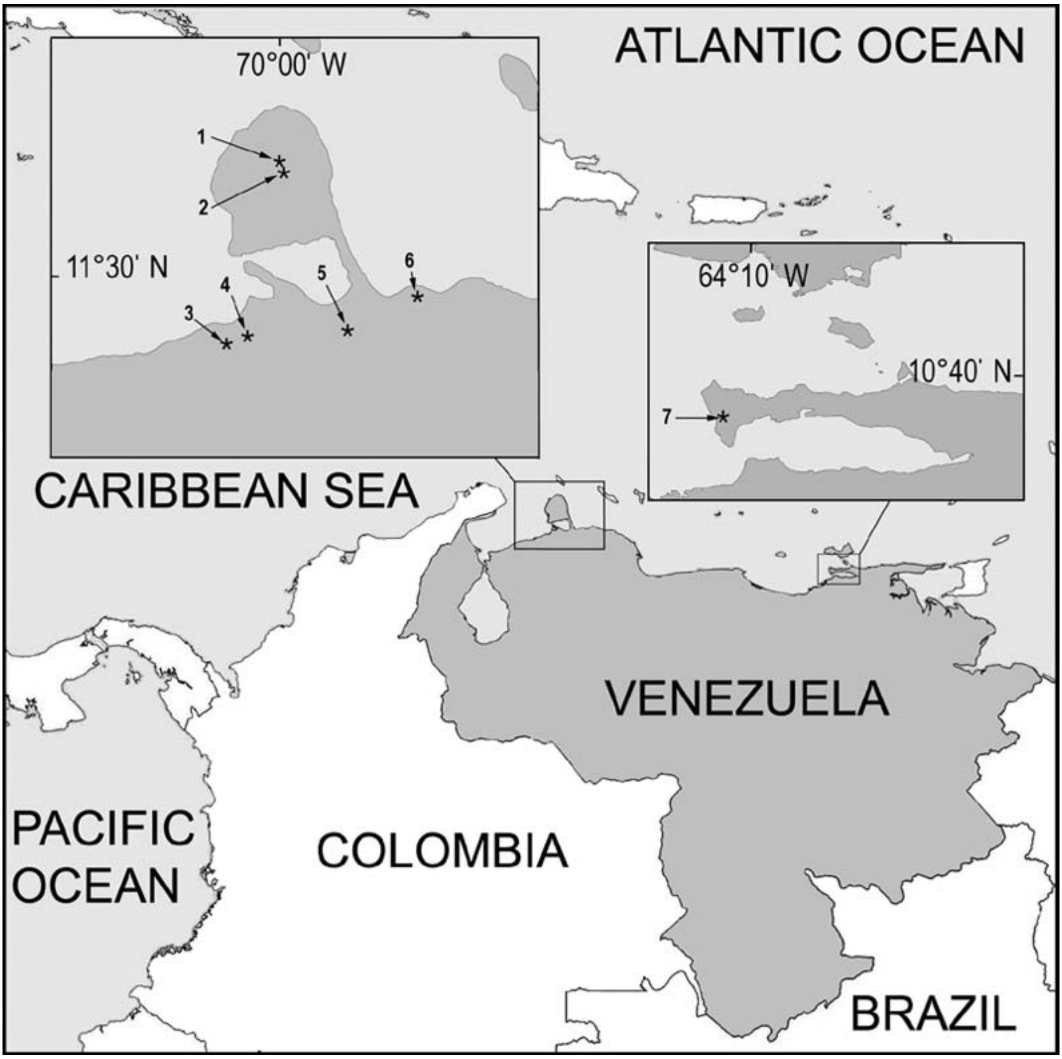

FIG. 1. Location of the Venezuelan sampling sites discussed in the text (see Table 1). 1, Cantaure Formation; 2, Paraguaná Formation; 3, Urumaco Formation; 4 Codore Formation; 5, Socorro Formation; 6, Caujarao Formation; 7, Cubagua Formation.

Purdy et al. (2001), and specimens were deposited in the Universidad Nacional Experimental Francisco de Miranda (UNEFM), Coro, Estado Falcón, Venezuela.

The geological unit from which teeth were obtained [Lower Miocene Cantaure, Middle Miocene Socorro, Upper Miocene Urumaco (Middle Member) and Caujarao (TaraTara Member), Upper Miocene to Lower Pliocene Cubagua (Cerro Verde Member), Upper Miocene to Pliocene Codore (Chiguaje Member) and Lower Pliocene Paraguaná formations (Amuay Member)] is the most complete Neogene sedimentary sequence preserved near the Caribbean Sea (Table 1). For additional information about the geology of these geological units see Ministerio de Energía y Minas (1997).

In order to reconstruct lower trophic levels in Neogene food webs we used published and unpublished data on fish assemblages (Table 1). The topology of the food web was suggested by E. Sala (pers.

comm.), and it is based on trophic relationships of present Caribbean food webs.

Results

The giant-toothed white shark *Carcharodon subauriculatus* (Agassiz) (Fig. 2.1-2.18) is the first record for the Caribbean; particularly from the Lower Miocene Cantaure Formation, Upper Miocene to Lower Pliocene Codore Formation, and Lower Pliocene Paraguaná Formation of Venezuela. Purdy et al. (2001) and Purdy (1996, 1998) reported from US an early record of the Oligocene Chandler Bridge Formation, Middle Miocene Calvert Formation, Miocene Purgo River Formation, and Lower Pliocene Yorktown Formation. *Carcharodon subauriculatus* is distinguished from *C. megalodon* by a low, slender, curved crown, strong marginal serration and by the presence of lateral heels feebly serrated. According to Purdy (1996), giant-toothed sharks *Carcharodon sokolowi* (Jaekel) (Eocene), *C. angustidens* (Agassiz) (Oligocene), *C. subauriculatus* (Oligocene), and *C. megalodon* (Miocene/Pliocene) were more common in warm waters and fed on whales. However, their discovery of *C. subauriculatus* in shallow-waters of the Caribbean suggests that this species may change habitat preferences through time, or it may have enough behavioral flexibility to occupy different environments at different times.

Carcharodon megalodon (Fig. 2.19-2.28) represents an additional fossil record for the Caribbean Neogene; particularly from the Lower Miocene Cantaure Formation, Upper Miocene Urumaco Formation, Middle Miocene Socorro Formation, Upper Miocene Caujarao Formation, Upper Miocene to Lower Pliocene Codore Formation, and Lower Pliocene Paraguaná Formation of Venezuela.

Kruckow and Thies (1990) compiled an early record of *C. megalodon* from the Caribbean, with additional published records by Aguilera (2004), Aguilera and Rodrigues de Aguilera (2001), Donovan and Gunter (2001), Flemming and MacFarlane (1998), Iturralde-Vinent et al. (1996), Laurito (1999), and Nieves-Rivera et al. (2003). This reinforces the information about the presence of giant-toothed white sharks in the Neogene Caribbean.

Carcharodon megalodon is characterized by a triangular, broad, high and slightly curved crown; cutting edge incised by numerous, small, and regular serrations; neck very marked, strongly curved toward the top; labial boundary of the enameled with a median obtuse angle directed toward the top. The presence of *C. megalodon* along the wide Neogene geochronologic sequence in the tropical Caribbean neritic deposit is contradictory, with warm and cold water preferences noted by Purdy (1996). In the Neogene Caribbean tropical environment, *C. megalodon* probably fed mainly on small cetaceans, sirenids, turtles, and fish.

The wide-toothed mako *Isurus xiphodon* (Agassiz) (Fig. 2.29-2.34) is the first record for the Caribbean; particularly from the Upper Miocene to Lower Pliocene Cubagua Formation of Venezuela. *Isurus xiphodon* is characterized by a long and stronger crown without lateral cusplets, cutting edges completely smooth reaching the base; root bulky with short divergent asymmetric lobes. According to Purdy et al. (2001), the wide-toothed mako with convergent teeth to those of the white shark may have been the main predator of tropical monk seals in the north Atlantic coast, reaching 7.6 m in length. A single Caribbean fossil record of wide-toothed mako is associated with coastal upwelling (Aguilera and Rodrigues de Aguilera 2001), and probably they fed on fish, turtles and cetaceans.

