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A New Eastern North Pacific Smoothhound Shark (Genus *Mustelus*, Family Triakidae) from the Gulf of California

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A new Smoothhound shark, *Mustelus hacat*, is described from the eastern North Pacific. Four species of the genus *Mustelus* had been previously recognized in this area: *M. californicus*, *M. henlei*, *M. lunulatus*, and *M. dorsalis*. *Mustelus hacat* is described on the basis of 36 specimens caught in the Gulf of California. Among the Smoothhound sharks in the eastern North Pacific, *M. hacat* is distinguished mainly by having color uniform dark gray-brown above, white below, with conspicuously white tips and trailing edges of dorsal, pectoral, anal, and caudal fins; upper jaw teeth cuspidate and distinctly asymmetric, with low rounded cusp and prominent cusplet present in teeth of juveniles; upper jaw labial folds notably longer than lower jaw labial folds; and inter-nostril and inter-orbital space wide. Because these species have long been misidentified, we present a key to species using morphological and morphometric features found to be useful taxonomic characters to distinguish them.

En este trabajo describimos una nueva especie de tiburón Musola, *Mustelus hacat*, del Pacífico Noreste. Previamente, en esta área habían sido reconocidas cuatro especies del género *Mustelus*: *M. californicus*, *M. henlei*, *M. lunulatus*, y *M. dorsalis*. *Mustelus hacat* es descrita con base en 36 especimenes que fueron capturados en el Golfo de California. Entre los tiburones del género presentes en el Pacífico Noreste, *M. hacat* es distinguido principalmente por su patrón de coloración, el cual es café-gris oscuro uniforme arriba, blanco abajo, con puntas y bordes posteriores blancos en aletas dorsales, pectorales, anal y caudal; la forma de sus dientes, los cuales son notablemente asimétricos, con una cúspide redonda, y una cúspide accesoria prominente en los dientes de juveniles; por tener pliegues labiales superiores notablemente más largos que los pliegues labiales inferiores; y espacios inter-narial e inter-orbital amplios. Debido a que estas especies han sido mal identificadas desde hace mucho tiempo, presentamos una clave dicotómica usando características morfológicas y morfométricas que han mostrado ser caracteres taxonómicos útiles para distinguirlas.

THE Smoothhounds, genus *Mustelus*, are small to medium-sized sharks with slender bodies, large oval eyes, low or blunt teeth, and a large second dorsal fin about three-quarters the size of the first dorsal fin. Some species of *Mustelus* are of local economic importance, and others are a nuisance to fishermen (Castro, 1996). There are some 25 species in the genus, all of which are primarily benthic sharks that inhabit temperate and tropical waters over continental shelves of all oceans (Heemstra, 1997).

Members of this genus are difficult to separate from one another, particularly without the use of internal characters, because many of the morphological, morphometric, and meristic characters that distinguish species partially overlap and considerable variation occurs within species (Compagno, 1984). The key for these species provided in Compagno (1984) was based on the revision of the genus *Mustelus* of the world carried out by Heemstra (unpubl. data) and, according to Compagno (1984), should be used with extreme caution, because not every individual of a given species may fit the criteria given. Currently, the taxonomic confusion of this genus has not been adequately resolved in the Mexican Pacific, where at least four species are recognized: *M. californicus* Gill, 1864; *M. henlei* Gill, 1863; *M. lunulatus* Jordan and Gilbert, 1882; and *M. dorsalis* Gill, 1864, with three of them present in the Gulf of California.

In some areas of the Gulf of California Smoothhounds represent 79% of the catch in the artisanal elasmobranch fishery (Márquez-Farias, 2000). However, because these species have never been adequately distinguished, very little is known about their biology. Here we describe a new species and provide a key to the species of the genus *Mustelus* for the eastern North Pacific.

Materials and Methods

We took morphometric measurements to the nearest millimeter following Compagno (2002).

