A review of the smooth-hound sharks (GENUS *Mustelus,* FAMILY TRIAKIDAE) of the western Atlantic Ocean, with descriptions of two new species and a new subspecies

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A REVIEW OF THE SMOOTH-HOUND SHARKS (GENUS *MUSTELUS*, FAMILY TRIAKIDAE) OF THE WESTERN ATLANTIC OCEAN, WITH DESCRIPTIONS OF TWO NEW SPECIES AND A NEW SUBSPECIES

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ABSTRACT

The taxonomy and distribution of sharks of the genus *Mustelus* in the western Atlantic Ocean are treated. Seven species are recognized, and all are endemic to the western Atlantic. A new species from the Gulf of Mexico and another new species from the Southern Caribbean are described. *Mustelus canis* is divided into two subspecies: a continental form and an insular form restricted to the Caribbean islands, the Bahamas, and Bermuda. Morphometric features, denticle and tooth configurations, buccopharyngeal denticle patterns, and vertebral numbers are shown to be useful taxonomic characters within the genus.

The genus *Mustelus* comprises some 25 species of small (less than 2 m total length), benthic sharks that inhabit temperate and tropical waters over the continental shelves of all oceans. In some countries, smooth-hounds (also called "smooth dogfish" or "gummy sharks") are an important food resource. And in areas where they are abundant, smooth-hounds are also important as predators of more valuable marine resources such as crabs and lobsters.

The present paper is based on a M.Sc thesis (Heemstra, 1969) completed at the University of Miami under the supervision of Prof. C. Richard Robins. Much of the information in the original thesis was incorporated (with the author's permission) in the FAO Catalogue, *Sharks of the World* by Leonard J.V. Compagno (1984). The main purpose of the present paper is to provide descriptions and names for the three undescribed taxa recognized in my original thesis. A key to species and a brief diagnosis for each species are also presented here to complement the accounts given by Compagno (1984).

The principal difficulty in taxonomic research on fishes that grow to one meter or more in length is that of assembling adequate series of specimens, including adults of all species. Because of the difficulty of collecting, preserving, and shipping sharks that are a meter or more in length, many species are represented in collections by only a few newborn or juvenile specimens. The confidence one places in a particular taxonomic work is a function of the size and quality of the samples studied. Although the limitations imposed by inadequate samples should be obvious, they are often not considered in works on shark taxonomy.

METHODS AND MATERIALS

Institutional acronyms are as given by Leviton et al. (1985).

Measurements.—Springer's (1964) remarks on measurements of sharks are apt here: "Measurements on sharks are notoriously difficult to obtain with accuracy, and it is rare that one investigator can reproduce exactly another's measurements or even his own; nevertheless, proportions based on measurements are one of the few types of characters available for the description of sharks. But many errors originate in the twisted and distorted shapes that result from preservation procedures. The snout tip is one of the most important reference points on a shark, yet in numerous preserved specimens the tip has been pushed in, mashed, or crushed beyond reconstruction because the specimen has been forced into too small a bottle."

In the present study, measurements of distances on the snout or from the snout tip of specimens with badly mashed snouts were either listed as approximate or omitted altogether. Long measurements

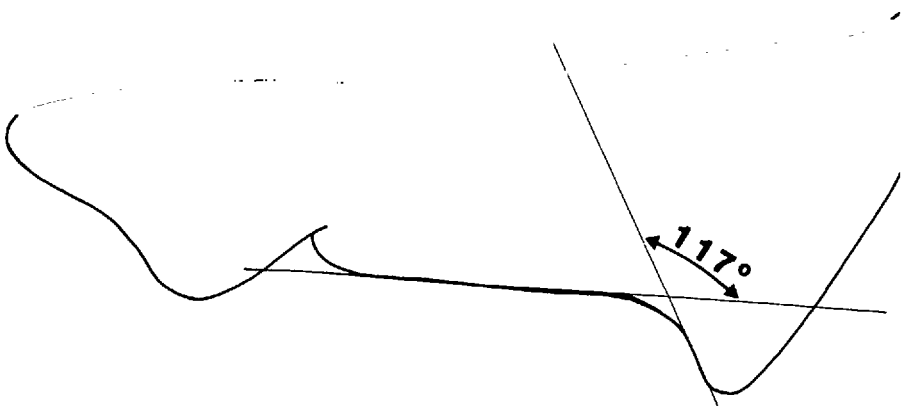

Figure 1. Caudal fin of *Mustelus canis canis*, 58 cm TL to show measurement of ventral caudal fin lobe angle.

on the body of sharks preserved in a distorted or curled position are accurate only to the nearest centimeter. All of the following measurements are of straight-line distances, and, unless stated otherwise, were made with dividers or a beam compass applied to a meter ruler and read to the nearest millimeter.

TOTAL LENGTH. With dorsal lobe of caudal fin placed in line with longitudinal axis of body, the total length was measured from tip of snout to end of caudal fin. For badly distorted or curled specimens, and for all sharks more than 1 m long, this measurement was read to only the nearest centimeter. SNOUT TO DORSAL CAUDAL LOBE: from tip of snout to origin of dorsal caudal fin lobe. SNOUT TO FIRST DORSAL, SECOND DORSAL, AND ANAL FIN: measured from tip of snout to origin of fin. SNOUT TO PELVIC FINS: from tip of snout to midpoint of a line across ventral surface of body joining origins of pelvic fins. SNOUT TO PECTORAL FINS: same as for "snout to pelvic fins." SNOUT TO FIRST GILL OPENINGS: from tip of snout to midpoint of a line across ventral surface joining ends of first gill openings. SNOUT TO ORBITS: from tip of snout to midpoint of a line across dorsal surface of head joining anterior ends of dermal eye openings. SNOUT LENGTH: from tip of snout to anterior edge of upper jaw symphysis. SNOUT TO NOSTRILS: from tip of snout to a line joining front edges of nostrils. INTER-NOSTRIL: least distance between nostrils; measured with dial calipers to the nearest 0.1 millimeter. MOUTH WIDTH: least distance between corners of mouth. MOUTH LENGTH: from anterior edge of upper jaw symphysis to midpoint of a line joining corners of mouth. LABIAL FOLD LENGTHS: lengths of upper (= lateral) and lower (= medial) labial folds; measured with dial calipers to nearest half millimeter. ORBIT DIAMETER: horizontal diameter of dermal eye opening. INTER-ORBITAL WIDTH: least distance between supraorbital crests, measured across dorsal surface of head (with upper eyelids depressed to delimit dorsal margins of chondrocranial orbits). BODY DEPTH: least distance from origin of dorsal fin to ventral midline of body. BODY WIDTH: width of body across ventral surface at pectoral fin origins. FIRST DORSAL FIN TO SECOND DORSAL FIN: from axil of first dorsal fin to origin of second dorsal fin. (The axil of the dorsal or anal fins is the point at which the frenum joins the free tip of the fin to the body.) SECOND DORSAL FIN TO CAUDAL FIN: from second dorsal fin axil to dorsal origin of caudal fin. CAUDAL PEDUNCLE LENGTH: from axil of anal fin to ventral origin of caudal fin. MEASUREMENTS OF DORSAL AND ANAL FINS: Base: from origin to axil of fin. Height: perpendicular distance from apex of fin to line along which base of fin was measured. Tip: from axil to end of free tip of fin. MEASUREMENTS OF PECTORAL AND PELVIC FINS: Anterior margin: from origin to distal tip of fin. Posterior margin: from distal tip to medial corner of fin. Proximal margin of pectoral fin: from point at which proximal margin joins body to medial corner of fin. PELVIC FINS TO ANAL FIN: from midpoint of a line joining rear ends of pelvic fin bases to origin of anal fin. DORSAL LOBE OF CAUDAL FIN: from origin of caudal fin to posterior tip of fin. VENTRAL LOBE OF CAUDAL FIN: from ventral origin of caudal fin to tip of ventral lobe of fin. VENTRAL CAUDAL FIN LOBE ANGLE: in species with a distinct ventral caudal lobe, the caudal fin was traced onto a piece of paper, and the angle between straight lines drawn tangent to the ventral edge of the fin and the posterior edge of the lobe (Fig. 1) was measured. TIP OF CAUDAL FIN: from rear end of fin to postero-ventral end of subterminal notch.

Tooth Counts.—A tooth row is a line of teeth approximately transverse to the longitudinal jaw axis that includes functional teeth and their replacements (Compagno, 1988). Tooth counts in the present paper are given as a ratio of the ranges in the number of rows in the upper and lower jaws.

Vertebral Counts.—The use of vertebral numbers as a taxonomic character has proved of considerable

benefit for distinguishing species in this difficult group. The transition from monospondylic to diplospondylic vertebrae occurs at about the level of the cloaca, and is indicated by a marked shortening in the length of the centra. During development of the embryo shark, the diplospondylic vertebrae are formed by secondary division of the posterior monospondylic vertebrae (Šećerov, 1911). This developmental process is either easily disturbed or inherently irregular, as there were many specimens that exhibited abnormally long (undivided monospondylic?) centra in the region of diplospondyly. In fact, two species (*M. mento* and *M. fasciatus*) are characterized by a more or less regular alternation of long and short centra throughout the region of diplospondyly. This accounts for the increased variation in the numbers of precaudal and precaudal-minus-monospondylic vertebrae in these two species (Figs. 24, 25). A similar condition of alternating long and short, diplospondylic (?) centra was noted in *Galeus* (= *Galeorhinus galeus*) by Ridewood (1899: 46). All but a few of the vertebral counts were made from radiographs. In some sharks, a centrum of intermediate length occurs between the last monospondylic centrum and the first diplospondylic centrum. For these specimens, I added one half to the number of pre-transitional vertebrae to account for this extra (transitional) vertebra in the count of monospondylic vertebrae.

Precaudal vertebrae are distinguished from the anterior caudal vertebrae by the presence (on the latter) of calcified cartilages that are fused to the centra and project postero-ventrally to support the ventral lobe of the caudal fin. These cartilages are termed, by various authors, haemapophyses, haemal spines, or basal cartilages. Springer and Garrick (1964) used the origin of the dorsal caudal lobe to delimit caudal from precaudal vertebrae. This point is located three or four vertebrae posterior to the first caudal vertebra as defined above.

Denticles.—Dermal denticles were routinely examined, in situ, at a point midway between the origins of the first dorsal and pectoral fins. The ridges on the scales are easiest to see if the denticles are dried and illuminated using a strong light directed posteriorly, at a low angle to the skin, and at about 90° to the line joining the origins of the dorsal and pectoral fins. There is considerable intraspecific variation in the shape of the denticles in certain species of *Mustelus*. On seven *M. minicanis*, for example, more than 90% of the midlateral denticles are lanceolate; but on two other specimens, the denticles are mostly tridentate. Other species show little variation in denticle shape (e.g., in *M. canis* almost all of the midlateral denticles are lanceolate). The scales of adults are generally broader, and their ridges are lower and less distinct than those on younger sharks of the same species.

Study of the denticle patterns in the buccopharyngeal cavity was accomplished following the methods of Nelson (1970). The use of hydrogen peroxide solution to bleach the naked skin areas should be avoided for older (alcohol-fixed) and poorly preserved specimens. Such specimens will disintegrate rapidly, even in weak (2–3%) peroxide solutions. The distribution of denticles within the buccopharyngeal cavity is distinctive for many species of sharks (Nelson, 1970). These buccopharyngeal denticle patterns exhibit little intraspecific variation and are diagnostic for most species of *Mustelus*.

Mustelus Linck

Mustelus Linck, 1790: 31 (type-species *Squalus mustelus* Linnaeus, 1758: 235 by decision of the International Commission on Zoological Nomenclature, Opinion 93). Placed on the Official List of Generic Names in Zoology by the same Opinion (Hemming, 1958).

Mustellus Fischer, 1813: 78. Not available; incorrect subsequent spelling for *Mustelus* Linck, 1790. Placed on Official Index of Rejected and Invalid Generic Names in Zoology.

Galeus Leach, 1818: 62 (type-species *Squalus mustelus* Linnaeus, 1758 by monotypy; preoccupied by *Galeus* Rafinesque). Leach listed in the synonymy of *Galeus mustelus* the species *S. mustelus* Linnaeus which, therefore, must stand as the type of his genus; however, his description of *Galeus mustelus* is probably based on a specimen of *Galeorhinus galeus* (Linnaeus) since the length (six feet) and the number of unborn young (26) are both a little too large for *M. mustelus*, but just right for *G. galeus*.

Mustelus Cuvier, 1816: 128 (type-species *Squalus mustelus* Linnaeus, 1758: 235 by absolute tautonomy; preoccupied by *Mustelus* Linck).

?*Emissola* Jarocki, 1822: 448 (The name was probably derived from "l'émissole", the French vernacular for the smooth-hound [*Mustelus mustelus*]. Jarocki mentions three species: "*Emissole commune* Risso, *Emissole Lentillat albo tachetée de blanc* Risso, and *Squalus Mustelus*. Type species *Squalus mustelus* Linnaeus, 1758 by subsequent designation of Hubbs, 1938: 12.).

Myrmillo Gistel, 1848: X (substitute name for *Mustelus* Cuvier, 1816 and therefore taking the same type-species: *Squalus mustelus* Linnaeus).

Rhinotriacis Gill, 1863: 486 (type-species *R. henlei* Gill, by monotypy.)

Pleuracromylon Gill, 1864: 148 (type-species *Mustelus laevis* Müller and Henle, 1841: 190, by monotypy [= *Squalus mustelus* Linnaeus]. Müller and Henle (1841: pp. 64–65) listed *M. laevis* in the synonymy of their *M. vulgaris* [= *M. asterias* Cloquet, 1819, a species without a yolksac

placenta]; but Müller later (1842: 214) restricts the name *M. laevis* to the species (with *M. mustelus* and *M. punctulaus* regarded as varieties) which has a placenta, and *M. vulgaris* was used for the species without a placenta. Since Gill's genus *Pleuracromylon* was erected specifically to house the *M. laevis* with a placenta, he apparently had in mind Müller's 1842 concept of this species.

Cynias Gill, 1903: 960 (type-species "*Mustelus canis*" of Jordan [*non Squalus canis* Mitchill 1815: 486]. Hubbs (1938) discussed the misidentification of *M. canis* by Jordan and Evermann, 1896 and Gill, and (as first reviser) Hubbs nominated "*Mustelus asterias,* the 'spotted hound' " as the type species for *Cynias.* The genus *Cynias* Gill is poorly defined, and this case should be presented to the International Commission on Zoological Nomenclature for clarification of the type-species.

Diagnosis.—The species of *Mustelus,* as here understood, are distinguished from the species of other triakid and carcharhinid genera by the following suite of characters: First dorsal fin origin over base or inner margin of pectoral fin; second dorsal fin relatively large, its height more than 70% of first dorsal fin height and its origin distinctly in advance of anal fin origin; anal fin height about half height of second dorsal fin. Nictitating lower eyelid separated from secondary lower eyelid by a shallow subocular pouch and not freely movable; spiracles obvious. Caudal peduncle without precaudal pits or lateral keels; mid-dorsal ridge between dorsal fins present. Nostrils without a barbel, but anterior margins with a short, flat, external lobe extending over middle third of nasal aperture; labial folds well developed. Teeth blunt, small and numerous, arranged in a pavement with several series functional at the same time; height of crown or cusp less than width of tooth; inner face of root with a peg ("... the peg of one tooth extends into the basal groove of the next tooth in succession in the same row, an arrangement that may serve to interlock the teeth in the pavement dentitions of these forms"; Compagno, 1970); fifty or more rows in each jaw; teeth of adults with a low rounded crown or bluntly rounded cusp; teeth of juveniles of most species with one or two, small, lateral cusplets at base of primary cusp and several short ridges at base of crown. Siphon sacs between skin and ventral body wall of mature males, well developed, reaching to axils of pectoral fins. Intestinal valve of the spiral type, with six to nine turns. Chondrocranium with a well-developed supraorbital crest; rostral cartilages longer than anterior fontanelle; median rostral cartilage with a terminal U-shaped notch or oval foramen. Vertebral centra with calcification pattern of radiating lamellae (Fig. 2).

Remarks.—The definition of the genus *Mustelus* and its relationships with other triakid and carcharhinoid genera were discussed in detail by Compagno (1988). I accept Compagno's (1988) conclusion that the species *Allomycter dissutus* Guitart, 1972 was based on photographs of an abnormal specimen of *Mustelus* with a deformed head (lacking a rostrum) and unusually wide, open nostrils without nasal flaps. Unfortunately, the holotype was lost before Dr Guitart could examine it.