Discussion

Most of the sedimentary basins included in the present study are neritic environments. Among them some exceptional deposits and their associated assemblages may be used to interpret and discuss different paleoenvironments along with their the trophic setting.

Coastal shallow water environments (Fig. 3).—The Cantaure Formation (Lower Miocene, northwestern Venezuela) is characterized by a diverse association of

TABLE 1. Venezuelan Neogene marine sedimentary basins with giant-toothed sharks.

Age	Formation/Member	Lithology	Marine vertebrate biota/Paleoenvironments	Reference
Lower Miocene	Cantaure Formation, northwestern Venezuela.	Gypsies slime claystone, with sandy intervals in the lower part. Claystone intercalated with thin limestone in the upper part	GINGLYMOSTOMATIDAE *Ginglymostoma delfortriei* Daimeries; LAMNIDAE *Carcharodon megalodon* (Agassiz), *Carcharodon subauriculatus* Agassiz; HEMIGALEIDAE *Hemipristis serra* Agassiz, *Paragaleus* sp.; CARCHARHINIDAE *Carcharhinus ackermani* Santos and Travasos, *Carcharhinus egertoni* (Agassiz), *Galeocerdo aduncus* Agassiz, *Negaprion eurybathrodon* (Blake), *Rhyzoprionodon* sp.; SPHYRNIDAE *Sphyma* sp.; PRISTIDAE *Pristis* sp.; RHINOBATIDAE *Rhynchobatus* sp.; DASYATIDAE *Dasyatis* sp.; MYLIOBATIDAE *Aetobatus arcuatus* (Agassiz), *Myliobatis* sp., *Rhinoptera* sp., *Plinthicus stenodon* Cope; MOBULIDAE *Mobula* sp.; ALBULIDAE *Albula* sp.; HETERENCHELYIDAE *Pythonichthys* sp.; CONGRIDAE *Conger* sp., *Paraconger guianensis* Kanagawa, *Rhynchoconger* aff. *flavus* (Goode and Bean), *Ariosoma balearicum* (DeLaRoche); CLUPEIDAE *Harengula* aff. *clupeola* Cuvier, *Illisha* sp., *Neopistopterus* sp., *Pellona* sp.; ARIIDAE *Arius* aff. *keesleri* Steindachner, *Cathorops* sp., *Genidens* sp.; PLOTOSIDAE *Plotosus* sp.; MYCTOPHIDAE *Diaphus* aff. *problematicus* Parr, *Diaphus* aff. *regani* Taaning, *Diaphus* sp., *Hygophum hygomi* (Lutken), *Myctophum* aff. *punctatus* Rafinesque; BREGMACEROTIDAE *Bregmaceros* sp.; MERLUCCIIDAE *Steindachneria* sp.; BATRACHOIDIDAE *Porichthhys* sp.; ATHERINIDAE *Membras* sp.; HEMIRHAMPHIDAE *Hyporhamphus* aff. *unifasciatus* (Ranzani); HOLOCENTRIDAE *Myripristis* sp.; CENTROPOMIDAE *Centropomus* aff. *undecimalis* (Bloch); OPISTHOGNATIDAE *Opisthognathus* sp.; APOGONIDAE *Apogon* sp.; LACTARIIDAE *Lactarius* aff. *atlanticus* Steurbaut and Jonet; CARANGIDAE *Trachurus* sp.; MENIDAE *Mene* sp.; LUTJANIDAE *Ocyurus* sp., *Pristipomoides* sp.; GERREIDAE *Diapterus* sp.; HAEMULIDAE *Haemulon* sp., *Haemulon* aff. *aurolineatus* Cuvier, *Orthopristis* aff. *ruber* Cuvier, *Orthopristis* sp, *Pomadasys* sp.; SCIAENIDAE *Aplodinotus longecaudatus* Nolf and Aguilera, *Aplodinotus hoffmani* Nolf and Aguilera, *Ctenosciaena* aff. *gracilicirrhus* (Metzelaar), *Equetus davidandrewi* Nolf and Aguilera, *Equetus* aff. *punctatus* (Bloch and Schneider), *Larimus henrii* Nolf and Aguilera, *Larimus steurbauti* Nolf and Aguilera, *Pachyurus jungi* Aguilera and Rodrigues de Aguilera, *Paralonchurus schwarzhansi* Aguilera and Rodrigues de Aguilera *Plagioscion marinus* Aguilera and Rodrigues de Aguilera, *Protosciaena neritica* Aguilera and Rodrigues de Aguilera, *Sciaena* sp., *Sciaenops reyezi* Aguilera and Rodrigues de Aguilera;	Geology: Díaz de Gamero 1974 Hunter and Bartok 1974 Jung 1965 Ministerio de Energía y Minas 1997 MacDonald 1968 Rey 1996 Rodríguez 1968 Thomas and MacDonald 1970 Paleontology: Aguilera and Rodrigues de Aguilera 2003, 2004a, b Nolf and Aguilera 1998.

TABLE 1. Continued.

Age	Formation/Member	Lithology	Marine vertebrate biota/Paleoenvironments	Reference
			MUGILIDAE *Mugil* aff. *cephalus* Linnaeus, *Peprilus* sp.; PARALICHTHYIDAE *Citharichthys* sp.; CYNOGLOSSIDAE *Symphurus* sp. The fish associations reflect a tropical, sublittoral environment.	
Middle Miocene	Socorro Formation, northwestern Venezuela,	Sandstone, clay stone, fossiliferous marl and limestone in the lower interval, and sandstone, turf and laminate clay stone without calcareous or fossiliferous horizon in the upper ones	LAMNIDAE *Carcharodon megalodon* (Agassiz); HEMIGALEIDAE *Hemipristis serra* Agassiz; CARCHARHINIDAE *Carcharhinus* sp., *Galeocerdo* sp., *Rhyzoprionodon* sp., *Negapriom eurybathrodon* (Blake); SPHYRNIDAE *Sphyrna* sp.; MYLIOBATIDAE *Aetobatus arcuatus* (Agassiz), *Mylobatis* sp., *Rhinoptera* sp. The fish associations reflect a tropical, sublittoral environment.	Geology: Gamero and Díaz de Gamero 1963 Ministerio de Energía y Minas 1997 Paleontology: Leriche, 1938 Present paper
Upper Miocene	Urumaco Formation, middle member, northwestern Venezuela	Clay stone, sand and calcareous rock	PODOCNEMIDIDAE *Bairdemys venezuelensis* Wood and Díaz de Gamero; LAMNIDAE *Carcharodon megalodon* (Agassiz); HEMIGALEIDAE *Hemipristis serra* Agassiz; CARCHARHINIDAE *Carcharhinus* sp., *Galeocerdo cuvier* (Peron and Lasueur), *Rhyzoprionodon* sp., *Negapriom eurybathrodon* (Blake); SPHYRNIDAE *Sphyrna* sp.; PRISTIDAE *Pristis* aff. *pectinata* Latham; DASYATIDAE *Dasyatis* sp.; MYLIOBATIDAE *Mylobatis* sp., *Rhinoptera* sp.; ARIIDAE *"Arius" couma Valenciennes, "Arius" dowii* (Gill), *"Arius" herzbergii* (Bloch), *"Arius" kessleri* Steindachner, *"Arius" quadriscutis* Valenciennes, *"Arius" rugispinis* Valenciennes, *Bagre marinus* (Mitchill), *Sciaedeops troschelli* Gill; SCIAENIDAE *Equetus* sp., *Larimus henrii* Nolf and Aguilera, *Larimus steurbautti* Nolf and Aguilera, *Larimus* sp., *Nebris* sp., *Ophioscion lundbergi* Aguilera and Rodrigues de Aguilera, *Cynoscion* sp., *Plagioscion urumacoensis* Aguilera and Rodrigues de Aguilera, *Micropogonias coatesi* Aguilera and Rodrigues de Aguilera; HAEMULIDAE *Haemulon* sp.; SERRANIDAE *Epinephelus itajara* (Lichtenstein). The fish associations reflect inner sublittoral and coastal lagoons environments with riverine and estuarine influence.	Geology: Ministerio de Energía y Minas 1997 Díaz de Gamero and Linares 1989 Díaz de Gamero 1996 Paleontology: Aguilera 2004 Aguilera and Rodrigues de Aguilera 2003, 2004a, b Wood and Díaz de Gamero 1971
Upper Miocene	Caujarao Formation, TaraTara Member, northwestern Venezuela	Microfossiliferous gray/blue clay and claystone	LAMNIDAE *Carcharodon megalodon* (Agassiz); HEMIGALEIDAE *Hemipristis serra* Agassiz; CARCHARHINIDAE *Carcharhinus* sp., *Galeocerdo* sp., *Rhyzoprionodon* sp., *Negapriom eurybathrodon* (Blake); SPHYRNIDAE *Sphyrna* sp.; MYLIOBATIDAE *Mylobatis* sp., *Rhinoptera* sp. The fish associations reflect a tropical, sublittoral environment.	Geology: Ministerio de Energía y Minas 1997 Petzall 1959 Vallenilla 1961 Paleontology: Present paper

