

A set of jaws possibly from the Seychelles (D. Ward, pers. comm.) has the dentitional characters of this species, and is the basis for the Indian Ocean record of *O. noronhai*. Sadowsky et al. (1984) indicated that a possible alternative locality for this jaw set was the South China Sea.

Literature: Maul (1955); D'Aubrey (1964b); Sadowsky, Amorim and Arfelli (1984); Compagno (1984); Quero (1984); Branstetter and McEachran (1986); Humphreys, Moffitt and Seki (1989); Springer (1990); McEachran and Fechhelm (1998); D. Brogan (pers. comm.); D. Guitart-Manday (pers. comm.); V. Sadowsky (pers. comm.).

2.2.2 Family MITSUKURINIDAE

Family: Family Mitsukurinidae Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 201.

Type Genus: *Mitsukurina* Jordan, 1898.

Number of Recognized Genera: 1.

Synonyms: Family Scapanorhynchidae White, 1936: 4. Type genus: *Scapanorhynchus* Woodward, 1889, a Cretaceous fossil genus (see remarks below).

FAO Names: **En** - Goblin sharks; **Fr** - Requins lutin; **Sp** - Tiburones duende.

Diagnostic Features: Head as long as trunk or slightly shorter. Snout greatly elongated, blade-like and flattened. Eyes small, length 1.0 to 2.4% of precaudal length. Gill openings short, length of first 4.6 to 5.9% 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 protrusible to about opposite snout tip but not greatly distensible laterally. Teeth large, anteriors and laterals very narrow and awl-like, in 35 to 53/31 to 62 (66 to 115 total) rows; three rows of large anterior teeth on each side of upper and lower jaws, the uppers separated from the smaller upper lateral teeth by a gap without intermediate teeth; a pair of lower symphyseal teeth present. Trunk compressed and moderately slender, very soft and flabby. Caudal peduncle compressed and without keels or precaudal pits. Dermal denticles small and rough, with erect spike-like crowns with narrow cusps and ridges; cusps of lateral denticles pointing perpendicular to surface of skin. Pectoral fins short and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, larger than dorsal fins; fin skeleton aplesodic. Dorsal fins small, low, and rounded, or semi-angular, first and second dorsals equal-sized and smaller than the large, rounded anal fin; first dorsal skeleton aplesodic. Second dorsal and anal fins with broad, nonpivoting bases. Caudal fin not lunate, dorsal lobe long but half length of rest of shark or less, ventral lobe not developed. Neurocranium low, with a greatly elongated compressed rostrum, depressed internasal septum and widespread nasal capsules, small orbits with the supraorbital crests reduced to isolated preorbital and postorbital processes, tiny stapedia foramina, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii but no annuli. Total vertebral count 122 to 125, precaudal count 53 to 56, diplospondylous caudal count 68 to 69. Intestinal valve of ring type with 19 turns. Size large, with adults 2.6 to 3.6 m long.

Local Names: Goblin sharks, Chien wên sha k'o; Mitsukurizame-ka (Japan); Akuly domovye (Russia).

Remarks: The living genus *Mitsukurina* has often been synonymized with the Upper Cretaceous fossil genus *Scapanorhynchus* Woodward, 1889 (Woodward, 1899; Regan, 1906a; Goodrich, 1909; Engelhardt, 1913; Garman, 1913; White, 1936, 1937; Berg, 1940; Fowler, 1941; Romer, 1945, 1966; Bigelow and Schroeder, 1948; Berg and Svedovidov, 1955; Matsubara, 1955; Garrick and Schultz, 1963; Norman, 1966; Bass, D'Aubrey and Kistnasamy, 1975a), but the two are apparently generically distinct (Signeux, 1949; Arambourg and Bertin, 1958; Glikman, 1967; Cappetta, 1980, 1987; Compagno, 1973, 1984). The type species of *Scapanorhynchus*, *S. lewisi* (Davis, 1887) is known from whole-bodied specimens that show many differences from *Mitsukurina owstoni* (Cappetta, 1987). Thus *Scapanorhynchus lewisi* has angular dorsal fins, a very long, low subangular anal fin, a more angular, much larger pectoral fin, a caudal fin with a discrete ventral caudal lobe and a more angular terminal lobe, more normal denticles with flattened, expanded tricuspidate crowns, and somewhat different teeth with less expanded and flattened root lobes and often stouter cusps. Some palaeontologists (Glikman, 1967; Shelton P. Applegate (pers. comm.)) place *Scapanorhynchus* in a separate family (Scapanorhynchidae) from *Mitsukurina*, but others (Herman, 1977; Cappetta, 1980, 1987; Carroll, 1988) include them both in the Mitsukurinidae. Despite dentitional and other differences, the presence of a greatly expanded, paddlefish-like rostrum, anteriorly extended subethmoid fossa, elongated anal fin, and bent palatine processes on the palatoquadrates in both genera is strongly suggestive of a relationship between them.

Jordan (1898) proposed a new family, Mitsukurinidae, for the living goblin shark, which was recognized by several subsequent authors (Jordan, 1923; Lozano y Rey, 1928; Whitley, 1940; Glikman, 1967; Compagno, 1973, 1981b, 1984, 1999; Carroll, 1988; Nelson, 1994; Shirai, 1996; Helfman, Collette and Facey, 1997; Eschmeyer, 1998). Following White (1936, 1937), many workers used the family Scapanorhynchidae for the goblin shark (Fowler, 1941, 1947, 1967a, b; Romer, 1945; Bigelow and Schroeder, 1948; Matsubara, 1955; Budker and Whitehead, 1971; Lindberg, 1971; Rass and Lindberg, 1971; Pinchuk, 1972; Bass, D'Aubrey and Kistnasamy, 1975a; Nelson, 1976; Gubanov, Kondyurin and Myagkov, 1986), but Mitsukurinidae Jordan 1898 has priority (Compagno, 1984). Cappetta (1987) and Carroll (1988) also include the fossil

genus *Anomotodon* Arambourg, 1952 in the Mitsukurinidae, and include as a synonym of Mitsukurinidae the family Anomotodontidae Herman, 1979. Several authors (Regan, 1906a; Engelhardt, 1913; Garman, 1913; Bertin, 1939a; Berg, 1940; Fowler, 1941; Berg and Svedovidov, 1955; Arambourg and Bertin, 1958; Norman, 1966; Romer, 1966; Patterson, 1967; Blot, 1969; Nelson, 1984; Eschmeyer, 1990), included *Mitsukurina* as a separate genus or as a synonym of *Scapanorhynchus* in the family Odontaspidae or Carchariidae, while Goodrich (1909) included it in the Lamnidae.