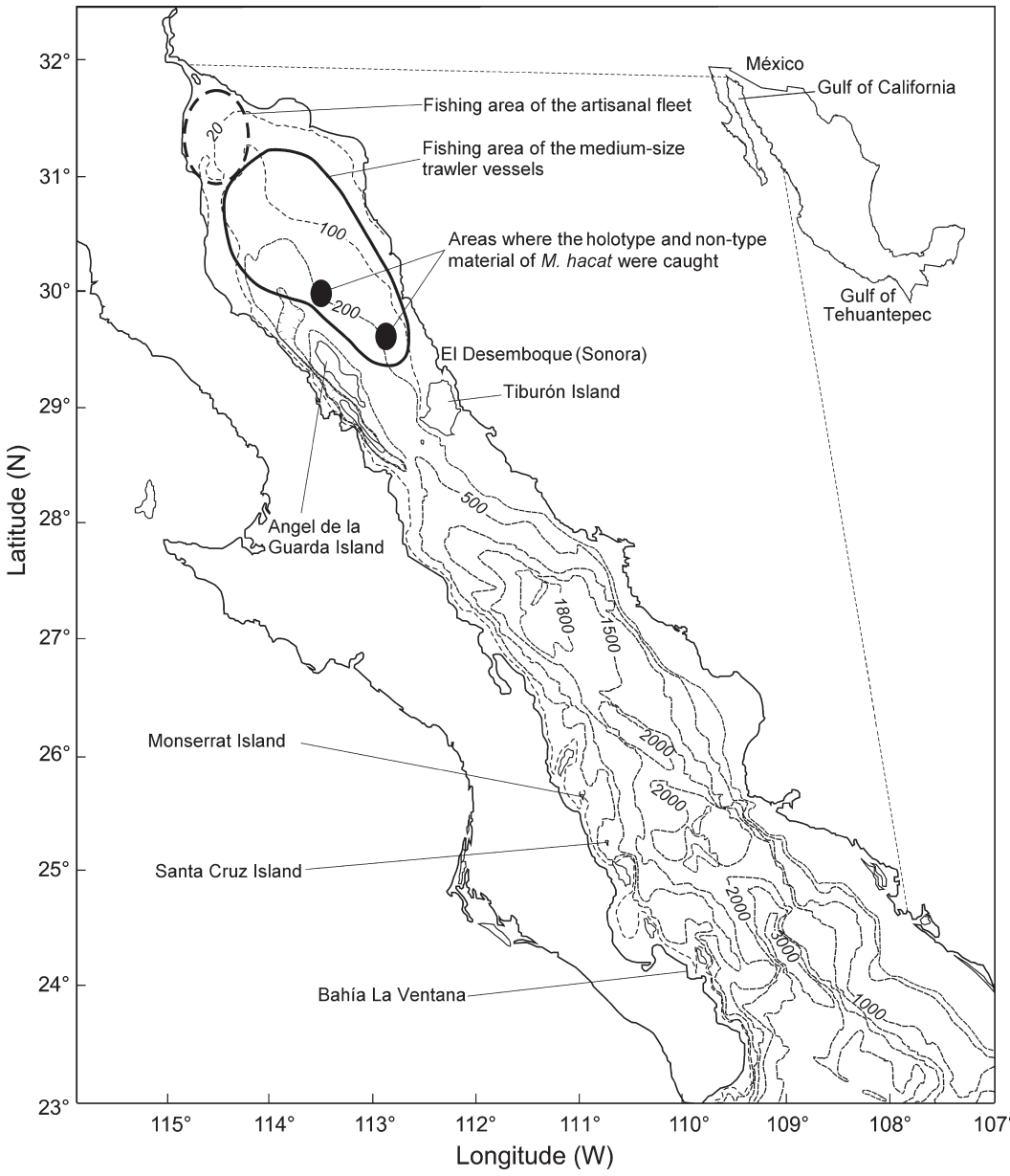

Fig. 1. Map of the Gulf of California showing fishing areas of the artisanal small boats and medium-size trawler vessels and the areas where the specimens of *M. hacat* were caught. Isobaths are in meters. (Map modified from Lavin et al., 1997.)

We analyzed specimens of the four previously described species of *Mustelus* from the eastern North Pacific to provide comparisons for the new species. Most specimens (except those of *M. dorsalis*) were sampled from the artisanal (small-boat) fishery and aboard two medium-size trawler vessels in the northern Gulf of California. The small boats using bottom gill-nets operated at depths from 6 to 55 m, whereas the trawlers were operating from 30 to 281 m (Fig. 1). We collected complete specimens when possible. In some cases, when we previously measured the total length in the field, we only obtained the shark heads (including pectoral fins) for later measurements and analysis in the laboratory of useful characters for identification that are present in jaws (tooth morphology and palato-quadrates subdivision). All specimens were ana-

lyzed in the field or laboratory to quantify reproductive parameters. In addition, five specimens of the new species were analyzed from the Marine Vertebrate Collection of the Scripps Institution of Oceanography (MVCSIO), where they were catalogued as *Mustelus* sp. Also, the thirteen specimens of *M. dorsalis* were analyzed from MVCSIO (three: SIO 63-517) and the Fish Collection of Los Angeles County Museum (eight: LACM 7010; two: LACM W58-278). The number of specimens and morphometric measurements (as % of TL) of the new species and the other four species of *Mustelus* from the eastern North Pacific are presented in Table 1. The number of tooth rows (except for *M. dorsalis*) and pre-caudal vertebrae were also recorded following Compagno (1988) and Springer and Garrick (1964), respectively. Because of the undefined pattern of tooth rows in the lower jaw of *M. californicus* and in both jaws for specimens smaller than about 70 cm TL of *M. henlei*, we could not count them. In all species, except in the new species, *M. hacat*, the tooth shape of upper and lower jaws is identical. Therefore, comparison of tooth morphology was based on the upper jaws. The number of pre-caudal vertebrae of the holotype (SIO 04-187, 113 cm TL) and one paratype (SIO 65-344-5A, 91 cm TL) of the new species, *M. hacat*, as well as for three specimens of *M. dorsalis* (SIO 63-517, 19–27 cm TL) were obtained by using x-rays.

According to Heemstra (1997), buccopharyngeal denticle patterns exhibit little intraspecific variation and are diagnostic for most species of *Mustelus*. However, because our observations of these denticle patterns for some specimens of *M. californicus* exhibited intraspecific variation, we did not consider this character as adequate to distinguish the species of *Mustelus* in the eastern North Pacific. On the other hand, dermal denticles were examined at a point midway between the origins of the first dorsal and pectoral fins following the methods of Heemstra (1997).

Mustelus hacat, new species
Figure 2

Holotype.—SIO 04-187, adult female, 113 cm TL, northeast of Angel de la Guarda Island, Gulf of California, 29°58.5′N, 113°37.8′W, trawler net, J. L. Castillo-Geniz, 10 March 2004.

Paratypes.—SIO 65-344-5A, three females, 80–91 cm TL, west side of Santa Cruz Island, southern Gulf of California, 25°15.5′N, 110°44.3′W, July 1965; SIO 65-247-5A, one female, 85 cm TL, Bahia La Ventana, southern Gulf of California, 24°04.9′N, 109°54.8′W; SIO 65–292–5, one female, 30 cm TL, west side of Monserrat Island, southern Gulf of California, 25°39.1′N, 111°04.8′W.

Non-type material.—Eleven females, 75–118 (mean 99) cm TL, 19 males 72–109 (mean 97) cm TL, caught by the trawler fishing vessel ESCAMA VI at north and east of Angel de la Guarda Island, Gulf of California, March of 2003 and 2004 at depths ranging from 204 to 281 m.

Diagnosis.—*Mustelus hacat* is the only member of the genus *Mustelus* with color uniform dark gray-brown above and conspicuously white tips and trailing edges of dorsal, pectoral, anal, and caudal fins. Although some specimens of *M. lunulatus* and newborn pups and juveniles of *M. canis* from the western Atlantic have tips and trailing edges of first dorsal, pectoral, anal, and caudal fins transparent or pale white, they clearly differ from *M. hacat* in having less contrasted dorsal color compared with tips and trailing edges of fins. This new species is distinguished from the other eastern North Pacific species of *Mustelus* in having 1) upper jaw teeth cuspidate and distinctly asymmetric, with low rounded cusp (teeth of *M. californicus* and *M. lunulatus* are from molariform to cuspidate and slightly asymmetric, with blunt to low rounded cusp, whereas *M. henlei* and *M. dorsalis* have teeth cuspidate and slightly asymmetric, with high sharp cusp); 2) upper jaw labial folds notably longer than lower jaw labial folds, only similar to *M. henlei* (*Mustelus californicus* has upper and lower jaw labial folds about equal in length, *M. lunulatus* has upper jaw labial folds notably shorter than lower jaw labial folds, and *M. dorsalis* has upper jaw labial folds slightly longer than lower jaw labial folds); 3) posterior margin of first dorsal fin vertical from apex, only similar to *M. lunulatus* (*Mustelus californicus*, *M. henlei*, and *M. dorsalis* have the first dorsal fin with sloping posterior margin); 4) inter-nostril space wide (49–58 vs. 33–49% pre-oral length for all other four species); and 5) inter-orbital space wide (5.6–6.8 vs. 4.3–5.6% TL for *M. californicus*, *M. henlei*, and *M. lunulatus*), similar to *M. dorsalis* (5.7–7.5% TL).

