AN EXCEPTIONAL COASTAL UPWELLING FISH ASSEMBLAGE IN THE CARIBBEAN NEOGENE*

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ABSTRACT—We report the discovery of an extremely rich, previously undescribed Caribbean late Miocene to early Pliocene ichthyofauna represented by one hundred forty species of elasmobranchs and teleosteans from the Cubagua Formation, northeastern Venezuela. The fauna exhibits significant ecological differences compared with common neritic Caribbean Neogene assemblages. The bathymetric distributions of taxa, based on living counterparts, ranges from 0 to 100 m depth. The exceptional co-occurrence of deep water (epipelagic, mesopelagic and benthopelagic), and shallow water (neritic) taxa is best interpreted as the consequence of ocean upwelling in the proximity to the deep-water Cariaco Trench. Patterns of predator and prey are established and corroborate upwelling. Special remarks are made regarding previously unknown late Miocene to early Pliocene Caribbean ichthyofaunas, the absence or rarity of reported fossil taxa in the Recent Caribbean fauna, and a paleo- upwelling indicator (*Lampadena jacksoni* new species).

INTRODUCTION

IN TROPICAL Middle America, the closure of the Isthmus of Panama (Coates, 1999; Coates et al., 1992; Coates and Obando, 1996) resulted in major geographic and environmental changes. Principal freshwater drainage systems into the south Caribbean changed course, including the Magdalena River (Kay et al., 1997), the Orinoco River (Diaz de Gamero, 1996), and the Amazon-Orinoco systems (Lundberg et al., 1998). This resulted in progressive oceanographic and environmental changes in the Caribbean during the Tertiary. The paleoecology, diversity, and composition of Caribbean Neogene fish faunal assemblages reveal the prevalence of neritic environments in many sedimentary basins, including Panama (Gillette, 1984), Panama and Costa Rica (Aguilera and Aguilera, 1999; Collins et al., 1999), Trinidad (Nolf, 1976), northwestern Venezuela (Nolf and Aguilera, 1998), the Dominican Republic (Nolf and Stringer, 1992), Jamaica (Stringer, 1998), and Cuba (Iturralde-Vinent et al., 1996).

The ichthyofaunas of the Cubagua Formation, treated herein, are ecologically very different from those previously documented Caribbean Neogene fish assemblages. The Cubagua fauna is a spectacular coastal upwelling faunal association that existed during the late Miocene to early Pliocene in northeastern Venezuela. The association is characterized by the high abundance of mesopelagic, epipelagic, and benthopelagic elasmobranchs (sharks and rays), teleosteans (bony fish), and the exceptional co-occurrence with shallow water elasmobranch and teleostean species. In terms of species composition and abundance, the teleostean fossil fauna is dominated by the most diverse groups of oceanic midwater fish, such as the myctophids (lantern fish). The elasmobranch fauna is dominated by the squaliformes (spiny dogfish) that, as a group, have the broadest bathymetric and geographical distribution of all sharks. For comparative purposes, we use the fauna of the early Miocene Cantaure Formation of northwestern Venezuela to represent a typical neritic environment. The Cantaure fauna is the best known Caribbean neritic fish assemblage (Nolf and Aguilera, 1998) and starkly contrasts the Cubagna fauna. It is dominated by shallow water sciaenids (croakers) and carcharhinid sharks (Fig. 1).

Today, the ecological environments in coastal northeastern Venezuela are controlled by the interplay among topographic setting, oceanographic conditions, and seasonal variation in the flux of nutrients from the Orinoco outflow, and variability of wind forces. Together, these conditions produce the exceptional upwelling phenomenon in the Caribbean Sea (Akl et al., 1997; Febres-Ortega and Herrera, 1975; Ginés, 1972; Herrera and Febres-Ortega, 1976; Okuda, 1974; Varela et al., 1997), which may have been present under similar circumstances during the late Miocene to early Pliocene.
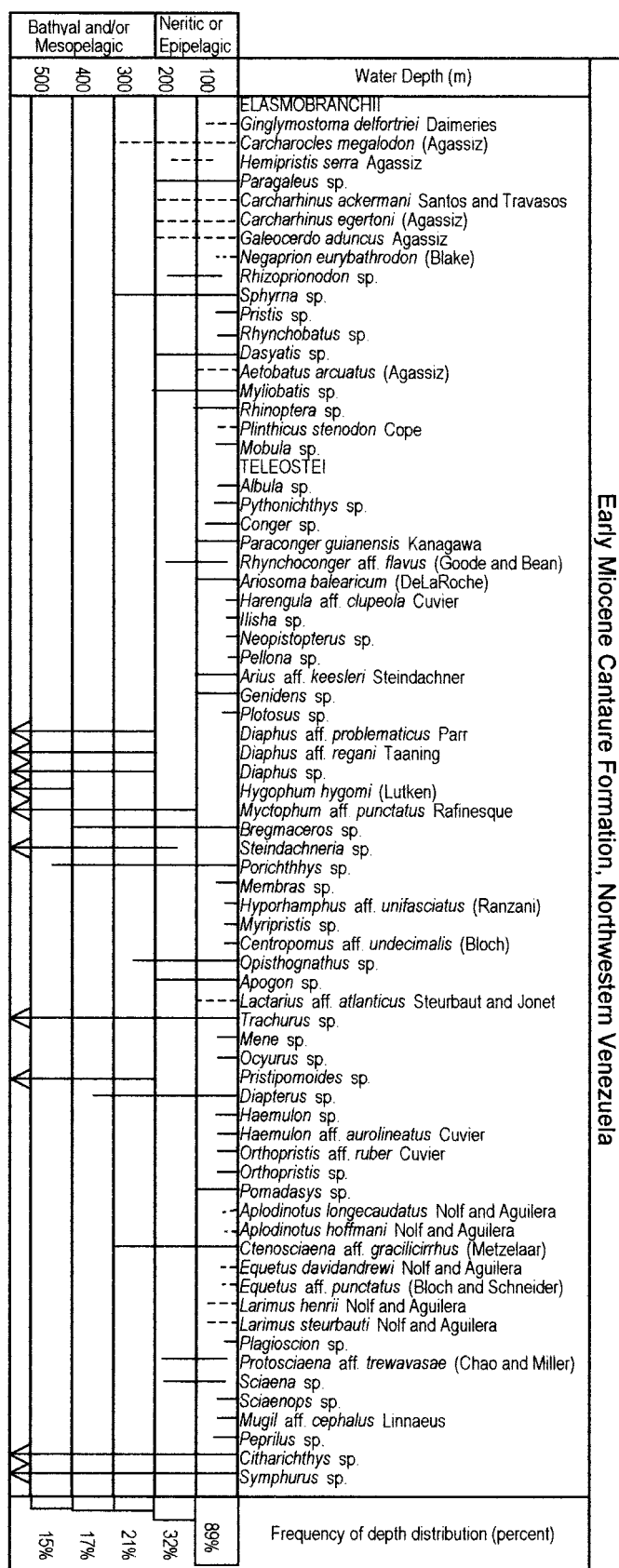
PHYSICAL AND GEOLOGICAL SETTING, STRATIGRAPHY AND COLLECTIONS

The geologic unit treated in the present study is the late Miocene to early Pliocene Cubagua Formation exposed along the Araya Peninsula, Cubagua Island, Margarita Island and the northern Paria Peninsula (northeastern Venezuela) (Fig. 2). This northern continental shelf of Venezuela represents the southeastern margin of the Caribbean Sea and forms the southern prolongation of the Lesser Antillian Arch (Sellier, 1974), which is clearly influenced by the waters of the Atlantic Ocean (Okuda, 1974; Febres-Ortega and Herrera, 1976). The coast is topographically complex and forms the Cariaco Gulf, between the Araya Peninsula and the continental coast. The Cubagua and Coche islands are located on the continental platform to the north of the Araya Peninsula, separated by a body of water of approximately 42 m depth. Margarita Island is located just to the north of both islands and is separated from them by the Margarita Channel, which has a depth of approximately 30 m.

