

## FIRST PALEOGENE SELACHIFAUNA OF THE MIDDLE AMERICAN-CARIBBEAN-ANTILLEAN REGION, LA MESA DE COPOYA, WEST-CENTRAL CHIAPAS, MEXICO—SYSTEMATICS AND PALEONTOLOGICAL SIGNIFICANCE

Ismael Ferrusquía-Villafranca\*,  
Shelton P. Applegate\* and  
Luis Espinosa-Arrubarrena\*

### ABSTRACT

La Mesa de Copoya Selachifauna, middle Eocene San Juan Formation, the Tuxtla Gutiérrez-Chiapa de Corzo-Suchiapa area, west-central Chiapas, southeastern Mexico, consists of these taxa: *Nebrius* sp., *Striatolamna macrotia*, *Carcharias* sp., *Odontaspis*? sp., *Isurus* cf., *I. praecursor*, *Carcharodon auriculatus*, *Hemipristis* sp., *Galeocerdo* sp., an indetermined odontaspid, and a possible carcharhinid. The genera are cosmopolitan, include tropical, frequently shallow marine, near shore, piscivorous species, plus a few scavengers (like *Galeocerdo* sp.), and small invertebrate crushers (like *Nebrius* sp.). This selachian assemblage is but a small, biased sample of the rich fish fauna that inhabited the extensive Middle American-Caribbean Antillean tropical realm during the Paleogene; it affords, however, a tantalizing view of shark life in that age, which is an exceedingly important, but poorly known and documented episode of carcharian evolution and diversification in the tropics.

Key words: Selachifauna, Paleogene, La Mesa de Copoya, Chiapas, Mexico.

### RESUMEN

La Salacifauna Mesa de Copoya, Formación San Juan del Eoceno medio del área Tuxtla Gutiérrez-Chiapa de Corzo-Suchiapa, Chiapas centro-occidental, sureste de México, consiste de estos taxa: *Nebrius* sp., *Striatolamna macrotia*, *Carcharias* sp., *Odontaspis*? sp., *Isurus* cf., *I. praecursor*, *Carcharodon auriculatus*, *Hemipristis* sp., *Galeocerdo* sp., un odontáspido indeterminado y un posible carcarínido. Los géneros son cosmopolitas, con especies tropicales piscívoras, frecuentemente habitantes de mares someros en sitios cercanos a la costa; algunas como *Galeocerdo* sp. son carroñeras, o como *Nebrius* sp., son depredadoras de invertebrados bentónicos pequeños.

Este conjunto saláceo es apenas una muestra pequeña y sesgada de la rica ictiofauna que poblaba el extenso dominio tropical Mesoamericano-Caribeño-Antillano durante el Paleógeno, y proporciona una visión prometedora—pero incompleta—de la carcarofauna de esa edad, la cual es una etapa poco conocida y documentada de la evolución y diversificación del grupo en el trópico.

Palabras clave: Salacifauna, Paleógeno, La Mesa de Copoya, Chiapas, México.

### INTRODUCTION

#### HISTORY OF RESEARCH

The paleontologic literature on Chiapas marine vertebrates is exceedingly scarce: Müllerried (1932, 1943, 1951), reported on ?Oligocene sirenians, and early Tertiary turtle and teleost (pycnodont) remains; Maldonado-Koerdell (1953) did it on Paleogene sirenians. The only reference to fossil sharks is that of Müllerried (1957, p. 101, 102 and 123), in his book on the geology of Chiapas, which is a synopsis aimed at the general public, without formal description and characterization of lithostratigraphic units, structural features nor of fossil taxa.

The presence of sharks teeth in La Mesa de Copoya was known by the ranchers living there, it became widely known in

the early 1980's, during the construction of the buildings for the Instituto de Historia Natural de Chiapas and the Zoological Garden, in El Zapotal Natural Reserve, located in the northern slope of La Mesa, just southeast of Tuxtla Gutiérrez. The limestone slabs removed, frequently bore fossils—corals, pelecypods, megaforaminifera, and dasycladacean and vertebrate remains, including sharks teeth; the vertebrates were much less abundant. No attempt was made to scientifically collect the fossils. Later, Biology teachers of the local state college (ICACH, Instituto de Ciencias y Artes de Chiapas, in Tuxtla Gutiérrez), regularly conducted informal field trips to see and collect fossils in La Mesa de Copoya, thus furthering the knowledge on the presence of sharks teeth there.

In 1992, one ICACH student informed Ferrusquía-Villafranca on this fact, he checked it out, became interested and invited S.P. Applegate and L. Espinosa-Arrubarrena, fellow researchers in the Instituto de Geología's Department of Paleontology, to set up a project to collect and study the selachi-

\*Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, 04510 D.F., Mexico.

an record of La Mesa de Copoya. The results are reported in these papers.

#### METHODS AND MATERIAL

The fossil sharks teeth occur in several localities at La Mesa de Copoya (Figure 1), all developed in the erosion-resistant limestone blanket of the middle Eocene San Juan Formation that caps La Mesa, which consists of some 6–12 m of thin- to medium-bedded, very well indurated, richly fossiliferous microspathite. Fossils are exposed by weathering of the limestone strata; however, no isolated teeth have ever been found, probably because once out of the limestone matrix, they are quickly destroyed. Teeth are relatively rare (perhaps on the average, about one per every 50 square meters of outcrop area), and appear to be randomly distributed; to discover them, a careful prospecting was conducted. Whenever a fossil tooth was

found, the portion of the bearing strata where it occurred was carefully chiseled out and removed. The resulting blocks vary in size from 10 to 80 cm in length, 10 to 30 cm in width and 10 to 20 cm in height; larger blocks usually contain more than one specimen.

The blocks were taken by foot from the locality to the field vehicle, and then transported to the Instituto de Geología's Laboratorio de Paleontología, in Mexico City. The full load weighed some 480 kg. There the fossils were prepared by acetic acid dissolution of the limestone, following a modified version of the method described by Rutzky and collaborators (1994). The blocks were diamond-sawed into cuboid blocklets no greater than 5 cm long, each containing at least a single visible fossil. The blocklets were immersed in plastic containers having a water solution of acetic acid at 10%, held at room temperature, and left standing by periods of one to six days. The jars were grouped in sets of 20, which were treated as a processing unit. The jars were placed in a "lab bell" (*i.e.*, a confined table with an air-extracting device); everyday each blocklet was manipulated: It was removed to be examined, washed in faucet water, and the fossil bearing face was dried up with warm air; the fossil was coated with lacquer (or shellack) to avoid corrosion, and the blocklet was immersed back in the solution; this was stirred, and impurities were screened out. Should the solution be weak (*i.e.*, it no longer bubbled), it was replaced by a fresh one. This procedure was repeated over and over again, till all fossils were freed from the limestone matrix, and a new batch of blocklets and jars was taken up for processing.

Once freed, the fossils were washed, dried up, and treated with acetone to remove the lacquer coating; by means of a translucent, high grade epoxy-like cement. Later the fossils were catalogued and lodged in plastic jars.

To establish the identity of the taxa represented by the isolated sharks teeth, the artificial-set method of Leriche (1905), modified by Applegate (1965) was applied, thus reducing uncertainty due to heterodony. Artificial sets are putative upper and lower dentitions, at least from one side (left or right), that include all tooth positions known to correspond to a single taxon. The criterion to make a set is an analogical comparison with full dentitions of closely related extant or well-known fossil species.

The material basis of this work includes 240 individual specimens, mostly isolated sharks teeth, a few fish vertebrae and miscellaneous bone fragments. The completeness of the teeth varies from fair to good. The teeth were arranged in artificial sets, as complete as possible, and then described. Measurements are in mm; descriptive terminology is that of Leriche (1905, 1910) and Applegate (1965). Each set was assigned a catalogue number; other teeth were given lot numbers. The material is housed in the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, in Mexico City. The equipment used was already mentioned.

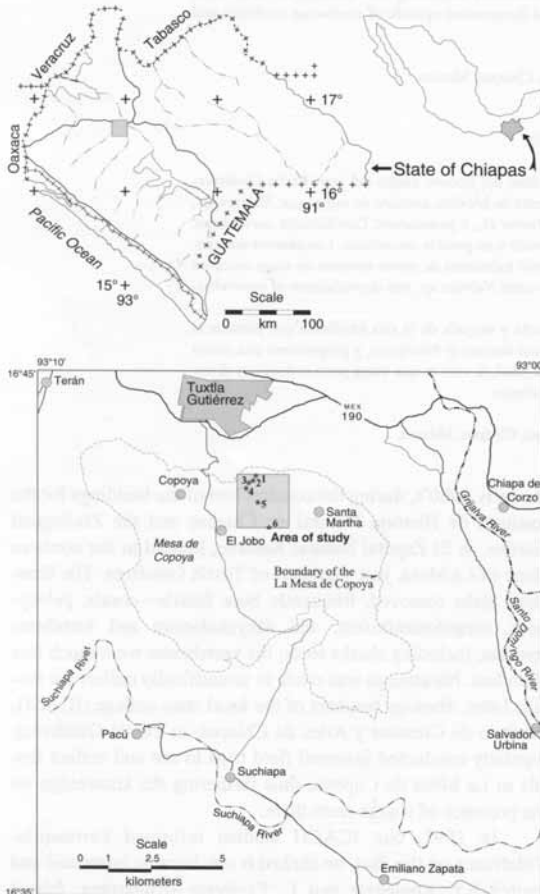


Figure 1. Location of the Tuxtla Gutiérrez-Chiapa de Corzo-Suchiapa area, Chiapas, where La Mesa de Copoya occurs.

## SYSTEMATIC PALEONTOLOGY

## INTRODUCTORY REMARKS

As mentioned in the history of research, the previously known Tertiary vertebrate record of Chiapas only includes sirenian (Müllerried, 1932; Maldonado-Koerdell, 1953), turtle (Müllerried, 1943) and pycnodont (Müllerried, 1951) remains; sharks teeth are mentioned (Müllerried, 1957), but not described. The sharks teeth assemblage here designated as La Mesa de Copoya local fauna, is the first to be described from the Paleogene of the Middle American-Caribbean-Antillean region (Figure 2), records a modest biodiversity (three orders, eight families and 11 genera) of seemingly tropical, shallow marine, near shore taxa, that probably constitute but a small biased sample of the rich marine vertebrate fauna that inhabited this vast region during the middle Eocene, mirroring the invertebrate one, as evidenced among others by the larger foraminifera, corals and mollusks (*cf.* Woodring, 1966; Frost and Langenheim, 1974; Butterlin, 1981).

