2.2 Order LAMNIFORMES - Mackerel sharks

Order: Group Lamnae Garman, 1885, *Bull. Mus. Comp. Zool. Harvard*, 12(1): 30. Emended here to Order Lamniformes Garman, 1885.

Number of Recognized Families: 5.

Synonyms: Part 1 Squali, Abtheilung 2: Müller and Henle, 1838d: 27; Müller and Henle, 1839: 27. Part 1 Squali, Abtheilung 2, Unterabtheilung 3: Müller and Henle, 1839: 66. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859: xi. Order Squali, Suborder Squali: Gill, 1862b: 394, 396. Order Squali, Suborder Galei: Gill, 1872: 22, 23. Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 2 Scylliolamnidae: Hasse, 1879: 51. Order Selachii, Suborder Asterospondyli: Woodward, 1889: 157. Order Asterospondyli: Gill, 1893: 130; Fowler, 1941: 4, 13; Smith, 1949: 37, 39. Order Asterospondyli, Suborder Galei: Jordan and Evermann, 1896: 19, 21. Order Euselachii, Suborder Pleurotremata, Division Galeoidei: Regan, 1906: 723. Order Selachii, Group 2, Division B, Subdivision 1, Suborder Scylliodei: Goodrich, 1909: 148. Order Pleurotremata, Suborder Galeoidei: Engelhardt, 1913: 97. Order Plagiostoma, Suborder Antacea, Group Carcharoidei: Garman, 1913: 10, 11. Order Plagiostoma, Suborder Antacea, Group Isuroidei: Garman, 1913: 10, 12. Order Euselachii, Suborder Galei, Series Lamnoidei: Jordan, 1923: 99. Order Plagiostomi, Suborder Galeiformes: Lozano y Rey, 1928: 280. Order Galea, Suborder Isurida, Superfamily Odontaspoidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Galea, Suborder Isurida, Superfamily Isuroidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Euselachii, Suborder Lamniformes: Bertin, 1939a: 9. Order Lamniformes: Berg, 1940: 137; Berg and Svetovidov, 1955: 65; Patterson, 1967: 670; Rass and Lindberg, 1971: 303; Lindberg, 1971: 8, 257; Compagno, 1973: 28; Applegate, 1974: 743; Nelson, 1976: 33; Compagno, 1984: 212; Nelson, 1984: 51; Gubanov, Kondyurin and Myagkov, 1986: 3, 49; Cappetta, 1987: 26, 85; Compagno, 1988: 382; Eschmeyer, 1990: 435; Nelson, 1994: 51; de Carvalho, 1996: 55; Shirai, 1996: 32; Eschmeyer, 1998. Order Lamniformes, Suborder Lamnoidei: Berg, 1940: 137; Berg and Svedovidov, 1955: 65; Patterson, 1967: 670; Lindberg, 1971: 8, 257; Nelson, 1976: 33; Nelson, 1984: 51. Order Euselachii, Suborder Galei, Superfamily Odontaspoidea: Whitley, 1940: 68. Order Euselachii, Suborder Galei, Superfamily Isuroidea: Whitley, 1940: 68. Order Selachii, Suborder Galeoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 77, 95; Romer, 1966: 350. Order Lamnoidea, Suborder Galeoidea: Schultz and Stern, 1948: 224. Order Lamnida, Suborder Lamnina: Matsubara, 1955: 1-789. Order Galeiformes, Suborder Isuroidea: Arambourg and Bertin, 1958: 2029. Order Pleurotrema, Suborder Galeoidea: Norman, 1966: 7. Order Carchariida, Suborder Carchariina, Superfamily Carchariicae: Fowler, 1967a: 92, 140. Order Carchariida, Suborder Carchariina, Superfamily Lamnicae: Fowler, 1967a: 92, 104. Order Squatinida, Suborder Squaloidei: Glikman, 1967: 215. Superorder Lamnae, Order Odontaspidida: Glikman, 1967: 229, 230. Order Odontaspidida, Superfamily Odontaspidoidea: Glikman, 1967: 230. Order Odontaspidida, Superfamily Isuroidea: Glikman, 1967: 232. Order Odontaspidida, Superfamily Scapanorhynchoidea: Glikman, 1967: 233. Order Euselachii, Suborder Galeoidei: Blot, 1969: 702-776. Order Pleurotremata, Suborder Galeiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Carcharhiniformes: Rass and Lindberg, 1971: 303; Gubanov, Kondyurin and Myagkov, 1986: 3, 61. Order Isuriformes: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Carcharioidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Isuroidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Cetorhinoidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Alopioidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, Suborder Lamnoidea: Carroll, 1988: 599.

FAO Names: En - Mackerel sharks.

Field Marks: Large active pelagic sharks without nictitating eyelids, no barbels or nasoral grooves, nostrils free from mouth, long mouths that extend behind eyes, usually with enlarged anterior teeth and a gap or small intermediate teeth between anteriors and laterals on each side of the upper jaw, five broad gill openings, two spineless dorsal fins and an anal fin.

Diagnostic Features: Head conical to moderately depressed, not expanded laterally. Snout very short to moderately elongated, truncated to conical or blade-like and flattened, not greatly elongated and without lateral teeth or rostral barbels. Eyes usually on sides of head (dorsolateral in ***Carcharias***), without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Nostrils of the ordinary shark type, transverse on snout, without barbels, nasoral grooves or circumnarial grooves, separate from mouth, anterior nasal flaps short and not reaching mouth. Five pairs of gill openings present on sides of head, with the posteriormost two in front of pectoral-fin origins or above them. Spiracles present and very small, well behind and about opposite to level of eyes. Mouth large, arched and elongated, extending well behind eyes. Labial furrows reduced or absent, when present on both jaws or on the lower jaw only. Teeth weakly to strongly differentiated along the jaws, with or without (***Megachasma***) enlarged anterior teeth but without enlarged molariform posterior teeth; usually with a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw (absent in ***Megachasma***); teeth with osteodont histological structure. Trunk cylindrical, fusiform, or somewhat compressed, not flattened and ray-like. Caudal peduncle without thin lateral dermal ridges but with lateral keels variably present or absent. Dermal denticles covering entire body, not enlarged as thorns or spines. Pectoral fins small to moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill slits. Pectoral girdle (scapulocoracoid) high, U-shaped, with or (usually) without a medial joint, and with superscapulae directed posterodorsally and not contacting vertebral column. Pectoral-fin skeleton primitively tribasal, with propterygium in contact with radials and metapterygium without a proximal segment; pectoral fins primitively aplesodic, with radials confined to the fin bases, but plesodic in derived taxa and supporting the fin webs; radial count 15 to 46 with 2 to 13 segments. Pelvic fins small to moderately large, with vent continuous with their inner margins. Claspers with siphons in the abdomen but without large clasper sacs; clasper glans with a pseudosiphon, cover rhipidion, rhipidion (sometimes absent), and clasper spurs or spines; dorsal and ventral marginals of clasper skeleton rolled into a tube for the clasper canal. Two spineless dorsal fins present, with origin of first over abdomen and well in front of pelvic-fin origins; dorsal-fin skeleton with segmented radials but without segmented basal plates. Anal fin

present. Caudal fin with a long dorsal lobe and the ventral lobe very strong to absent; vertebral axis elevated into the dorsal caudal lobe (heterocercal caudal fin). Vertebral calcification usually strong, secondary calcification usually in form of strong branched radii in intermedial spaces, sometimes with annular rings but without diagonal lamellae or other calcifications in the basal spaces (***Megachasma*** with vertebral calcification greatly reduced). Total vertebral count 109 to 477, precaudal vertebrae 50 to 125. Neurocranium with a short to greatly elongated, tripodal rostrum without ventral keel and open dorsally; nasal capsules spherical, oval or flattened and without subnasal fenestrae (basal communicating canals) or antorbital cartilages; orbits with complete preorbital walls (except ***Mitsukurina***), strong supraorbital crests (reduced to isolated preorbital and postorbital processes in ***Mitsukurina***), strong suborbital shelves, separate foramina for superficial ophthalmic nerves and hyomandibular nerves, and incomplete postorbital walls without lateral commissures for lateral head vein; occipital condyles low, occipital hemicentrum present between them. Jaws elongated, upper jaws (palatoquadrates) with or without short vertical orbital processes that articulate with cranial orbits in orbital notches of suborbital shelves or with basal plate; orbital processes when present do not penetrate supraorbital crests. Hyobranchial skeleton with narrow elongated basihyoid; posterior two pharyngobranchials and last epibranchial fused into a yoke-shaped element. Head muscles include elongated horizontal preorbitalis, elongated broad levator palatoquadrati that extend far behind the orbits, adductor mandibulae muscles not segmented and notched anteriorly for mouth gape; no craniomandibular muscle between the lower jaw and orbital walls; no mandibulocutaneous muscle between upper jaw and skin; and no postocular eyelid muscles. Intestinal valve of ring type, with 19 to 55 turns. Reproduction ovoviviparous (aplacental viviparous), foetal nutriment in at least some species from uterine cannibalism (eating of eggs and, in ***Carcharias taurus*** at least, eating other foetuses), but without placental vivipary or nutritive trophonemata.

Distribution: Circumglobal in temperate and tropical seas, with some lamnoids penetrating cold boreal and subantarctic waters. Some species favour temperate to cold boreal or subantarctic waters (basking shark, porbeagle and salmon shark) while most other species occur in warm-temperate to tropical seas; the white shark has one of the most extensive ranges of any cartilaginous fish.

Habitat: Mackerel sharks or lamnoids occur in a variety of marine habitats from shallow open and enclosed bays, rocky and coral reefs, and sandy beaches on the continental shelves to the epipelagic zone and possibly the mesopelagic zone of the open ocean, with a few species occurring on the continental and insular slopes. They range in depth from the intertidal to at least 1 600 m on the lower slopes, in the open ocean from the surface to at least 450 m, and on the abyssal plains over bottoms down to over 5 000 m depth. Although a few species are found in shallow bays and off beaches in the intertidal zone lamnoid sharks are not known to penetrate brackish estuaries and are not recorded from freshwater rivers and lakes.

Biology: The lamnoids are a small group of possibly 15 living species but are remarkably varied and often specialized in their form and habits. Except for the smallish crocodile shark, all living lamnoids are medium-sized to gigantic. Their ranks include sharks of littoral morphotype (Compagno, 1990a: sand tiger shark, ***Carcharias taurus***), but also high-speed tachypelagic predators (shortfin mako), macroceanic and microceanic specialists of the open ocean (longfin mako and crocodile shark), two very different filter feeders (basking and megamouth sharks), bathic and rhynchobathic deepwater specialists (bigeye sand tiger and goblin sharks), and an archipelagic shark or top predator (white shark). There are no living durophage (shell-crushing) or specialized bottom-dwelling lamnoids. The prey range of lamnoids is vast, from microscopic zooplankton to large bony fishes, marine mammals, other chondrichthyans, marine birds and reptiles, cephalopods, crabs, large gastropods, and carrion. Most lamnoids are active swimmers, some are highly migratory, and some may seasonally visit favoured areas including concentrations of food (fish banks, areas and current systems with plankton blooms, and seal colonies). At least some of the species are social (sand tiger shark, Lamnidae), and some may practice cooperative hunting. Mode of reproduction is known for only some of the lamnoid species which practice uterine cannibalism in the form of egg-eating or oophagy (Lamnidae, Alopiidae, crocodile shark, sand tiger shark, and possibly basking and megamouth sharks), but also foetus-eating or adelphophagy (sand tiger shark, possibly crocodile shark).

Interest to Fisheries and Human Impact: Several are important fisheries sharks in coastal and oceanic waters, particularly members of the families Alopiidae, Cetorhinidae, Lamnidae, and some Odontaspididae. These are regular components of targeted commercial or sport fisheries including some fisheries specifically targeting certain species (basking, shortfin mako and white sharks), and as bycatch of other fisheries targeting teleost fishes or marine invertebrates. Some species are rare to common and often discarded bycatch of high-seas and deepwater fisheries (crocodile shark, bigeye sand tiger, goblin shark). Lamnoids are caught in bottom and pelagic trawls, in pelagic and fixed gill nets (including anti-shark nets to protect bathing beaches), in fish traps, on bottom and pelagic longlines, in purse seines, with harpoons, and with hook-and-line and rod-and-reel. Many species are used for human consumption; the flesh of some species is excellent, and large fins are of high value in the oriental soup-fin trade. Several inshore and offshore species are caught by sportsfishing anglers, and some species (makos, white shark, porbeagle, threshers) are sought by big-game anglers and are recognized by the International Game Fish Association.

