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PHYLETIC STUDIES; PART I; TIGER SHARKS

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RESUMEN

Se describe una nueva especie de tiburón tigre *Galeocerdo rosaliaensis,* de la formación conocida como "Gloria", de Baja California Sur. Esta especie está basada sobre la discernible heterodoncia entre los dientes superiores e inferiores y parece ser la transición entre *Galeocerdo aduncus* y *G. cuvier.*

La lista de tiburones de la Formación "Gloria", muestra hasta la fecha 29 especies, comparadas con 43 vivientes en el Golfo de California. Seis especies de esta formación están extintas y cuatro representan, hasta donde se conoce, especies que ya no ocurren en el golfo.

La fauna de tiburones (localidad B.C.S. 2 del Instituto de Geología), sugiere que se trata de depósitos de mar abierto con amplitud de 10 a 100 m de profundidad. Se piensa que los carcharhinidos descritos por Cappetta (1975) parecen ser galeocerdidos primitivos y deberían haber sido colocados en el género *Alopiopsis.* Se cree que *Gaelocerdo* se originó de este tipo de tiburones durante el Paleoceno tardío o Eoceno temprano, ambos géneros tomando un origen a partir de un ancestro primitivo parecido a *Galeorhinus.*

El redescrito *Alopiopsis* muestra muchas características que uno esperaría en tal transición.

ABSTRACT

A new species of tiger shark *Galeocerdo rosaliaensis* is described from the so called "Gloria" Formation of Baja California Sur. This species is based on easily discernible heterodonty between the upper and lower teeth and is thought to be transitional between *Galeocerdo aduncus* and *G. cuvier.* A list of sharks from the "Gloria" Formation shows todate 29 species, compared with 43 living today in the Gulf of California. Six species from this formation are extinct and 4 represent, so far as known, species that no longer occur in the gulf. The shark fauna from the Santa Rosalia locality (IGCUBCS 2) suggests open sea offshore deposits, in waters that may have ranged from 10 to 100 m.

The carcharhinids described by Cappetta (1975) are thought to be primitive galeocerdids and should have been placed in the genus *Alopiopsis. Galeocerdo* is though to have originated from this sort of shark in the late Paleocene or early Eocene, both genera, having an origin from an early galeorhinid-like ancestor. The redescribed *Alopiopsis* shows many of the features that one would expect in such a transition.

INTRODUCTION

Tiger sharks of which there is only one living species *Galeocerdo cuvier,* have an excellent but complex fossil history dating back to the early Eocene. It seems reasonable to suppose that the tiger sharks arose from the genus *Galeorhinus* or a galeorhinid-like shark. Not only do the teeth of the tiger sharks become more soupfin-like as one traces them back in geological time, but the soupfin lacks many of the tiger shark specializations, such as the keel so characteristic of *Galeocerdo.* The genus *Galeorhinus* is known by good specimens (teeth) from the Paleocene. The genus *Alopiopsis* is known from the lower Eocene of Monte Bolca, Italy. Though inappropriately named, this genus lies between the tiger shark and the soupfin and in this sense warrants retention.

It is here contended that two major problems have retarded our acquisition of knowledge of the fossil history of genus *Galeocerdo:* One is the almost complete lack of attempts to erect artificial tooth sets, which if it accomplished nothing more, the erection of sets, real or artifical, could help eliminate extraneous and spurious species. Another problem is the unwillingness of past and present workers to be aware that Pliocene and older species of tiger sharks, may and often, do show marked heterodonty between the upper and lower teeth as has been suggested by Leriche (1926).

Eocene tiger sharks were quite diversified with at least one other lineage besides that exemplified by *G. aduncus.* The *G. aduncus* lineage, which appears quite early, may have arisen from the transitional genus *Alopiopsis.* The aduncus lineage dominates the Oligocene and the Miocene, it is present in the middle Eocene and abundant in the upper Eocene. It is not proper at this time to discuss the seemingly numerous species that compose this lineage, but that they do exist is clear from the unpublished work that has been done in California, Mexico, and the eastern United States.

THE SANTA ROSALIA LOCALITY (B.C.S. 2)

The copper deposits at Santa Rosalia, Baja California Sur, known since 1868, have a long history of geologic investigation and exploitation, yet it is only in the last twenty five years that the existence of sharks teeth has been known. The first report appeared in a popular article in the Mineralogist (July-August and Sept-Oct. 1963), which illustrated a few teeth but gave neither the exact locality or any identifications.

On August 4, 1965, Mr. Reynoso, of Santa

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Rosalía directed the writer, and Messrs. Pat Royce and Harli Garbani to a site about 5 km north of the town of Santa Rosalía. Here we collected hundreds of sharks teeth, fish and marine mammal bones. At this locality were unusual solidified burrows more than 2 m in height, about 5 cm in diameter, that spiraled downward like a corkscrew into the sediments; because of these features the locality was given the name of "Loma del Tirabuzón", ("Corkscrew Hill' in English; Figure 1).

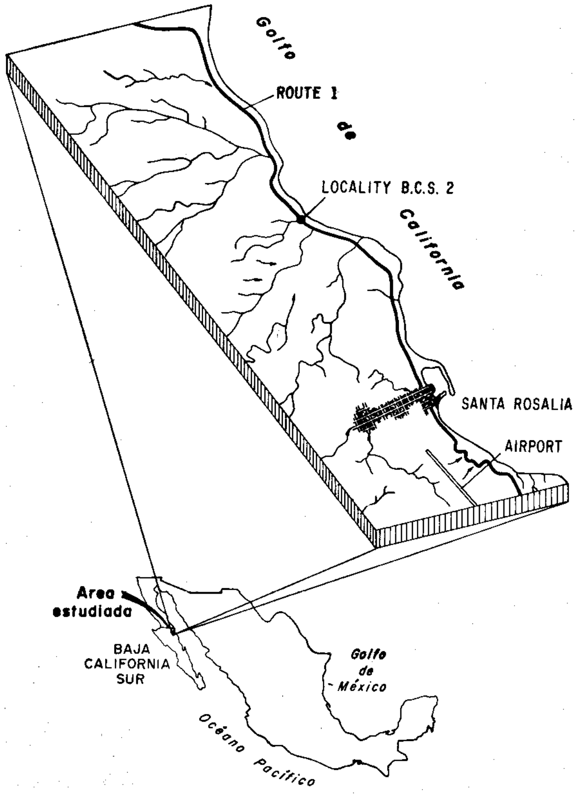

Figure 1.—Index map, showing the location of fossil locality.