In most species of *Mustelus* the teeth are asymmetric, with the rounded apex or cusp directed away from the symphysis, and the edge towards the rictus is more or less concave or even notched; on juveniles the cusps are higher and the notching may be so deep that it forms an smaller accessory cusp at the base of the main cusp. Small juveniles may have a small accessory cusp at one or both sides of the main cusp. In large adults of *M. canis,* the tooth crowns are so low that a cusp is not discernible but the tooth is still slightly asymmetric, with the crown slightly higher on the rictal half of the tooth. In two species, *M. mento* Cope 1877 and *M. fasciatus,* the teeth are symmetric, with low, evenly-rounded crowns, and the tooth shape is similar in juveniles and adults.

Within the genus *Mustelus,* there appears to be little variation in the anatomy of the intromittent organs, or claspers. Chondrocrania of all the species were compared from radiographs, and a few dissections were made for direct compar-

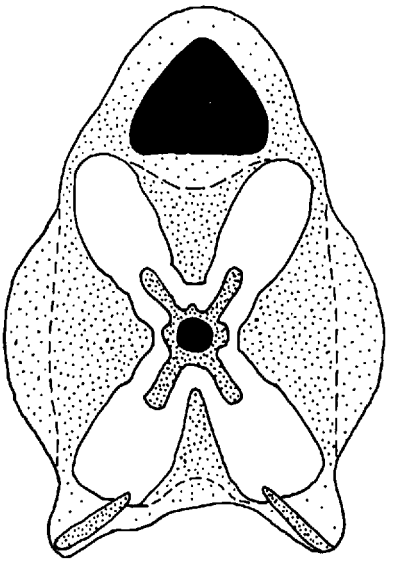

Figure 2. Cross-section of trunk (monospondylic) vertebra to show calcification pattern of centrum. Neural and notochordal canals black; calcified cartilage stippled. Drawn from a radiograph of the 36th vertebra of *Mustelus canis insularis*, 98 cm, ANSP 124249.

ison of skulls. Only slight differences were noted between species (e.g., the absence of an epiphyseal notch on the rear edge of the anterior fontanelle of *Mustelus fasciatus,* or the reduction of the suborbital shelf of *M. higmani*).

Among the species of *Mustelus,* there are two kinds of upper jaw skeleton (Fig. 3). In some species (e.g., *M. californicus*), the upper jaw cartilages comprise four separate palato-quadrate elements (Fig. 3A). In most species, including all of the western Atlantic species, the upper jaw skeleton comprises only two (left and right) palatoquadrate cartilages (Fig. 3B).

Key to Western Atlantic Species of *Mustelus*

1a. Snout long (pre-oral snout length 8.0–9.1% TL); ventral caudal fin lobe obtuse, the ventral margin approximately straight; caudal peduncle length 4.2–5.6% TL; teeth without cusps, tooth crown low, evenly rounded, symmetric . . . . . *M. fasciatus*
(Rio Grande do Sul, Brazil and Uruguay)

1b. Snout length 4.2–8.0% TL in most species (6.9–9.6% TL in *M. higmani,* but it has an acuminate ventral caudal fin lobe); caudal peduncle length 5.8–9.7% TL; teeth with more or less distinct cusps, asymmetric 2

2a. Trailing edges of dorsal fins usually with a narrow dark margin of bare ceratotrichia; small white spots often present on dorsal surface of body; inter-nostril distance narrow (1.8–2.4% TL) . . . . . *M. schmitti*
(southern Brazil to southern Argentina)

2b. Trailing edges of dorsal fins without dark margins; dorsal surface of body immaculate grey or greyish tan; inter-nostril distance 2.3–3.8% TL 3

3a. Denticles (from area midway between origins of first dorsal fin and pectoral fin) tridentate AND orbit diameter 2.2–3.4% TL 4

3b. Denticles lanceolate OR (if most denticles are tridentate) diameter of orbit = 3.2–4.3% TL 5

4a. Upper-jaw labial folds long (1.9–2.5% TL), distinctly longer than labial folds of lower jaw; snout short (5.4–6.3% TL); size large (maturity not attained until a length of at least 75 cm) . . . . . *M. sinusmexicanus*
(Gulf of Mexico)

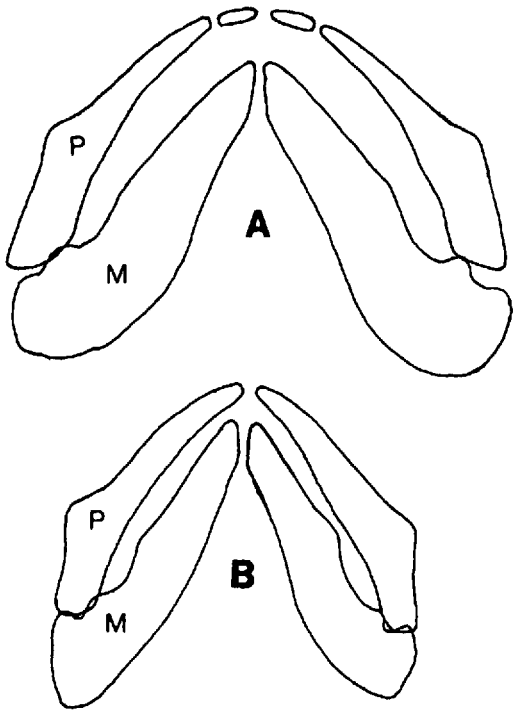

Figure 3. Diagrammatic representation of two types of upper jaw (palatoquadrate) cartilages in species of *Mustelus*. A) 4-part upper jaw cartilages typical of *M. californicus* and some other Pacific species of *Mustelus*. B) 2-part upper jaw cartilages of Atlantic species of *Mustelus*. P = palatoquadrate, M = Meckel's cartilage. Traced from radiographs.

4b. Upper-jaw labial folds short (0.8–1.8% TL), about equal to lower-jaw labial folds; snout long (6.9–10% TL); maximum size 65 cm (maturity attained at 50 cm) ..... *M. higmani* (Gulf of Venezuela to Santos, Brazil)

5a. Upper-jaw labial folds long (1.6–2.7% TL), distinctly longer than lower-jaw labial folds; internostril distance wide (2.7–3.6% TL); maximum size 150 cm (maturity not attained until a length of at least 80 cm) 6

5b. Upper-jaw labial folds 1.0–1.7% TL, not much longer than lower-jaw folds 7

6a. Height of first dorsal fin of adults usually more than 10% TL; monospondylic vertebrae 34–39; precaudal vertebrae 85–93 ..... *M. canis canis* (continental shelf from Bay of Fundy to Uruguay)

6b. First dorsal fin height of adults usually less than 10% TL; monospondylic vertebrae 39–41.5; precaudal vertebrae 94–100 ..... *M. canis insularis* (Bermuda and Caribbean islands)

7a. Orbit diameter small (2.3–3.4% TL); inter-nostril distance narrow (2.3–2.8% TL); mouth narrow (width 4.6–5.6% TL) ..... *M. norrisi* (Gulf of Mexico, continental coast of Caribbean and Atlantic coast of South America to Rio de Janeiro)

7b. Orbit diameter large (3.2–4.3% TL); inter-nostril distance wide (2.7–3.1% TL); mouth wide (width 5.4–6.9% TL) ..... *M. minicanis* (Caribbean coast of Venezuela)

Species Accounts

Mustelus canis canis (Mitchill)
Figure 4

Squalus canis Mitchill, 1815: 486 (type-locality, New York; type specimens not preserved).
Mustelus canis: De Kay, 1842: 355, fig. 209. Storer, 1867: 227, pl. 37, fig. 2. Field, 1907: 10

(stomach contents). Breder, 1921; Nichols and Breder, 1927: 13 (in part, confused with *M. mustelus*; description, illustration, biological data). Hubbs, 1938 (nomenclature). Springer, 1939a (compared with *M. norrisi* and *M. schmitti*). Bigelow and Schroeder, 1940 (in part, the MCZ 503 shark from Brazil is *M. norrisi*; measurements, illustrations of teeth, denticles, caudal and pectoral fin shapes, compared with other species of *Mustelus*); 1948: 244–54, figs. 42 A–E, 43C (in part, all MCZ specimens identified by Bigelow and Schroeder as *M. canis* from Brazil are *M. norrisi*, and specimens from Texas (collected by J.L. Baughman) are *M. sinusmexicanus*; description, illustrations, biology, compared with other *Mustelus*). Ifft and Zinn, 1948 (tooth replacement). ?Baughman and Springer, 1950: 99 (applies, at least in part, to *M. sinusmexicanus*). TeWinkel, 1950 (ovulation, ova and early development). Bigelow and Schroeder, 1953: 34–36 (description, illustration, habits, and range). ?Hildebrand 1954: 281 (life history data; probably applies to *M. sinusmexicanus*). ?Briggs, 1958: 248 (distribution, probably applies to *M. sinusmexicanus*). Barcellos, 1961 (detailed description, morphometric data, photograph, comparison with *M. fasciatus* and *M. schmitti*). Schwartz, 1960 (reported from Chesapeake Bay, Maryland). Hoese, 1962: 167 (reported from Virginia). TeWinkel, 1963 (notes on eggs and fetal development). Springer and Garrick, 1964: 87 (vertebral data). Cervigon, 1966: 47–49 (reported from La Blanquilla, Venezuela; size, coloration, morphometric data, food, reproduction, habitat, and distribution). Graham, 1967 (function of placenta). Gilbert and Heath, 1972 (function of clasper/siphon-sac mechanism). Moss, 1973 (tooth replacement and body growth rates). Figueiredo, 1977: 15, fig. 21 (distinguished from other Brazilian species in key; not common on south coast). Uyeno and Sasaki, 1983 (diagnosis, photograph of 621 mm immature male from 173–225 m off Surinam or French Guiana). Schwartz, 1984: 40 (diagnosis, figure of prenatal pup). Menni et al., 1984: 98 (record from Mar del Plata, Argentina). Rountree and Able, 1996 (biology of juveniles in estuarine nursery habitats in New Jersey).

Mustelus mustelus (non Linnaeus): Fowler, 1908 (mention of embryo with placenta); 1918: 15, pl. 2 (description and illustration of uterus with pups and placentae). Hildebrand and Schroeder, 1927: 47, fig. 27 (description and illustration based on Garman, 1913; recorded from Chesapeake Bay).

Galeorhinus laevis (non Linck): Garman, 1913: 176, pl. 4, figs. 6–9 (in part, description based on *M. mustelus* from France, but figs 6–9 of plate 4 are of a specimen from Long Island, New York). Radcliffe, 1916: 267, fig. 19 & pl. 42, fig. 3 (description and illustration of denticles and teeth).

Diagnosis.—Morphometric data are listed in Table 1. Ventral caudal fin lobe of adults prominent, but not pointed, the ventral caudal lobe angle 89–110°; ventral lobe of juveniles smaller and ventral lobe angle more obtuse (110–134°). Trailing edges of dorsal fins not frayed. Rear (distal) edge of pectoral and pelvic fins concave. Head moderate, pre-pectoral distance 17–21% TL; inter-orbital distance 3.7–4.6% TL; snout moderate, pre-oral snout length 8.0–9.1% TL; inter-nostril distance wide, 2.7–3.6% TL; eye large, the orbit diameter 2.2–4.2% TL; upper-jaw labial folds (1.6–2.7% TL) longer than lower-jaw labial folds. Teeth of large adults (> 110 cm) with a low, broadly-rounded, asymmetric crown and no basal ridges; teeth of large juveniles and small adults (70–100 cm) with a shallow indentation (more pronounced on smaller specimens) on postero-lateral margin of cusp (Fig. 4C) and indistinct basal ridges; teeth of small juveniles (40–60 cm) with a low accessory cusp on one or both sides of main cusp (Fig. 4B) and numerous low basal ridges, which are usually hidden by adjacent teeth. Tooth counts 64–74/58–75. Denticles mostly (60–100%) lanceolate; but on some specimens, up to a third of the midlateral flank denticles are weakly tridentate; denticles with 2–6 (usually 4) ridges extending to posterior margin of scales. Buccopharyngeal denticles of palate and tongue not extending past first gill arch (Fig. 18A). Diagnostic vertebral numbers are given in figures 23–25. Spiral valve of intestine with 7 or 8 turns.

Adults immaculate grey or brownish dorsally, paler ventrally; specimens from dark environments are much darker than those from pale sandy habitats. Newborn pups and juveniles with sooty smudges on apices of dorsal fins and tip of caudal fin, and the rear margins of dorsal fins and/or ventral margin of caudal fin white or pale grey.

Remarks.—*M. canis canis* is a placental viviparous species, with 4 to 20 pups in

Table 1. Morphometric data from western Atlantic species of *Mustelus* (ranges of measurements in % TL): *Mustelus canis canis* (*M. c.c.*), *M. canis insularis* (*M. c.i.*), *M. norrisi* (*M. no.*), *M. sinusmexicanus* (*M. si.*), *M. minicanis* (*M. mi.*), *M. higmani* (*M. hi.*), *M. schmitti* (*M. sc.*), *M. fasciatus* (*M. fa.*)

Species	*M. c.c.*	*M. c.i.*	*M. no.*	*M. si.*	*M. mi.*	*M. hi.*	*M. sc.*	*M. fa.*
N =	61	19	47	18	9	67	42	9
Size range (cm)	36–122	28–117	26–82	38–140	31–57	20–59	22–75	37–62
Depth of body	8.8–14	9.5–13	9.5–12	9.4–12	10–13	9.5–13	8.2–12	9.0–15
Width of body	9.2–12	9.8–11	8.2–10	8.7–11	10–12	8.0–13	9.7–11	11–13
Snout to upper jaw	5.6–8.0	5.5–7.1	4.2–6.5	4.8–6.3	6.1–7.3	6.9–9.6	5.6–8.0	8.0–9.1
Snout to nostrils	3.4–5.1	3.4–4.4	3.2–4.3	3.2–4.2	3.5–4.4	4.3–6.7	3.0–4.9	5.2–6.2
Mouth width	4.7–6.8	4.8–6.3	4.6–5.6	4.7–6.1	5.4–6.9	5.1–7.3	4.4–6.4	6.7–7.7
Mouth length	2.6–3.5	2.3–3.5	2.5–3.7	2.2–2.9	3.0–3.6	2.3–3.6	2.3–3.2	3.4–4.2
Upper labial fold	1.6–2.7	1.8–2.4	1.0–1.7	1.9–2.5	1.3–1.7	0.8–1.8	1.8–2.6	2.0–2.4
Lower labial fold	1.3–2.0	1.4–1.7	1.0–1.6	1.0–1.6	1.0–1.5	1.0–1.8	1.3–1.8	1.6–2.1
Inter-nostril	2.7–3.6	2.9–3.5	2.3–2.8	2.6–3.3	2.7–3.1	2.7–3.8	1.8–2.4	2.9–3.4
Orbit diameter	2.2–4.2	2.5–3.7	2.3–3.4	1.9–3.1	3.2–4.3	2.2–3.4	2.1–3.5	1.9–2.5
Inter-orbital	3.7–4.6	3.6–4.3	3.3–4.2	3.9–4.6	4.2–4.8	4.5–6.3	4.3–5.3	4.8–5.2
Snout to orbits	6.1–8.3	5.9–7.3	5.9–7.2	6.2–8.1	6.4–7.5	6.9–9.9	6.0–8.2	9.4–10
Snout to D_1	23–32	24–29	25–34	25–28	27–29	28–33	25–30	28–31
D_1 to D_2	16–23	20–23	18–26	17–23	20–25	17–23	17–23	16–19
D_2 to caudal fin	8.7–13	9.0–11	9.9–13	8.2–11	10–12	8.1–12	10–13	8.6–9.3
Dorsal caudal fin lobe	17–22	20–22	18–23	20–23	19–21	17–22	17–22	20–22
Snout to P_1	17–21	17–20	16–20	17–23	18–21	19–24	16–21	22–25
Snout to 1st gill slits	14–18	15–17	14–17	14–16	15–17	16–21	14–17	18–21
Anterior margin P_1	11–16	12–16	12–15	13–16	13–14	11–14	12–16	13–15
Posterior margin P_1	8.0–13	10–14	7.9–12	8.5–12	9.2–11	6.7–10	8.6–13	11–13
Proximal margin P_1	6.0–8.6	6.5–7.6	5.1–7.1	6.1–7.6	7.1–8.0	5.9–8.9	7.2–9.6	7.5–8.8
Anterior margin P_2	6.6–8.3	6.9–8.8	6.7–8.5	7.0–8.3	6.0–7.1	6.2–8.9	6.7–8.7	7.4–9.2
Posterior margin P_2	4.6–6.9	5.5–7.1	4.2–6.2	4.6–6.4	5.5–7.5	4.3–6.7	5.9–8.5	6.1–7.9
Pelvic fin tip	3.9–5.4	4.2–5.2	3.4–4.8	4.2–5.3	4.6–5.7	3.5–5.8	4.4–6.3	4.2–5.7
Pelvic fins to anal fin	13–17	13–16	14–20	13–17	15–19	11–18	13–18	11–14
Anal fin to caudal fin	6.3–9.2	6.3–9.1	7.3–9.7	6.7–8.3	6.4–8.6	6.0–9.2	5.8–7.8	4.2–5.6
Height of anal fin	2.5–3.9	2.9–4.5	2.6–3.7	2.6–3.4	2.8–4.0	2.9–4.6	2.5–3.5	2.8–3.2
Base of anal fin	4.6–7.2	4.5–7.1	5.2–7.6	5.4–7.3	5.2–7.3	5.7–8.0	5.5–8.0	5.7–7.3
Anal fin tip	1.6–3.2	2.3–2.9	1.6–2.3	1.9–2.9	2.2–3.0	1.9–3.4	1.8–3.0	1.9–3.0
D_1 height	7.2–11	9.3–11	8.3–10	9.3–11	9.3–11	6.8–11	8.2–10	7.5–8.9
D_1 base	9.7–14	10–14	10–13	11–14	11–13	9.4–14	11–13	12–14
D_1 tip	3.2–5.1	3.5–5.1	2.6–3.9	3.2–4.5	3.7–4.5	2.5–4.7	3.0–4.5	2.6–4.6
D_2 height	5.1–7.6	5.1–7.8	5.5–7.6	5.8–6.8	6.0–7.3	5.1–7.7	5.7–7.4	5.6–7.0
D_2 base	7.9–11	8.4–11	8.1–10	9.2–10	7.9–11	7.7–11	8.7–12	9.2–11
D_2 tip	1.9–3.3	2.5–3.3	1.9–3.1	2.4–3.0	2.3–3.0	1.8–3.3	2.2–3.4	2.1–3.2
Ventral caudal fin lobe	7.2–10	8.0–10	7.7–9.4	7.6–9.1	7.4–8.7	7.1–10	7.2–8.7	6.9–8.6
Caudal fin tip	4.6–7.0	6.5–8.6	4.6–6.6	5.0–7.0	5.7–7.1	3.8–6.0	4.8–7.7	5.9–6.8
Snout to D_2	55–63	57–62	57–64	57–62	58–62	57–63	56–62	58–61
Snout to anal fin	60–68	62–66	60–68	61–65	61–64	62–68	63–68	64–67
Snout to P_2	39–48	41–46	38–44	40–44	41–44	40–48	41–47	44–48