The Araya saddle (depth 300 to 450 m) and the Cubagua saddle (depth 150 to 260 m) represent the submarine western prolongation of the Araya Peninsula and the Cubagua Bank, and help form the submarine valley located between the Araya Peninsula, Cubagua Bank, and Margarita Island. This submarine valley has the same orientation as the Cariaco Trench, which is a depressed tectonic zone in the continental platform of northern Venezuela, between the Unare Platform and the Tortuga Bank. It consists of two small sub-basins, each reaching depths of about 1,400 m, which are separated by a central saddle that shoals to a depth of about 900 m. A distinctive characteristic of this trench is a zone of anoxia below 330 m depth, a product of restricted water circulation (Febres-Ortega and Herrera, 1975; Herrera and Febres-Ortega, 1976).

According to the Léxico Estratigráfico de Venezuela (1997), the holostratotype section of the late Miocene to early Pliocene Cubagua Formation is located in the Cañón de La Caldera (Cubagua Island) and is 70 m thick. The hypostratotype section is located in the borehole of well Rio Caribe-1, the top of which is

Water Depth (m) — Bathyal and/or Mesopelagic (500, 400, 300) / Neritic or Epipelagic (200, 100)

ELASMOBRANCHII
- *Ginglymostoma delfortriei* Daimeries
- *Carcharocles megalodon* (Agassiz)
- *Hemipristis serra* Agassiz
- *Paragaleus* sp.
- *Carcharhinus ackermani* Santos and Travasos
- *Carcharhinus egertoni* (Agassiz)
- *Galeocerdo aduncus* Agassiz
- *Negaprion eurybathrodon* (Blake)
- *Rhizoprionodon* sp.
- *Sphyrna* sp.
- *Pristis* sp.
- *Rhynchobatus* sp.
- *Dasyatis* sp.
- *Aetobatus arcuatus* (Agassiz)
- *Myliobatis* sp.
- *Rhinoptera* sp.
- *Plinthicus stenodon* Cope
- *Mobula* sp.

TELEOSTEI
- *Albula* sp.
- *Pythonichthys* sp.
- *Conger* sp.
- *Paraconger guianensis* Kanagawa
- *Rhynchoconger* aff. *flavus* (Goode and Bean)
- *Ariosoma balearicum* (DeLaRoche)
- *Harengula* aff. *clupeola* Cuvier
- *Ilisha* sp.
- *Neopistopterus* sp.
- *Pellona* sp.
- *Arius* aff. *keesleri* Steindachner
- *Genidens* sp.
- *Plotosus* sp.
- *Diaphus* aff. *problematicus* Parr
- *Diaphus* aff. *regani* Taaning
- *Diaphus* sp.
- *Hygophum hygomi* (Lutken)
- *Myctophum* aff. *punctatus* Rafinesque
- *Bregmaceros* sp.
- *Steindachneria* sp.
- *Porichthhys* sp.
- *Membras* sp.
- *Hyporhamphus* aff. *unifasciatus* (Ranzani)
- *Myripristis* sp.
- *Centropomus* aff. *undecimalis* (Bloch)
- *Opisthognathus* sp.
- *Apogon* sp.
- *Lactarius* aff. *atlanticus* Steurbaut and Jonet
- *Trachurus* sp.
- *Mene* sp.
- *Ocyurus* sp.
- *Pristipomoides* sp.
- *Diapterus* sp.
- *Haemulon* sp.
- *Haemulon* aff. *aurolineatus* Cuvier
- *Orthopristis* aff. *ruber* Cuvier
- *Orthopristis* sp.
- *Pomadasys* sp.
- *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
- *Plagioscion* sp.
- *Protosciaena* aff. *trewavasae* (Chao and Miller)
- *Sciaena* sp.
- *Sciaenops* sp.
- *Mugil* aff. *cephalus* Linnaeus
- *Peprilus* sp.
- *Citharichthys* sp.
- *Symphurus* sp.

(Right vertical label: Early Miocene Cantaure Formation, Northwestern Venezuela)

Frequency of depth distribution (percent): 15% | 17% | 21% | 32% | 89%

FIGURE 1—Present-day bathymetric ranges of taxa represented in the early Miocene Cantaure Formation (northwestern Venezuela). Teleostean records following Nolf and Aguilera (1998), that for elasmobranchs are original data. Interrupted lines indicate extinct species.

located at 649 m of depth sediment below sea level, with the bottom at 2,708 m of depth. The Cubagua Formation sits conformably upon the Tres Puntas Formation and extends conformably up into the overlying Cumaná Formation.

The lower Cubagua Formation consists of gray shale with glauconite, abundant pyrite nodules, gray limonite, and some sandy intercalation with fine clastics probably carried out by turbidity currents. Occasionally clastic metamorphic and volcanic components are present. The upper Cubagua Formation consists of bioclastic banks of reef, mollusk and bryozoans, quartz sandstone, calcareous sandstone, bioclastic limestone, with interstratified olive gray shale, laminar glauconitic clay and gray limonite. The sediments of the lower part appear to have been deposited in deep water, and the upper part in shallow tropical water.

The Cubagua Formation is divided into four formal members: the Cerro Verde Member, exposed on the Cubagua Island and westernmost Araya Peninsula; the Cerro Negro Member, exposed along the Western Araya Peninsula and Cubagua Island; and the La Tejita and Las Hernandez members, exposed on Margarita Island.

The oldest of these, the Cerro Verde Member (late Miocene to early Pliocene), consists of conglomerate with sandy matrix, that continues vertically into fossiliferous conglomerate sandstone, bioclastic sandstone, and shale. This member has a thickness of 45 m at the type section. The Cerro Verde Member rests unconformably upon the metamorphic rocks of the Late Jurassic to Early Cretaceous Manicuare Formation. It passes transitionally up into the overlying Pliocene Cerro Negro Member.

The Cerro Negro Member (Pliocene) consists of a 2 m thick basal sandy marl, which is highly fossiliferous with *Ostrea haitensis* and *O. crassissima,* followed by thin intercalations of sandy lime, fossiliferous marl, and limestone marl. The total thickness of the member is 22 m at the type locality. The Cerro Negro Member sits conformably and transitionally on the Cerro Verde Member. It appears to continue conformably up into the overlying Pleistocene to Quaternary Barrigón Formation.

The La Tejita Member (late Miocene to early Pliocene) consists of a 45 m thick basal conglomerate with quartz pebbles, schist and igneous rocks, followed by gypsum clay, calcareous argillaceous sandy and fossiliferous marl, which is highly fossiliferous with *O. crassissima.* The La Tejita Member rests unconformably upon metamorphic rocks and the Eocene Punta Carnero Group. It passes unconformably up into the overlying Pliocene Manguillo Formation.

The Las Hernandez Member (Early Pliocene) consists of unconsolidated marl, clay, and lime. The thickness of this member is unknown and is overlain by alluvium.

The sample area (Fig. 2) includes the following localities in the Araya Peninsula: northwest of Cerro Barrigón, south of Cerro El Macho, north of Cerro La Cruz, north of Cerro Cangrejero, southwestern of Castillo de Araya, ENSAL Pyramid, south of Araya Salina. The localities on the Cubagua Island are Cañón de La Caldera and Cañón de Charagato, both in the northern part of the island. The locality on Margarita Island was the Santiago Mariño International Airport, close to Laguna de Las Marites.

