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Additions to a Revision of the Shark Genus *Carcharhinus*: Synonymy of *Aprionodon* and *Hypoprion*, and Description of a New Species of *Carcharhinus* (Carcharhinidae)

J. A. F. Garrick

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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John V. Byrne, Administrator
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Additions to a Revision of the Shark Genus *Carcharhinus*: Synonymy of *Aprionodon* and *Hypoprion*, and Description of a New Species of *Carcharhinus* (Carcharhinidae)

J. A. F. GARRICK[1]

ABSTRACT

Features of the valid nominal species of *Aprionodon* Gill (*isodon* Valenciennes) and *Hypoprion* Müller and Henle (*hemiodon* Valenciennes, *macloti* Müller and Henle, and *signatus* Poey), plus those of a previously unrecognized species here described as *Carcharhinus leiodon* n.sp., are examined and compared with those of *Carcharhinus* Blainville. Features studied include morphometrics, vertebral numbers and other vertebral characteristics, tooth numbers, color pattern, and some other aspects of external morphology. It is concluded that on these features *C. leiodon* n.sp. is entirely encompassed within the parameters of *Carcharhinus*, and that, although *A. isodon*, *H. hemiodon*, *H. macloti*, and *H. signatus* each extend the range of diversity of *Carcharhinus* in one or more features, *A. isodon* is not uniquely different from *Carcharhinus*, and there is no common pattern of difference between the three species of *Hypoprion* and *Carcharhinus*. Accordingly, and because the nature of the teeth of *Aprionodon* and *Hypoprion* has been found insufficient to warrant generic distinction from *Carcharhinus*, the genera *Aprionodon* and *Hypoprion* are synonymised with *Carcharhinus*.

A diagnosis and description are given for each of the above species. The descriptions include measurements, counts, and line illustrations that show the whole shark in lateral view, underside of head, nostril, and teeth. The geographic distribution is summarized, as are also the meager biological data available on number of embryos, size at birth, size at sexual maturity, and maximum size.

INTRODUCTION

At the time of completion of a revision (Garrick 1982) of *Carcharhinus* I accepted the validity of the genera *Aprionodon* and *Hypoprion*. However, my subsequent study of these last two genera now convinces me that they should be incorporated as junior synonyms of *Carcharhinus*. Therefore a major purpose of the present account is to provide detailed information on features of the species that were assigned to *Aprionodon* and *Hypoprion*, to allow comparison with *Carcharhinus*, and to provide a basis for the synonymy of these genera. A second purpose is to describe and illustrate each of these species, plus a new species of *Carcharhinus*, and to document and collate information on their distribution and some aspects of their biology. These latter aims are necessary because, in general, the nominal species of *Aprionodon* and *Hypoprion* are rather poorly known.

The history of *Aprionodon* Gill, 1861 and *Hypoprion* Müller and Henle, 1841 (including *Hypoprionodon* Gill, 1862 as a synonym) is covered fully in Compagno (1979), who detailed the nominal species that have been referred to these genera and concluded that *Aprionodon* is represented by only one valid species (*isodon* Valenciennes *in* Müller and Henle, 1841) and *Hypoprion* by three (*hemiodon* Valenciennes *in* Müller and Henle, 1841; *macloti* Müller and Henle, 1841; and *signatus* Poey, 1868). Compagno (1979) further concluded from his studies that both *Aprionodon* and *Hypoprion* should be synonymised with *Carcharhinus* Blainville, 1816, an action that he had earlier taken (1973, 1978) with respect to *Aprionodon* but without substantiating it.

As noted by Compagno (1979), the only reasons that have been advanced for separating *A. isodon* from *Carcharhinus* are that it is distinctive in having smooth-edged (upper) teeth and extremely long gill openings. However, he found these reasons insufficient because juveniles of one species of *Carcharhinus* (*brevipinna*) have smooth-edged upper teeth while, conversely, an adult female *A. isodon* has weak serrations on the bases of the upper teeth, and three species of *Carcharhinus* (*limbatus*, *amblyrhynchoides*, and *brevipinna*) not only have gill opening sizes approaching those of *A. isodon* but also agree closely with *isodon* in dentition, external morphology, and vertebral counts.

Compagno's (1979) review of the diagnostic features of *Hypoprion* led him to the view that the similarity between the three included species in having upper teeth with enlarged basal serrae and essentially or completely smooth-edged cusps is not indicative of close relationship nor clearly distinctive from *Carcharhinus*, and that overall "*Hypoprion* is a heterogeneous assemblage with different members closest to different species of *Carcharhinus*." Compagno found the upper teeth of *H. macloti* unique in being low-based and in having the large serrae restricted to the bases (thus the cusps are completely smooth-edged), whereas in *H. hemiodon* and *H. signatus* the upper teeth are high-based and in some specimens have irregular serrations continuing on to the medial edges of the cusps (thereby approximating the condition in *Carcharhinus*). He further noted that several species of *Carcharhinus* have upper teeth similar to those of *hemiodon* and *signatus*.

Other features evaluated by Compagno and found insufficient as generic indicators for *Hypoprion* were nipple-shaped anterior nasal lobes, a long first dorsal rear tip, a low and long second dorsal fin, and a long snout. He concluded that the only one of these features

[1]Department of Zoology, Victoria University of Wellington, Private Bag, Wellington, New Zealand.

common to all three species was nipple-shaped nasal lobes, but that these, as well as the fin and snout features, also have counterparts in *Carcharhinus* species.

Although the above findings did not support recognition of *Hypoprion* in its accustomed sense, Compagno noted that *H. macloti* had cranial differences (hypercalcified rostrum and presence of an epiphysial foramen) from *H. hemiodon*, *H. signatus*, and those *Carcharhinus* species that he had been able to examine. These differences, together with its unique teeth, could favor retention of *Hypoprion* for *H. macloti* alone, but Compagno deemed this inadvisable because of the "absence of cranial material for several *Carcharhinus* species and the close similarity that *H. macloti* has with *Carcharhinus*, especially *C. sorrah*. . . ."

In the present study, based on a wider range of material than was available to Compagno (1979), the morphometrics, vertebral numbers and other vertebral characteristics, tooth numbers, color pattern, and some other aspects of the external morphology of the species of *Aprionodon* and *Hypoprion* are compared with those of *Carcharhinus* as a whole. Included in the comparison are data from an undescribed species, so far known from only one specimen, which has smooth-edged upper teeth conforming to the generic diagnosis of *Aprionodon*. Following the generic comparison in which the conclusion is reached that *Aprionodon* and *Hypoprion* are synonyms of *Carcharhinus*, a detailed account of each of the nominal species of *Aprionodon* and *Hypoprion* is given, and the undescribed species is described as *C. leiodon* n.sp.

MATERIALS AND METHODS

Specimens examined by me and identified as *Aprionodon* and *Hypoprion* in this study came from the museums listed below. Abbreviations preceding the names of each of these museums are those used in the text.

BMNH	British Museum (Natural History), London
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
ISZZ	Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
MNHN	Museum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NMV	Naturhistorisches Museum, Vienna
RNH	Rijksmuseum van Natuurlijke Historie, Leiden
SU	Division of Systematic Biology, Stanford University (this collection has since been transferred to the California Academy of Sciences, San Francisco)
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum of Natural History, Washington, D.C.

Data on *Carcharhinus* used there for comparison with *Aprionodon* and *Hypoprion* in Figures 1-4 are the combined ranges of the 25 species recognized by Garrick (1982) and presented in his figures 2-8, 10, 11 and tables 1, 2, and 4.

The methods used for taking measurements from which proportional dimensions were calculated, and for making counts of teeth and vertebrae, were the same as those described in Garrick (1982).

RESULTS AND CONCLUSIONS

Figures 1-4 present comparative data on proportional dimensions, vertebral numbers, and tooth numbers in *Aprionodon*, *Hypoprion*, and *Carcharhinus*. The data for each species of *Aprionodon* and *Hypoprion* and for *C. leiodon* n.sp. are presented separately, whereas those shown for *Carcharhinus* are the combined ranges of the 25 species recognized in Garrick (1982). The ranges and means of the data for each species of *Aprionodon* and *Hypoprion* are based principally on the small samples of specimens examined in the present study, and for the most part the values for individual specimens are shown in Tables 1-4 and the accompanying species descriptions. For *C. leiodon* n.sp. only one specimen was available; for the other species the numbers of specimens from which the majority of the data was taken were as follows: *A. isodon*, 6; *H. hemiodon*, 5; *H. macloti*, 7; and *H. signatus*, 5.

The items selected for inclusion in Figures 1-4 are the same as those used by Garrick (1982) in his study of *Carcharhinus*, and were chosen for the same three reasons, i.e., they are features which have commonly been used in the past to distinguish carcharhinid taxa, or they have been found to have value for that purpose in the present study, or they contribute to a broad picture of morphometrics and meristics of these taxa.

Data for *Aprionodon isodon* are almost entirely encompassed within the ranges of the data for *Carcharhinus* in Figures 1-4 where 31 characters are treated. The exceptional data (Fig. 2c) are those for gill opening lengths, in which the values for *A. isodon* exceed the ranges of values for *Carcharhinus* species. Taking the first gill opening length as an example, since it is the most obviously different from *Carcharhinus*, its mean length in *A. isodon* (4.9% TL) is clearly greater than in any *Carcharhinus* species, among which the highest means occur in *amblyrhynchoides* (4.0%) and *limbatus* (3.9%). However, four *Carcharhinus* species (*amblyrhynchoides*, *limbatus*, *brevipinna*, and *leucas*) have first gill opening length ranges overlapping the *A. isodon* range, thus establishing that *A. isodon* is not uniquely different from *Carcharhinus* in that feature.

Although *A. isodon* shares with *C. leiodon* n.sp. the unusual feature of having essentially smooth-edged upper teeth, the generally low degree of congruence between the data for *A. isodon* and *C. leiodon* n.sp. in Figures 1-4 offers little support for the possibility that these species are more closely related to each other than to other species of *Carcharhinus*. The same conclusion can be reached for most other characters examined in the present study but not shown in Figures 1-4; for example, color pattern and the position where diplospondyly begins. In *C. leiodon* n.sp. the fins are prominently black-tipped and diplospondyly begins above the anterior part of the pelvic base, whereas in *A. isodon* the fins lack black tips and diplospondyly begins much further posteriorly, above or behind the pelvic axil.

Based on the above findings, *A. isodon* and *C. leiodon* n.sp. are sharks of predominantly "average" *Carcharhinus* morphology, smooth-backed, and with pointed snouts. These characters, even in

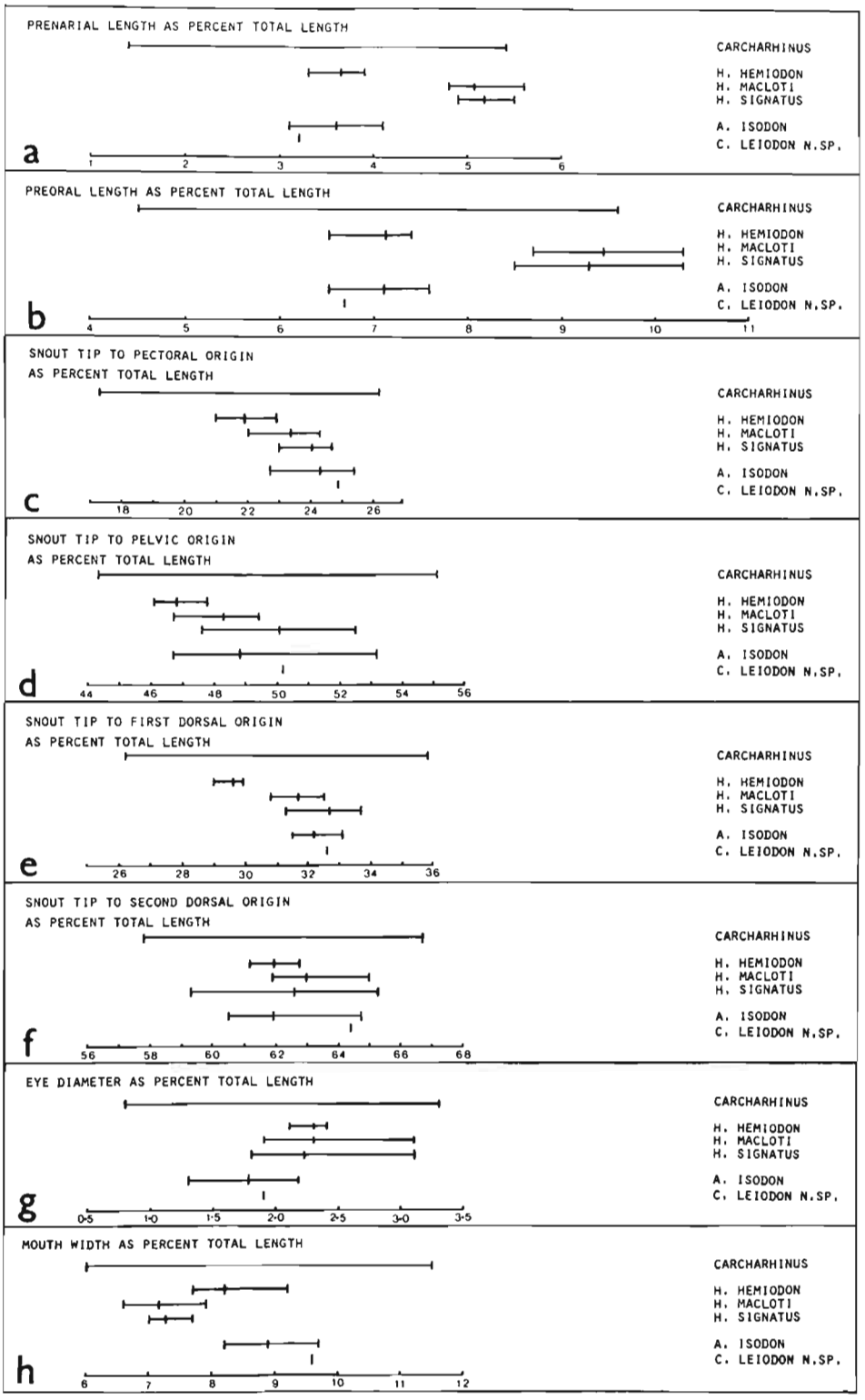

Figure 1.—Proportional dimensions of the species formerly referred to *Hypoprion* (*H. hemiodon*, *H. macloti*, and *H. signatus*) and *Aprionodon* (*A. isodon*), and those of *Carcharhinus leiodon* n.sp. expressed as ranges and means. For each dimension the range in 25 species of *Carcharhinus* is also shown for comparison.

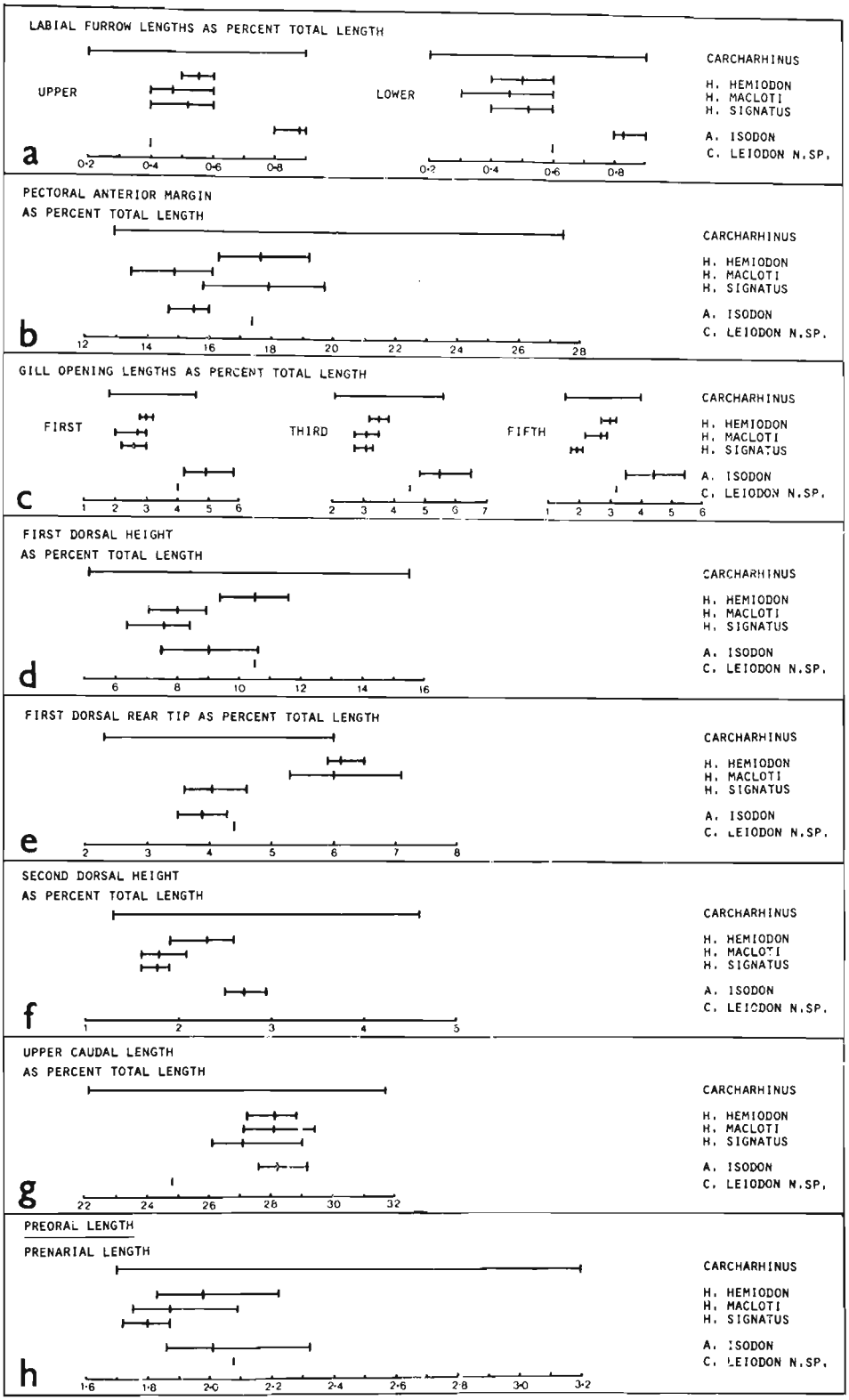

Figure 2.—Proportional dimensions of the species formerly referred to *Hypoprion* (*H. hemiodon*, *H. macloti*, and *H. signatus*) and *Aprionodon* (*A. isodon*), and those of *Carcharhinus leiodon* n.sp. expressed as ranges and means. For each dimension the range in 25 species of *Carcharhinus* is also shown for comparison.