This locality (IGCUBCS 2), was visited in 1974 and again in 1975 and a list of the fauna was prepared for a unpublished progress report for the National Geographic Society. In 1976, the area was visited by a crew from the Instituto de Geología from Mexico City, who collected additional fossil material. The material from these collections form the bases for the following list of sharks (Table 1). At Corkscrew Hill at least 15 m of sediments are exposed. These sediments were mapped by Wilson and Rocha (1955) as part of the "Gloria" Formation, and considered to be middle Pliocene in age (Figure 2).

The sharks teeth are from the upper 6.6 m of this section. The teeth were collected by a physical search of the area, bagging the sediments and later screening the matrix and washing the residue.

Unpublished work, done by the University of Southern California, on the basis of the microfauna suggested a late Pliocene or Pleistocene age for the beds (Dr. Robert Douglas, personal communication), a conclusion that is not in keeping with what we know from the sharks. The shark fauna appears older, that is middle Pliocene. The fauna is extensive and there is little doubt that future collecting will add more species to the list of sharks.

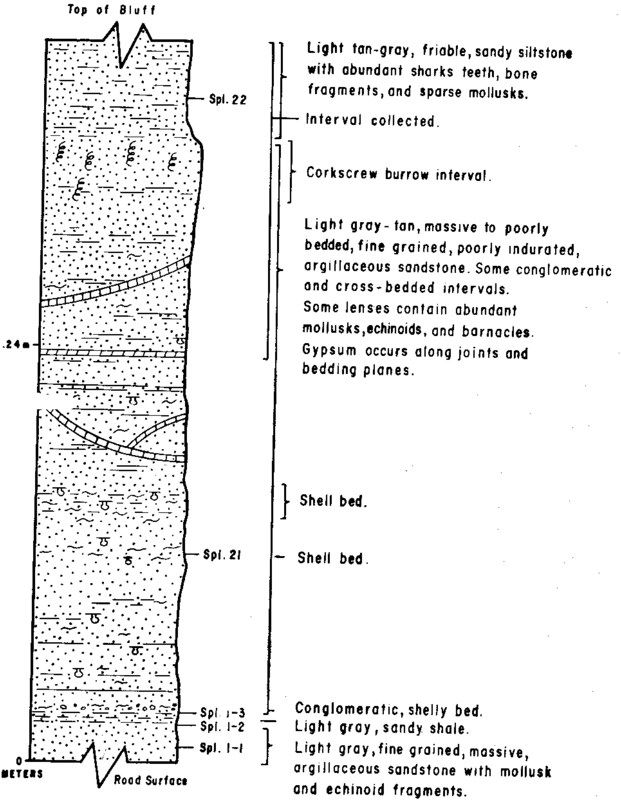

Figure 2.—Columnar section a Corkscrew Hill.

Of the 29 sharks known to date from Santa Rosalía, 6 are extinct (approximately 20 percent); 4 sharks are not known to live in the Gulf of California at the present; 2 genera that would be expected to be present are: the lemon shark, *Negaprion* and the nurse shark, *Ginglymostoma* have not been found. The fauna as a whole points to a moderately deep environment with a depth of 20 to 30 m. Such a depth might have excluded these two shallow water species.

A GENERAL DISCUSSION OF TIGER SHARK TEETH

The artificial tooth set.—The construction of artificial tooth sets has been discussed by Applegate (1965, 1967). The first requirement is that one have a sufficent number of teeth, preferably from one locality, that can reasonably be assigned to a genus or even better a single species. One should try, of course, to pick teeth that would belong to the same size shark. The material should be compared with a living member of the same genus, species, family or with other related tooth sets, natural or artificial. The teeth are first split into uppers and lowers and then are separated into lefts and rights. The right side as viewed from the rear is the prefered side to work with. The teeth are sorted into anteriors, laterals and posteriors and other types as necessary. If gaps in size or shape seem too large, a space is left for the missing tooth or teeth.

In the summer of 1976, we collected at Santa Rosalia (locality IGCUBCS 2). The work involved 7 persons, on August 1-3. At this time we collected 169 teeth that could be identified as to belong to

Table 1.—Sharks from the "Gloria' Formation at Loma del Tirabuzón, 5 km north of Santa Rosalía, Baja California Sur. Geological Institute Museum of Vertebrate Paleontology B.C.S. 2.

Scientific Name	Remarks
1. *Hexanchus* cf. *griseus*	Not yet reported from the Gulf of California fauna.
2. *Notorhynchus* sp.	Not yet reported from the Gulf of California fauna.
3. *Heterodontus* sp.	2 or 3 species living in the Gulf of California.
4. *Squalus* sp.	Not yet reported from the Gulf of California fauna.
5. *Odontaspis acutissima*	Known by only one tooth (extinct).
6. *Isurus benedeni*	Fairly common (extinct).
7. *Isurus oxyrinchus*	Fairly common living in the Gulf.
8. *Carcharodon megalodon*	Rare (extinct).
9. *Carcharodon sulcidens*	Common (extinct).
10. *Carcharodon carcharias*	Not as common as *C. sulcidens* living in the Gulf.
11. *Cetorhinus* sp.	Living, but rare in the Gulf of California.
12. *Rhizoprionodon longurio*	Living in great numbers in the Gulf of California.
13. *Sphyrna zygaena*	Living in the Gulf of California.
14. *Sphyrna lewini*	Living in the Gulf of California.
15. *Sphyrna tiburo vespertina*	Living in the Gulf of California.
16. *Sphyrna media*	Living in the Gulf of California.
17. *Sphyrna mokarran*	Living in the Gulf of California.
18. *Prionace glauca*	Not yet reported from the Gulf of California.
19. *Hemipristis serra*	Extinct.
20. *Galeocerdo rosaliaensis* n. sp.	Extinct.
21. *Carcharhinus leucas*	Living in the Gulf of California.
22. *Carcharhinus obscurus*	Living in great numbers in the Gulf of California.
23. *Carcharhinus brachylurus*	Living in the Gulf of California.
24. *Carcharhinus falciformis*	Living in the Gulf of California.
25. *Carcharhinuis* cf. *galapagensis*	Living in the Gulf of California.
26. *Carcharhinus albimarginatus*	Living in the Gulf of California.
27. *Carcharhinus velox*	Living in the Gulf of California.
28. *Carcharhinus limbatus*	Living in the Gulf of California.
29. *Carcharhinus altimus*	Living in the Gulf of California.