The present report deals with the sharks teeth, so only passing comments are made on the accompanying vertebrate

fauna. Besides the sharks, chondrichthyan remains include also a few broken and worn ray dental plates, probable assignable to *Myliobatis* sp. Teleost fossils are fairly common in the collection, and consist of isolated teeth and vertebrae, some resemble mackerel or tunid skeletal elements. A few distinctive snout spine fragments are assigned to the Eocene teleost *Cylindracanthus* sp.

## SYSTEMATICS

Class Chondrichthyes Huxley, 1880  
 Subclass Elasmobranchii Bonaparte, 1838  
 Cohort Euselachii Hay, 1902  
 Subcohort Neoselachii Compagno, 1977  
 Order Orectolobiformes Applegate, 1972  
 Family Ginglymostomatidae Gill, 1862  
 Genus *Nebrius* Rüpel, 1837

*Nebrius* sp.

(Plate 1, figures A and B)

**Referred material**—A tooth lot composed of five teeth designated as IGM-6981 (series 1–5).

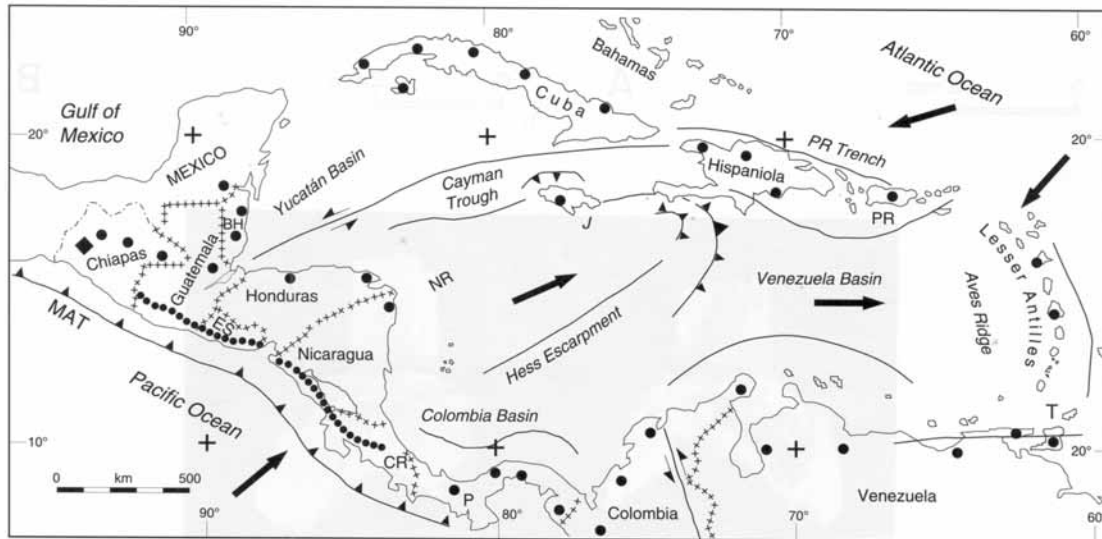


Figure 2. Chief Paleogene (largely middle Eocene) marine fossil-bearing localities of the Middle American-Caribbean-Antillean region; main neotectonic features are also depicted. **Abbreviations:** BH, British Honduras; CR, Costa Rica; J, Jamaica; MAT, Middle American Trench; NR, Nicaraguan Rise; P, Panama; PR, Puerto Rico; and T, Trinidad. **Symbols:** Dots, Middle America Volcano Chain, it may include El Chichón Volcano, just north of Chiapas. Black circles, invertebrate fossil localities, most include both planktonic micro- and benthonic larger foraminifera; corals, mollusks and echinoderms are also common. Heavy arrow, relative lithospheric plate motion. Opposite arrows, strike-slip fault. Heavy toothed line, active subduction zone. Black diamond, La Mesa de Copoya site, only known Paleogene shark-bearing locality in the region.

**Sources:** Geographic plot modified from Schuchert (1935), and Maurrasse (1990b); bathyal elements modified from Holcombe (1990); tectonic elements mainly from Case and Holcombe (1980). Invertebrate fossil-bearing localities: General: Schuchert (1935); Judoley and Furrázola-Bermúdez (1971); Dengo (1973); Butterlin (1977); and Maurrasse (1990 a–c). Foraminifera: Loeblich and Tappan (1964); Cole (1956, 1958, 1959); Cole and Aplin (1964); Bolli (1966); Frost and Langenheim (1974); and Butterlin (1981). Corals: Wells and Hill (1956); Frost and Langenheim (*op. cit.*). Mollusks: Woodring (1954, 1957, 1966, 1978). Echinoderms: Buitrón-Sánchez (1978).

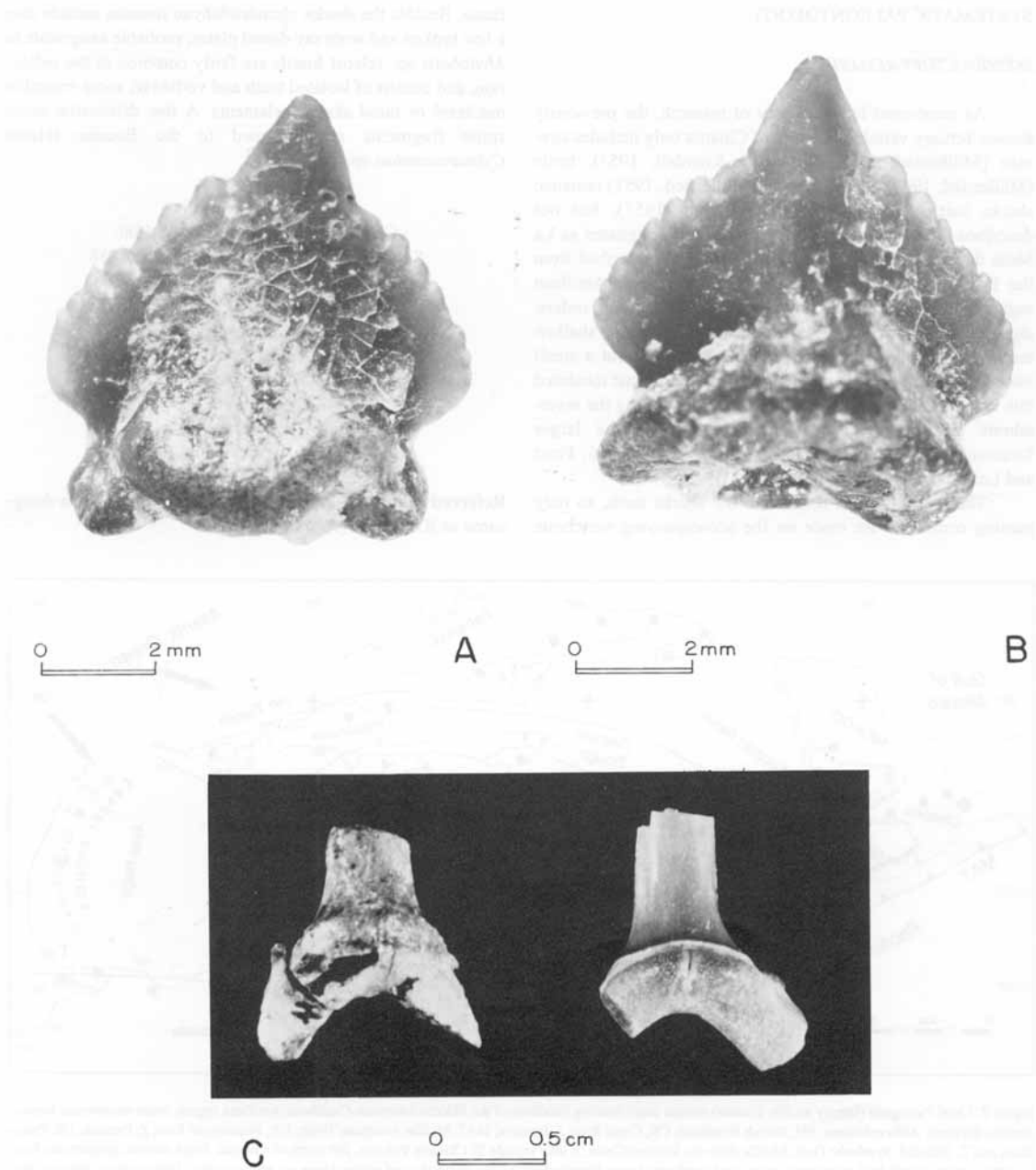


Plate I. *Nebrius* and *Striatolamia*. Figure A, IGM 6981-1, a symmetrical medial tooth referred to *Nebrius* sp., shown in labial view. Figure B, *idem.*, lingual view. Figure C, left side, IGM 6982-1, a first anterior right lower tooth referred to *Striatolamia macrota*. Right side, IGM 6982-2, a right lateral lower tooth referred to the same taxon.

**Geochronologic range**—*Nebrius* is known from the early Paleocene to the Recent (Cappeta, 1987).

**Geographic distribution**—The fossil record is wide, includes Europe, North America and northwestern Africa (Cappeta, 1987). The only living species of this genus *N. ferrugineus* has only been reported from the Indo-West and Central Pacific Oceans (Compagno, 1984).

**Description**—Within this genus, the teeth are mostly asymmetrical. The main cusp of the crown in many teeth is small, inconspicuous and shows several lateral cusplets (eight or more in number) that decrease in size towards the edge of the tooth. These structures can be pointed or lobed as shown in Plate 1, figures A and B. The apron (lower part of the crown) is large and tongue-like. The shape of the roots is markedly different from other shark taxa. Instead of branching, they tend to flatten out with a labio-lingual ridge behind the apron. Their bases are heart shaped and when seen from below, the appearance tends to be triangular with a large elliptical foramen (not illustrated) behind the labio-lingual ridge.

#### Discussion

**Taxonomic assessment.** There are four nominal species known in this Cenozoic genus: *Nebrius bequaerti* (Paleocene); *N. blanckenhorni* and *N. thielensis*, from the middle Eocene of Belgium, Egypt and the late Eocene of Georgia (Cappeta, 1987); and the extant *N. ferrugineus*. Due to the scarcity of the referred material, it is not possible at this time to make a taxative specific assignment; obviously it will take a larger sample to decide to which Paleogene species the Copoya *Nebrius* material can be referred.