The late Miocene to early Pliocene Cubagua Formation age is based on local geological and stratigraphic relations (Bermudez, 1966; Gonzalez de Juana et al., 1980; Léxico Estratigráfico de Venezuela, 1997; Sellier, 1959; Vignali, 1965). A preliminary biostratigraphic age of 4.2 Ma (early Pliocene) is used throughout this paper and is based on the median value of the age ranges of planktonic foraminifera obtained from all sampled areas (L. S. Collins, personal commun., 1998) except from the Margarita Island locality: La Tejita and Las Hernandez members. The taxa examined include *Dentgloboquadrina altispira* (Cushman and Jarvis), last appearance datum (LAD = 2.5 Ma), *Globigerinoides*
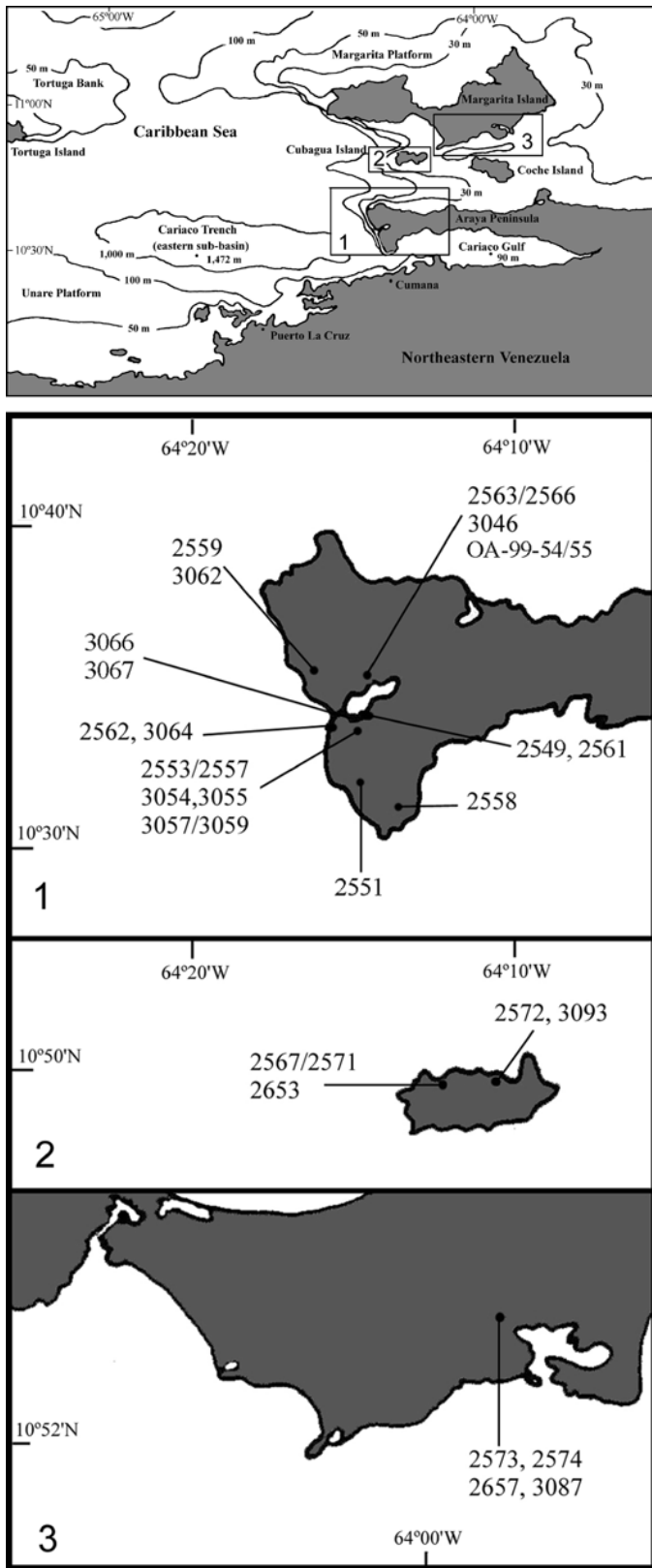
FIGURE 2—Location of the sampling sites in northeastern Venezuela. IN-SETS OF FIGURE 2.— Detailed map showing the sampling locations.
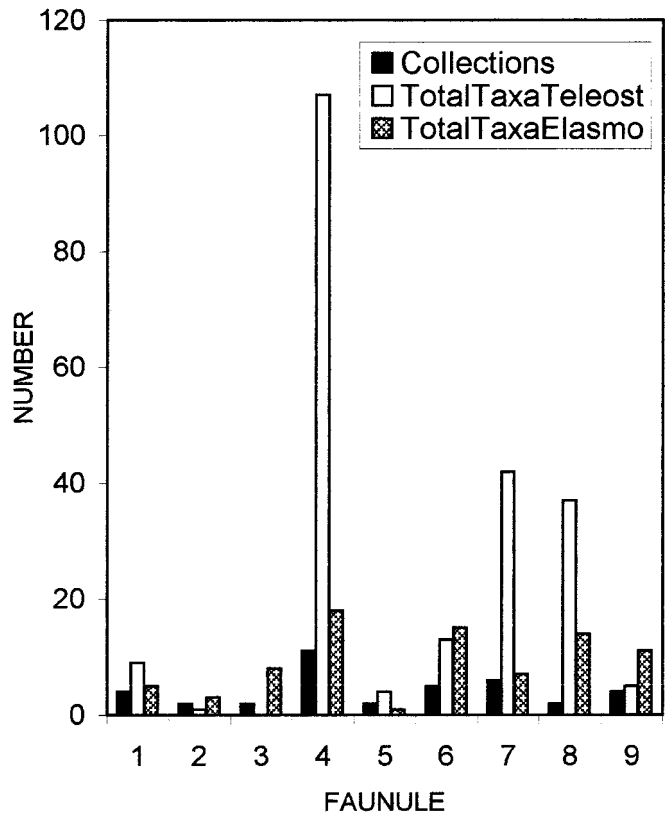