Description (holotype and paratypes).—*Mustelus hacat* is a slender medium-sized shark having the characteristics of the genus *Mustelus* as given in Compagno (1984) and Castro (1996). Snout relatively short (5.6–7.5% TL); inter-orbital space wide (5.6–6.8% TL); eyes oval and large (2.6–3.4% TL); spiracles small (0.4–0.8% TL); nostrils without barbell and narrow (1.1–2.1% TL), anterior nasal flaps elongated; mouth short

TABLE 1. MORPHOMETRIC DATA FROM SPECIES OF *Mustelus*. Ranges of measurements in % total length. *Non-type material.

Measurements	*M. hacat*	*M. hacat*	*M. hacat*	*M. californicus*	*M. henlei*	*M. lunulatus*	*M. dorsalis*
N =	Holotype	5 Paratypes	30*	96*	126*	83*	13*
Size range (cm)	113	30–91	72–118	42–95	36–90	28–162	19–45
Head length	21	20–25	20–21	18–21	20–24	19–22	23–25
Pre-branchial length	16	15–20	15–17	14–16	16–19	14–18	17–19
Pre-spiracular length	9.8	9.5–14	10–12	9.4–11	10–13	9.6–12	10–13
Pre-orbital length	6.4	6.0–8.1	6.9–7.7	6.7–7.8	7.1–8.8	6.9–8.2	7.2–10
Pre-pectoral length	21	19–24	18–22	17–20	19–23	19–21	20–23
Pre-nostril length	4.7	4.1–5.2	4.6–5.2	3.9–4.9	4.6–6.0	4.0–5.1	3.7–5.7
Pre-oral length	5.8	5.6–7.5	5.8–6.7	5.2–6.4	5.5–7.7	5.3–6.5	6.6–8.3
Eye length	2.6	2.9–3.4	2.4–3.0	2.0–3.1	2.4–3.6	1.8–2.7	2.2–3.0
Inter-gill length	5.1	3.9–5.6	4.1–4.8	3.4–5.3	3.6–5.4	4.1–5.8	4.5–5.5
First gill slit height	2.3	2.1–2.9	2.3–2.5	1.9–2.6	1.7–2.6	2.2–2.8	1.9–2.5
Fifth gill slit height	1.9	1.7–2.1	2.0–2.1	1.7–2.2	2.1–2.6	1.6–2.0	1.6–1.9
Pectoral anterior margin	17	13–15	13–15	12–14	12–14	13–15	13–14
Pectoral inner margin	6.8	5.6–7.3	5.5–7.1	6.3–7.2	6.7–8.2	5.8–7.6	6.7–7.7
Pectoral posterior margin	13	9.5–12	10–12	8.3–11	8.0–11	9.4–12	7.6–10
Mouth length	2.8	2.6–3.4	2.4–3.0	2.3–2.7	2.5–3.4	2.8–3.2	3.1–3.7
Mouth width	5.8	5.6–6.1	5.0–5.9	4.4–6.2	5.4–7.4	5.1–6.1	5.3–7.0
Upper labial fold length	1.8	1.4–2.0	1.6–2.1	1.2–1.6	1.6–2.1	0.8–1.1	1.3–1.9
Lower labial fold length	1.3	1.2–1.5	1.1–1.5	1.1–1.6	0.9–1.4	1.2–1.5	1.1–1.6
Inter-nostril space	3.2	3.1–4.2	2.9–3.2	2.1–2.6	2.5–3.3	2.2–2.8	2.4–3.1
Nostril width	1.3	1.1–2.1	1.1–1.6	1.3–2.0	1.5–2.3	1.3–2.0	2.2–2.7
Spiracle length	0.6	0.4–0.8	0.4–0.7	0.3–0.8	0.4–0.8	0.3–0.8	1.0–1.2
Inter-orbital space	5.8	5.6–6.8	5.2–6.5	4.3–5.4	4.8–5.6	4.9–5.6	5.7–7.5
Head height	9.6	8.1–8.8	8.1–8.6	6.6–8.2	6.8–8.9	7.5–9.3	7.2–9.9
Trunk height	11	9.4–11	10–12	8.5–11	9.2–11	10–12	9.3–12
Abdomen height	10	8.0–10	11	8.3–10	8.9–12	10–12	8.4–10
Tail height	6.6	5.0–6.7	6.1–6.2	5.1–7.0	5.3–7.5	6.0–7.7	6.4–7.5
Pre-caudal length	81	79–82	80–81	80–82	80–84	79–82	79–82
Pre-first dorsal length	29	28–32	28–29	28–30	27–32	27–30	31–33
Pre-second dorsal length	63	60–63	62	59–63	61–66	59–64	61–63

TABLE 1. CONTINUED.