**Biogeographic considerations.** Today, this genus is confined to the Central Pacific and Indian Oceans (Compagno, 1984). However, the fossil records encompass Africa, Europe and the eastern United States, suggesting a drastic reduction in its distribution from the Eocene to Recent times. It is worth noticing that the closest previous record of the Copoya *Nebrius*, is that of the late Eocene *N. thielensis* of Georgia, U.S.A.

**Ecological significance.** The tawny nurse shark *Nebrius*, represents a tropical near-shore elasmobranch taxon; specimens are small to large, nocturnal, inshore bottom sharks with a Central and Western Pacific and Indian Oceans distribution. They live in continental and insular waters, in depths that range from the intertidal down to at least 70 m, feeding on (crushing) small invertebrates. The fact that *Nebrius* has such a long stratigraphic range and that has always been associated with near shore shallow water deposits (e.g., coral or rocky reefs and sandy bottoms), implies that the presence of this genus can serve as a dependable environmental index.

**Phyletic significance.** Although recent specimens are available in the Family Ginglymostomidae, no tooth sets have been constructed, neither are there studies related to the ontogenetic changes intooth morphology; the intraspecific dental variation is practically unknown. Therefore, regardless of the four nominal species (three fossil and one Recent), no attempt has been done to establish any lineage or evolutionary trend within this taxon.

Order Lamniformes Berg, 1958

Family Carcharidae Müller and Henle, 1939

Genus *Striatolamia* Glückman, 1810

*Striatolamia macrotota* (Agassiz) 1843

(Plate 1, figure C)

**Synonymy**—*Otodus macrotus* Agassiz, 1843; *Odontaspis macrotota* Leriche, 1951.

For a more extensive synonymy regarding this taxon, see Leriche (1951) and Cappeta, (1987).

**Referred material**—A lot of two teeth, designated as IGM-6982-1 (series 1-2).

**Geochronologic range**—So far, *Striatolamia macrotota* is a common species that has been reported ranging throughout the Eocene (Leriche, 1951; Cappeta, 1987).

**Geographic distribution**—*S. macrotota* is a taxon that is widely known from shallow water deposits from the Eocene of the world, although the reports that are better documented pertain to Europe and North America.

**Description**—As illustrated in Plate 1, figure C, the tooth shown on the left is a first lower anterior from the right lower jaw. Although the crown is broken above the midsection, it can be seen that it shows a straight shape and that there are definite striations on its lingual side. The presence of striations and small single lateral denticles represents diagnostic characters for *Striatolamia macrotota*. The position of this tooth in the jaw is given by a conspicuous protuberance at the center of the root, a condition that in Lamniformes is characteristic of the first lower position (Applegate, 1965). The anterior branch of the root is elongated, markedly narrow and its tip is broken, while the posterior side is short and slightly wider. Both branches (or root interspace) form a wide open U. The tooth shown at the right side of Plate 1, figure C, corresponds to a lower right lateral (between the third and the sixth positions). In this specimen, the crown is also broken and the diagnostic striations, although present, are weak. The anterior branch of the root is broken, but appears to be narrower and longer than the posterior limb. At the center of the root there is a strong nutrient groove. The posterior side of the root is complete and its tip is bluntly rounded. These two teeth are somewhat smaller than the typical *Striatolamia*

*macrota*, however, this may be due to the immature nature of the material, and as such, it does not represent another species.

#### Discussion

**Taxonomic assessment.** Though fragmentary and with only two teeth, we still feel confident in the specific assignment of this taxon. The presence of striations and small single lateral denticles, plus the shape of the teeth regarding their position in the jaw, confirm this taxonomic identification.

**Biogeographic considerations.** This is a form known from numerous Eocene localities, either in tropical or temperate waters, therefore its occurrence in Middle America, though reported here for the first time.

**Ecological significance.** At present, the closest relative to this species is *Carcharias taurus*, a species of a wide distribution, which is a common littoral shark in temperate and tropical waters (Compagno, 1984). The resemblance of the dental elements between the extant *C. taurus* and *S. macrota*, as well as the depositional environments in which *S. macrota* has been reported, likewise suggest similar distribution and living conditions, ranging from the surf zone, in shallow bays, to no more than 200 m deep, on the outer shelves.

**Phyletic significance.** The Genus *Striatolamia* includes only two species restricted to the Paleogene, *Carcharias striata* (from the Paleocene), and *S. macrota* (in the Eocene). Though derived from Cretaceous carcharhinid, the precise ancestor of this taxon is still unknown. The fact indicates that there are no known descendants of *S. macrota* after the end of the Eocene, and that this lineage has a quite limited stratigraphic range.

#### ***Carcharias* sp. Rafinesque, 1810** (Plate 2, figure A)

**Generic synonym**—*Synodontaspis* (see Cappetta, 1987).

**Referred material**—A partial artificial set from the right side of the jaw, composed of 16 teeth, designated as IGM-6983 (series 1-16).

**Geochronologic range**—This taxon has been reported from the Albian of Texas in North America (Welton and Farish, 1993) to the Holocene, when its extant species occur in practically all oceans.

**Geographic distribution**—The numerous fossil records of the genus *Carcharias*, also known as the "sand tiger shark", are wide spread, including Antarctica, as well as all the equatorial, subtropical and tropical areas. There are 52 nominal species, most of which are fossils. Nevertheless, very few can be con-

sidered valid. Today, only one species, *C. taurus*, is recognized in the Mediterranean Sea (where the first recent specimen was described), as well as to the Atlantic, Western Pacific and Indian Oceans (Compagno, 1984).

**Description**—These teeth were included under the genus *Carcharias* due to the presence of short lateral denticles and smooth lingual crowns (lacking striations).

**Upper jaw.** The two anterior teeth in Plate 2, figure A, are poorly preserved but show narrow crowns and lateral denticles. Within the sample, there was neither a third upper anterior nor any intermediate position found. The upper lateral teeth (the next five to the right) show large lateral denticles with irregular edges. One tooth of the lot (not illustrated) shows two lateral denticles in the only side that was preserved.

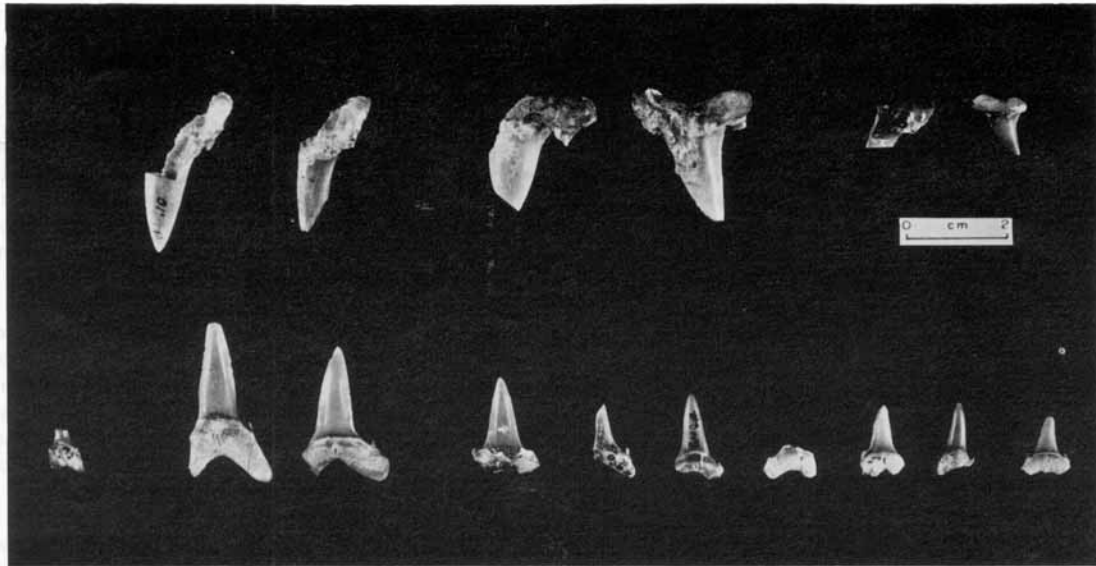
**Lower jaw.** The first tooth of the left side in Plate 2, figure A, corresponds to what Applegate (1965) has described for *Carcharias* as a lower symphyseal. This small tooth shows a large nutrient canal and a smooth broken crown. The next two teeth in the artificial set, correspond to the second and third anterior positions, respectively. Though incomplete (both lack the symphyseal branch of the root), their shapes coincide to the same positions in *Carcharias* (Applegate, 1965). It is important to notice that in the dental set the first anterior position is missing. There are seven lower laterals that show straight narrow crowns and small lateral denticles. The fragmentary nature of these lower lateral teeth precludes a more detailed description as to position in the jaw.

#### Discussion

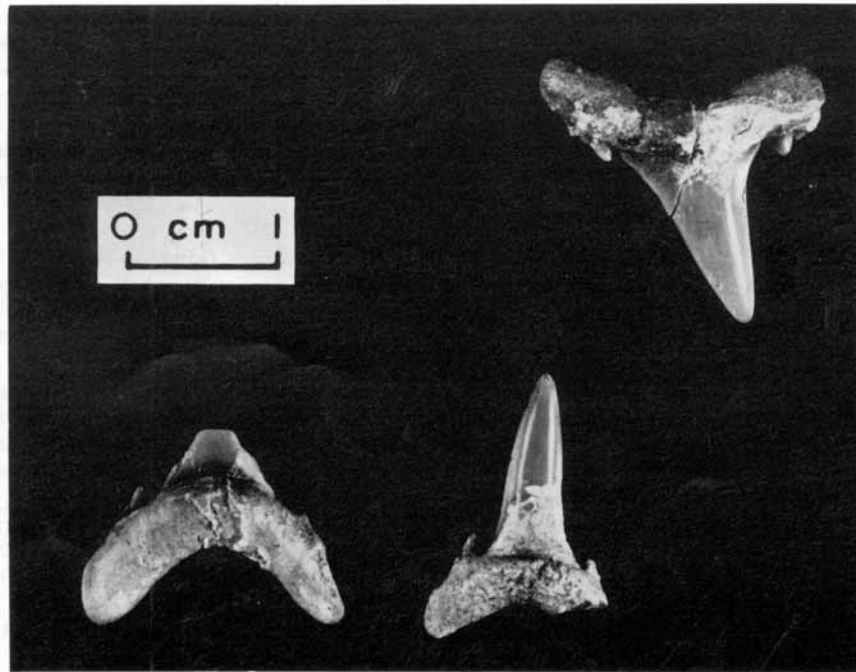
**Taxonomic assessment.** Though assigned with certainty to the genus *Carcharias*, the precise species of the material herein described is unknown, because of its fragmentary nature and to the fact that some key positions are missing. Also, a large number of spurious species described for *Carcharias* in the Paleogene, curtails a more detailed taxonomic assignment. Nevertheless, with better preserved materials and with complete tooth sets, there are as many as three possibilities of species that could be related or belong to La Mesa de Copoya material: *C. cuspidata*, *C. hopei* and *C. koerti*.