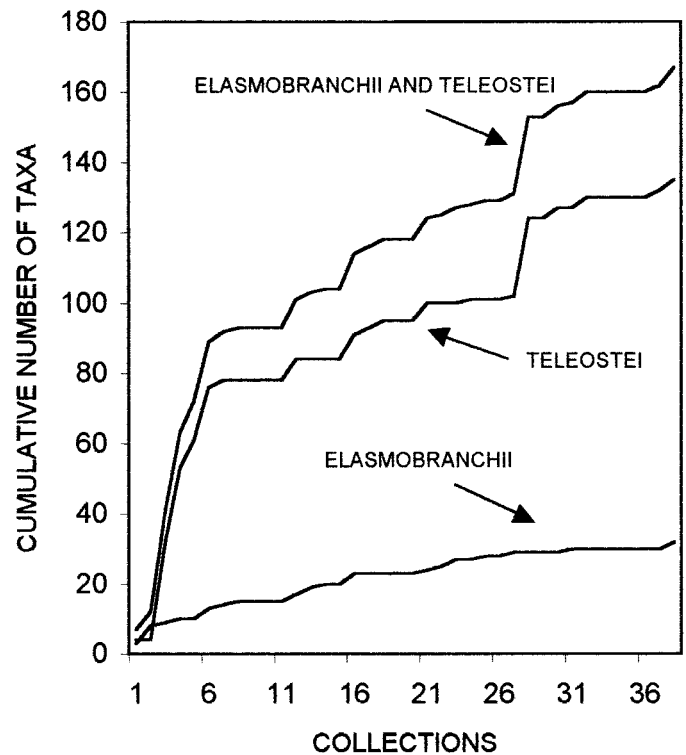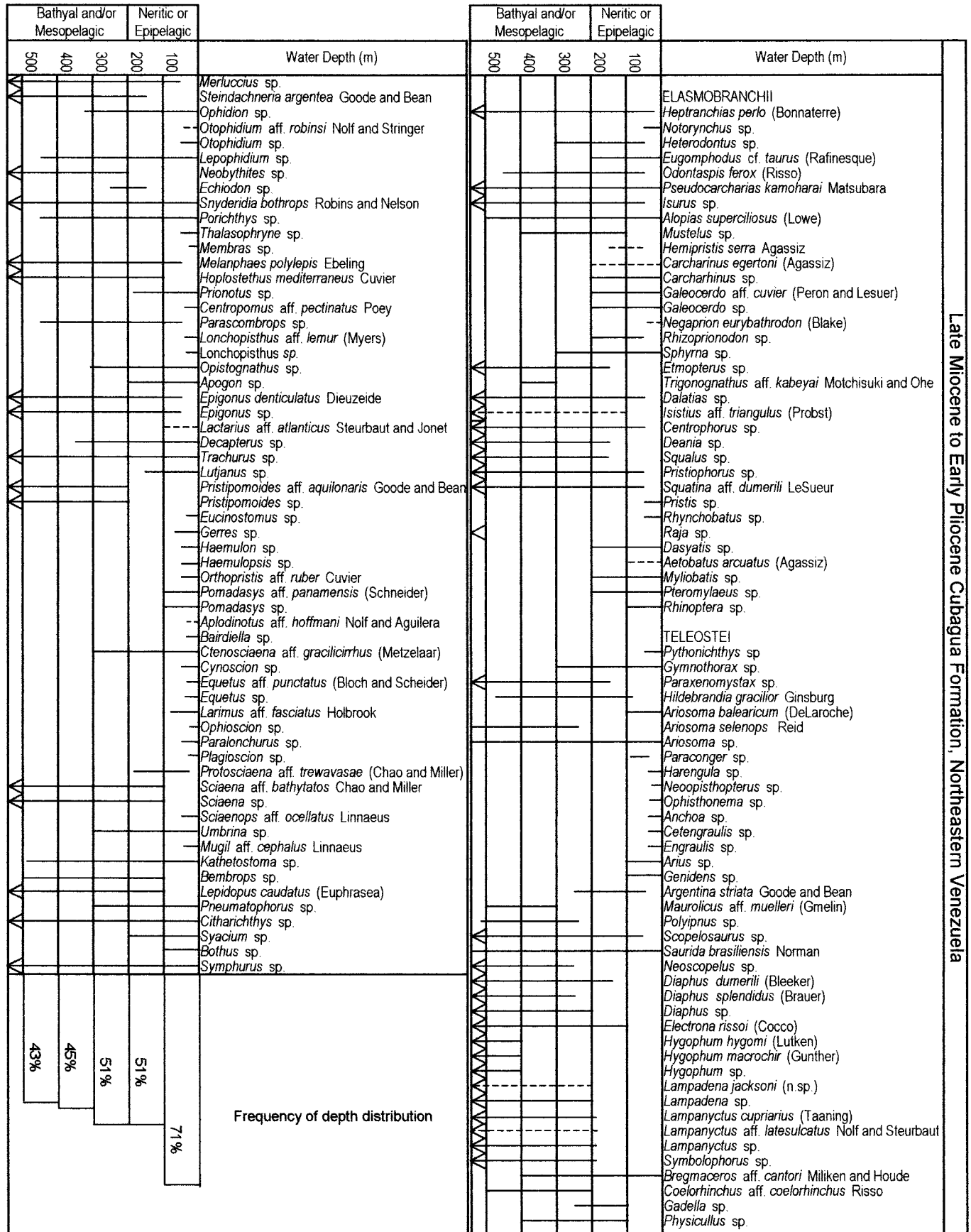FIGURE 3—Distribution of the collections, the total number of elasmo-branchs and teleosts by faunule.
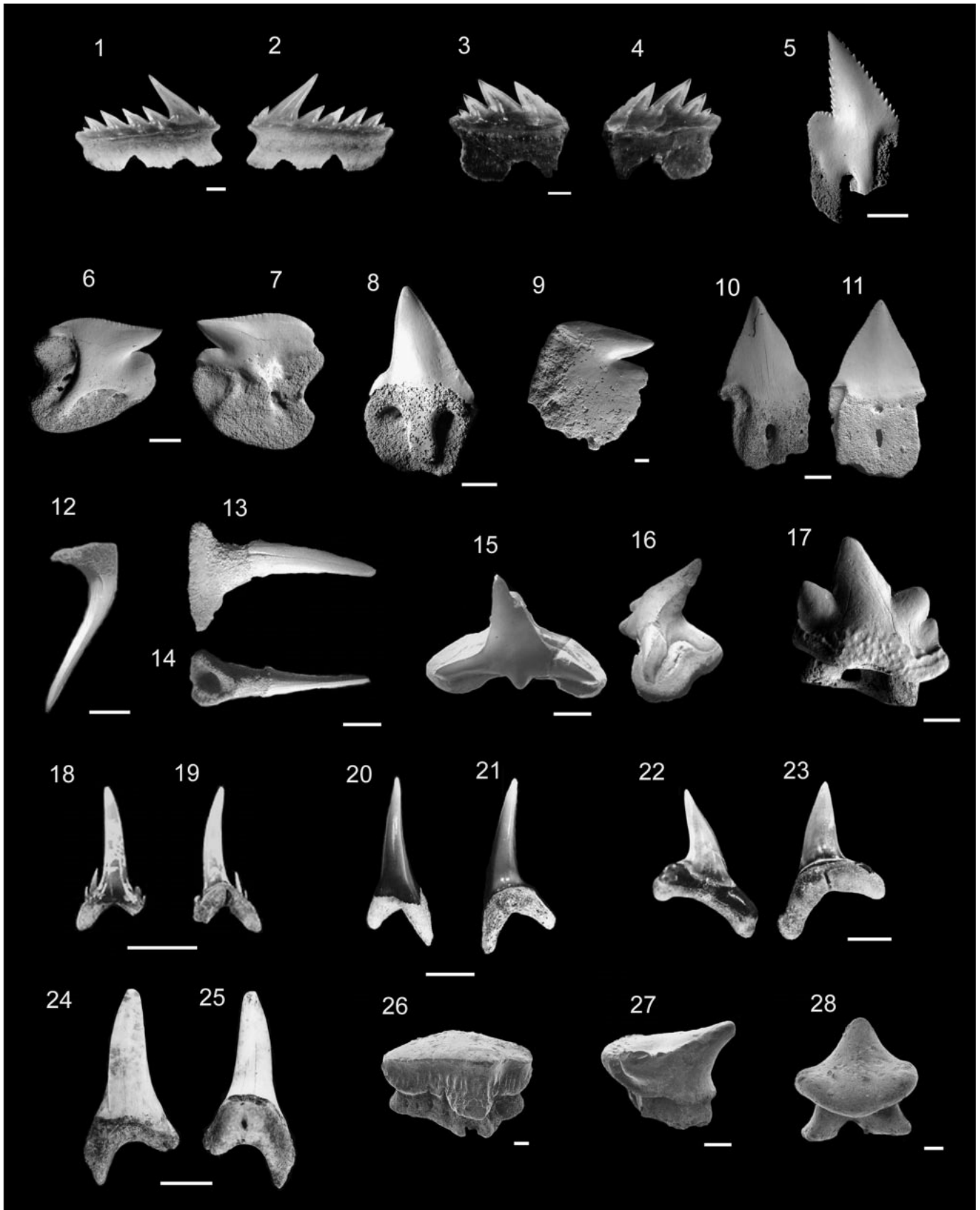

FIGURE 4—Cumulative curve of the number of taxa (Elasmobranchii, Teleostei and both) as a function of the number of collections.

Left panel

Bathyal and/or Mesopelagic			Neritic or Epipelagic		Water Depth (m)
500	400	300	200	100	

Merluccius sp.
Steindachneria argentea Goode and Bean
Ophidion sp.
Otophidium aff. robinsi Nolf and Stringer
Otophidium sp.
Lepophidium sp.
Neobythites sp.
Echiodon sp.
Snyderidia bothrops Robins and Nelson
Porichthys sp.
Thalasophryne sp.
Membras sp.
Melanphaes polylepis Ebeling
Hoplostethus mediterraneus Cuvier
Prionotus sp.
Centropomus aff. pectinatus Poey
Parascombrops sp.
Lonchopisthus aff. lemur (Myers)
Lonchopisthus sp.
Opistognathus sp.
Apogon sp.
Epigonus denticulatus Dieuzeide
Epigonus sp.
Lactarius aff. atlanticus Steurbaut and Jonet
Decapterus sp.
Trachurus sp.
Lutjanus sp.
Pristipomoides aff. aquilonaris Goode and Bean
Pristipomoides sp.
Eucinostomus sp.
Gerres sp.
Haemulon sp.
Haemulopsis sp.
Orthopristis aff. ruber Cuvier
Pomadasys aff. panamensis (Schneider)
Pomadasys sp.
Aplodinotus aff. hoffmani Nolf and Aguilera
Bairdiella sp.
Ctenosciaena aff. gracilicirrhus (Metzelaar)
Cynoscion sp.
Equetus aff. punctatus (Bloch and Scheider)
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.
Sciaenops aff. ocellatus Linnaeus
Umbrina sp.
Mugil aff. cephalus Linnaeus
Kathetostoma sp.
Bembrops sp.
Lepidopus caudatus (Euphrasea)
Pneumatophorus sp.
Citharichthys sp.
Syacium sp.
Bothus sp.
Symphurus sp.