a litter and a gestation period of 10–11 months. This is one of the larger species of *Mustelus*. Males are not mature until about 82–89 cm, and females not until approximately 90 cm. Pups are born between 34 and 39 cm in length. The largest specimen that I examined was a female of 122 cm; Bigelow and Schroeder (1948) give "about five feet" (1.5 m) as the maximum size for *M. canis*.

M. canis canis has not been reported from Georgia or the east coast of Florida, but as can be seen from the list of material examined below, it is not uncommon there. Although coral reef habitats are included within the geographic range of this subspecies, *M. canis canis* appears to avoid well-developed reef areas. Except for a few records beyond 230 m, most specimens that I examined were collected

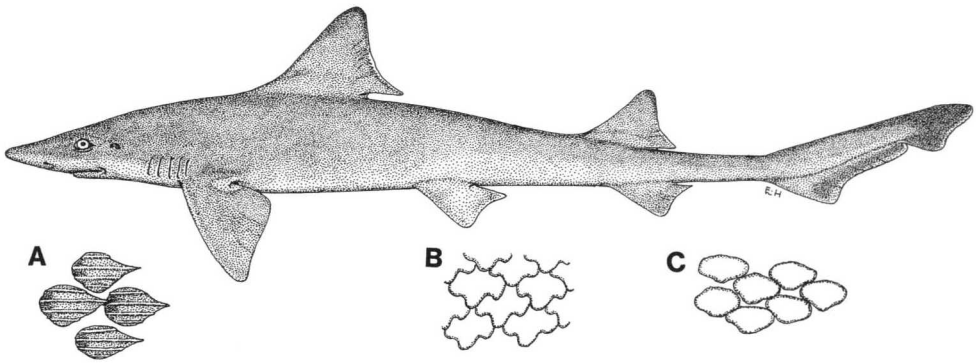

Figure 4. *Mustelus canis*, 68 cm juvenile female from Long Island, New York (redrawn from Garman, 1913); A) denticles from flank, midway between origins of dorsal and pectoral fins; B) teeth from upper jaw of 41 cm neonate; C) teeth from 78 cm juvenile.

from shore out to about 200 m. The deepest record is 360 m, (UF 46016, 86 cm male, from off Tamaulipas, Mexico).

Distribution (Fig. 26).—*M. canis canis* is known from the Bay of Fundy to Florida and the Gulf of Mexico, Venezuela, Surinam, French Guiana, Brazil (south of Rio de Janeiro), Uruguay and Mar de Plata, Argentina. It is replaced in the Caribbean Islands, the Bahamas, and Bermuda by *M. canis insularis*. Contrary to Springer and Lowe (1963: 249), it is not "absent either inshore or offshore around peninsular Florida." (See material examined below.)

Comparisons.—*M. canis canis* is, of course, most closely related to the insular form of this species, *M. canis insularis*; see account of the latter (below) for a discussion of their similarities and differences. *Mustelus canis* is also similar to *M. norrisi* of the western Atlantic, an undescribed eastern Pacific species, and the eastern Atlantic *M. mustelus*. *M. canis* will be compared with *M. norrisi* under the account of the latter species.

Mustelus canis and *M. mustelus* are similar in size, color, morphometric features, fin shapes, denticle and tooth morphology (including arrangement of denticles in the buccopharyngeal cavity), fetal development, and depth distribution. These two species are also similar in their wide latitudinal ranges and in the fact that each species has given rise to an isolated population (herein considered subspecies) that inhabits the islands off their respective continental shelves. *Mustelus canis* differs from *M. mustelus* in vertebral numbers (34–39 monospondylic centra [n = 47] versus 25–32 monospondylic centra in *M. mustelus* [n = 89]), in having only a single point of transition from the long (monospondylic) centra of the body region to the shorter (diplospondylic) centra of the tail, upper-jaw labial folds distinctly longer than lower-jaw folds (upper and lower labial folds equal or nearly equal in *M. mustelus*) and in having a somewhat wider inter-nostril distance (2.7–3.6% TL versus 2.4–3.0% TL in *M. mustelus*).

Material Examined.—70 specimens, 36–122 cm. RHODE ISLAND, NEW JERSEY and DELAWARE: ANSP 601, 2: 36–96 cm; ANSP 23473, 2: 41–47 cm; ANSP 24170, 4: 41–44 cm; ANSP 41038, 2: 38–39 cm; ANSP 124250, 89 cm; USNM 197676, 38 cm. VIRGINIA and MARYLAND: Uncat. 5: 88–103 cm; UF 101294, 46 cm; UF 101295, 2: 43–56 cm. NORTH CAROLINA and SOUTH CAROLINA: UF 32392, 57 cm; UF 32393, 52 cm; UF 32398, 50 cm; UF 101293, 47 cm; UF 101320, 14: 105–122 cm. GEORGIA: USNM 164520, 60 cm; UF 32394, 58 cm. FLORIDA (East Coast): UF 15579, 50 cm; UF 32396, 65 cm; UF 32397, 48 cm; UF 66549, 2: 58–61 cm; UF 101324, 51 cm; UF 228457, 2: 58–60 cm; UF 208888, 4: 63–72 cm; UF 209881, 56 cm; UF 213458, 45 cm; UF

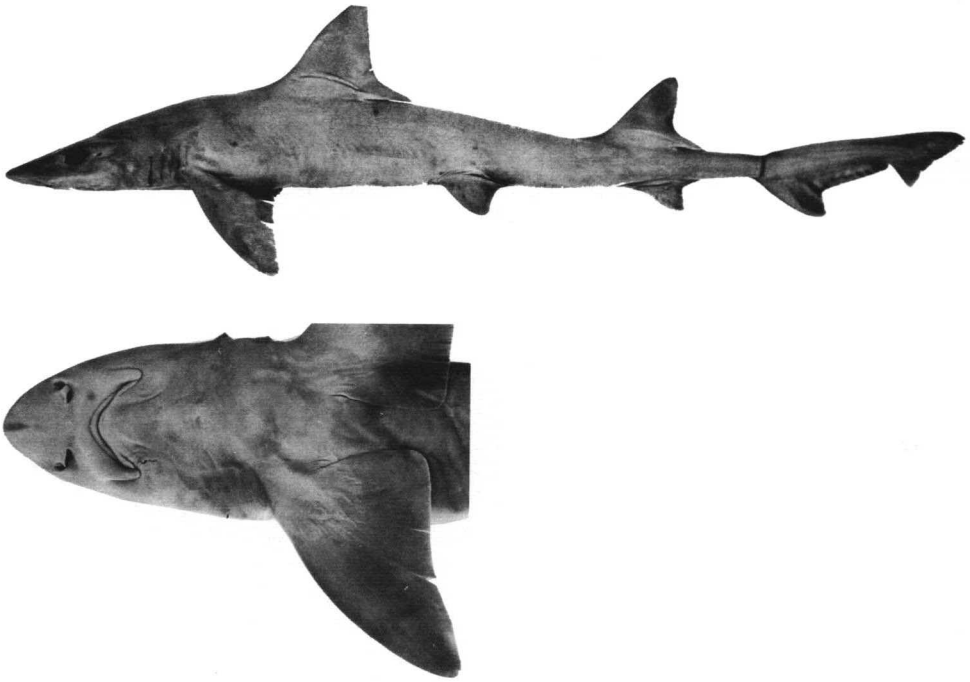

Figure 5. *Mustelus canis insularis*, 111 cm female, holotype, USNM 208012; black line at base of caudal is a stain from a wire used to affix a label to the peduncle. Lower figure: ventral view of head and pectoral fin.

224063, 69 cm; UF 224101, 65 cm; UMML 4996, 66 cm. NORTHERN GULF OF MEXICO: UF 230476, 3: 38–47 cm (29°33'N, 86°35'W; off Panama City, FL; depth 229 m; R/V OREGON II sta. 10122); USNM 188078, 56 cm (29°11.5'N, 88°11.5'W; off Mississippi Delta; depth 275 m; R/V OREGON, sta. 4002). MEXICO: UF 46016, 87 cm; UF 46017, 87 cm; uncataloged: R/V OREGON II sta. 10994, 40 cm. BRAZIL (Rio de Janeiro and Southward): CAS-SU 53725, 68 cm; ISH 2027–68, 56 cm. URUGUAY: ISH 1008–66, 2: 86–90 cm; ISH 1068–66, 61 cm; ISH 2036–68, 101 cm.

Mustelus canis insularis new subspecies
Figure 5

Mustelus canis (non Mitchill): Bigelow and Schroeder, 1940 (in part, specimen from Cuba); 1948 (in part, specimens from Bermuda, Cuba and Jamaica). Nelson, 1970: fig. 7 (illustration of denticles in buccopharyngeal cavity). (In view of the insular distribution of this subspecies, it is probable that all literature references to *M. canis* from Bermuda, the Bahamas, Cuba, Jamaica, and Puerto Rico apply to *M. canis insularis.*)

Mustelus sp: Clark and Kristof, 1990: 279, fig. 14.

Holotype.—USNM 208012, female, 111 cm, Bahamas, Cay Sal Bank, 5 miles NW of Cay Sal Island; depth 214 m; 1 December 1966. The holotype and all paratypes from Cay Sal Bank were collected by Mr. Frank Williams.

Paratypes.— BAHAMAS: ANSP 103924, female, 112 cm, Cay Sal Bank, 24°00'N, 80°26'W; depth 229 m; 12 August 1967; Frank Williams and William D. Anderson, Jr, colls.; BMNH 1972.10.3.1, female, 650 mm, same locality and collection data as for holotype; FMNH 71555, female, 708 mm, same locality and collection data as for holotype; UF 46039, female, 875 mm, same locality and depth as for holotype, November 1966; UF 101336, female, 117 cm, Cay Sal Bank, 24°00'N, 80°26'W; depth 192 m; 1 November 1966; UF 203360, female, 107 cm, Bimini; depth 366–427 m; August 1958; UF 224064, female, 595 mm, Bahama Bank, 50 miles south of Orange Key, 24°10'N, 79°10'W; depth 213 m; 21 June 1966; UF 228458, female, 330 mm, Bimini, off Picket Rock; depth 366 m; 9 June 1952; USNM 20813, female, 100 cm, Cay Sal Bank, 24°00'N,

80°26'W; depth 214 m; 10 August 1967; William D. Anderson, Jr and Frank Williams, colls. BARBADOS: UF 19141, female, 746 mm, 13°16'N, 59°40'W; depth 137 m; 20 March 1969. BERMUDA: AMNH 19475, 2: female 267 mm, male 287 mm; ANSP 124249, female, 98 cm (only cranium retained); BMNH 1879.1.8.1, male, 865 mm; USNM 21376, 2: 274 & 285 mm; USNM 154808, 307 mm. CUBA: MCZ 35233, male, 546 mm, Havana; USNM 25234, male, 89 cm. JAMAICA: USNM 37679, female, 974 mm. LEEWARD ISLANDS: CAS 15051, male, 97 cm, Nevis Island (17°15'N, 62°22'W), depth 579 m, 8 December 1969, OREGON II stn. 10842; ZMA 110.193, female, not measured, Saint Eustatius. PUERTO RICO: UF 46075, male, 885 mm TL (18°31'N, 66°23'W), depth 234 m, 10 September 1982, R/V OREGON II stn. 37204; UF 46076, male, 970 mm TL (18°3'N, 67°28'W), depth 322 m, 2 September 1982, R/V OREGON II stn. 37103; UF 46077, male, 940 mm TL (18°29'N, 66°3'W), depth 269 m, 11 September 1982, R/V OREGON II stn. 37217.

Diagnosis.—Morphometric data are given in Table 1. Caudal fin of adults with a prominent (but not pointed) ventral lobe, the ventral lobe angle 95–105°. Trailing edges of dorsal fins not frayed. Rear (distal) edge of pectoral and pelvic fins concave. Head moderate, pre-pectoral distance 17–20% TL; inter-orbital distance 3.6–4.3% TL; snout moderate, pre-oral snout length 5.5–7.1% TL; inter-nostril distance wide (2.9–3.5% TL); orbit diameter 2.5–3.7% TL; upper-jaw labial folds (1.8–2.4% TL) slightly longer than lower-jaw labial folds. Teeth asymmetric, with a low, broadly-rounded cusp and numerous indistinct basal ridges; tooth counts 77/70 (one specimen). Denticles mostly lanceolate (fewer than 10% with accessory cusps) with 4–6 ridges extending at least half the distance to the posterior margins. Buccopharyngeal denticles of palate and tongue not extending past first gill arch, similar to *M. canis canis* (Fig. 18A). Upper jaw skeleton comprising a single cartilage on each side. Diagnostic vertebral numbers are given in Figures 23–25.

Adults immaculate grey dorsally, paler ventrally; trailing edges of fins often with a pale or white margin; most specimens with a greyish smudge on midline of underside of snout tip. Newborns and young juveniles with sooty smudges on apices of dorsal fins and tip of caudal fin, the trailing edges of all fins with a pale or white margin.

Remarks.—As is the case in the nominal subspecies, *M. canis insularis* also develops a placental connection between the mother and fetus.

The largest specimen examined was a 117-cm female. Males are not mature until 80–84 cm, and females mature at about 90 cm. A 33-cm pup was not quite ready for birth.

M. canis insularis is usually found in deeper water (137–808 m) than the continental subspecies; most of the specimens that I examined were caught in depths greater than 200 m. Also unlike *M. c. canis,* the insular subspecies seems to prefer rugged rocky bottom.

Distribution (Fig. 26).—*M. canis insularis* is an insular subspecies that occurs at several Caribbean islands (Cuba, Jamaica, Grand Cayman, Puerto Rico, Nevis Island, Sint Eustatius the Bahamas and Bermuda; and it appears to be the only species of *Mustelus* occurring at these islands.

Comparisons.—Externally, *M. c. insularis* and *M. c. canis* are virtually identical; but *M. c. insularis* differs in usually having a slightly higher dorsal fin (Fig. 6) and a longer caudal fin tip (6.5–8.6 versus 4.6–7.0% TL in *M. c. canis*). The white margins on the fins of juvenile *M. c. insularis* are generally more distinct than those of *M. c. canis.* The most significant difference between these two subspecies is in the numbers of vertebrae (Figs. 23–25).