**Biogeographic considerations.** Given that the Paleogene record of *Carcharias* includes in any given site several nominal species, we refrain from working out the biogeographic considerations of the Copoyan *Carcharias* sp., for want of its specific identity.

**Ecological significance.** As other members of La Mesa de Copoya shark fauna, *Carcharias* sp. represents a fish feeder. The elongated, narrow and pointed anterior teeth were used for grasping the prey, whereas the robust spike-like lower laterals



A



B

Plate 2. *Carcharias* and *?Odontaspis*. Figure A, IGM 6983, a lot of 16 upper and lower teeth (series 1-16) that form a partial artificial set (right side) referred to *Carcharias* sp. Figure B, IGM 6984, a lot formed by two lower and a single upper lateral teeth referred to *?Odontaspis* sp.

held the fish so they could be sliced by the wide and triangular upper laterals. Such a large and successful predator speaks for the presence of an abundant fish fauna, as it is found today in near shore shallow waters (from the surf zone to over 90 m in the outer shelves) of temperate and tropical regions of the world. Further, stomachal contents of *C. taurus* have shown remains of large fish; also individuals of this species have been observed cutting large baits into smaller pieces (J.L. Castro-Aguirre, written communication, January, 1999).

**Phyletic significance.** Until the taxonomy of the Genus *Carcharias* is worked out through the use of tooth sets, and critical comparisons are established between *C. cuspidata*, *C. hopei* and *C. koerti*, it is unneeded to speculate on the phyletic significance of the *Carcharias* form from La Mesa de Copoya.

Family Odontaspidae Müller and Henle, 1839  
Genus *Odontaspis* Agassiz, 1838

*Odontaspis?* sp.  
(Plate 2, figure B)

**Synonym for the genus**—*Squalus ferox*, Risso, 1810; and *Carcharias ferox*, Risso (Cappeta, 1987).

**Referred material**—A small lot of three lateral teeth designated as IGM-6984 (series 1-3).

**Geochronologic range**—*Odontaspis* ranges from the Late Cretaceous (Campanian) to the Recent (Cappeta, 1987), with two living species, *O. ferox* and *O. noronhai* (Compagno, 1984). Nevertheless, in opinion of the authors of this paper, *O. noronhai* warrants generic separation, based on the number and shape of the teeth.

**Geographic distribution**—The extant *Odontaspis ferox*, the living form recognized in this paper, has a deep water, cosmopolitan distribution (Compagno, 1984). On the other hand, the known distribution of the fossil Genus *Odontaspis*, as we recognize it, includes shallow and deep water of North America, Europe, Asia, North Africa, and Greenland.

**Description**—The three teeth shown in Plate 2, Figure B, are tentatively assigned to the Genus *Odontaspis*. The top tooth is an upper lateral. The crown is triangular and points towards the distal side of the jaw. The anterior branch of the root is longer than the posterior. The lateral denticles are short and rounded, but this could be due to wear. The space between the root branches is very wide, describing a shallow concavity. The first lower tooth under the scale of Plate 2, figure B, corresponds to a lower lateral position of the left side of the jaw. Most of the crown is missing, but still it can be seen that the symphyseal branch of the root is narrower than the posterior one (a typical character of the lateral positions). The next lower tooth is char-

acterized by a straight crown and erect double denticles. Although the anterior limb of the root is missing, a strong nutrient groove can be seen.

#### Discussion

**Taxonomic assessment.** It appears that specimen IGM 6984 has more features in common with *Odontaspis* than with any lamniform genera, such as *Carcharias* (also present in this fauna), warranting their tentative assignment to the former; the presence of the double lateral denticles, clearly discernible in Plate 2, figure B, is of particular significance.

**Biogeographic considerations.** At present, much of the geographic range of the Recent *O. ferox*, is based on single occurrences (isolated records); there is little doubt that future work will extend its range. On the other hand, the fossil Copoya material needs to be identified within a better taxonomic framework. This should provide a better picture of the distribution and biographic implications of this taxon.

**Ecological significance.** Although Compagno (1984) reported that the extant *O. ferox* has been caught in depths between 10 to 500 m, of continental and insular shelves and upper slopes of warm and temperate waters of the Northeastern Atlantic, Pacific and Indian Oceans, as well as the Mediterranean Sea; the species of this genus normally dwells at great depths. The teeth of *Odontaspis* are similar to those of *Carcharias*, except that *Odontaspis* normally has only two upper anterior teeth, and that in general the dental elements of *Odontaspis* are smaller and more delicate, suggesting that this active piscivorous shark feeds on smaller, and possibly less active prey (Compagno, 1984).

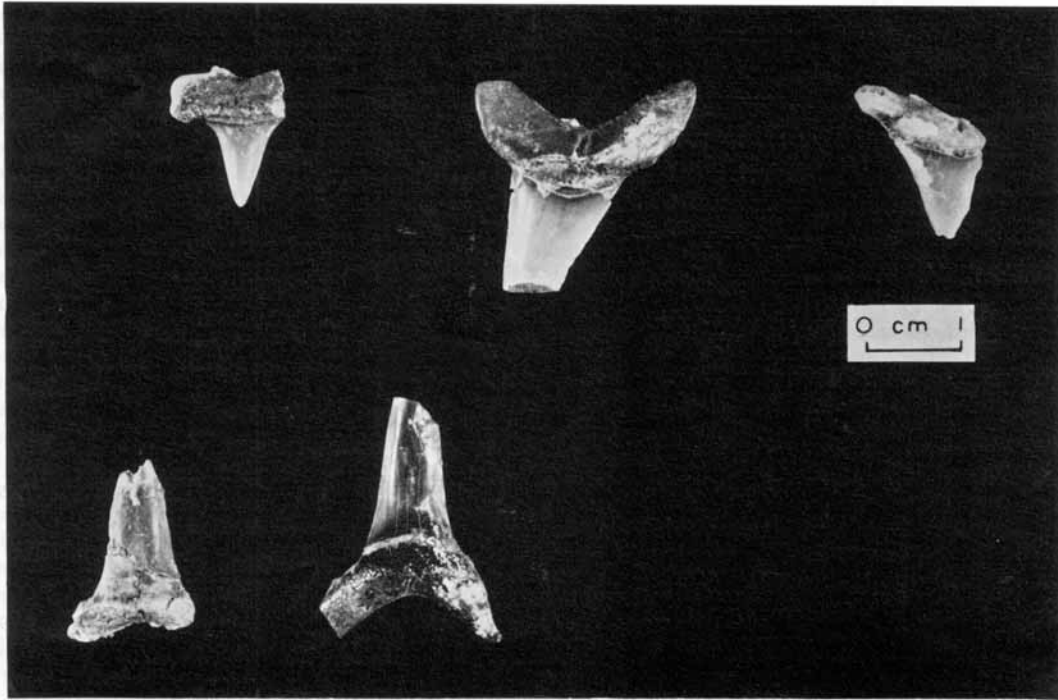
**Phyletic significance.** *Odontaspis* belongs to a lineage of well-known shark species throughout the Tertiary. Nevertheless, recent work carried out by Applegate in 1997 on specimens housed in the collections of the US National Museum, shows that the lineage is much older, going back at least to the Cenomanian. So far, no documented study regarding the relationships within this genus has been published. In the future and with more diagnostic material, the phyletic implications of this Eocene *Odontaspis* could add meaningful information to the *O. ferox* lineage.

Family Lamnidae Müller and Henle, 1838  
Genus *Isurus* Rafinesque, 1810

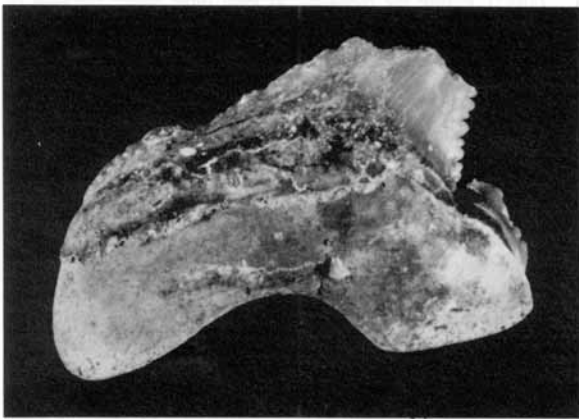
*Isurus* cf. *I. praecursor* Leriche, 1905  
(Plate 3, figure A)

**Referred material**—An incomplete tooth lot composed of five teeth, three uppers and two lowers, designated as IGM-6985 (series 1-5).

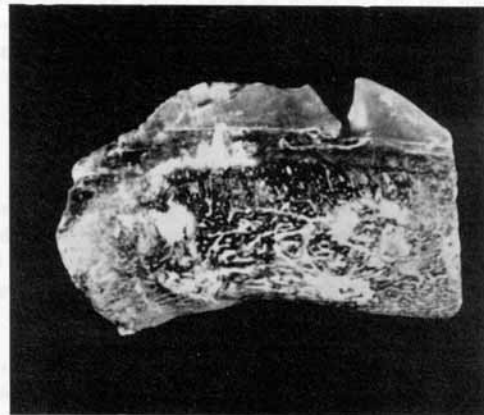




A



B



C

Plate 3. *Isurus*, *Carcharodon* and *Otodus*. Figure A, IGM 6985, a lot consisting of three upper and two lower teeth referred to *Isurus* cf. *I. praecursor*. Figure B, IGM 6986, an incomplete lower right lateral tooth referred to *Carcharodon auriculatus*. Figure C, IGM 6987, a basal tooth fragment possibly referable to *Otodus* sp.

**Geochronologic range**—This species ranges from the early to the middle Eocene (Cappeta, 1987).

**Geographic distribution**—*Isurus praecursor* is known from the early Eocene of England and from the middle Eocene of Belgium, Syria, Egypt and Nigeria (Cappeta, 1987). Also, this taxon has been identified by one of the authors of this paper in several major collections in the United States.