White sharks rarely but regularly bite swimmers, surfers, divers and boats, but less than a third of such incidents result in fatalities and very rarely result in consumption of the victim. Sand tigers and shortfin makos sporadically bite but do not consume people, and shortfin makos sometimes cause problems by jumping into sportsfishing boats after being hooked by anglers. *Jaws* and more recent shark-monster Hollywood films have inspired social phenomena leading to conservation problems for white sharks and sharks in general but have also been instrumental in promoting public awareness of the issues of shark conservation. Hollywood lamnoid stars have suffered from increased fishing pressure and demand for trophies and food including jaws, teeth, meat and fins, but have also received public support for their protection and conservation.

White sharks, shortfin makos, sand tiger sharks, and even the smalltooth sandtiger (***Odontaspis ferox***) are currently sought by ecotouristic divers and film-makers in the Indian Ocean, western Atlantic, western Pacific and eastern Pacific. Although the white shark has been subject to repeated and unsuccessful attempts to keep it in captivity in large public aquaria, the sand tiger shark is the only lamnoid that is readily kept for public viewing and is currently living in numerous aquaria in the USA, Europe and South Africa.

There are conservation concerns over several lamnoid species, including the white, basking and sand tiger sharks, some of which have declined locally from overfishing and possibly other environmental problems. Certain species yield products of extremely high value comparable to rhinoceros horns and elephant tusks, including the jaws, teeth and fins of white sharks and the fins of basking sharks. More abundant oceanic fisheries species, including makos and threshers, are in need of rational management, while less abundant to rare offshore species such as crocodile and bigeye sand tiger sharks are threatened as bycatch of fisheries driven by abundant, wide-ranging scombroid fishes. The conservation status of some uncommon to rare deepwater lamnoids, including the goblin, megamouth and bigeye sand tiger sharks, is poorly known and is of concern as these sharks are found in areas subject to intensive deepwater and oceanic fisheries and are not being monitored.

Local Names: Lamnoid sharks, Mackerel sharks.

Remarks: Garman (1885) was the first author to propose a higher group name applicable to this order but the concept of an order Lamniformes or equivalent ordinal taxon to include only lamnoid families is far more recent. Early writers and even some modern authors generally grouped orectoloboids and sometimes carcharhinoids and other shark groups together with the lamnoids. Garman's Lamnae included most living sharks except hexanchoids, heterodontoids and squatinoids. Garman (1913) later recognized two primarily lamnoid 'groups' (equivalent to infraorders or superfamilies) in his suborder Antacea (sharks), the Carcharoidei (for odontaspidids and mitsukurinids), and the Isuroidei, for alopiids, lamnids, cetorhinids, and the orectoloboid whale shark, but did not place the two groups in a common higher lamnoid group. White (1936, 1937) and Whitley (1940) essentially followed Garman's arrangement of dividing the lamnoids into two groups. An influential modern arrangement was Bigelow and Schroeder's (1948) order Selachii, suborder Galeoidea, which included the lamnoid, orectoloboid, and carcharhinoid families in a single undifferentiated group. This has been followed by several authors in various forms.

Jordan (1923) was the first author to propose an exclusive group for the lamnoids, the series Lamnoidei (equivalent to an infraorder or superfamily). Bertin's (1939a) suborder Lamniformes included all lamnoids but also (inexplicably) the carcharhinoid ***Pseudotriakis***. Rass and Lindberg (1971) used the order Lamniformes exclusively for all lamnoids except the basking shark, which was placed in the order Carcharhiniformes along with orectoloboids. Glikman (1967) proposed an order Odontaspidida for all lamnoids except the basking shark, which was placed in the order Squatinida in a suborder Squaloidei including the squaloids. Compagno (1973) and Applegate (1974) reinvented the order Lamniformes in its modern form, essentially the same as Jordan's series Lamnoidei, which has been followed by several authors including Compagno (1984, 1988, 1990b, 1999), Cappetta (1987), Eschmeyer (1990, 1998), Nelson (1994), de Carvalho (1996), and Shirai (1996). Chu and Meng (1979) used the order Isuriformes as an equivalent taxon to Lamniformes and Carroll (1988) used the order Galeomorpha, suborder Lamnoidei exclusively for lamnoids.

Continuing work on the morphology of sharks by the writer as an extension of previous work (Compagno, 1990b) supports the retention of the Lamniformes as a monophyletic but morphologically and ecologically varied group. The arrangement of lamnoid families recognized in Compagno (1984, 1990b, 1999) are retained here, but the possibility remains that the Odontaspididae is paraphyletic, and that the two genera, ***Carcharias*** and ***Odontaspis***, may be separable into two families, Carchariidae and Odontaspididae.

Key to Families:

1a. Snout greatly elongated and flattened, forming a dagger-like blade; no precaudal pits; ventral caudal lobe absent; anal fin broadly rounded (Fig. 42) . . . . . **family Mitsukurinidae**

Fig. 42 ***Mitsukurina***

1b. Snout very short to moderately elongated, conical to flattened and broadly rounded but not blade-like; precaudal pits (upper pits, and often lowers) and ventral caudal lobe present; anal fin angular (Fig. 43) . . . . . **→ 2**

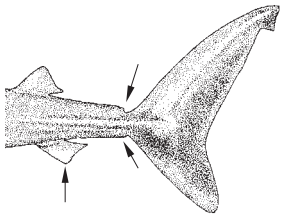


Fig. 43 ***Cetorhinus***

2a. Snout very short and broadly rounded in dorsoventral view; mouth terminal on head (Fig. 44); teeth in dental bands continuously varying, no row groups; internal gill openings with densely packed papillose gill rakers . . . . . **family Megachasmidae**

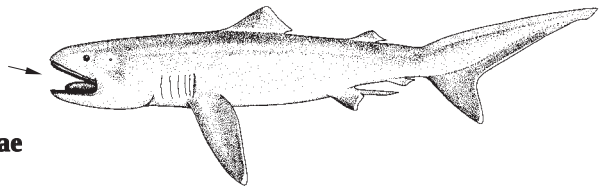


Fig. 44 ***Megachasma***

2b. Snout longer and narrowly to broadly parabolic in dorsoventral view; mouth subterminal on head (Fig. 45); teeth differentiated into anteriors and lateroposteriors in upper jaw (Cetorhinidae), and anteriors, laterals and often intermediates and symphysials in other taxa; internal gill openings either without gill rakers or with rows of elongated gill raker denticles (Cetorhinidae). . . . . → **3**

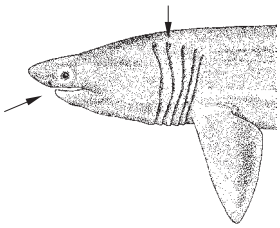


Fig. 45 ***Cetorhinus***

3a. Caudal fin about as long as rest of shark; last two gill openings above pectoral-fin base (Fig. 46) . . . . . **family Alopiidae**

3b. Caudal fin much shorter than rest of shark; all gill openings in front of pectoral-fin base (Fig. 47) . . . . → **4**

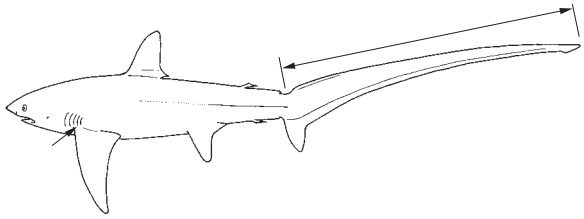


Fig. 46 ***Alopias***

4a. Caudal fin asymmetrical, not lunate, ventral caudal lobe short, preventral caudal margin much shorter than dorsal caudal margin; caudal peduncle without lateral keels or with weak ones (Fig. 47) . . . . . → **5**

4b. Caudal fin nearly symmetrical and lunate, with a long ventral lobe and preventral caudal margin nearly as long as dorsal caudal margin; caudal peduncle with very strong lateral keels (Fig. 48) . . . . → **6**

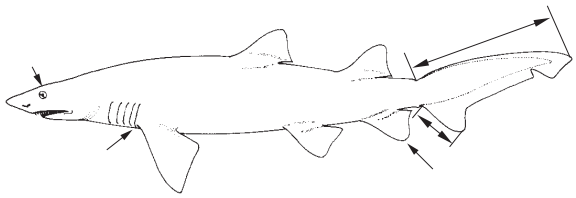


Fig. 47 ***Carcharias***

5a. Eyes very large, body slender; anal fin narrow-based, pivoting; caudal peduncle with both upper and lower precaudal pits and low lateral keels on each side; gill openings extending onto dorsal surface of head (Fig. 49) . . . . . **family Pseudocarchariidae**

5b. Eyes relatively small, body stout; anal fin broad-based, not pivoting; caudal peduncle with an upper precaudal pit but without a lower pit or lateral keels; gill openings not extending onto dorsal surface of head (Fig. 47) . . **family Odontaspididae**

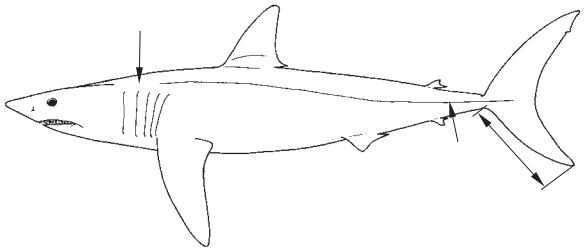


Fig. 48 ***Isurus***

6a. Teeth relatively few, enlarged and blade-like, with less than 40 rows in each jaw; gill openings large but ending far lateral to mid-dorsal surface of head (Fig. 48); internal gill openings without gill rakers . . . . . **family Lamnidae**

6b. Teeth numerous, minute, hooked and not blade-like, with over 150 rows in each jaw; gill openings extremely large, extending nearly to mid-dorsal surface of head (Fig. 45); internal gill openings with prominent gill rakers formed from modified dermal denticles . . . . . **family Cetorhinidae**

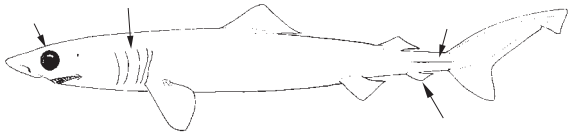


Fig. 49 ***Pseudocarcharias***

2.2.1 Family ODONTASPIDIDAE

Family: Family Odontaspides Müller and Henle, 1839, *Syst. Beschr. Plagiost.*, pt. 2: 73. Emended to Family Odontaspididae Müller and Henle, 1839. The corrected form Odontaspididae was placed on the Official List of Family-Group Names in Zoology (Name no. 385) but Odontaspides was placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (Name no. 414) by the International Commission on Zoological Nomenclature (1965, Opinion 723, *Bull. Zool. Nomencl.*, 22: 33, 34). Odontaspididae was given special endorsement by the International Commission on Zoological Nomenclature (1987, Opinion 1459.6, *Bull. Zool. Nomencl.*, 44(3): 216) to take precedence over Carchariidae Müller and Henle, 1838 when the two are synonymized.

Type Genus: ***Odontaspis*** Agassiz, 1838.

Number of Recognized Genera: 2.

Synonyms: Subfamily Triglochidini Bonaparte, 1838: 208 (Family Squalidae). Type genus: ***Triglochis*** Müller and Henle, 1837. Family Carchariae Müller and Henle, 1838d: 27. Type genus: ***Carcharias*** Rafinesque, 1810. Rejected by the International Commission on Zoological Nomenclature (1965, Opinion 723: 33) but reinstated by the Commission (1987, Opinion 1459.5: 216) in the corrected form Family Carchariidae Müller and Henle, 1838 on the Official List of Family-Group Names in Zoology, with the special endorsement that it is not to be given precedence over Odontaspididae Müller and Henle, 1839 when considered a synonym of it. This name was widely used by earlier writers for members of the Carcharhinidae, following Müller and Henle's original usage, but Jordan and Gilbert (1883: 27) and many subsequent writers used it for members of the Odontaspididae with the assignment of ***Carcharias*** to this family. Family Carchariidae Jordan and Gilbert, 1883: 27. Emended spelling for Family Carchariae Müller and Henle, 1838. Type genus: ***Carcharias*** Rafinesque, 1810. Family Eugomphodidae Applegate, Espinosa, Menchaca and Sotelo, 1979: 130. Type genus: ***Eugomphodus*** Gill, 1862. Also *ibid.*: 30, as Eugonphodidae, error for Eugomphodidae.