Upper Miocene to Lower Pliocene	Cubagua Formation, Cerro Verde Member, northwestern Venezuela	Conglomerates with sandy matrix, which continues vertically into marine fossiliferous conglomeratic sandstones, bioclastic sandstones, and claystone	HEXANCHIDAE *Heptranchias perlo* (Bonnaterre), *Notorynchus* sp; HETERODONTIDAE *Heterodontus* sp.; ODONTASPIDIDAE *Eugomphodus* cf. *taurus* (Rafinesque), *Odontaspis ferox* (Risso); PSEUDOCARCHARIIDAE *Pseudocarcharias kamoharai* Matsubara; LAMNIDAE *Isurus xiphodon* (Agassiz); ALOPIIDAE *Alopias superciliosus* (Lowe); TRIAKIDAE *Mustelus* sp.; HEMIGALEIDAE *Hemiprisitis serra* Agassiz; CARCHARHINIDAE *Carcharhinus egertoni* (Agassiz), *Carcharhinus* sp, *Galeocerdo* aff. *cuvier* (Peron and Lesuer), *Galeocerdo* sp., *Negaprion eurybathrodon* (Blake), *Rhyzoprionodon* sp.; SPHYRNIDAE *Sphyrna* sp; DALATIIDAE *Etmopterus* sp., *Trigonognathus* aff. *kabeyai* Motchisuki and Ohe, *Dalatias* sp., *Isistius* aff. *triangulus* (Probst); CENTROPHORIDAE *Centrophorus* sp., *Deania* sp., SQUALIDAE *Squalus* sp., PRISTIOPHORIDAE *Pristiophorus* sp.; SQUATINIDAE *Squatina* aff. *dumerili* LeSeur; PRISTIDAE *Pristis* sp.; RHINOBATIDAE *Rhynchobatus* sp.; RAJIDAE *Raja* sp.; DASYATIDAE *Dasyatis* sp.; MYLIOBATIDAE *Aetobatus arcuatus* (Agassiz), *Myliobatis* sp., *Pteromylaeus* sp., *Rhinoptera* sp.; HETERENCHELYIDAE *Pythonichthys* sp.; MURAENIDAE *Gymnothorax* sp.; CONGRIDAE *Paraxenomystax* sp., *Hildebrandia gracilior* Ginsburg, *Ariosoma balearicum* (DeLaroche), *Ariosoma selenops* Reid, *Ariosoma* sp., *Paraconger* sp.; CLUPEIDAE *Harengula* sp., *Neopisthopterus* sp., *Opisthonema* sp.; ENGRAULIDAE *Anchoa* sp., *Cetengraulis* sp., *Engraulis* sp.; ARIIDAE *Arius* sp., *Genidens* sp.; ARGENTINIDAE *Argentina striata* Goode and Bean; STERNOPTYCHIDAE *Maurolicus* aff. *muelleri* (Gmelin), *Polyipnus* sp.; NOTOSUDIDAE *Scopelosaurus* sp.; SYNODONTIDAE *Saurida brasiliensis* Norman; NEOSCOPELIDAE *Neoscopelus* sp.; MYCTOPHIDAE *Diaphus dumerili* (Bleeker), *Diaphus splendidus* (Brauer), *Diaphus* sp. 1, *Diaphus* sp. 2, *Diaphus* sp. 3, *Electrona rissoi* (Cocco), *Hygophum hygomi* (Lutken), *Hygophum macrochir* (Gunther), *Hygophum* sp., *Lampadena jacksoni* Aguilera and Rodrigues de Aguilera, *Lampadena* sp., *Lampanyctus cupriarius* (Taaning), *Lampanyctus* aff. *latesulcatus* Nolf and Steurbaut, *Lampanyctus* sp., *Symbolophorus* sp.; BREGMACEROTIDAE *Bregmaceros* aff. *cantori* Miliken and Houde; MACROURIDAE *Coelorhinchus* aff. *coelorhinchus* Risso; MORIDAE *Gadella* sp., *Physicullus* sp.; MERLUCCIIDAE *Merluccius* sp., *Steindachneria argentea* Goode and Bean; OPHIDIIDAE *Ophidion* sp., *Otophidium* aff. *robinsi* Nolf and Stringer, *Otophidium* sp., *Lepophidium* sp., *Neobythites* sp.; CARAPIDAE *Echiodon* sp., *Snyderidia bothrops* Robins and Nelson; BATRACHOIDIDAE *Porichthys* sp., *Thalassophryne* sp.; ATHERINIDAE *Membras* sp.; MELAMPHAIDAE *Melamphaes polylepis* Ebeling; TRACHICHTHYIDAE *Hoplostethus mediterraneus* Cuvier; TRIGLIDAE *Prionotus* sp.; CENTROPOMIDAE *Centropomus* aff. *pectinatus*	Geology: Bermúdez 1966; Ministerio de Energía y Minas 1997; Kugler 1957; Sellier 1959; Paleontology: Aguilera and Rodrigues de Aguilera 2001

TABLE 1. Continued.

Age	Formation/Member	Lithology	Marine vertebrate biota/Paleoenvironments	Reference
			Poey; ACROPOMATIDAE *Parascombrops* sp.; OPISTOGNATHIDAE *Lonchopisthus* aff. *lemur* (Myers), *Lonchopisthus* sp., *Opistognathus* sp.; APOGONIDAE *Apogon* sp. 1, *Apogon* sp. 2; EPIGONIDAE *Epigonus denticulatus* Dieuzeide, *Epigonus* sp.; LACTARIIDAE *Lactarius* aff. *atlanticus* Steubaut and Jonet; CARANGIDAE *Decapterus* sp., *Trachurus* sp.; LUTJANIDAE *Lutjanus* sp., *Pristipomoides* aff. *aquilonaris* Goode and Bean, *Pristipomoides* sp.; GERREIDAE *Eucinostomus* sp., *Gerres* sp.; HAEMULIDAE *Haemulon* sp., *Haemulopsis* sp., *Orthopristis* aff. *ruber* Cuvier, *Pomadasys* aff. *panamensis* (Schneider), *Pomadasys* sp.; SCIAENIDAE *Aplodinotus* aff. *hoffmani* Nolf and Aguilera, *Bairdiella* sp., *Ctenosciaena* aff. *gracilicirrhus* (Metzelaar), *Cynoscion* sp., *Equetus* aff. *punctatus* (Bloch and Schneider), *Equetus* sp., *Larimus* aff. *fasciatus* Holbrook, *Ophioscion* sp., *Paralonchurus* sp., *Plagioscion* sp., *Protosciaena* aff. *trewavasae* (Chao and Miller), *Sciaena* aff. *bathytatos* Chao and Miller, *Sciaena* sp. 1, *Sciaena* sp. 2, cf. *Sciaena* sp., *Sciaenops* aff. *ocellatus* Linnaeus, *Umbrina* sp., Stelliferini; MUGILIDAE *Mugil* aff. *cephalus* Linnaeus; URANOSCOPIDAE *Kathetostoma* sp.; PERCOPHIDAE *Bembrops* sp.; GOBIIDAE Ind.; TRICHIURIDAE *Lepidopus caudatus* (Euphrasea); SCOMBRIDAE *Pneumatophorus* sp.; PARALICHTHYIDAE *Citharichthys* sp., *Syacium* sp.; BOTHIDAE *Bothus* sp.; CYNOGLOSSIDAE *Synphurus* sp. The fish associations reflect inner sublittorial environments influenced by coastal upwelling conditioned.	
Upper Miocene to Pliocene	Codore Formation, Chiguaje Member, northwestern Venezuela	Calcareous clay and slime, with consolidate coquinoids limestone. In the central section exists calcareous sandstone with fine to medium grain size, massif or cross stratigraphy, usually with bioturbate burrows	LAMNIDAE *Carcharodon megalodon* (Agassiz); HEMIGALEIDAE *Hemipristis serra* Agassiz; CARCHARHINIDAE *Carcharhinus* sp., *Galeocerdo* sp., *Rhyzoprionodon* sp., *Negapriom eurybathrodon* (Blake): SPHYRNIDAE *Sphyma* sp.; MYLIOBATIDAE *Mylobatis* sp., *Rhinoptera* sp. The fish associations reflect inner sublittoral environments.	Geology: Ministerio de Energía y Minas 1997 Rey 1994 Paleontology: Present paper
Lower Pilocene	Paraguaná Formation, Amuay Member, northwestern Venezuela	3 m thick compact algal limestone	LAMNIDAE *Carcharodon megalodon* (Agassiz); HEMIGALEIDAE *Hemipristis serra* Agassiz; CARCHARHINIDAE *Carcharhinus* sp., *Galeocerdo* sp., *Rhyzoprionodon* sp., *Negapriom eurybathrodon* (Blake); SPHYRNIDAE *Sphyrna* sp.; MYLIOBATIDAE *Mylobatis* sp., *Rhinoptera* sp. The fish associations reflect inner sublittoral environments.	Geology: Hunter and Bartok 1974 Ministerio de Energía y Minas 1997 MacDonald 1968 Rey 1996 Rodríguez 1968 Paleontology: Present paper