Galeocerdo; most of the time was spent collecting other sharks teeth. Since only the writer could identify *Galeocerdo* teeth, the sample is assumed to be unbiased. Of the 169 teeth 2 were medials, and can be excluded from the following considerations. It proved to be the case, however, that one of the medials was an upper and the other a lower. When the distinctiveness of the lower teeth was discovered, it was possible to identify teeth from the right side as opposed to those from the left. In this sample 81 were right and 86 were left; 78 teeth were interpreted to be lower teeth and 89 teeth are thought to be uppers. This approximately 50/50 ratio adds confidence to the supposition that we are dealing with a single species of shark. The fact, that it is possible to pick out a fairly complete tooth set (Figure 3) from such a small number of teeth, was a happy surprise and one would consider this to be an exception, as a much larger number of teeth is usually required.

The living tiger shark shows a marked variation in the total number of teeth; the smallest number that was seen is 36 and the largest 49. The last number was used in the present case, though there is, as yet, no exact proof, the variation appears to occur mainly in the number of posteriors.

The dental formula has been described by Leriche (1926) for the side of the jaw as follows:

$$\frac{\text{S1-A4-L7}}{\text{S1-A4-L8}}$$

Using Applegate's (1965) modifications of Leriche's formula, it would be written as follows:

$$\frac{\text{M1-A4-L5-P2}}{\text{S1-A4-L5-P3}}$$

Leriche (1926) did not attempt to separate posteriors from laterals and used the term symphyseals in a wider sense than appears necessary. The term medial may be applied to the example used by Leriche (1926). Other specimens of tiger sharks have medials in both the upper and lower jaws. In the example figured by Bigelow and Schroeder (1948), it is evident that the medials may be symmetrical or point to either corner of the jaw. The formula for the tiger shark, figured by Bigelow and Schroeder (1948), would be:

$$\frac{\text{M1-A4-L5-P3}}{\text{M1-A5-L5-P3}}$$

The dental formula used for the Santa Rosalía artificial set was:

$$\frac{\text{P3-L5-A4-M1-A4-L5-P3}}{\text{P2-L5-A4-M1-A4-L5-P3}}$$

The individual tooth.—Tiger shark teeth when sectioned display the orthodont condition, that is, they posses a prominent internal chamber surrounded by bands of orthodentine which are capped by an enamel layer; for a discussion of this type of tooth, the reader is referred to Applegate (1967). The short root almost forms a simple rectangular band at the lower part of the tooth (Figure 4); the double nature

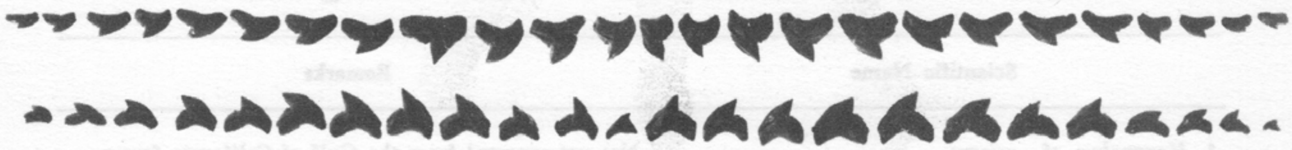

Figure 3.—*Galeocerdo rosaliaensis*, cotypes and type in an artificial set IGCU 1280 and 1281 respectively. The dental formula of the set is:

P-3-L5-A4-M1-A4-L5-P3

P-2-L5-A4-M1-A4-L5-P3

of the root is often suggested by a simple open v-shape (Figure 4A). On the inner face in the center of the root, there is a root furrow that posses a simple single root canal.

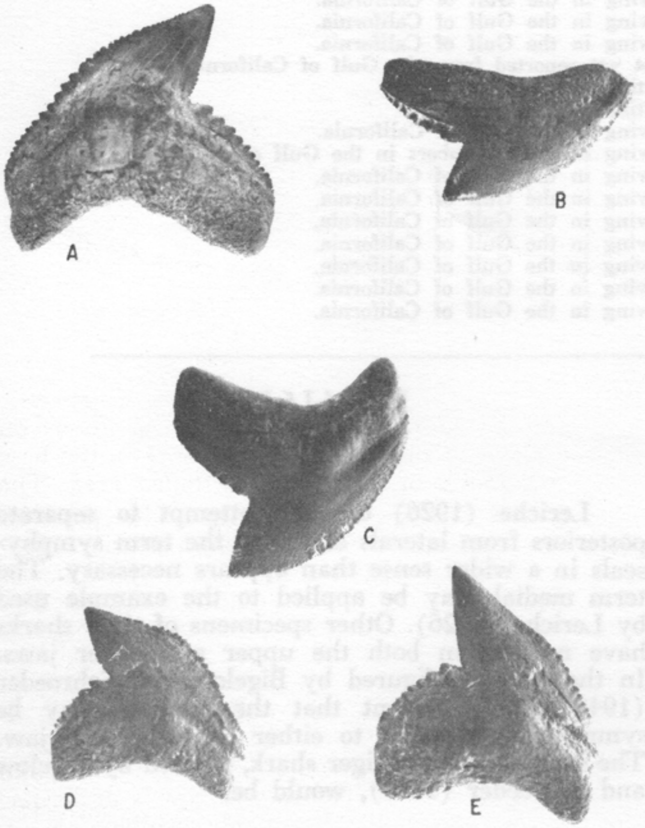

Figure 4.—(A)-*Galeocerdo rosaliaensis*, type, a lower right I.G.C.U. 1280 Loc. BCS 2, Corkscrew Hill, Santa Rosalía. (B, C, D, E) .— Cotypes I.G.C.U. 1281, Loc. BCS 2, from artificial set, fig. B, upper 1st posterior; C, upper anterior; D, lower posterior lateral; E, lower lateral. B-E are all from the left side of the artificial set.

The crown is usually strongly curved toward the corner of the mouth, except for symmetrical medials. The asymmetrical medials and the symphyseals show a similar, if less pronounced, curvature. Below and posterior to the tip of the crown, the edge forms a shelf which is related to the strongly serrated shelf in *Galeorhinus* or the blade in *Rhizoprionodon* and *Sphyrna*. The shelf or blade in the living *Galeocerdo cuvier* possesses a series of step-like serrations, each increasing in size as the edge ascends anteriorly (Figure 5A); the blade ends in a notch followed by the posterior upper crown edge. Above the notch on the upper posterior edge of the crown, there are regular small serrations. The upper anterior edge of the tooth in *G. cuvier* makes a smooth rounded curve, the serrations reach there maximun size in the center of the arch and diminish toward both the tip and the anterior base of the crown. The larger serrations of the upper portions of the shelf and the central portion of the crown bare small secondary serrae, as shown on Figure 5A.