43% 45% 51% 51% 71%

Frequency of depth distribution

Right panel

Bathyal and/or Mesopelagic			Neritic or Epipelagic		Water Depth (m)
500	400	300	200	100	

ELASMOBRANCHII
Heptranchias perlo (Bonnaterre)
Notorynchus sp.
Heterodontus sp.
Eugomphodus cf. taurus (Rafinesque)
Odontaspis ferox (Risso)
Pseudocarcharias kamoharai Matsubara
Isurus sp.
Alopias superciliosus (Lowe)
Mustelus sp.
Hemipristis serra Agassiz
Carcharinus egertoni (Agassiz)
Carcharhinus sp.
Galeocerdo aff. cuvier (Peron and Lesuer)
Galeocerdo sp.
Negaprion eurybathrodon (Blake)
Rhizoprionodon sp.
Sphyrna sp.
Etmopterus sp.
Trigonognathus aff. kabeyai Motchisuki and Ohe
Dalatias sp.
Isistius aff. triangulus (Probst)
Centrophorus sp.
Deania sp.
Squalus sp.
Pristiophorus sp.
Squatina aff. dumerili LeSueur
Pristis sp.
Rhynchobatus sp.
Raja sp.
Dasyatis sp.
Aetobatus arcuatus (Agassiz)
Myliobatis sp.
Pteromylaeus sp.
Rhinoptera sp.

TELEOSTEI
Pythonichthys sp.
Gymnothorax sp.
Paraxenomystax sp.
Hildebrandia gracilior Ginsburg
Ariosoma balearicum (DeLaroche)
Ariosoma selenops Reid
Ariosoma sp.
Paraconger sp.
Harengula sp.
Neoopisthopterus sp.
Ophisthonema sp.
Anchoa sp.
Cetengraulis sp.
Engraulis sp.
Arius sp.
Genidens sp.
Argentina striata Goode and Bean
Maurolicus aff. muelleri (Gmelin)
Polyipnus sp.
Scopelosaurus sp.
Saurida brasiliensis Norman
Neoscopelus sp.
Diaphus dumerili (Bleeker)
Diaphus splendidus (Brauer)
Diaphus sp.
Electrona rissoi (Cocco)
Hygophum hygomi (Lutken)
Hygophum macrochir (Gunther)
Hygophum sp.
Lampadena jacksoni (n.sp.)
Lampadena sp.
Lampanyctus cupriarius (Taaning)
Lampanyctus aff. latesulcatus Nolf and Steurbaut
Lampanyctus sp.
Symbolophorus sp.
Bregmaceros aff. cantori Miliken and Houde
Coelorhinchus aff. coelorhinchus Risso
Gadella sp.
Physicullus sp.

Late Miocene to Early Pliocene Cubagua Formation, Northeastern Venezuela

FIGURE 5—Present-day bathymetric ranges of taxa represented in the late Miocene to early Pliocene Cubagua Formation, northeastern Venezuela. Interrupted lines indicate extinct species.

obliquus Bolli (LAD = 1.8 Ma), *G. obliquus* Bolli var. *extremus* Bolli and Bermudez (LAD = 1.8 Ma), *Globorotalia crassaformis* (Galloway and Wissler) first appearence datum (FAD = 4.3 Ma), *G. margaritae* Bolli and Bermudez (FAD = 5.6 Ma, LAD = 3.4 Ma), *G. miocenica* Palmer (FAD = 3.4 Ma, LAD = 2.2 Ma), *G. pseudomiocenica* Bolli and Bermudez (LAD = 2.2 Ma), *Neobloloquadrina acostaensis* (Blow) (LAD = 1.8 Ma), *N. dutertrei* (d'Orbigny) (FAD = 3.0 Ma, LAD = 1.8 Ma) and *Orbulina universa* d'Orbigny. These preliminary results are consistent with the earlier age estimates reported by Bermudez (1966).

In several cases, the precise stratigraphic placement of samples in relation to unit boundaries is not known, however, studies of the physical stratigraphy are in progress (A. Coates, personal commun., 1999). We have followed the collections and processing methods used in the Panama Paleontology Project (see Jackson et al., 1999). Samples were processed using 2 mm and 500 micron sieves. Teeth and otoliths were picked at 6 to 10× magnification using a stereomicroscope. All teeth and otoliths were identified to species. The basic references use to identify the Elasmobranch teeth and Teleostean otolith are Cappetta (1987) and Nolf (1985) respectively. We have posted digital images of otoliths and the diagnostic character used for identification on the NMITA website (nmita.geology.uiowa.edu).

A total of 38 collections were grouped into nine "faunules" in an attempt to lessen the effects of sample size on the analysis of patterns and trends of faunal assemblages. The groupings were made on the basis of location, while taking into consideration the continental and insular outcrop of the Cubagua Formation. Each faunule corresponds to a single fossiliferous stratigraphic horizon at a single outcrop. Due to pervasive bioturbation at the great majority of sites, bedding could not usually be observed, therefore, packages of lithologically identical sediment, typically amounting to a few meters of section, were treated as a single horizon. Nearby but physically separate outcrops of the same stratigraphic horizon were treated as separate faunules for purposes of replication in the analyses (e.g., faunule 7: Cañón de La Caldera, and faunule 8: Cañón de Charagato, both on Cubagua Island).

All of the samples from the late Miocene to early Pliocene Cubagua Formation were used to make one estimate of paleobathymetry, using both elasmobranch and teleostean data following the methods described in Aguilera and Aguilera (1999). The method is based on the assumption that the taxa encountered lived together in the same environment represented by the sedimentary horizons sampled. All of the identifiable teeth and otoliths from the samples were identified and depth ranges were assigned to each taxon based on the known depths of living counterparts.

COMPOSITION OF THE FAUNA

Sixty-three families, 115 genera, and 140 species in the 38 collections (Appendix 1) represent the late Miocene to early Pliocene Cubagua Formation ichthyofauna. One hundred or more specimens in the 38 collections comprise only 16 out of the total 152 taxa. These include 69 percent Myctophidae with other minor groups of less than five percent in abundance (e.g., Gobiidae, Sternoptychidae, and Merluccidae). The presence and abundance of Myctophidae (including six genera and 11 species) in almost 47 percent of the collections, can be attributed to upwelling conditions.

Taxonomic diversity in these nine faunules ranges from a minimum of three to a maximum of 125 taxa, and abundance ranges from three to 1,989 specimens (medians: 33 taxa, 2,327 specimens per faunule). Elasmobranch diversity varies a few fold but teleostean diversity varies enormously (three to 55 fold). This variation is not due to differences in numbers of samples (Fig. 3). Elasmobranchs are clearly well sampled, as demonstrated by the leveling off of the sampling effort curve (Fig. 4), but teleosts appear to be less thoroughly sampled, with diversity still increasing with numbers of collections.

The bathymetric distribution based on living representative counterparts is 0 to 100 m (Fig. 5). However, this ichthyofauna is characterized mostly by the co-occurrence of oceanic and neritic fish.

Faunules 1, 2, and 3 (Appendix 1) at the Araya Peninsula show very low diversity and abundance, and an analysis of the faunal associations was not possible.

Faunule 4 at the Cerro Barrigón (Araya Peninsula) is the most diverse and abundant faunule from the Cubagua Formation. The sampled horizon corresponds to the calcareous fine sandstone and shale levels, presumably from the middle part of the Cerro Verde Member. The assemblage is characterized by the co-occurrence of epipelagic, mesopelagic and benthopelagic taxa together with neritic taxa. This mixture of faunas is strongly indicative of upwelling conditions close to the Cariaco Trench.

Faunule 5 at the Castillo de Araya (Araya Peninsula) is very poorly fossiliferous and is not considered in the present analysis.

Faunule 6 at the Cerro El Macho (Araya Peninsula) is significantly lower in diversity and abundance compared to Faunule 4.