Mitsukurina shows a curious mix of numerous primitive and derived characters that isolate it from other living lamnoids. Compagno (1990b), using morphological characters for a phyletic analysis of Lamniformes, and Long and Waggoner (1996), using dental morphology, suggested that Mitsukurinidae is the sister group of all other living Lamniformes. Recent molecular phyletic studies (Naylor et al., 1997; Martin and Naylor, 1997) have not given unambiguous results on the relationship of Mitsukurinidae to other lamnoids, but one possibility is that Mitsukurinidae is sister to all other taxa. Morphological and molecular studies apparently support the retention of *Mitsukurina* in its own family.

This family includes only a single living species, *Mitsukurina owstoni*, along with fossil species of *Anomotodon*, *Mitsukurina* and *Scapanorhynchus*. Morphological definition of the family is based on the living species.

Mitsukurina Jordan, 1898

Genus: *Mitsukurina* Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 199.

Type Species: *Mitsukurina owstoni* Jordan, 1898, by monotypy.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Mitsukurinidae above.

Mitsukurina owstoni Jordan, 1898

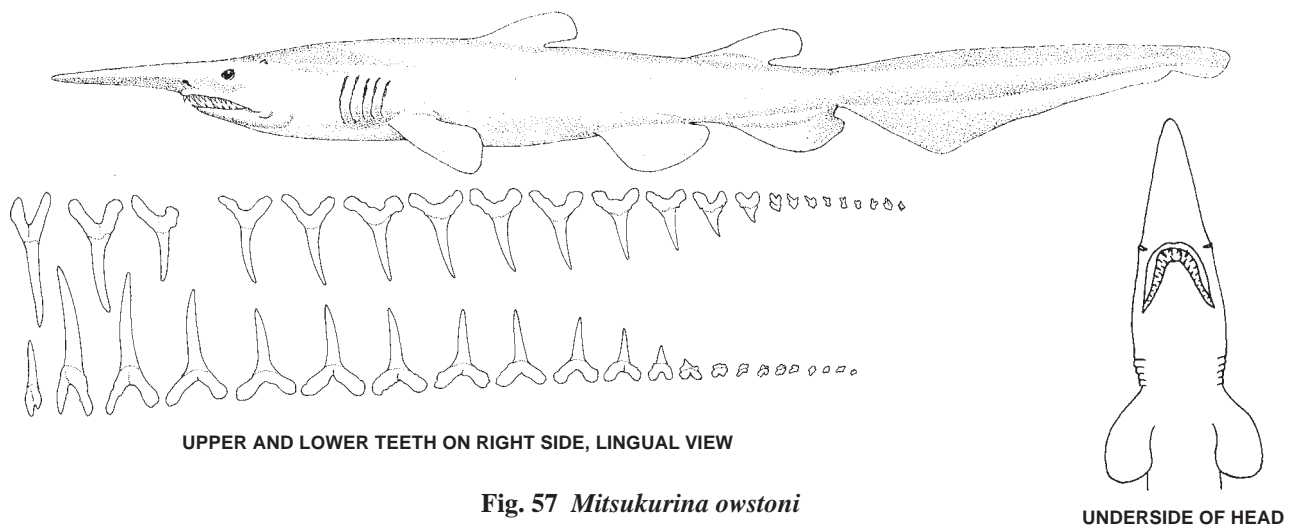
Fig. 57

Mitsukurina owstoni Jordan, 1898, *Proc. Calif. Acad. Sci. ser. 3 (Zool.)*, 1: 200, pls. 11-12. Holotype: Zoological Museum, University of Tokyo, 107 cm immature male, near Yokohama, Japan, in deep water. Holotype lost, according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: *Odontaspis nasutus* de Braganza, 1904: 49, 104, pl. 1, figs. 1-1c. Type locality, Mare de Sezimbra, Portugal, 603 m. Types unknown according to Eschmeyer (1998). *Scapanorhynchus jordani* Hussakof, 1909: 257, text-figs., pl. 44. Syntypes (2): American Museum of Natural History, AMNH-00004SW, jaws, model on display from 1 300 mm female; 1 155 mm female, formerly in the Zoological Department at Columbia University. Type locality, Japan. *Scapanorhynchus dofleini* Engelhardt, 1912: 644. Holotype: Zoologischen Staatssammlung München, 2 100 mm female, Mayegawa, Sagami Sea, Japan. Locality of holotype unknown according to Eschmeyer (1998: CD-ROM). *Scapanorhynchus mitsukurii* White, 1937: 29 (error for *Mitsukurina owstoni* Jordan, 1898). Japan.

Other Combinations: *Scapanorhynchus owstoni* (Jordan, 1898).

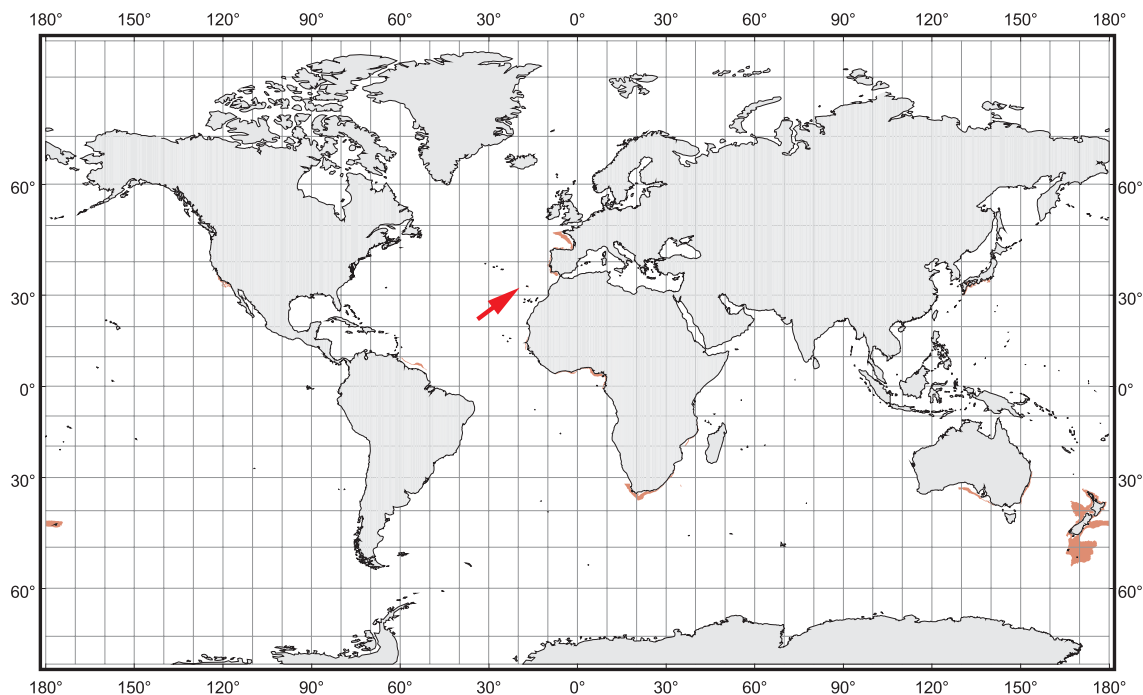
FAO Names: En - Goblin shark; Fr - Requin lutin; Sp - Tiburón duende.