Clark and Kristof (1990) reported three specimens caught at Bermuda and "observed at least 14 individuals 45–120 cm TL during sub dives in Cayman,

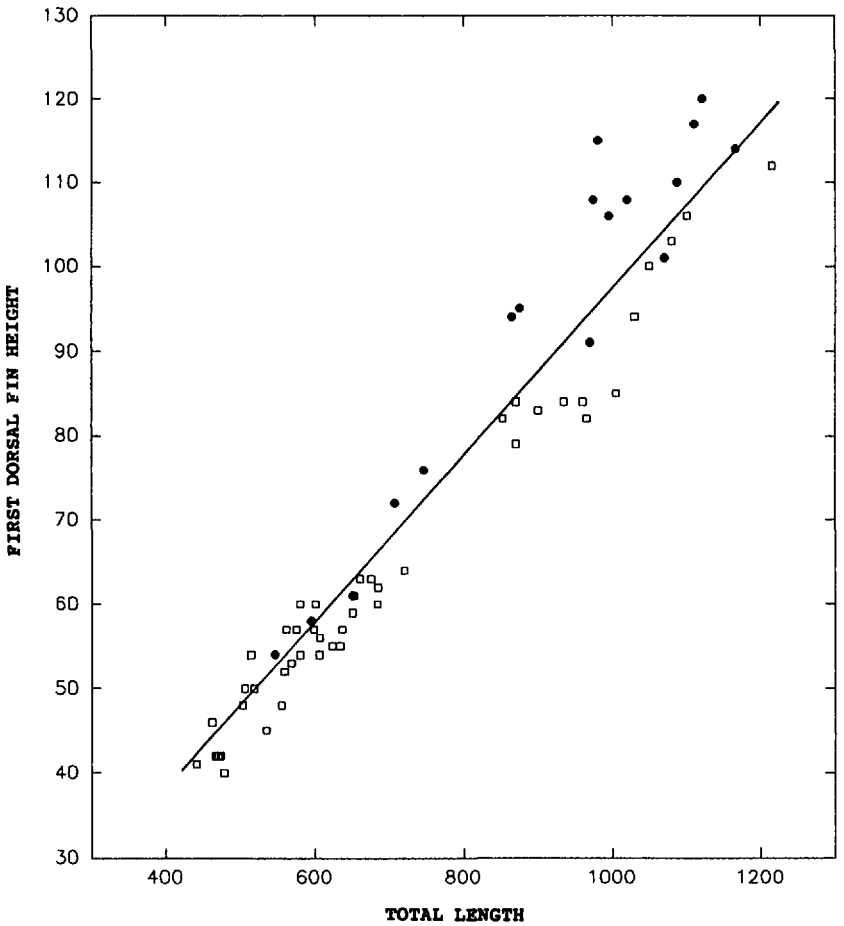

Figure 6. Scatter diagram of first dorsal fin height plotted against total length for *Mustelus canis canis* (squares) and *M. canis insularis* (circles). Straight line represents first dorsal fin height as 10% of total length.

Bermuda and Bahama at depths from 300 to 808 m." They mentioned that "The two dorsal and pectoral fins seem larger and the first dorsal more pointed than the shallow-water *M. canis*." They also claimed that specimens from deepwater at Bermuda exhibited "differences in the dermal denticles between the two types [i.e., the deep-water insular population and the shallow-water continental population] of *Mustelus* that may prove them to be separate species or subspecies." However, all 25 specimens of *M. canis insularis* that I examined had lateral body denticles of the same configuration as *M. canis canis* (mostly lanceolate with 4–6 ridges that usually extended to the rear margin of the scale).

Bigelow and Schroeder (1948: 251) wrote, "The coastwise nature of this species (*M. canis*) makes it likely that the Bermudian population has long been entirely isolated."

Mustelus fasciatus (Garman)
Figure 7

Galeorhinus fasciatus Garman, 1913: 172 (type-locality Rio Grande do Sul, Brazil; syntypes MCZ nos. 154, 315).

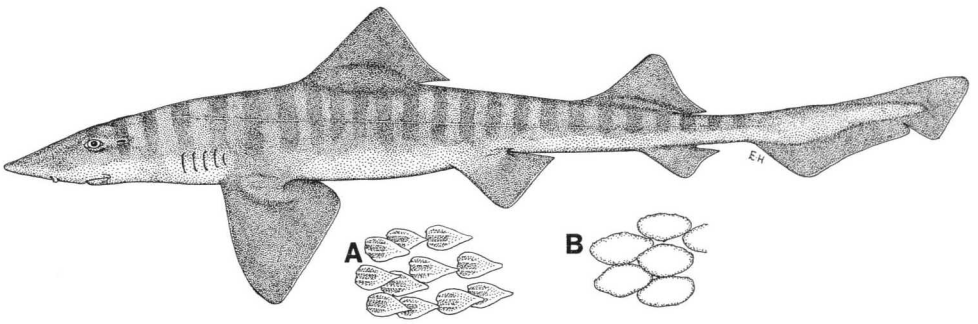

Figure 7. *Mustelus fasciatus,* 62 cm immature male, syntype, MCZ 154; A) denticles from flank, midway between origins of dorsal and pectoral fins; B) teeth from upper jaw.

Mustelus striatus Devincenzi, 1920: 122, pl. 12 (type-locality Montevideo, Uruguay; holotype MHNM CI 135). Olazarri et al., 1970: 2 (holotype listed among type-specimens deposited in the Museo Nacional de Histoire Natural de Montevideo).

Mustelus fasciatus: Tortonese, 1938: 305 (description, measurements, illustration). Springer, 1939a: 467 (separated from other species of *Mustelus* in key). Bigelow and Schroeder, 1940 (compared with other species of *Mustelus; M. striatus* listed in synonymy). Bigelow and Schroeder, 1948: 256, fig. 43 (diagnosis, description, illustration, range, and synonymy). Barcellos, 1961 (reported as common off southern Brazil; compared with *M. canis*). Ximénez, 1962 (synonymy, reported from Montevideo; separated [inadequately] from *M. schmitti* in key). Figueiredo, 1977: 14, fig. 18 (distinguished from other Brazilian species of *Mustelus* in key; reported from northern Argentina to Rio Grande do Sul, Brazil). Sadowski, 1977 (adult female, 1467 mm and adult male, 1455 mm reported from Sâo Paulo, Brazil). Lopez Cazorla and Menni, 1983 (950 mm female from Bahia Blanca, Argentina; photograph). Menni et al., 1984 (Argentina, references, distinguished from *M. mento, M. schmitti* and *M. canis*). Vooren, 1992 (reproduction compared with *M. canis* and *M. schmitti*).

Diagnosis.—Morphometric data are listed in Table 1. Ventral lobe of caudal fin not well-developed, the ventral lobe angle obtuse. Trailing edges of vertical fins not frayed. Rear (distal) edge of pectoral and pelvic fins straight or very nearly straight. Head large, pre-pectoral distance 22–25% TL, inter-orbital distance 4.8–5.2% TL; snout large, pre-oral snout length 8.0–9.1% TL; inter-nostril distance wide, 2.9–3.4% TL; eye small, orbit diameter 1.9–2.5% TL. Upper-jaw

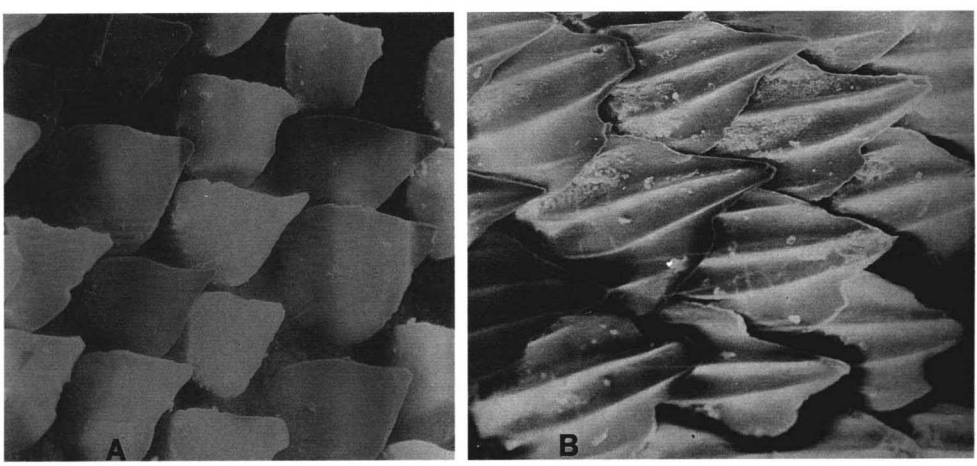

Figure 8. Midlateral flank denticles: A) *Mustelus fasciatus,* magnification 20×; B) *M. norrisi,* magnification 25×.

labial folds longer than lower-jaw labial folds, 2.0–2.4% TL. Teeth hemispherical, similar in adults and juveniles, with crowns very low, evenly rounded and symmetric; tooth counts 64–66/56–58. Denticles lanceolate, with 2–4 low ridges extending no more than half length of scales (Fig. 7A) or without ridges (Fig. 8A). Buccopharyngeal cavity mostly covered by denticles (Fig. 19). Anal fin close to caudal fin, distance from anal-fin base to caudal-fin origin 4.2–5.6% TL. Diagnostic vertebral numbers are given in Figures 23–25.

Color.—Grey to greyish-tan dorsally; newborn *M. fasciatus* and juveniles (up to about 80 cm) with several darker bars of irregular width and shape across dorsal surface of head and body. Adults dark grey dorsally, with faint (slightly darker) transverse bars across the dorsal surface.

Remarks.—This is a large species of *Mustelus.* A male of 62 cm (the largest specimen that I examined) still had undeveloped claspers. On a 39-cm shark, the "umbilical" scar had not yet completely healed. Vooren (1992) mentions that *M. fasciatus* has a placenta, but the weights of the pups at birth are not different from the aplacental *M. schmitti*; and fecundity (litter size) is not correlated with size of the mother. The largest female *M. fasciatus* that he examined was 155 cm (15.7 kg, eviscerated). Figueiredo (1977) reported that this species is often captured near shore and that it occurs to depths of 70 m. But in otter trawls at depths of 10 to 500 m off the coast of Rio Grande do Sul (from 28°40'S to 33°44'S), Vooren (1992) found that *M. fasciatus* was much less common (only 1 or 2 individuals caught per h trawl) than *M. canis* and *M. schmitti* (which were caught in large numbers).

Distribution (Fig. 26).—*M. fasciatus* is known only from southern Brazil to off the Rio de la Plata in Argentina.

Comparisons.—*M. fasciatus* is one of the most distinctive species of *Mustelus.* It and *M. mento* Cope, 1877 of the Galapagos and coast of Peru and Chile (south to at least Isla de Chiloé at 43°S) are the only species with symmetric, evenly rounded (hemispherical) teeth with no discernible cusp and no differences in tooth shape of juveniles and adults. These two sister species represent the end stages of the phyletic trend in teeth adapted for feeding on hard-bodied prey such as crustaceans and molluscs. The disproportionately large head of *M. mento* and *M. fasciatus* also sets them apart from other species of *Mustelus.* In addition, the shapes of the pectoral and pelvic fins (with the rear edge straight or almost straight) of *M. fasciatus* (Fig. 9) and *M. mento* are different from those of the other western Atlantic species. The color pattern of juveniles of these two species (with several dark bars across the dorsal surface of the body) is also unique for species of *Mustelus.* But the most remarkable feature of these two species is the high incidence (more than half of 45 *M. mento* and all 10 *M. fasciatus* x-rayed) of "monospondylic" centra posterior to the point of transition from the anterior, long, monospondylic centra to the posterior, short, diplospondylic centra. In some specimens there was an almost regular alternation of long and short centra from the point of transition back to the caudal fin.

These two sister species differ in the number of precaudal vertebrae (58–63 for *fasciatus* and 64–90 for *mento*). Although I examined only nine juveniles (37–62 cm TL) and no adults of *M. fasciatus,* it appears to have a longer snout (snout to upper jaw 8.0–9.1 versus 6.0–7.9% TL for *mento*), wider mouth (6.7–7.7 versus 4.5–6.4% TL for *mento*), and shorter distance between anal-fin base and caudal-fin origin (4.2–5.6 versus 5.7–7.5% TL for *mento*). Other differences are that *M. mento* has a row of papillae along the posteromedial side of the lower half of the

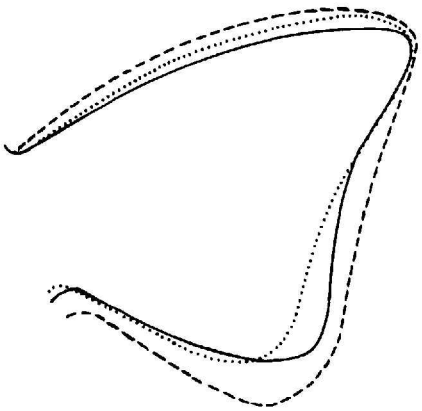

Figure 9. Pectoral fin shapes of *Mustelus canis,* 77 cm, Massachusetts (dotted line); *M. schmitti,* 59 cm, Uruguay (solid line) and *M. fasicatus,* 60 cm, holotype, Rio Grande do Sul, Brazil (dashed line). After Bigelow and Schroeder (1948).

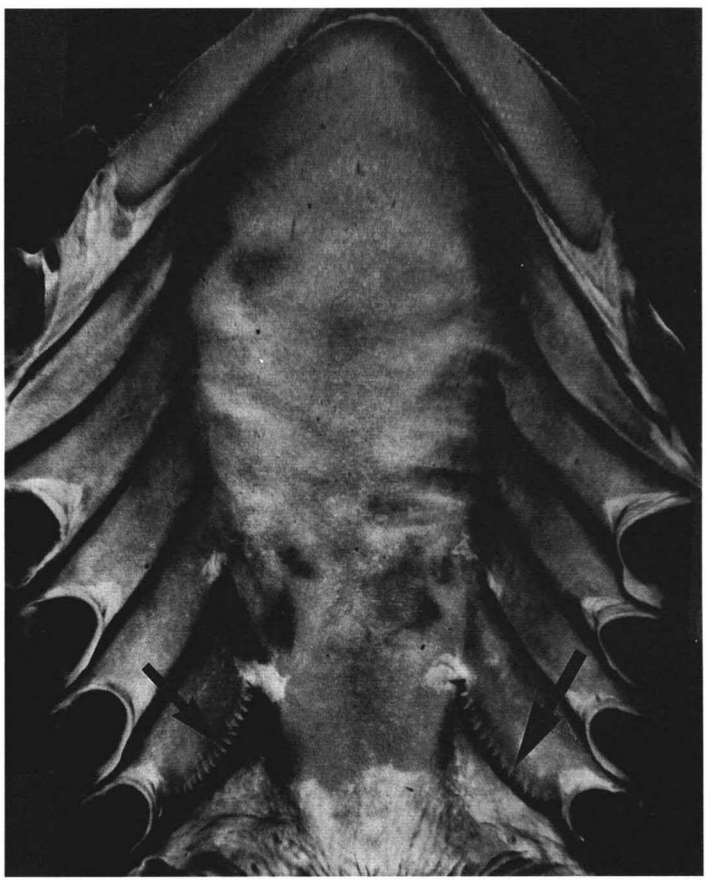

Figure 10. Ventral surface of buccopharyngeal cavity of *Mustelus mento,* 61 cm, Peru. Note papillae (arrows) along posteromedial side of fifth gill arch.

fifth gill arch (Fig. 10), whereas *M. fasciatus* has no such papillae (Fig. 19B), and adults of *M. mento* usually have numerous, more or less conspicuous, small pale spots on the dorsal surface of the body (no pale spots in adults of *M. fasciatus*).

Material Examined.—Brazil (Rio Grande do Sul): BMNH 1886.1.21.43–44, 2: 44–52 cm; MCZ 154, syntype 62 cm; MCZ 315, syntype 48 cm; CAS-SU 52867, 2: 37–39 cm. Uruguay: LACM 30616, 44 cm; CAS-SU 13432, 2: 59–60 cm; USNM 104936, 2: 49–50 cm.

Mustelus higmani Springer and Lowe

Mustelus higmani Springer and Lowe, 1963: 245, Fig. 1 (type-locality, northeast of Parimaribo, Surinam (06°23′–21′N, 54°47′–51′W) depth approximately 12 fathoms; holotype USNM 156930). Cervigon, 1966: 49–51, fig. 18 (diagnosis, coloration, habitat, photograph, distribution). Figueiredo, 1977: 14, figs 17 and 62 (compared with Brazilian species in key, good illustration of shark and denticle; reported from Esperíto Santo and Sâo Paulo). Uyeno and Sasaki, 1983: 58 (color photo of adult male, 442 mm, from off Surinam or French Guiana).