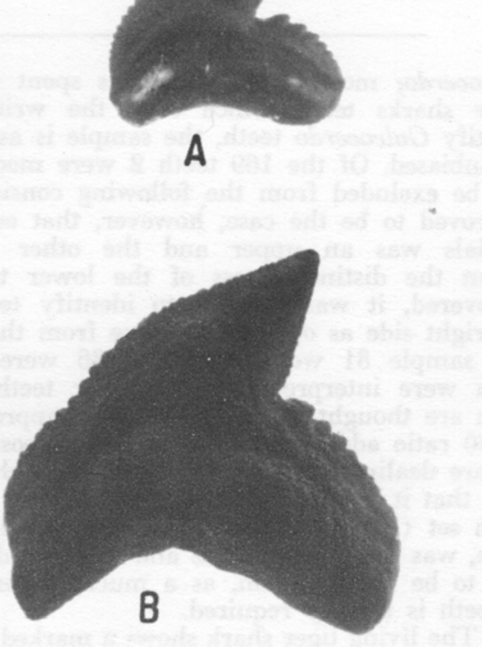

Figure 5.—(A).—*Galeocerdo cuvier*, first lower right lateral from M.V.C.E. 162. Total length 246 CM. Female from Tecolutla, Veracruz, Mexico. (B).—*Galeocerdo rosaliaensis* type a lower right lateral IGCU. 1280.

The late Miocene tiger sharks.—The most characteristic form and the latest member of the aduncus lineage is *Galeocerdo aduncus* Agassiz, 1843, which has a good record from the middle to the late Miocene and probably to the early Pliocene. The major difference between the living *G. cuvier* and *G. aduncus* is that *G. aduncus* shows a decided flattening of the anterior upper edge of its lower teeth, a thinner crown and a smaller overall tooth size (Figure 6). Early Miocene teeth are even smaller and probably represent another species. In the living *G. cuvier*, there is an almost homodont relationship between the upper and lower teeth, both exhibit a curved anterior upper edge. The variations that exist between the upper and the lower jaws are therefore slight. The difference of anterior edge shape in the lower teeth of *G. aduncus* has caused past workers to split the species in to two, a point that was not justified in the opinion of Leriche (1926).

This opinion is substantiated in the present paper. One of the arguments that could be made is that no link existed between *G. aduncus* and *G. cuvier*. The new species described here satisfies the requirements for such a link.

Figure 6 shows a tentative artificial tooth set of the Miocene *Galeocerdo aduncus*. The teeth are in the collections of the Los Angeles County Museum of Natural History and come from Locality 1945, Leasure World, El Toro, Orange County, California. The associated fauna is late Miocene. This set was picked from several hundred teeth. The dental formula for this set is believed to be:

$$\frac{\text{P2-L5-A3-M1-A3-L5-P2}}{\text{P2-L5-A3-S1-M1-S1-A3-L5-P2}}$$

There is a possibility that this count is low, as suggested by the small number of laterals and lower anteriors. The differentation of symphysials is very different from the later Galeocerdids. The general heterodonty of the uppers and lowers is as marked as is that of the individual tooth files making such a set much more highly differentiated than in the living *Galeocerdo cuvier*.

Figure 6.—*Galeocerdo aduncus*, artificial set from L.A.C.M. Loc. 1945 Leasure World. El Toro, Orange Co.

DESCRIPTION OF A NEW TIGER SHARK FROM BAJA CALIFORNIA SUR

Phylum: Chordata
Subphylum: Elasmobranchimorphi
Class: Euselachi
Order: Carcharhiniformes
Family: Carcharhinidae

Galeocerdo rosaliaensis n. sp.

Holotype.—A lower right lateral tooth, thought to belong to the 1st. file (I.G.C.U. No. 1280) deposited in the Museo de Vertebrados del Departamento de Paleontología del Instituto de Geología de la Universidad Nacional Autónoma de México (Figure 4A).

Cotypes: an artificial tooth set containing 49 teeth (I.G.C.U. No. 1281; Figure 3).

Paratypes.—133 teeth collected in 1976 (I.G.C.U. No. 1282).

Diagnosis of the type tooth (Figure 4A).—A tooth that differs from all other species of *Galeocerdo* by having the combination of large size and shape similar to *Galeocerdo cuvier*, but with the upper half of the anterior border flattened.

Description.—The holotype (Figure 4A) is a tooth with the following dimensions: the greatest height is 23.9 mm; the greatest width is 29.9 mm; the height of the root at the median furrow is 10 mm; the length from the tip of the crown to the lower anterior corner of the edge of the crown is 30.1 mm; the length of the posterior shelf is 14.3 mm; the posterior upper edge of the crown is 10.3 mm.

Serration counts.—There are 41 serrations on the anterior edge of the crown and 19 from the base to the beginning of the upper flattened area. The flattened area possesses 22 serrae. The posterior shelf possesses 11 serrations and the posterior upper edge has 19. The largest serrations of the anterior border occur from serrae 15 to 19. On the posterior border from 2 to 4. The last upper serration on the shelf is the largest. The 3 upper serrations on the shelf bare secondary serrations. Secondary serrations are also present on the serrae of the middle of the anterior border; there may be as many as three or four per primary serration, they are weak and difficult to distinguish. The root furrow is ill-defined and the central canal is hardly discernible.

Cotypes.—The lower jaw; the diagnostic features of the type exist in all of the teeth of the artificial lower jaw except the medial tooth. The medial tooth (Figure 3), in the cotype set is very waterworn and does not exhibit the flattening, but the symmetry of the root and unique shape suggest that this is the lower medial tooth. It might, of course, belong to the upper jaw but, for the present, it is assigned to the lower. The crown of this tooth points strongly to the right, and is quite low. The 4 lower anteriors (Figures 3 and 7B) increase in size laterally. In Figure 4D, the teeth appear to be slightly more narrowly pointed, the roots bare high arches. The lower anterior teeth in the living *G. cuvier* (Figures 5A and 7A), in some specimens tend to show a straight instead of a curved border. In *G. rosaliaensis* there is a tendency in some lower anterior teeth to be curved. The general straightness of the other lower teeth is not affected. The last anterior or the first lateral appear to be the largest tooth in the lower jaw. The laterals decrease in size until they meet the posteriors. The upper portion of the crowns of the lateral teeth become wider. The posteriors are much wider than high.