FAO Names: En - Sand tiger sharks; **Fr** - Requins de sable; **Sp** - Solrayos, Toros.

Field Marks: Large heavy-bodied sharks with conical to slightly depressed pointed snouts, long mouths extending behind eyes, small to moderately large eyes without nictitating eyelids, moderately long gill openings in front of pectoral origins, large teeth with slender cusps and lateral cusplets, small intermediate teeth separating anterior and lateral teeth in the upper jaw, two large dorsal fins and an anal fin, small pectoral fins, a compressed caudal peduncle without keels but with an upper precaudal pit only, and an asymmetrical caudal fin with a strong but short ventral lobe.

Diagnostic Features: Head much shorter than trunk. Snout short to moderately long, pointed and bulbously conical or moderately depressed, not greatly elongated, flattened or blade-like. Eyes small to moderately large, length 1.4 to 4.1% of precaudal length. Gill openings moderately large, length of first 6.2 to 9.2% of precaudal length, not extending onto dorsal surface of head; all gill openings anterior to pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusable to almost opposite snout tip but not greatly distensible laterally. Teeth large, anteriors narrow and awl-like but laterals moderately compressed and blade-like, in 34 to 56/36 to 46 (71 to 102 total) rows, less than 60 rows in either jaw; 2 or 3 rows of large anterior teeth on each side of upper jaw, three rows in lower jaw, the uppers separated from the smaller upper lateral teeth by 1 to 5 rows of small intermediate teeth (rarely absent); one or more pairs of symphysial teeth present in the lower jaw or both jaws. Trunk compressed-cylindrical and moderately stout, firm and not flabby. Caudal peduncle compressed and without keels but with a crescentic upper precaudal pit only. Dermal denticles moderately large and smooth, with flat crowns, small ridges and cusps, and with cusps directed posteriorly on lateral denticles. Pectoral fins moderately long and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, nearly or quite as large as first dorsal fin; fin skeleton aplesodic. First dorsal fin large, moderately high, erect and angular; first dorsal-fin skeleton aplesodic. Second dorsal and anal fins about as large as first dorsal fin or second dorsal smaller than first and as large or larger than anal fin; second dorsal and anal fins with broad nonpivoting bases. Caudal fin not lunate, dorsal lobe moderately long, less than half as long as rest of shark, ventral lobe short but strong. Neurocranium low to moderately high, with a short to moderately elongated rostrum, depressed internasal septum and widespread nasal capsules, small to large orbits with the supraorbital crests strong, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified with well-developed double cones and radii but no annuli. Total vertebral count 156 to 183, precaudal count 80 to 95, diplospondylous caudal count 71 to 88. Intestinal valve of ring type with 28 to 32 turns. Size large with adults 2.2 to at least 3.6 m.

Distribution: Odontaspidids have a wide but sporadic geographic distribution in virtually all warm-temperate and tropical seas, and further deepwater exploration and fisheries efforts with appropriate gear will undoubtedly reveal range extensions.

Habitat: Sand tiger sharks are tropical to warm-temperate, inshore to offshore, littoral and deepwater sharks. They occur in continental and insular waters from the outer shelves and down the slopes to possibly 1 600 m, on seamounts, and with one species (***Odontaspis noronhai***) also oceanic in the epipelagic and possibly the mesopelagic zone.

Biology: Sand tiger sharks are relatively slow but active littoral, epibenthic and oceanic swimmers. They feed on a wide variety of bony fishes, other sharks, rays, squids and bottom crustaceans. Development is ovoviviparous (aplacental viviparous), without a yolk-sac placenta but with uterine cannibalism in the genus ***Carcharias***, in the form of both oophagy and adelphophagy (egg and embryo-eating).

Interest to Fisheries and Human Impact: Sand tiger sharks, particularly ***Carcharias taurus*** and to a lesser extent ***Odontaspis ferox*** are or have been important for inshore and offshore fisheries wherever they occur, but are far less important and less abundant than requiem sharks (Carcharhinidae) or hammerheads (Sphyrnidae). ***Odontaspis noronhai*** is primarily a rare or uncommon bycatch of oceanic and slope line fisheries. In some areas of relative abundance, such as the east coast of North America and Australia, ***C. taurus*** has severely declined due to fishing pressure (including attacks by divers in Australia), but other areas that supported important fisheries (west Africa off Senegal, and the South China Sea) have not been monitored and local populations may need attention. Population trends in ***Odontaspis*** are essentially unknown, and potentially worrisome because of known catches by fisheries. Sand tiger sharks are presently protected in the eastern USA and Australia, and ***Carcharias taurus*** is to be decommercialized in South Africa and will only be fished by sports anglers.

These sharks are inoffensive and usually not aggressive to humans in the water and are the subject of ecotouristic viewing by divers in South Africa, Australia, the east coast of the USA, the Mediterranean Sea, and Malpelo Island in the eastern Pacific. Swimmers, divers and fishermen commonly encounter (or formerly encountered) ***C. taurus*** and more recently ***Odontaspis ferox*** in areas of abundance, but despite their impressive teeth there have been few incidents of ***Carcharias taurus*** biting people, and none currently known for ***Odontaspis***. As with other large sharks, sand tigers should be treated with respect and not harassed underwater.

Carcharias taurus is important for aquarium displays worldwide, but ***Odontaspis*** species have not been kept in captivity to the writer's knowledge. The former has the ideal combination of a fearsome, showy, large 'sharky' appearance, combined with docility, hardiness, and great longevity in captivity.

Local Names: Sand tiger sharks, Sand sharks, Ragged-tooth sharks, Grey or gray nurse sharks, Gray sharks, Patings, True sharks, Chuich'ih sha k'o; Mizuwani ka (Japan); Dlinnozubye akuly, Peschanye akuly (Russia); Tubaroes de areia.

Remarks: The family Odontaspididae was recognized by many authors following Müller and Henle (1839). However, considerable confusion was caused by these authors (Müller and Henle, 1838d), who proposed Carchariidae for carcharhinids but based it on Rafinesque's (1810) genus ***Carcharias***, which has as its type species the sand tiger shark ***C. taurus***. Several authors followed Müller and Henle in using Carchariidae for carcharhinids and Odontaspididae (or Odontaspidae) for sand tiger sharks (Bleeker, 1859; Dumeril, 1865; Günther, 1870; Regan, 1906; Engelhardt, 1913), while others used Odontaspididae for sand tiger sharks and other names for carcharhinids (Gray, 1851; Gill, 1862b, 1872; Bertin, 1939a; Berg, 1940; Berg and Svedovidov, 1955; Arambourg and Bertin, 1958; Norman, 1966). Carchariidae was reestablished and widely used as a family for sand tiger sharks rather than carcharhinids (Jordan and Gilbert, 1883; Gill, 1893; Jordan and Evermann, 1896; Garman, 1913; Jordan, 1923; Lozano y Rey, 1928; White, 1936, 1937; Whitley, 1940; Fowler, 1941, 1947; Bigelow and Schroeder, 1948; Matsubara, 1955; Garrick and Schultz, 1963; Romer, 1966; Pinchuk, 1972; Chu and Meng, 1979; Carroll 1988). However, this was curtailed by White, Tucker and Marshall (1961), who proposed to validate the name Odontaspididae over Carchariidae due to greater use in the palaeontological literature. The International Commission on Zoological Nomenclature (1965) suppressed Carchariidae for zoological literature. Various authors who published subsequent to this ruling have used Odontaspididae (Glikman, 1967; Patterson, 1967; Blot, 1969; Bailey et al, 1970; Budker and Whitehead, 1971; Lindberg, 1971; Rass and Lindberg, 1971; Compagno, 1973, 1981b, 1982, 1984, 1999; Nelson, 1976, 1984, 1994; Gubanov, Kondyurin and Myagkov, 1986; Cappetta, 1987; Eschmeyer, 1990; Robins et al., 1991a; Shirai, 1996; Helfman, Collette and Facey, 1997; Eschmeyer, 1998). Applegate et al. (1979) used Eugomphodidae. However, following a petition by Compagno and Follett (1986), the International Commission on Zoological Nomenclature (1987) reinstated Carchariidae as a valid family-group name for sand tiger sharks, but not having precedence over Odontaspididae unless removed from synonymy of that family. This leaves Carchariidae available for the genus ***Carcharias*** and its fossil relatives if considered a distinct family from Odontaspididae and ***Odontaspis***.

Although most writers have recognized only one genus of Odontaspididae (or Carchariidae), two genera are recognized here for the living species. This follows recent palaeontological and neontological work (Glikman, 1964, 1967; Herman, 1977; Compagno, 1981b, 1982, 1984; Cappetta, 1987) that treats the ***taurus*** and ***ferox*** groups of species as separate genera, but also morphological studies on the living species that revealed their distinctness (Compagno, 1984, 1990b; Compagno and Follett, 1987).

The oldest genus-group names for the ***taurus*** group are ***Carcharias*** Rafinesque, 1810, and ***Triglochis*** Müller and Henle, 1837, but these were rejected by the International Commission on Zoological Nomenclature (1965), following a proposal by White, Tucker and Marshall (1961). These authors reasoned that ***Carcharias*** Rafinesque, 1810 should be suppressed because the genus ***Odontaspis*** Agassiz, 1838 has been used far more frequently in the literature for odontaspidids (especially fossils) than ***Carcharias***. A key point to their reasoning is that "...since the respective nominal type species of ***Carcharias*** Rafinesque,1810, and ***Odontaspis*** J.L.R. Agassiz, 1838, are *congeneric*, it is the latter name which is threatened by the former" (emphasis added). However, subsequent work indicated that the two type species, ***taurus*** and ***ferox***, were not congeneric, and, provided two genera of living odontaspidids are recognized, ***Odontaspis*** is not threatened by ***Carcharias***. Compagno (1977, 1981b, 1982, 1984), Welton and Zinsmeister (1980) and various subsequent writers used the genus ***Eugomphodus*** Gill, 1862 as the next valid name that could substitute for ***Carcharias***. Cappetta (1987) used ***Synodontaspis*** in favour of ***Eugomphodus***, but the latter has priority. However, following the petition by Compagno and Follett (1986) the International Commission on Zoological Nomenclature (1987) reinstated the genus ***Carcharias*** Rafinesque, 1810.

The genus ***Odontaspis*** as presently delimited is restricted to ***O. ferox***, ***O. noronhai***, and fossil species (Compagno, 1984; Cappetta, 1987), while the genus ***Carcharias*** has a single living species, ***C. taurus***, and numerous fossil species.

Carcharias kamoharai Matsubara, 1936 (and its synonyms) have previously been placed in the genus ***Odontaspis*** or ***Carcharias*** (D'Aubrey, 1964a, b; Bass, D'Aubrey and Kistnasamy, 1975a), but this was placed in the genus ***Pseudocarcharias*** and the family Pseudocarchariidae (Compagno, 1973, 1984).

Phyletic studies by Compagno (1990b) based on external and skeletal morphology and dentition of living lamnoids, and a genetic study by Martin and Naylor (1997) suggested that Odontaspididae might be paraphyletic, with ***Carcharias*** and ***Odontaspis*** separate since the Cretaceous (Cappetta, 1987) and rating separate families. However, a phyletic study of the dentition of lamnoid sharks by Long and Waggoner (1996) suggested that Odontaspididae is monophyletic. Pending further study ***Odontaspis*** and ***Carcharias*** are retained in the family Odontaspididae following Compagno (1984).