Field Marks: This unmistakable shark has a flat blade-like elongated snout, tiny eyes without nictitating eyelids, soft flabby body, slender very long-cusped teeth in long highly protrusible jaws, two spineless dorsals and an anal fin, and a long caudal fin without a ventral lobe. **Colour:** live and newly-captured individuals are pinkish white, but usually fade to brownish in alcohol.

Diagnostic Features: See family Mitsukurinidae above.

Distribution: Western Atlantic: Guiana, Surinam, French Guyana. Eastern Atlantic: France (Bay of Biscay), Madeira, Portugal, Senegal, Gulf of Guinea, South Africa (Western Cape). Western Indian Ocean: South Africa (Eastern Cape, KwaZulu-Natal), Mozambique (Mozambique seamount range). Western Pacific: Japan, Australia (South Australia, New South Wales), New Zealand. Eastern Pacific: USA (southern California).



Habitat: A poorly known, bottom-dwelling shark that inhabits the outer continental shelves and upper slopes and is found off seamounts, but rarely occurs at the surface or in shallow water close inshore. Most records are on or near the continental slopes between 270 and 960 m deep but down to at least 1 300 m, sometimes in shallower shelf waters at 95 to 137 m. Seamount records suggest that the species is oceanic or semioceanic in addition to its known occurrences off continental slopes.

Biology: Very little is known of the biology of this bizarre shark, which is rare in most places where it is known apart from Japan and possibly Portugal. The long flexible caudal fin, without a ventral lobe, the soft, flabby body, and small, soft paired and unpaired fins, suggest that the goblin shark is a relatively inactive, slow swimming species with a density close to seawater. Its remarkable blade-like snout is superficially similar to those of the chondrosteian paddlefishes (Polyodontidae), and like these fishes may use it as a forward-projecting prey detector. Its slender, pick-like anterior and lateral teeth suggests small, soft-bodied prey including fishes, shrimp and squid, and one specimen was found with fish remains in its stomach. As in *Carcharias taurus*, the posterior teeth of the goblin shark are modified for crushing.

The jaws of the goblin shark are highly specialized for rapid projection from the head as in some mesopelagic teleosts, propelled in part by a double set of elastic tensioning ligaments at the mandibular joints. The first set of ligaments are at the hinge joint between the ceratohyal head and Meckel's cartilage on each side; and the second set extends across the head of the hyomandibula in a cavity between the ceratohyal and Meckel's cartilage on each side. The ligaments are stretched when the jaws are retracted rearward into the mouth but are relaxed when the jaws are shot forward, and apparently function (along with the long preorbitalis muscles) like a catapult to project the jaws forward and snap up small animals.

This shark is often illustrated and preserved with the jaws more or less protruded but a live goblin shark in captivity in the Marine Science Museum, Tokai University, Shimizu, Japan, held its jaws tightly retracted while swimming (Shiobara, 1990, Y. Shiobara, pers. comm. and photographs). Early catch records (Bean, 1905) suggested that mature females visited the east coast of Honshu during the springtime only. Mode of reproduction unknown; a pregnant female has never been reported.

Size: Maximum total length at least 384 cm. Size at birth unknown, smallest recorded specimen 107 cm; mature males 264, 320 and 384 cm, females reaching 373 cm, one mature at 335 cm. Weight 210 kg at 384 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal, taken as untargeted bycatch of deepwater trawl fisheries and occasionally taken with deepwater longlines, deep-set gill nets, and possibly purse seines. Utilized dried-salted for human consumption. Harmless to people. A spectacular aquarium exhibit, but seldom kept in captivity; one lived for a week in an aquarium at Tokai University, Shimizu, Japan. Conservation status unknown.

Local Names: Nasuta (Portugal), Elphin or Elfin shark, Japanese goblin shark, Tenguzame or Tengu (goblin) shark, Mitsukurizame or Mitsukuri's shark (Japan); Kabouterhaai (South Africa).

Literature: Jordan (1898); Bean (1905); Hussakof (1909); Garman (1913); Fowler (1941); Bigelow and Schroeder (1948); Stead (1963); Bass, D'Aubrey and Kistnasamy (1975a); Uyeno, Nakamura and Mikami (1976); Piotrovsky and Prut'ko (1980); Uyeno, Matsuura and Fujii (1983); Cadenat and Blache (1981); Quero (1984); Compagno (1984); Davison and van Berkel (1985); Stevens and Paxton (1985); Shcherbachev (1987); Compagno, Ebert and Smale (1989); Springer (1990); Shiobara (1990); Compagno, Ebert and Cowley (1991); Last and Stevens (1994); Shinohara and Matsuura (1997); P. Duarte (pers. comm.); D.A. Ebert (pers. comm.); Y. Shiobara (pers. comm.); J.D. Stevens (pers. comm.); J. Ugoretz (pers. comm.).

2.2.3 Family PSEUDOCARCHARIIDAE

Family: Family Pseudocarchariidae Compagno, 1973, *J. Linn. Soc.(Zool.)*, 53, suppl. 1: 28.

Type Genus: *Pseudocarcharias* Cadenat, 1963.

Number of Recognized Genera: 1.

Synonyms: Family Pseudocarcharinidae Shirai, 1996: 34. Probably error for Pseudocarchariidae.

FAO Names: **En** - Crocodile sharks; **Fr** - Requins crocodile; **Sp** - Tiburones cocodrilo.