The upper jaw; the upper medial (Figures 3 and 7B) is asymmetrical and points to the right. The tooth is higher than wide and the left side is very straight, almost vertical, the root is asymmetrical in contrast to the lower medial. The upper anterior edges of the anteriors (Figures 3 and 7B), are strongly curved in the 4 upper teeth. The 4th upper anterior is the largest tooth in the upper jaw. The posterior teeth are very wide and low. The set viewed from the rear is shown in Figure 3.

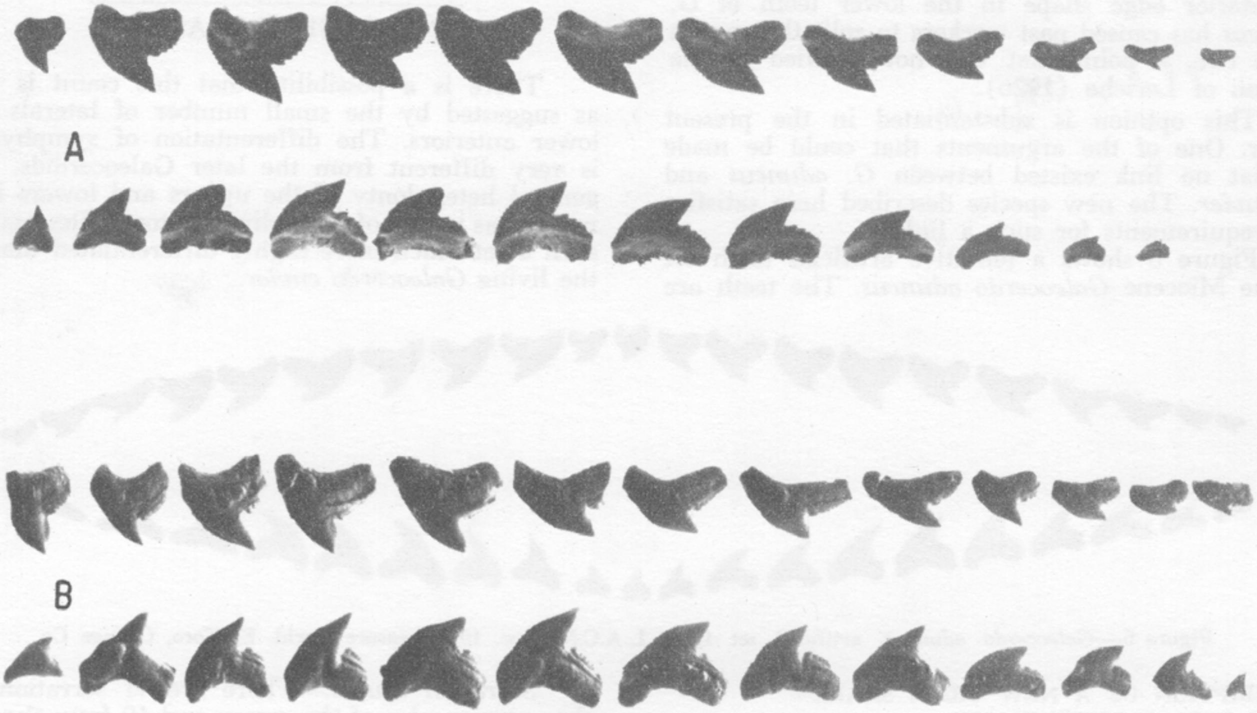

Figure 7.—(A).—Teeth from the right side of a natural set of *Galeocerdo cuvier* M.V.C.E.—163-Female from Tecolutla, Veracruz, México. (B).—Teeth from the right side of the artificial set IGCU 1280, 1281 of *Galeocerdo rosaliaensis* BCS 2.

Paratypes.—The 133 other teeth collected from Locality IGCUBCS 2, that can be assigned to *Galeocerdo rosaliaensis*, are well distributed as far as variety is concerned. The small number of posterior teeth is believed due to a collecting bias.

Type locality and horizon.—The teeth including the holotype, were collected in an area of less than 100 m^2, on the west side of Locality IGCUBCS 2, (Loma del Tirabuzón), which is the same as, Los Angeles Country Museum Locality No. 6597, which is referred to in the National Geographic Report (unpublished) as Locality No. BNG. 1. The teeth all have come from the upper 6.6 m. (Figure 2) of the section; this, however, is not the top of these beds in the area.

SOME COMMENTS ON THE MONTE BOLCA CARCHARHINIDS

In considering Cappetta's (1975) results, it was thought best to make some closer comparisons with living sharks. So, contrary to Cappetta (1975), *Prionace glauca* is not considered to have even a remote relationship to the Bolca sharks and the problem at hand. It differs from the Bolca sharks in snout shape and size, body shape, fins and teeth. *Prionace* has a record of being no older than the late Miocene (L.A.C.M. Loc. 1945, near El Toro, Orange County, California). There is no indication that the Bolca beds are open sea deep water deposits and *Prionace* is certainly a pelagic shark.

Fin position.—Fin position has long been used as taxonomic tool in recent sharks particularly in the carcharhinids. In fossil sharks, however, fin position may be quite risky since changes may and do occur with decay, shifting of the enclosing sediments and compression. In the present discussion I will consider four separate fin arrangements to gain a proper perspective on the Monte Bolca sharks described by Cappetta (1975).

(1) — In *Galeocerdo cuvier* (Lesueur), 1822 (Figure 8E), fin position is known only in the living genus. The first dorsal's origin or front basal edge is over or a little posterior to the insertion of the pectoral fin. The second dorsal fin originates over or a little in front of the origin of the anal. The origin of the pelvics is 2/3 of the distance posteriorly between the origin of the pectorals and the anal fin.

(2) — *Mustelus canis* (Mitchill), 1815 is a member of a family that is considerably more primitive than either *Galeocerdo* or *Galeorhinus*. *Mustelus canis* is used in the following comparison as a pre-carcharhinid (Figure 8A). The moundlike teeth set it aside as a specialized genus, through it has a record no older than Oligocene. This poor record may be due more to the exceedingly small size and simple nature of its teeth which make collecting and identification difficult. The fact that the Triakidae, the family that *Mustelus* belongs to, is well known from the Cretaceous, however, gives

validity to this comparison. The first dorsal originates over the midpoint of the inner margin of the pectoral. The second dorsal origin is above a point about midway between the tips of the pelvics and the origin of the anal. The pelvics are about 1/2 the distance between the origin of the pectoral and the origin of the anal.