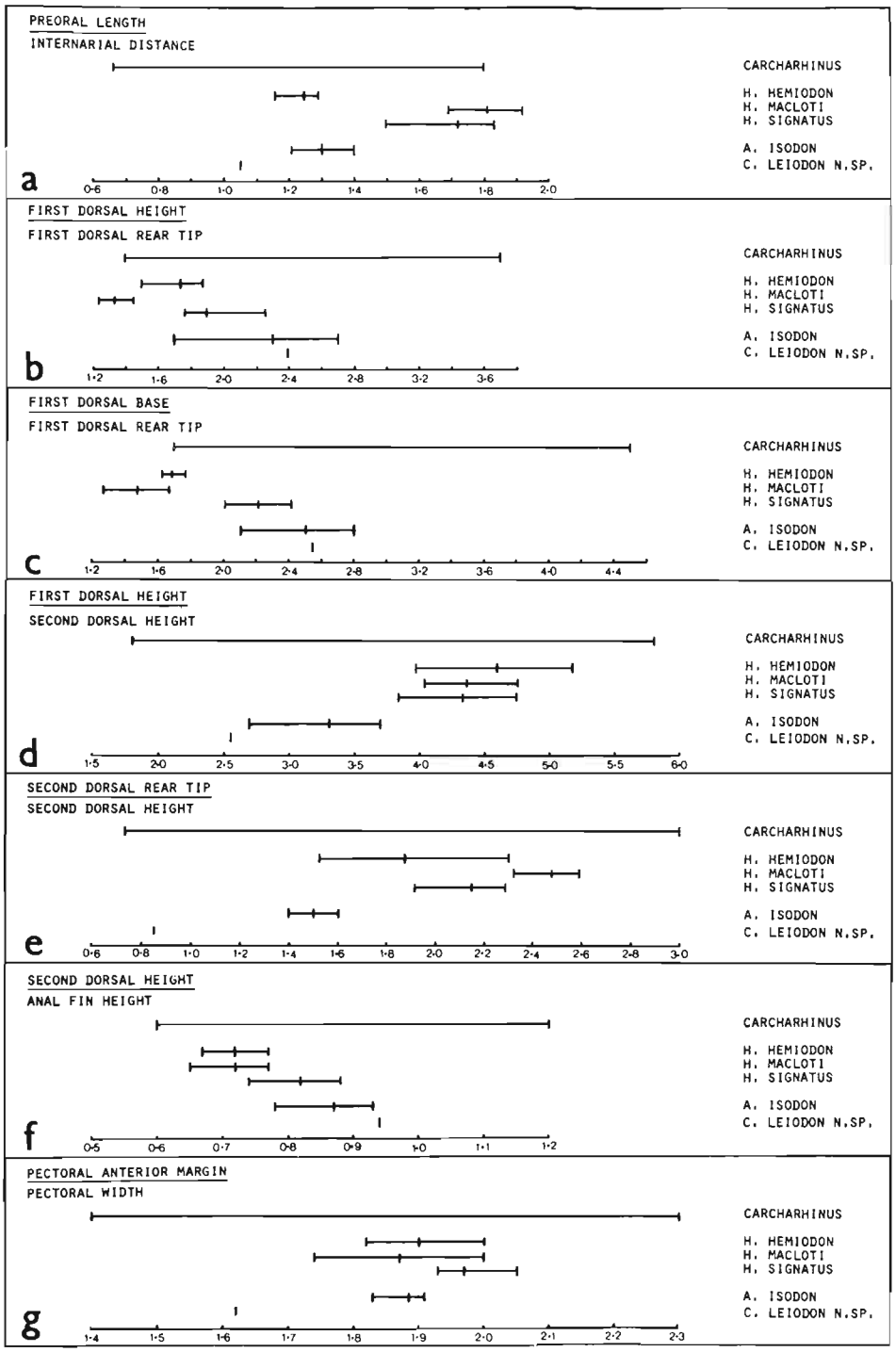

Figure 3.—Proportional dimensions of the species formerly referred to *Hypoprion* (*H. hemiodon*, *H. macloti*, and *H. signatus*) and *Aprionodon* (*A. isodon*), and those of *Carcharhinus leiodon* n.sp. expressed as ranges and means. For each dimension the range in 25 species of *Carcharhinus* is also shown for comparison.

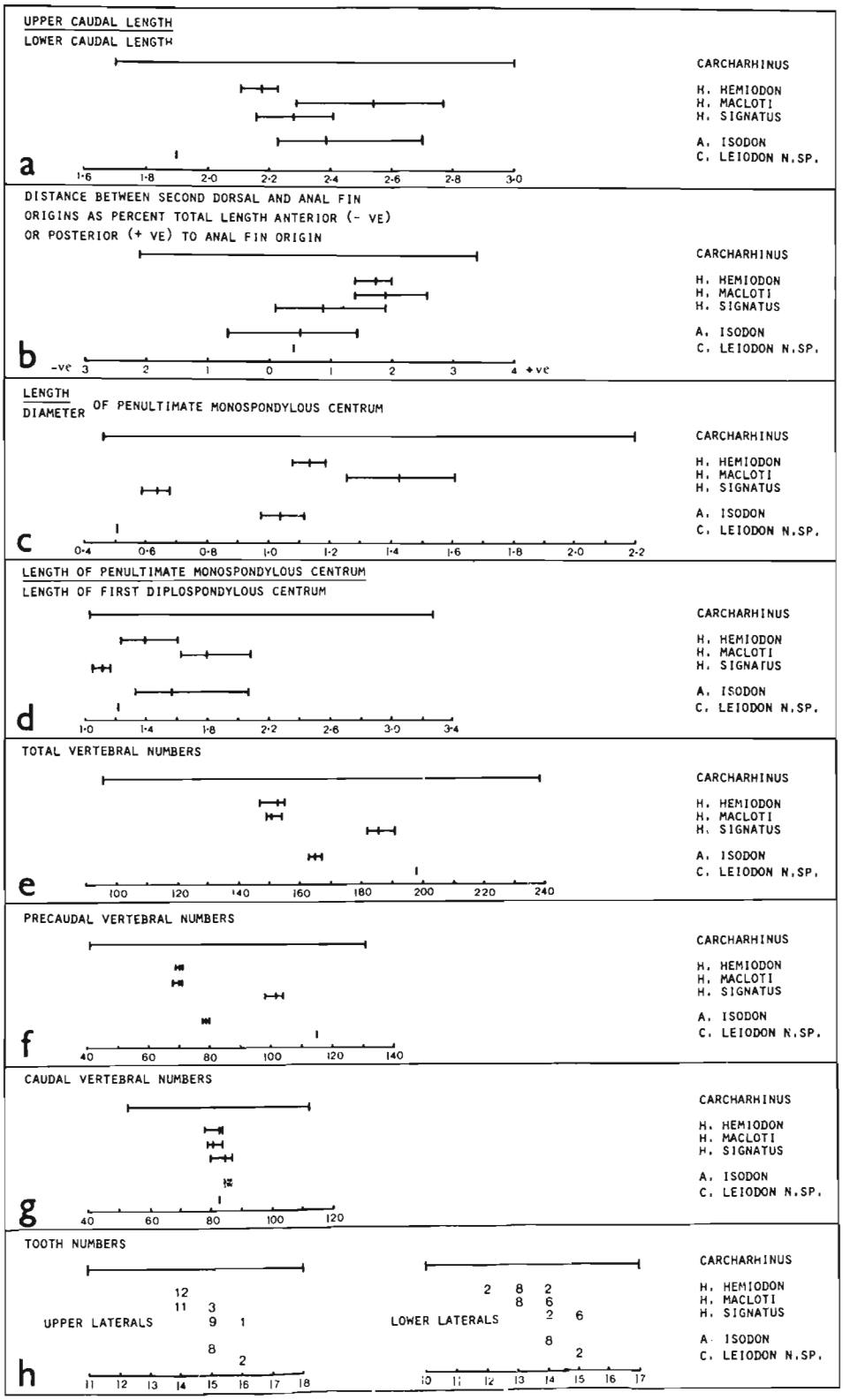

Figure 4.—Proportional dimensions, vertebral numbers, and tooth numbers of the species formerly referred to *Hypoprion* (*H. hemiodon*, *H. macloti*, and *H. signatus*) and of *Aprionodon* (*A. isodon*), and those of *Carcharhinus leiodon* n.sp. In a-g, data are expressed as ranges and means. In h, tooth numbers are given as a frequency table. For a-h, the range in 25 species of *Carcharhinus* is also shown for comparison.

combination, are shared by several *Carcharhinus* species and hence offer no grounds for aligning *A. isodon* and *C. leiodon* n.sp. in a genus separable from *Carcharhinus*. Therefore the only remaining feature that might be used to support such action is the nature of the teeth, but as already demonstrated by Compagno (1979) these are insufficiently distinctive for that purpose. Accordingly, *A. isodon* is here treated as a species of *Carcharhinus*, in line with Compagno's (1979) findings.

Decision on the status of *Hypoprion* versus *Carcharhinus* is similarly, but less obviously, resolved. As can be seen from Figures 1-4, the three *Hypoprion* species have values for several characters that variously exceed the ranges of *Carcharhinus* (including *Aprionodon*). In particular, these characters include three simple dimensions (prenarial length, preoral length, and first dorsal rear tip as percent total length) and three ratios incorporating these and other simple dimensions (preoral length/internarial distance, first dorsal height/first dorsal rear tip, and first dorsal base/first dorsal rear tip). Since there is a direct correlation between some of these characters (e.g., between prenarial and preoral lengths, and between the simple dimensions and the ratios incorporating them), attention is focused here on only two of them, i.e., preoral length as percent total length and first dorsal rear tip as percent total length.

The mean values for preoral length in *H. macloti* (9.5%) and *H. signatus* (9.3%) are slightly greater than in any *Carcharhinus* species, in which the highest means occur in *borneensis* and *porosus* (each with 8.7%). However, eight *Carcharhinus* species have ranges overlapping the range for *H. macloti* and ten the range for *H. signatus*. By contrast *H. hemiodon*, with a mean of 7.1%, has a preoral length like an "average" *Carcharhinus*, and there are 20 species of *Carcharhinus* with ranges that overlap its range.

The mean values for first dorsal rear tip in *H. hemiodon* (6.1%) and *H. macloti* (6.0%) are distinctly greater than in any *Carcharhinus* species, in which the highest means are in *borneensis* (4.8%), *porosus* (4.7%), and *altimus* (4.7%). Only one *Carcharhinus* species (*porosus*) has a range overlapping the range for *H. hemiodon*, and only four overlap that for *H. macloti*. In marked contrast, *H. signatus* with a mean of 4.0% is "average" for *Carcharhinus*, and there are 22 species of *Carcharhinus* with ranges overlapping that for *H. signatus*.

A third simple dimension, length of second dorsal rear tip as percent total length, although not included in Figures 1-4, also shows a difference between *H. macloti* and all *Carcharhinus* and a similarity between *H. macloti* and *H. hemiodon* comparable with that provided by first dorsal rear tip. The mean value for *H. macloti* (4.5%) is minimally greater than in any *Carcharhinus* species, where the highest means are in *borneensis* (4.4%) and *falciformis* (4.3%). The mean in *H. hemiodon* is 4.2%, and in *H. signatus* 3.8%. However, 14 *Carcharhinus* species have ranges overlapping the range for *H. macloti*, and 21 and 25 species have ranges overlapping those for *H. hemiodon* and *H. signatus*, respectively.

It is clear from the above analysis that the data in Figures 1-4 offer no basis for recognizing *Hypoprion* as distinct from *Carcharhinus*. On the one hand, the few differences that are apparent are all mean differences, and on the other hand none of the differences is common to all three *Hypoprion* species. A long preoral length is shared by *H. macloti* and *H. signatus* but not by *H. hemiodon*. A long first dorsal rear tip, and less trenchantly a long second dorsal rear tip, are common to *H. macloti* and *H. hemiodon* but not to *H. signatus*. Based on these data, *H. macloti* is the most distinctive of the three species relative to *Carcharhinus*.

Other characters examined, but not shown in Figures 1-4, yield findings parallel to the above. With respect to color, *hemiodon* has black-tipped fins but not so *signatus* and *macloti*, though the last-named is distinctive in having white trailing edges on the paired fins, the anal fin, and the lower lobe of the caudal fin. Both *signatus* and *macloti* have diplospondyly beginning above the pelvic base, whereas in *hemiodon* it is further posterior, from the level of the pelvic axil to between the pelvic tip and anal fin origin. An interdorsal ridge is common to *signatus* and to some, but perhaps not all, specimens of *macloti* and *hemiodon*. A discrete series of enlarged hyomandibular pores is present in *macloti* but not in *signatus* or *hemiodon*; it may be meaningful that the only *Carcharhinus* species with comparable pores is *borneensis* which agrees further with *macloti* in having a long preoral length; long first and second dorsal rear tips; the second dorsal origin over the middle of the anal fin base; white trailing margins on the pectoral, pelvic, and anal fins; very large basal serrae on the lateral margins of the upper teeth; and a nipple-shaped anterior nasal lobe. All three species of *Hypoprion* have similar anterior nasal lobes, but so do several species of *Carcharhinus*.

The overall conclusion that must be reached from the present study is that although *hemiodon*, *macloti*, and *signatus* each extend the range of diversity of *Carcharhinus* in one or more features, there is no common pattern of difference from *Carcharhinus* other than in the nature of the upper teeth—and even this dental difference is not consistent, as indicated by Compagno (1979). Were this difference in the upper teeth matched by even one other common but singular distinction from *Carcharhinus*, the case for retaining *Hypoprion* as a separate genus could be readily made. Since this is not so, the distinction based on the teeth alone, i.e., on the presence of large basal serrae coupled with essentially smooth-edged margins distally, must also come under more stringent scrutiny. Several *Carcharhinus* species (including *borneensis*, *cautus*, *dussumieri*, *porosus*, and *sealei*, amongst others) have comparably large basal serrae, and one (*brevipinna*) has smooth-edged margins at least in juveniles, thus supporting Compagno's (1979) conclusion that *Hypoprion* should by synonymised with *Carcharhinus*. I agree with Compagno's conclusion. It is also evident that the present data further support Compagno's findings that *macloti* is the most divergent of the three nominal species of *Hypoprion*. These data, even when combined with the cranial and dental peculiarities of *macloti* noted by Compagno, seem insufficient to warrant retaining *Hypoprion* as a separate genus for *macloti* alone, because of the various features shared by *macloti* and either *hemiodon* or *signatus*, and *macloti* and various species of *Carcharhinus*.

Carcharhinus isodon (Valenciennes *in* Müller and Henle, 1841)
Figures 5, 6, Table 1

Carcharias (*Aprion*) *isodon* Valenciennes *in* Müller and Henle, 1841:32-33. One spirit specimen in the Paris Museum from Milbert; no locality mentioned in original description, but Paris Museum data give it as New York.