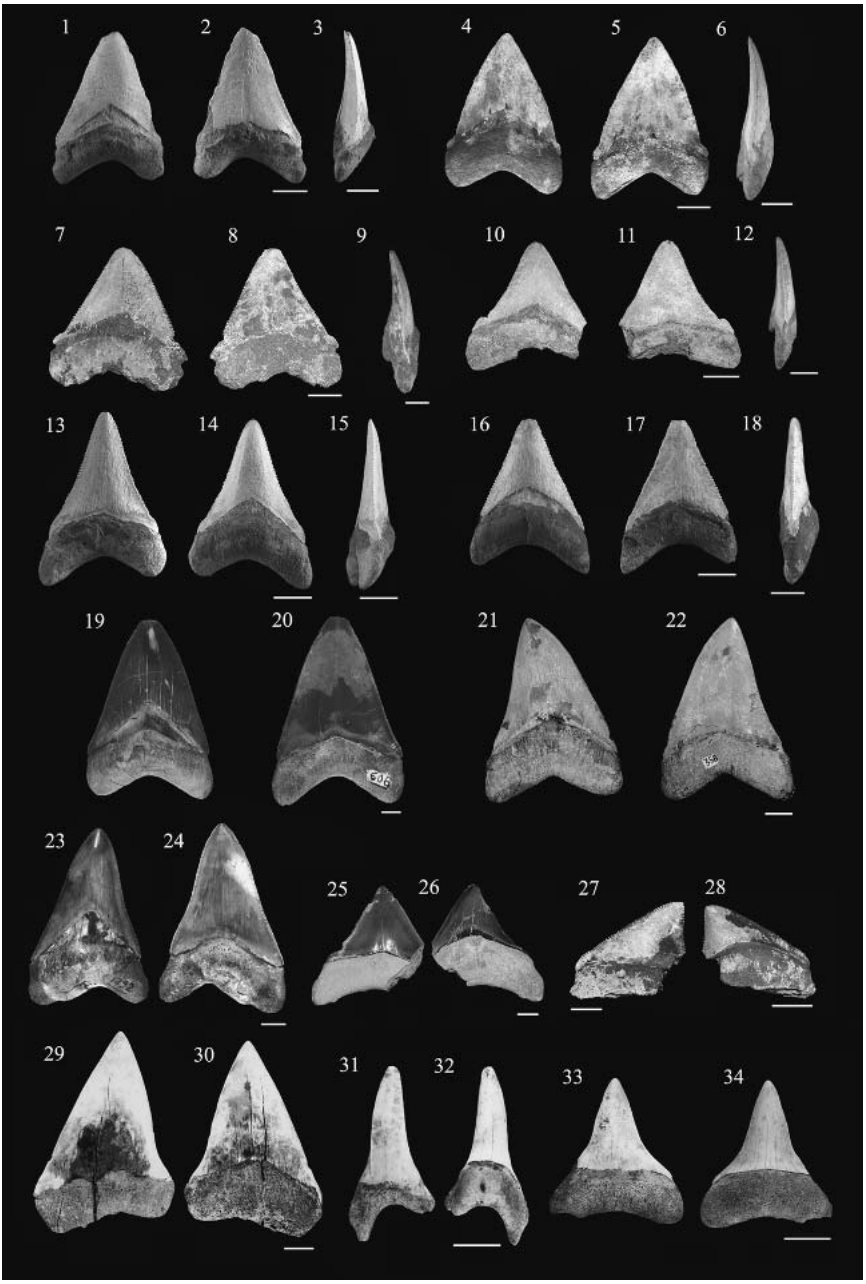

FIG. 2. Giant-toothed shark *Carcharodon subauriculatus* Agassiz, *1-18*, UNEFM-PF-0324, UNEFM-PF-00349/0340, from the Lower Pliocene Paraguaná Formation, Paraguaná Peninsula, Venezuela. Giant-toothed white shark *Carcharodon megalodon* (Agassiz), *19-20*, UNEFM-CIAAP-606 from the Upper Miocene Urumaco Formation, El Mamón, Urumaco, Venezuela; *21-22*, UNEFM-CIAAP-358 from the Upper Miocene Caujarao Formation (TaraTara Member), TaraTara, Venezuela; *23-24*, UNEFM-CIAAP-1292 from the Upper Miocene Urumaco Formation, El Mamón, Urumaco, Venezuela; *25-26*, UNEFM-PF-0322 from the Lower Miocene Cantaure Formation, Paraguaná Peninsula, Venezuela; *27-28*, UNEFM-PF-0321 from the Lower Pliocene Paraguaná Formation, Paraguaná Peninsula, Venezuela. Wide-toothed mako *Isurus xiphodon* (Agassiz), *29-34*, UNEFM-PF-015, UNEFM-PF-0297/0298, from the Upper Miocene to Lower Pliocene Cubagua Formation (Cerro Verde Member), Araya Peninsula, Venezuela. Scale bar equal to 1 cm.