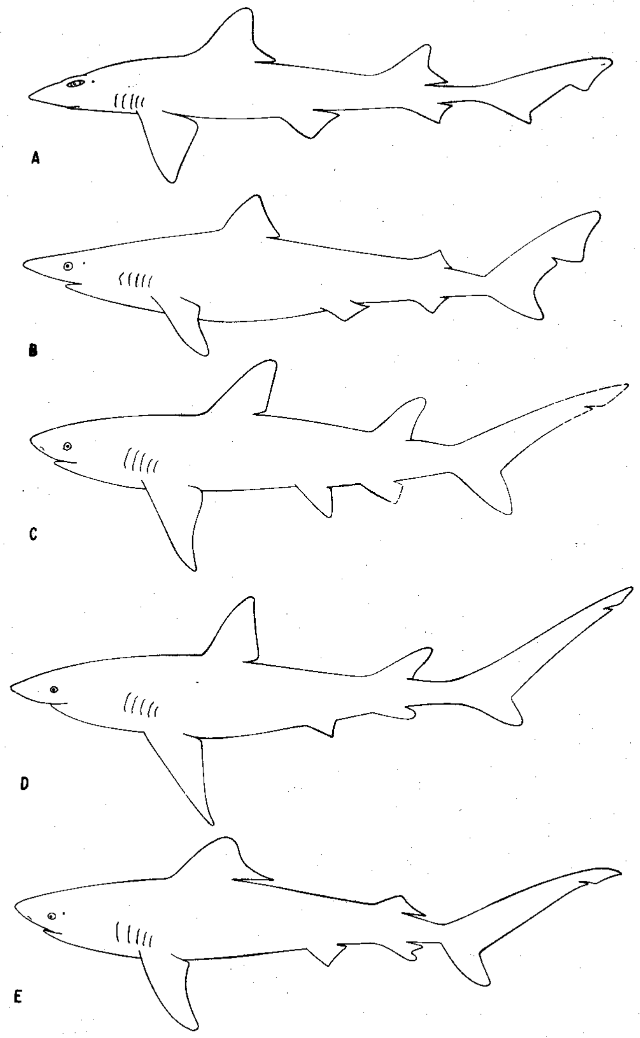

Figure 8.—Sharks showing fin position. (A).—*Mustelus canis*. (B).—*Galeorhinus galeus*. (C).—*Alopiopsis plejodon*. (D).—*Alopiopsis cuvieri*. (E).—*Galeocerdo cuvier*.

(3) — In the living *Galeorhinus galeus* (Linneaus), 1758 (Figure 8B), the origin of the first dorsal is definitely posterior to the inner posterior corner of the pectoral fin. The second dorsal originates directly above the origin of the anal. The pelvic fin origin lies 2/3 the distance behind the rear corner of the pectoral fin and the origin of the anal fin.

(4) — **The two species of sharks treated by** Cappetta (1975) appear to have the following fin positions (Figure 8D). The first dorsal fin originates over the posterior corner of the pectoral fin, a character similar to that of *Galeocerdo* and *Mustelus*, but very different from that of *Galeorhinus*. The second dorsal fin originates directly over or slightly in front of the anal fin, a trait found in *Galeocerdo* and *Galeorhinus*, but not in *Mustelus*. The origin of the pelvics is approximately 2/3 the distance between the origin of the pectoral and the origin of the anal, a condition found in the genera *Galeocerdo* and *Galeorhinus*.

In summary, the position of the dorsal fin alone would eliminate the placing of either Bolca sharks in the genus *Galeorhinus*. The position of the pelvic fin and the second dorsal fin are similar to that of *Galeocerdo* and *Galeorhinus*, but different from that of *Mustelus*.

Fins of the trunk shape and size.—Fin size and shape are known to be highly variable within a single species of shark (Garrick, 1967). Absolute judgements based on these features alone should be cautious. Major differences have, however, at times proved to be of important taxonomic value. The dorsal fins in *Mustelus* (Figure 8A) are similar in shape. The first dorsal fin's free tip is 1/3 as long as the base. The fin is not as high as the length of its base. The anterior edge is slightly convex. The posterior edge is concave, the tip is acutely rounded, the 2nd dorsal is large, being about 2/3 to 4/5 the height of the first (Bigelow and Schroeder, 1948). The anal fin is longer than high, the anterior border is straight, the posterior slightly concave. The free tip of the anal is not as large as that of the second dorsal. The pelvics are only slightly smaller than the 2nd dorsal, both the anterior and posterior borders are almost straight, the outline of the free edge is an acute angle.

The pectoral fin has a narrow base, about equal to the inner margin, the fin is short and broadly triangular.

The trunk fins of *Galeorhinus* (Figure 8B), are short, except for the pectoral fin that may be slightly elongate though not so much as in *Galeocerdo*. The anal fin and the second dorsal are of approximately the same height, triangular in shape with the posterior edges having a slight convexity. The dorsal fin is much larger than the 2nd dorsal, the anterior edge is almost straight, the tip is only slightly rounded, the posterior edge may be straight to slightly concave. The pelvic fin is only slightly larger than the anal, it is more or less triangular in outline.

The dorsal fin of *Galeocerdo* (Figure 8E) is slightly curved in front with a narrowly rounded top. The posterior edge is concave. The free flap is large, long, pointed, and slender. The second dorsal is about 1/3 as high as the first dorsal and about 1/2 as long. The anterior edge is low and the free tip is longer than its base. The anal is almost as long as the second dorsal but slightly higher. The posterior margin is more deeply concave. The free tip is relatively shorter than the second dorsal. The pelvics have straight edges with narrowly rounded corners. The pectoral fin's outer margin is moderately concave, the posterior margin is convex. The fin is fairly elongate, its length is about equal to the length from the first gill slit to the tip of the snout. It is here considered that the type *Alopiopsis plejodon* and *Eogaleus bolcensis* (Figure 8C), the latter was named by Cappetta, both belong to the same species. The poor quality of the material still leaves many questions. The first dorsal fin is poorly preserved. In the known specimens, it appears to be fairly low with the front inclined at a remarkably low angle and having anteriorly a very convex outline, the tip is quite rounded. The posterior border is straight, but inclined in the specimens posteriorly above the base.