Diagnostic Features: Head much shorter than trunk. Snout moderately long, pointed and bulbously conical, not greatly elongated or flattened and blade-like. Eyes very large, length 3.6 to 4.9% of precaudal length. Gill openings moderately long, length of first 5.4 to 8.2% of precaudal length, extending onto dorsal surface of head; all gill openings in front of pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusible to almost opposite snout tip but not greatly distensible laterally. Teeth large, the anteriors narrow and awl-like, the laterals more compressed and blade-like, with 26 to 29/21 to 26 (45 to 52 total) rows; two rows of enlarged anterior teeth on each side of upper jaw, the uppers separated from the smaller upper lateral teeth by a row of small intermediate teeth; three rows of lower anteriors on each side, the first two rows enlarged but the third about as large as laterals; symphysials absent. Trunk cylindrical and slender. Caudal peduncle slightly depressed and with low lateral keels and upper and lower crescentic precaudal pits present. Dermal denticles small and smooth, with flat crowns, small ridges and cusps, and with cusps directed posteriorly on lateral denticles. Pectoral fins small, short and broad, much shorter than head in adults; pectoral skeleton aplesodic with radials confined to fin bases. Pelvic fins large, somewhat smaller than pectoral and first dorsal fins; fin skeleton aplesodic. First dorsal fin small, low, and angular; fin skeleton aplesodic. Second dorsal fin smaller than first but larger than anal fin; second dorsal fin with a broad nonpivoting base but anal fin pivotable. Caudal fin not lunate, dorsal lobe moderately long but less than half as long as rest of shark, ventral lobe short but strong. Neurocranium moderately high, with a short to moderately elongated rostrum, depressed internasal septum and narrowly separated nasal capsules, large orbits with the supraorbital crests strong, small stapedia 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 146 to 158, precaudal count 80 to 88, diplospondylous caudal count 60 to 71. Intestinal valve of ring type with 24 to 27 turns. Size small with adults 0.74 to 1.10 m.

Local Names: Crocodile sharks, Tubarões crocodilos (Mozambique).

Remarks: The single living genus and species in this family, *Pseudocarcharias kamoharai*, was formerly placed in the family Odontaspidae and genus *Odontaspis* or *Carcharias* (Matsubara, 1936; Teng, 1959; D'Aubrey, 1964a, b; Bass, D'Aubrey and Kistnasamy, 1975a). Anatomical work by the writer has shown that this species is very distinct and rates a separate family Pseudocarchariidae. Characters of the family are presented and discussed in Compagno (1973, 1977, 1982, 1984, 1990b, 1999). Pseudocarchariidae has been recognized by a number of subsequent writers (Last and Stevens, 1994; Nelson, 1994; Shirai, 1996; Helfman, Collette and Facey, 1997). Eschmeyer (1990) reduced its rank to a subfamily Pseudocarchariinae of the family Odontaspidae, but subsequently recognized it as a full family (Eschmeyer, 1998).

Pseudocarcharias was proposed by Cadenat (1963) as a subgenus of *Carcharias* Rafinesque, 1810 but was synonymized with *Carcharias* by D'Aubrey (1964a, b) and *Odontaspis* Agassiz, 1838 by Bass, D'Aubrey and Kistnasamy (1975a). It is strongly divergent from either *Odontaspis* or *Carcharias* as delimited here and has been recognized by many writers (Abe et al., 1969; Compagno, 1973, 1977, 1981a,b, 1982, 1984, 1990b, 1999; Krefft, 1980; Fujita, 1981; Cadenat and Blache, 1981; Nakaya, 1984; Springer, 1990; Cigala-Fulgosi, 1992; Last and Stevens, 1994). The synonymy of the species follows D'Aubrey (1964a, b), Bass, D'Aubrey and Kistnasamy (1975d) and Compagno (1973, 1984).

Compagno (1990b) suggested, on morphological characters, that Pseudocarchariidae might be the sister group of Megachasmidae, Alopiidae, Cetorhinidae, and Lamnidae within Lamniformes. Recent molecular phyletic studies (Naylor et al., 1997; Martin and Naylor, 1997) have not given unambiguous results on the relationship of Pseudocarchariidae to other lamnoids, but suggest relationships with Odontaspidae and Megachasmidae. Long and Waggoner (1996), using dental morphology for a phyletic analysis of Lamniformes, suggested that Pseudocarchariidae is the immediate sister group of Alopiidae plus Lamnidae within the Lamniformes.

***Pseudocarcharias* Cadenat, 1963**

Genus: Subgenus *Pseudocarcharias* Cadenat, 1963 (Genus *Carcharias* Rafinesque, 1810), *Bull. Inst. Francaise Afrique Noire*, ser. A, 25(2): 526 (proposed as a subgenus of *Carcharias* Rafinesque, 1810, but used throughout in generic form).

Type Species: *Pseudocarcharias pelagicus* Cadenat, 1963, by original designation, a junior synonym of *Carcharias kamoharai* Matsubara, 1936.

Number or Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Pseudocarchariidae above.

***Pseudocarcharias kamoharai* (Matsubara, 1936)**

Fig. 58

Carcharias kamoharai Matsubara, 1936, *Zool. Mag. Tokyo*, 48(7): 380. Holotype: Imperial Fisheries Institute, Japan, Kyoto University, Department of Fisheries, Faculty of Agriculture, Japan (housed at Maizuru, Japan) FAKU, Fish Spec. 1823, 735 mm male, Koti Fish Market, Koti, Japan, apparently lost according to Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Synonyms: *Carcharias yangi* Teng, 1959: 1, fig. 1. Holotype, Taiwan Fisheries Research Institute, TFRI 2895, 1 000 mm TL adult male, Su-ao fish market, from off Su-ao, Taiwan (Province of China). Type status confirmed by Eschmeyer (1998: CD-ROM). *Pseudocarcharias pelagicus* Cadenat, 1963: 529, figs. 1-5. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 1963-1, 975 mm adult male, off the Guinea coast, West Africa. Type status confirmed by Eschmeyer (1998: CD-ROM).

Other Combinations: *Odontaspis kamoharai* (Matsubara, 1936).

FAO Names: **En** - Crocodile shark; **Fr** - Requin crocodile; **Sp** - Tiburón cocodrilo.