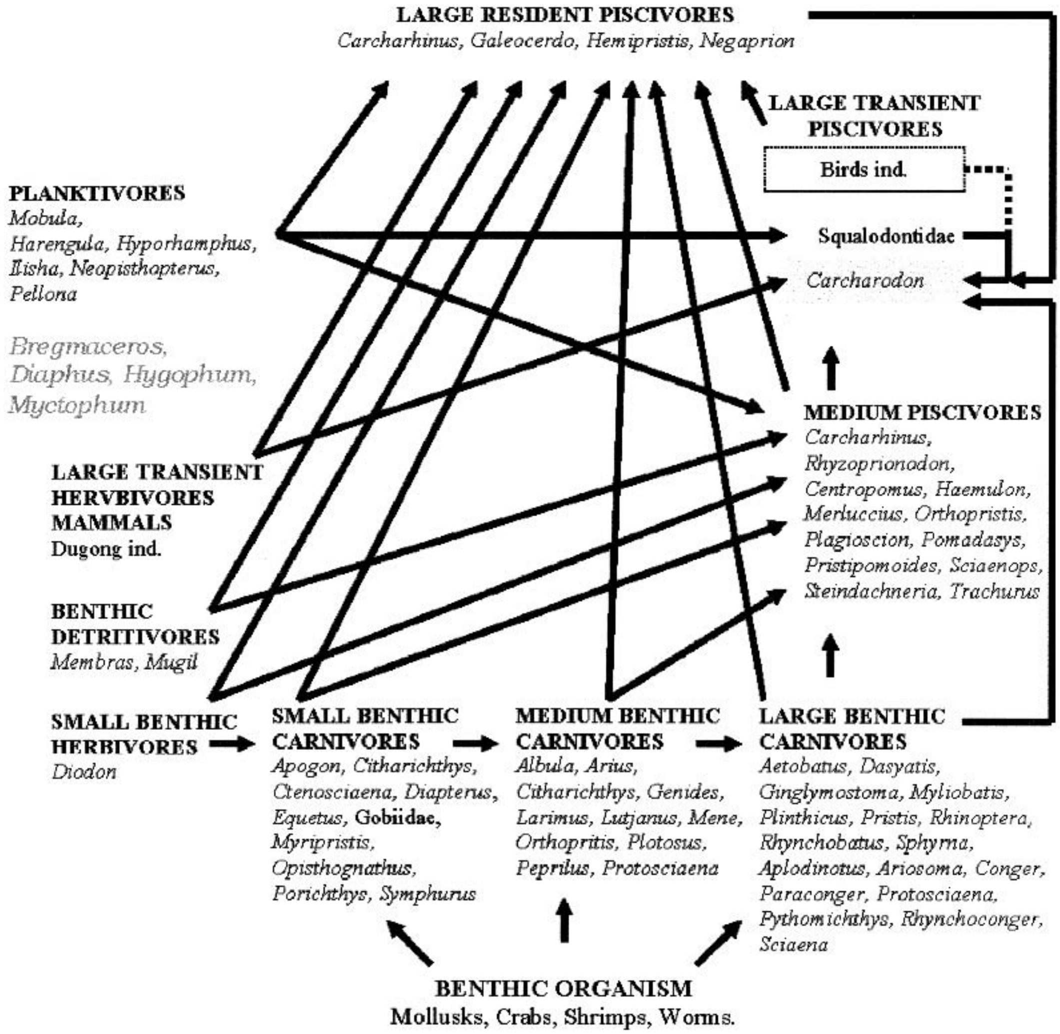

FIG. 3. Cantaure Formation fish assemblage. Genera name in black font is referred to marine shallow water occurrence, and genera name in gray font is referred to upwelling relationship.

mollusks (737 species, Jackson et al. 1999), crustaceans (13 species, Aguilera and Rodrigues de Aguilera unpubl. data), fish (72 species, Aguilera and Rodrigues de Aguilera 2001, 2003, 2004a, b, Nolf and Aguilera 1998), and marine mammals (3 species, Aguilera and Rodrigues de Aguilera unpubl. data). This biodiversity (Table 1) suggests rich assemblages associated to the coastal upwelling around the Paraguaná Peninsula of Venezuela, similar to the present process (Akl et al. 1997; Ginés 1982; Monente and Astor 1987). The benthic fauna, comprised by annelids, mollusks, and crustaceans, is consumed by benthic carnivores (small to large fish) that inhabit muddy to sandy bottoms, either in rocks or isolated corals. These fishes were also prey of medium to large piscivores. Among planktivores, there were shallow water fishes, and bathyal fishes which ascended to shallower depths at night. Both planktivores groups are eaten by large and medium piscivores, and also by large transient piscivores such as cetaceans. The Cantaure coastal upwelling deposits show a high abundance of otoliths of bathyal lantern fish (21.6% of the total fish remains in the

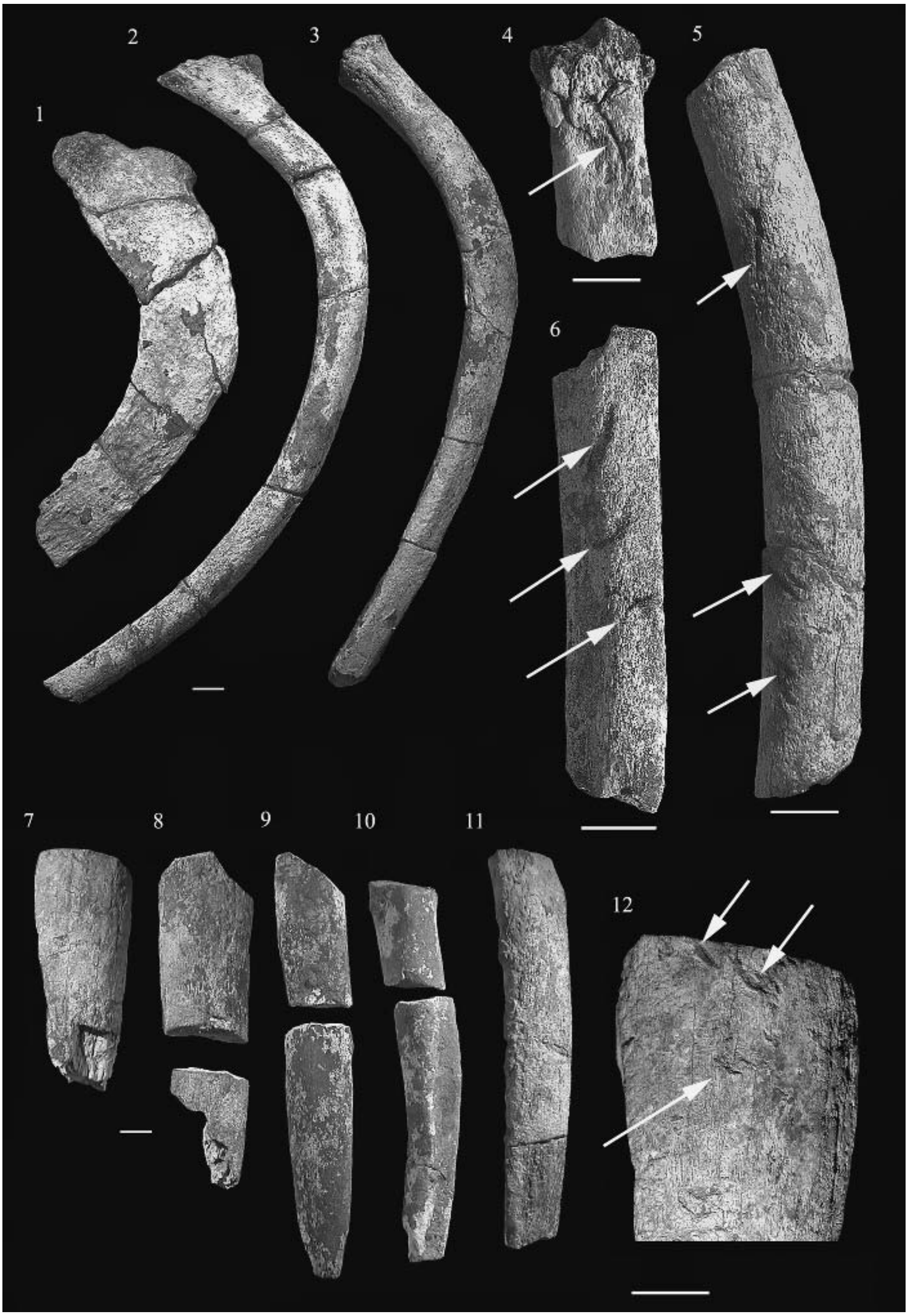

FIG. 4. Bitten marks in fossil mammals ribs from the Lower Miocene Cantaure Formation, northwestern Venezuela, *1-6*, cetacean ribs (squalodontids), *7-12*, sirenids ribs (dugongids). White arrows shows the bitten marks details. Scale bar equal to 1 cm.