DIAGNOSIS.—Moderately large sharks, up to 1.55 m long, lacking an interdorsal ridge; fin tips without dark markings though the leading margins of the dorsals and both margins of the upper caudal may be narrowly dark-edged; snout moderately long and sharply pointed; internarial width 1.2 to 1.4 in preoral length; origin of first dorsal fin over or just behind middle of inner pectoral margin; apex of first dorsal sharply rounded to pointed; origin of second dorsal from slightly in front of to slightly behind anal fin origin; height of second dorsal 2.5-2.9% TL and 1.4-1.6 in length of its rear tip; dental formula usually 15-2-15/14-3-14; upper teeth narrow, erect to slightly oblique, concave laterally and medially, and smooth-edged; lower teeth erect, smooth-edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 78-80; caudal centra 85-87; total centra 163-167; diplospondyly begins from pelvic axil to behind pelvic tip; anterior diplospondylous centra alternate slightly but regularly in length; penultimate monospondylous centrum 1.0-1.1 times longer than wide.

The species most likely to be confused with *isodon* are *amblyrhynchoides*, *brevipinna*, *limbatus*, and *C. leiodon* n.sp. which have in common with it all or most of the following features: narrow and essentially erect upper teeth, no interdorsal ridge, a pointed and moderately long snout, large gill openings, and long labial furrows. It differs from all of these species in lacking black fin tips; from *amblyrhynchoides*, *brevipinna*, and *limbatus* in having the first dorsal origin over the middle of the pectoral inner margin (over the pectoral axil in *amblyrhynchoides* and *limbatus*, and over or behind the pectoral inner corner in *brevipinna*) and in details of the teeth; and from *C. leiodon* n.sp. in having a much lower second dorsal fin.

NOMENCLATURAL DISCUSSION.—The holotype of *isodon* Valenciennes *in* Müller and Henle (1841) is in good condition and agrees well with the original description where *isodon*, although not illustrated, was compared with *brevipinna* Müller and Henle and placed with that species, and also *acutidens* Rüppell (= *Negaprion acutidens*), in the new subgenus *Aprion* Müller and Henle. Gill (1862), who recognized that *Aprion* was preoccupied (see Bigelow and Schroeder 1948), proposed the replacement name *Aprionodon* with *punctatus* as type-species, an action based on his belief that *Squalus punctatus* Mitchill, 1815 was a senior synonym of *isodon* (see Gill 1864). However, as evident from Mitchill's description of *punctatus* in Gill (1864), where the upper lobe of the caudal fin is said to be "almost thrice as large as the lower" these two species cannot be synonymous. There are no other primary synonyms of *isodon*. Springer's (1950) suggestion "that there are two American forms of *Aprionodon* and that the Texas and north Gulf of Mexico population may represent an undescribed species" has not been further substantiated.

DESCRIPTION (see also Table 1).—Moderately large sharks, growing to at least 1.55 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles in small specimens close-packed and overlapping, subcircular in outline, each with three longitudinal ridges and corresponding posterior marginal teeth, the latter sharp-pointed but rather short.

Snout of moderate length and sharply pointed in contour. Anterior margin of eye above front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula 15-2-15/14-3-14 in five specimens counted. Upper teeth narrow, erect near the center of the mouth but slightly oblique laterally, medial and lateral margins concave, both margins essentially smooth-edged, although there are slight irregularities basally, particularly on the lateral margins; two small symphysial teeth. Lower teeth narrow, erect, with both margins deeply concave, and smooth-edged; three small symphysial teeth.

First dorsal fin moderately low, erect rather than falcate, its apex sharply rounded to pointed; origin of first dorsal over or slightly behind middle of posterior (inner) pectoral margin. Second dorsal fin moderately low and long, almost equal to anal fin; length of second dorsal rear tip 1.4 to 1.6 (mean 1.5 in six specimens) times its height; origin of second dorsal from slightly anterior to slightly posterior to anal fin origin. Pectoral fin short, slightly falcate, and pointed distally; origin of pectoral fin below or only just anterior to fifth gill opening; outer corner of pectoral, when fin is adpressed to trunk so that its anterior margin is horizontal, reaches almost or quite to first dorsal axil.

After preservation in alcohol, the color of the back and sides is grey to dark grey while the underside is pale, and a tongue of the pale color may extend forward along the side from the pelvic region to below the first dorsal fin. The leading margins of the two dorsal fins and both margins of the upper caudal lobe are usually narrowly edged with a dusky color or black.

Vertebral counts as in Table 1. Centrum diameter greater than centrum length except in longest monospondylous centra at posterior of abdomen where diameter and length are approximately equal. Anterior diplospondylous centra alternate slightly but regularly in length. Diplospondyly occurs from above the pelvic axil to behind the pelvic tip. Length/diameter of penultimate monospondylous centrum is 0.98 to 1.12 (mean 1.04 in four specimens), and length of penultimate monospondylous centrum/length of first diplospondylous centrum is 1.33 to 2.07 (mean 1.57 in four specimens).

Of the five specimens of *isodon* examined by me, four were newborn or juveniles, 413-631 mm TL, and the fifth was a mature female, about 1,500 mm. A similar disparity of sizes and a relative paucity of adult records are evident from the literature. The few records of adults include those of Springer (1950) who noted that adults "appear in relatively large numbers in less than 10 fathoms (18 m) off Salerno, Florida, during December and January" but not in other months. He gave the lengths of 20 adult females as 1,473-1,549 mm and of 6 adult males as 1,397-1,524 mm. Dahlberg and Heard (1969) listed only one presumably adult specimen, 1,445 mm long, in a collection of 30 specimens from off Georgia in July to September. Branstetter and Shipp (1980) reported five adults, two of them females 1,270-1,390 mm, and three males 1,120-1,270 mm, taken off Alabama in June and July. Branstetter (1981) summarized unpublished data from Moran (1972)[2] on six females 1,230-1,420 mm from the northern Gulf of Florida. All other records from the

[2]Moran, J. L. 1972. The occurrence of sharks in two bays off the northern Gulf coast of Florida. Unpubl. senior research project, 26 p. Florida State University, Tallahassee.

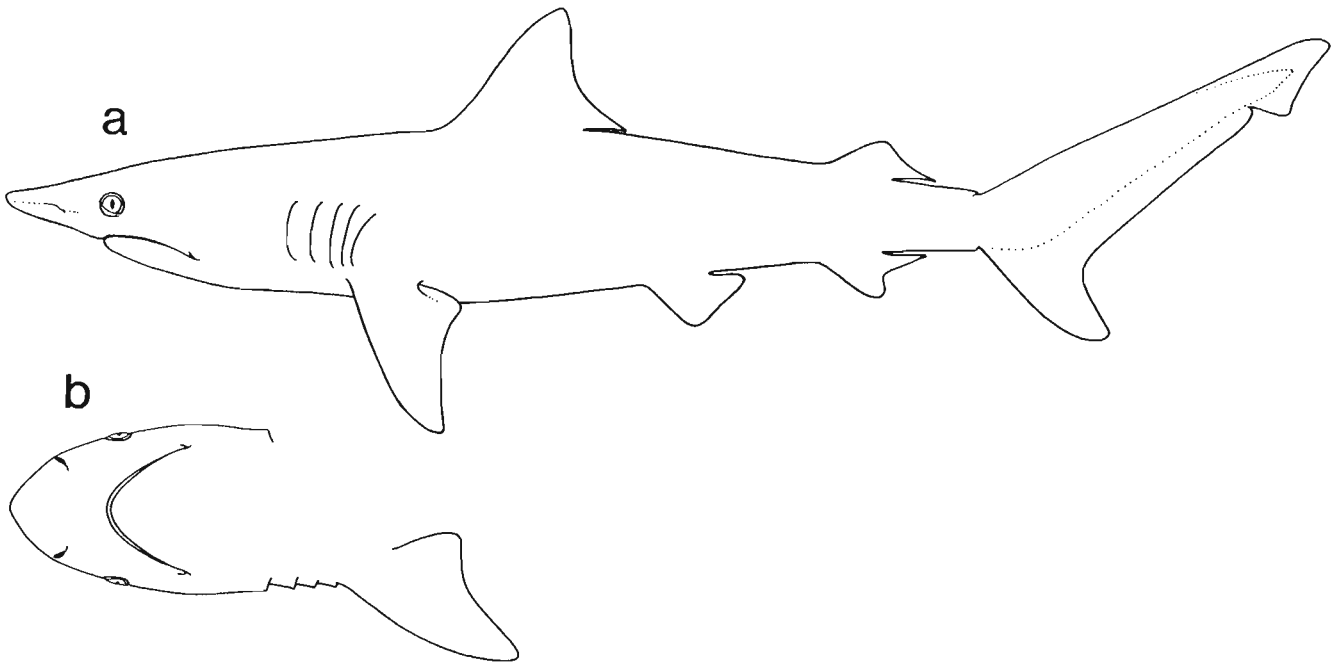

Figure 5.—*Carcharhinus isodon*, USNM 118457, 496 mm TL, female from Texas: a, left side (redrawn and modified from Bigelow and Schroeder 1948, fig. 51); b, underside of head.

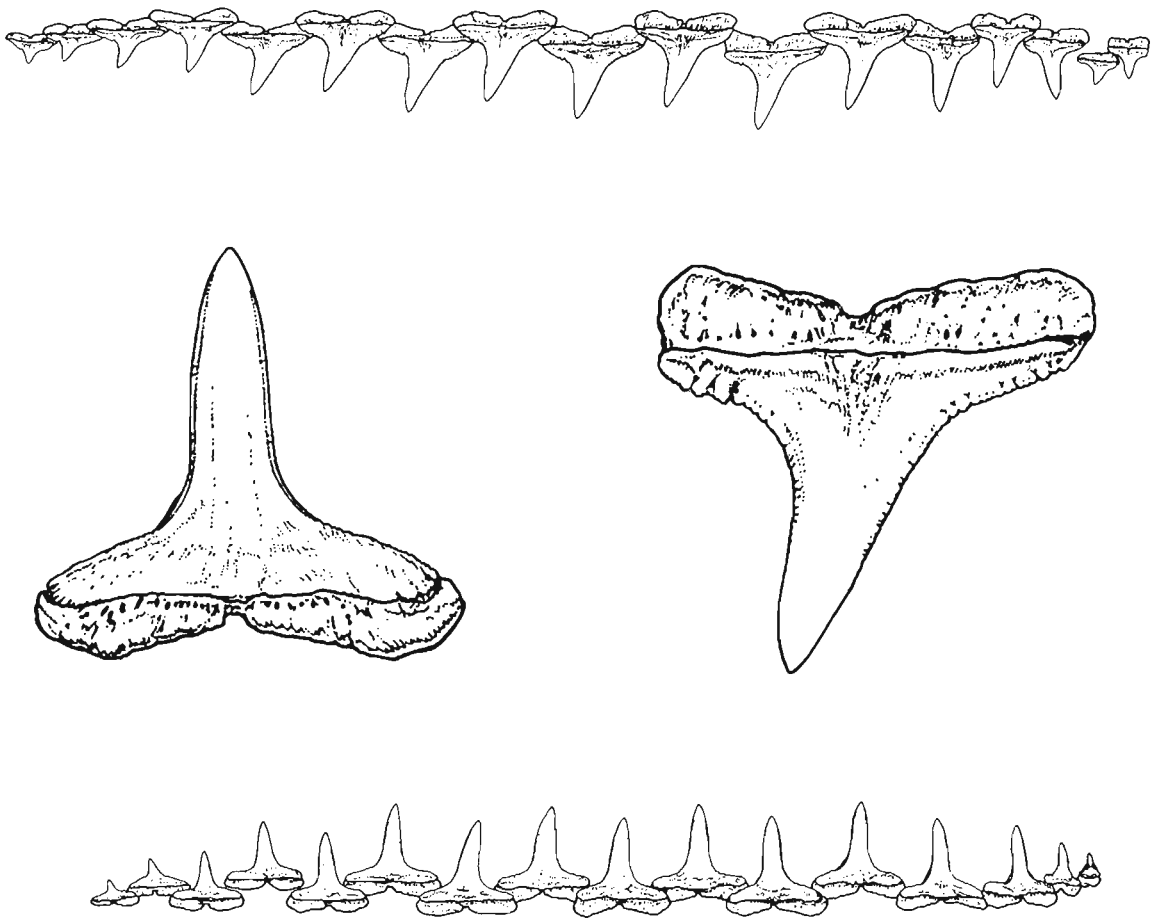

Figure 6.—*Carcharhinus isodon*, USNM 143761, ca. 1,500 mm TL, female from Florida; right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Table 1. — Carcharhinus isodon and C. leiodon n.sp., proportional dimensions in percent of total length.

	C. isodon						C. leiodon n.sp.
	♀ 413 mm Texas USNM 130651	♀ 453 mm Mississippi USNM 126118	♀ 496 mm Texas USNM 118457	♂ 510 mm[1] Alabama USAIC 6278	♂ 631 mm[2] New York MNHN 1037	♀ 1390 mm[1] Alabama USAIC 6278	♂ 750 mm Gulf of Aden NMV 61-465
Snout tip to: outer nostrils	3.6	4.1	3.1	-	3.6	-	3.2
: eye	7.0	7.6	7.1	-	6.8	-	6.7
: mouth	7.0	7.6	7.3	7.6	6.8	6.5	6.7
: 1st gill-opening	21.5	21.8	19.4	-	19.6	-	19.8
: 3rd gill-opening	23.9	24.0	23.0	-	22.5	-	22.5
: 5th gill-opening	25.2	25.6	25.0	-	24.7	-	25.3
: pectoral origin	24.7	25.4	24.6	23.9	24.4	22.7	24.9
: pelvic origin	47.4	47.4	48.2	49.8	46.7	53.2	50.2
: 1st dorsal origin	32.0	32.2	32.1	32.4	31.5	33.1	32.6
: 2nd dorsal origin	61.0	60.7	62.5	61.8	60.5	64.7	64.4
: anal fin origin	60.5	60.3	61.5	62.5	60.2	63.3	64.0
: upper caudal origin	73.1	72.0	74.2	-	72.4	-	76.1
: lower caudal origin	72.1	71.9	73.6	-	71.4	-	75.7
Nostrils: distance between inner corners	5.8	5.7	5.4	5.3	5.3	5.0	6.3
Mouth: width	8.5	8.2	8.7	8.6	8.7	9.4	9.6
: length	6.3	6.2	5.8	-	5.9	-	5.5
Labial furrow lengths: upper	0.8	0.9	0.9	-	0.9	-	0.4
: lower	0.8	0.8	0.8	-	0.9	-	0.6
Gill-opening lengths: 1st	4.2	5.0	4.3	4.5	5.7	5.8	4.0
: 3rd	4.8	5.4	4.9	5.3	5.9	6.5	4.5
: 5th	4.0	4.4	4.3	3.5	4.5	5.4	3.2
Eye: horizontal diameter	2.2	2.2	1.9	1.6	1.7	1.3	1.9
1st dorsal fin: length base	9.7	8.8	10.0	9.0	10.1	10.1	11.2
: posterior margin	3.8	4.0	3.5	4.3	4.0	4.0	4.4
: height	8.5	8.8	8.9	7.5	9.7	10.6	10.5
2nd dorsal fin: length base	4.1	4.1	4.3	4.3	4.4	4.7	5.1
: posterior margin	4.1	4.0	3.7	4.3	4.0	4.0	3.5
: height	2.8	2.5	2.5	2.7	2.9	2.9	4.1
Anal fin: length base	5.0	4.9	4.8	4.7	4.6	5.3	5.6
: posterior margin	3.6	3.6	3.3	3.7	4.0	3.5	3.3
: height	3.1	3.1	3.2	2.9	3.4	3.1	4.4
Pectoral fin: length base	5.8	5.3	5.6	5.1	5.3	5.8	6.5
: anterior margin	16.0	15.4	14.7	-	16.0	-	17.4
: distal margin	10.2	9.9	10.1	-	11.4	-	14.5
: greatest width	8.5	8.2	8.1	-	8.2	-	10.8
Pelvic fin: length base	5.1	5.1	5.1	-	5.1	-	6.3
: anterior margin	5.7	5.5	5.1	5.1	5.8	4.7	6.7
: distal margin	4.8	5.4	5.1	5.7	5.1	6.3	7.1
: length claspers	-	-	-	-	2.8	-	2.8
Caudal: length upper lobe	27.8	28.5	27.6	29.2	27.7	28.1	24.8
: length lower lobe	12.1	11.9	11.3	10.8	12.3	12.6	13.1
Trunk at pectoral origin: width	10.4	10.6	10.5	-	10.4	-	14.2
: height	10.6	11.0	11.3	-	11.1	-	12.8
Dental formula	$\frac{15-2-15}{14-3-14}$	$\frac{15-2-15}{14-3-14}$	$\frac{15-2-15}{14-3-14}$	-	$\frac{15-2-15}{14-3-14}$	-	$\frac{16-3-16}{15-3-15}$
Vertebrae: precaudal	80	78	79	-	80	-	115
: caudal	87	85	85	-	86	-	83
: total	167	163	164	-	166	-	198

1. Data from Branstetter & Shipp (1980) on specimens in the University of South Alabama Ichthyological Collection.

2. Holotype of Carcharias (Aprion) isodon.

western North Atlantic which I have seen are clearly of newborn or juveniles. They include Baughman and Springer (1950—432 mm), Bigelow and Schroeder (1948—460 to 567 mm), Radcliffe (1916—508 mm), Dahlberg and Heard (1969—520 to 940 mm), Müller and Henle (1841)—631 mm, holotype of *isodon*), Bearden (1965—695 mm), Burton (1940—747 mm), Clark and von Schmidt (1965—760 mm), and Springer (1938—762 mm). For the western South Atlantic, Sadowsky (1967) recorded two males from southern Brazil of 1,101 and 1,148 mm which he described as half-grown. Springer's works (1950, 1960) contribute to estimates of probable birth size and litter number in *isodon*. Of 20 adult females from Salerno, Florida, (Springer 1950) 13 had 1-6 embryos 432-483 mm long and 7 had recently pupped. His estimate of birth size (1960—from his fig. 3) was about 435-610 mm. Branstetter and Shipp (1980) reported four late embryos, 490-510 mm long, two in each uterus, from a 1,390 mm female taken off Alabama in June, and proposed birth size of 450-550 mm. They estimated that males become mature at lengths between 1,150 and 1,200 mm (based on their immature male of 1,120 mm and two mature males of 1,200 and 1,270 mm). For females they proposed a larger size at maturity, noting that their 1,270 mm specimen was still immature whereas their 1,390 mm female was gravid. Branstetter (1981) supplemented these data with information from Moran (footnote 2) on four immature females (1,230, 1,260, 1,370, and 1,420 mm) and two gravid females (1,370 and 1,420 mm) from the northern Gulf coast of Florida, and concluded that females become mature at lengths near 1,400 mm. The maximum size so far reported for *isodon* is 1,524 mm for males and 1,549 mm for females (Springer 1950).