**Description**—Regarding the shape of the teeth of *Isurus* (large and elongate), in a broad sense they resemble *Carcharias* and *Odontaspis*, but it must be noticed that the lingual surfaces at the crowns in *Isurus* are completely smooth (contrary to the striations found in *Carcharias*), and that there are no lateral denticles present toward the base of the crowns, whereas *Odontaspis* and *Carcharias* bear conspicuous lateral cusplets. The roots are bulky with long branches, that are more divergent on the upper positions than on the lower teeth. This feature can be observed in Plate 3, figure A, where the second upper left anterior (the tooth in the center of the three uppers) shows both (complete) branches of the root. Unfortunately, the small number of teeth and the incompleteness of the elements limited a more accurate taxonomic determination as to a specific level. From the teeth depicted in Plate 3, figure A, the incomplete upper tooth (right corner of the illustration, above the scale) was determined to be a right lateral. The next tooth to the left (upper central part of the figure) lacks a little less than one third of the crown and was determined as a second upper left anterior. The smaller tooth next to the anterior (upper left corner), was identified as an upper left lateral posterior position. The two lower teeth, although very incomplete, were assigned to the left side of the jaw and the one below the upper central was designated as a possible third lower anterior, whereas the one at the lower left corner of the figure may correspond to one of the first laterals, but its incompleteness makes this determination highly questionable.

#### Discussion

**Taxonomic assessment.** The width of the base of the second anterior tooth, along with the narrowness of its root and the lack of lateral denticles, suggest that the species might be *Isurus praecursor*. The general tooth shapes of the remaining four specimens, also agree with this assignment.

**Biogeographic considerations.** *Isurus praecursor* occurs associated with large fish faunas (composed of many species). Therefore, it is to be expected in any place where large ichthyofaunas are found. This includes the Southern Hemisphere, although, in South America, this isurid might have received different names.

**Ecological significance.** Although there are two species of mako sharks living today: *Isurus oxyrinchus* (the short fin

mako), and *I. paucus* (the long fin mako), much of what is known about the habitat and biology of mako sharks has been derived from *I. oxyrinchus*, a cosmopolitan, coastal and pelagic species. The short fin mako is a common, extremely active and epipelagic species found in tropical and warm temperate seas, but seldom occurring in water below 16°C (Compagno, 1984). From the shape of the teeth, and the feeding preferences recorded for *I. oxyrinchus*, it can be implied that the mako sharks are primarily fish-feeders, that use their elongated and pointed teeth to grasp their prey. Since early Paleocene times, teeth with "isurid" tooth shapes have been found in shallow water deposits, as part of abundant and diverse ichthyofaunas (that include many teleostean species). This association (makos and bony fishes) has also been known and documented in younger Pale- and Neogene local faunas, as it occurs in the Oligocene Sand Member of the Jewett Sand, Pyramid Hill California (Mitchel and Tedford, 1973); in the middle Miocene Sharktooth Hill Bonebed, in Kern Co., California (Barnes, 1976, 1978); and in the middle Pliocene "Loma del Tirabuzón", in Baja California Sur, Mexico (Applegate, 1978; Carreño, 1981), among many other local faunas, where 14 species of *Isurus* have been recorded (Espinosa-Arrubarrena, 1987). For what has been mentioned, it is not difficult to imagine that the "isurid" material from La Mesa de Copoya, as coming from a medium sized shark ([?] 3 m long) that could inhabit depths ranging from almost the surf of tropical or warm-temperate waters to around 150 m, and having an almost exclusive diet of other elasmobranch species and of bony fishes.

**Phyletic significance.** According to Espinosa-Arrubarrena (1987), during the Neogene, at least three major lineages of mako sharks (*Isurus*) can be recognized. One possesses teeth with elongated crowns associated with fish predation; another is a group with large and totally labio-lingually flattened teeth, adapted for preying on marine mammals; and a third one, with robust and moderately flattened teeth intermediate between the first and second categories. More recently, Martin (1996), through comparative analysis of the mitochondrial DNA sequences of extant species of *Isurus* and the fossil record, inferred that the origin of *Isurus* may have occurred some time in the Paleocene or early in the Eocene. Therefore, to understand the origin and evolution of this interesting taxon in terms of the major Neogene radiation of the isurid lineages (*sensu* Espinosa-Arrubarrena, 1987), it is necessary to study and assess the relationships of the Paleogene species (e.g., *I. winkleri*, *I. sheppeyensis*, etc.). Within this phyletic framework, when eventually complete tooth sets be available, La Mesa de Copoya isurid material will contribute important elements to the *Isurus* fish-predator lineage.

Family Carcharodontidae *sensu* Applegate and Espinosa-Arrubarrena, 1996

Genus *Carcharodon* Müller and Henle, 1938

***Carcharodon auriculatus* Blainville, 1818**

(Plate 3, figure B)

**Synonymy**—For an extensive discussion on the synonyms of this species, see Applegate and Espinosa-Arrubarrena (1996).

**Referred material**—One incomplete tooth designated as IGM-6986.

**Geochronologic range**—*Carcharodon auriculatus* is a middle Eocene species known from practically all the world (Applegate and Espinosa-Arrubarrena, 1996). It is important to notice that from all the shark taxa present in La Mesa de Copoya local fauna, *C. auriculatus* is the one having the shortest stratigraphic range, which is confined to the middle Eocene.

**Geographic distribution**—*C. auriculatus* has been reported from Belgium and other European countries, as well as from North America, and Japan (Applegate and Espinosa-Arrubarrena, 1996).

**Description**—Teeth with triangular and comparatively sharp crowns (particularly the anterior positions) that tend to broaden towards the base. Contrary to other Lamniformes (*Carcharias*, *Odontaspis*, *Isurus* and *Lamna*), that show crowns with smooth sides, in *Carcharodon* the cutting edges bear conspicuous serrations, and in the case of *C. auriculatus*, the serrations are strong and irregular. At the sides of the crown's bases, there is a pair of lateral denticles that is also strongly serrated. The roots tend to be flat, and the branches are not as elongated as in other *Carcharodon* species. With the only exception of the Paleocene *C. orientalis*, the teeth of *C. auriculatus* are the smallest in all the *Carcharodon* lineage (Applegate and Espinosa-Arrubarrena, 1996). Unfortunately, the single tooth recovered from La Mesa de Copoya is broken (two thirds of the crown are missing), and moderately worn. However, the size and shape of the root, the presence of serrated denticles, and the strong and irregular serrations (that can be seen in what little is left along the sides of the crown), allow its reliable taxonomic assignment to *C. auriculatus*.

**Discussion**

**Taxonomic assessment.** Although with many synonyms reported in the literature, perhaps *C. auriculatus* is one of the best documented Paleogene shark species; it is easily distinguished from other great white taxa, because of its small tooth size (for *Carcharodon* standards), less than 4 cm in height. The upper lateral teeth are strongly curved towards the rear of the jaw and the interspace between the root branches is shallow. It bears large serrations similar to those of the Paleocene and early Eocene *C. orientalis*. The taxonomic assignment of the Copoya specimen to *C. auriculatus*, is based on the artificial set assembled by Applegate from material housed in the US National

Museum of Natural History, and in the British Museum of Natural History.

**Biogeographic significance.** Because its cosmopolitan tropical distribution (Purdy, 1996), *C. auriculatus* is a species that has little value to assess the biogeographic affinities of La Mesa de Copoya local fauna.

**Ecological considerations.** This middle Eocene cosmopolitan "great white" species reached a similar size to that of extant *Carcharodon carcharias* average adult specimens, but there is a striking difference to notice, individuals of *C. carcharias* are born with elongated crowns and conspicuous lateral denticles, thus having almost the same shape as those of *C. auriculatus*. Later, as *C. carcharias* matures, the teeth grow, lateral denticles disappear and the bases of crowns broaden considerably, whereby changing the teeth's functional morphology from grasping devices to effective cutting blades; this is concomitant to a change in the shark's feeding habits from a fish feeder to a marine mammal predator (prey includes seals, sea lions, dolphins and occasionally whales); the change is also reflected in the distribution. On the other side of this haeckelian recapitulation lies *C. auriculatus*, retaining the grasping fish-feeder dental structure throughout its life. This obvious feeding strategy difference between Paleogene and Recent members of the *Carcharodon* lineage can be interpreted in terms of: (a) a fairly abundant ichthyofauna during the middle Eocene at La Mesa de Copoya, that allowed the presence of so many shark species adapted to fish predation; and (b) a significant local deficit of large prey (e.g., marine mammals) during the Paleogene. Therefore, with the paleobiological information at hand, the middle Eocene *Carcharodon auriculatus* from Copoya can be regarded as an expected element in terms of the other fish-feeder taxa recovered in this coastal, shallow water, tropical or subtropical deposit.

**Phyletic significance.** *Carcharodon auriculatus* is a species that in the last 35 years has been variously interpreted in terms of its phyletic implications. For some European paleontologists (e.g., Casier, 1960; Cappetta, 1987), *C. auriculatus* does not belong to the Genus *Carcharodon* at all, but it is placed within the Genus *Carcharocles*, Jordan & Hannibal 1923. Alternatively, other authors include *C. auriculatus* in *Carcharodon*, but disagree on the origination time of at least two lineages. For Purdy (1996), *C. auriculatus* is a branch of the Paleocene *C. orientalis*, that since the middle Eocene developed a distinct lineage of "small-toothed" *Carcharodon* species, out of which, the extant *C. carcharias* was derived. Applegate and Espinosa-Arrubarrena (1996) agree with Purdy (1996) in the age and ancestry of *C. auriculatus*, but disagree in the splitting time between the small and large-toothed species. Contrary to Purdy's (1996) middle Eocene branching scheme, Applegate and Espinosa-Arrubarrena (*op. cit.*) suggest that such splitting could have occurred between the late early or middle

Oligocene, or even much later (maybe as late as early Miocene), thus bringing the splitting episode much closer timewise to the ocean cooling event, that started during the late Eocene (Savin *et al.*, 1975), and to the middle Miocene periods of greater diversity and abundance of marine mammals (Barnes, 1976; Espinosa-Arrubarrena, 1987). Therefore, additional Paleogene carcharodontid material from La Mesa de Copoya, may become essential to elucidate the true *Carcharodon* lineage-splitting time.