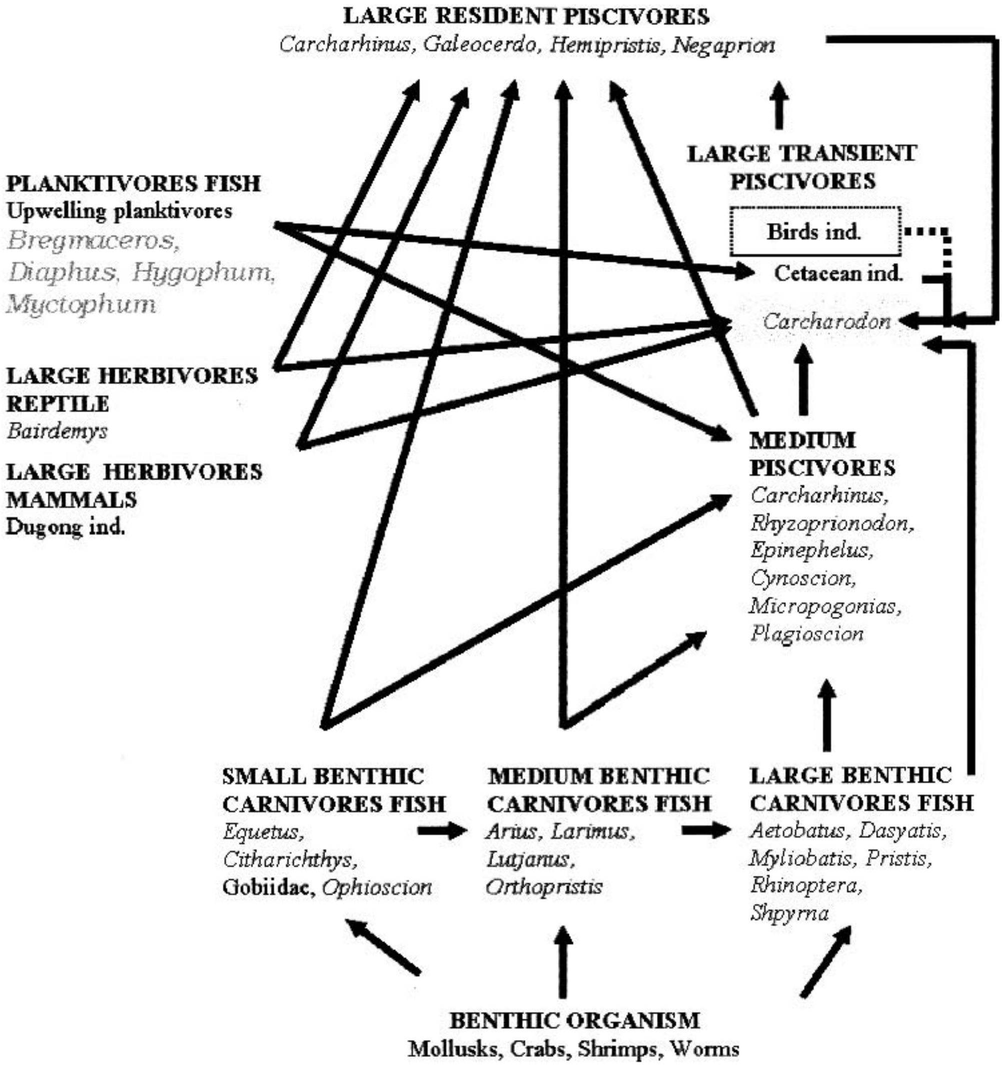

FIG. 5. Urumaco Formation fish assemblage.

sediments, Nolf and Aguilera 1998). Lantern fishes represent the main food of marine cetaceans (Fitch and Brownell 1968), which in turn were main food items to *C. megalodon* (Purdy 1996, Purdy et al. 2001). Preliminary research shows cetacean (squalodontids, Fig. 4.1-4.6) and sirenid (dugongids, Fig. 4.7-4.12) skeletal remains, with some of them exhibiting bite marks suggesting predator-prey relationships with sharks in the Cantaure Formation. Cigala-Fulgosi (1990) described similar bite marks on cetacean remains from the European Pliocene attributed to the great white shark, and Bianucci et al. (2000) described the trophic interaction between Pliocene and recent white shark and cetaceans from the central Mediterranea sea. Purdy (1996) also described bite marks on cetacean remains attributed to white sharks. Large transient piscivores, such as *C. megalodon*, accumulated high corporal biomass from rich food sources in tropical water subject to upwelling.

We can only speculate about the role of the large sharks in those ancient ecosystems. Although the topology of the Neogene food web in terms of trophic links among major taxa is different to that today, we cannot determine real changes in the food web due to extinction of large sharks. Despite the former high abundance of large predatory fishes (Jackson and Sala 2001), otoliths and teeth of large fishes are still less abundant in the fossil record than those of small fishes, because of obvious scale reasons. Today, almost 441 demersal fishes are distributed around the Paraguaná Peninsula in a no pristine assemblage (Aguilera 1998; Valdez and Aguilera 1987) and no direct assemblage relationship can be made based on the comparative low fossil diversity recorded in the Cantaure Formation. The role carried out from the large consumer sharks represents the higher trophic category, the type of selective pressure and the control performed in marine environment. The dynamics of these associations during Neogene is deeply different. Until taphonomic issues are resolved, our only look into the past organization of food webs is still limited to topology.

Swampy, coastal lagoon and sandy littoral environments (Fig. 5).—The Urumaco For-

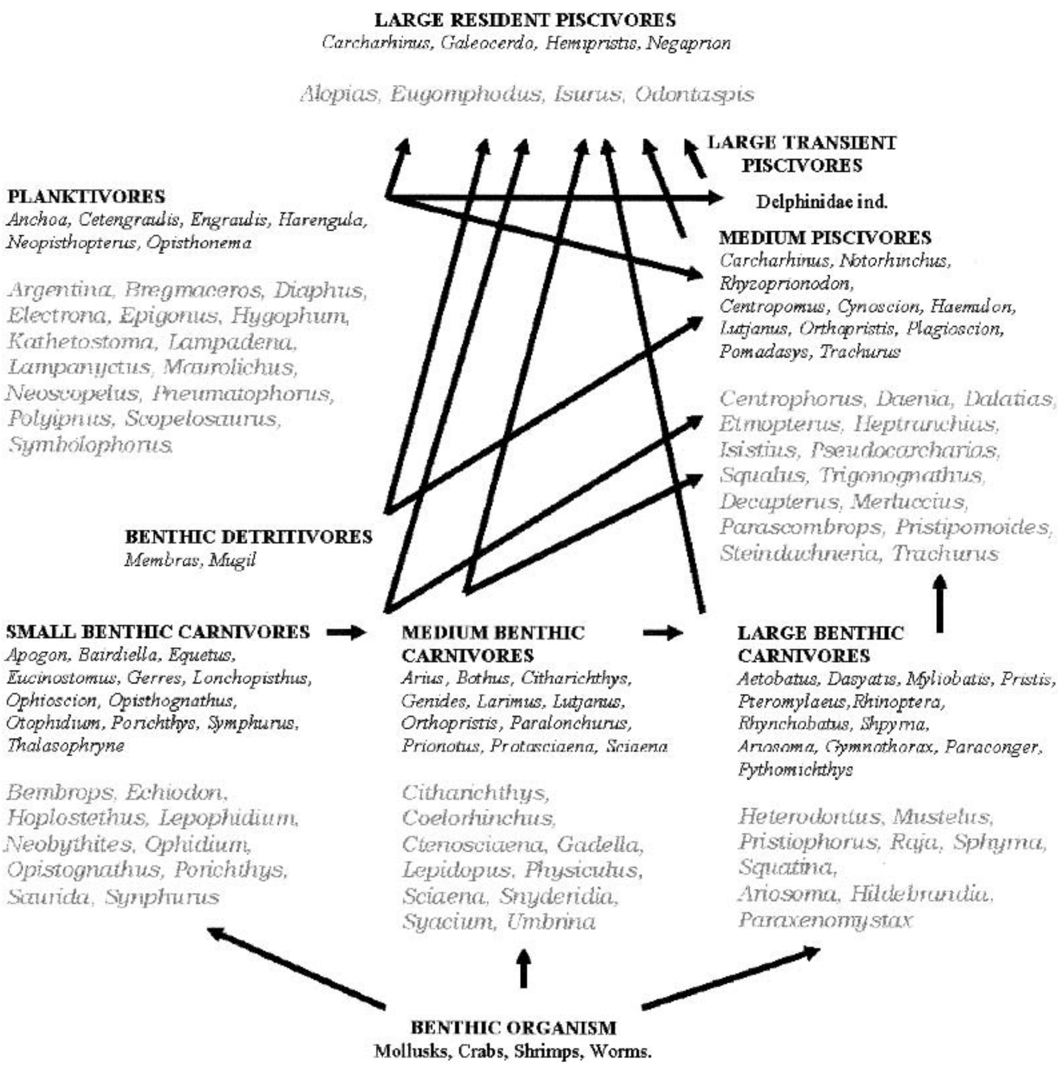

FIG. 6. Cubagua Formation fish assemblage. Genera name in black font refers to marine shallow water occurrence. Genera name in gray font refers to upwelling relationship.