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Lindberg (1971); Shiino (1972, 1976); Compagno (1973, 1982, 1984, 1990b, 1999); D'Aubrey (1964a, b); Bass, D'Aubrey and Kistnasamy (1975a).

Key to Genera:

1a. Snout short and flattened; three rows of large upper anterior teeth on each side of symphysis; first dorsal fin about as large or slightly larger than second dorsal fin and anal fin; first dorsal fin closer to pelvic-fin bases than pectoral-fin bases (Fig. 50) . . . . . ***Carcharias***

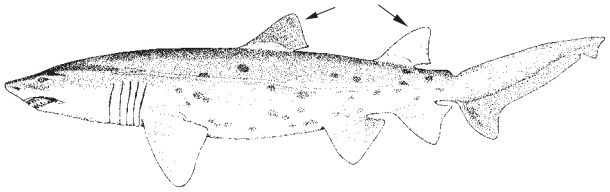


Fig. 50 ***Carcharias***

1b. Snout long and conical; two rows of large upper anterior teeth on each side of symphysis; first dorsal fin noticeably larger than second dorsal fin and anal fin; first dorsal fin closer to pectoral-fin bases than pelvic-fin bases (Fig. 51) . . . . . ***Odontaspis***

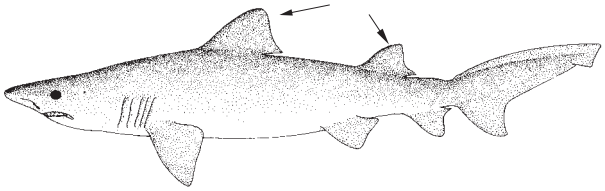


Fig. 51 ***Odontaspis***

Carcharias Rafinesque, 1810

Genus: ***Carcharias*** Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 10. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 1746) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5a, *Bull. Zool. Nomencl.*, 22(1): 33) following a proposal by White et al. (1961, *Bull. Zool. Nomencl.*, 18(4): 277-278). However, Compagno and Follett (1986, *Bull. Zool. Nomencl.*, 43(1): 89-92) argued for the reinstatement of ***Carcharias*** because its rejection on nomenclatural grounds interfered with taxonomic work on the family. This was accepted by the International Commission on Zoological Nomenclature with near-unanimity, and ***Carcharias*** was placed on the Official List of Generic Names in Zoology (1987, Opinion 1459.2, *Bull. Zool. Nomencl.*, 44(3): 216), with the special endorsement that it is not to be given precedence over ***Odontaspis*** Agassiz, 1838, whenever the two are considered synonyms.

Type Species: ***Carcharias taurus*** Rafinesque, 1810, by monotypy (International Commission on Zoological Nomenclature, 1912, Opinion 47, *Smithsonian Pub.*, (2060): 108).

Number of Recognized Species: 1.

Synonyms: Genus ***Triglochis*** Müller and Henle, 1837a: 113. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 1747) by the International Commission on Zoological Nomenclature (1965, Opinion 723.5b: 33). Genus ***Eugomphodus*** Gill, 1862a: 60 (name only, but without allocated species); Gill, 1864: 260 (description). Type species, ***Eugomphodus griseus*** Gill, 1862, by monotypy, equals ***Carcharias griseus*** Storer, 1846 and ***C. griseus*** Ayres, 1843, and a junior synonym of ***Carcharias taurus*** Rafinesque, 1810. Subgenus ***Synodontaspis*** White, 1931 (Genus ***Odontaspis*** Agassiz, 1838): 51. Type species, ***Carcharias taurus*** Rafinesque, 1810 by original designation. Subgenus White, 1931 (Genus ***Odontaspis*** Agassiz, 1838): 63. Type species, ***Odontaspis platensis*** Lahille, 1928, by original designation.

Diagnostic Features: Snout short with preoral length 0.3 to 0.5 times mouth width and 3.2 to 4.7% (usually 4.0 or less) of total length; snout somewhat flattened but not bulbously conical. Eyes smaller and about 0.9 to 1.4% of total length, dorsolateral in position with prominent lateral head ridges below them. Upper symphysial teeth usually absent; three rows of large upper anterior teeth on either side of symphysis; anterior teeth with stout broad-tipped cusps and short and strongly hooked cusplets; anterior teeth enlarged with largest (second lower anterior) about 1.3 to 1.5% of total length; lateral teeth compressed, blade-like and with flattened cusps; posterior teeth strongly differentiated from lateral teeth, with cusps and cusplets reduced or absent and teeth molariform and carinate. Claspers tapering. First dorsal-fin base far posterior and closer to pelvic-fin bases than to pectoral-fin bases, with pre-first dorsal-fin length 48 to 58% of precaudal length; first dorsal-fin origin well behind inner margins of pectoral fins, insertion about over pelvic-fin origins. Second dorsal fin about as large as first dorsal fin. Anal fin about as large or slightly larger than dorsal fins; anal-fin origin under midbase of second dorsal fin. Irises of eyes light greenish.

Carcharias taurus Rafinesque, 1810 — Fig. 52

Carcharias taurus Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1:10, pl. 14, fig. 1. Holotype unknown; type locality, Sicily, Mediterranean Sea. Placed on the Official list of Specific Names in Zoology by the International Commission on Zoological Nomenclature (1987, Opinion 1459.4, *Bull. Zool. Nomencl.*, 44(3): 216).

Synonyms: ***Squalus americanus*** Mitchell, 1815: 483. No types known according to Eschmeyer (1998: CD-ROM). Type locality, New York. Not ***Squalus americanus*** Gmelin, 1788, = ***Dalatias licha*** (Bonnaterre, 1788). ***Squalus macrodous*** Mitchell, 1818: 328. Replacement name for ***S. americanus*** Mitchell, 1815. ***Squalus littoralis*** Le Sueur, 1818: 224. Holotype: 91 cm specimen, New York, possibly not extant. ***Squalus littoralis*** Mitchell, 1818: 328. Types unknown. Apparently a junior homonym of ***S. littoralis*** Le Sueur, 1818 according to Eschmeyer (1998: CD-ROM). ***Carcharias griseus*** Ayres, 1842: 58-59 (*nomen nudum*); Ayres, 1843a: 288 (no distinguishing features), Ayres, 1843b: 293, pl. 12, fig. 4. Type locality, Long Island, New York. No types according to Eschmeyer (1998: CD-ROM). ***Odontaspis americanus*** Abbott, 1861: 400 (new combination validates name?). ?***Carcharias tricuspidatus*** Day, 1878: 713, pl. 186, fig. 1. Figured from a skin about 373 cm TL, apparently lost (P.K. Talwar, pers. comm.), India (see remarks below). ?***Odontaspis cinerea*** Macleay, *in* Ramsay, 1880: 96. Port Jackson, New South Wales, name only, in footnote. ?***Carcharias cuspidatus*** Ogilby, 1888?: 1767. Reference in Fowler (1941: 122), but Ogilby, 1888 spelled it correctly as ***C. tricuspidatus***, hence possibly an error by Fowler? Australia. ***Lamna ecarinata*** Hemprich and Ehrenberg, 1899: 8, pl. 6, fig. 1. Holotype, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB 4532, a stuffed 846 mm female according to Paepke and Schmidt (1988: 163), Alexandria, Mediterranean Sea. ***Carcharias arenarius*** Ogilby, 1911: 37. Holotype: Queensland Museum, Brisbane, QM I.1884 (dry mount) according to Eschmeyer (1998: CD-ROM), Moreton Bay, Queensland. ***Carcharias owstoni*** Garman, 1913: 24. Holotype, Museum of Comparative Zoology, Harvard, MCZ-1278, 920 mm TL newborn or late foetal male, Sagami Sea, Japan. Status confirmed by Hartel and Dingerkus (1997) with catalogue number MCZ-1278-S. ?***Squalus lixa*** Larrañaga, 1923: 391. Reference from Eschmeyer (1998: CD-ROM); apparently a *species dubium* and *nomen nudum*, possibly referable to this species). ***Odontaspis platensis*** Lahille, 1928: 324, figs 13-16, pl. 3 (upper fig.). Syntypes: Possibly three syntypes, a 2.33 m specimen from Panela, near Montevideo, Uruguay, a jaw from Necochea, Quequen, Argentina, and a 2.27 m female (on which the description is primarily based) from Bahia Blanca, Argentina, status uncertain. ***Odontaspis tricuspitatus*** Fang and Wang, 1932: 241, fig. 12. Chefoo, China, apparently a spelling error for ***Carcharias tricuspidatus***.

Other Combinations: ***Eugomphodus taurus*** (Rafinesque, 1810), ***Odontaspis taurus*** (Rafinesque, 1810), ***Triglochis taurus*** (Rafinesque, 1810), ***Synodontaspis taurus*** (Rafinesque, 1810), ***Carcharias littoralis*** (Le Sueur, 1818), ***Odontaspis griseus*** (Ayres, 1843), ***Eugomphodus griseus*** (Ayres, 1843), ***Odontaspis littoralis*** (Le Sueur, 1818), ***Eugomphodus littoralis*** (Le Sueur, 1818), ***Carcharias americanus*** (Mitchell, 1815), ***Odontaspis tricuspidatus*** (Day, 1878), ***Carcharias platensis*** (Lahille, 1928).

FAO Names: En - Sand tiger shark; **Fr** - Requin taureau; **Sp** - Toro bacota.

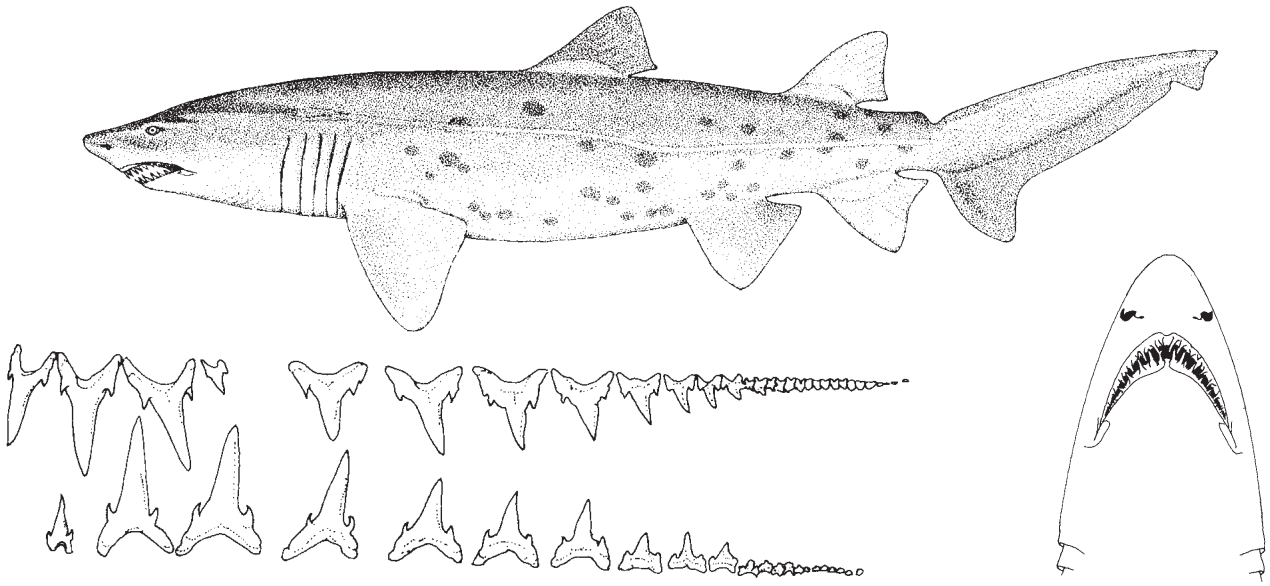
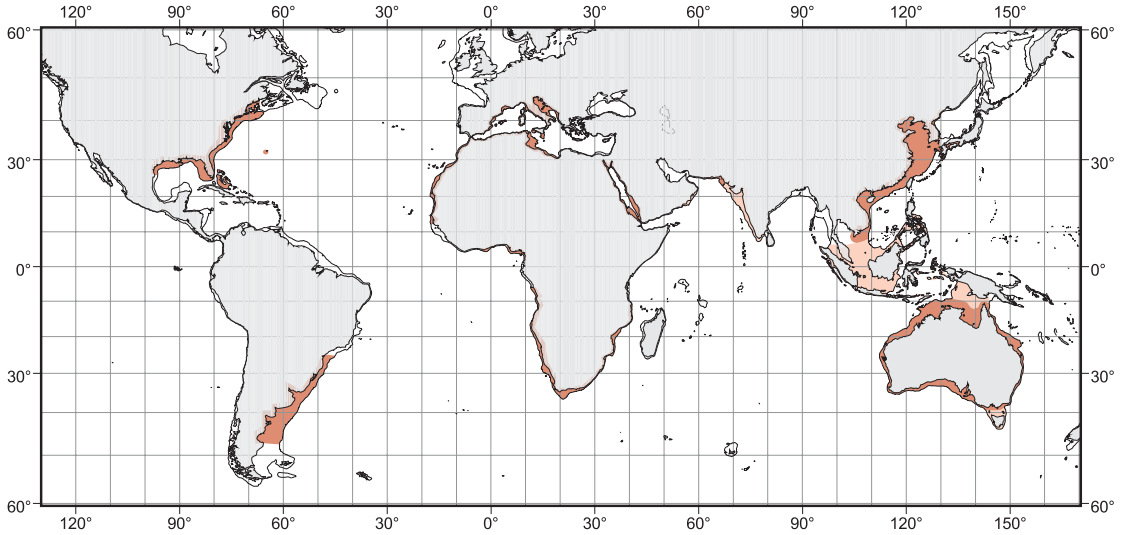