Measurements	*M. hacat*	*M. hacat*	*M. hacat*	*M. californicus*	*M. henlei*	*M. lunulatus*	*M. dorsalis*
Pre-pelvic length	48	43–47	44–46	41–46	44–48	42–47	44–48
Pre-anal length	66	65–66	65–66	64–68	64–69	64–68	66–67
Inter-dorsal space	23	20–24	23	20–24	21–26	21–24	17–22
1st dorsal midbase-pelvic origin	13	9.5–12	10–11	8.0–10	9.1–13	9.2–13	8.8–11
1st dorsal midbase-pectoral insertion	12	8.3–12	11	12–15	10–13	11–12	8.8–13
Dorsal-caudal space	10	10–11	9.1–10	9.5–11	9.6–12	9.5–11	9.3–10
Pectoral-pelvic space	24	18–24	21–23	21–25	20–25	21–24	18–22
Pelvic-anal space	15	15–17	15–17	16–19	15–18	14–18	13–18
Anal-caudal space	8.2	7.5–8.3	7.1–7.6	6.5–7.8	7.2–8.8	6.5–8.0	6.1–7.0
Pelvic-caudal space	28	29–30	28–30	28–33	28–32	27–31	26–30
Dorsal caudal margin	19	20–21	20	18–21	17–20	18–21	19–21
Lower postventral caudal fin margin	2.5	1.5–2.7	1.8–2.4	1.1–1.6	1.2–1.6	1.3–2.3	1.0–1.6
First dorsal base	11	11	11	10–12	11–12	11–13	12–13
First dorsal height	9.0	9.0–10	9.1–9.9	8.0–9.4	7.8–9.7	9.3–11	7.4–9.4
First dorsal inner margin	4.2	4.4–4.7	4.3–4.6	3.5–4.2	3.5–4.3	3.3–4.3	3.2–4.5
Second dorsal base	8.5	7.6–8.8	8.2	8.4–9.7	8.0–9.5	8.0–9.6	8.3–10
Second dorsal height	6.1	5.9–6.4	6.2–6.3	5.8–7.1	5.2–6.8	5.8–7.0	5.8–7.2
Second dorsal inner margin	2.9	2.9–3.2	2.7–2.9	2.6–3.1	2.3–2.9	2.5–3.1	2.7–3.6
Pelvic anterior margin	8.1	7.0–8.3	8.3–8.6	7.4–9.0	6.7–8.1	8.1–9.7	6.9–8.8
Pelvic inner margin	5.3	4.4–5.0	4.6–5.0	4.3–5.8	3.9–5.8	4.1–5.0	4.7–5.8
Pelvic posterior margin	6.5	5.5–6.9	6.0–6.4	5.3–6.6	5.3–6.4	5.2–7.2	4.7–5.6
Anal base	5.8	5.4–5.7	5.6–5.7	4.9–6.1	5.4–6.2	5.6–6.6	6.1–7.3
Anal height	3.8	2.5–3.5	3.2–3.3	2.7–3.4	2.6–3.3	3.1–3.7	2.6–3.7
Anal inner margin	2.5	2.5–2.9	2.5	2.2–2.6	2.1–2.7	2.0–2.5	2.5–3.0
Mouth length as % pre-oral length	48	40–49	39–48	34–51	37–53	46–59	41–51

TABLE 1. CONTINUED.

Measurements	*M. hacat*	*M. hacat*	*M. hacat*	*M. californicus*	*M. henlei*	*M. lunulatus*	*M. dorsalis*
Inter-nostril space as % pre-oral length	55	49–58	45–55	34–40	41–49	36–44	33–40
Nostril width as % inter-nostril space	41	34–51	38–50	63–77	51–72	53–74	84–95
Upper jaw tooth rows	—	—	62–72	68–76	72–76	73–88	—
Lower jaw tooth rows	—	—	62–68	—	71–75	70–87	—
Pre-caudal centra	102	102	101	96–100	103–107	79–84	99–100

(40–49% pre-oral length); inter-nostril space wide (49–58% pre-oral length); jaw labial folds long, uppers (1.4–2.0% TL) notably longer than lowers (1.2–1.5% TL; Fig. 2B). Teeth different among upper and lower jaws and not bladelike. Upper jaw teeth cuspidate and distinctly asymmetric, with low rounded cusp (Fig. 2C). Lower jaw teeth molariform and asymmetric, with blunt cusp (Fig. 2D). Teeth of 30 cm TL neonate (SIO 65-292-5) with prominent accessory cusplet (Fig. 2E). Accessory cusplet rudimentary or absent in adults. Tooth rows in upper and lower jaws 62–72 and 62–68, respectively (non-type material). Palatoquadrates not subdivided near the symphysis. Denticles lanceolate with 2–4 (usually two) ridges extending almost three-quarters the length of scales (Fig. 2F).

Pectoral fins distinctly pointed (anterior margin 13–17% TL), moderately pointed in the 30 cm TL specimen (SIO 65-292-5). First dorsal

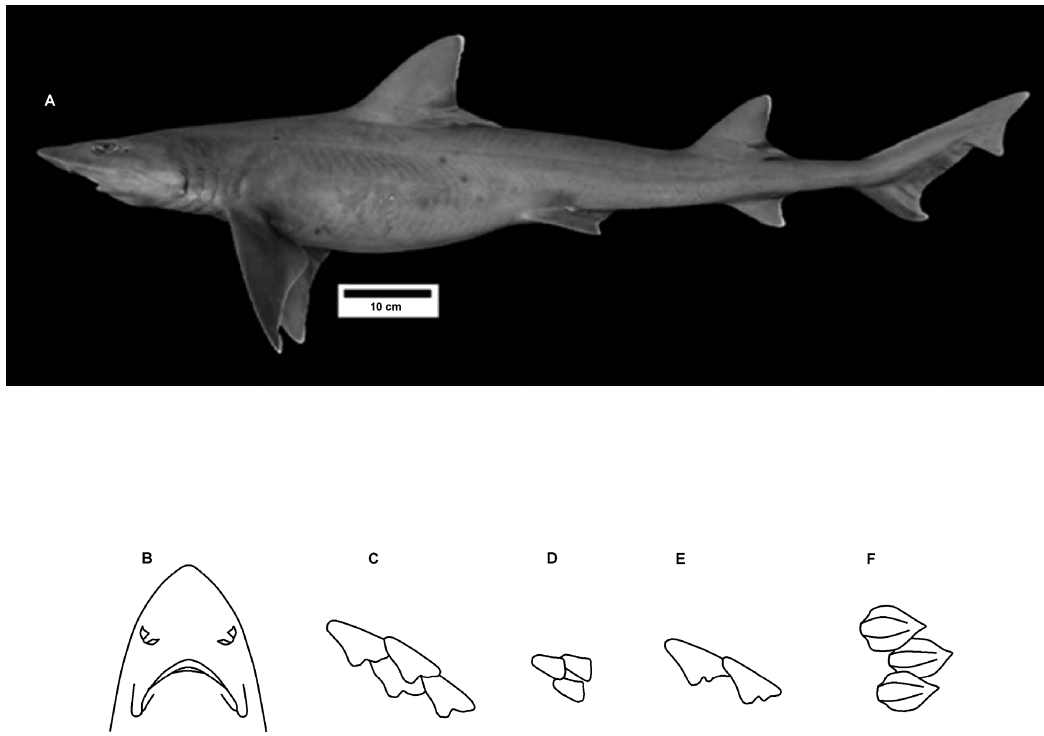

Fig. 2. Holotype of *Mustelus hacat*, SIO 04-187, female, 113 cm TL. (A) Holotype, (B) ventral view of head, (C) upper teeth, (D) lower teeth, (E) upper teeth of a 30 cm TL neonate, paratype SIO 65-292-5, and (F) denticles.