mation is characterized by diverse faunal associations in coastal marine (coastal lagoon, salt marsh and sandy littoral), freshwater (swampy and rivers), estuarine (brackish), and continental (savannas) assemblages (Table 1). Each assemblage corresponds with the typical biostratigraphy facie. However, it is possible to observe shallow water marine sediments rich in mollusks and fishes (Aguilera, 2004; Aguilera and Rodrigues de Aguilera 2003, 2004a, b), swampy paleoenvironments rich in crocodilians and gavialids (Aguilera, 2004; Bocquentin-Villanueva 1984; Bocquentin-Villanueva and Buffetaut 1981; Bocquentin-Villanueva et al. 1989; Medina 1976; Sill 1970), marine and freshwater turtles (Aguilera, 2004; Gaffney and Wood 2002; Sánchez-Villagra et al. 1995; Wood 1976; Wood and Díaz de Gamero 1971; Wood and Patterson 1973), and freshwater catfish (Aguilera, 2004; Lundberg and Aguilera 2004; Lundberg et al. 1988), or brackish water rich in marine catfish (Aguilera, 2004; Aguilera and Rodrigues de Aguilera 2004a). These general sequences are repeated several times in the outcrop (see Ministerio de Energía y Minas 1997). Some marine living transient fishes such as the swan-fish *Pristis perotteti* Müller and Henle are found around Manaus in the Brazilian Amazon river about 1,340 km from the sea. Also, *Carcharhinus leucas* (Müller and Henle) is found in Puerto Leticia (Colombian Amazon) at 3,840 km from the sea, in Iquitos at 4,000 km, or Ucazali at 4,200 km from the sea (Cervigón and Alcalá 1999). The presence of the *C. megalodon* in these tropical paleoenvironments may reflects the capacity or tenacity to use very shallow-waters to obtain food, maybe following migrating prey such as turtles, which are more abundant from the Urumaco Formation.

Coastal upwelling (Fig. 6).—The Cubagua Formation (Upper Miocene to Lower Pliocene, eastern Venezuela), is characterized by a co-occurrence of deep-water fish assemblages (epipelagic, mesopelagic, and benthopelagic), and shallow water fish assemblages (neritic) (Table 1). The presence of the *I. xiphodon* as large piscivore residents probably is related to the presence of coastal upwelling, and is thus subject to seasonal oceanographic changes. Today, the Caribbean area around the Cubagua Formation in the Araya Peninsula, Cubagua and Margarita Islands (northeastern Venezuela) has a different fish assemblage but similar neritic and pelagic environments (Cervigón 1991, 1993, 1994, 1996, Cervigón and Alcalá 1999; Cervigón et al. 1993).

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Literature Cited

Aguilera, O. 1998. Los peces marinos del occidente de Venezuela. *Acta Biol. Venez.* 18:43-57.

Aguilera, O. 2004. *Tesoros paleontológicos de Venezuela: Urumaco, patrimonio natural de la Humanidad*. Caracas: Editorial Arte.

Aguilera, O., and D. Rodrigues de Aguilera. 1999. Bathymetric distribution of Miocene to Pleistocene Caribbean Teleostean fishes from the coast of Panama and Costa Rica. In *A Paleobiotic Survey of the Caribbean Faunas from the Neogene of the Isthmus of Panama*. ed. L. S. Collins and A. G. Coates, 251-269. *Bull. Am. Paleontol*. 357.

Aguilera, O., and D. Rodrigues de Aguilera. 2001. An Exceptional Upwelling Fish Assemblages in the Caribbean Neogene. In *Morphology and evolution of the late Cenozoic marine biota of tropical America*. ed. A. A. Budd and D. Miller, 732-742. J. Paleontol. 75.

Aguilera, O., and D. Rodrigues de Aguilera. 2003. Two new otolith-based sciaenid species of the genus *Plagioscion* from South American Neogene marine sediments. *J. Paleontol.* 77:937-942.

Aguilera, O., and D. Rodrigues de Aguilera. 2004 a. Amphi-American Neogene Sea catfishes (Siluriformes, Ariidae) from northern South America. In *Fossils from the Miocene Castillo Formation, Venezuela*. ed. M. R. Sánchez-Villagra and J. A. Clack, 29-48. Contrib. Neotrop. Palaeontol Spec. Pap. Palaeontol. 71.

Aguilera, O., and D. Rodrigues de Aguilera. 2004 b. New Miocene Otolith-based Sciaenidae species (Pisces, Perciformes) from Venezuela. In *Fossils from the Miocene Castillo Formation, Venezuela*. ed. M. R. Sánchez-Villagra and J. A. Clack, 49-59. Contrib. Neotrop. Palaeontol. Spec. Pap. Palaeontol. 71.

Akl, J., R., Varela and F. Muller-Kerger. 1997. *Influencia de la batimetría y línea de costa en algunas áreas de surgencia al sur del Mar Caribe, observaciones con el AVHRR*. Mem. VII Simp. Lat. Percepción Remota, Mérida, Venezuela, CD-ROM, Doc. OCE_004.

Bermúdez, P. J. 1966. Consideraciones sobre los sedimentos del Mioceno Medio al Reciente de las costas central y oriental de Venezuela. (Primera parte). *Bol. Geol.* 7:333-411.

Bianucci, G. et al. 2000. Trophic interaction between white shark, *Carcharodon carcharias,* and cetaceans: A comparison between Pliocene and Recent data from central Mediterranean Sea. ed. Vacchi, M., La Mesa G., Serena F., and B. Séret, 33-48. Proc. IV Europ. Elasm. Assoc. Meet., Italy.

Bocquentin-Villanueva, J. 1984. Un nuevo Nettosuchidae (Crocodylia, Eusuchia) proveniente de la Formación Urumaco (Mioceno Superior), Venezuela. *Ameghiniana* 21:3-8.

Bocquentin-Villanueva, J., and E. Buffetaut. 1981. *Hesperogavialis cruxenti* n. gen., n. sp., nouveau gavialide (Crocodylia, Eusuchia) du Miocene Superieur (Huayquerien) đUrumaco (Venezuela). *Géobios* 14: 415-419.

Bocquentin-Villanueva, J., J. Pereira de Souza, E. Buffetaut, and F. R. Negri. 1989. Nova intrepretação do gênero *Purussaurus* (Crocodylia, Alligatoridae). *An. XI Cong. Brasileiro Paleontol.* pp. 427-438.

Cassier, E. 1958. Contribution à l'étude des Poissons fossiles des Antilles. *Mém. Suiss. Paléontol.* 74, 95 pp., 3 pl.

Cervigón, F. 1991. *Los peces marinos de Venezuela. Vol. 1.* Venezuela: Fundación Científica Los Roques.

Cervigón, F. 1993. *Los peces marinos de Venezuela. Vol. 2.* Venezuela: Fundación Científica Los Roques.

Cervigón, F. 1994. *Los peces marinos de Venezuela. Vol. 3.* Venezuela: Fundación Científica Los Roques.

Cervigón, F.1996. *Los peces marinos de Venezuela. Vol. 4.* Venezuela: Fundación Científica Los Roques.

Cervigón, F., and A. Alcalá. 1999. *Los peces marinos de Venezuela. Vol. 5.* Venezuela: Fundación Museo del Mar.

Cervigón, F., R. et al. 1993. Field guide to the commercial marine and brackish-water resources of the northern coast of South America. *FAO Fish. Synops.* 513 pp., 40 pl.

Cigala-Fulgosi, F. 1990. Predation (or possible scavenging) by a great white shark on an extinct species of bottlenose dolphin in the Italian Pliocene. *Tertiary Res.* 12:17-36.

Díaz de Gamero, M. L. 1974. Microfauna y edad de la Formación Cantaure, Península de Paraguaná, Venezuela. *Bol. Inf. Asoc. Venez. Geol. Mineral. Petról.* 17:41-47.

Díaz de Gamero, M. L. 1996. The changing course of the Orinoco River during the Neogene: a review. *Palaeontol.* 123:385-402.

Díaz de Gamero, M. L., and O. J. Linares. 1989. Estratigrafia y paleontología de la Formación Urumaco, del Mioceno Tardío de Falcón noroccidental. *Séptimo Congr. Geol. Venez. Mem.* 1:419-438.