Fig. 52 ***Carcharias taurus***

Field Marks: A large, bulky shark with a flattened-conical snout, eyes without nictitating eyelids, mouth long and extending behind eyes, teeth large with prominent narrow cusps and lateral cusplets, upper anterior teeth separated from lateral teeth by small intermediate teeth, anal fin and both dorsal fins equally large and broad-based, first dorsal fin on back closer to pelvic fins than to pectoral fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe. **Colour:** light brown, often with darker reddish or brownish spots scattered on body, eyes with light green irises.

Diagnostic Features: See genus ***Carcharias*** above.

Distribution: Wide-ranging in warm-temperate and tropical coastal waters of the Atlantic Ocean, Mediterranean Sea, and Indo-West Pacific Ocean; absent from the Central Pacific and eastern Pacific Oceans. Western Atlantic: Canada (Gulf of Maine: New Brunswick, rare), USA (Cape Cod, Massachusetts, New York, Rhode Island, Connecticut, New Jersey, Delaware, Maryland, Virginia, North Carolina, South Carolina to Florida, northern Gulf of Mexico including western Florida, Louisiana and Texas), Bahamas, Bermuda; southern Brazil to Uruguay and Argentina. Eastern Atlantic: Mediterranean to Canary Islands, Morocco, Western Sahara, Mauritania, Sao Tome and Principe, Cape Verde Islands, Senegal, Ghana, southern Nigeria to Cameroon, Angola, Namibia, and South Africa (Western Cape). Indo-West Pacific: South Africa (entire east coast), Mozambique, possibly Providence, Farquhar and Cerf Islands (western Indian Ocean), Red Sea, ?Oman, Pakistan, ?India. Western Pacific: ?Indonesia (Laiwui, Obi Major, Aru Islands), ?Malaysia, Viet Nam, ?Philippines, Japan, Taiwan (Province of China), China; Australia (Queensland, New South Wales, Victoria, South Australia, Northern Territory, Western Australia; Tasmanian records need confirmation).



Habitat: An inshore and offshore, littoral shark. This shark occurs in the surf zone off sandy and rocky beaches, in shallow bays, on offshore banks and reefs, in underwater caves, in troughs on sandy areas, and around coral and rocky reefs from the intertidal less than 1 m deep down to at least 191 m, with most at depths of 15 to 25 m. This species is often found near or on the bottom but also occurs in midwater or at the surface.

Biology: A common or formerly common to abundant shark, present in large aggregations during breeding. It is a strong but slow midwater swimmer that is more active at night. This shark is denser than water, but it swallows air at the surface and holds it in its stomach to maintain approximately neutral buoyancy. Like a bony fish with a swim bladder, it can readily halt and hover motionless in the water (*stalling*).

This species occurs as solitary individuals or in small to large aggregations or schools, ranging from 20 to at least 80 individuals in Australia and South Africa. It is strongly migratory in parts of its range, particularly in its northern and southern extremities where pronounced poleward migrations occur in summer and equatorial movements in autumn and winter (Australia, the east coast of the USA, and the east coast of South Africa). Aggregations of individuals occur for feeding, courtship, mating and birth. In Australia sexual segregation and separate migration of the sexes may occur off the east coast of Australia, with males predominant off southern Queensland during the winter and females off New South Wales. Off South Africa courtship and mating apparently occurs in the more tropical parts of its range, while pregnant females give birth in warm-temperate waters. In North America, nursery areas are not well-defined, and it may give birth along its entire range there during March and April.

The behaviour of this shark has been studied in captivity (Gordon, 1993), in a large shark tank housing sand tigers (young and adult), wobbegongs (***Orectolobus***), grey sharks (***Carcharhinus***), sevengills (***Notorynchus***), stingrays, and reef and pelagic teleosts. These studies have shown evidence of complex behaviour, including social interactions (with courtship and mating) between three adult sharks and asocial interactions with other marine vertebrates and divers. A dominance hierarchy was recorded among three adult sharks (two males and a female). Behaviour patterns observed include stalling (shark stops swimming and hovers above the bottom), *nosing* (male comes behind and below female, and places his snout just below her cloaca); *tailing* (male closely follows another male, his head interfering with normal caudal movement of the leading shark), *submissive behaviour* (or *bowing*, female swims slowly, with body angled about 15° downward, exposing the pelvic fins, and just prior to copulation), *cupping* and *flaring* (female depresses her pelvic fins into a cup-shape, then flares them outward, exposing the cloaca), *snapping* (males give quick bites to other fishes in the tank and then withdraws), *stalking* (close circling and passing of other fishes and divers), *clasper flexion* (movements of individual claspers forward and rearward), *clasper splaying* (claspers spread laterally), *clasper crossing* (claspers crossed with tips posterolateral), *shielding* (female swims close to bottom to protect her cloaca), and *scarring* (infliction of light bites by both males and females).

Most of the behaviours were observed during courtship and mating. The two adult males became reluctant to feed, and aggressive toward other fishes, particularly the grey sharks. The adult female slowed over large sand flats, cupped her pelvic fins when a male approached, and the two males lightened in colour and began ‘defending’ the sand flat area and presumably the female, snapping, stalking and tailing at immature sand tigers, other sharks and divers. Snapping and tailing resulted in one male driving off the other without scarring it. The dominant male then would bite the female on the anal fin forward to the pectoral fin, and the female would turn and bite the male, then return to patrol the sandy areas. Shielding also occurred, and cupping and flaring of the female’s pelvic fins, while the male responded by nosing. Over a few days of courtship between the dominant male and the female, the dominant male eventually grabbed the female by the right flank and pectoral fin, contorted his body toward the female, and inserted his right clasper in her cloaca for a few minutes, then broke away and showed little further interest. Additional scarring on the female suggested that a secondary mating had occurred in one instance.

Reproduction in this species is better known than in most other lamnoids and features uterine cannibalism or cannibal vivipary. Gilmore, Dodrill and Linley (1983) give a detailed and fascinating account of the reproduction of the sand tiger shark, documenting the sequence of intrauterine nourishment in this species, in which a successful embryo progresses from using stored yolk through killing and eating other embryos to eating unfertilized eggs, for a 9 to 12-month gestation period. There are normally two young in a litter, one per uterus. Eggs leave the ovaries, and while in transit in the oviducts are fertilized and enclosed in groups of 16 to 23 in egg cases. However, at some time between fertilization and birth only one embryo of its group prevails, apparently by devouring its rivals, and this proceeds to eat fertilized eggs and smaller potential siblings *in utero* until birth. Unlike ovoviviparous non-cannibal and viviparous species, the yolk sac is reabsorbed at a small size, less than 17 cm, and the umbilical scar may be lost. At 17 cm, foetuses have sharp, functional teeth and are feeding; at about 26 cm, they can swim *in utero*; late foetuses are near 1 m long and one bit the hand of an investigating scientist (Stewart Springer). This species may breed every other year, with a rest year between pregnancies.

This species is thought to deposit two growth rings in its vertebrae per year, with males becoming adult at about five years and females at over six. Growth rings indicate animals growing to at least ten years old, with one adult male surviving nearly 17 years in captivity in South Africa. Growth is rapid over the first five years, but declines beyond 10 years and is virtually absent at 16 years.

The sand tiger primarily feeds on a wide variety of bony fishes (teleosts), with elasmobranchs an important secondary prey; crustaceans, cephalopods, and marine mammals are also taken. Bony fish prey includes herring (Clupeidae), anchovies (Engraulidae), hake (Merluccidae), eels (Anguillidae), monkfish or anglers (Lophiidae), cusk eels (Ophidiidae), lizardfish (Synodontidae), sea catfish (Ariidae), croakers (Sciaenidae), Australian salmon (Arripidae), morwong (Cheilodactylidae),

rock blackfish or opaleyes (Girellidae), bluefish, elf or taylor (Pomatomidae), mackerel and bonito (Scombridae), butterfishes (Stromateidae), snappers (Lutjanidae), wrasses (Labridae), mullet (Mugilidae), spadefish (Chaetodipteridae), sea robins (Triglidae), flatheads (Platycephalidae), duckbills (Percophidae), midshipmen (Batrachodidae), sea basses (Serranidae), porgies or sea bream (Sparidae), jacks (Carangidae), remoras (Echeneidae), flatfish (Pleuronectiformes) including soles (Soleidae), American soles (Achiridae), Atlantic flounders (Scophthalmidae), and righteye flounders (Paralichthyidae), and undoubtedly many others. Elasmobranch prey includes requiem sharks (Carcharhinidae), houndsharks (Triakidae), angel sharks (Squatinidae), skates (Rajidae) and their egg cases, and eagle rays (***Aetobatus*** and ***Myliobatis***, Myliobatidae). Invertebrate prey includes squid (Loliginidae), crabs, lobsters and hermit crabs (Paguridae). Plant material is rarely found in stomach contents, and presumably is accidentally ingested along with animal prey. Off Uruguay, Praderi (1985) found pinniped remains (7 individuals out of 12 identified as sea lion, ***Otaria***) in 2% of 557 stomachs of the sand tiger shark, as well as wounds attributable to this species on two Franciscana dolphins (***Pontoporia blainvillei***; not necessarily from predation). Schools of this shark have been observed feeding cooperatively, surrounding and bunching schooling prey and then feeding on them, and may use tail-slapping to scare and confuse schooling carangids. Australian and South African sharks sometimes have hydroid growths on their teeth, suggesting that the sharks were not feeding at the time.

Size: Maximum total length at least 318 cm, with recent records from shark meshing operations in Australia suggesting a maximum of at least 4.3 m. Older accounts attribute a size of at least 6.1 m to this species (Day, 1878), but this is unlikely. Size at birth 95 to 105 cm. Males maturing at about 190 to 195 cm with adults 220 to 257+ cm; females maturing at 220 cm or more and reaching 300+ cm, with immatures up to 225 cm.

Interest to Fisheries and Human Impact: This shark is generally fished commercially wherever it occurs, but particularly in the western North Pacific (where it is highly prized for food), off tropical west Africa, in the northern Indian Ocean (India and Pakistan), and in the western Atlantic (where it has a lesser value as a food-fish in the western North Atlantic but has been fished for hides and fins). Caught with line gear, but also with fixed bottom gill nets and in pelagic and bottom trawls. It is of only moderate importance to commercial fisheries in comparison to more abundant carcharhinids. The meat of this shark is utilized for human consumption (utilized fresh, frozen, smoked and dried-salted), carcasses for fishmeal, hides for leather (the skin is very thick and tough, but hides can be spoiled by mating scars), liver for oil, fins for the oriental sharkfin trade, and jaws and teeth for trophies and ornaments. In Australia (New South Wales) the flesh has been found to have high mercury levels (about ten times the permitted maximum), making the species unsuitable for human consumption.