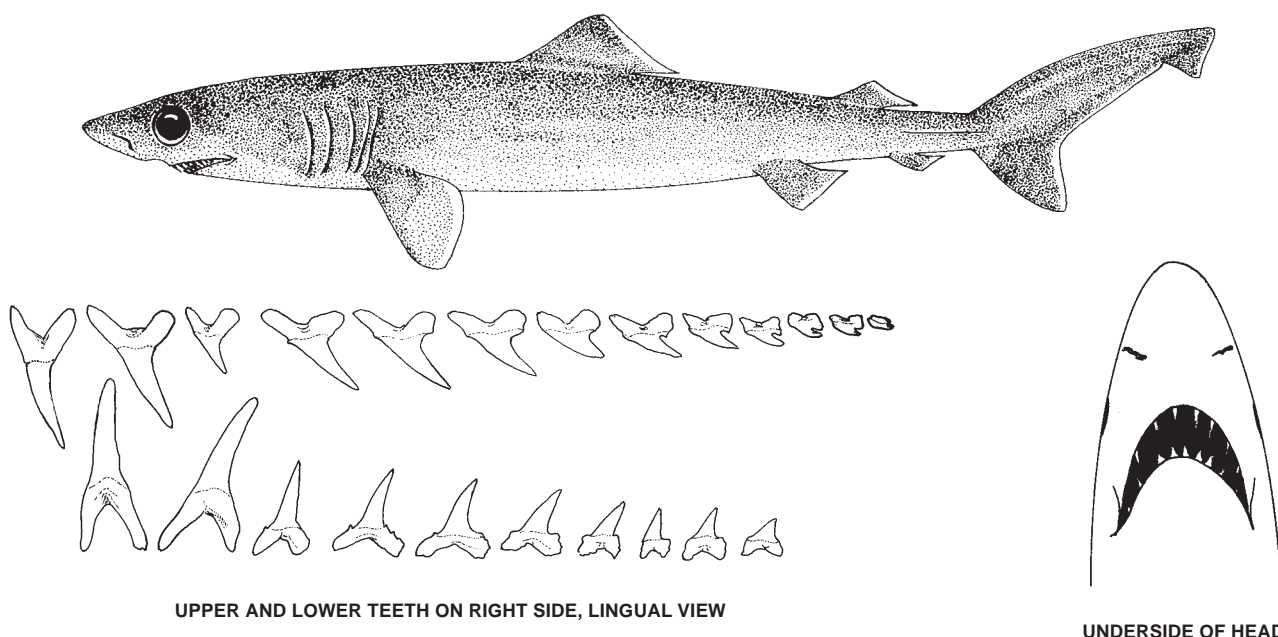
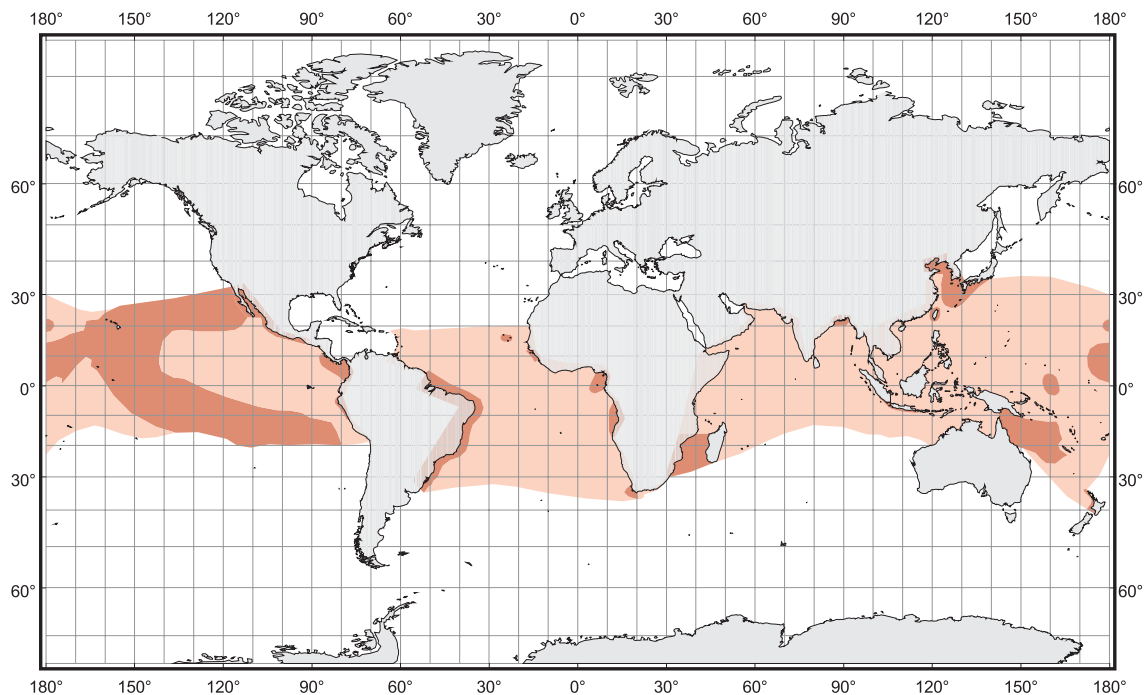


Fig. 58 *Pseudocarcharias kamoharai*

Field Marks: A small, very distinctive oceanic shark, with huge eyes lacking nictitating eyelids, long gill slits, slender, spindle-shaped body, long-cusped prominent teeth in a long angular mouth with highly protrusible jaws, small pectoral fins, two small spineless dorsal fins and an anal fin, weak keels and precaudal pits on the caudal peduncle, an asymmetrical caudal fin with a long ventral lobe. **Colour:** grey or grey-brown dorsal surface, lighter ventral surface, and light-edged fins.

Diagnostic Features: See family Pseudocarchariidae above.

Distribution: Oceanic and circumtropical. Western Atlantic: Off Brazil. Eastern Atlantic: Southeast of Cape Verde Islands, between them and Guinea-Bissau, Guinea, Angola, and South Africa (Western Cape, vicinity of Cape Town and Cape Peninsula). Western Indian Ocean: Mozambique Channel between southern Madagascar, southern Mozambique and KwaZulu-Natal, South Africa, possibly south within Agulhas Current to off Eastern Cape. ? Eastern Indian Ocean: Bay of Bengal (possibly erroneous). Western North Pacific: Off Japan, Taiwan Island and Korean Peninsula; area between Marshall, Howland and Baker, Palmyra, Johnston and Hawaiian Islands. Western South Pacific: Australia (northeastern Queensland), west of New Zealand (North Island), Coral Sea, Indonesia (south of Sumatra near Sunda Straits and off Java). Central Pacific: Marquesas Islands, Hawaiian Islands, open ocean between Marquesas and Hawaiian Islands, open ocean between Hawaiian Islands and Baja California, around Line Islands, open water between Line Islands and southern Peru. Eastern Pacific: Mexico (off west coast of Baja California), Costa Rica, Panama and northern Peru.