Donovan, S. K., and G. C. Gunter. 2001. Fossil sharks from Jamaica. *Bull. Mizunami Fossil Mus.* 28:211-215.

Flemming, D., and D. A. MacFarlane. 1998. New Caribbean locality for the extinct great white shark *Carcharodon megalodon*. *Caribb. J. Sci.* 34:317-318.

Fitch, J. E., and R. L. Brownell. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Broad Canada* 25:2561-2574.

Gaffney, E. S., and R. Wood. 2002. *Bairdemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of the Caribbean. *Am. Mus. Novit.* 3359:1-28.

Gamero, G. A., and M. L. Díaz de Gamero. 1963. Estudio de una sección de referencia de las formaciones Cerro Pelado y Socorro en la región de El Saladillo, Estado Falcón, Venezuela. *GEOS* 9:7-44.

Gillette, D. D. 1984. A marine ichthyofauna from the Miocene of Panama, the Tertiary faunal province. *J. Verteb. Paleontol.* 4:172-186.

Gines, Hno. 1982. *Carta Pesquera de Venezuela, 2.—áreas Central y Occidental*. Fundación la Salle de Ciencias Naturales 27. 227 pp.

Hunter, V. F., and P. Bartok, 1974. The age and correlation of the Tertiry sediments of the Paraguaná Península, Venezuela. *Bol. Inf. Asoc. Venez. Geol., Min. Petról.* 17:143-154.

Iturralde-Vinent, M., G. Hubbell, and R., Rojas. 1996. Catalogue of Cuban fossil Elasmobranchii (Paleocene to Pliocene) and paleogeographic implications of their lower to middle Miocene occurrence. *J. Geol. Soc. Jamaica* 31:7-21.

Jackson, J. B. C., and E. Sala. 2001. Unnatural Oceans. *Scientia Marina* 65(2):273-281.

Jackson, J. B. C., J. A. Todd, H. Fortunato, and P. Jung. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. In *A Paleobiotic Survey of the Caribbean Faunas from the Neogene of the Isthmus of Panama.* ed. L. S. Collins and A.G. Coates, 193-230. Bull. Am. Paleontol. 357.

Jung, P. 1965. Miocene Mollusca from the Paraguaná Peninsula, Venezuela. *Bull. Am. Paleontol.* 49:389-652.

Kruckow, T., and D. Thies. 1990. Die Neoselachier der Paleokaribik (Pisces: Elasmobranchii). *Cour. Forsch.-Inst. Senckemberg* 119:1-102.

Kugler, H. G. 1957. Contribution to the geology of the islands Margarita and Cubagua, Venezuela. *Geol. Soc. Amer. Bull.* 68:555-566.

Laurito, C. A. 1999. *Los seláceos fósiles de la localidad de Alto Guayacán (y otros ictiolitos asociados), Mioceno Superior-Plioceno Inferior de la Formación Uscari, Provincia de Limón, Costa Rica*. Costa Rica: Editora San José.

Leriche, M. 1938. Contribution á L'étude des poisson fossiles des pays riverains de la Méditerranée Americaine (Venezuela, Trinité, Antilles, Mexique). *Mém. Soc. Paleontol. Suisse* 61. 42 pp.

Ministerio de Energía y Minas, 1997. Léxico Estratigráfico de Venezuela (Tercera Edición). *Bol. Geo.* 12, 828 pp.

Lundberg, J. G., and O. Aguilera. 2003. The late Miocene *Phractocephalus* catfish (Siluriformes: Pimelodidae,) from Urumaco, Venezuela: Additional specimens and reinterpretation as a distinct species. *Neotrop. Ichthyol.* 1:97-109.

Lundberg, J. G., O. J. Linares, M. E. Antonio, and P. Nass. 1988. *Phractocephalus hemiliopterus* (Pimelodidae, Siluriformes) from the Upper Miocene Urumaco Formation, Venezuela: A further case of evolutionary stasis and local extinction among South American fishes. *J. Verteb. Paleontol.* 8:131-138.

MacDonald, W. D. 1968. Estratigrafía, estructura y metamorfismo de las rocas del Jurásico Superior, Península de Paraguaná, Venezuela. *Bol. Geol.* 9: 441-457.

Medina, C. J. 1976. Crocodilians from the late Tertiary of Northwestern Venezuela: *Melanosuchus fisheri* sp. nov., *Breviora* 438:1-14.

Monente, J., and Y. Astor. 1987. Observaciones hidrográficas superficiales en la región noroccidental del Mar Caribe venezolano. *Mem. Soc. Cienc. Nat. La Salle* 47:125-148.

Nieves-Rivera, Á. M., M. Ruiz-Yantín, and Michael D. Gottfried. 2003. New record of the Lamnid shark *Carcharodon megalodon* from the Middle Miocene of Puerto Rico. *Caribb. J. Sci.* 39:223-227.

Nolf, D., and O. Aguilera. 1998. Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela). *Bull. Inst. Royal Sc. Nat. Belgique, Sciences de la Terre* 68: 237-262.

Petzall, C. K. 1959. Estudio de una sección de la Formación Caujarao en el anticlinal de La Vela, Estado Falcón. *Asoc. Venez. Geol. Min. y Petról.* 10:269-320.

Purdy, R. W. 1996. Paleoecology of Fossil White Shark. In *Great White Sharks: The biology of Carcharodon carcharias*. ed. A. P. Kinklei and D. G. Ainley, 67-78. USA: Academy Press.

Purdy, R. W. 1998. The early Miocene fish fauna from the Pollack Farm Site, Delaware. In *Geology and paleontology of the lower Miocene Pollack Farm Fossil Site, Delaware.* ed. R. N. Benson, 133-139. Delaware Geol. Surv. Spec. Publ. 21.

Purdy, R. W., et al. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In *Geology and Paleontology of the Lee Creek Mine, North Carolina, III*. ed. C. Ray and D. Bohaska, 71-202. Smithson. Contrib. *Paleobiol.* 90.

Rey, O. 1994. Miembro Chiguaje: Formación La Vela, o Formación Codore. *Bol. Soc. Venez. Geol.* 19:50-53.

Rey, O. 1996. Estratigrafía de la Península de Paraguaná, Venezuela. Revista de la Facultad de Ingeniería, Universidad Central de Venezuela, 11:35-45.

Rodríguez, S. E. 1968. Estratigrafía y Paleontología del Mioceno en la Península de Paraguaná, Estado Falcón. *Asoc. Venez. Geol. Min. y Petról.* 11:127-152.

Sánchez-Villagra, M. R., O. J. Linares, and A. Paolillo. 1995. Consideraciones sobre la sistemática de las tortugas del género *Chelus* (Pleurodira: Chelidae) y nuevas evidencias fósiles del Mioceno de Colombia y Venezuela. *Ameghiniana* 32:159-167.

Sánchez-Villagra, M. R., O. Aguilera, and I. Horovitz. 2003. The anatomy of the world's largest extinct rodent. *Science* 301:1678-1679.

Sellier de Civrieux, J. M. 1959. Apuntes bioestratigráficos sobre una nueva sección del Mioceno en la Isla de Margarita. *Bol. Geol.* 5:81-91.

Sill, W. D. 1970. Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusión de los gaviales sudamericanos. *Ameghiniana* 7:151-159.

Thomas, D., and W. MacDonald. 1970. The Cantaure Formation of the Paraguaná Península. *Asoc. Venez. Geol. Min. y Petról.* 13:177-179.

Valdez. J., and O. Aguilera. 1987. *Los Peces del Golfo de Venezuela*. Fondo Editorial CONICIT, Caracas. 215 pp.

Vallenilla, L. P. 1961. Estratigrafía de las formaciones Caujarao, La Vela y Coro en sus localidades tipo, Estado Falcón. *Asoc. Venez. Geol. Min. y Petrol.* 4: 29-78.

Wood, R. C. 1976. *Stupendemys geographicus*, the world's largest turtle. *Breviora* 436:1-31.

Wood, R. C., and M. L. Díaz de Gamero. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleudira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America. *Breviora* 376:1-23.

Wood, R. C., and B. Patterson. 1973. A fossil Trionychid turtles from South America. *Breviora* 405:1-10.