Family ?Otodontidae Glückman, 1964

**Genus *et species* indet.**

(Plate 3, figure C)

This fragmentary specimen (IGM-6987), probably represents the Genus *Otodus*, characterized by massive teeth with robust crowns that bear smooth cutting edges (although sometimes show fine serrations), and conspicuous lateral denticles. Plate 3, figure C, shows part of the massive root of the lateral denticle that resembles those of this genus, or of an *Otodus*-like form. Interestingly, the oldest records of *Otodus* come from beds of the Early Paleogene of Europe, North America and West Africa. According to Applegate and Espinosa-Arrubarrena (1996), *Otodus* became extinct by the middle Eocene.

Order Carchariniiformes Compagno, 1973

Family Hemigaleidae Hasse, 1879

Genus *Hemipristis* Agassiz, 1843

***Hemipristis* sp.**

(Plate 4, figure A)

**Referred material**—An almost complete tooth, with the tip of the left branch of the root missing, designated as IGM-6988.

**Geochronologic range**—Although *Hemipristis* became widespread during the Miocene, it has been recorded since the middle Eocene, and throughout the Tertiary (Cappetta, 1987). In 1984, Compagno synonymized the only living form *Durrhizodon* (from the Indian Ocean) with *Hemipristis*, hence, the range of this taxon can be considered from Early Paleogene to the Recent.

**Geographic distribution**—In general, the Tertiary reports of *Hemipristis* (mostly from the Miocene) come from Europe, North and South America, North and West Africa, India, and Indonesia. The Paleogene species have been reported in Egypt, U.S.A., Western Africa, and South America (Cappetta, 1987). Applegate (1986) has reported its presence from Late Paleogene beds of Baja California Sur, Mexico.

**Description**—Teeth that have triangular crowns, with characteristic and numerous well marked serrations along their cutting

edges that start at the base and disappear toward the apex. In the tooth illustrated in Plate 4, figure A (identified as a left upper lateral), the central part of the crown, devoid of serrations, is so incomplete and worn, that hardly stands out from the serrations level. The roots are not very high (although in some teeth they are robust and high). The incompleteness of the specimen precludes a more detailed description, however, the taxonomic assignment of the Copoya specimens to a generic level, can be justified on the basis of the serrations and its small size (8 mm long and 7 mm high). This taxon is noted by its remarkable heterodonty, particularly between the upper and the lower positions.

**Discussion**

**Taxonomic assessment.** Even though over half of the crown is missing in the available specimen, it is possible to infer that the heights of the crown and the root are equal. This condition places the tooth within the Genus *Hemipristis*. Also, the fact that there are only step-like serrations at the base of both sides of the crown (the smallest being at the bottom), easily separates this genus from others with similar serrations (*e.g.*, *Galeocerdo*).

**Biogeographic considerations.** The living species of *Hemipristis* is confined to the Indian Ocean. However, the fossil taxa show a worldwide distribution, as late as the late Pliocene (where they attained their largest size). Therefore, *Hemipristis* can be considered an expected element in a middle Eocene tropical ichthyofauna.

**Ecological significance.** The extant *Hemipristis elongatus* is confined to the Indian Ocean, where it lives in warm coastal waters (Compagno, 1984). In the fossil record, *Hemipristis* is a genus that has been found abundantly in tropical neritic and coastal Paleogene and Neogene deposits of the world, becoming scarce in more boreal areas. Although in some Neogene deposits the teeth of *Hemipristis* have been associated with large prey or carrion (*e.g.*, marine mammals), their elongated lower teeth could have served as a grasping mechanism, that allowed a piscivorous diet for *Hemipristis* sp. in La Mesa de Copoya.

**Phyletic significance.** *Hemipristis* is a widely distributed and abundantly collected taxon in the Neogene deposits of the world, whereas in the Paleogene local faunas, teeth of this taxon are not common. Nevertheless, at least there are two nominal Eocene species; *H. curvatus* Dames 1833, and *H. wyattdurhami* White 1956. Unfortunately, with this isolated and fragmentary tooth, it is impossible to know if the La Mesa de Copoya *Hemipristis* belongs to either, or if it represents a separate species. The available record of the beginning of the *Hemipristis* lineage is very scarce; therefore, the presence of *Hemipristis* sp. in La Mesa de Copoya, is a significant addition.

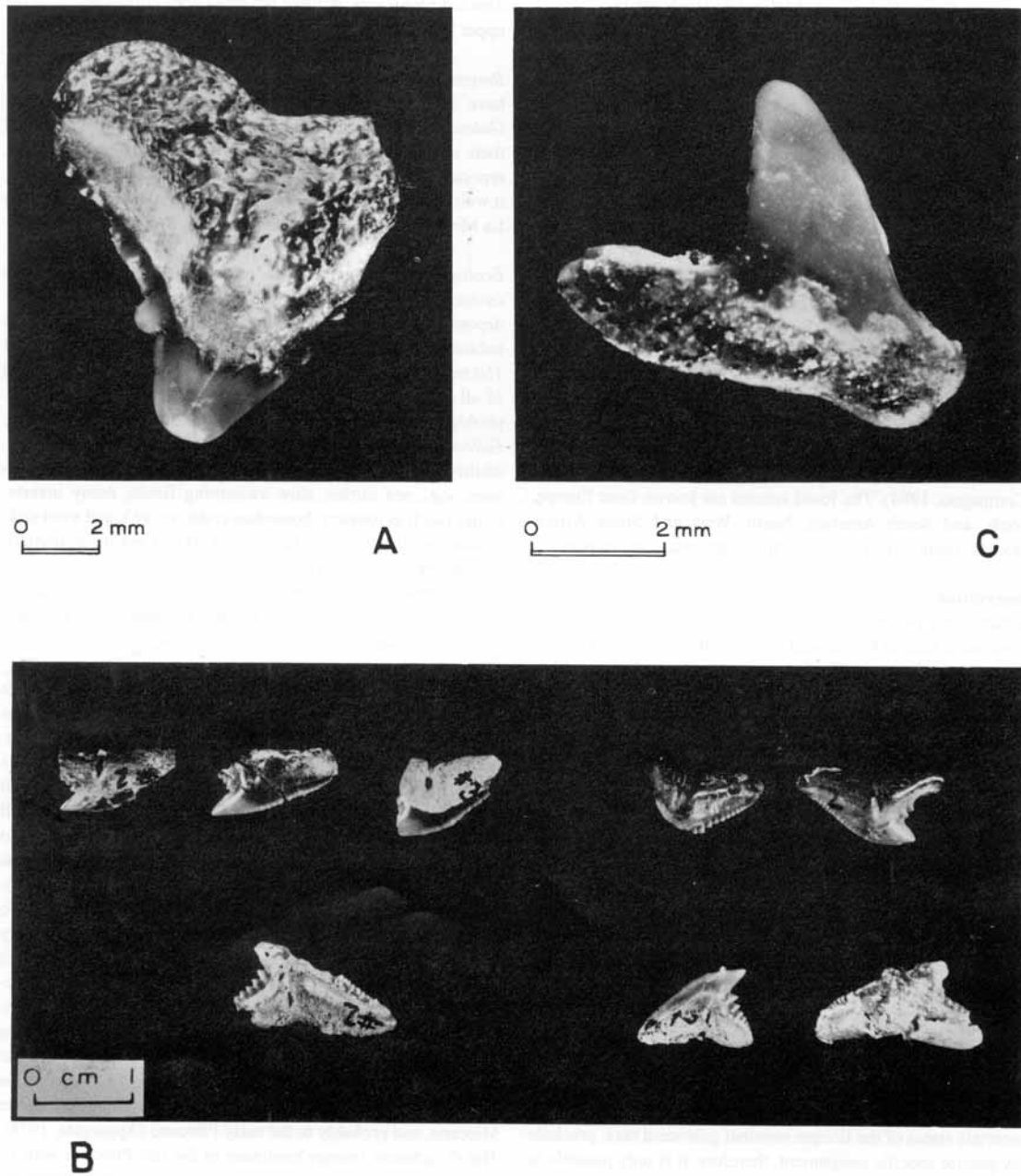


Plate 4. *Hemipristis*, *Galeocerdo* and a possible carcharhiniform. Figure A, IGM 6988, a nearly complete upper lateral tooth referred to *Hemipristis* sp. Figure B, IGM 6989, a lot of five upper and three lower teeth that form an artificial set referred to *Galeocerdo* sp. Figure C, IGM 6990, a very small specimen (5 mm long and 4 mm high) that may correspond to a lower tooth of a primitive carcharhiniform.

Family Carcharhinidae Jordan and Everman, 1896  
Genus *Galeocerdo* Müller and Henle, 1838

*Galeocerdo* sp.  
(Plate 4, figure B)

**Referred material**—An incomplete tooth set composed of eight teeth (five uppers and three lowers) designated as IGM-6989 (series 1-5).

**Geochronologic range**—*Galeocerdo* ranges from the early Eocene, occurring in the Monte Bolca beds, Italy (Applegate, 1978), to the Recent, where it is represented by a single species, *G. cuvier*, that reaches a length of five meters. *G. cuvier* bears large teeth, whereas early Eocene species show significantly smaller teeth (Applegate, 1978); individual Paleogene tiger sharks seem not to have exceeded 1.5 m in length (Applegate, *op. cit.*).

**Geographic distribution**—The extant *G. cuvier* has a well-documented cosmopolitan temperate and tropical distribution (Compagno, 1984). The fossil species are known from Europe, North, and South America, North, West and South Africa, Celebes, India, Japan and Australia (Cappetta, 1987 in part).

**Description**—Small teeth, less than 1 cm high and 15 cm long, including the two branches of the root. The mesial edge of the upper teeth tend to be rounded, whereas the lower teeth tend to be straight and narrow. The incomplete tooth set shown in Plate 4, figure A, is composed of five upper and three lower teeth. There are two laterals from the right side of the upper jaw and three laterals from the left side. In the remaining lower positions, there is one lateral (incomplete and worn), from the left side of the jaw and two from the right side. One is well preserved and the adjacent is larger, broken and incomplete. One feature that can be seen in all the teeth (typical of the genus) is the serration pattern of the crown. Along the mesial side of the cutting edges the serrations are comparatively fine, regular and gradually fade towards the tip of the crown. On the distal side, at the base of the cusps (forming a blade) the step-like serrations increase their size towards the tip of the crown, where they disappear sharply, making the upper part of the crown a completely smooth structure.

**Discussion**

**Taxonomic assessment.** The incompleteness of the teeth and the uncertain status of the Eocene nominal galeocerd taxa, preclude any precise specific assignment, therefore, it is only possible to state that La Mesa de Copoya material belongs to *Galeocerdo*, and within the genus, it shows some characteristics of what Applegate (1978) described as the "*G. aduncus*" lineage, which includes at least four galeocerd Neogene species. The shared characters consist of upper teeth with curved edges toward the

back of the jaw, and lower teeth with narrow crowns (at the tip) directed backwards, without the pronounced curved edges of the upper positions.