Diagnosis.—Morphometric data are listed in Table 1. Ventral lobe of caudal fin well-developed, acuminate in some adult males, the lobe angle 86°–138°. Trailing edges of dorsal fins fins not frayed. Rear (distal) edge of pectoral and pelvic fins distinctly concave. Head large, pre-pectoral distance 19–24% TL; inter-orbital distance 4.5–6.3% TL; snout large, pre-oral snout length 6.9–9.6% TL; internostril distance wide, 2.7–3.8% TL; orbit diameter 2.2–3.4% TL. Upper-jaw labial folds short (0.8–1.8% TL), equal or about equal to lower-jaw labial folds. Teeth with a low, rounded asymmetric cusp and 8–15 short ridges at base; tooth counts 66–78/62–69. Denticles mostly tridentate, with four prominent ridges extending the length of the scale. Denticles of palate and tongue extend posterior to first gill arch (Fig. 20); gill arches and pharyngeal pads on fifth epibranchial cartilages mostly covered with denticles, but dorsal and ventral surfaces of pharyngeal cavity otherwise free of denticles. Diagnostic vertebral numbers are given in Figures 23–25.

Color in alcohol: immaculate grey dorsally, paler ventrally. In life, some individuals are golden yellow.

Remarks.—*M. higmani* is another species in which the fetus develops a yolk-sac placenta. Litters comprise 1–7 (usually 3–5) pups.

This is one of the smallest species of *Mustelus*. The largest specimen known (Springer and Lowe, 1963: 249) was a 635 mm female. My data on sizes at maturity and birth for *M. higmani* agree with figures published by Springer and Lowe (1963). Males are mature at about 43 cm, females at about 48 cm, and pups are born between 21 and 24 cm.

Springer and Lowe (1963) published considerable information on the ecology of *M. higmani*. The species was common in trawls over shallow (16–110 m) mud, mud and sand, or mud and shell bottom from the Gulf of Venezuela to the coast of Brazil; and there was some indication of sexual segregation of schools. *M. higmani* was reported by Cervigon (1966) as abundant at Margarita and adjacent islands and frequently captured in shallow, brackish water at the mouth of the Orinoco River.

Distribution (Fig. 26).—*M. higmani* is known from Curaçao, Trinidad and the coast of South America from the Gulf of Venezuela to Santos on the south coast of Brazil. Contrary to the statement by Springer and Lowe (1963): ". . . there is no overlap in the ranges of the three species, *canis, norrisi,* and *higmani.*", all three species occur together on the coasts of Venezuela and Brazil. According to Cervigon (1966), *M. higmani, M. norrisi,* and probably *M. canis* are sympatric

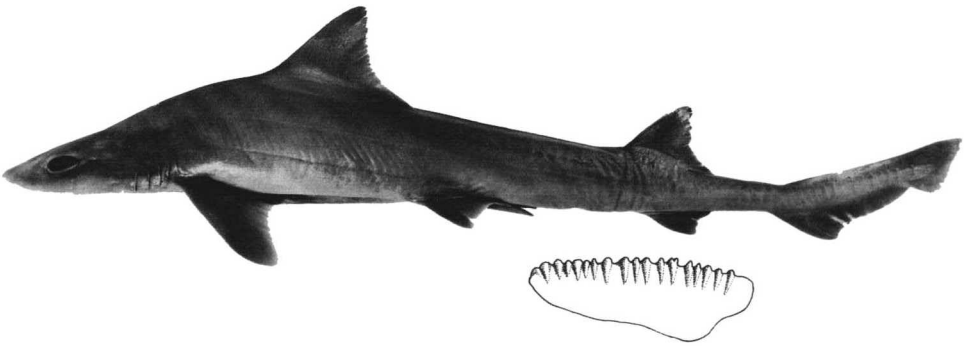

Figure 11. *Mustelus minicanis*, 48 cm adult male, holotype, USNM 207961, from Venezuela; inset: camera lucida sketch of tooth.

along part of the Venezuelan coast. In addition, I have examined specimens of all three species from southern Brazil.

A surprising geographic and bathymetric range extension is the *M. higmani* that was collected by the R/V OREGON II in the northern Gulf of Mexico on the edge of the DeSoto Canyon at a depth of at least 1281 m. This 482 mm TL female (UF 41634) was caught, along with 935 lbs of "deepwater fishes", on 2 September 1970 at station 11206 (29°11'N, 87°17'W) with a 191-ft prawn trawl. The depth was recorded as "800 fms" in the station list, but according to the Cruise Report, the tow was in 700–900 fms. This record is 400 m deeper than any previously recorded catches or sightings of *Mustelus* species.

Relationships.—The relationships of *M. higmani* are unclear. I do not agree with the vague statement by Springer and Lowe (1963): "A close relationship between *higmani* and *canis* is suggested by their similarities in head, body, and fin shapes.".

Material Examined.—98 specimens, 20–59 cm. NORTHERN GULF OF MEXICO: UF 41634, 48 cm. CURAÇAO: RMNH 23320, 59 cm. Uncataloged: R/V OREGON Sta. 4473, 3: 20–21 cm. VENEZUELA: FMNH 66693, 24 cm; FMNH 66697: 6, 42–52 cm; UF 233646, 53 cm; Uncataloged: R/V OREGON Sta. 4490, 24 cm; OREGON Sta. 5620, 46 cm; UF 224215, 50 cm; USNM 221717, 3: 20–21 cm; USNM 221723, 25 cm. TRINIDAD: BMNH 1931.12.5.114, 53 cm; BMNH 1932.2.8.1, 51 cm. GUYANA: BMNH 1950.5.15.1, 48 cm, 1961.8.31.8, 48 cm; USNM 187693, 52 cm. SURINAM: UF 36963, 47 cm; UF 36962, 47 cm; UF 224215, 50 cm; USNM 156930, holotype, 49 cm; USNM 187695, 48 cm; USNM 187698, 2: 39–39 cm; USNM 187720, 13: 31–54 cm; USNM 187721, 4: 45–49 cm; USNM 187723, 6: 32–37 cm; USNM 187938, 3: 22–23 cm; USNM 221722, 45 cm. FRENCH GUIANA: ANSP 103923, 51 cm; FMNH 66691, 45 cm; USNM 187706, 45 cm; USNM 187707, 3: 29–33 cm; USNM 187720, 14: 31–54 cm; USNM 187723, 2: 33–37. BRAZIL (North of Recife): FMNH 66692, 18 cm; UF 211533, 20 cm; USNM 187692, 2: 17–20 cm; USNM 187696, 19 cm; USNM 187704, 2: 27–36 cm; USNM 188020, 2: 27–27 cm; USNM 188021, 20 cm; USNM 188022, 22 cm. BRAZIL (South of 20° S): ANSP 120467, 58 cm; FMNH 74164, 35 cm; FMNH 74164, 35 cm; USNM 100836, 31 cm; ZMH 13247, 55 cm.

Mustelus minicanis new species
Figure 11

Holotype.—USNM 207961, male 478 mm; between Peninsula de Paraguaná Venezuela and Aruba (12°19'N, 70°34'W), depth 73 m; 27 September 1963; R/V OREGON Sta. 4402; shrimp trawl.

Paratypes.—VENEZUELA: ANSP 120342, female 574 mm, Peninsula de Araya, 23 August 1960; W.A. Lund, Jr, collector; UF 19140, male 477 mm, (11.5°N, 63°W), depth 71–73 m, 20 July 1968, M/V CALAMAR Sta. 491; UF 230376, female 371 mm, (11.5°N, 63°W), depth 93–95 m, 20 July 1968, M/V CALAMAR Sta. 492. COLOMBIA: USNM 207962, 2 males 348 & 473 mm, off Cape La Vela (12°13'N, 72°34'W), depth 183 m, 1 June 1964, R/V OREGON Sta. 4402; USNM 208016, female 431

mm, off Bahia Honda (12°29'N, 71°54'W), depth 174 m, 9 October 1965, R/V OREGON Sta. 5685; USNM 208017, 2: male 348 mm, female 312 mm, same data as for holotype.

Diagnosis.—Morphometric data are listed in Table 1. Ventral lobe of caudal fin not well developed; the ventral lobe angle obtuse (129°–163°). Trailing edges of dorsal fins not frayed. Rear (distal) edge of pectoral and pelvic fins slightly concave. Head moderate, pre-pectoral distance 18–21% TL; inter-orbital distance 4.2–4.8% TL; pre-oral snout length 6.1–7.3% TL; inter-nostril distance 2.7–3.1% TL; eye large, orbit diameter 3.2–4.3% TL. Upper-jaw labial folds 1.3–1.7% TL, slightly longer than lower-jaw folds. Teeth wide, asymmetric, with a low rounded cusp and prominent basal ridges (Fig. 11); tooth width about 3 times crown height; tooth counts 60–67/60–61. Denticles lanceolate and/or tridentate with four ridges extending to rear margin of scale. Buccopharyngeal denticles (Fig. 18D) confined to a triangular patch at front of palate, front and rear sides of gill arches, posterior margin of pharyngeal pads on fifth gill arch, and a triangular patch at tip of tongue. Upper jaw skeleton comprises a single cartilage on each side. Spiral valve of intestine with seven turns. Diagnostic vertebral numbers are given in Figures 23–25.

Head and body immaculate grey dorsally; newborn young and juveniles with sooty smudges on apices of dorsal fins and tip of caudal fin.

Remarks.—*M. minicanis* pups develop a placental connection with the mother. Although the sample size of available specimens is small (n = 9) it is obvious that this is a small species of *Mustelus*: males are mature at 47 cm, and a 57-cm female contained five, near-term pups of 20–21 cm total length.

Comparisons.—*M. minicanis* is easily distinguished from all other species of *Mustelus* by its small size, increased number of vertebrae, large eye, and poorly developed ventral lobe of the caudal fin. *M. minicanis* is the only species of *Mustelus* in which the orbit diameter is distinctly greater than the inter-nostril distance. Seven of the nine specimens examined had lanceolate denticles with 4–6 prominent ridges extending the length of the scale; on two specimens (UF 230376, female 371 mm and USNM 207962, male 348 mm) however, the denticles were mostly tridentate. Although the small size at maturity and presence of tridentate denticles on some *M. minicanis* is similar to *M. higmani,* there are other trenchant differences (vertebral numbers, size of eye, pre-oral and pre-nasal snout lengths, and configuration of the caudal fin) that belie a close relationship between these two species.

Distribution (Fig. 26).—*M. minicanis* is known only from the coast of South America between Cape La Vela, Colombia (72°W) and Rio Caribe, Venezuela (63°W), in 71 to 183 meters.

Mustelus norrisi Springer
Figure 12

Mustelus norrisi Springer, 1939a: 462 (type-locality off Englewood, Florida in about 3 fathoms). Springer, 1939b: 15 (illustration, compared with *M. lunulatus* and *M. canis*). Bigelow and Schroeder, 1940: 417, pls. 14, 15 and 17 (illustrations of fin shapes and teeth; compared with other species of *Mustelus*). Bigelow and Schroeder, 1948: 254, fig. 43 D–F (diagnosis, illustration, compared with *M. canis*). Briggs, 1958: 248 (reported from west coast of Florida). V.G. Springer, 1961: 480 (reported from Tampa Bay, Florida; notes on fetuses). Cervigon, 1963: 113 (reported from Cubagua and Margarita islands off Venezuela). ?Briggs et al., 1964: 113 (reported from northwestern Gulf of Mexico; may have been either *M. canis* or *M. sinusmexicanus*). Springer and Garrick, 1964: 87 (vertebral data). Clark and von Schmidt, 1965: 47, Tables 13 and 14 (in part, the CHML No. 1 shark from the northern Gulf of Mexico is either *M. canis* or *M. sinus-*

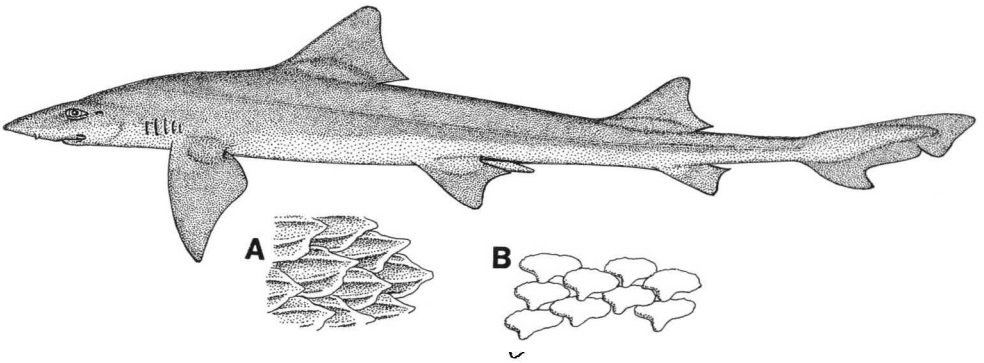

Figure 12. *Mustelus norrisi,* 64 cm adult male from Florida Keys, MCZ 442 (redrawn from Bigelow and Schroeder, 1948: fig. 43); A) denticles from flank, midway between origins of dorsal and pectoral fins (composite of adults); B) upper jaw teeth of 64 cm male (redrawn from Bigelow and Schroeder, 1948).

mexicanus; data on fetuses and stomach contents, morphometric data). Heemstra, 1965: 8 (separated from *M. canis* in key). Cervigon, 1966: 45, fig. 17 (photograph, reported from Margarita Island; compared with *M. canis*; notes on coloration, size, food and habitat). Figueiredo, 1977: 15, fig. 19 (key, compared with other Brazilian species).

Mustelus canis (non Mitchill): Bigelow and Schroeder, 1940: Table, col. C (in part, the MCZ 503 shark from Brazil, referred to *M. canis,* is *M. norrisi*). Bigelow and Schroeder, 1948: 244 and 251 (in part, all of the MCZ specimens that I have examined identified as *M. canis* from Brazil by Bigelow and Schroeder are *M. norrisi*).

Diagnosis.—Morphometric data are listed in Table 1. Caudal fin of adults with a prominent, falcate ventral lobe, the ventral lobe angle acute, 57°–84°; ventral lobe of juveniles distinct but rounded, the lobe angle 84°–101°. Trailing edges of dorsal fins not frayed. Rear (distal) edge of pectoral and pelvic fins concave. Head moderate, pre-pectoral distance 16–20% TL; inter-orbital distance narrow, 3.3–4.2% TL; snout small, pre-oral snout length 4.2–6.5% TL; inter-nostril distance narrow, 2.3–2.8% TL; orbit diameter 2.3–3.4% TL. Upper-jaw labial folds short, 1.0–1.7% TL, and not much longer than lower-jaw folds. Teeth asymmetric, with a relatively high, rounded cusp and numerous short basal ridges; tooth counts 58–65/57–60. Denticles (Figs. 8B, 12A) lanceolate, with 4, 5 or 6 ridges extending to rear margins of scales. Buccopharyngeal denticles of palate extend to base of first gill arch; tongue, gill arches and pharyngeal pads of fifth gill arch also covered with denticles. Upper jaw comprising a single cartilage on each side. Diagnostic vertebral numbers are given in Figures 23–25.

Immaculate grey or greyish brown dorsally, paler ventrally; some specimens with apex of first dorsal fin and/or trailing edges of fins with a pale or white margin. Newborn pups and juveniles with sooty smudges on apices of dorsal fins and tip of caudal fin.

Remarks.—*Mustelus norrisi* is a placental viviparous species with 7 to 14 pups in a litter. It is a moderate-sized species of *Mustelus*: males are mature at 57–61 cm, and females at about 65 cm. The young are born at a length of 29–30 cm, and the maximum total length for this species is about 98 cm.