Although Springer (1950) suggested that "comparison of new-born summer young from the coast of Texas with winter late embryos from Salerno indicates that there are two American forms of *Aprionodon* and that the Texas and north Gulf of Mexico population may represent an undescribed species" he did not give further information on this phenomenon.

DISTRIBUTION (see also Material Examined).—Western Atlantic from New York to southern Brazil but generally not well documented. The few specimens I have seen have been from New York (holotype of *isodon*), the east coast of Florida (Salerno), and the northern Gulf of Mexico (Texas and Mississippi). Specimens from these latter regions (Florida and the northern Gulf of Mexico) have also been the subject of the most extensive or detailed accounts of *isodon* in the literature, including particularly those of Bigelow and Schroeder (1948—Mississippi and Texas) and Springer (1950—both coasts of Florida and Mississippi). Supplementary accounts for the same regions are by Springer (1938—Florida), Baughman and Springer (1950—Texas), Clark and von Schmidt (1965—Florida), Applegate et al. (1979—who include an illustration of *isodon* in their account of Mexican sharks but do not give a detailed locality or record for the Gulf of Mexico), Branstetter and Shipp (1980—Alabama), and Branstetter (1981—Alabama and Florida). Northward of these regions there are scattered records or listings from Georgia (Dahlberg and Heard 1969), South Carolina (Burton 1940; Bearden 1965), North Carolina (Radcliffe 1916—specimen in Beaufort Laboratory but without data), Virginia (Jordan and Evermann 1896), and New York (holotype of *isodon*). Southwards the records of *isodon* are likewise meager and confined to Cuba (Poey 1876 and also Manday 1968 who commented that *isodon* has been reported only once from that locality), British Guiana (Lowe (McConnell) 1962), and southern Brazil (Sadowsky 1967 who noted that his two specimens from Cananéia at lat. 25°S were a new record for Brazil).

Reports of *isodon* from the eastern Atlantic cannot be regarded as confirmed, and are probably based on other species including particularly *Carcharhinus brevipinna*. Bigelow and Schroeder (1948) cited Rochebrune (1883-85) and Metzelaar (1919) as references for the occurrence of *isodon* off West Africa, but despite these listings I note that Cadenat (1950) did not observe *isodon* off the Senegalese coasts, and Poll (1951) likewise did not report it in the collection of 21 species of sharks taken by the Expédition Océanographique Belge (1948-49) from the Equator south to lat. 22°30′S. Poll's (1951) description of an *Aprionodon* as a new species, *A. caparti*, from that expedition was, in fact, based on juvenile *C. brevipinna*. The same may be true of Gonçalves' (1955) listing of a small (650 mm) specimen, as *A. isodon*, from Portuguese Guinea.

MATERIAL EXAMINED.—USNM 130651, female, 413 mm, Texas, Galveston, 7-14 July 1940, J. L. Baughman; USNM 126118, female, 453 mm, Mississippi, Biloxi Light, 4 July 1933, S. Springer; USNM 118457, female, 496 mm, Texas, Galveston, 14 July 1940, J. L. Baughman; MNHN 1037, male, 631 mm (holotype of *Carcharias* (*Aprion*) *isodon*), New York, Milbert; USNM 143761, skinned-out, female, ca. 1,500 mm, Florida, Salerno, January 1948, S. Springer.

Carcharhinus leiodon n.sp.
Figures 7, 8, Table 1

Holotype (the only specimen known) NMV 61-465, immature male, 750 mm, from southern Arabia (Gulf of Aden) probably at Qishn (variously spelt as Keschin, Kischin, or Gischin), collected by W. Hein, 1902.

DIAGNOSIS.—Sharks lacking an interdorsal ridge; all fins with black tips; snout moderately long and bluntly pointed; internarial width 1.1 in preoral length; origin of first dorsal fin slightly behind middle of inner pectoral margin; apex of first dorsal pointed; origin of second dorsal slightly behind anal fin origin; height of second dorsal 4.1% TL and 0.8 in length of its rear tip; dental formula 16-3-16/15-3-15; upper teeth narrow, erect to slightly oblique, concave to notched medially, notched laterally, and smooth-edged; lower teeth erect and smooth-edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 115; caudal centra 83; total centra 198; diplospondyly begins above anterior third of pelvic base; diplospondylous centra regular; penultimate monospondylous centrum 0.5 times as long as wide.

The narrow, erect, and smooth-edged upper teeth of *leiodon*, when compared with those of other *Carcharhinus* species, have close counterparts only in *isodon* and in juvenile *brevipinna*, although comparably shaped teeth, but with serrated edges, occur also in *amblyrhynchoides*, *limbatus*, and adult *brevipinna*. Other common features which *leiodon* shares with these same four species include the lack of an interdorsal ridge, a pointed snout, and rather large gill openings. *Carcharhinus leiodon* differs from *isodon* in having black fin tips, a much higher second dorsal fin (4.1% TL versus 2.5-2.9% TL), and more precaudal vertebrae (115 versus 78-80). It is readily separable from the black-tips *amblyrhynchoides*, *limbatus*, and *brevipinna* by having its first dorsal fin origin over the middle of the pectoral inner margin (*amblyrhynchoides* and *limbatus* have it over the pectoral axil, *brevipinna* over or behind the pectoral inner corner), by its greater number of precaudal vertebrae, and to a less obvious extent by several differences in fin sizes and proportions (see Garrick 1982 for comparative data on these black-tips).

On external features alone, *leiodon* is most likely to be confused

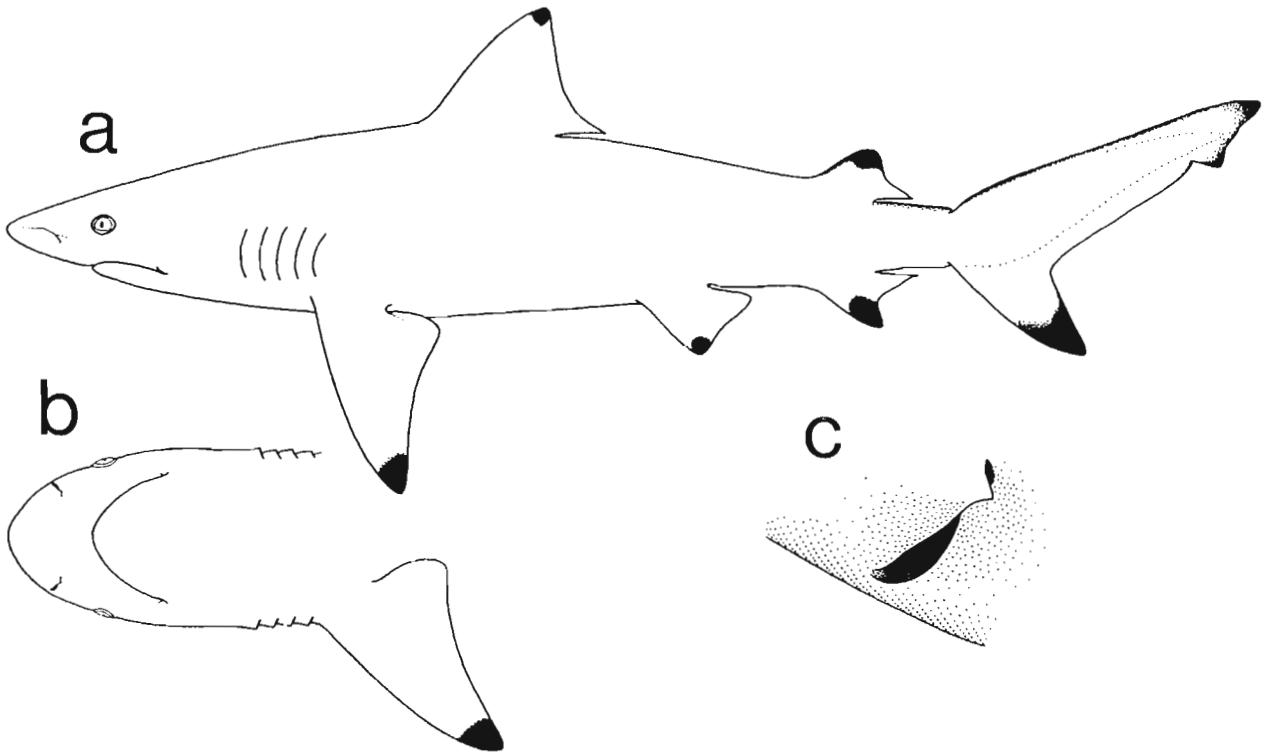

Figure 7.—*Carcharhinus leiodon* n.sp., NMV 61-465, 750 mm TL, male from Gulf of Aden, Qishn: a, left side; b, underside of head; c, enlarged right nostril.

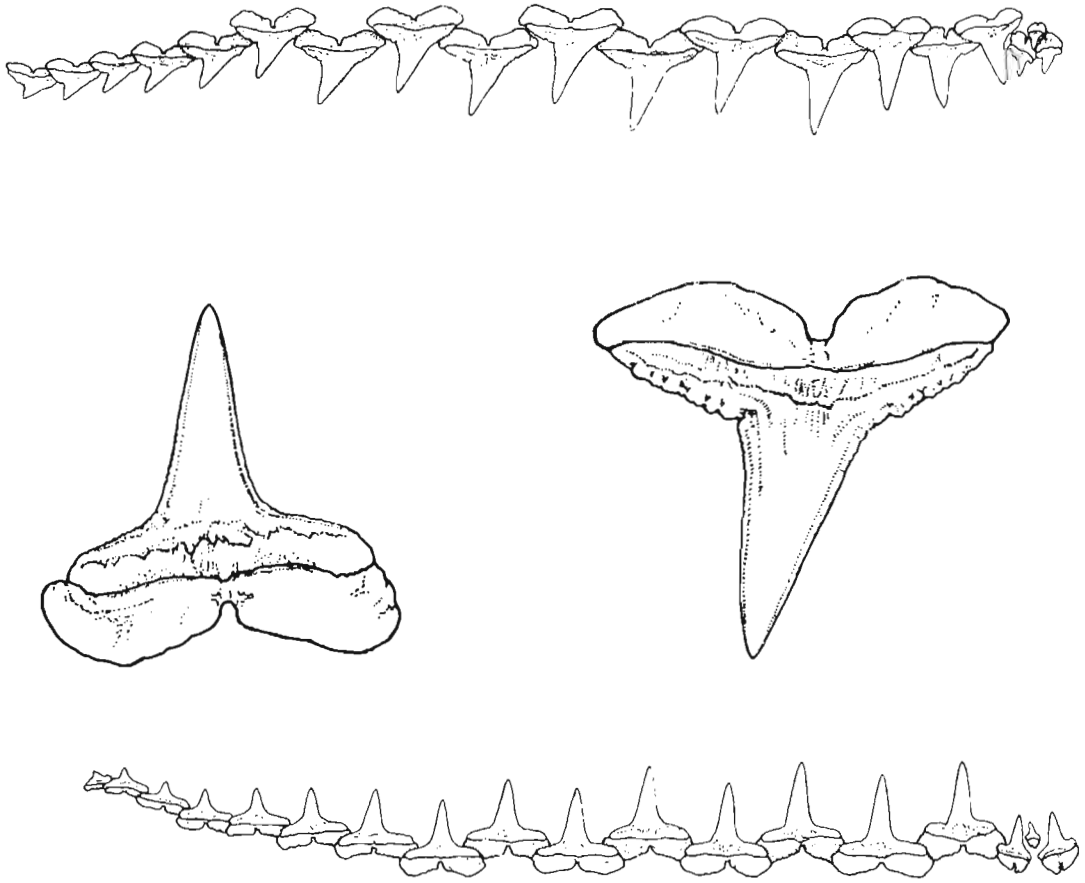

Figure 8.—*Carcharhinus leiodon* n.sp., NMV 61-465, 750 mm TL, male from Gulf of Aden, Qishn: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

with *melanopterus*, and perhaps also with *hemiodon*. It agrees further with *melanopterus* in its number of precaudal vertebrae (115 versus 111-122) but differs in its pointed snout, upper tooth shape, and dental formula (16/15 lateral teeth on each side versus 12 or 13/10 to 12). It is readily distinguished from *hemiodon* by its much shorter first dorsal rear tip (4.4% TL versus 5.9-6.5% TL), its higher second dorsal (4.1% TL versus 2.3-2.6% TL), and upper tooth shape.

In terms of vertebral numbers alone, the precaudal count of 115 for *leiodon* is encompassed only by counts for *amblyrhynchos* (110-119), *wheeleri* (110-117), *melanopterus* (111-122), and *leucas* (101-123), species which, apart from *melanopterus* discussed above, differ trenchantly from *leiodon* in numerous other features.

DESCRIPTION (see also Table 1).—Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles slightly overlapping, ovoid in outline, wider than long, each with three strong, longitudinal ridges and three, or occasionally five, sharp-pointed, posterior marginal teeth.

Snout of moderate length and bluntly pointed in contour. Anterior margin of eye above front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula 16-3-16/15-3-15. Upper teeth narrow, erect near the center of the mouth but slightly oblique laterally, medial margins notched to concave, lateral margins notched, both margins essentially smooth-edged, although there are slight irregularities basally, particularly on the lateral margins; three small symphysial teeth. Lower teeth narrow, erect, with both margins deeply concave to almost notched, and smooth-edged; three small symphysial teeth.

First dorsal fin of moderate height, erect rather than falcate, its apex pointed; origin of first dorsal slightly behind middle of posterior (inner) pectoral margin. Second dorsal fin large and high, almost equal to anal fin; length of second dorsal rear tip 1.2 in its height; origin of second dorsal slightly posterior to anal fin origin. Pectoral fin moderately short, weakly falcate, and pointed distally; origin of pectoral fin below and between the fourth and fifth gill openings; outer corner of pectoral, when fin is adpressed to trunk so that its anterior margin is horizontal, reaches to first dorsal axil.

Color after preservation is yellowish-brown above, and yellowish on the underside, with a tongue of this paler underside color extending forward along the side of the trunk from the pelvic region to below the first dorsal fin; the upper surface of the caudal peduncle behind the second dorsal is dusky. All fins are black-tipped, with the black clearly demarcated from the background color; the black markings on the apices of the first dorsal and pelvic fins are smaller than those on the other fins; on the upper lobe of the caudal the black tip is extended forwards along both margins as a narrow black edging.

Vertebral count as in Table 1. Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centra regular. Diplospondyly begins above the anterior third of the pelvic base. Length/diameter of penultimate monospondylous centrum is 0.51, and length of penultimate monospondylous centrum/length of first diplospondylous centrum is 1.22.

The size of the claspers (2.8% TL) indicates that the specimen is immature.

DISCUSSION.—Although my information on *leiodon* is based on only one specimen, I have no hesitation in describing it as a new species because it very clearly differs from all other species of *Carcharhinus* including even those that superficially are very similar to it.