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FIGURE 6—Common upwelling elasmobranchs species, late Miocene to early Pliocene Cubagua Formation, Cerro Verde Member, Venezuela. *1, 2, Heptranchias perlo* (Bonnaterre), labial and lingual view of lower tooth, UNEFM-PF-01, loc. OA-99–55, Cerro El Macho, Araya Peninsula. Scale bar equal to 1 mm. *3, 4, Notorynchus* sp., labial and lingual view of lower tooth, UNEFM-PF-02, loc. OA-99–55, Cerro El Macho, Araya Peninsula. Scale bar equal to 1 mm. *5, Dalatias* sp., labial view of lower tooth, UNEFM-PF-03, loc. PPP2556, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *6, 7, Centrophorus* sp., labial and lingual view of lower tooth, UNEFM-PF-04, loc. PPP3058, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *8, Deania* sp., lingual view of upper tooth, UNEFM-PF-05, loc. PPP2557, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *9, Etmopterus* sp., lingual view of lower tooth, UNEFM-PF-06, loc. PPP2565, Cerro Barrigón, Araya Peninsula. Scale bar equal to 100 μm. *10, 11, Isistius* aff. *triangulus* (Probst), labial and lingual view of lower tooth, UNEFM-PF-07, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *12, Trigonognathus* aff. *kabeyai* Mochizuki and Ohe, lateral view of anterior tooth, UNEFM-PF-08, loc. PPP2555, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *13, 14, Pristiophorus* sp., dorsal and anterior view of rostral tooth, UNEFM-PF-09, loc. PPP3054, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *15, 16, Squatina* aff. *dumerili* LeSeur, labial and lateral view of lateral tooth, UNEFM-PF-010, loc. PPP2563, Cerro El Macho, Araya Peninsula. Scale bar equal to 1 mm. *17, Heterodontus* sp., lingual view of anterior tooth, UNEFM-PF-011, loc. PPP3058, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *18, 19, Odontaspis ferox* (Risso), labial and lingual view of anterior tooth, UNEFM-012, loc. PPP2563, Cerro El Macho, Araya Peninsula. Scale bar equal to 10 mm. *20, 21, Pseudocarcharias* aff. *kamoharai* (Matsubara), labial and lingual view of anterior tooth, UNEFM-PF-013, loc. PPP2556, Cerro Barrigón, Araya Peninsula. Scale bar equal to 5 mm. *22, 23, Alopias* aff. *superciliosus* (Lowe), labial and lingual view of upper lateral tooth, UNEFM-PF-014, loc. OA-99–54, Cerro El Macho, Araya Peninsula. Scale bar equal to 5 mm. *24, 25, Isurus* sp., labial and lingual view of anterior tooth, UNEFM-PF-015, loc. OA-99–54, Cerro El Macho, Araya Peninsula. Scale bar equal to 10 mm. *26, Mustelus* sp., occlusal view of lateral tooth, UNEFM-PF-016, loc. PPP2563, Cerro El Macho. Scale bar equal to 0.1 mm. *27, 28, Raja* sp., lateral and lingual view of lateral tooth, UNEFM-PF-017, loc. PPP2554, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm.
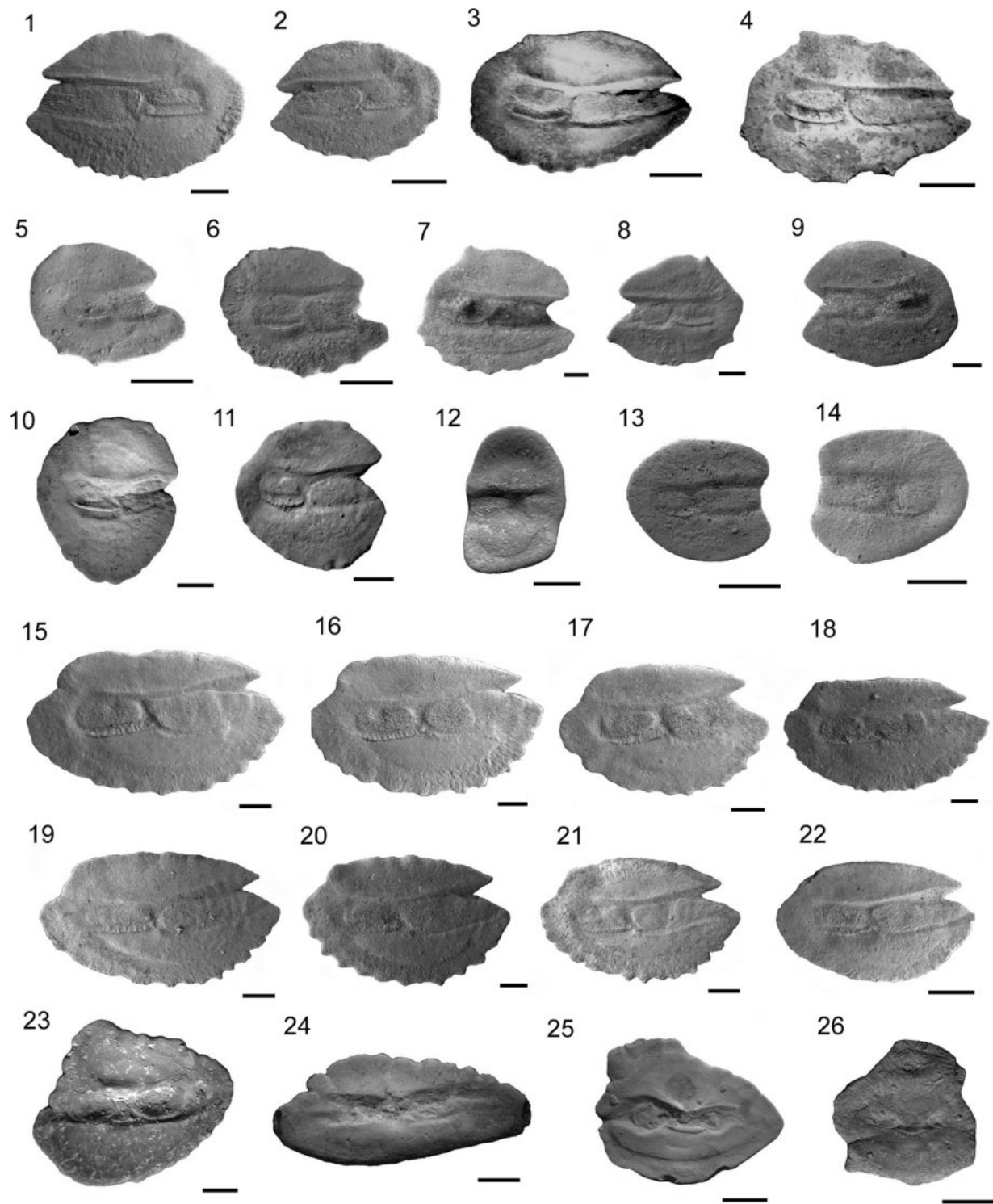
FIGURE 7—Common upwelling teleostean species, late Miocene to early Pliocene Cubagua Formation, Cerro Verde Member, Venezuela. *1, 2, Diaphus dumerili* (Bleeker), right otolith (inner view), UNEFM-PF-018, UNEFM-PF-019, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *3, 4, Diaphus splendidus* (Brauer), left otolith (inner view), UNEFM-PF-020, UNEFM-PF-021, loc. PPP2553, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *5, 6, Diaphus* sp. 1, left otolith (inner view), UNEFM-PF-022, UNEFM-PF-023, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *7, 8, Diaphus* sp. 2, left and right otolith respectively (inner view), UNEFM-PF-024, UNEFM-PF-025, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *9, Diaphus* sp. 3, right otolith (inner view), UNEFM-PF-026, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *10, Electrona rissoi* (Cocco), left otolith (inner view), UNEFM-PF-027, loc. PPP2572, Cañón de Charagato, Cubagua Island. Scale bar equal to 1 mm. *11, Hygophum macrochir* (Gunther), left otolith (inner view), UNEFM-PF-028, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *12, Lampanyctus cupriarius* (Taaning), right otolith (inner view), UNEFM-PF-029, loc. PPP2553, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *13, 14, Lampanyctus* aff. *latesulcatus* Nolf and Stringer, left and right otolith respectively (inner view), UNEFM-PF-030, UNEFM-PF-031, loc. PPP3055, Cerro Barrigón,

The ichthyofauna is characterized primarily by the presence of elasmobranchs and a relative scarcity of teleosteans, and the presence of deep-water shark species suggests an external neritic environment. The horizon sampled corresponds to calcareous sandstone and marl, apparently from the upper part of the Cerro Verde Member of the Cubagua Formation.

Faunule 7 at Cañón de La Caldera and Faunule 8 at Cañón de Charagato (Cubagua Island) have similar fish assemblages which are moderately abundant and characterized by a typical neritic ichthyofauna. The horizon sampled corresponds to calcareous sandstone and marl, probably from the middle to upper part of the Cerro Verde Member of the Cubagua Formation.