Habitat: A rare to locally abundant oceanic, epipelagic and possibly mesopelagic shark, usually found offshore and far from land but sometimes occurring inshore and near the bottom, at depths from the surface to at least 590 m. Its bicolorate, countershaded colour pattern, lack of an expanded iris and prominent green or yellow retinal reflection, and frequent occurrence in pelagic longline catches suggests that it primarily inhabits the epipelagic zone. There are several records of strandings in the Cape Town area, South Africa, possibly due to upwelling of cold water that may stun these sharks but in at least one instance as a discarded catch of an offshore longliner.

Biology: The long body cavity, large liver, and small fins of this shark (microoceanic habitus, Compagno, 1990a) give it a superficial resemblance to *Isistius*, *Squaliolus*, *Euprotomicrus*, *Scymnodalatias*, and other oceanic squaloids, as well as *Odontaspis noronhai*, and like these sharks its extremely large and oily liver is probably important in maintaining neutral buoyancy. Its habits are little known, but its firm body musculature, tough skin, small precaudal fins, and large caudal fin suggests that it is a relatively active species, which is also suggested by its behaviour when captured. Off Cape Point, South Africa, one jumped out of the water after a bait and was caught. It snaps strongly and vigorously when captured (S. Kato, pers. comm.) and can bite very hard. The large but nonreflective eyes of the crocodile shark suggest nocturnal activity in the epipelagic zone, and possibly a diel pattern of movement toward the surface at night and away from it in the day.

The crocodile shark is ovoviviparous and a uterine cannibal, with the young having yolk sacs at 3 to 4 cm long but reabsorbing them and subsisting on eggs and possibly other young beyond this size. Number of young in a litter four, two per uterus; egg cases formed in the oviducts have 2 to 9 fertilized eggs, but apparently only two of these survive, possibly through elimination of extra rivals. An interesting question is why two young survive in each uterus in this shark and some other lamnoids, while in *Carcharias taurus* only one foetus per uterus is normally produced.

Feeding habits of this shark are sketchily known. Its long, flexed teeth, strong and long jaws, and its vigorous activity when captured adapt it to moderately large, active oceanic prey. Of seven specimens examined by the writer for stomach

contents, the stomachs of four were empty and three others had a number of small bristlemouths (gonostomatids), possibly lanternfish (myctophids), unidentified fish scales, small shrimp, and squid beaks, including onychoteutids (*Moroteuthis robsoni*), mastigoteuthids (*Mastigoteuthis*), pholidoteuthids (*Pholidoteuthis ?boschmai*), and cranchiids (*Megalocranchia?*) in their stomachs (M. Roeleveld and M. Lipinski, pers. comm., on identification of squid beaks). The jaws of the crocodile shark can be protruded for a considerable distance from its head.

Size: This is the smallest living lamnoid, with maximum size at least 110 cm; size at birth about 41 cm; males adult at 74 to 110 cm; adolescent females examined 96 to 110 cm and adults recorded at 89 to 110 cm and presumably greater.

Interest to Fisheries and Human Impact: This shark is primarily caught as a discarded bycatch of pelagic longline fisheries for scombroids, but details are sketchy. Abe et al. (1969) noted that the species is often caught on tuna longlines, but discarded because of its small size and meat that is apparently unsuitable for the Japanese market. The liver of this species is very large and very high in squalene, and hence is of potential value. It also has been caught on squid jigs and occasionally washes up on beaches in the Cape Town area of South Africa. It may also be a discarded bycatch of pelagic squid fisheries as well as of pelagic net fisheries for scombroid fishes.

The crocodile shark is small and has never bitten people in the water, but should be treated with respect because of its strong jaws. It apparently has not been kept by large public aquaria but its small size and poorly-known behaviour suggests it may be more amenable to captivity than larger pelagic lamnoids and might be an interesting animal to observe in captivity.

Conservation status is uncertain but of concern because of its epipelagic habitat and because it is an apparently widespread, discarded, and largely unrecorded bycatch of the burgeoning pelagic longline fisheries. It is too small to be of much value for fins, and is little-utilized for flesh, but has a large mouth and strong teeth and is readily caught on longline hooks fished near the surface. It does not appear to be abundant anywhere with the known exception of the Mozambique Channel in the western Indian Ocean during the 1960s, and catch records are very limited and largely confined to a small number of specimens (less than 50) deposited in museums. It was assessed as Limited Risk (Near Threatened) for the Red List of the IUCN Shark Specialist Group (L.J.V. Compagno and J.A. Musick, pers. comm.).

Local Names: Kamohara's sand shark, Mizu-wani, Mizuwani, Water crocodile, Water alligator (Japan); Japanese ragged tooth shark, Grootoog-skeurtandhaai, Bigeye ragged-tooth (South Africa).

Literature: Matsubara (1936); Teng (1959); Lindberg and Legeza (1959); Cadenat (1963); Chen (1963); D'Aubrey (1964a, b); Merrett (1965); Abe et al. (1969); Abe (1973); Bass, D'Aubrey and Kistnasamy (1975a); Compagno (1973, 1981, 1982, 1984, 1990a, b); Krefft (1980); Fujita (1981); Cadenat and Blache (1981); Nakaya (1984); Sadowsky, Amorim and Arfelli (1987); Kashkin (1989); Fischer et al. (1990); Springer (1990); Cigala-Fulgosi (1992); Last and Stevens (1994); Long and Seigel (1996); L.J.V. Compagno and J.A. Musick (pers. comm.); S. Kato, (pers. comm.).

2.2.4 Family MEGACHASMIIDAE

Family: Family Megachasmidae Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 89.

Type Genus: *Megachasma* Taylor, Compagno and Struhsaker, 1983.

Number of Recognized Genera: 1.

Synonyms: None.

FAO Names: **En** - Megamouth sharks; **Fr** - Requins grande gueule; **Sp** - Tiburones bocudos.