**Biogeographic considerations.** At least three nominal species have been recognized worldwide from the middle Eocene: *Galeocerdo eaglesomi*, *G. latidens*, and *G. semilevi*; should their distribution be similar to that of the extant *G. cuvier*, reported from temperate and tropical regions through the world, it would be expected that at least one such species be present in La Mesa de Copoya local fauna.

**Ecological significance.** The extant tiger shark *Galeocerdo cuvier*, has been reported in tropical and temperate marine deposits of the world, showing a wide tolerance to different habitats, from the surface and intertidal zone to depths of almost 150 m (Compagno, 1984). This species is the least specialized of all sharks, as borne out by its undifferentiated dental morphology (fully displayed in complete tooth sets), thus making *Galeocerdo cuvier* primarily an active scavenger, with the possibility of opportunistically preying upon slow moving organisms, *e.g.*, sea turtles, slow swimming fishes, many invertebrates (such as lobsters, horseshoe crabs, *et cet.*); and even sick, injured or otherwise handicapped sharks or marine mammals. The presence of *Galeocerdo* sp. as a possible scavenger-opportunistic predator in La Mesa de Copoya deposit is expected, in terms of the rich ichthiofauna needed to support the recorded shark assemblage.

**Phyletic significance.** The occurrence of the *G. aduncus* lineage (*sensu* Applegate, 1978) in the middle Eocene is important, as it points to an early origin of this clade of tiger sharks. However, with the limited material at hand, the specific placement of La Mesa de Copoya *Galeocerdo* is still open. Tentatively, it appears to be close to *G. semilevi* White, 1926, and certainly it is not related to *G. latidens* Agassiz, 1843. According to Applegate (1978), some time in the Paleocene, *Galeocerdo* was derived from *Galeorhinus* or, a close related form (of soupfin-like shark), and the oldest positively identifiable *Galeocerdo* teeth come from undescribed materials from Nanjamoy, early Eocene of Virginia, and from the middle Eocene Red Hot Locality of Mississippi, U.S.A. Tiger sharks form a very distinctive line of scavenger-opportunistic predator species, that started with the Eocene form (including the La Mesa de Copoya specimens) through the Paleogene. Later in Early Neogene times, arose the *Galeocerdo aduncus* Agassiz, 1843 part of the lineage, which has a good record from the middle to the late Miocene, and probably to the early Pliocene (Applegate, 1978). The *G. aduncus* lineage continues in the late Pliocene with *G. rosaliaensis* Applegate, 1978, a species that has been commonly found in middle and late Pliocene deposits of the Baja California Peninsula. Finally, probably since Pleistocene times, the Recent *Galeocerdo cuvier* arose, becoming the youngest member of this clade of tiger sharks.

**?Carchariniformes**Family, Genus *et* species indet.

(Plate 4, figure C)

A very small tooth, less than 5 mm long and 4 mm high (Plate 4, figure C). The specimen (IGM-6990) is incomplete, lacks one branch of the root, and bears a smooth edged crown (suggesting that corresponds to a lower position). There are no lateral denticles present toward the base of the crown. This is a "primitive" taxon that has not been recorded yet in the Early Paleogene. Nevertheless, the tooth shows already some carcharhinid characteristics that are indicative of an important "pre-gray shark" radiation, from which the Genus *Carcharhinus* itself perhaps originated some time during the early or middle Eocene. A larger sample from La Mesa de Copoya (with more complete specimens), will provide important information regarding the origin and early records of *Carcharhinus*, the dominant group of sharks living today in all the seas of the world.

## DISCUSSION: PALEONTOLOGICAL SIGNIFICANCE OF LA MESA DE COPOYA SELACHIFAUNA

## TAPHONOMIC ASPECT

The present-day Middle American-Caribbean-Antillean region (Figure 2) is indeed vast, spans 27 longitude degrees length-wise, and averages 10 latitude degrees width-wise, its inner perimeter is about 11,200 km, the sea surface alone exceeds 10,000,000 km<sup>2</sup>, and the surrounding land adds at least 1/10 that much; during the middle Eocene it was just as large, if not larger, and was inhabited by a rich, tropical marine fauna, of which some invertebrate groups such as larger foraminifera, corals and mollusks have left a record long known throughout the region (*cf.* among others Schuchert, 1935; Woodring, 1954, 1957, 1966, 1978; Durham *et al.*, 1955; Cole, 1956, 1958, 1959; Cole and Aplin, 1964; Frost and Langenheim, 1974; Butterlin, 1977, 1981). The vertebrates so far, have eluded discovery for the most part, and this in itself is quite paradoxical: Were the fishes—sharks included—rare at the time in the region, or their preservation as fossils was a rare event? The actualistic approach leads us to exclude the first alternative, so at least for the sharks teeth, the second alternative should be explored; here the taphonomic information may shed light on the riddle.

Sharks teeth do not occur in a bone bed, nor in concentrations, such as those of Loma del Tirabuzón, Santa Rosalía, Baja California Sur (Carreño, 1981) or Monte Bolca, Italy (Applegate, 1978). On the contrary, the sharks teeth of Copoya sparsely appear in the San Juan Formation strata that cap La Mesa de Copoya, forming an erosion resistant limestone blanket, no thicker than 6 to 12 m, thus making only 2% of the estimated thickness of this unit in the area. These strata are largely composed of the Lithovarieties 1, 2, 5 and 6; the first two, as

discussed elsewhere (Ferrusquía-Villafranca *et al.*, in press), are sedimentological riddles themselves, because they seem to incorporate sediments laid down in two contrasting flow regimes (high and low energy), somehow coexisting in the same place.

The sharks teeth are spacially separated from each other by distances of 5 to 10 m (or more), appear frequently broken, and show some degree of abrasion. This taphonomic pattern is not what could have resulted from teeth accumulated by carcass decay, or shedded off by sharks while eating; in both instances a closer spacing and no fractures nor abrasion could be expected. This indicates that the teeth underwent transport after being laid down in the sea bottom, perhaps by the same type of currents that transported the quartz-granules and grains (that make a very distinctive feature of Lithovarieties 1–2) to their final resting place. A possible scenario could be afforded by short lived intertidal channels that soon became sites of nearly standing water (*i.e.*, with little kinematic energy), perhaps as a result of abrupt changes in sea level (rising beyond tidal influence), not uncommon in a tectonically active region, as it is and was the Middle American-Caribbean-Antillean one. This set of conditions falls in a very narrow sector of the tectono-depositional spectrum, which in turn may account for the rarity of fossil-bearing sharks teeth sites in the region.

## TAXONOMIC AND GEOCHRONOLOGIC ASPECTS

The methodology employed (using artificial sets), assures confidence to the taxonomic identifications, leading to caution and precluding the formal recognition and/or generation of species based on single or very few isolated teeth. To be most effective, this methodology requires large amounts of individual teeth of the various dental positions; in turn, this is best accomplished in localities bearing large quantities of already isolated teeth. The collection from La Mesa de Copoya, consists only of less than 200 specimens, resulting from acetic acid-dissolution of nearly half a ton of limestone rock, and out of these, a little less than half were taxonomically useful. Therefore, of the 10 possible recorded species, only three could be identified at the specific level, and other five at the generic level (Table 1). This level of resolution limits La Mesa de Copoya Selachifauna's usefulness as a geochronologic and sedimentary-environmental indicator. Neither aspect is critical for the present study, however, because evidence from the associated invertebrate fauna and the lithostratigraphic units themselves (*cf.* Ferrusquía-Villafranca *et al.*, in press, stratigraphic section), more than offset this limitation.

The fauna includes 10 species referable to eight named genera, to as many families, and to three orders (*cf.* Ferrusquía-Villafranca *et al.*, in press, Table 1); it records a small portion of the selachian fauna that inhabited the Middle American-Caribbean-Antillean region during the middle Eocene. The total diversity of such fauna is at present unknown, but probably was at least as big as that of the extant selachifauna, which com-

Table 1. Geochronological range, environmental parameters and geographic distribution of recorded shark taxa at La Mesa de Copoya, west-central Chiapas, south-eastern Mexico.

FEATURES	<i>Nebrius</i> sp.	<i>Striatolamia</i> <i>macrota</i>	<i>Carcharias</i> sp.	<i>Odontaspis</i> sp.	<i>Isurus</i> cf. <i>I.</i> <i>praecursor</i>	<i>Carcharodon</i> <i>auriculatus</i>	<i>Hemipristis</i> sp.	<i>Galeocerdo</i> sp.
A. Geochronological range	Paleocene-Holocene	Eocene	Albian-Holocene	Campanian-Holocene	early-middle Eocene	Middle Eocene	middle Eocene-Holocene	early Eocene-Holocene
B. Inferred ecological conditions								
1. Water temperature *	Tropical	Tropical warm-temperate	Tropical warm-temperate	Tropical warm-temperate	Tropical warm-temperate	Tropical warm-temperate	Tropical	Tropical warm-temperate
2. Water depth	Shallow (< 70 m)	Shallow-moderately deep (< 200 m)	Shallow-moderately deep (< 200 m)	Shallow-deep (< 500 m)	Shallow-deep (< 500 m)	Shallow-?moderately deep (< 200 m)	Shallow-deep (< 500 m)	Shallow-deep (< 500 m)
3. Littoral nearness *	Near shore	Near shore	Near shore-off shore	Near shore-off shore	Near shore-off shore	Near shore-off shore	Near shore-off shore	Near shore-off shore
4. Feeding habits	Small-invertebrate crusher	Piscivorous	Piscivorous	Piscivorous	Piscivorous	Piscivorous	Piscivorous	Scavenger
C. Geographic distribution								
North America	√	√			√	√	√	√
South America				√	√		√	√
Atlantic Ocean			Extant					
Europe	√	√	Mediterranean	√	√	√	3 (Miocene)	
Africa	√			√	√		√	√
Indian Ocean	Extant		Extant				Extant	
Australia						√		√
Antarctica						√		
Pacific Ocean			Extant					
Asia				√		√	√	√

\* Qualitative description.