The sand tiger is sought by anglers in fishing competitions because of its size (South Africa), but it is sluggish when hooked and generally does not give much of a fight. Divers using powerheads and poisoned spears found this slow-moving species an easy target in Australia and to a much more limited extent in South Africa. Such crude and barbaric sport, analogous to shooting domestic cattle with a pistol, caused a severe decline in the number of these sharks in Australia and has been banned since 1984. South African divers stopped shooting ragged-tooth sharks many years ago. Australian anglers agreed to a ban on catching sand tiger sharks in 1979. These sharks are caught live for the public aquarium trade, but the number of sharks involved in the trade is not recorded and is probably small. Separate catch statistics for this shark are not reported to FAO.

This species formerly had a bad reputation as a ‘maneater’ in Australian waters, but apart from shark-attack hyperbole this is apparently due to confusion with other species, particularly requiem sharks (Carcharhinidae) but possibly the white shark. Observations of this shark underwater suggest that it is primarily inoffensive and not aggressive toward people when not provoked, though its size and jagged dentition should invite respect. However, it occasionally harasses and rarely bites divers, particularly when they are spearfishing or possibly when adults are courting. This shark will steal fish off stringers and spears underwater, underlining the desirability of boating one’s catch when this shark or others are about. Relatively few valid instances of this shark biting people have been reported, and minimalist bites on divers off South Africa and elsewhere suggest non-predatory behaviour and possibly agonistic activity similar to scarring bites delivered to conspecifics, other species of sharks and occasionally to divers in aquaria. Divers view aggregations of these sharks off Australia (particularly off New South Wales), South Africa and the east coast of North America. There are regular charter tours that include places frequented by congregations of these sharks. Interest in ecotouristic diving on sand tiger sharks is high in Australia, leading to potential problems such as too many divers driving away sharks in a given area, and feeding of sharks resulting in possible incidents of biting. Management of diving contact with sand tiger sharks may be required in the future, as with white sharks. Capture, tagging and live release of sand tiger sharks by recreational anglers and scientists occurs in South Africa and elsewhere, and sonic tagging is planned in Australia to trace movements.

This shark is prized as an exhibit in large aquaria and oceanaria and is regularly shown in the United States, Europe, Australia and South Africa. It is very hardy and docile in captivity, grows to adult size and can live for decades in aquaria, can be kept with other sharks and fishes (although it sometimes may prey on fishes and will bite and sometimes kill other sharks), and makes an impressive display because of its showy, toothy, ‘sharky’ appearance, large size, and amenability to being approached and even fed underwater by divers. An aquarium in Cape Town, South Africa allows ecotouristic divers to swim with these sharks in their giant oceanic tank. Adults will court and even give birth in adequate tank facilities.

The conservation status of this species is of concern because of its vulnerability to fisheries and recorded declines off eastern North America and Australia. It is listed as a vulnerable species by IUCN in its Red List of Threatened Animals. It congregates in large numbers in coastal areas during the breeding season, and is readily accessible to commercial fishers who can catch it with little effort. It began to decline dramatically off New South Wales, Australia, in the 1960s due to fisheries, including shooting by sports divers, and catches in anti-shark nets dropped thirty-fold. It was fully protected off

New South Wales in 1984, and later off Queensland and in all Commonwealth waters of Australia, as well as in federal waters of the eastern coast of the USA. However, despite it having a midrange intrinsic rebound potential (Smith, Au and Show, 1998), the population off New South Wales has not shown signs of recovery and a new recovery plan is being drafted by the Australian Government (Environment Australia, 2000a).

A burgeoning fishery for sand tigers along the east coast of the United States during the 1990s caused local catches to plummet off North Carolina, Florida and Chesapeake Bay, and the species was given total protection from sports and commercial fisheries in 1997.

There is a proposal under consideration by the South African Sea Fisheries Research Institute (now Marine and Coastal Management) to decommercialize catches of this species, allowing it only to be fished by sports anglers. Unfortunately, relatively little is known of trends in other places in which sand tiger sharks have been heavily fished, including the western North Pacific, western South Atlantic and eastern North Atlantic.

Local Names: Sand shark, Sand tiger shark, Sand tiger (USA); Tiburón, Sarda, Tiburón de leznas (Argentina); Lamio, Verdoun, Odontaspide taureau (France); Odontaspe tauro, Carcharia tauro, Triglochide tauro, Pisci cani (Italy); Pez toro (Spain); Psina zmijozuba sivka (Adriatic); Sarda (Canaries); Requin sable, Requin sable tachete (Senegal); Grey nurse shark, Grey nurse, Sand shark, Shovel-nosed shark (Australia); Shirowani, Umiwani, Owston's sand shark (Japan); Shovelnose shark, Sand tiger, Yellow shark, Brown shark, Grey shark, Tiger shark, Grey-nurse (English); Ragged-tooth or Raggedtooth shark, Spotted ragged-tooth or Raggedtooth shark, Raggie, Yellow belly, Blue nurse shark, Spikkel-skeurtandhaai (South Africa); Indian sand tiger, Requin taureau bambak, Toro bambaco, Blue nurse shark, Blue nurse, Dundanee (India); Ca nham nhon, Ca nham nhan (Viet Nam).

Remarks: Included as synonyms of ***Carcharias taurus*** are a number of regional species that have often been considered valid in the older literature, but which are most likely local representatives (or at most local subspecies) of a single, wide-ranging species. The dentitional characters most often used to distinguish several of these species (see Bigelow and Schroeder, 1948) apparently vary considerably within samples from a given area (Applegate, 1965; Sadowsky, 1970; Taniuchi, 1970). Regional names include ***Squalus americanus*** and its synonyms from the western North Atlantic, ***Odontaspis platensis*** from the western South Atlantic, ***Carcharias tricuspidatus*** from the Indian subcontinent, ***C. owstoni*** from the western North Pacific, and ***C. arenarius*** from Australia. Abe et al. (1968, 1969), Sadowsky (1970), Taniuchi (1970), and Whitley and Pollard (1980) have all used the species name ***taurus*** for the local representatives of the species formerly named ***owstoni***, ***arenarius*** and ***platensis***. ***Carcharias taurus*** itself has been placed in different genera as ***Odontaspis taurus***, ***Eugomphodus taurus*** and ***Synodontaspis taurus***.

Carcharias tricuspidatus was distinguished by Compagno (1984) from ***C. taurus*** by characters from Day's (1878) original description. A problem was that these characters could not be confirmed in recent accounts or specimens of this species from the Indian subcontinent. Compagno (1984) suggested that ***C. tricuspidatus*** may be a junior synonym of ***C. taurus*** as with other regional species of ***Carcharias***. Day's (1878) original description stated that ***C. tricuspidatus*** lacked labial furrows and pictured it as having a broadly rounded snout (***C. taurus*** has a rounded-angular snout and well-developed labial furrows). However, since the species was described from a skin, now lost, it is possible that the reported snout shape is in error and that the labial furrows were overlooked. Day's (1878, pl. 186, fig. 13) drawing of the snout of his ***C. tricuspidatus*** may even be based on ***Negaprion acutidens***, though the lateral view and tooth illustrated are very similar to those of ***Carcharias taurus***. An alternative is that the drawing is inaccurate and sketchy, as with several others of Day's shark drawings, and might reflect problems Day had in interpreting the holotype. During a trip to India in 1982, the writer was unable to examine any specimens of ***Carcharias*** from India (which is apparently much less common there than large carcharhinids) and was unable to confirm or deny the validity of this species. Compagno (1984) left this as a species dubium, but further consideration leads me to place it as a tentative synonym of ***C. taurus*** as suggested by ***C. taurus*** material I examined in the Pakistan collection of the Los Angeles County Museum of Natural History.

Literature: Rafinesque (1810); Day (1878); Garman (1913); Whitley (1940); Bigelow and Schroeder (1948); Springer (1948); Cadenat (1956); D'Aubrey (1964a,b); Applegate (1965); Abe et al. (1968, 1969); Lineaweaver and Backus (1970); Taniuchi (1970); Sadowsky (1970); Bass, D'Aubrey and Kistnasamy (1975a); Gilmore, Dodril and Linley (1983); Compagno (1984); Govender, Kistnasamy and van der Elst (1991); Gordon (1993); Michael (1993); Musick, Branstetter and Colvocoresses (1993); Branstetter and Musick (1994); Last and Stevens (1994); Pollard, Smith and Smith (1996); Hoese and Moore (1998); McEachran and Fechhelm (1998); Smith, Au and Show (1998); Castro, Woodley and Brudek (1999); Gelsleichter, Musick and Nichols (1999); Environment Australia (2000a).

Odontaspis Agassiz, 1838

Genus: ***Odontaspis*** Agassiz, 1838, *Recher. Poiss. Foss.*, 3: 86, 87. Placed on the Official List of Generic Names in Zoology (Name no. 1659) by the International Commission on Zoological Nomenclature (1965, Opinion 723.3c, *Bull. Zool. Nomencl.*, 22(1): 33).

Type Species: ***Carcharias ferox*** Risso, 1826 by monotypy, equals ***Squalus ferox*** Risso, 1810. This genus takes precedence over ***Carcharias*** Rafinesque, 1810 when the two are considered synonyms, by special endorsement of the International Commission on Zoological Nomenclature (1987, Opinion 1459.3, *Bull. Zool. Nomencl.*, 44(3): 216).

Number of Recognized Species: 2.

Synonyms: None.

Field Marks: Large bulky sharks with bulbous conical snouts, eyes without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and lateral cusplets, upper anterior teeth separated from lateral teeth by small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin, all three broad-based, first dorsal fin on back closer to pectoral fins than to pelvic fins, only upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe. **Colour:** blackish to light brown, eyes with black irises.

Diagnostic Features: Snout longer with preoral length 0.8 to 1.2 times mouth width and 4.4 to 7.8% (usually over 5%) of total length; snout long and bulbously conical. Eyes moderately large and about 1.6 to 2.8% of total length, lateral in position without lateral-head ridges below them. A pair of upper symphysial tooth rows present or absent; two rows of large upper anterior teeth on either side of symphysis; anterior teeth with slender narrow-tipped cusps and long straight or weakly curved but not hooked cusplets; anterior teeth smaller with largest (second lower anterior) about 1% of total length; lateral teeth little compressed and not blade-like and with little-flattened cusps; posterior teeth grading into lateral teeth, with prominent cusps and cusplets and not molariform. Claspers cylindrical and blunt-tipped. First dorsal-fin base more anterior and closer to pectoral-fin bases than to pelvic-fin bases and with pre-first dorsal-fin space 43 to 49% of precaudal length; first dorsal-fin origin over inner margins of pectoral fins, insertion well anterior to pelvic-fin origins. Second dorsal fin about half as large as first dorsal fin. Anal fin subequal to or somewhat smaller than second dorsal; anal-fin origin under or behind second dorsal-fin insertion. Irises of eyes black.

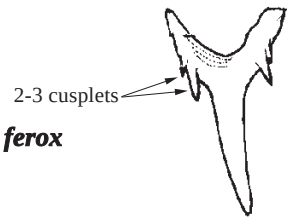
Local Names: Deepwater sand tigers.

Remarks: Following Compagno (1984) and Cappetta (1987), this account restricts the genus ***Odontaspis*** to species related to ***O. ferox***, including the living ***O. ferox***, ***O. noronhai***, and fossil species. ***O. noronhai*** needs further study of its anatomy to clarify differences between it and ***O. ferox*** and between ***Odontaspis*** and ***Carcharias***. Data on vertebral counts, vertebral calcification patterns, cranial and fin skeletal morphology, and clasper morphology were unavailable for ***Odontaspis noronhai***.