Faunule 9 from the La Tejita Member exposed at the Margarita International Airport (Margarita Island) has low abundance; however, the presence of elasmobranch species suggests an inner neritic environment.

Many distinctive circumstances produce the general paleoecological conditions of this remarkable coastal upwelling (Araya Peninsula horizon) and inner neritic (Cubagua and Margarita Islands horizon) assemblage fauna in the late Miocene to early Pliocene Cubagua Formation. Additional evidence supporting upwelling can be found by examining the ecological associations of the common living fish, particularly those relating to diet and feeding habits.

Ebert et al. (1992) clearly showed that the dominant fish prey in the diets of fifteen species of spiny dogfish sharks, *Centrophorus* (collected between 380 to 800 m of depth), *Deania* (400 to 800 m of depth), *Etmopterus* (450 to 925 m of depth) and *Squalus* (50 to 550 m of depth) was mainly myctophids and merlucciids. Species such as, *Diaphus* sp., *Epigonus* sp., *Merluccius* sp., *Coelorinchus* sp., *Maurolicus muelleri* (Gmelin), and *Lepidopus caudatus* (Euphrasea) are present in the squalid diet.

These predatory bathyal sharks and the mesopelagic prey relationship from the west coast of South Africa, can be used in the analysis of the fossil Cubagua Formation fish assemblages (upwelling fauna), because both groups (predators and prey) are very well represented in the collections (Appendix 1).

Other living epibenthic and benthic predators in the northeastern Atlantic, such as *Mustelus* sp., *Squatina* sp., and *Raja* sp., feed primarily on crustaceans, but also on fish such as ammodytids, callyonimids, gadoids, gobiids, and pleuronectiforms (Ellis et al., 1996), which also are present in the fossil associations.

In contrast, the diet of neritic predators such as the bonnethead shark, *Sphyrna tiburo* (Linnaeus), from southwest Florida (Cortes et al., 1996) is dominated by crustaceans, principally shallow water blue crabs (*Callinectes sapidus* Rathbun). The diet of the lemon shark, *Negaprion brevirostris* (Poey), collected from the Bahamas, is dominated by inner neritic fish, like sparids, lutjanids and gerreids (Cortes and Gruber, 1990). In addition, the diet of the southern stingray, *Dasyatis americana* Hildebrand and Schroeder, is dominated by crustaceans, mainly decapods and portunids (Gillian and Sullivan, 1993).

Coastal upwelling is the principle oceanographic phenomenon in the Caribbean associated with higher biological productivity. Upwelling of colder water, less than 24°C and rich in nutrients, stimulates phytoplankton growth which, in turn, supports the secondary productivity and fisheries in the region. Upwelling is the product of the seasonal winds along the northeastern Venezuelan coast during February to April, when maximal wind speeds reach 5 m/s (Herrera and Febres-Ortega, 1975), and chlorophyll concentration reaches a maximal value in the same period (Varela et al., 1997). Seasonal productivity increases due to upwelling over much of the northeastern Venezuelan coast, and produces the most important fishery activity in the country (Gimenez et al., 1993).

Evidence that higher biological productivity also occurred in this area during the geologic past is found in the Neogene sedimentary basin along the northeastern Venezuela. The sequence of Cubagua Formation (late Miocene to early Pliocene), Barrigón Formation (Pliocene), Cumaná Formation (Pliocene), Castillo de Araya Formation (Pleistocene) exhibits high mollusk diversity (see: Bermudez, 1966; Macsotay, 1965). Also, the presence of large specimens (at least 30 cm length) of *Lyropecten* and *Ostraea,* and taxa that typically inhabit deep water or superficial cold waters, are indicative of higher phytoplankton productivity.

In particular the mesopelagic and bathypelagic Cubagua Formation ichthyofauna from the Araya Peninsula horizon, contrast markedly with the neritic assemblages from the insular area (Cubagua and Margarita islands). These differences in faunal composition are probably also the result of the influence of submarine topography (the Araya Peninsula horizon close to the Cariaco trench, and Cubagua and Margarita islands surrounded by shallow continental platform).

Based on this preliminary evidence, coastal upwelling was apparently persistent in the geological past and probably varied in intensity.

Compared with other Caribbean Neogene fish assemblages that are reported in the literature, such as Cantaure Formation in Venezuela (Nolf and Aguilera, 1998: 61 teleostean taxa; herein: 18 elasmobranch taxa), Gatun Formation in Panama (Gillette, 1984: 24 teleostean and 17 elasmobranch), Bowden Formation in Jamaica (Stringer, 1998: 68 teleostean; Kruckow and Thies, 1990: one elasmobranch), Nariva, Brasso, Manzanilla, and Tarama formations in Trinidad (Nolf, 1976: 66 teleostean; Kruckow and Thies, 1990: 35 elasmobranch), and Baitoa, Cercado, Gurabo and Mao Formations (Nolf and Stringer, 1992: 65 teleostean taxa; no record of elasmobranch is available), the Cubagua Formation with 140 species, and approximately 714 elasmobranch teeth and 20,105 teleostean otoliths, is the more diverse and abundant Caribbean Neogene fish assemblages.

NOTE OF SPECIES OCCURENCES

Additional comments are made below regarding the distribution of epipelagic, mesopelagic, and benthopelagic elasmobranchs and teleosts in the upwelling assemblages. It was observed that some fossils of living species are not present in the Recent Caribbean ichthyofauna. Figures 6 and 7 show thirty one species that are distinctive and support the upwelling interpretation.

The sharpnose sevengill shark (Fig. 6.1, 6.2), *Heptranchias perlo* (Bonnaterre) is the first fossil record for the Caribbean late

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Araya Peninsula. Scale bar equal to 0.5 mm; *15–21, Lampadena jacksoni* n. sp., left otolith (inner view), UNEFM-PF-032 to UNEFM-PF-038, loc. PPP3055, Cerro Barrigón, Araya Peninsula (Holotype UNEFM-PF-035), Scale bar equal to 0.5 mm. *22, Symbolophorus* sp., left otolith (inner view), UNEFM-PF-039, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *23, Coelorinchus* aff. *coelorinchus* Risso, right otolith (inner view), UNEFM-PF-040, loc. PPP2556, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *24, Merluccius* sp., right otolith (inner view), UNEFM-PF-041, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm. *25, Steindachneria argentea* Goode and Bean, left otolith (inner view), UNEFM-PF-042, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 1 mm. *26, Bregmaceros* aff. *cantori* Miliken and Houde, otolith (inner view), UNEFM-PF-043, loc. PPP3055, Cerro Barrigón, Araya Peninsula. Scale bar equal to 0.5 mm.

Miocene to early Pliocene. An earlier Caribbean species, *Heptranchias tenuidens* (Leriche, 1938) was recorded from the late Oligocene of Venezuela. The first recorded catch of living *Heptranchias, H. perlo,* was made in 1998 along the Venezuelan coast from a depth of 166 fathoms (Crevigón and Alcalá, 1999).

The broadnose sevengill shark (Fig. 6.3, 6.4), *Notorynchus* sp. is the first fossil record for the Caribbean late Miocene to early Pliocene, although the recent monotypic *Notorynchus cepedianus* (Peron) is known in mostly temperate seas (Compagno, 1984).

Deep water squaliform sharks (Fig. 6.5–6.12), *Dalatias* sp., *Centrophorus* sp., *Deania* sp., *Etmopterus* sp., *Isistius* aff. *triangulus* (Probst) and *Squalus* sp. (no figure), represent additional fossil records for the Caribbean late Miocene to early Pliocene. The Miocene species C*entrophorus* sp., *Squalus stehleni* (Leriche), *Etmopterus acutidens* Casier, and *Isistius triangulus* (Probst) are the only previous Caribbean records cited by Kruckow and Thies (1990).

The present record of monotypic squalid shark *Trigonognathus* aff. *kabeyai* Mochisuki and Ohe (Fig. 6.12) is the first in the Caribbean late Miocene to early Pliocene. Cappetta and Sylvain (H. Cappetta, personal commun., 1999) reported an early record of *Trigonognathus* in the Paleogene of southern France. The living species is known from only two specimens collected from the coastal waters of Japan at depths of 330 m and 360 m, respectively (Mochisuki and Ohe, 1990).