The 118 cm gravid female caught by the R/V SILVER BAY about 26 miles east of the Mississippi Delta at a depth of 90 m and reported as *M. norrisi* (CHML No. 1) by Clark and von Schmidt (1965, p. 47 and Tables 13 and 14) was certainly not this species. This shark was 22 cm longer than any *M. norrisi* that has yet been collected, the pups were larger (34–37 cm) than any full-term foetus of *M.*

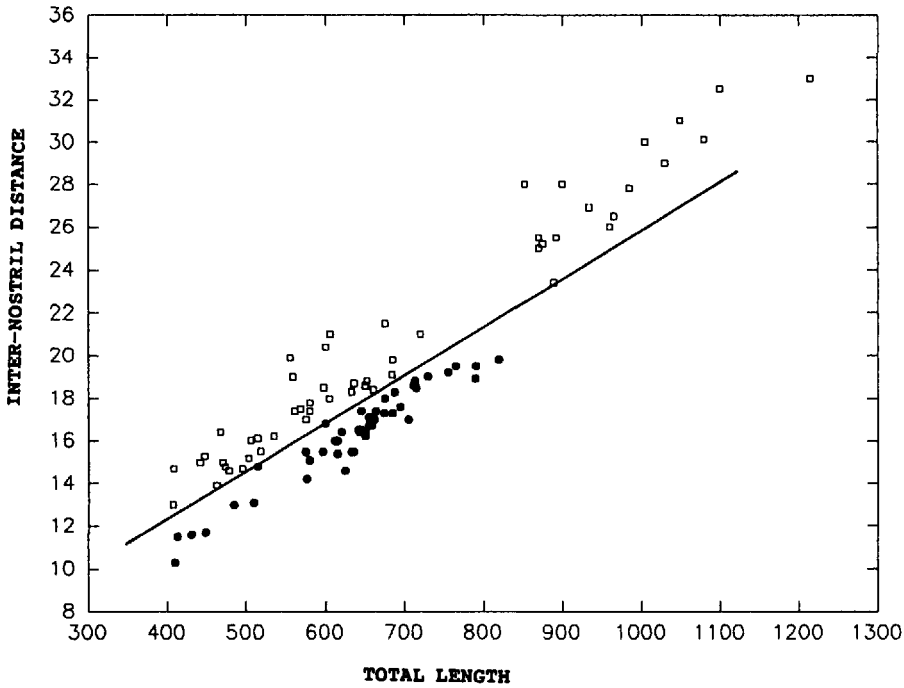

Figure 13. Scatter diagram of inter-nostril distance plotted against total length for *Mustelus canis canis* (squares) and *M. norrisi* (circles).

norrisi would be, and the depth of capture is considerably deeper than other Gulf of Mexico records (< 55 m) for *M. norrisi.* Unfortunately, Clark and von Schmidt did not examine the denticles or determine the number of vertebrae of this specimen; and it appears not to have been deposited in any museum fish collection. But on the basis of its size and provenance (26 miles east of the Mississippi Delta in 90 m of water), their specimen probably was *M. sinusmexicanus* sp nov. (See below.)

M. norrisi apparently prefers shallow sandy or mud bottom; the deepest record for this species is 84 m at the mouth of the Gulf of Venezuela (UF 101345). The Gulf of Mexico population of *M. norrisi* appears to be migratory. All specimens that I examined from this area were collected between October and May in depths less than 55 m. And the specimens seen by Springer, (1939b: 15) and Clark and von Schmidt, (1965: 47) were also collected from near-shore areas only during the winter months. Segregation by size and sex was indicated by Springer (1939a), who reported that all of the more than 50 *M. norrisi* that were caught during the winter months of 1935 to 1938 were adult males.

Distribution (Fig. 26).—West coast of Florida, Texas, southern Caribbean (Colombia and Venezuela), and southern Brazil from Recife to Cananéia. Contrary to the statement by Springer and Lowe (1963: 249), the ranges of *M. norrisi, canis,* and *higmani* do overlap.

Comparisons.—M. norrisi is similar to *M. canis canis* and an undescribed species of the eastern Pacific. *M. canis* is similar in vertebral numbers (except for the precaudal minus monospondylic count, for which there is only a slight overlap), denticle morphology, coloration, dorsal and anal fin configuration, and most mor-

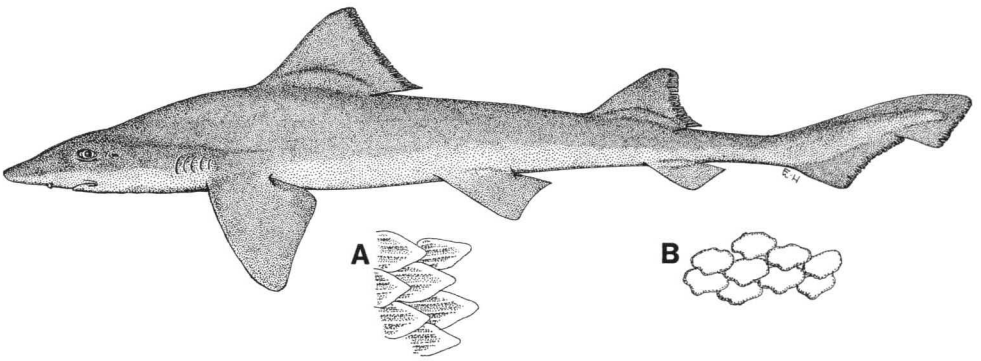

Figure 14. *Mustelus schmitti,* composite, subadult female about 59 cm; A) denticles from 59 cm female (MCZ 530); B) teeth from same specimen.

phometric features. *M. norrisi* differs from *M. canis* in having a narrower internostril distance (Fig. 13), shorter upper-lip folds (1.0–1.7 versus 1.6–2.7% TL for the upper-lip folds of *M. canis*) with upper and lower-lip folds subequal, denticle-covered portion of buccopharyngeal cavity more extensive (compare Figs. 18A and 18B), and in having more diplospondylic precaudal vertebrae (54–65 versus 48–55 in *M. canis*). In addition, *M. norrisi* differs from *M. canis* in several less definitive features: *M. norrisi* is a smaller, more slender shark (maximum size 98 cm versus 150 cm; body width 8.2–10.3 versus 9.2–12.5% TL), the inter-orbital distance is narrower (3.3–4.2 versus 3.7–4.6% TL), the teeth have a slightly higher, more distinct cusp than in like-sized *canis,* and the ventral lobe of the caudal fin is acuminate in adults of *M. norrisi* (Fig. 12).

Some characters used by previous authors to distinguish *M. norrisi* from *M. canis* and other species have proved, upon comparison of the larger samples used in the present study, to be of doubtful or no value in this regard. According to Bigelow and Schroeder (1948: 255), *M. norrisi* has the middle of the first dorsal-fin base "nearer to origin of pelvics than to axil of pectoral by a distance about equal to horizontal diameter of eye," whereas *M. canis* has the first dorsal midpoint "as near to axil of pectoral as to origin of pelvics, or nearer;". But (contrary to Bigelow and Schroeder) Compagno (1984: 400) states that the first dorsal-fin base midpoint of *M. norrisi* is "about equidistant between pectoral and pelvic fins" compared with *M. californicus,* which has the dorsal-fin base midpoint "somewhat closer to pelvic fins than pectorals." The amount of intraspecific variation in this feature, as revealed by the large numbers of sharks examined for this study (Table 1), and the lack of precision in quantifying the supposed differences in the relative positions of the first dorsal fin vis-a-vis the pectoral and pelvic fins, precludes the use of the position of the first dorsal fin as a taxonomic character that will separate these species.

The position of the origin of the pelvic fins relative to the pectoral-fin and anal-fin origins, used by Bigelow and Schroeder (1940: 420) and Figueiredo (1977) to separate *M. norrisi* from *M. canis* is also subject to considerable variation. Generally, females have the pelvic-fin origin located more posteriorly (i.e., closer to anal-fin origin than to pectoral-fin origins) than do males. This is probably a consequence of the greater demand for space in the abdominal cavity of gravid females. Bigelow and Schroeder's claim (1940, p. 420 and 1948, p. 254) that *M. norrisi* has the pelvic-fin origins about midway between the origins of the pectoral and anal fins, whereas *M. canis* has the pelvic-fin origins considerable nearer the

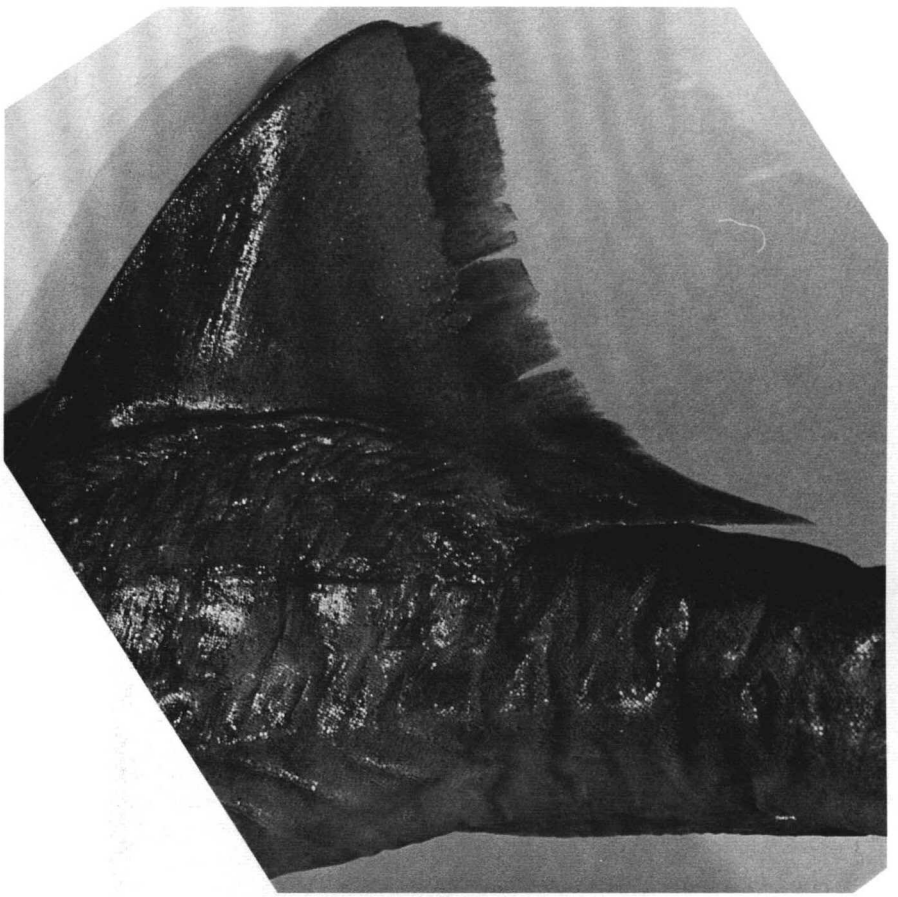

Figure 15. *Mustelus schmitti*, second dorsal fin of 60 cm male, USNM 87680.

anal-fin origin, probably reflects the fact that their sample of *M. norrisi* comprised all males.

Material Examined.—56 specimens, 26–82 cm. FLORIDA: Holotype, USNM 106639, male 71 cm, Englewood. Paratypes: BMNH 1939.5.5.1, male, 65 cm, Englewood; USNM 57369, 82 cm female with pups, Sawyer's Key Channel (a few miles NW of Key West); ANSP 10260, male 71 cm, Englewood; USNM 104333, male 69 cm, Englewood; USNM 116444, male 66 cm, Englewood. Other specimens from FLORIDA: FDNR 3994, 6: 56–77 cm, Manatee County; FDNR uncat. 4, 64–65 cm, central west coast of Florida. ANSP 103921, 66 cm; FDNR 3794, 3: 58–76 cm; FDNR 3996, 52 cm; FDNR 3997, 7: 58–66 cm; Pinellas County. UF 59031, 3: 60–72 cm; UF 65267, 63 cm; UF 65964, 2: 61–64 cm; Franklin County. ALABAMA: UF 46073 63 cm. TEXAS: FMNH 45042, 31 cm, off Corpus Christi; MCZ 35853, 28 cm; TIMS 680, 8 prenatal pups, 26–27 cm, off Port Aransas. COLOMBIA: UF 101345, 51 cm; USNM 201920, 79 cm. VENEZUELA: UF 46072, 2: 62–79 cm. BRAZIL: CAS-SU 52724, 41 cm; CAS-SU 52866, 49 cm; Recife; CAS-SU 730, 73 cm, Vitoria; MCZ 161, 3: 39–45 cm; MCZ 437, 35 cm; MCZ 503, 41 cm.

Mustelus schmitti Springer
Figures 14–16

Mustelus schmitti Springer, 1939a: 465 (type-locality Uruguay; holotype, USNM 106640). Bigelow and Schroeder, 1940: (misspelt as *M. schmidti*; compared with *M. canis*; measurements, illustrations of pectoral and caudal fins and teeth). 1948: 261, figs. 42F, G and 43C (measurements, same

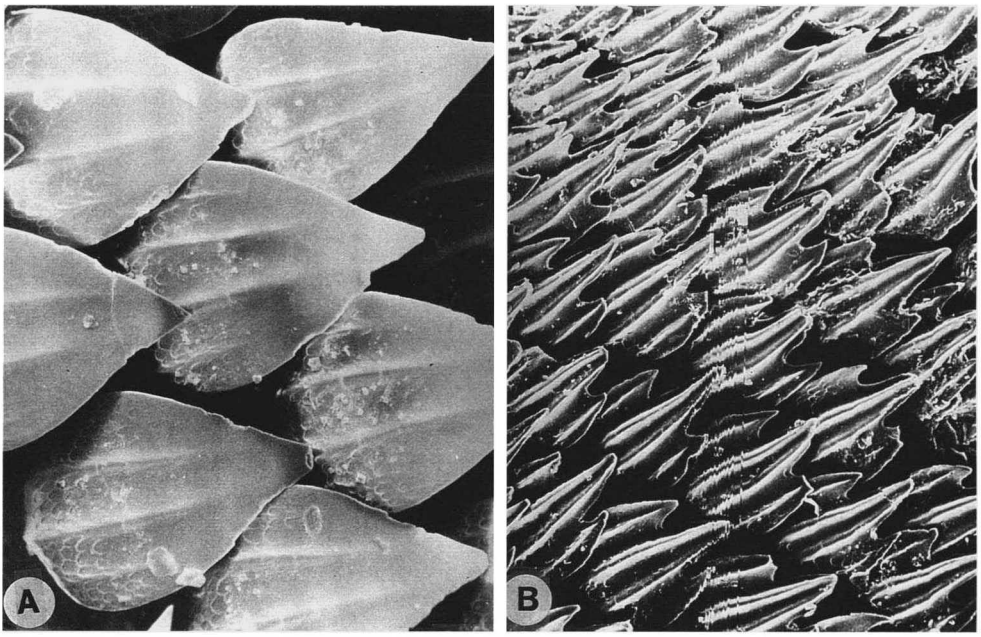

Figure 16. Denticles: A) *Mustelus schmitti,* 60 cm male, USNM 87680, magnification 70×; B) *M. sinusmexicanus,* 70 cm, male, ANSP 103921, magnification 40×.

illustrations as in 1940 paper, compared with *M. canis,* synonymy, range). Barcellos, 1961: 107 (reported as common on coasts of southern Brazil; compared with *M. canis*). Ximénez, 1962: 37–44 (reported from coast of Uruguay, synonymy, separated (incorrectly) from *M. fasciatus* in key). Figueiredo, 1977: 15, fig. 20 (key, compared with Brazilian species of *Mustelus*) Menni, 1985 (biology and distribution). Vooren, 1992 (reproduction).

Diagnosis.—Morphometric data are listed in Table 1. Ventral lobe of caudal fin not well-developed. Trailing edges of dorsal fins and caudal fin with a denticle-free margin of exposed ceratotrichia, giving the fins a "frayed" appearance (Fig. 15). Rear edge of pectoral and pelvic fins slightly concave. Head moderate, pre-pectoral distance 16–21% TL; inter-orbital distance wide, 4.3–5.3% TL; pre-oral snout length 5.6–8.0% TL; inter-nostril distance narrow, 1.8–2.4% TL; orbit diameter 2.1–3.5% TL. Upper-jaw labial folds long (1.8–2.6% TL), longer than lower-jaw folds. Teeth asymmetric, with a low, rounded cusp (Fig. 14B); tooth counts 55–60/52. Denticles (Figs. 14A, 16A) lanceolate with 2–4 ridges extending at least half length of the scale. Buccopharyngeal denticle patch of palate (Fig. 21) narrowing posteriorly to end at level of third gill arch; lingual patch roughly triangular; a few denticles scattered over gill arches and on pharyngeal pads of fifth gill arch. Postero-medial surface of lower limbs of fifth gill arch with a series of rudimentary papillae. Diagnostic vertebral numbers are given in Figures 23–25.

Body grey dorsally, often with more or less prominent, minute, white spots.

Remarks.—The lack of placentae in *M. schmitti* was confirmed by my dissection of a 60-cm female (NMW 11188) which contained two 15–16 cm pups, each with a 7-mm diameter yolk-sac at the end of a 15-mm yolk stalk. Another gravid female contained seven pups of 16–20 cm. Vooren (1992: 304) pointed out that, although the pups do not develop a placenta, the 39 g weight of a neonate compared with a weight of 2 g for a mature egg, indicates that the pups are [somehow] supplied with additional nutrients by the mother during the gestation period.