Sources: see Systematic Paleontology section in this paper.

prises *circa* 350 species, 98 genera, 28 families and eight orders (Compagno, 1984), as befits a tropical fauna inhabiting a vast geographic realm. As to how many species of sharks might coexist in a given site, is a problem that could be approached by direct systematic observations; these are scarce, so that for Chiapas, the only study is that of Castillo-Geniz and collaborators (1997), who reported that fishers home-based in Puerto Madero, Chis., captured in the 1996-1997 fiscal year 14 shark species in the adjacent Pacific. In this regard, the recorded diversity in La Mesa de Copoya is not far below this actualistic standard.

Another indirect mean of estimating the selachian middle Eocene diversity of the region, is its linkage with the tropical invertebrate coexisting fauna (Figure 2), which was fairly diverse (*cf.* Schuchert, 1935; Woodring, 1954, 1966; Frost and Langenheim, 1974; Butterlin, 1981). All points to the great potential of the area for future discoveries, and as a much needed window to shark diversification in the tropics during the Paleocene. In this regard, the phyletic significance of the recorded taxa, has already been discussed.

#### BIOGEOGRAPHIC AND ECOLOGICAL ASPECTS

Most genera recorded in La Mesa de Copoya have living species with a wide geographic distribution in tropical and

warm-temperature waters in the Atlantic, Pacific and Indian Oceans (*cf.* Compagno, 1984; Cappetta, 1987); something similar occurs with the Paleogene species (Figure 3) (Compagno and Cappetta, *op. cit.*). Hence, the Copoya selachifauna consists of cosmopolitan genera (Table 1), not amenable to be ascribed to any particular marine province.

The geographic position of west-central Chiapas (where La Mesa de Copoya is located) during the middle Eocene was very close to the present-day one (*cf.* Ross and Scotese, 1988; Pindell and Barrett, 1990; Smith *et al.*, 1994) (Figure 3), *i.e.*, it lay in the tropical region. The sedimentary-environmental and paleontological evidence presented and discussed for the San Juan Formation (Ferrusquía-Villafraña *et al.*, in press), indicates that this unit, which bears the Copoya selachifauna, was laid down in tropical, nearshore, shallow marine waters, probably covering a bank or platform set in an epicontinental sea. This interpretation agrees with that given by previous authors to this or equivalent units in Chiapas (*cf.* Durham *et al.*, 1955; Gutiérrez-Gil, 1956; Müllerried, 1957; De La Rosa *et al.*, 1993; Frost and Langenheim, 1974; Sánchez-Montes de Oca, 1978; *et cet.*). The environmental information recorded in the Copoya selachifauna, summarized in Table 1, calls for a similar scenario.

The odontography of most Copoya sharks indicates a piscivorous habit, and by implication the coexistence of an abun-



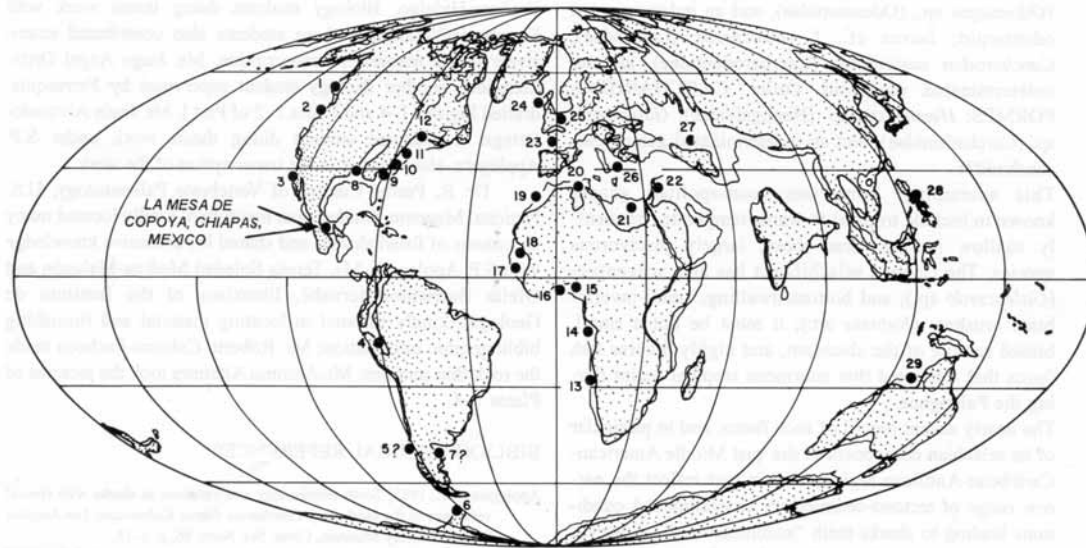


Figure 3. Chief selachian fossil localities of the recorded taxa at La Mesa de Copoya, Chiapas, Mexico, displayed on a middle Eocene paleogeographic reconstruction (*sensu* Smith *et al.*, 1994). For each locality, its geographic occurrence and reported middle Eocene taxa are given. Some taxa's age is Eocene, without any further precision. (1) Oregon, USA: *Striatolamia macroti*; (2) California, USA: *Striatolamia macroti*; (3) Baja California Sur, Mexico: *Hemipristis* and possibly *Isurus*, *Carcharodon auriculatus* and *Galeocerdo*; (4) Peru: *Hemipristis*; (5) Chile?: *Striatolamia macroti* and possibly *Isurus* and *Hemipristis* (with different nominal designations); (6) Antarctica (Meseta Formation, Seymour Island): *Striatolamia macroti*, and *Carcharodon auriculatus*; (7) Argentina?: possibly *Isurus*, *Hemipristis*, and *Striatolamia macroti* with different nominal designations; (8) Alabama, USA (Jackson Formation): *Galeocerdo*; (9) Georgia, USA: *Nebrius*, *Hemipristis*; (10) South Carolina, USA: *Striatolamia macroti* and many primitive carcharhinid forms; (11) Virginia, USA: *Galeocerdo* (doubtful); (12) Maryland, USA: *Odontaspis*; (13) Angola: *Striatolamia macroti*, *Odontaspis*, *Galeocerdo*, *Otodus*; (14) Landana Cabinda: *Striatolamia macroti*; (15) Nigeria: *Carcharodon auriculatus*, *Galeocerdo*; (16) Togo: *Nebrius*, *Carcharias*, *Isurus praecursor*, *Carcharodon auriculatus*, *Galeocerdo*; (17) Guinea Bissau: *Nebrius*, *Isurus praecursor*, *Hemipristis*, *Galeocerdo*; (18) Senegal: *Nebrius*; (19) Morocco: *Nebrius*, *Striatolamia macroti*, *Carcharias*, *Galeocerdo*, *Otodus*; (20) Tunisia: *Nebrius*, *Galeocerdo*; (21) Cairo, Egypt: *Nebrius*, *Hemipristis*, *Galeocerdo*; (22) Syria: *Isurus praecursor*; (23) France: *Striatolamia macroti*, *Carcharodon auriculatus*; (24) England: *Carcharias*, *Otodus*; (25) Belgium: *Nebrius*, *Striatolamia macroti*, *Carcharias*, *Odontaspis*, *Isurus praecursor*, *Carcharodon auriculatus*, *Galeocerdo*, *Otodus*; (26) Bulgaria: *Otodus*; (27) Kazakhstan: *Striatolamia macroti*; (28) Japan: *Carcharodon auriculatus*; (29) Australia: several forms of primitive middle Eocene carcharhinid-like taxa.

**Chief sources** (*cf.* this paper's Systematics section for details): **Published:** Leriche (1951); Casier (1960); Welton and Zinsmeister (1980); Applegate (1986); Cappetta (1987); Applegate and Espinosa-Arrubarrena (1996). **Unpublished:** Written and personal communication from Dr. Bruce J. Welton (Mobil Exploration and Producing Technical Center in Dallas, Texas); S.P. Applegate and L. Espinosa-Arrubarrena, personal record of their revisions of major fossil shark's teeth collections in Mexico, United States and Europe.

dant and diverse fish fauna, able to support taxa such as *Carcharias* sp., which preys on large fishes, or *Odontaspis* sp., a predator of smaller, perhaps less rapid swimmers. It should be noted that species of this genus are usually deep water inhabitants, but some are also known to occur in very shallow waters (Compagno, 1984), therefore the presence of *Odontaspis* sp. in Copoya is not incongruent with the rest of the fauna or with the assessed environmental scenario. Finally trophic-wise, scavengers like *Galeocerdo* sp., and bottom-prone, small invertebrate eaters (crushers), such as *Nebrius* sp., also known to prefer reef environs where it preys upon coral buds, complete the roster of recorded sharks in La Mesa de Copoya.

During the middle Eocene, the coexistence in the Copoya area of sharks and sirenians (already known there [Müllerried, 1932]), and perhaps other marine mammals as well, may have

occurred, but it is not reflected in the recorded shark species, neither of which show the typical flesh-slicing adaptations displayed by the teeth of sharks commonly preying on marine mammals. The scant available evidence does not allow to decide whether this fact reflects a sample bias, or a true absence of marine mammals (other than sirenians) in the region at the time.

#### SUMMARY AND CONCLUSIONS

1. La Mesa de Copoya Selachifauna is the first Paleogene shark fauna described from the vast Middle American-Caribbean-Antillean region, and consists of these taxa: Order. ORECTOLOBIFORMES: *Nebrius* sp. (Gynglimostomidae). Order LAMNIFORMES: *Striatolamia macroti*, *Carcharias* sp. (Carcharidae);

- ?*Odontaspis* sp., (Odontaspidae), and an indetermined odontaspid; *Isurus* cf., *I. praecursor* (Lamnidae), *Carcharodon auriculatus* (Carcharodontidae), and an indetermined otodontid. Order. CARCHARHINI-FORMES: *Hemipristis* sp. (Hemigaleidae), *Galeocerdo* sp. (Carcharhinidae), and an indetermined genus (carcharhinid?).
2. This assemblage comprises cosmopolitan genera known to include tropical to warm-temperate, frequently shallow marine, near shore, largely piscivorous species. The Copoya selachifauna has also scavengers (*Galeocerdo* sp.), and bottom-dwelling, small-invertebrate crushers (*Nebrius* sp.); it must be but a small, biased sample of the abundant, and highly diverse fish fauna that inhabited this enormous tropical realm during the Paleogene.
  3. The nearly absent record of such fauna, and in particular of its selachian component in the vast Middle American-Caribbean-Antillean region, may in part reflect the narrow range of tectono-sedimentary environmental conditions leading to sharks teeth "accumulations"—however scarce—in strata and deposits such as those of La Mesa de Copoya; this in turn lends additional scientific importance to this fauna.

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