The longnose sawshark (Fig. 6.13, 6.14) *Pristiophorus* sp. is the first fossil record for the Caribbean late Miocene to early Pliocene. This genus is represented in the fossil record from Europe, Japan, New Zealand, U.S.A., and South America (Pacific of Peru) (Cappetta, 1987). The living Atlantic species *Pristiophorus schroederi* Springer and Bullis, is known only from the Bahamas region (Compagno, 1984).

The angleshark (Fig. 6.15, 6.16) *Squatina* aff. *dumerili* Le Seur, is an uncommon fossil occurrence for the Caribbean (Kurckow and Thies, 1990). The living counterpart can be found in water depths reaching 1,390 m (Compagno, 1984).

The horn shark (Fig. 6.17) *Heterodontus* sp. is the first fossil record for the Caribbean late Miocene to early Pliocene. Earlier fossil occurrences in the Caribbean of *Heterodontus* (*H. pineti* Case, *H.* cf. *woodwardi* Casier and *H. janefirdae* Case) were reported by Kruckow and Thies (1990) from Eocene and early Miocene deposits of the U.S.A. The living species is known only from the eastern and western Pacific, and western Indian Ocean (Compagno, 1984).

The small-tooth sand tiger shark (Fig. 6.18, 6.19) *Odontaspis ferox* (Risso) is the first fossil record for the Caribbean late Miocene to early Pliocene. Landini (1977) reported an early record of *Odontaspis ferox* in the early Pliocene of Tuscani, Italy. Although this species is also known from the northeastern Atlantic; eastern, central and western Pacific, and the Western Indian Ocean (Compagno, 1984).

The crocodile shark (Fig. 6.20, 6.21) *Pseudocarcharias kamoharai* Matsubara, is represented in the Mediterranean fossil record (Cigala-Fulgoi, 1992). This present fossil record is the first for the Caribbean late Miocene to early Pliocene. The living species is also known in the eastern and western south Atlantic; eastern, central and western Pacific, and in the western Indian Ocean (Compagno, 1984; Lessa et al., 1991). Alcalá (1993) reports a single Caribbean record of a live specimen of *Pseudocarcharias kamoharai* caught off the Venezuelan coast. Crevigón and Alcalá (1999) comment that additional specimens are occasionally obtained by sport-fisherman.

The bigeye thresher (Fig. 6.22, 6.23) *Alopias superciliosus* Lowe, represents an additional fossil record for the Caribbean Neogene. The depth distribution of the living counterpart ranges from the surface to at least 500 m of depth (Compagno, 1984).

The mako (Fig. 6.24, 6.25) *Isurus* sp. is a genus common in all Recent Oceans (Compagno, 1984). Miocene to middle Pliocene species are widely distributed in Europe, Africa, Australia, North and South America (Cappetta, 1987; Kruckow and Thies, 1990). Leriche (1938) reported an earlier Venezuelan record of *Isurus* cf. *desori* from the late Oligocene San Lorenzo Formation.

The dusky smooth hound (Fig. 6.26) *Mustelus* sp. is a new fossil record for the Caribbean Pliocene. According to Compagno (1984), it is found in tropical waters ranging from shallow inshore and intertidal zones most commonly down to 200 m of depth, but occasionally down to 579 m.

The skates are represented by a deep tropical batoid, *Raja* sp. (Fig. 6.27, 6.28). The fossil record shows them to be uncommon in the entire Caribbean area (Kruckow and Thies, 1990).

There is a high diversity and abundance of lantern fish (Fig. 7), such as, *Diaphus dumerili* (Bleeker), *D. splendidus* (Brauer), approximately four additional undetermined *Diaphus* species, *Electrona rissoi* (Cocco), *Hygophum macrochir* (Gunther), *Lampanyctus cupriarius* (Taaning), *L.* aff. *latesulcatus* Nolf and Steurbaut, and *Symbolophorus* sp., represent additional fossil records for the Caribbean Neogene.

Special attention is given to a new extinct species of lantern fish, *Lampadena jacksoni* n. sp., because of its abundance and distribution in the Cubagua Formation (Araya Peninsula horizon, Cerro Barrigón, faunule 4), which perhaps might be used as a fossil indicator of Miocene-Pliocene upwelling events in the Caribbean Sea.

Associated with the myctophids (lantern fishes) is the presence of marine benthopelagic gadiforms (Fig. 7.23–7.26) such as, the hollowsnout grenadier, *Coelorhinchus* aff. *coelorhinchus* (Risso), the hake, *Merluccius* sp., the luminous hake, *Steindachneria argentea* Goode and Bean, and the codlets, *Bregmaceros* aff. *cantori* Miliken and Houde are indicative of deep-water in the tropics (Cohen et al., 1990).

SYSTEMATIC PALEONTOLOGY

Family MYCTOPHIDAE Gill, 1893
Genus LAMPADENA Goode and Bean *in* Gill, 1893
LAMPADENA JACKSONI new species
Figure 7.15–7.22

Diagnosis.—Otolith uniform oval to oblong-ovate shape, with a markedly straight dorsal margin, distinctly notched in the postero-dorsal angle and well developed and sharply rostrum and antirostrum.

Description.—Otolith oval to oblong-ovate. Moderately thin and slightly convex. Dorsal margin markedly straight; sculptures irregular, and distinctly notched in the postero-dorsal angle. Ventral margin rounded and serrate, with nine to ten denticles. Posterior margin rounded, irregular, and notched dorsally. Elongated slightly and flares ostium, anteriorly with large, low, and oblong colliculum. Short cauda, with oblong colliculum. Ostio-caudal differentiation slightly ventrally constricted. Ostium/cauda relation 1:0.5. Pseudocolliculum, as long as posterior colliculum. No collum. Crista superior low ridges from ostium to mid-cauda, poorly developed posteriorly, and absent at caudal tip. Crista inferior poorly developed along entire sulcus, and absent under cauda. Oval and shallow dorsal depression. No ventral depression, and shallow groove near margin. Large, broad, and angled rostrum, with sharply rounded tip. Small, narrows, and sharply rounded antirostrum. Excisura moderately wide, notch shallow, and angle acute.

Etymology.—Dedicated to Dr. J. Jackson, Smithsonian Tropical Research Institute, Panama, for his valuable contribution in the Panama Paleontology Project.

Types.—The holotype, UNEFM-PF-035, and six paratypes,

UNEFM-PF-032 to UNEFM-PF-034, and UNEFM-PF-036 to UNEFM-PF-038, are deposited in the Universidad Francisco de Miranda, Coro, Edo. Falcón, Venezuela.

Occurrence.—The material was collected from the late Miocene to early Pliocene Cubagua Formation, Cerro Verde Member, north of Cerro Barrigón, Araya Peninsula, northeastern Venezuela at locality PPP3055 (Fig. 2).

Discussion.—This otolith can be distinguished from the otoliths of recent species *Lampadena chavesi* Collett, *L. luminosa* (Garman), *L. notialis* Nafpaktitis and Paxton, and *L. speculigera* Goode and Bean [Smale et al., 1995 (pl. 21, fig. E1–G2; pl. 22, fig. A1–A3)], and from the fossil species *Lampadena dea* Fraser-Brunner, *L. speculigeroides* Brzobohaty and Nolf, and *L. gracile* (Schubert) [Brzobohaty and Nolf, 1996 (pl. 4, fig. 1–10, 12–16)] by the uniform oval to oblong-ovate shape otolith, with a markedly straight dorsal margin, distinctly notched in the postero-dorsal angle, and well developed and sharply rostrum and antirostrum. *Lampadena jacksoni* n. sp. occurs on the lower part of the Cubagua Formation (Cerro Verde Member) exposed at Araya Peninsula (Appendix 1, faunule 4) associated with high diversity upwelling assemblages. Its unique presence and abundance in a specific horizon suggests that it may be a useful fossil indicator of Caribbean upwelling events during the late Miocene to early Pliocene.

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APPENDIX I

Elasmobranchs and teleosteans from the Cubagua Formation discussed in the text. Frequencies are available on the Journal of Paleontology's Supplemental Database (http://www.journalofpaleontology.org).