Diagnostic Features: Head very elongated and about length of trunk. Snout extremely short, flattened and broadly rounded, not elongated and blade-like. Eyes moderately large, length 1.6 to 1.8% of precaudal length. Gill openings moderately long, length of first 6.4 to 8.6% of precaudal length, not extending onto dorsal surface of head; last two gill openings over pectoral-fin bases; unique gill rakers of finger-like dermal papillae with cartilage cores fringing internal gill slits. Mouth very large and arcuate, terminal on head; jaws greatly protrusible anteriorly beyond snout tip but not greatly distensible laterally. Teeth small, continuously varying and more or less awl-shaped, in 55 to 115/75 to 121 (130 to 236 total) rows, no differentiation between anterior, intermediate, lateral, or symphyseal teeth. Trunk cylindrical and somewhat compressed, stout, and relatively flabby. Caudal peduncle compressed and without lateral keels but with small fossate-shaped upper precaudal pit only. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins large, narrow and elongated, much shorter than head in adults; pectoral skeleton plesiodic with radials extending far into fin webs. Pelvic fins moderate-sized, smaller than pectoral and first dorsal fins; fin skeleton probably aplesiodic, not extending into fin web. First dorsal fin moderately large, semierect and angular; fin skeleton aplesiodic. Second dorsal fin less than half size of first but moderately large. Anal fin smaller than second dorsal fin and with its base slightly behind second dorsal-fin base, bases of both fins not pivotable. Caudal fin not

lunate, dorsal lobe long but less than half as long as rest of shark, ventral lobe short but strong. Neurocranium depressed, with short wide rostrum, greatly depressed internasal septum and widespread nasal capsules, small orbits with strong supraorbital crests, small stapedia fenestrae, and with hyomandibular facets not extended outward. Vertebral centra weakly calcified, with rudimentary radii and double cones and no annuli. Total vertebral count 151, precaudal count 64, diplospondylous caudal count 82 to 87. Intestinal valve of ring type with 23 or 24 turns. Size very large with adults 4.5 to 5.5 m long.

Remarks: Taylor, Compagno and Struhsaker (1983) proposed a new monotypic family of lamnoid sharks, Megachasmidae, for the new genus and species of megamouth shark (*Megachasma pelagios*), and suggested that it might be either the sister group of all other lamnoids or could be grouped with more derived lamnoids having plesodic pectoral fins. The family Megachasmidae has received recognition from various authors, including Compagno (1984, 1990b, 1999), Gubanov, Kondyurin and Myagkov (1986), Eschmeyer (1990, 1998), Nelson (1994), Last and Stevens (1994), Shirai (1996), and Helfman, Collette and Facey (1997). Maisey (1985) adopted the second suggestion of the megamouth shark being related to derived plesodic lamnoids, but maintained that the megamouth shark was the sister group of the basking shark and confamilial with it in the family Cetorhinidae on derived characters of its jaw suspension, cranial morphology, dentition and filter-feeding. Robins et al. (1991a) followed Maisey's classification. Compagno (1990b) noted that Maisey's derived characters for grouping the basking and megamouth sharks did not hold, and listed numerous characters separating these sharks. He suggested on morphological grounds that the Megachasmidae was distinct from Cetorhinidae, that Cetorhinidae was the immediate sister group of Lamnidae, that Megachasmidae was a valid taxon, that filter-feeding was independently derived in the basking and megamouth sharks, and that the Megachasmidae, on the basis of plesodic pectoral fins, was the sister group of all other plesodic lamnoids (Alopiidae, Cetorhinidae and Lamnidae). Two molecular studies confirmed the separation of the Megachasmidae and Cetorhinidae and refuted the common evolution of filter-feeding in these sharks, but disagreed on the relationships of Megachasmidae within the Lamniformes. Martin and Naylor (1997), using cytochrome b mitochondrial genes, suggested that *Cetorhinus* was sister to the Lamnidae but could not resolve the position of *Megachasma* robustly except for its arising from the basal root of lamnoids; their work suggested no common grouping of plesodic lamnoids but a possible relationship of *Megachasma* to *Pseudocarcharias* plus *Odontaspis*. Morrissey, Dunn and Mulé (1997) using the 12S messenger RNA mitochondrial gene suggested that *Megachasma* was the sister of all other lamnoids that they examined. Long and Waggoner (1996), using dental morphology for a phyletic analysis of Lamniformes, suggested that the basking and megamouth sharks were immediate sister groups within the Lamniformes, and formed a sister taxon to Odontaspidae, Pseudocarchariidae, Alopiidae, and Lamnidae. As noted in Compagno (1990b), similarities in tooth morphology between these sharks could be the result of parallelism and may not reflect a common immediate origin within the Lamniformes. Particularly problematical is the absence of disjunct monognathic heterodonty in *Megachasma*, while *Cetorhinus* retains disjunct upper anteriors and a gap between laterals and anteriors as in all other lamnoids. Although the phylogeny of Lamniformes remains unsettled, morphological and molecular studies support the retention of the Megachasmidae as distinct from the Cetorhinidae or any other lamnoid family.

Megachasma Taylor, Compagno and Struhsaker, 1983

Genus: *Megachasma* Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 96.

Type Species: *Megachasma pelagios* Taylor, Compagno and Struhsaker, 1983, by original designation.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: See family Megachasmidae above.

Megachasma pelagios Taylor, Compagno and Struhsaker, 1983

Fig. 59

Megachasma pelagios Taylor, Compagno and Struhsaker, 1983, *Proc. California Acad. Sci.*, ser. 4, 43(8): 87, 96, figs. 1-15. Holotype: Bernice P. Bishop Museum, BPBM-22730, 4 460 mm adult male, off Oahu, Hawaiian Islands, 21° 51' N, 157° 46' W, about 42 km northeast of Kahuku Point, at 165 m depth in water about 4 600 m deep.

Synonyms: None.

Other Combinations: None.

FAO Names: En - Megamouth shark; Fr - Requin grande gueule; Sp - Tiburón bocudo.