The collection data with the holotype are meager, giving the locality only as "Gischin," the collector as "Hein," and the date 1902. I was unable to locate Gischin in atlases, but Rainer Hacker[3] of the Vienna Museum informed me that the name may be an old spelling or a misspelling for Qishn in southern Arabia, which latter region was where Wilhelm Hein collected specimens, including the holotype, at the beginning of this century. Other alternative spellings in older atlases are Keschin and Kischin.

Etymology of the Name.—*leiodon* is a noun in the nominative singular in apposition, formed from Greek *leios*, adjective = smooth, and Greek (Ionic) *odon*, noun, masculine = tooth.

Carcharhinus hemiodon (Valenciennes *in* Müller and Henle, 1841)
Figures 9, 10, Table 2

Carcharias (*Hypoprion*) *hemiodon* Valenciennes *in* Müller and Henle, 1841:35, plate 19 (teeth). Four spirit specimens in the Paris Museum, from Bélanger. India—Malabar and Pondicherry.

Hypoprion atripinnis Chu, 1960:80, figures 75-76 (not seen; data from Chu (1962:26, fig. 19) in which four females, 519 to 675 mm, and two males, 542 and 564 mm, are listed). South China Sea.

DIAGNOSIS.—Small sharks, probably up to 1.0 m long, with or without an interdorsal ridge; pectoral, lower lobe of caudal, and to a lesser extent second dorsal, black-tipped; upper caudal leading margin and tip and apex of first dorsal dusky-edged; snout moderately long and bluntly pointed; internarial width 1.2-1.3 in preoral length; origin of first dorsal fin above or slightly in front of middle of inner pectoral margin; apex of first dorsal pointed; rear tip of first dorsal 5.9-6.5% TL; origin of second dorsal one-third to almost halfway along anal base; height of second dorsal 1.9-2.6% TL and 1.5-2.3 in length of its rear tip; dental formula usually 14-1 or 2-14/13-1 or 2-13 but may be 14-1 or 2-14/12 to 14-1 or 2-12 to 14; upper teeth narrow, erect to slightly oblique, notched laterally and notched to concave or straight medially, with very large serrae basally but smooth-edged distally; lower teeth erect and smooth-edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 69-71; caudal centra 78-84; total centra 147-155; diplospondyly begins from between pelvic axil and tip to midway between pelvic tip and anal fin; diplospondylous centra regular; penultimate monospondylous centrum 1.1-1.2 times longer than wide.

The black fin tips of *hemiodon*, coupled with its distinctively long first dorsal rear tip (5.9-6.5% TL) and features of its upper teeth (teeth smooth-edged distally but with large serrae basally), effectively separate it from all other *Carcharhinus* species including even the black-tipped species (*amblyrhynchoides*, *brevipinna*, *limbatus*, *melanopterus*, *sorrah*, and *C. leiodon* n.sp.) with which it could, at first glance, be confused. Of these latter, *melanopterus* comes closest to it in having a long first dorsal rear tip (3.8-5.0% TL), but *melanopterus* differs immediately in its much blunter snout contour and higher second dorsal fin.

NOMENCLATURAL DISCUSSION.—The spirit-preserved holotype and three paratypes of *hemiodon* Valenciennes *in* Müller and Henle (1841) in the Paris Museum permit amplification of the original

[3]R. Hacker, former Curator of Fishes, Naturhistorisches Museum, Wein, Burgring 7, A-1014 Vienna, Austria, pers. commun. July 1980.

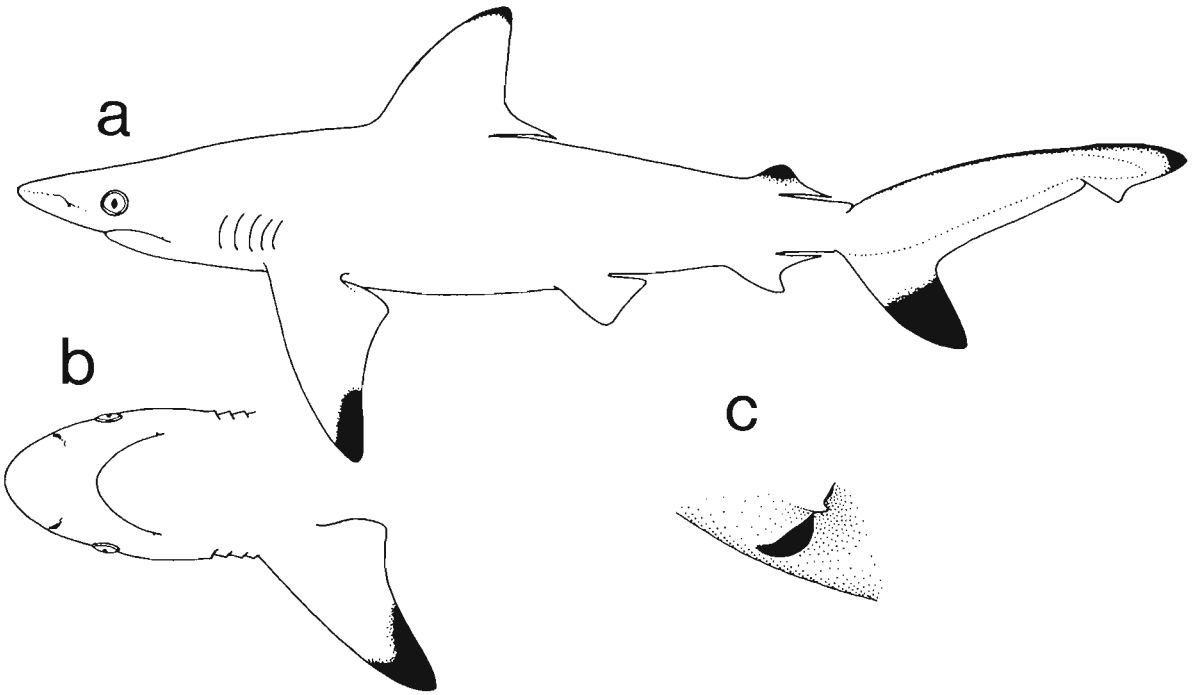

Figure 9.—*Carcharhinus hemiodon*, SU 14501, 553 mm TL, male from India, Calicut: a, left side; b, underside of head; c, enlarged right nostril.

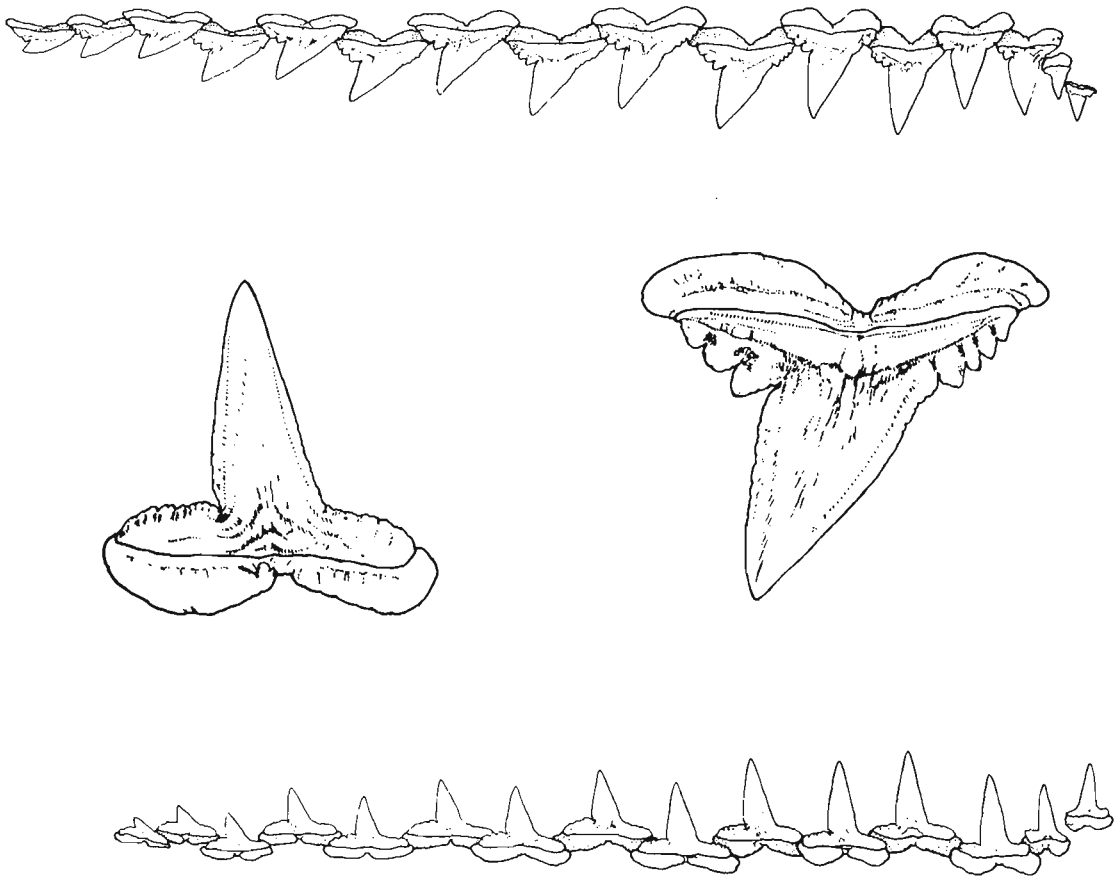

Figure 10.—*Carcharhinus hemiodon*, SU 14501, 553 mm TL, male from India, Calicut: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Table 2. — Carcharhinus hemiodon, proportional dimensions in percent of total length.

	♂ 368 mm[1]. India Malabar MNHN 7774	♂ 444 mm India Canara BMNH 89.2.1.4174	♂ 467 mm[2]. India Pondicherry MNHN 1040	♂ 553 mm India Calicut SU 14501	♀ 665 mm India Calicut BMNH 89.2.1.4171
Snout tip to: outer nostrils	3.9	3.8	3.5	3.3	3.6
: eye	7.2	7.2	6.5	7.0	7.3
: mouth	7.2	7.2	6.5	7.2	7.4
: 1st gill-opening	-	17.3	18.6	17.2	18.5
: 3rd gill-opening	-	19.8	21.2	19.7	21.2
: 5th gill-opening	22.7	22.3	23.6	21.7	23.2
: pectoral origin	21.9	21.6	22.9	21.0	22.3
: pelvic origin	46.4	46.8	47.8	46.1	46.9
: 1st dorsal origin	29.9	29.0	30.0	29.5	29.6
: 2nd dorsal origin	61.2	61.9	62.7	62.4	61.5
: anal fin origin	59.8	59.9	60.8	60.5	60.1
: upper caudal origin	72.0	72.3	72.3	72.3	71.9
: lower caudal origin	70.6	71.1	71.5	70.9	70.7
Nostrils: distance between inner corners	5.7	5.8	5.7	5.8	5.7
Mouth: width	7.7	8.0	9.2	8.4	7.8
: length	5.4	4.5	5.5	5.1	5.1
Labial furrow lengths: upper	0.5	0.5	0.6	0.5	0.6
: lower	0.5	0.5	0.6	0.5	0.4
Gill-opening lengths: 1st	-	3.2	3.1	2.8	-
: 3rd	3.3	3.7	3.6	3.2	3.8
: 5th	-	3.2	2.9	2.7	-
Eye: horizontal diameter	2.4	2.3	2.2	2.3	2.1
1st dorsal fin: length base	10.3	9.9	10.3	10.4	10.5
: posterior margin	6.2	5.9	6.0	5.9	6.5
: height	9.4	10.9	9.6	10.8	11.6
2nd dorsal fin: length base	3.5	2.9	2.7	3.4	3.0
: posterior margin	4.5	4.3	4.3	4.2	3.9
: height	2.4	2.3	1.9	2.4	2.6
Anal fin: length base	4.3	4.5	4.3	4.2	4.7
: posterior margin	4.1	3.9	4.1	4.2	3.8
: height	3.1	3.2	2.8	3.2	3.8
Pectoral fin: length base	6.5	6.2	5.8	6.3	6.0
: anterior margin	16.3	17.1	16.8	19.2	18.6
: distal margin	10.8	12.6	11.8	13.7	15.2
: greatest width	8.7	8.6	9.2	9.8	10.2
Pelvic fin: length base	5.2	4.6	4.6	5.4	5.3
: anterior margin	5.7	5.2	4.8	5.9	5.6
: distal margin	4.5	5.2	4.5	5.7	6.0
: length claspers	2.6	2.7	2.4	2.5	-
Caudal: length upper lobe	28.8	28.1	27.2	28.0	28.3
: length lower lobe	13.2	12.6	12.6	13.0	12.8
Trunk at pectoral origin: width	10.8	-	11.3	11.7	-
: height	9.5	-	10.7	11.5	-
Dental formula	$\frac{14\text{-}1\text{-}14}{12\text{-}1\text{-}12}$	$\frac{14\text{-}1\text{-}14}{14\text{-}1\text{-}14}$	$\frac{14\text{-}1\text{-}14}{13\text{-}1\text{-}13}$	$\frac{14\text{-}2\text{-}14}{13\text{-}2\text{-}13}$	$\frac{14\text{-}2\text{-}14}{13\text{-}2\text{-}13}$
Vertebrae: precaudal	-	70	69	71	71
: caudal	-	84	78	84	83
: total	-	154	147	155	154

1. Paratype of Carcharias (Hypoprion) hemiodon.

2. Holotype of Carcharias (Hypoprion) hemiodon.

description, which although adequate was not accompanied by an illustration other than of the teeth.

I have not seen Chu's (1960) original description of his *atripinnis* from the South China Sea, but his later description (1962) and illustrations (lateral view and underside of head) agree so well with *hemiodon* that I find no reason for regarding *atripinnis* as distinct from *hemiodon*. Chu (1962) compared *atripinnis* only with *macloti* from which he found obvious differences.

Gill (1862) designated *hemiodon* as the type-species of a new genus *Hypoprionodon* differing from *Hypoprion* Müller and Henle in the more anterior position of the first dorsal fin relative to the pectoral fins. Subsequent authors have not found this generic separation compelling.

DESCRIPTION (see also Table 2).—Small sharks, growing to about 1 m TL. Midline of back between dorsal fins with or without a low interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles in small specimens overlapping, ovoid in outline, wider than long, each with three strong longitudinal ridges and three, or occasionally five, rather short, posterior marginal teeth.

Snout of moderate length and bluntly pointed: anterior margin of eye above or slightly forward of front of mouth. Nostrils strongly oblique, with rather broadly ovate apertures, the anterior margin of each with a narrow, pointed lobe.

Dental formula 14-1 or 2-14/13-1 or 2-13 in four of six specimens counted, 14-1-14/12-1-12 in one, and 14-1-14/14-1-14 in one. Teeth of an immature male as in Figure 10, where the upper teeth are narrow, erect near the center of the mouth but increasingly oblique laterally, their lateral margins deeply notched, their medial margins notched in the teeth near the center of the mouth but weakly concave to straight in those towards the corner of the mouth; two to four very large basal serrae on the lateral margin of each tooth, and a comparable number of rather smaller and less well defined basal serrae on the medial margin [these medial serrae are lacking in smaller specimens judging by descriptions in Müller and Henle (1841) and Day (1889)]; distally both margins of each tooth are smooth-edged; one or two small symphysial teeth. Lower teeth of the same specimen narrow, more erect than the upper, with both margins notched, and smooth-edged except for some slight basal irregularities, particularly on the lateral margins; one or two small symphysial teeth.

First dorsal fin moderately high, erect to weakly falcate, its apex pointed, its rear tip noticeably long (5.9-6.5% TL); origin of first dorsal above or slightly in front of the middle of the posterior (inner) margin of the pectoral fin. Second dorsal fin moderately low but long, and considerably lower than the anal fin; length of second dorsal rear tip 1.5 to 2.3 (mean 1.9 in five specimens) times its height; origin of second dorsal behind anal fin origin, ranging from one-third to almost halfway along anal base. Pectoral fin moderately short, falcate, pointed distally; origin of pectoral fin below the fourth gill opening; outer corner of pectoral, when fin is adpressed to trunk so that its anterior margin is horizontal, reaches from almost to first dorsal axil to as far back as one-third along first dorsal rear tip.

After preservation in alcohol, the color of the back and sides is dark greyish while the underside is pale; on some specimens a tongue of the paler color extends forward along the side from the pelvic region to below the first dorsal fin. The pectoral fin and the lower lobe of the caudal are extensively black-tipped, and to a lesser extent the apex of the second dorsal is dusky to black; the upper caudal leading margin and tip and the apex of the first dorsal are dusky-edged.

Vertebral counts of four specimens as in Table 2. One further specimen (BMNH 1889.2.1.4172 from Madras) has a count of 70 precaudal, 84 caudal, and a total count of 154 centra. Centrum diameter greater than centrum length except in longest monospondylous centra at posterior of abdomen where the length is about equal to or slightly greater than the diameter. Diplospondylous centra regular. Diplospondyly begins from between the pelvic axil and tip to as far back as midway between the pelvic tip and anal fin origin. Length/diameter of penultimate monospondylous centrum is 1.08 to 1.19 (mean 1.14 in five specimens), and length of penultimate monospondylous centrum/length of first diplospondylous centrum is 1.24 to 1.61 (mean 1.40 in five specimens).