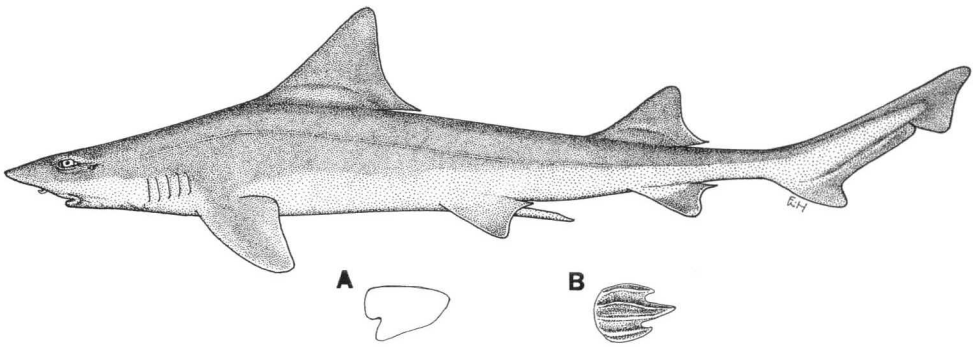

Figure 17. *Mustelus sinusmexicanus,* 83 cm adult male, holotype, USNM 208345, from off Alabama. A) tooth from right side of upper jaw, B) midlateral flank denticle.

This is a moderate-sized species of *Mustelus.* Menni (1985) reported a maximum size (females) of 109 cm, with males mature at 62–67 cm, and females at 60–62 cm. The young are born at about 36 cm, with 2–13 pups per litter.

According to Menni (1985), the major prey for *M. schmitti* are crustaceans and polychate worms, with lesser amounts of benthic fishes (*Dules auriga, Symphurus sp* and other pleuronectiforms), holothurians, actinians, *Branchiostoma platae* and cephalopods.

In the original description of *M. schmitti,* Springer (1939: 466) stated "Color uniform gray, without light or dark spots or bands." He apparently did not notice the minute, faint pale spots that are particularly numerous along the lateral line on one of the paratypes (USNM 87680). The light spots that are often found on this species vary from noticeable, small, white spots to very faint, minute, pale dots. The latter condition would only be noticed by someone familiar with the range of expression of this feature.

In their second account of *M. schmitti* (1948, p. 261), Bigelow and Schroeder mention a specimen from Rio Grande do Sul, Brazil (MCZ 35316) which was apparently received at Harvard subsequent to their 1940 paper on *Mustelus.* I examined this shark, a 58-cm male, and regard it as *M. henlei* (Gill, 1863). The rather wide inter-nostril distance (2.6% TL) and short lower labial folds (1.0% TL) are both outside the ranges for *M. schmitti,* but within those for *M. henlei.* The teeth are of the usual *M. henlei* configuration (with a rather well-developed, narrow primary cusp and often one or two accessory cusplets at the base) and unlike those of *M. schmitti.* Even more decisive for this identification is the number of monospondylic (41) and precaudal vertebrae (100) for this specimen. These counts are both well outside the ranges for *M. schmitti* (35–39 and 82–88 respectively), but well within the ranges for *M. henlei* (39–45 and 97–106). It seems more reasonable to question the provenance of this specimen, than to extend the distribution of *M. henlei* from the northern coast of Peru (its present southern limit) to southern Brazil.

Distribution (Fig. 26).—The range of *M. schmitti* extends from Florianopolis, Brazil to the Golfo San Jorge, Argentina, and the depth distribution from 60 to 195 m.

Relationships.—The phylogenetic relationships of *M. schmitti* are obscure. It appears not to be closely related to any of the other southern white-spotted species of *Mustelus* (*fasciatus, mento, palumbes, antarcticus,* or *lenticulatus*). The exposed ceratotrichia at the posterior margin of the dorsal and caudal fins is an

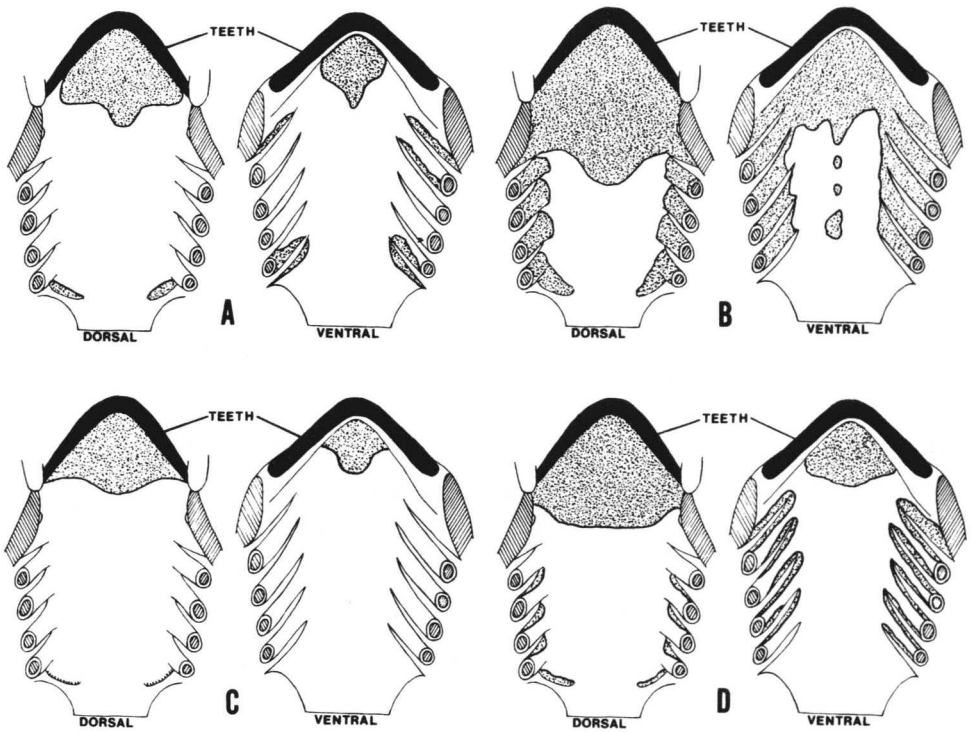

Figure 18. Buccopharyngeal denticle patterns: A) *Mustelus canis canis,* 88 cm, female; B) *M. norrisi,* 63 cm, male, UF 65267; C) *M. sinusmexicanus,* 67 cm, female, UF 230476; D) *M. minicanis,* 312 mm, female, USNM 208017.

unusual character shared (in the genus) only with the Mediterranean species *M. punctulatus* Risso, 1826 and the eastern Pacific species *M. henlei* and *M. whitneyi* Chirichigno, 1973. However, *M. schmitti* differs from these species (and all other species of *Mustelus*) in its combination of tooth morphology, narrow inter-nostril distance, lanceolate denticles, long upper lip folds, vertebral numbers, small white spots (usually discernible) on body, and lack of a placenta.

Material Examined.—45 specimens, 22–75 cm. BRAZIL (Florianopolis to Rio Grande): CAS-SU 52869, 38 cm; ISH 1017–66, 6: 30–32 cm; ZMB 21722, 3: 48–53 cm; ZMB 21725, 63 cm. URUGUAY TO LA PLATA, ARGENTINA: BMNH 1878.10.29.1–2, 60 and 71 cm; ISH 27–1950 52 and 54 cm; ISH 1081–66, 4: 33–49 cm; MCZ 529, 56 cm; 530, 60 cm; NMW 11188, 60 cm; USNM 55582, 45 cm; USNM 86724, 22 and 23 cm; USNM 87680, paratypes 60 & 60 cm; USNM 106640, holotype 74 cm; USNM 164571, 3: 43–57 cm; ZMB 4503, 56 cm. ARGENTINA (Mar del Plata to Golfo San Jorge): FRSKU S 360, 56 cm; FRSKU S 361, 70 cm; FRSKU S 362, 75 cm; FRSKU S 363, 67 cm; ISH 1466–66, 5: 35–46 cm; ISH 1643–66, 3: 58–74 cm; NMW 11187, 40 cm; ZMH 10196, 33 cm.

Mustelus sinusmexicanus new species
Figure 17

Mustelus canis (non Mitchill): Baughman and Springer, 1950: 99 (in part; pups taken from female caught 24 March 1940 off Freeport, Texas). Springer and Lowe, 1963: 249 (in part; see "Remarks" below). Dawson, 1966: 179 (reported from 20 fms. off Grand Isle, Louisiana [GCRL 288]).

?Mustelus norrisi (non Springer): Clark and von Schmidt, 1965: 47–50 (in part, see Remarks section below).

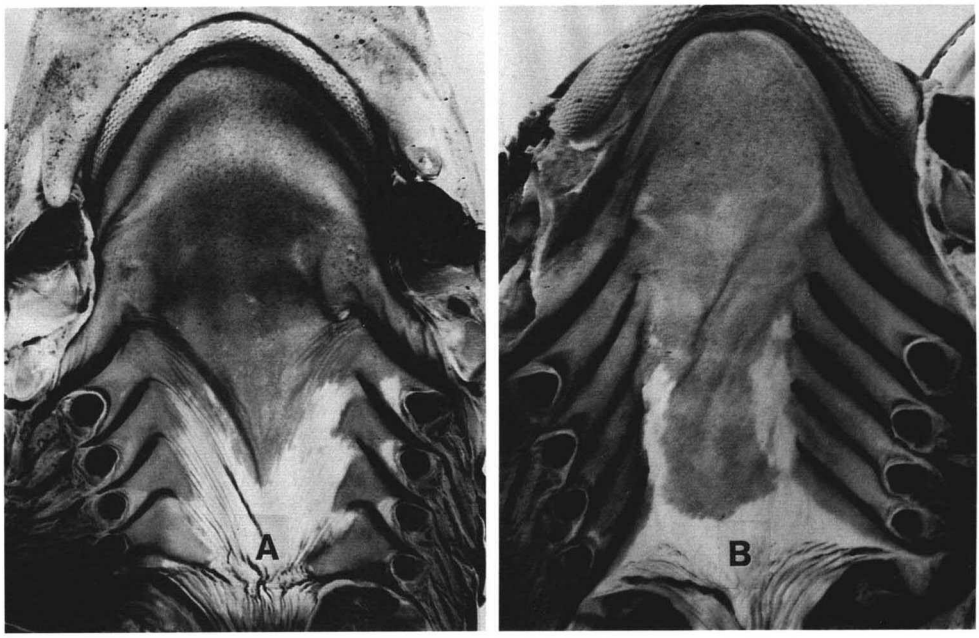

Figure 19. Buccopharyngeal denticle pattern of *Mustelus fasciatus*, 60 cm female, CAS SU 13432: A) dorsal surface, B) ventral surface.

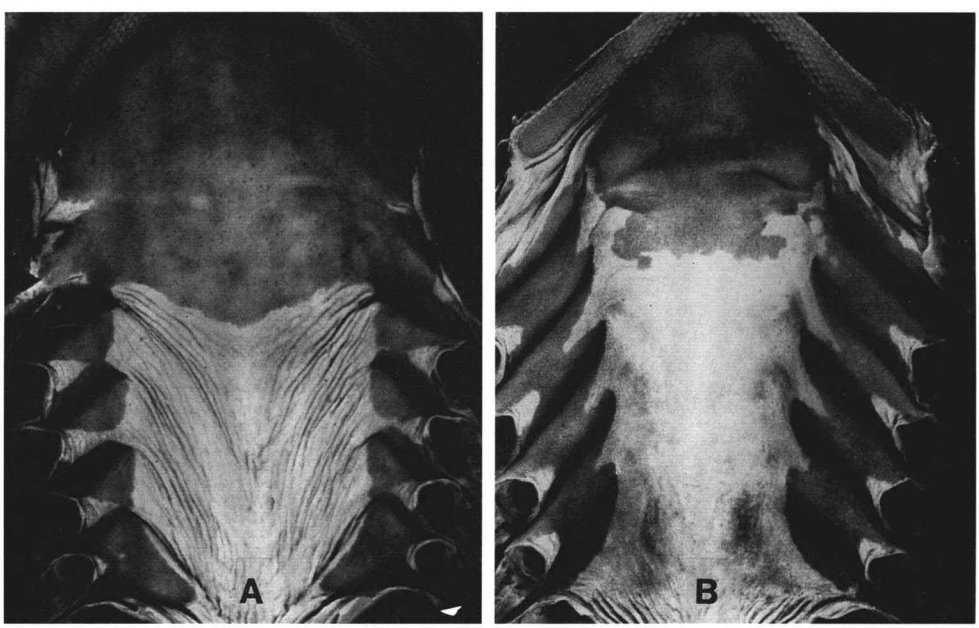

Figure 20. Buccopharyngeal denticle pattern of *Mustelus higmani*, 53 cm female, UF 233646; A) dorsal surface, B) ventral surface.

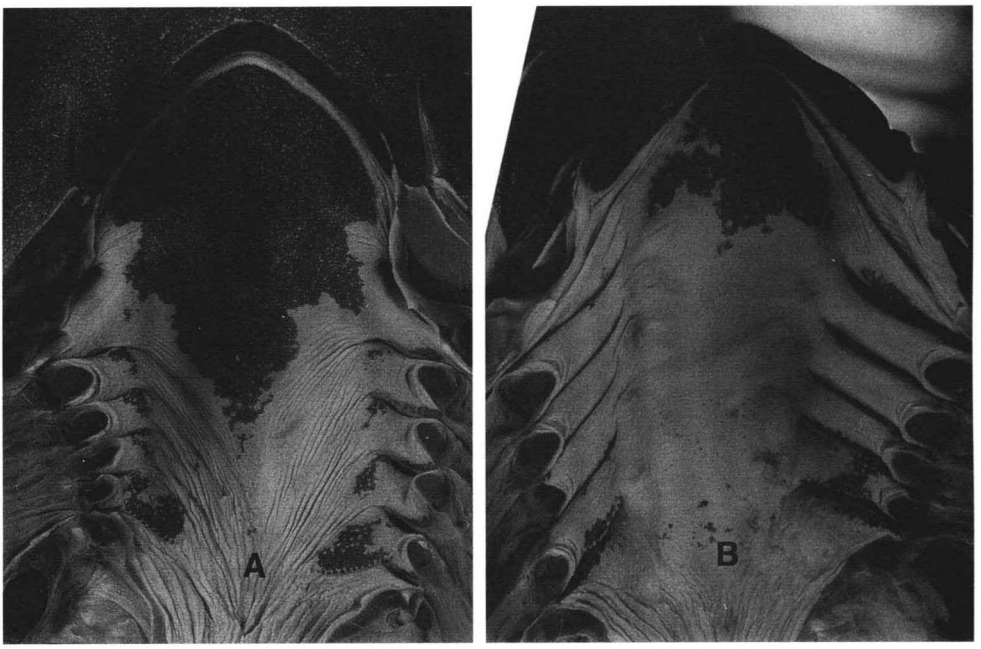

Figure 21. Buccopharyngeal denticles of *Mustelus schmitti*, 57 cm, female FRSKU S 360: A) dorsal surface, B) ventral surface.

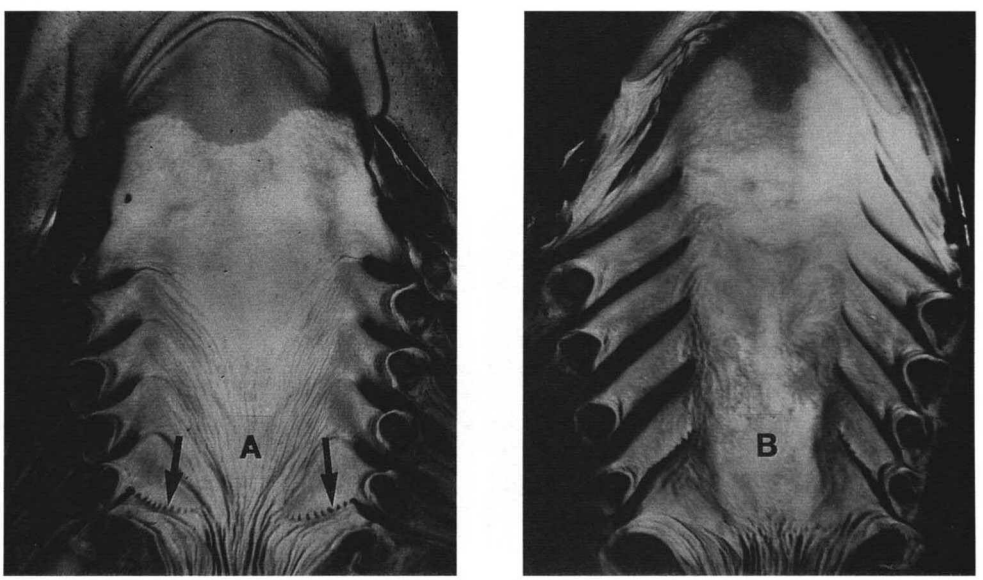

Figure 22. Buccopharyngeal denticles of *Mustelus sinusmexicanus*, 67 cm female, UF 230476: A) dorsal surface (arrows indicate posterior margin of fifth epibranchial pharyngeal pads with series of denticle-covered, shallow notches); B) ventral surface.