fin with anterior margin from semifalcate to falcate and posterior margin vertical from apex. First dorsal fin moderately high (9.0–10% TL); origin slightly behind free rear tips of pectoral fins. In the 30 cm TL specimen (SIO 65-292-5), first dorsal-fin origin clearly over free rear tips of pectoral fins. Mid-base of first dorsal fin about equidistant between pelvic origin and pectoral insertion: first dorsal midpoint–pelvic origin 9.5–13% TL; first dorsal midpoint–pectoral insertion 8.3–12% TL. Free rear tip of first dorsal fin does not extend over pelvic fins origins, however, in the 30 cm TL specimen it does. Second dorsal-fin height (5.9–6.4% TL) about two-thirds of first dorsal-fin height. Anal-fin height (2.5–3.8% TL) about one-half of second dorsal-fin height. Interdorsal space long (20–24% TL); mid-dorsal ridge between dorsal fins present. Ventral caudal-fin lobe well developed, even prominent (2.5–2.7% TL); poorly developed in the 30 cm TL specimen (1.5% TL). Caudal peduncle has no pre-caudal pits or lateral keels. Trailing edges of dorsal and caudal fins not frayed. Color uniform dark gray-brown above, white below, with conspicuously white tips and trailing edges of dorsal, pectoral, anal, and caudal fins. Preserved specimens (paratypes) have color uniform brownish above, yellowish below, without white tips and trailing edges of fins. Pre-caudal vertebrae 101–102 (n = 4, holotype SIO 04-187, one paratype SIO 65-344-5A, and two specimens of the non-type material).

Remarks.—The mode of reproduction of *M. hacat* is placental viviparity, having a brood size of 3 to 23 (mean 16). The size of embryos analyzed (only March) was 25–34 cm TL (mean 29 cm). Young are born probably between 30–35 cm TL. Females mature between 94–98 cm and males between 90–99 cm TL.

Distribution.—Although medium-size trawler vessels were fishing in a wide area of the northern Gulf of California, including depths from 30 to 281 m, the holotype and specimens of the non-type material of *M. hacat* analyzed from that region were caught only at east and north of Angel de la Guarda Island, at depths greater than 200 m. The five paratypes were collected from the southern Gulf of California at the west side of Santa Cruz and Monserrat Islands and in Bahia La Ventana, at depths that probably exceeded at least 100 m (Fig. 1).

Etymology.—The word *hacat* means shark in the dialect of the Seri Indians from Tiburón Island and ''El Desemboque,'' Sonora, Mexico. The Seri Indians have fished sharks since several decades ago, and they distinguish among several shark species the Smoothhounds, which were named *hacat imitáast* by them.

Discussion

The existence of this new species of *Mustelus* has been suspected since the 1960s, because according to Compagno (1984), Kato et al. (unpubl. data) called attention to the existence of at least two unidentified Smoothhound species with characters similar to *M. lunulatus* in the eastern Pacific. Heemstra (unpubl. data) studied the matter and indicated that these were undescribed tropical species (which we called here ''species a'' and ''species b'') distributed from the Gulf of California south to Ecuador and the Galapagos Islands, however, he did not publish descriptions of these unnamed species. *Mustelus hacat* and ''species a'' are clearly the same species. The specimens that we designated as paratypes of *M. hacat* are part of the material that Heemstra (unpubl. data) used to conclude that they belong to an undescribed species (''species a'').

Mustelus hacat and ''species a'' have the same color. *Mustelus hacat* has dark gray-brown color, and, according to Heemstra (unpubl. data), the color in ''species a'' is immaculate gray, grayish-tan, or brown dorsally. In addition, these species are similar in most of their morphometric features; specifically, they have upper jaw labial folds notably longer than lowers, inter-nostril space wide, and about equal number of pre-caudal vertebrae (101–102 in *M. hacat* vs. 96–101 in ''species a''). On the other hand, *Mustelus hacat* differs from ''species b'' in having upper jaw labial folds notably longer than lower jaw labial folds. In ''species b'' upper jaw labial folds are shorter than lowers. Also, *Mustelus hacat* has wider inter-nostril space (3.1–4.2% TL vs. 2.1–3.0% TL in ''species b'') and more pre-caudal vertebrae (101–102 vs. 83–93 in ''species b'') than ''species b.'' This undescribed species of *Mustelus* (''species b'') in most morphometric features partially or totally overlaps with *M. lunulatus*. According to Heemstra (unpubl. data) the number of pre-caudal vertebrae is the unique useful character to distinguish among these species (74–82 *M. lunulatus* vs. 83–93 in ''species b''). We do not have any evidence for the presence of ''species b'' in the northern Gulf of California.

Comparisons.—*Mustelus hacat* differs from the other four eastern North Pacific species of *Mustelus* in having color uniform dark gray-brown, with conspicuously white tips and trailing edges of dorsal, pectoral, anal, and caudal fins. The color of *M. californicus*, *M. lunulatus*, and *M.*

dorsalis is uniform brown or gray brown, and the color of *M. henlei* is uniform dark brown, however, some specimens of this species caught in shallow water are less dark than those from deep water. Fins of these four species of *Mustelus* have tips and trailing edges not white. Although some specimens of *M. lunulatus* have tips and trailing edges of first dorsal, pectoral, anal, and caudal fins transparent or pale white, they clearly differ from *M. hacat* in having less contrasted dorsal color compared with tips and trailing edges of fins. *Mustelus hacat*, *M. henlei*, *M. lunulatus*, and *M. dorsalis* differ from *M. californicus* in having palatoquadrates not subdivided near the symphysis. The upper jaw cartilages comprising four separate palatoquadrate elements (palatoquadrates subdivided) in *M. californicus*, whereas only two elements in the other four species. *Mustelus hacat* has smaller number of tooth rows than *M. lunulatus* and *M. henlei*. In *M. lunulatus* considerable variation with size was observed (the larger specimens have highest number of tooth rows). Upper jaw teeth of the new species, *M. hacat*, are cuspidate and distinctly asymmetric, with low rounded cusp. Teeth of *M. californicus* and *M. lunulatus* are from molariform to cuspidate and slightly asymmetric, with blunt to low rounded cusp, whereas *M. henlei* and *M. dorsalis* have teeth cuspidate and slightly asymmetric, with high sharp cusp and accessory lateral cusplet on each side of primary cusp base of most teeth in juveniles.