The smallest specimens seen by me were a female of 317 mm TL and a male of 368 mm (paratype), while the largest were a female of 1,020 mm (mounted skin) and an immature male of 553 mm. These sizes encompass specimens mentioned in the literature available to me, except for Boulenger's (1889) report of an adult female of 8 ft 4 inches (2,540 mm) from Muscat which was undoubtedly a misidentification insofar as *hemiodon* appears to be an inshore species and hence could be expected to be represented in collections by other comparably large specimens were it to grow to that size. Because of the overall paucity of material of *hemiodon* and the lack of any data on size at maturity and reproduction, there is no gauge by which to estimate the approximate maximum size except that if the smallest specimens seen (female, 317 mm and male, 368 mm) were free-living and not embryos, then it is likely that maximum size does not greatly exceed 1 m. Clasper length of the largest male examined (553 mm TL and immature) was 2.5% TL, and in three other immature males, 368 to 467 mm (including the holotype and a paratype) clasper length ranged from 2.4 to 2.7% TL. Compagno (1984) reported immature specimens up to 600 mm long.

DISTRIBUTION (see also Material Examined).—Tropical Indo-Pacific, virtually confined to the Indo-Australian archipelago. Specimens I have examined have been from the Gulf of Oman (Muscat) in the west, eastwards at both sides of India (Malabar, Canara, Madras, and Pondicherry) which is the type locality, and southwards at Borneo and Java (Batavia). Literature reports, frequently as mere listings and hence not verifiable, extend this distribution to Calcutta (Day 1878), Vietnam (Chevey 1929; Tirant 1929), South China Sea (Chu 1962—as *atripinnis*), Philippines (Meyer 1885 and Elera 1895 according to Fowler (1941) though I have not seen these accounts), Indonesia (Damar Island in the Moluccas from Weber 1913 and north Celebes from Meyer 1885—latter not seen), and northwest New Guinea at Waigeu (Weber 1913). As well there are unsubstantiated and conflicting reports of *hemiodon* from Australia, dating from Macleay (1878) who identified it from Port Darwin but later (1882) amended his identification to *Carcharhinus melanopterus*. Zeitz (1888) subsequently reported a 17-inch (432 mm) specimen from Port Adelaide Creek, South Australia, as *hemiodon*, noting that as its upper teeth were denticulated only at the base, it was referable to *Hypoprion* according to criteria from Günther (1870). Whitley (1934) listed *H. hemiodon* in the Australian fauna.

Although Day (1878) reported that *hemiodon* ascended rivers such as the Hooghly at Calcutta, and Tirant (1929) observed that he had seen *hemiodon* several times in the Saigon River above Saigon at Thudaumot, it remains to be established whether these reports indicate that *hemiodon* can tolerate substantially reduced salinity.

MATERIAL EXAMINED.—RNH 7387, female, 317 mm, Batavia,

1852, Bleeker; MNHN 7774, two males, 368 and 397 mm (paratypes of *Carcharias* (*Hypoprion*) *hemiodon*), India, Malabar, Bélanger; BMNH 89.2.1.4172, female, 435 mm, India, Madras, F. Day; MNHN 1042, female, 437 mm (paratype of *Carcharias* (*Hypoprion*) *hemiodon*), India, Pondicherry, Bélanger; BMNH 89.2.1.4174, male, 444 mm, India, Canara, F. Day; MNHN 1040, male, 467 mm (holotype of *Carcharias* (*Hypoprion*) *Hemiodon*), India, Pondicherry, Bélanger; ISZZ 6967, mounted skin of female, 480 mm, East Indies, Besnard; NMV —, female, 540 mm, Borneo, 1897; SU 14501, male, 553 mm, India, Calicut, 1941, A. W. Herre; BMNH 89.2.1.4171, female, 665 mm, India, Calicut, F. Day; BMNH —, mounted skin of female, ca. 1,020 mm, Muscat, A. S. G. Jayrakar.

Carcharhinus macloti (Müller and Henle, 1841)
Figures 11, 12, Table 3

Carcharias (*Hypoprion*) *Macloti* Müller and Henle, 1841:34-35, plate 10 (lateral view, underside of head, teeth and dermal denticles). One dried specimen in the Leyden Museum, from Macklot. New Guinea.

DIAGNOSIS.—Small sharks, up to 1.0 m long, usually with an interdorsal ridge in preserved specimens; no prominent black tips on the fins, but the leading margins of the second dorsal and the upper caudal, and sometimes the first dorsal and pectoral, have a narrow dusky or black edge; trailing margins of pectoral, pelvic, anal, and lower caudal white or pale; snout very long (8.7-10.3% TL) and sharply pointed; internarial width 1.7-1.9 in preoral length; origin of first dorsal fin above posterior one-third or tip of inner pectoral margin; apex of first dorsal pointed; rear tip of first dorsal 5.3-7.1% TL; origin of second dorsal above middle of anal base; height of second dorsal 1.6-2.1% TL, and 2.3-2.6 in length of its rear tip; dental formula commonly 14-1 to 3-14/13-1-13 but may be 14 or 15-2-14 or 15/13 or 14-1-13 or 14; upper teeth narrow, erect to oblique, concave to notched laterally, concave to straight or convex medially, with very large serrae basally but smooth-edged distally; lower teeth erect to slightly oblique, and smooth-edged; a discrete series of 7-12 enlarged hyomandibular pores alongside corner of mouth; precaudal centra 68-71; caudal centra 79-84; total centra 149-154; diplospondyly usually begins at pelvic origin but may be as far back as two-thirds along pelvic base; diplospondylous centra regular except for one or two enlarged centra alternating with the normal centra anteriorly; penultimate monospondylous centrum 1.3-1.6 times longer than wide.

This species, together with *hemiodon* and *signatus*, differs from all other *Carcharhinus* in having upper teeth which are smooth-edged distally, the only serrations present being very large serrae basally. *Carcharhinus macloti* is separable from *hemiodon* in snout length (8.7-10.3% TL in *macloti*, 7.2-7.4% TL in *hemiodon*) and in lacking prominent black tips on the fins, and from *signatus* in having a much longer first dorsal rear tip (5.3-7.1% TL in *macloti*, 3.6-4.6% TL in *signatus*). It further differs from both these species, and from all other *Carcharhinus* species except *borneensis*, in having a discrete series of enlarged hyomandibular pores alongside each corner of the mouth. Its resemblance to *borneensis* includes not only this feature but also several other shared attributes such as the unusually long, low second dorsal fin originating over the middle portion of the anal fin base, the nipplelike nasal lobes, and the presence of large basal serrae on the upper teeth. However, it can be distinguished from *borneensis* by its longer snout (8.7-10.3% TL versus 4.1-5.2% TL in *borneensis*), by having the upper teeth smooth-edged distally, and to a lesser extent by its longer pectoral fin and longer first dorsal rear tip.

NOMENCLATURAL DISCUSSION.—Although I have not examined the holotype of *macloti* Müller and Henle (1841), the original description of this very distinctive little shark plus the accompanying illustrations leave no doubt as to its identity. There are no primary synonyms of *macloti*. Gill (1862) designated *macloti* as type-species of *Hypoprion* Müller and Henle, 1841, an action that seems to have been overlooked by subsequent workers (Fowler 1941; Bigelow and Schroeder 1948) who attributed that type-species designation to Jordan and Gilbert (1883).

DESCRIPTION (see also Table 3).—Small sharks, probably growing to 1 m TL. Midline of back between dorsal fins with a low interdorsal ridge in most preserved specimens and perhaps in all in life. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles overlapping, subcircular to ovoid in outline, slightly wider than long, each with three strong longitudinal ridges and corresponding short posterior marginal teeth in small specimens; in adults the denticles are essentially the same but a few denticles have five posterior teeth.

Snout very long (8.7-10.3% TL) and sharply pointed. Anterior margin of eye forward of front of mouth by a distance equal to one-third to half of eye diameter. Nostrils strongly oblique, with rather broadly ovate apertures, the anterior margin of each with a narrow, pointed lobe. A discrete longitudinal row of enlarged hyomandibular pores lateral to each corner of the mouth, their number ranging from 7 to 12 (mean of 8.6 on left side, 9.0 on right side in five specimens).

Dental formula 14-1 to 3-14/13-1-13in three of seven specimens counted, and within the range 14 or 15-2-14 or 15/13 or 14-1-13 or 14 in the remaining four. Upper teeth narrow, erect near center of mouth but increasingly oblique laterally, their lateral margins concave to notched, their medial margins concave in the teeth near the center of the mouth but straight to convex or sinuous in those towards the corner of the mouth; distally both margins are smooth-edged but basally there are very large serrae, particularly on the lateral margin, but their number is variable and in part related to size or age; in four juveniles and subadults (both sexes) of 323-526 mm TL from China, Hong Kong, and the Gulf of Aden, there were 1-2 serrae laterally and 0-1 medially, whereas in a mature female of 718 mm from Burma there were up to 4 laterally and 3 medially; contrasting with this, a mature male of 734 mm from Borneo had not more than 2 or 3 laterally (and these poorly defined) and 0 medially; the difference between these two adults may reflect either sexual dimorphism or geographic variation; one to three small symphysial teeth. Lower teeth erect to slightly oblique, with both margins deeply concave to notched, and smooth-edged; one small symphysial tooth.

First dorsal fin low, erect to slightly falcate, its apex pointed, its rear tip very long (5.3-7.1% TL); origin of first dorsal at least two-thirds back along posterior (inner) pectoral margin in juveniles, and over posterior (inner) pectoral corner in larger specimens. Second dorsal fin very low and long, and considerably lower than the anal fin; length of second dorsal rear tip 2.3-2.6 (mean 2.5 in seven specimens) times its height; origin of second dorsal above middle of anal base. Pectoral fin short, moderately falcate, pointed distally; origin of pectoral fin below fourth gill opening; outer corner of pectoral, when latter is adpressed to trunk so that its anterior margin is horizontal, reaches at least two-thirds along first dorsal base in small specimens and to as far as first dorsal axil in adults.

After preservation in alcohol, the color of the back and sides is dark grey while the underside is white or pale, and a tongue of this

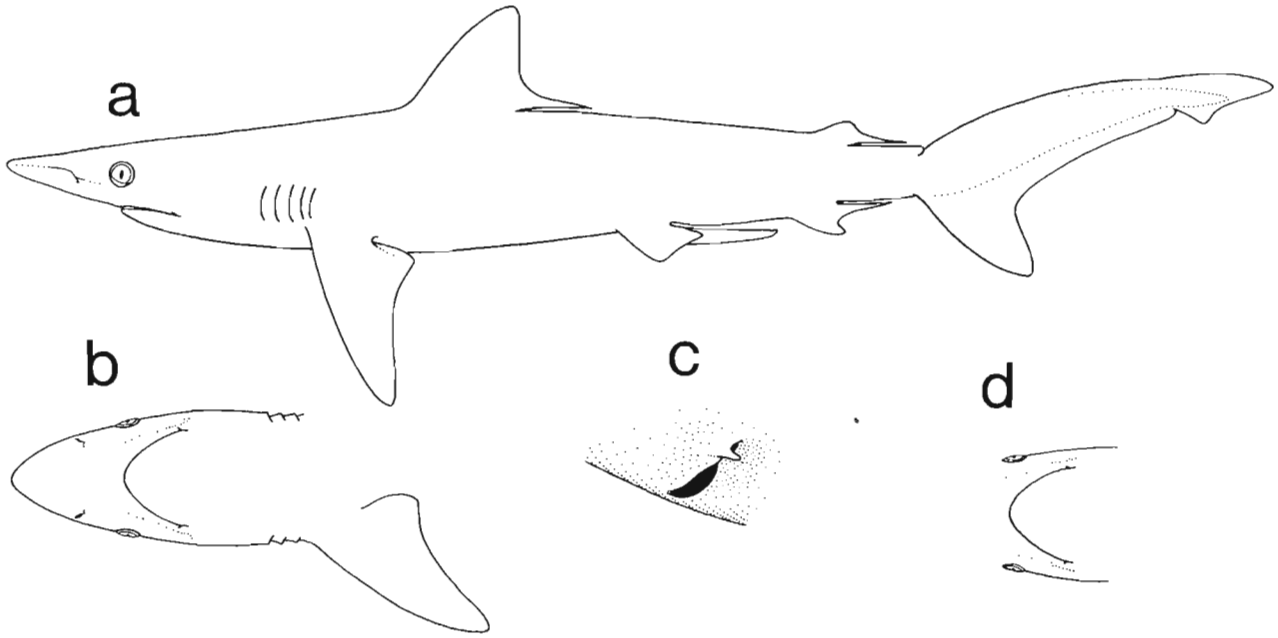

Figure 11.—*Carcharhinus macloti*: a, left side of USNM 197385, 734 mm TL, male purportedly from Borneo; b, underside of head of same; c, enlarged right nostril of same; d, mouth region of SU 14488, 718 mm TL, female from Burma to show arrangement of enlarged hyomandibular pores.

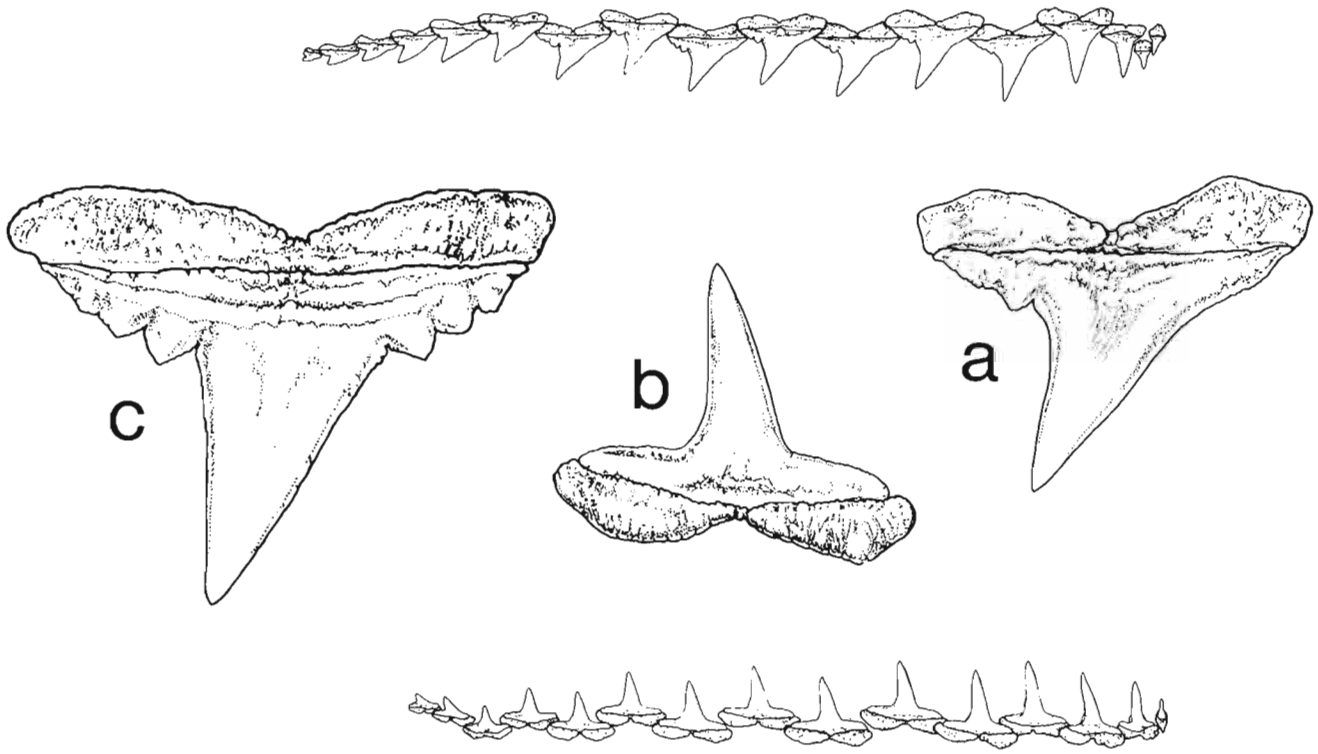

Figure 12.—*Carcharhinus macloti*: right upper and lower teeth (symphysis to the right) of USNM 197385, 734 mm TL, male purportedly from Borneo; inset teeth a and b are enlarged fifth upper and lower teeth of same; c, fourth upper tooth of SU 14488, 718 mm TL, female from Burma.

Table 3. — Carcharhinus macloti, proportional dimensions in percent of total length.