Key to Species:

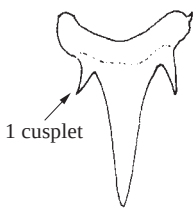
1a. Teeth mostly with two or three cusplets on each side of cusp (Fig. 53); colour grey or grey-brown above, lighter below, often with darker spots on sides but without a white-tipped first dorsal fin . . . . ***Odontaspis ferox***

1b. Teeth mostly with only one cusplet on each side of cusp (Fig. 54); colour dark reddish brown to blackish brown or black above and below, first dorsal fin often with a white blotch on its tip . . . . . ***Odontaspis noronhai***



UPPER ANTERIOR TOOTH

Fig. 53 ***Odontaspis ferox***



UPPER ANTERIOR TOOTH

Fig. 54 ***Odontaspis noronhai***

Odontaspis ferox (Risso, 1810) Fig. 55

Squalus ferox Risso, 1810, *Ichthyol. Nice, Paris*: 38. Holotype unknown; type locality off Nice, France, in the Mediterranean Sea. Also, ***Carcharias ferox*** Risso, 1826, *Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons*, 3: 122. Description virtually verbatim that of ***Squalus ferox*** Risso, 1810, and quite evidently a generic translocation, not a new species name. Placed on the Official List of Specific Names in Zoology (Name no. 2057) by the International Commission on Zoological Nomenclature (1965, Opinion 723.4.c: 33).

Synonyms: ***Odontaspis herbsti*** Whitley, 1950: 234, fig. 1, pl. 17, fig. 1. Holotype: Australian Museum, Sydney, AMS-IB.2136, 168 cm immature male, Gabo Island, New South Wales, 137 m depth.

Other Combinations: None.

FAO Names: En - Smalltooth sandtiger; **Fr** - Requin féroce; **Sp** - Solrayo.

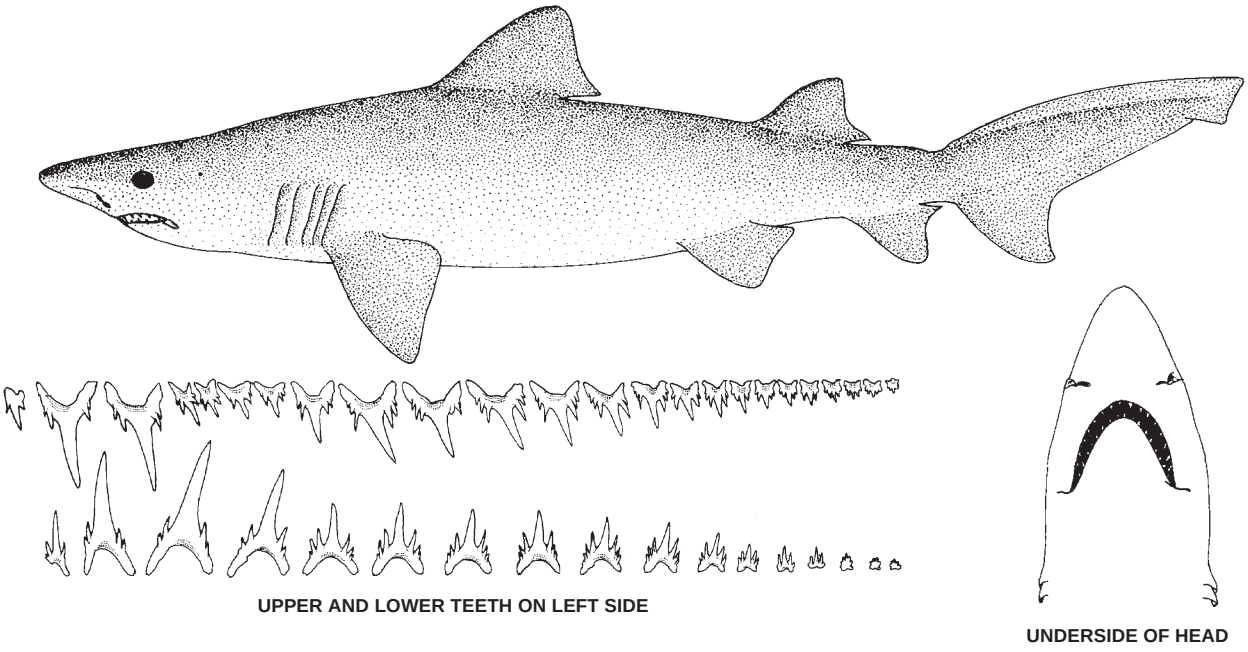
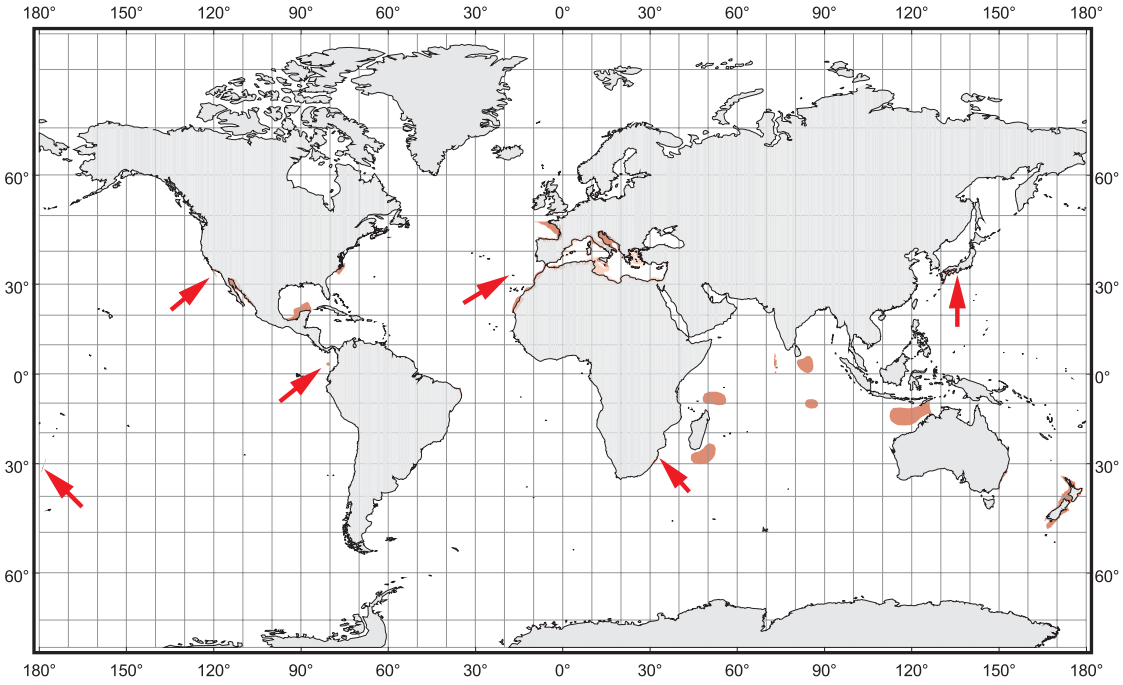


Fig. 55 ***Odontaspis ferox***

Field Marks: A large, bulky shark with a long bulbously conical snout, eyes moderately large without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and two or more pairs of lateral cusplets, upper anterior teeth separated from lateral teeth by 2 to 5 rows of small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin but broad-based, first dorsal fin on back and closer to pectoral fins than pelvic fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe, colour medium grey or grey-brown above, usually lighter below, sometimes with darker spots scattered on body.

Diagnostic Features: Two to five (mostly four) rows of small intermediate teeth between upper anterior and lateral tooth rows; a pair of upper and a pair of lower symphysial teeth present; tooth rows numerous, 48 to 56/36 to 46 (88 to 102 total); root lobes of anterolateral teeth deeply arched and narrow; anterolateral teeth usually with 2 or 3 pairs of lateral cusplets. Pectoral fins angular. First dorsal apex subangular in adults. Anal fin with height 4.6 to 6.0% of total length. Anal fin with strongly concave posterior margin. Caudal fin with ventral caudal lobe short but stout. **Colour:** medium grey or grey-brown above, lighter below, with darker dusky spots on sides of some individuals; fins dusky with blackish edges in young but uniform dusky in adults, first dorsal fin without a white blotch.

Distribution: Possibly circumglobal in warm-temperate and tropical waters but spottily distributed. Western Atlantic: Mexico (Campeche Bank), United States (North Carolina), Brazil (NE Natal). Eastern North Atlantic: France (Bay of Biscay), Madeira, Morocco, Western Sahara, Mediterranean (Algeria, Italy, Adriatic, Lebanon). Western Indian Ocean: South Africa (KwaZulu-Natal), NE and SE of Madagascar in open ocean?, Maldives, open ocean SSE of Sri Lanka, SW of Sumatra and W of northern Australia. Western Pacific: Japan (Oshina Islands, SE Honshu off Izu-Shichito Islands), Australia (New South Wales), New Zealand and Kermadec Islands. Central Pacific: Hawaiian Islands (Oahu; record of "***O. owstoni***" from Pedestal Seamount in the Hawaiian range possibly this species or ***O. noronhai***?). Eastern Pacific: United States (southern California), Mexico (Gulf of California, Baja California), Colombia (Malpelo Island). A cosmopolitan distribution has been proposed for this species (Bonfil, 1995) and further exploration of deepish waters around the world might unveil its presence in still unknown parts of its range.



Habitat: This shark is a little-known inhabitant of deepish water in warm-temperate and tropical seas, on or near the bottom on continental and insular shelves and upper slopes at depths of 13 to 420 m, also possibly epipelagic zone in 140 to 180 m over the ocean floor. Sometimes observed by divers near dropoffs on coral reefs.

Biology: An active-swimming offshore shark, caught and seen as individuals and in small groups. Reproduction is sketchily known in the species, with litter size unknown. An adult female from the Gulf of California had its right ovary filled with hundreds of small eggs and suggests that the species practices uterine cannibalism in the form of oophagy. It is not known if developing foetuses attack and devour each other until only one is left in each uterus as in ***Carcharias taurus***, or if larger litters are possible.

This species feeds on small bony fishes, squid and shrimp. The teeth of this species and of ***Odontaspis noronhai*** are noticeably smaller and less robust than those of ***Carcharias taurus*** (with this species having larger anterior teeth than ***Odontaspis noronhai***), suggesting that both species take smaller and possibly less active prey than ***Carcharias taurus***. Also, the dentitions of both species are more weakly differentiated along the jaws, with their lateral teeth less specialized for cutting than ***Carcharias taurus*** and their posterior teeth not differentiated into specialized crushers. This suggests a more uniform diet of softer prey than in ***C. taurus***.

Apparently the offshore and deepish-water habitat of this species does not allow this shark to regulate its buoyancy by gulping air as in ***C. taurus***; it does however, have a longer body cavity than ***C. taurus***, with a very large, oily liver, and presumably uses this organ as its primary hydrostatic structure.

Off Lebanon, adult individuals confronted by scuba divers may approach quite closely or slowly flee, and have been seen to hover (*stall*), *gape*, do a *U-turn* and do *tail-shake* (shaking their caudal fins vigorously) which may indicate ambiguity or mild agonistic reactions to divers or possibly conspecifics. Individuals have been seen with scars possibly from courtship or possibly low-intensity *scarring*. They occur singly and in small groups and seem to prefer swimming near the bottom, in sandy areas and on rocky reefs, sometimes following gullies or depressions in the reef (I.K. Fergusson, L.J.V. Compagno, K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie, unpublished data).

Size: Maximum total length at least 410 cm and possibly larger; size at birth above 105 cm; male mature at 275 cm, females adult at 364 cm. Specimens recently seen by divers at Malpelo Island are said to be considerably larger than the known maximum, but specimens have not been measured or photographed in such a way as to confirm this.

Interest to Fisheries and Human Impact: This uncommon to rare but wide-ranging species is primarily fished in the Mediterranean Sea and off Japan with bottom gill nets, line gear, and bottom trawls, and less commonly elsewhere. It forms a discarded or utilized bycatch of deepwater line and net fisheries in areas where it occurs. It is used in Japan for human consumption and for its liver, which is very large and oily, and has a reasonably high squalene content. Its flesh is considered far inferior to that of ***Carcharias taurus*** in Japan. This shark has not been recorded as biting people, and recent underwater observations by ecotouristic divers in the Mediterranean and off Malpelo Island in the eastern Pacific suggest that it is essentially docile although sometimes inquisitive when confronted by people. Its conservation status is essentially unknown. It has been protected in Australia since 1984.