In addition, *M. hacat* differs from *M. californicus*, *M. lunulatus*, and *M. dorsalis* in having upper jaw labial folds notably longer than lower jaw labial folds ($t = 8.23$, $df = 70$, $P < 0.001$; Fig. 3A). In this character *M. hacat* is similar to *M. henlei* (Fig. 3C). *Mustelus californicus* has upper and lower jaw labial folds about equal in length ($t = 2.07$, $df = 190$, $P = 0.04$; Fig. 3B), *M. lunulatus* has upper jaw labial folds notably shorter than lower jaw labial folds ($t = -7.05$, $df = 164$, $P < 0.001$; Fig. 3D), and *M. dorsalis* has upper jaw labial folds slightly longer than lower jaw labial folds ($t = 2.91$, $df = 24$, $P < 0.01$; Fig. 3E). The new species, *M. hacat*, has inter-nostril space wider than the other four species (49–58 vs. 33–49% pre-oral length) and inter-orbital space wider than *M. californicus*, *M. henlei*, and *M. lunulatus* (5.6–6.8% TL vs. 4.3–5.6% TL), only similar to *M. dorsalis* (5.7–7.5% TL). *Mustelus hacat* has mouth short (39–49% pre-oral length) similar to *M. californicus*, *M. henlei*, and *M. dorsalis* (34–53% pre-oral length), differing only from *M. lunulatus*, which has mouth relatively long (46–59% pre-oral length). This new species of *Mustelus* has nostrils narrower than the other species (34–51% inter-nostril space). *Mustelus*

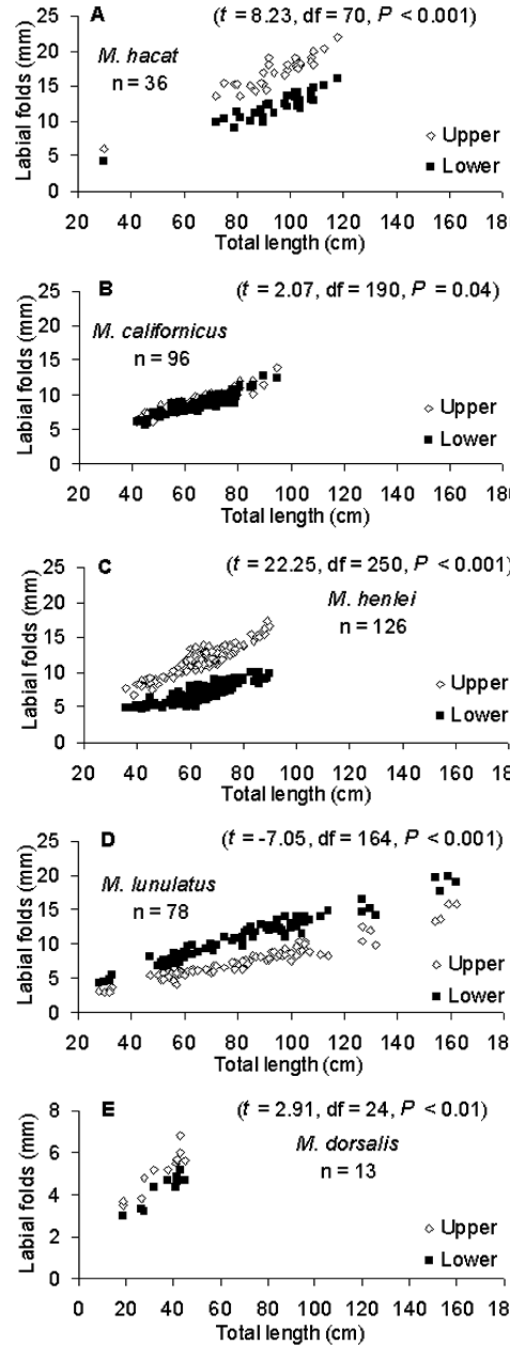

Fig. 3. The relation between total length versus upper and lower labial folds in (A) *M. hacat*, (B) *M. californicus*, (C) *M. henlei*, (D) *M. lunulatus*, and (E) *M. dorsalis*. The X and Y axes of the graphic of *M. dorsalis* have smaller scale than the X and Y axes of graphics of other species.

TABLE 2. PAIRWISE PERCENT SEQUENCE DIVERGENCE BETWEEN SMOOTHHOUND SHARKS FROM THE GULF OF CALIFORNIA. Values are mean ± SD.

	M. hacat	*M. californicus*	*M. henlei*	*M. lunulatus*
M. hacat	—			
M. californicus	3.01 (0.0)	—		
M. henlei	2.34 (0.18)	2.87 (0.18)	—	
M. lunulatus	5.60 (0.09)	3.95 (0.09)	5.32 (0.19)	—

californicus, *M. henlei*, and *M. lunulatus* have moderately sized nostrils (51–77% inter-nostril space), whereas *M. dorsalis* has nostrils wide, being almost the size of the inter-nostril space (84–95%). *Mustelus hacat*, *M. californicus*, *M. henlei*, and *M. lunulatus* differ from *M. dorsalis* in having spiracles short (0.3–0.8% vs. 1.0–1.2% TL).

Also, *M. hacat* has the posterior margin of first dorsal fin vertical from apex similar to *M. lunulatus*, whereas *M. californicus*, *M. henlei*, and *M. dorsalis* have the first dorsal fin with sloping posterior margin, being distinctly sloped in *M. dorsalis*. *Mustelus hacat* is similar to *M. californicus*, *M. lunulatus*, and *M. dorsalis* because it has trailing edges of dorsal and caudal fins not frayed, differing from *M. henlei*, which has trailing edges of those fins frayed, visible as a conspicuous dark band. The new species, *M. hacat*, as well as *M. lunulatus*, *M. henlei*, and adults of *M. dorsalis* differ from *M. californicus* in having the mid-base of first dorsal fin about equidistant between pelvic origin and pectoral insertion. *Mustelus californicus* has the mid-base of first dorsal fin closer to pelvic origin than to pectoral insertion, similar to specimens less than about 25 cm of *M. dorsalis*. *Mustelus hacat* differs from *M. californicus*, *M. henlei*, and *M. dorsalis* in having pectoral anterior margin long (13–17 vs. 12–14% TL for all other three species), similar to *M. lunulatus* (13–15% TL). Pectoral fins of the new species are distinctly pointed similar to *M. lunulatus*, whereas *M. californicus* has those fins moderately pointed, and *M. henlei* and *M. dorsalis* have them almost rounded. *Mustelus hacat* has denticles lanceolate similar to *M. californicus*, *M. lunulatus*, and *M. dorsalis*, differing only from *M. henlei* which has mostly denticles tricuspidate. *Mustelus hacat* has a similar number of pre-caudal vertebrae as *M. californicus* and *M. dorsalis* (101–102 vs. 96–100) and clearly differs from *M. lunulatus*, which has a smaller number of pre-caudal vertebrae (79–84), and from *M. henlei* which has the highest number of pre-caudal vertebrae (103–107) in the eastern North Pacific among the species of *Mustelus*.