The first dorsal is almost twice as large as the second. The second dorsal is much larger than the anal, the anal is poorly preserved in all of the specimens. The pelvic fin is much smaller than the second dorsal, but is larger than the anal. The anterior edge of the pelvic fin appears to be straight, the fins seem erect instead of appressed to the trunk, the posterior edge is almost straight.

The other species of *Alopiopsis*, *A. cuvieri* (Figure 8D), consists of better preserved specimens, the snout is rounded but not quite as blunt in *A. plejodon*. The dorsal fin is high, the front edge is at a moderately low angle to the body, the posterior edge is straight and almost vertical. The tip is acutely rounded. The second dorsal fin is a little less than 1/2 the size of the first dorsal, the anterior edge is low, the tip is rounded. The posterior edge is convex and forms an acute angle with the body. The anal fin, though smaller than the 2nd dorsal, is very similar in shape. The pelvic fin is only slightly smaller than the anal, the anterior edge is straight as is the posterior.

Caudal fins.—In the sharks under consideration perhaps the most revealing differences and similarities occur in the caudal fins. Caudal fins as such are normally very conservative characters. In this discussion the terminology of Thomson (1976) is used.

The caudal fin is elongate, falcate and narrowly pointed in *Mustelus canis* (Figure 8A). The caudal fin has the overall shape of an obtuse triangle, the top side is the longest, the bottom anterior side is the shortest. Between the bottom anterior side and the bottom posterior side is an obtuse angle. The heterocercal angle is low, the epichordal lobe is well developed with an extensive edge above the notochordal mass. Posteriorly, it composes about 1/3 of the posterior flap. The other 2/3's consists of the subterminal lobe. The posterior border of the flap is straight. The longitudinal hypochordal lobe is narrow and is sharply delineated from the subterminal lobe by the caudal notch. Anteriorly, the longitudinal hypochordal lobe expands and grades into the ventral hypochordal lobe. The ventral lobe is low through it is distinct.

In *Galeorhinus galeus* (Figure 8B), the caudal fin has the aspect of an equilateral triangle. The epichordal lobe is large and similar to that of *Mustelus*; its posterior apex is pointed and the posterior surface large. The subterminal lobe is prominent and its lower apex is also pointed. The two form a posterior flap that is straight between the two points; the subterminal lobe makes up about 1/2 of this flap. The flap is quite large. There is a definite notch between the subterminal lobe and the longitudinal hypochordal lobe. The longitudinal hypochordal lobe is very low at the notch but increases anteriorly in height. The ventral hypochordal lobe is convex on both sides, the tip is pointed. The anterior edge of the ventral hypochordal lobe is longer than the edge of the longitudinal hypochordal lobe.

In *Galeocerdo cuvier* (Figure 8E), the caudal fin is lunate in shape or has the form that may be described as an elongate acutely pointed triangle. The epichordal lobe is present as a narrow edge above the notochordal mass. The epichordal and subterminal lobes form a point and both are quite small. The longitudinal hypochordal lobe is very long but narrow. The ventral hypochordal is convex posteriorly and anteriorly, it is long and pointed.

In the genus *Alopiopsis* the caudal fin has the same general shape as that of the tiger shark *Galeocerdo*. The overall shape is that of an elongate triangle. In *A. plejodon* (Figure 8C), the ventral hypochordal lobe is convex on both sides. The longitudinal hypochordal lobe is elongate as in *Galeocerdo*. The end of the tail is too poorly preserved for comment. In *A. cuvieri* (Figure 8D), the posterior edge of the ventral hypochordal lobe is concave, the tip is rounded and the lobe is thin but long. The longitudinal hypochordal lobe is elongate, the epichordal lobe is pointed. The subterminal lobe has a small point. The minute size of these lobes is characteristic of the genus *Galeocerdo*. The fact that both lobes do not form a single point could be a slightly more primitive feature, but in any case a minor character.

Teeth.—Cappetta (1975) did not attempt to reconstruct even an artificial tooth set, nor did he investigate the associated sets in sufficient detail. Therefore, it is difficult to speak with exactness concerning the Monte Bolca sharks. The lack of a primitive galeocerdid artificial tooth set, futher complicates the problem. From Cappetta's figures, I can draw at least some tentative conclusions. Differences in the dentition do exist between his two forms, but not enough to warrant generic separation. In both species, heterodonty of the aduncus type exists between the upper and lower jaws. The tooth files show a marked tooth heterodonty with distinctive medials, symphyseals, anteriors, laterals, and posteriors; a condition which is unknown in the living *Galeocerdo cuvier* and *G. rosaliaensis*, but one that is present in *G. aduncus*, and the more primitive Eocene species that are thought to belong to this lineage. The anteriors, in both the Monte Bolca fossils and in the primitive galeocerdids, have erect crowns and are more carcharhinoid-like. Such teeth have been named *Physodon*, a generic name incorrectly applied to living sharks belonging to any number of genera. For the present, it is not possible to make a differentation of the Bolca specimens from these primitive galeocerdids by teeth alone.

Vertebral counts.—In recent species of sharks, vertebral counts may be useful taxonomic tools, as has been shown by Springer and Garrick (1964). It is certainly an exception to the rule when vertebral counts can be used in reference to fossil sharks.

Cappetta (1975) gives a vertebral count for his supposed new genus *Eogaleus* as approximately 150 vertebrae. This count would apply to the sharks referable to the genus and species *Alopiopsis plejodon*. For *Alopiopsis cuvieri* he gives the counts of 175 to 210. *Mustelus canis* has a count of 146 vertebra, according to Springer and Garrick (1964). *Galeorhinus galeus* has a count of 136. Bass *et al* (1973) give an average of 132.9. Compagno (1970) has removed *G. japonicus* from the genus *Galeorhi-*

nus and placed it in the genus *Hemitriakis*. so, this count does not apply in our case. The vertebral count for *Galeorhinus* would be 133 and furnishes the lower number. The range for *Alopiopsis* would be higher from 150 to 210, with *A. cuvieri* in the upper part of this range. *Galeocerdo cuvier*, on the other hand, has a range from 231 to 233 (Springer and Garrick, 1964). We may conclude, on the basis of the scanty information at hand, that *Alopiopsis* stands between *Galeorhinus* and *Galeocerdo* with *Alopiopsis cuvieri* being closest to *Galeocerdo*.