	♀ 323 mm Gulf of Aden BMNH 1925.7.20.9-13	♀ 490 mm Hong Kong ISZZ 5799	♂ 518 mm China Chusan Is. SU 14111	♂ 526 mm Hong Kong SU 12988	♂ 526 mm India Madras BMNH 89.2.1.4170	♀ 718 mm Burma South Moscos SU 14488	♂ 734 mm ? Borneo USNM 197385
Snout tip to: outer nostrils	5.0	5.5	4.8	4.8	5.6	5.0	4.8
: eye	8.8	9.1	8.1	8.2	9.0	8.3	8.0
: mouth	10.3	9.8	9.3	9.1	9.8	9.2	8.7
: 1st gill-opening	21.3	20.2	19.1	19.2	20.5	20.2	20.0
: 3rd gill-opening	23.5	22.4	21.0	21.5	22.6	22.4	22.2
: 5th gill-opening	25.2	24.6	22.8	23.0	24.8	24.1	23.7
: pectoral origin	24.2	24.3	22.0	22.4	24.1	23.4	23.2
: pelvic origin	48.0	48.5	46.7	48.3	49.4	49.4	47.9
: 1st dorsal origin	31.9	32.2	31.3	30.8	32.5	32.3	31.2
: 2nd dorsal origin	61.9	62.2	62.0	62.3	63.8	65.0	63.7
: anal fin origin	59.7	60.8	60.1	60.5	62.4	62.4	61.7
: upper caudal origin	70.3	71.4	71.4	72.0	72.8	73.6	72.9
: lower caudal origin	69.3	70.5	69.9	71.3	71.3	72.5	72.0
Nostrils: distance between inner corners	5.6	5.1	5.4	4.9	5.1	5.4	5.0
Mouth: width	7.0	7.1	6.6	6.7	7.6	7.9	7.2
: length	4.8	5.1	4.4	4.5	4.8	5.0	4.5
Labial furrow lengths: upper	0.6	0.4	0.4	0.4	0.6	0.4	0.5
: lower	0.5	0.4	0.3	0.4	0.5	0.6	0.5
Gill-opening lengths: 1st	-	2.7	3.0	2.2	-	2.9	2.9
: 3rd	2.9	2.9	3.5	2.7	3.5	3.3	3.1
: 5th	-	2.2	2.9	2.9	-	2.9	2.5
Eye: horizontal diameter	3.1	2.3	2.3	2.1	2.5	2.0	1.9
1st dorsal fin: length base	9.3	8.3	8.5	8.7	8.7	9.0	9.0
: posterior margin	5.6	5.7	5.6	5.3	6.4	7.1	6.3
: height	7.1	7.5	7.7	7.7	8.9	8.8+	8.2
2nd dorsal fin: length base	2.9	2.7	2.7	2.9	2.9	2.8	2.9
: posterior margin	4.2	4.4	4.2	4.2	4.8	5.2	4.8
: height	1.8	1.7	1.7	1.6	2.1	2.0	1.8
Anal fin: length base	4.2	3.5	3.7	3.8	3.2	4.2	3.7
: posterior margin	4.2	4.1	4.0	4.1	4.8	5.0	4.8
: height	2.6	2.2	2.3	2.5	2.8	2.6	2.7
Pectoral fin: length base	5.0	4.9	5.8	5.4	5.4	5.2	5.3
: anterior margin	14.5	15.1	14.5	13.5	15.2	16.1	15.4
: distal margin	9.9	10.6	10.2	10.2	10.6	13.0	11.8
: greatest width	8.4	7.6	-	7.6	8.2	-	7.9
Pelvic fin: length base	4.0	4.1	4.1	3.9	4.0	4.6	4.4
: anterior margin	4.6	4.4	4.3	3.9	4.4	5.2	4.3
: distal margin	4.6	4.1	4.2	4.2	4.0	5.2	4.5
: length claspers	-	-	2.1	2.3	2.5	-	9.1
Caudal: length upper lobe	29.4	28.6	28.6	28.0	27.6	27.1	27.1
: length lower lobe	10.8	10.6	11.4	10.1	11.0	11.8	11.6
Trunk at pectoral origin: width	10.5	9.2	9.5	9.5	-	10.2	9.9
: height	10.5	9.2	8.7	9.1	-	9.9	9.7
Dental formula	$\frac{14-2-14}{13-1-13}$	$\frac{14-2-14}{13-1-13}$	$\frac{14-2-14}{14-1-14}$	$\frac{14-2-14}{14-1-13}$	$\frac{14-3-14}{13-1-13}$	$\frac{15-2-14}{14-1-13}$	$\frac{15-2-15}{14-1-14}$
Vertebrae: precaudal	71	70	71	68	70	70	70
: caudal	79	84	83	82	79	82	80
: total	150	154	154	150	149	152	150

paler color may extend forward along the side from the pelvic region to below the first dorsal fin. There are no prominent dark markings on the fins, but in most specimens the leading margin of the second dorsal and both margins of the upper caudal are narrowly edged with duskyness or black, and in some specimens there is a similar dark edging on the leading margins of the first dorsal and pectoral; in most specimens the trailing margins of the pectoral, pelvic, anal, and lower lobe of caudal are white or pale.

Vertebral counts as in Table 3. Centrum diameter greater than centrum length anteriorly, but this relationship reversing in posterior half of abdomen where the length of the longest monospondylous centra is considerably greater than the diameter. Diplospondylous centra essentially regular except that most specimens have one or two longer centra interposed between the normal centra anteriorly. Diplospondyly, as evidenced by position of first short centrum, begins at pelvic fin origin in five of seven specimens, at one-third along pelvic base in one, and two-thirds along pelvic base in one. Length/diameter of penultimate monospondylous centrum is 1.26 to 1.61 (mean 1.43 in seven specimens), and length of penultimate monospondylous centrum/length first diplospondylous centrum is 1.63 to 2.08 (mean 1.80 in seven specimens).

The smallest specimens seen by me, and smaller than any reported in the literature, were two females of 320 and 323 mm TL and three males of 348 to 370 mm, all listed under the same collection number (BMNH 1929.7.20.9-13). The largest specimens seen were a mature male of 734 mm TL and a female of 790 mm. A male of 845 mm in Nakamura's (1936) account is the only specimen of either sex reported in the literature available to me that exceeds the size of my material. In the male it is likely that maturity is reached at a length of 700 mm or less. This estimate is based firstly on my material in which three males of 518 to 526 mm were immature with clasper lengths of 2.1 to 2.5% TL whereas one of 734 mm was obviously mature with a clasper length of 9.1%, and secondly on the holotype which, as illustrated, was mature with a clasper length equal to about 7.5% at a total length of 27.5 inches, which corresponds to 698 mm if Müller and Henle (1841) used imperial measures or 724 mm if they used Vienna measures. Nakamura (1936) illustrated a mature male of 845 mm in which the clasper length appears to be about 7.5%. For females my only information on maturity is from a 718 mm specimen which was clearly mature with well developed shell glands and uteri containing remnants of yolk. Judging by the above evidence on size at maturity it is likely that the maximum size of *macloti* does not exceed 1 m. Campagno (1984) reported that the number of embryos "is usually 2 (one per uterus), size at birth 45 to 50 cm."

DISTRIBUTION (see also Material Examined).—Northern Indian Ocean and tropical Indo-Pacific including most of the Indo-Australian archipelago and probably Australia itself. Specimens seen by me have been from Aden, both coasts of India (Malabar and Madras), Burma (S. Moscos Group), Hong Kong, China (including Chusan Island), and North Sulu Sea off Borneo. Literature records, in some cases as mere listings of *macloti*, which extend and fill out this distribution include Kenya (Compagno 1984), Bombay (Setna and Sarangdhar 1946), Pakistan (Qureshi 1977—not seen), Ceylon (Mendis 1954), South China Sea (Chu 1962), Taiwan (Nakamura 1936 and Chen 1963), New Guinea (type-locality—Müller and Henle 1841, and with several other listings including Papua, the D'Entrecasteaux Group and New Britain from Munro 1958) and Australia (see below). Fowler (1941) also included references for Mekran (Zugmayer 1913), Malaya (Fowler 1938), and the Philippines (Elera 1895), but I have not seen these. Australian listings date from Ramsay (1881) and Ogilby (1889) who reported *macloti* from Port Jackson, New South Wales, but I have seen no specimens to substantiate its occurrence there. Whitley (1940) noted that a record of *macloti* from the Gulf of Carpentaria, Northern Territory, by Paradice and Whitley (1927) was in error, being based on *Protozygaena taylori*, a species of *Rhizoprionodon*. However, McKay[4] informs me that a long-snouted *Hypoprion* is present off Darwin and this is very likely to be *macloti* in view of its occurrence at nearby New Guinea.

MATERIAL EXAMINED.—BMNH 1929.7.20.9-13, two females, 320 and 323 mm, and three males, 348 to 370 mm, Gulf of Aden, A. Ehrenreich; RNH 4575, female, 450 mm, from Bleeker; RNH 8576, female, 480 mm, India, Malabar; ISZZ 5799, female, 490 mm, Hong Kong; SU 14111, male, 518 mm, China, Chusan, A. W. Herre; SU 12988, male, 526 mm, Hong Kong, W. Finch; BMNH 89.2.1.4170, male, 526 mm, India, Madras, F. Day; NMV —, female, 537 mm, India, Madras, 1886, Day; SU 14488, female, 718 mm, Burma, South Moscos Group, November 1940, A. W. Herre; USNM 197385, male, 734 mm, Manila Fish Market, purportedly caught by fishermen off Borneo, North Sulu Sea, March 1962; NMV 24449 (old number), female, 790 mm, China, 1905, Konsul Post.

Carcharhinus signatus (Poey, 1868)
Figures 13, 14, Table 4

Hypoprion signatus Poey, 1868:452, plate 4, figures 7-8 (teeth). Based on a set of jaws only. Cuba.

Hypoprion longirostris Poey, 1876:394-395, plate 9, figures 8-9 (teeth). Male, 2,266 mm. Cuba.

Hypoprion bigelowi Cadenat, 1956:539-545, 5 figures. Female, 1,627 mm. Between the limits of the French Guinea and Portuguese Guinea coasts.

DIAGNOSIS.—Large sharks, up to 2.55 m long, with an interdorsal ridge; no prominent black tips on the fins, but in small specimens most fins are dusky margined and in adults the underside of the pectoral is dusky towards its tip; snout very long (8.5-10.3% TL), its tip sharply rounded; internarial width 1.5-1.8 in preoral length; origin of first dorsal fin varying from above middle of inner pectoral margin to as far back as inner pectoral corner; apex of first dorsal pointed; rear tip of first dorsal 3.6-4.6% TL; origin of second dorsal varying from above anal fin origin to about halfway along anal base; height of second dorsal 1.6-1.9% TL, and 2.0-2.3 in length of its rear tip; dental formula 15 or 16-2-15 or 16/14 to 16-1-14 to 16; upper teeth narrow, erect to oblique, notched laterally, straight to convex medially, with large serrae basally but smooth-edged distally; lower teeth erect to slightly oblique, and smooth-edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 98-104; caudal centra 80-87; total centra 182-191; diplospondyly begins about one-third along pelvic base; diplospondylous centra regular; penultimate monospondylous centrum 0.6-0.7 as long as wide.

The upper teeth of *signatus* (smooth-edged distally but with large serrae basally) together with the combination of a long snout (8.5-10.3% TL) and an only moderately long first dorsal rear tip (3.6-4.6% TL) enable it to be distinguished from all other *Carcharhinus* species including the only other two species (*hemiodon* and *macloti*) with comparable upper teeth.

[4]R. J. McKay, Curator of Fishes, Queensland Museum, Gregory Terrace, Fortitude Valley, Queensland 4006, Australia, pers. commun. November 1980.

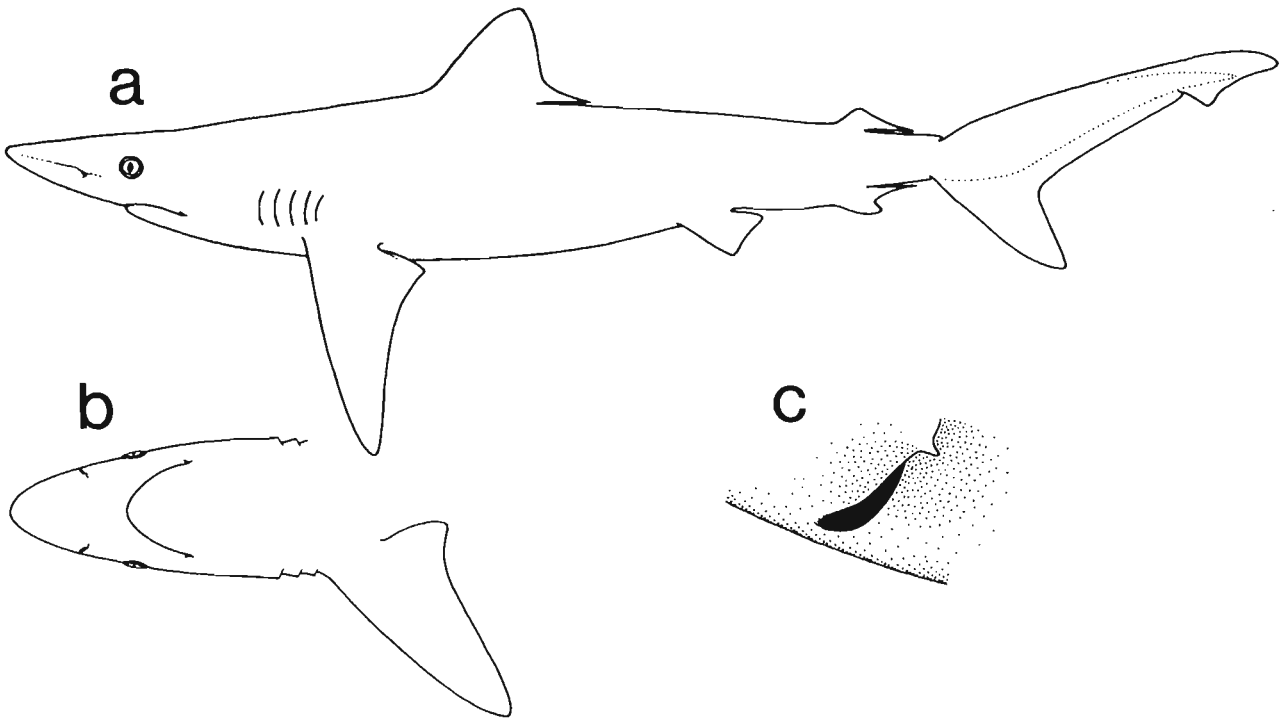

Figure 13.—*Carcharhinus signatus*, USNM 196131, 1,740 mm TL, female from Northwest Atlantic: a, left side; b, underside of head; c, enlarged right nostril.

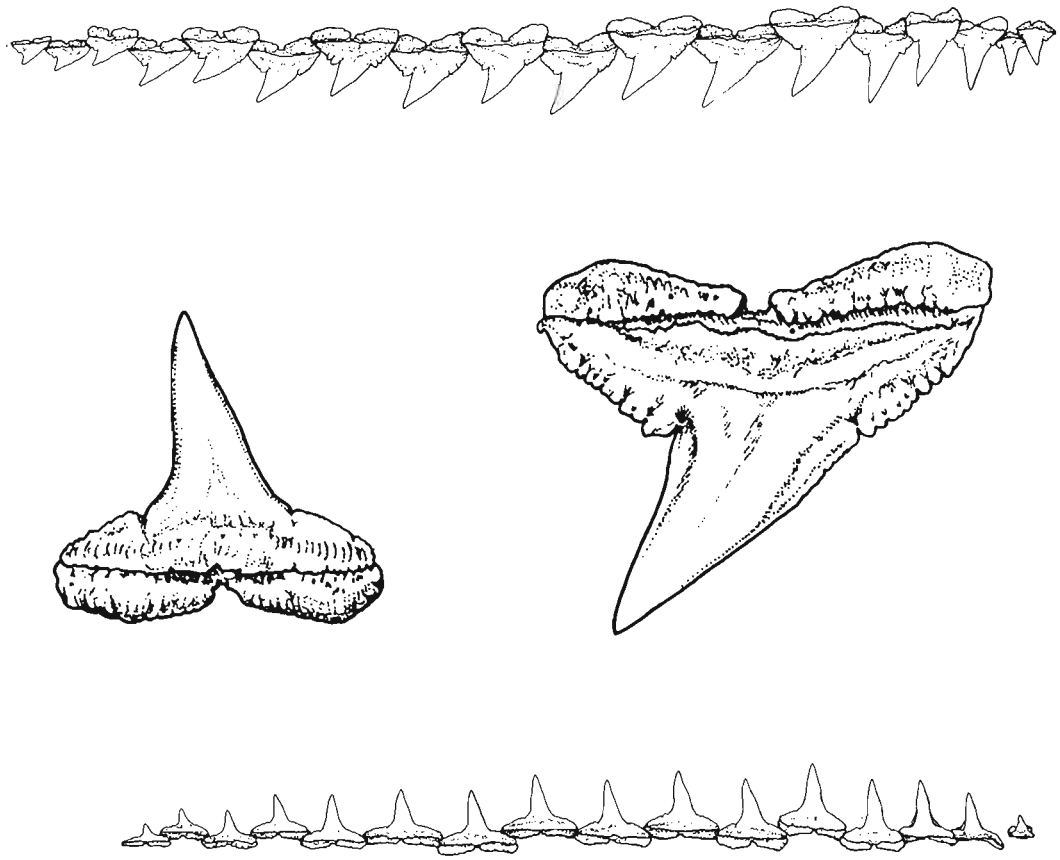

Figure 14.—*Carcharhinus signatus*, USNM 112582, 2,286 mm TL, male from Bahamas: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Table 4. — Carcharhinus signatus, proportional dimensions in percent of total length.