In the Gulf of California, the species that are most similar to each other are *M. californicus* and *M. lunulatus*. They are identical in color and in most of their morphometric features. The jaw labial folds are very useful characters to distinguish them from one another; in *M. californicus* the upper and lower folds are about equal in length, whereas in *M. lunulatus* upper folds are notably shorter than lower folds (Fig. 3B, D). In addition, *M. californicus* has a shorter mouth (2.3–2.7 vs. 2.8–3.2% TL), smaller first dorsal fin (8.0–9.4 vs. 9.3–11% TL), and more pre-caudal vertebrae (96–100 vs. 76–84) than *M. lunulatus*. The first dorsal fin of *M. californicus* has a sloping posterior margin, whereas in *M. lunulatus* the posterior margin is vertical from apex in most specimens. Teeth of *M. californicus* are very similar to those of adults of *M. lunulatus*, being molariform and slightly asymmetric with blunt cusp. However, specimens of *M. lunulatus* smaller than about 105 cm have teeth cuspidate with low rounded cusp.

In addition to the phenotypic distinction discussed above, molecular genetic analysis detailed elsewhere (Pérez-Jiménez et al., unpubl. data) clearly indicate that each species from the Gulf of California (*M. hacat, M. californicus, M. henlei*, and *M. lunulatus*) represents an independent genetic evolutionary lineage. For instance, molecular divergences computed from 620 base pairs, spanning the 3′ end of the cytochrome b gene intervening threonine and proline tRNA genes and the 5′ hypervariable segment of the mitochondrial control region, reveal fixed differences accounting for an order of magnitude increase of inter- versus intra-specific variation (Table 2).

The length of jaw labial folds has shown to be one of the most useful characters to distinguish these species. If we trace an imaginary horizontal line between upper folds, in *M. hacat* and *M. henlei* we could observe that lower folds do not extend to the horizontal line, whereas in *M. lunulatus* lower folds extend farther away of the traced line. In *M. californicus* and *M. dorsalis* lower folds extend to or almost to the horizontal line, even when upper labial folds are significantly longer than lower folds (Fig. 3B, E). This is because the origins of upper and lower folds are not at the same level (lower folds origins are

located above the upper folds origins). Some authors have proposed the use of labial folds as diagnostic features for species of *Mustelus* in the eastern North Pacific (Garman, 1913; Compagno, 1984), however, their use has not been generalized. In this paper, we strongly recommend the use of these taxonomic characters because we have observed that they do not show variation with size in any species. In addition, tooth morphology (strongly cuspidate in *M. henlei* and *M. dorsalis*) and trailing edges frayed in fins of *M. henlei* have also been proposed by other authors as useful diagnostic features (Compagno, 1984; Castro, 1996; Ebert, 2003).

We found that the position of the mid-base of the first dorsal fin is useful to distinguish *M. californicus* from the other four species in the eastern North Pacific. Since Jordan and Gilbert (1882) proposed the use of this character to distinguish *M. californicus* from *M. lunulatus* and *M. dorsalis*, other authors have made the same proposal (Beebe and Tee-Van, 1941; Compagno, 1984; Castro, 1996). Although some authors mentioned, based on the analysis of few specimens, that the mid-base of the first dorsal fin is closer to pectoral insertion than to pelvic origin in *M. lunulatus* (Jordan and Gilbert, 1882; Beebe and Tee-Van, 1941; Castro, 1996), and from equidistant between fins to closer to the pectoral insertion in *M. dorsalis* (Jordan and Gilbert, 1882; Beebe and Tee-Van, 1941), we found that the mid-base of first dorsal fin is about equidistant between pectoral insertion and pelvic origin in *M. lunulatus*, *M. henlei*, *M. hacat*, and adults of *M. dorsalis*. In specimens of *M. dorsalis* less than about 25 cm TL, the mid-base of the first dorsal fin is closer to pelvic origin than to pectoral insertion, as in all sizes of *M. californicus*.

We observed that the origin of the first dorsal fin varied with size in *M. hacat* and *M. californicus*. In *M. hacat* the origin of that fin is slightly behind the free rear tips of pectoral fins, however, in a 30 cm TL specimen the first dorsal fin origin is clearly over the free rear tips of pectoral fins. In *M. californicus* the origin of the first dorsal fin is behind the free rear tips of pectoral fins, however, in juveniles less than about 50 cm TL the origin is over the free rear tips of pectoral fins. The origin of that fin is over the free rear tips of pectoral fins at all sizes in *M. henlei*, *M. lunulatus*, and *M. dorsalis*. Although some authors proposed the use of the origin of the first dorsal fin as diagnostic character to distinguish *M. californicus* from *M. lunulatus* and *M. henlei* (Starks, 1917; Castro, 1996; Ebert, 2003), we do not recommend its use, or recommend it be used with caution, because of the variation associated with size in *M. californicus*.

Several authors have proposed, among other characters, the use of the ventral caudal lobe to distinguish *M. lunulatus* from *M. californicus*, *M. henlei*, and *M. dorsalis* (Jordan and Gilbert, 1882; Starks, 1917; Beebe and Tee-Van, 1941). Even though recent studies proposed the same (Castro, 1996; Ebert, 2003), we do not consider it a useful diagnostic feature for *M. lunulatus* because we have observed that it is well developed also in adults of *M. californicus* and poorly developed only in *M. dorsalis* and *M. henlei*. Furthermore, *M. hacat* also has a prominent ventral caudal lobe in adults as in *M. lunulatus*.

Geographical distribution.—The new species, *M. hacat*, is distributed at least in the Gulf of California. However, Heemstra (unpubl. data) stated that specimens of this species (considered by him as undescribed) have been collected from the Gulf of California, Ecuador, and Galapagos Islands. In the northern Gulf of California it is distributed mainly at depths greater than 200 m, overlapping its distribution only with *M. henlei*, which is observed mainly at depths from 100 to 266 m. The paratypes of this new species deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography (MVCSIO) lack information on the depth at which they were caught, however, we suppose they came from depths more than 100 m based on the information of the area where they were collected.