Scales.—Scales and their use in taxonomy have been discussed briefly by Applegate (1967). In most sharks the pitfalls are more evident than their advantages of utilization; among these can be cited the complete changes that occur as the shark matures, plus the great scope of convergence so that unrelated genera may posses almost identical scales. Applegate (1967) demonstrated that scales from different parts of the body may have distinctly different shapes.

In *Mustelus canis* the trunk denticles below the first dorsal fin are tear-shaped when seen from above (Figure 9A). The anterior edge being rounded and the posterior pointed respectively. The surface bears 3 raised ridges, the middle one is in the center of the scale.

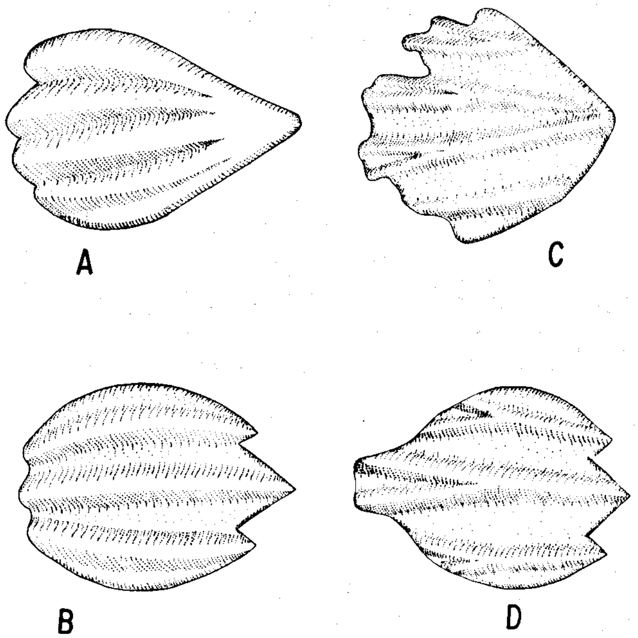

Figure 9.—Scales from 4 genera of sharks greatly enlarged. (A).—*Mustelus canis* after Bigelow and Schroeder, (1948). (B).—*Galerorhinus galeus*, taken from the specimen, M.V.C.E. 164 from Punta Eugenia, Baja California Sur. The scale is from directly in back of the head. (C).—*Alopiopsis plejodon* after Cappetta's (1975) figure of the scales of "Eogaleus bolcensis". (D).—*Galeocerdo cuvier*, after Bigelow and Schroeder (1948).

In the living *Galeocerdo cuvier* (Figure 9D), scales are diamond shaped with from one to three ridges, the main ridge is in the center of the scale. Anteriorly, the main ridge forks. The upper and lower sides of the scale are slightly curved, the anterior edge is bluntly pointed. The posterior edge has 3 small points. The middle point is the longest.

The scales of *Galeorhinus* (Figure 9B), that is those of a specimen from the west coast of Mexico, possess a three pronged, more or less, oval blade. The middle point is the longest. Each prong bares a pronounced ridge that runs the length of the scale on to a posterior projection. The middle posterior projection is the longest. The scales are similar to those of *Hypoprion signatus*, as figured by Bigelow Schroeder (1948), except that they are not as wide or as robust.

The scales of the Monte Bolca carcharhinids figured by Cappetta (1975, pl. II, fig. 3), bear little resemblance to those of either *Mustelus* or *Galeorhinus*, but are almost identical with those of *Galeocerdo*. The ridges show a similar anterior dichotomose branching and a near diamond shape. In itself, this might be just another example of convergence, but in light of the other evidence presented in this paper, these scales form what is considered almost foolproof evidence of a close relationship of *Alopiopsis* to *Galeocerdo* and not to *Galeorhinus*.

The origin of the genus Galeocerdo.—When one considers the total morphology of *Galeocerdo*, one is drawn to the conclusion that the tiger shark was derived from some sort of soupfin, *Galeorhinus* or a soupfin-like shark. Teeth referable to *Galeorhinus* are known from the Paleocene near Benton, Arkansas. In North America, the oldest positively identifible *Galeocerdo* teeth are from the Nanjamoy lower Eocene of Virginia and the Red Hot locality of middle Eocene of Mississippi. With this in mind, a lower Eocene or upper Paleocene origin of the genus is not unreasonable.

Cappetta (1975) reviewed the Monte Bolca carcharhinids that are early Eocene. Though he gives an interesting discussion of the specimens and good illustrations, Cappetta rejected the possibility that he was dealing with a *Galeocerdo* ancestor. For the sharks in question, he erected what appears to be an unnecessary new genus and species. In comparing the Monte Bolca sharks with the modern tiger shark, as opposed to the soupfin *Galeorhinus*, there is still much to recommend Jaekel's (1894) contention that we are dealing with a primitive tiger shark or a tiger shark ancestor. It is believed, that Cappetta would have followed a more proper course if he had retained the old genus *Alopiopsis*, which has every reason to be considered usable. Cappetta does not offer any reasonable explanation for not placing both of the Monte Bolca species into this genus. If the present suggestions are taken, the phylogeny would be *Galeorhinus* (or a related form), *Alopiopsis* and *Galeocerdo*. The proper names for the Monte Bolca species would be *Alopiopsis plejodon*, Lioy, (1865) and *Alopiopsis cuvieri* (Agassiz), 1835.

AMENDED DIAGNOSIS OF *ALOPIOPSIS* LIOY, (1865)

Sharks with the anterior most edge of the first dorsal directly over the posterior corner of the pectoral fin. The anterior edge of the second dorsal is directly over or in front of the anterior edge of the anal. The second dorsal is at least 1/3 as large as the first and much larger than the anal. The pelvic fin originates in the posterior portion of the distance between the pectoral and the pelvic fins. The head is bluntly rounded. The caudal fin is elongate triangular in overall shape, the ventral hypochordal lobe of the caudal fin is convex on both sides and is thin. The teeth show pronounced heterodonty with distinctive medials, symphyseals, anteriors, laterals and posteriors. Vertebral counts range from 150 to 210. The scales are diamond-shaped and the ridges show dichotomose branching anteriorly.

At the present, two species may be recognized, *Alopiopsis plejodon* Lioy, 1865 and *Alopiopsis cuvieri* (Agassiz) 1835. *Alopiopsis plejodon* differs from *A. cuvieri* in a blunter snout, lower second dorsal, more robust fins and evidently a thicker body. In *A. plejodon* the vertebral count is low 150, as opposed to the higher count in *A. cuvieri,* that ranges from 175 to 210.

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