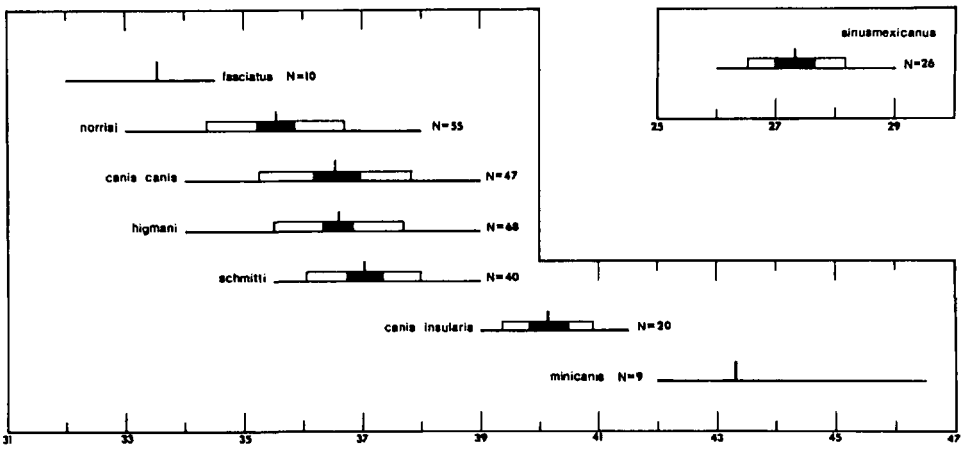

Figure 23. Monospondylic vertebral numbers of western Atlantic species of *Mustelus*. Black bars represent 3 standard errors of the mean (2 on either side of the mean); open bars represent 2 standard deviations (1 on either side of the mean).

Holotype.—USNM 208345, adult male, 83 cm, south of Dauphin Island, Alabama (29°15'N, 88°11'30"W) depth 91 m; 21 March 1967, R/V GULF RESEARCHER.

Paratypes.—NORTHERN GULF OF MEXICO: ANSP 103925, male 70 cm, same data as for holotype. BMNH 1972.10.3.2–4, 2 males 409–438 mm, female 415 mm, off Mississippi Delta. CAS 14978, female, 55 cm, off Galveston, Texas (28°28'N, 94°20'W) depth 51 m, 25 June 1957, R/V SILVER BAY; CAS-SU 38654 male (not measured) off Galveston; CAS-SU 38659, male 401 mm, Heald Bank, off Galveston, 17 March 1940; CAS-SU 38660, 2: female 427 mm, male 412 mm, 32-Mile Bank, off Freeport, Texas; 23 March 1940. FMNH 71556, 2 females 382–388 mm, off Cameron, Louisiana (28°06'N, 93°20'W), depth 82 m, 18 April 1961. GCRL 288, female 352 mm, off Grand Isle, Louisiana, 3 April 1959; GCRL 1183, female 405 mm, SE of Chandeleur Id, Louisiana, depth 42 m, 8 April 1960. MCZ 35853, 2 males 405–412 mm, off Freeport. TU 164146,

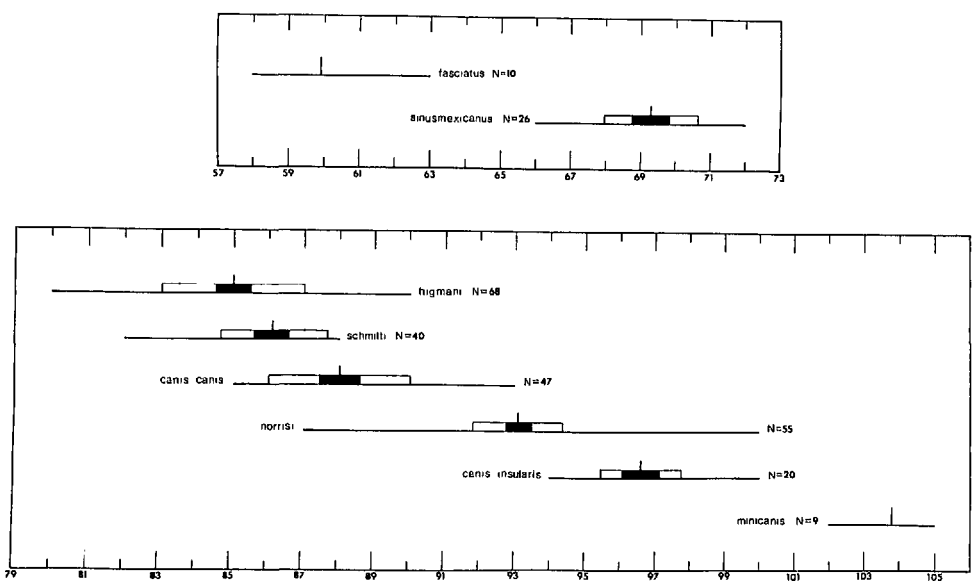

Figure 24. Precaudal vertebral numbers of western Atlantic species of *Mustelus*. Representation as in Figure 23.

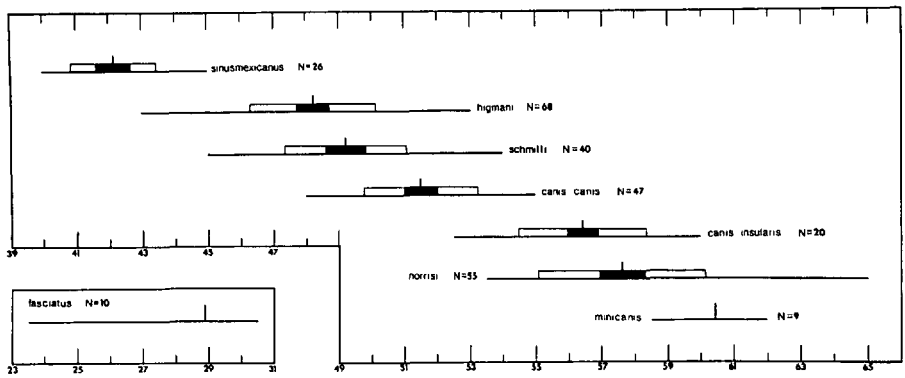

Figure 25. Diplospondylic precaudal vertebral numbers of western Atlantic species of *Mustelus*. Representation as in Figure 23.

female 140 cm, 17 mi SE of Grand Isle, Louisiana; TU 16544, female 86 cm, off Freeport, Texas (28°30'N, 94°25'W), depth 51 m, 28 June 1957, R/V SILVER BAY. UF 230476, 2: male 59 cm, female 67 cm, off Panama City, Florida (29°33'N, 86°35'W) depth 229 m, 25 January 1968, R/V OREGON II sta. 10122. USNM 116443, female 405 mm, Freeport, Texas 24 March 1940; USNM 158585, female, 58 cm, off Mississippi Delta (29°15.5'N, 88°48'W), depth 62 m, 27 Feb 1951; USNM 179120, 2 females, 48 cm and 54 cm, male 49 cm, Port Aransas, Texas. MEXICO (Campeche Bay): UF 27999, female 74 cm, (18°41'N, 93°36'W) depth 66 m, 9 June 1970; UF 46036, male 66 cm, (18°38'N, 93°44'W) depth 66 m, 8 June 1970; UF 46038, male 70 cm, (18°48'N, 95°37'W) depth 68 m, 11 June 1970.

Diagnosis.—Morphometric data are listed in Table 1. Caudal fin with prominent, narrowly-rounded ventral lobe, the lobe angle 79°–106° (11 specimens measured). Trailing edges of dorsal fins not frayed. Rear (distal) edge of pectoral and pelvic fins distinctly concave. Head moderate, pre-pectoral distance 17–23% TL; inter-orbital distance 3.9–4.6% TL; pre-oral snout length 5.4–6.3% TL; inter-nostril distance 2.6–3.3% TL; orbit diameter 2.3–3.1% TL. Upper-jaw labial folds long (1.9–2.5% TL), distinctly longer than lower-lip folds. Teeth (Fig. 17A) noticeably asymmetric, higher crowned than in most *Mustelus,* the primary cusp rounded, with a small accessory cusp on posterolateral margin of crown; tooth counts 58–69/60–62. Midlateral flank denticles (Figs. 16b, 17B) distinctly tridentate, strongly sculptured with 3–6 prominent ridges extending to rear margin of scale. Buccopharyngeal cavity (Figs. 18C, 22) almost devoid of denticles; patch of denticles at anterior end of palate not extending posterior to upper lip fold; lingual patch confined to tip of tongue; posterior margin of fifth epibranchial pharyngeal pads with evenly-spaced, denticle-covered, shallow notches (Fig. 22). Palatoquadrate a single cartilage on each side of jaw. Intestine with seven turns in spiral valve. Diagnostic vertebral numbers are given in Figures 23–25.

Head and body of adults immaculate grey or greyish-tan dorsally; juveniles usually with sooty smudges on apices of dorsal fins and sometimes on tip of caudal fin.

Remarks.—*M. sinusmexicanus* is a large species. Males are not mature until about 80 cm; and pups are born between 39 and 43 cm. The largest specimen that I examined was an adult female of approximately 140 cm (TU 164146).

Specimens of this species in the U.S. National Museum of Natural History, Museum of Comparative Zoology at Harvard and the Florida Museum of Natural History were labelled *Mustelus canis.* Unless one examines the denticles with a microscope, *M. sinusmexicanus* could easily be mistaken for *M. canis* or *M. nor-*

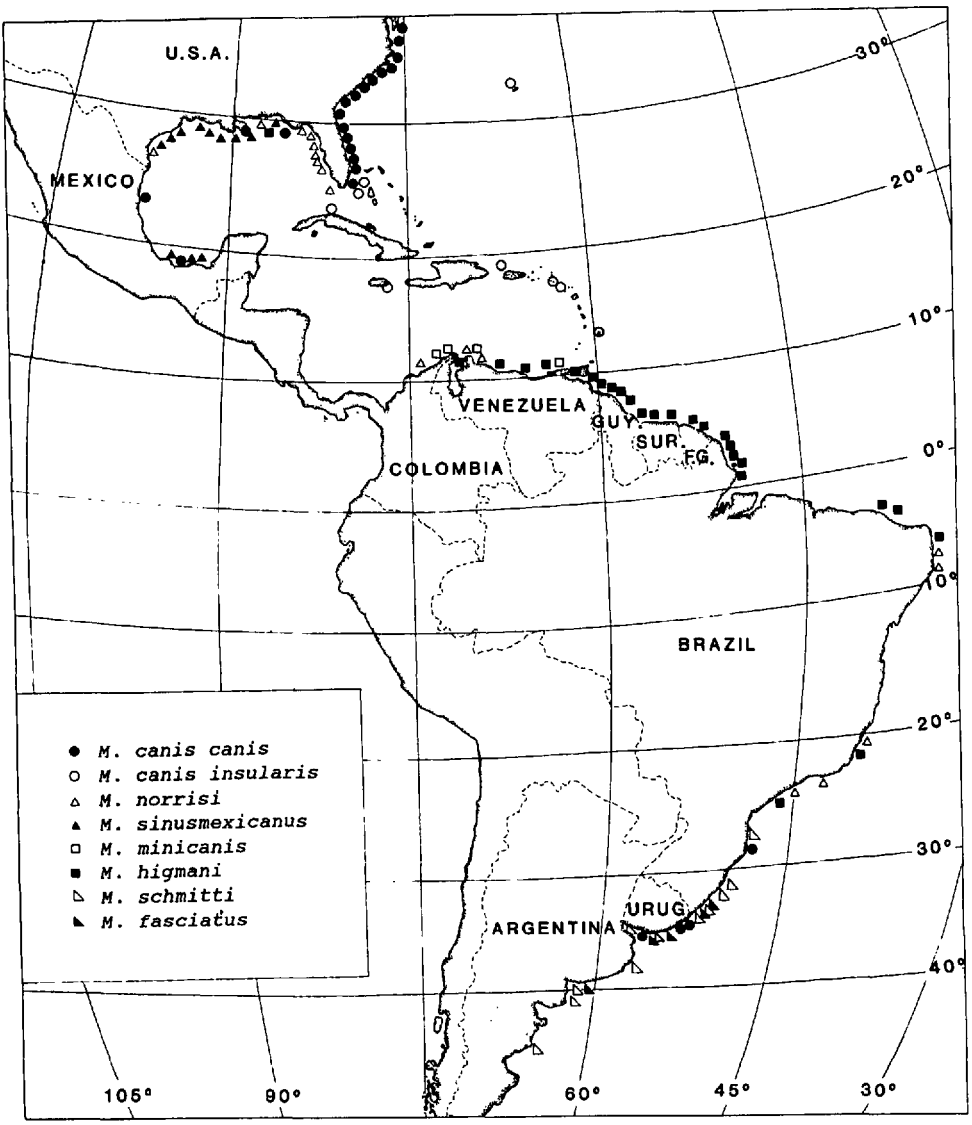

Figure 26. Distributions of western Atlantic species of *Mustelus* based on material examined. Northern distribution of *M. canis canis* (not shown on map) extends to the Bay of Fundy in Canada.

risi. Springer and Lowe (1963:249) state "It is remarkable that *M. canis* was regularly caught on set lines by commercial shark fishermen using 7-inch hooks made of ⅜ inch diameter steel whenever lines were set in areas of known abundance, as off the Carolinas or off the Mississippi Delta. The irregular localized occurrence of *M. canis* is illustrated in its distribution off the southeastern United States. It is commonly taken by snapper fishermen from offshore banks of the northern and western parts of the Gulf of Mexico but is practically unknown inshore." The reference to "*M. canis*" offshore in the Gulf of Mexico probably applies (at least in part) to *M. sinusmexicanus,* which seems to be more common than *M. canis* in this offshore habitat. Prenatal pups (CAS-SU 38660, MCZ 35853,

USNM 116443) taken from gravid females caught off Freeport Texas by J.L. Baughman in March of 1940, were reported by Baughman and Springer (1950) as *M. canis.*

If (as I believe) the specimen from the northern Gulf of Mexico identified as *M. norrisi* by Clark and von Schmidt (1965) was a specimen of *M. sinusmexicanus* (see the Remarks section of *M. norrisi,* above), then it seems likely that *M. sinusmexicanus* is another species with a placental connection between the mother and developing fetuses. Although Clark and von Schmidt (1965: 47) do not actually mention the presence of placentae in their specimen, they do give the number and size of the fetuses removed from this gravid female; and, since they considered this shark to be *M. norrisi,* they probably would have noted the absence of placentae if they were indeed lacking.

M. sinusmexicanus is sympatric with *M. norrisi* and *M. canis*; and *M. sinusmexicanus* and *M. canis* even share the same habitat, as proved by their having been caught on the same longline set in 229 m off Panama City, Florida by the Research Vessel OREGON II (Sta. 10122). *M. sinusmexicanus* seems to prefer deeper water (42–229 m) than *M. norrisi,* which (in the Gulf of Mexico) is not known from depths greater than 55 m.

Comparisons.—Superficially, *Mustelus sinusmexicanus* is similar to other species with a prominent ventral caudal fin lobe (*M. canis, M. norrisi,* and *M. higmani*). It differs from *M. canis* and *M. norrisi* in having distinctly tridentate lateral body denticles. Some *M. norrisi* have a few denticles with one or two smaller accessory cusps, and a few *M. canis* were found with numerous denticles (up to a third of midlateral flank denticles) with a short cusp on each side of the main cusp. *M. sinusmexicanus* has a shorter snout (4.8–6.3% TL) than *M. canis* (5.6–8.0% TL), and the upper lip folds are longer (1.9–2.5% TL) than in *M. norrisi.* The buccopharyngeal denticle pattern of *M. sinusmexicanus* (Fig. 22) is different from all other species of *Mustelus.* The teeth of adults of this new species are also higher (with more distinct cusps) than teeth of adults of other western Atlantic species. The low vertebral counts of *M. sinusmexicanus* are also unique (Figs. 23–25).

Distribution (Fig. 26).—*M. sinusmexicanus* appears to be endemic to the Gulf of Mexico—from off Panama City, Florida to the Bay of Campeche—in 36 to 229 m.

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