In the northern Gulf of California, *Mustelus hacat* was caught only in March of 2003 and 2004, because the trawler fishing vessels that targeted Pacific Hake (*Merluccius productus*) fished only from January to April (as in every year) at depths greater than 150 m, where *M. hacat* is distributed. After those months, the vessels operated at shallower waters targeting other teleost fishes, shrimp, and some elasmobranch species.

In the northern Gulf of California *M. hacat* and *M. henlei* clearly differ in distribution from *M. californicus* and *M. lunulatus*, which are distributed in shallower waters, mainly at depths less than about 100 m. These four species of *Mustelus* cooccur on the Gulf of California: *M. henlei* is distributed from northern California to Gulf of California, Ecuador, and Peru; *M. californicus* from northern California to Gulf of California; and *M. lunulatus* from southern California to Panama (Compagno, 1984), including the Gulf of California. *Mustelus dorsalis* is distributed from southern Mexico to the Gulf of Guayaquil, Ecuador (Compagno, 1984). However, Beebe and Tee-Van (1941), based on two references, one of which registered a 91 cm gravid female of

M. dorsalis from Tiburon Island in the Central Gulf of California, include this species as one which is distributed in the Gulf of California. Evidently, the specimen was misidentified with other congener, because it is well known that *M. dorsalis* probably does not exceed 64 cm TL (Compagno, 1984). The other reference on which the authors based their conclusion that *M. dorsalis* is distributed in the Gulf of California lacks information on size of the specimen and the specific locality where the shark was caught.

Natural history notes on Mustelus hacat *and congener species.*—The mode of reproduction of the new species, *M. hacat*, and the other four congeners (*M. californicus*, *M. henlei*, *M. lunulatus*, and *M. dorsalis*) is placental viviparity. Before this study, the mode of reproduction for *M. lunulatus* was considered unknown. We based our conclusion on the reproduction mode of *M. hacat* and *M. lunulatus* in the analysis of nine and 20 gravid females, respectively.

The size at maturity for *M. hacat* was calculated to be between 94–98 cm TL for females and between 90–99 cm TL for males. Similar sizes at maturity were observed for *M. lunulatus*, being between 94–99 cm TL for females and between 89–94 cm TL for males. These species clearly differ in this parameter from the other three species of *Mustelus* in the eastern North Pacific, all of which reach the size at maturity before they have a total length of 80 cm. The size at maturity for females and males of *M. californicus* is reached between 80–84 cm and 72–74 cm TL, respectively, while for females and males of *M. henlei* maturity is attained between 58–61 cm and 55–56 cm TL, respectively. According to Compagno (1984), *M. dorsalis* reach the size at maturity of about 43 cm TL.

Key to Eastern North Pacific species of *Mustelus*

1a. Trailing edges of dorsal and caudal fins frayed, visible as a conspicuous dark band ..... ***M. henlei***
1b. Trailing edges of dorsal and caudal fins not frayed, without dark band 2
2a. Teeth with high cusp; nostrils wide (2.2–2.7% TL and 84–95% inter-nostril space); spiracles long (1.1–1.2% TL) ..... ***M. dorsalis***
2b. Teeth with blunt to low rounded cusp; nostrils narrow (1.1–2.3% TL and 34–77% inter-nostril space); spiracles short (0.3–0.8% TL) 3
3a. Upper jaw labial folds (1.2–1.6% TL) and lower jaw labial folds (1.1–1.6% TL) about equal in length; mid-base of first dorsal fin closer to pelvic origin than to pectoral insertion ..... ***M. californicus***
3b. Upper jaw labial folds notably different in length than lower jaw labial folds; mid-base of first dorsal fin about equidistant between pelvic origin and pectoral insertion 4
4a. Upper jaw labial folds (0.8–1.1% TL) notably shorter than lower jaw labial folds (1.2–1.5% TL); inter-nostril space narrow (36–44% pre-oral length); mouth long (46–59% pre-oral length); inter-orbital space narrow (4.9–5.6% TL) ..... ***M. lunulatus***
4b. Upper jaw labial folds (1.4–2.0% TL) notably longer than lower jaw labial folds (1.2–1.5% TL); inter-nostril space wide (45–58% pre-oral length); mouth short (39–49% pre-oral length); inter-orbital space wide (5.6–6.8% TL) ..... ***M. hacat***

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Literature Cited

Beebe, W., and J. Tee-Van. 1941. Eastern Pacific Expeditions of the New York Zoological Society. XXV. Fishes from the Tropical Eastern Pacific. Sharks. Zoologica 26:93–122.

Castro, J. I. 1996. The Sharks of North American Waters. 2nd Ed. Texas A. & M. University Press, College Station, Texas.

Compagno, L. J. V. 1984. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO fisheries synopsis (125) 4:251–655.

———. 1988. Sharks of the Order Carcharhiniformes. Princeton Univ. Press, Princeton, New Jersey.

———. 2002. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO species catalogue for fishery purposes. Vol. 2. Rome, FAO. 2001. 269 p.

EBERT, D. A. 2003. Sharks, Rays, and Chimaeras of California. University of California Press, Berkeley, California.

GARMAN, S. 1913. The Plagiostomia (Sharks, Skates, and Rays). Memoirs of the Museum of Comparative Zoology at Harvard College. Vol. 36. Cambridge, Massachusetts.

HEEMSTRA, P. C. 1997. 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. Bull. Mar. Sci. 60:894–928.

JORDAN, D. S., AND C. H. GILBERT. 1882. Description of four new species of sharks, from Mazatlan, Mexico. Proc. U.S. Natl. Mus. 5:102–110.

LAVIN, M. F., E. BEIER, AND A. BADAN. 1997. Estructura hidrográfica y circulación del Golfo de California: Escalas estacional y interanual, p. 141–171. *In:* Contribuciones a la Oceanografía Física en México. M. F. Lavin (ed.). Monografía No. 3, Unión Geofísica Mexicana, México.

MÁRQUEZ-FARIAS, F. 2000. Tiburones del Golfo de California. p. 237–257. *In:* SEMARNAP ''Sustentabilidad y Pesca Responsable en México: Evaluación y manejo 1999–2000.'' INP, SEMARNAP, México.

SPRINGER, V. G., AND J. A. F. GARRICK. 1964. A survey of vertebral numbers in sharks. Proc. U.S. Natl. Mus. 116:73–96.

STARKS, E. C. 1917. On the differential characters between *Mustelus henlei* and *Mustelus californicus*. Copeia 1917:61–63.

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