	♂ 564 mm West Atlantic USNM 197373	♀ 930 mm North West Atlantic USNM 38508	♀ 998 mm East Atlantic MRAC 80256	♀ 1590 mm[1] East Atlantic MNHN 55-4915	♀ 1740 mm North West Atlantic USNM 196131
Snout tip to: outer nostrils	5.5	5.4	4.9	5.0	5.1
: eye	9.2	9.2	8.7	8.4	8.8
: mouth	10.3	9.5	9.1	8.5	9.1
: 1st gill-opening	21.8	20.2	19.2	20.1	21.0
: 3rd gill-opening	23.9	22.8	22.2	22.9	23.7
: 5th gill-opening	25.5	24.5	24.1	25.2	25.5
: pectoral origin	24.6	23.6	23.0	24.7	24.3
: pelvic origin	50.2	50.9	47.6	51.6	52.5
: 1st dorsal origin	33.3	33.7	31.3	32.6	32.7
: 2nd dorsal origin	62.9	65.3	61.1	64.4	59.3
: anal fin origin	62.6	63.4	59.6	63.8	59.2
: upper caudal origin	72.7	74.3	71.2	73.3	73.9
: lower caudal origin	71.8	73.3	70.2	72.2	72.8
Nostrils: distance between inner corners	5.8	5.2	5.4	4.8	5.2
Mouth: width	7.4	7.1	7.7	7.0	7.2
: length	4.6	5.1	4.5	5.1	4.5
Labial furrow lengths: upper	0.4	0.5	0.6	0.5	0.6
: lower	0.4	0.6	0.5	0.6	0.5
Gill-opening lengths: 1st	2.7	2.2	2.4	3.0	2.6
: 3rd	3.0	2.7	3.2	3.3	3.1
: 5th	2.0	1.7	1 9	2.1	2.0
Eye: horizontal diameter	3.1	2.3	2.2	1.9	1.8
1st dorsal fin: length base	8.6	8.8	9.3	9.0	9.0
: posterior margin	3.6	3.9	4.6	3.7	4.4
: height	6.4	7.4	8.1	8.4	7.9
2nd dorsal fin: length base	3.3	2.4	2.9	2.5	2.6
: posterior margin	3.6	3.7	4.0	3.6	4.0
: height	1.6	1.9	1.8	1.8	1.8
Anal fin: length base	3.5	3.0	4.3	3.5	3.0
: posterior margin	3.5	3.4	3.6	3.5	3.9
: height	2.0	2.2	2.1	2.4	2.1
Pectoral fin: length base	5.3	5.7	6.0	5.3	6.1
: anterior margin	15.8	16.8	19.7	19.0	18.3
: distal margin	9.6	12.9	15.0	15.8	15.5
: greatest width	8.2	8.6	9.6	9.7	9.4
Pelvic fin: length base	5.1	4.5	4.7	4.8	4.6
: anterior margin	5.1	4.7	5.1	5.1	5.3
: distal margin	4.1	4.2	5.1	5.5	4.5
: length claspers	1.9	-	-	-	-
Caudal: length upper lobe	27.0	26.1	29.0	27.3	26.3
: length lower lobe	11.2	11.3	12.7	12.3	12.2
Trunk at pectoral origin: width	11.3	11.5	11.8	-	10.7
: height	10.3	11.2	11.5	-	11.5
Dental formula	-	$\frac{15\text{-}2\text{-}15}{15\text{-}1\text{-}15}$	$\frac{15\text{-}2\text{-}15}{14\text{-}1\text{-}14}$	$\frac{15\text{-}2\text{-}15}{15\text{-}1\text{-}15}$	-
Vertebrae: precaudal	101	104	-	98	-
: caudal	87	87	-	84	-
: total	188	191	-	182	-

1. Holotype of Hypoprion bigelowi.

NOMENCLATURAL DISCUSSION.—Poey (1868) described *signatus* from jaws alone, and illustrated an upper tooth in which the medial margin had about six basal serrae which were approximately half the size of the seven basal serrae on the lateral margin. Subsequently Poey (1876) described a second species, *longirostris*, from Cuba from an adult male, 2,266 mm long, in which the upper tooth as illustrated had equal-sized serrae on both margins, with eight serrae on the medial margin and about seven on the lateral margin. In the same account Poey noted that he had also obtained an adult female, 2,270 mm long, which he initially thought to be *longirostris* on external features. However, examination of the teeth of this specimen led him to the conclusion that it was not *longirostris* but probably *signatus*, although he did not elaborate on the differences. Despite Poey's view that *signatus* and *longirostris* were distinct, it is now clear that the illustrations of the teeth of the holotypes could be encompassed by changes that occur with growth (see Raschi et al. 1982), *signatus* probably being based on a subadult and thus differing from the *longirostris* adult. Furthermore, although it is over a century since Poey described his two species, there is no subsequent evidence to support his belief that there are two species of *Hypoprion* off Cuba.

Cadenat's (1956) new species, *bigelowi*, from the tropical eastern Atlantic can be relegated to the synonymy of *signatus* on the same grounds that apply for *longirostris*. The holotype of *bigelowi*, an adult of 1,627 mm, with basal serrae on both the medial and lateral margins of the upper teeth, and with dermal denticles with five longitudinal ridges and five posterior marginal teeth, was regarded by Cadenat as distinct from *signatus* because the latter, as represented by juvenile specimens in Bigelow and Schroeder (1948), was thought to have basal serrae only on the lateral margins of the upper teeth, and dermal denticles with only three ridges and three marginal teeth. Detailed and extensive evidence establishing that these differences are simply the opposite end points of the normal pattern of ontogenetic change in *signatus* is given in Raschi et al. (1982), who, as a result, synonymise *bigelowi* with *signatus*, an action with which I agree.

DESCRIPTION (see also Table 4).—Large sharks, growing to 2.55 m TL. Midline of back between dorsal fins with a low interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles overlapping, subcircular to ovoid in outline, slightly wider than long, each with three strong longitudinal ridges and corresponding posterior marginal teeth in small specimens, but with five ridges and teeth in adults.

Snout very long (8.5-10.3% TL), its tip sharply rounded. Anterior margin of eye slightly forward of front of mouth. Nostrils strongly oblique, with rather slitlike apertures, the anterior margin of each with a narrow pointed lobe.

Dental formula 15-2-15/15-1-15 in two of five specimens counted, 15-2-15/14-1-14 in one, 15-2-16/15-1-15 in one, and 16-2-16/16-1-16 in one. Upper teeth narrow, erect near the center of the mouth but increasingly oblique laterally, their lateral margins deeply notched, their medial margins straight or slightly convex; distally both margins smooth-edged, but basally there are large serrae which in small specimens are confined to the lateral margin whereas in subadults and adults they are present on both lateral and medial margins; the number of serrae varies with size or age; in juveniles there may be only two or three serrae laterally, whereas in two adult females there are up to about five and nine medially, and two and six laterally, and in one adult male there are up to about ten medially and eight laterally; two small symphysial teeth. Lower teeth erect to slightly oblique, with both margins deeply concave to notched, and smooth-edged except for some slight basal irregularities particularly in larger specimens; one small symphysial tooth.

First dorsal fin low, erect, its apex pointed, its rear tip of moderate length (3.6-4.6% TL); origin of first dorsal varying from halfway back along posterior (inner) pectoral margin to as far as posterior (inner) pectoral corner. Second dorsal fin very low and long, and slightly lower than the anal fin; length of second dorsal rear tip 2.0-2.3 (mean 2.2 in five specimens) times its height; origin of second dorsal ranging from above anal fin origin to about halfway along anal base. Pectoral fin moderately short, weakly falcate, pointed distally; origin of pectoral fin below or just anterior to fourth gill opening; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from at least four-fifths along first dorsal base to as far as first dorsal rear tip.

After preservation in alcohol, the color of the back and sides is brownish grey while the underside is paler; in juveniles there are no obvious black-tipped fins but the pectoral tip is dusky as are the apical margins of both dorsal fins, the anal fin, and the upper caudal lobe; in adults the only obviously dusky marking is on the underside of the pectoral fin which is increasingly darker towards its tip.

Vertebral counts as in Table 4. Counts of one other specimen (USNM 133827 from Florida) are precaudal 104, caudal 80, and a total count of 184. Centrum diameter considerably greater than centrum length. Diplospondylous centra regular. Diplospondyly begins about one-third along pelvic base. Length/diameter of penultimate monospondylous centrum is 1.59 to 1.68 (mean 0.64 in three specimens), and length of penultimate monospondylous centrum/length of first diplospondylous centrum is 1.05 to 1.17 (mean 1.12 in three specimens).

The smallest free-living specimen I have seen was 930 mm TL while the largest embryo was 564 mm. Size at birth would appear to be about 650 mm judging by Raschi et al.'s (1982) report of embryos up to 634 mm long and free-living (trawled) specimens as small as 665 mm. Also, Applegate et al. (1979) illustrated a specimen, presumably free-living, of 660 mm. There are no firm data on size at first maturity in the male, except that Krefft[5] notes that males up to 1,560 mm were immature, whereas Cadenat and Blache (1981) reported two adult males, 1,535 and 1,700 mm, with claspers extending 5.9 and 4.6% TL beyond the extremity of the pelvic fins and hence presumably mature. Krumholz (1957) recorded a mature male of 1,978 mm. Springer and Thompson (1957) reported adult males of 2,007 and 2,159 mm. For females, Krefft (footnote 5) lists immature specimens up to 1,450 mm, Daiber (1960) inferred that one of 1,835 mm was immature since it had undeveloped gonads, and Branstetter (1981) reported one of ca. 1,900 mm which "did not appear to be mature." Contrasting with the last two specimens was a pregnant female of 1,740 mm recorded by Poll (1951) and three pregnant females of 1,776 to 1,790 mm reported by Cadenat and Blache (1981). Raschi et al. (1982) noted a mature female of 1,900 mm. The number of embryos per litter ranges from 4 to 18 according to seven accounts in the literature. The smallest litter (four embryos from a 1,740-mm female) was reported by Poll (1951). Litters of 10, 7, and 9 from females of 1,776, 1,790, and 1,790 mm, respectively, are recorded by Cadenat and Blache (1981), and two others of 10 and 12 from females of 2,200 and 2,550 mm are documented by Raschi et al. (1982). Bigelow and Schroeder (1948) also gave 12 as the litter size for *signatus*. Larger litters, 14 embryos in each, were reported by Springer and Thompson (1957) and by Daiber (1960) from females of 2,286 mm. Branstetter (1981) provided in-

[5]G. Krefft, Ichthyologie Seefischerei, Zoologisches Institut and Zoologisches Museum der Universität Hamburg, Martin-Luther-King Platz 3, D-2000 Hamburg 13, West Germany, pers. commun. January 1980.

formation on a litter of 18. The maximum size to which *signatus* grows was given by Manday (1968) as 3 m, although this may be an estimate of potential size insofar as I have not discovered any records of specimens of that length. Bigelow and Schroeder (1948) stated that recorded specimens reach 2,766 mm (male) and 2,270 mm (female); they did not give the source of their data but I suspect it was Poey (1876) in which case the 2,766 was an error of transcription for 2,266 which was the length of the holotype male of *longirostris*. If this is true, the only recorded male specimen to exceed 2,266 mm is one of 2,362 mm examined by S. Springer and reported in Springer and Thompson (1957). Since female carcharhinids attain a larger size than males of the same species, it is not surprising that the largest recorded female *signatus* is 2,550 mm (Raschi et al. 1982). The next smaller females are two of 2,388 mm, slightly larger than the largest male, listed in Springer and Thompson (1957).

DISTRIBUTION (see also Material Examined).—Both sides of the tropical Atlantic, and extending significantly into temperate latitudes both north and south in the western Atlantic. Specimens I have examined have had a much more limited distribution, from South Carolina, Florida, and the Bahamas in the northwestern Atlantic, and from about lat. 12°N (region of French Guinea and Portuguese Guinea) and from off the Congo and northern Angola in the eastern Atlantic.

Some of the accounts that further document and extend this distribution include, for the western Atlantic, those of: Mather and Gibbs (1957), who reported *signatus* from off Delaware at lat. 38°22′N, long. 69°35′W; Raschi et al. (1982), who noted that "recent records indicate that it is a common shark in the Florida Current and Gulf Stream, ranging as far north as the Middle Atlantic Bight along the Outer Continental Shelf during the warmer months of the year" and list many specimens supporting their statement; Krumholz (1957), who recorded it from the Bahamas; Boschung (1979) and Branstetter (1981), who each reported a specimen from the southeast Gulf of Mexico; Springer and Thompson (1957), who reported a specimen from the northern Gulf of Mexico off Mississippi; Applegate et al. (1979), who illustrated another from Veracruz in the southern Gulf (Bahia de Campeche); Bigelow and Schroeder (1948), who noted that *signatus* is abundant off the northern coast of Cuba, from which island also the holotypes of *signatus* and *longirostris* were described (Poey 1868, 1876) and from where *signatus* has recently been reported (Manday 1968, 1975—latter account not seen); and Krefft (footnote 5), who informs me of 12 juveniles taken off southern Brazil and Uruguay (lat. 33°-35°20′S, long. 51°20′-52°41′ W). These accounts leave a considerable gap in the western Atlantic distribution, with no records between the northern Caribbean Sea and southern Brazil other than a doubtful listing by Blosser (1909) from British Guiana.

For the eastern Atlantic coast, records by Cadenat (1956—holotype of *bigelowi*) from about lat. 12°N, by Cadenat and Blache (1981—as *bigelowi*) from Cap Vert (Senegal), Guinea, Ivory Coast, and Dahomey, and by Raschi et al. (1982) for the Gulf of Guinea region from lat. 4°14′-6°09′N document the occurrence of *signatus* north of the Equator, while those of Poll (1951) from lat. 5°51′-8°21′S cover the south.

Although Raschi et al. (1982) summarized the depth distribution of *signatus* as 200-600 m, "approaching the shallower end of this depth range during hours of darkness," they also report captures in the Florida Current at dawn in depths of <50 m and document another five *Anton Dohrn* stations off the east coast of the United States where *signatus* was taken in depths from 135 to 175 m. Other reports of shallow captures include those of Bigelow and Schroeder (1948)—26 m off South Carolina; Poll (1951)—100 m off the Congo; Boschung (1979)—near the surface in the southeast Gulf of Mexico; Branstetter (1981)—upper 80 m in the southeast Gulf of Mexico; and Krefft (footnote 5)—110 m in the southwestern Atlantic.

MATERIAL EXAMINED.—IRSN 8.458, four embryos, two males, 320 mm, and two females, 340 mm, Angola, 7°16′S, 12°08′E, 1 October 1948, *M'Bizi*; USNM 133827, male embryo, 457 mm, Florida, Key West, off Cosgrove Reef, April 1947, S. Springer; USNM 197373, male embryo, 564 mm, West Atlantic, *Oregon*; USNM 38508, female, 930 mm, North West Atlantic, 33°37′30″N, 77°36′30″W, 20 October 1885, *Albatross*; MRAC 80256, female, 998 mm, East Atlantic, 5°53′30″S, 11°40′30″E, 21 August 1948; MNHN 55-4915, female, 1,590 mm (holotype of *Hypoprion bigelowi*), within the region of the coasts of French Guinea and Portuguese Guinea, 8-10 March 1955; USNM 196131, female, 1,740 mm, North West Atlantic, 29°46′N, 80°12′W, 30 April 1961, *Silver Bay*.

Also IRSN 8.397, uterus with four embryos, 325 to 340 mm, Angola, 7°16′S, 12°08′E, 1 October 1948, *M'Bizi*; MRAC 8.452, head and tail of specimen from Angola, 8°21′S, 12°46′E, 8 February 1949, *M'Bizi*; MRAC 8.451, head of specimen from Angola, 7°16′S, 12°08′E, 1 October 1948, *M'Bizi*; IRSN 8.459, jaws of specimen from South Atlantic, 1948-49, *M'Bizi*; UMMZ —, jaws of specimen 2,170 mm, Florida, the Hump off Islamorada, 24 June 1961, H. Brown; USNM 112582, jaws of adult male, 2,286 mm, Bahamas, Bimini, 3 June 1948, S. Springer.

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