Local Names: Bumpytail ragged-tooth shark, Bumpytail ragged-tooth, Ragged-tooth, Knopstert-skeurtandhaai (South Africa); Sand tiger shark, Herbsts or Herbst's nurse shark, Smalltooth sand tiger (Australia); Tiger ragged-tooth (Malpelo Island); Cagnia, Can da denti, Cagnassown de foundo, Carcaria feroce, Lamia, Odontaspe feroce, Pisci cani, Smidiru, Squalo feroce, Triglochide feroce (Italy); Salroig, Surraig, Solraig (Spain); Smalltooth sand tiger, Ragged-tooth shark (Azores); Psina zmij ozuba ruzicua (Adriatic); Ragged-tooth shark (USA, California), Fierce shark, Ôwanizame (Japan).

Remarks: Garrick (1974) recognized ***Odontaspis herbsti*** for members of the genus from New Zealand, Australia, California and Madeira that differed from the Mediterranean ***O. ferox*** only in lacking spots. This was followed by Bass, D'Aubrey and Kistnasamy (1975a) for South African spotless individuals, but Robins et al. (1980: 69) note that specimens from California may have spots or lack them. Observations of live ***O. ferox*** underwater in the Mediterranean Sea and off Malpelo Island also reveals individuals with and without spots (I.K. Fergusson, L.J.V. Compagno. K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie, unpublished data). Apparently presence of spots reflects individual variation in a single species. ***Carcharias taurus*** is also variable in presence or absence of spots.

Literature: Risso (1810); Garman (1913); Maul (1955); Tortonese (1956); Daugherty (1964); D'Aubrey (1964a, b); Abe et al. (1968); Garrick (1974); Bass, D'Aubrey and Kistnasamy (1975); Taniuchi (1983); Compagno (1984); Nakaya (1984); Quero (1984); Gubanov (1985); Seigel and Compagno (1986); Springer (1990); Anderson and Ahmed (1993); Michael (1993); Last and Stevens (1994); Bonfil (1995, 1997); Menni, Hazin and Lessa (1995); Pollard, Smith, and Smith (1995); Villavicencio-Garayzar (1996); Santos, Porteiro and Barreiros (1997); Sheehan (1998); I.K. Fergusson, L.J.V. Compagno, K.J. Graham, F. Fakhoury, W. Noshie and W. Noshie (unpublished data); R. Bonfil (pers. comm.); D. Perrine (pers. comm.); C. Roessler (pers. comm.).

Odontaspis noronhai (Maul, 1955) **Fig. 56**

Carcharias noronhai Maul, 1955, *Notul. Nat. Acad. Nat. Sci. Philadelphia*, (279): 3, figs. 1-4. Holotype: Museu Municipal do Funchal, Madeira, MMF-2691, 1 710 mm female, from off Camara de Lobos, Madeira, between 600 and 1 000 m depth and most likely at 800 to 1 000 m depth.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Bigeye sand tiger; **Fr** - Requin noronhai; **Sp** - Solrayo ojigrande.

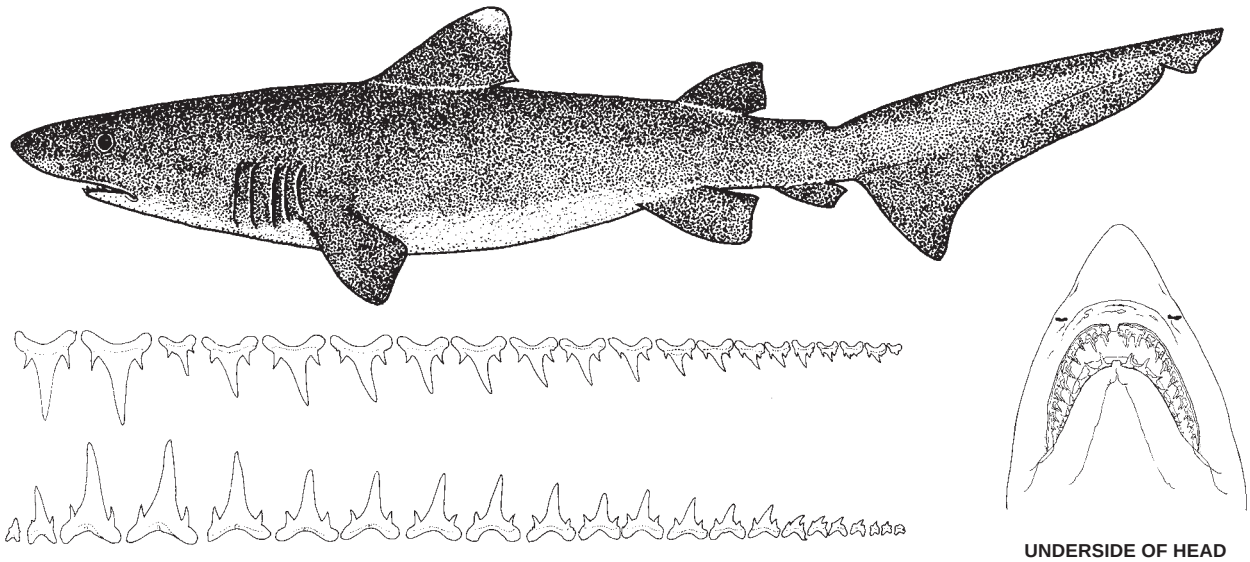
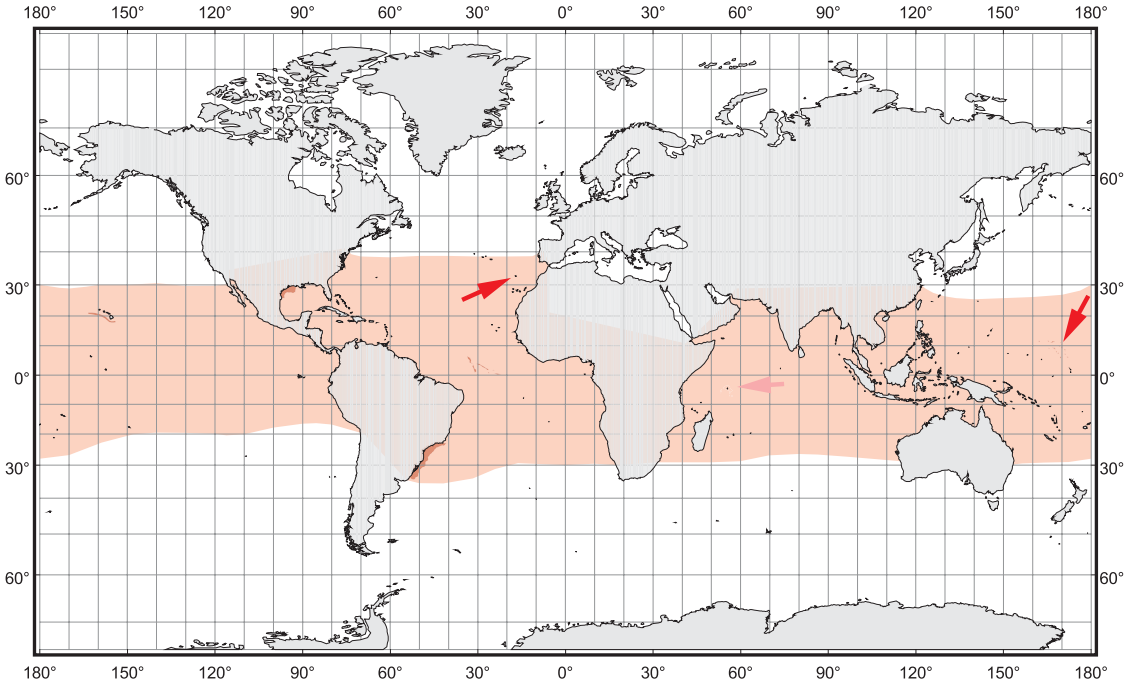


Fig. 56 ***Odontaspis noronhai***

Field Marks: A large, bulky shark with a long bulbously conical snout, eyes very large without nictitating eyelids, mouth long and extending behind eyes, teeth moderately large with prominent narrow cusps and a single pair of lateral cusplets, upper anterior teeth separated from lateral teeth by one or two rows of small intermediate teeth, anal fin and second dorsal fin smaller than first dorsal fin but broad-based, first dorsal fin on back and closer to pectoral fins than to pelvic fins, upper precaudal pit present but lateral keels absent from caudal peduncle, caudal fin asymmetrical but with a strong ventral lobe, colour uniform blackish, dark chocolate brown or reddish brown, without spots, first dorsal fin with a light apical blotch.

Diagnostic Features: One row (occasionally two rows) of small intermediate teeth between upper anterior and lateral tooth rows; a pair of rows or a single row of upper symphysial teeth present, but sometimes absent; usually 2 to 4 pairs of lower symphysial tooth rows present; tooth rows 34 to 43/37 to 46 (71 to 83 total); root lobes moderately arched and broad; anterolateral teeth with a single pair of lateral cusplets. Pectoral fin rounded. First dorsal-fin apex broadly rounded in adult. Anal fin with height 2.4 to 4.5% of total length. Anal fin with straight posterior margin. Caudal fin with ventral caudal lobe hardly developed. **Colour:** background colour of surface black, chocolate brown or dark reddish brown dorsally and ventrally, without dark spots on sides of body; fins black, first dorsal fin often with a white blotch at tip.

Distribution: Possibly circumglobal in all warm seas but as presently known sporadically distributed with very few records in the Atlantic and Central Pacific. Western North Atlantic: USA (Texas, Gulf of Mexico). Central Atlantic off Mid-Atlantic Ridge just north of the Equator. Western South Atlantic: Southern Brazil. Eastern North Atlantic: Madeira. ?Western Indian Ocean: possibly Seychelles. Pacific: South of Hawaiian Islands, USA; off Marshall Islands, possibly South China Sea.



Habitat: Apparently an inhabitant of the continental and insular slopes near the bottom at 600 to 1 000 or more metres and well off it near the surface at 100 m in water 640 m deep, and in the epipelagic and mesopelagic zone of the open ocean at 60 to 450 m in water 4 500 to 5 300 m deep. Its uniform dark coloration, similar to many deepwater oceanic teleosts, suggests a mesopelagic rather than epipelagic habitat, and it could be primarily an oceanic shark rather than a primarily slope-dwelling epibenthic species.

Biology: This is a poorly known deepwater shark. One was caught at night near the Marshall Islands at 75 m with a longline set over water between 4 500 and 5 300 m deep, suggesting that it may migrate vertically to the epipelagic zone at night and descend in the daytime but this cannot be confirmed at present. It may also be migratory and seasonal in distribution, as Brazilian catches were made only during the springtime. Reproduction unknown, feeding habits little known; one specimen had squid beaks and fish otoliths in its stomach. One caught near Hawaii writhed and snapped vigorously when captured.

Size: Maximum at least 3.6 m; males possibly adolescent at 217 cm, three males adult at 326 to 342 cm long; a female immature at 321 cm and another adult at about 326 cm.

Interest to Fisheries and Human Impact: Incidental and apparently rare bycatch of pelagic longliners but little-utilized. The holotype was taken on a vertical longline set by fishermen for black scabbardfish (***Aphanopus carbo***). Presumably taken occasionally by deepwater fisheries with line and net gear, including pelagic gill nets, purse seines and deep-set longlines. It may live mostly below the depths normally fished by horizontal pelagic longlines and purse seines, and is possibly too large to be a regular bottom or pelagic trawl catch. Conservation status unknown.

Local Names: Bigeye sand tiger, Black sand tiger, Oceanic sand tiger.

Remarks: Compagno (1981a) recognized this species on the type description (Maul, 1955) but suggested that it possibly was only an extreme variant of ***O. ferox***. However, descriptions of additional specimens convinced the writer that it is a valid species, readily separable from ***O. ferox*** (Compagno, 1984; Sadowsky et al., 1984; Branstetter and McEachran, 1986; Humpreys, Moffitt and Seki, 1989). Some characters used by Compagno (1984), including the position of the first dorsal-fin origin, more vertical position of the first dorsal-fin margin, and position of the second dorsal-fin origin relative to the pelvic-fin bases, apparently do not hold due to individual variation in ***O. noronhai*** and ***O. ferox***.

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