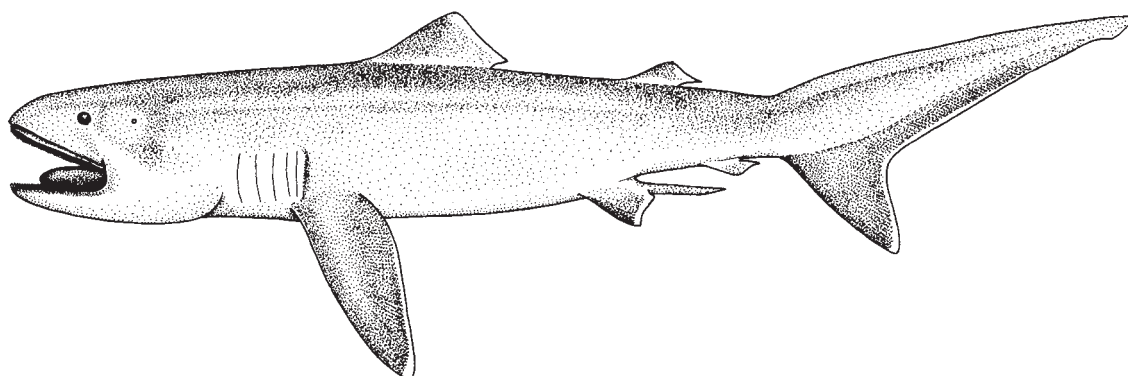
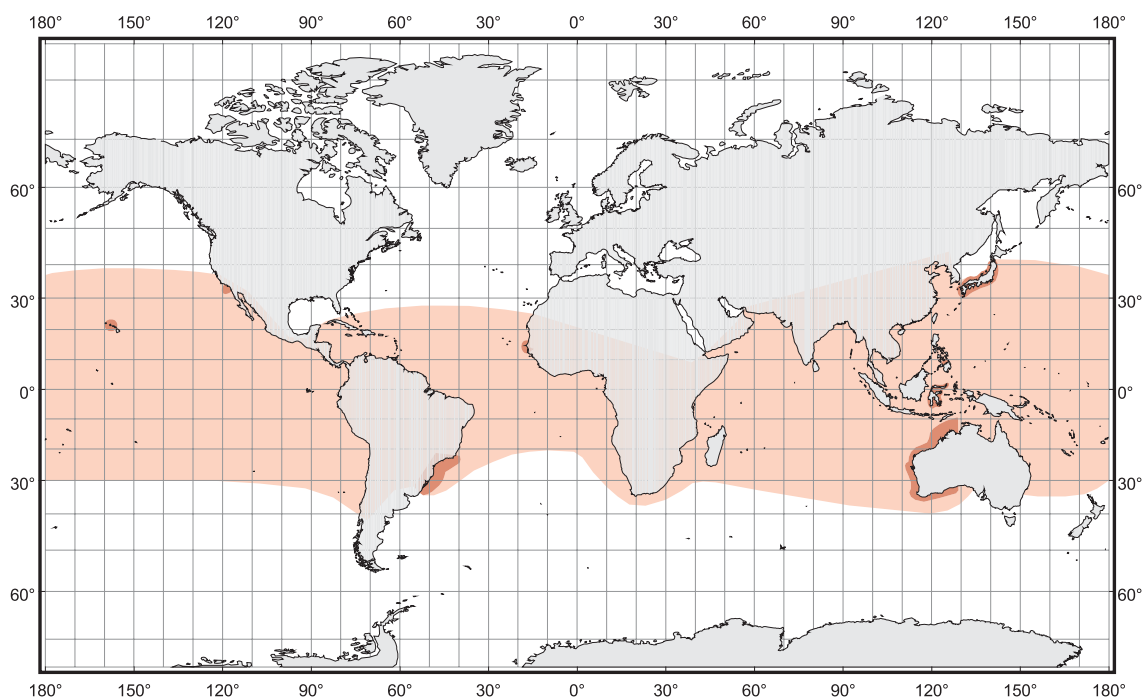


Fig. 59 *Megachasma pelagios*

Field Marks: One of three species of gigantic filter-feeding non-batoid sharks, unmistakable with its extremely short but broadly rounded snout, very large and long head, huge terminal mouth that extends behind the eyes, numerous small hooked teeth, moderately long gill slits, internal gill slits lined with dense rows of papillose gill rakers, eyes without nictitating eyelids, two dorsal fins and an anal fin, caudal peduncle without keels, caudal fin asymmetrical not lunate, but with a short and strong ventral lobe, and no light spots. **Colour:** upper surface of body grey or grey-black above, without light spots, underside white, mouth dusky blackish with dark spotting on lower jaw, and dorsal surfaces of pectoral and pelvic fins blackish with conspicuous light margins.

Diagnostic Features: See family Megachasmidae above.

Distribution: Spottily known from less than 20 specimens but probably circumtropical and wide-ranging. Western Atlantic: Brazil. Eastern Atlantic: Senegal. Southeastern Indian Ocean: Australia (Western Australia). Western North Pacific: Japan, Philippines (Macabalan Bay, Cagayan de Oro), Indonesia (Sulawezi, Nain Island, Bunaken Archipelago). Central Pacific: Hawaiian Islands (Oahu). Eastern Pacific: USA (southern California near San Clemente and off Catalina Island and San Diego).



Habitat: A coastal and oceanic, epipelagic and neritic species, found in water as shallow as 5 m in a shallow bay and in water 40 m deep on the continental shelf, with at least one washed ashore alive on a sandy beach; also offshore in the epipelagic zone at 8 to 166 m depth in water 348 to 4 600 m deep. The coloration and catch records of the megamouth shark are suggestive of epipelagic rather than deepwater habitat, as is the composition of its liver oil (Itabashi, Yamaguchi and Nakaya, 1997).

Biology: This is a seldom reported, possibly rare or uncommon shark, with most examples from off Japan and southern California. As the megamouth shark has greatly reduced teeth, very numerous gill-raker papillae on its internal gill openings, and stomach packed with very small prey, it can be properly considered a specialized filter feeder like the basking shark (*Cetorhinus maximus*), whale shark (*Rhincodon typus*), and the devil rays (Mobulidae). However, the flabby body, soft fins, asymmetrical caudal fin without keels, and weak calcification of the megamouth shark suggested that it is much less active than the whale and basking sharks (Compagno, 1984, 1990b) and the mobulids. Observations and tracking of a live specimen off southern California confirmed its relative sluggishness (Nelson et al., 1997).

The only known prey of the megamouth shark are epipelagic and mesopelagic euphausiid shrimp, copepods, and jellyfish. The first megamouth shark from Hawaii had been feeding on an euphausiid shrimp, *Thysanopoda pectinata*, that averages 3.1 cm in length. The shrimp has a diel migration pattern with a range of 300 to 1 100 m depth during the day; at night it is commonest at 150 to 500 m with a maximum range of 75 to 525 m. When captured during the night the shark was apparently at the upper depths where these shrimp are commonest. It may have been feeding on them when it fouled itself by its mouth and teeth on a pair of parachutes being used as sea anchors by a US Navy research vessel. The second megamouth shark from California had euphausiids, copepods and deepwater jellyfish (*Atolla vanhoeffeni*) in its stomach. Two female sharks from Japan had macerated euphausiids in their stomachs (probably *Euphausia nana*). The feeding structures of this shark may allow it to feed on other pelagic invertebrates and even small midwater fishes, but so far the limited stomach contents available suggests that this shark primarily targets euphausiid shrimp as prey.

There has been considerable speculation on the feeding habits of this shark. Taylor, Compagno and Struhsaker (1983) compared the basking, whale, and megamouth sharks, and suggested that the megamouth shark slowly swam through schools of euphausiid shrimp with jaws widely open, occasionally closing its mouth and contracting its pharynx to concentrate prey before swallowing it. These authors noted the presence of a bright silvery mouth lining, which they suggested was possibly bioluminescent but could not prove it because of inadequate histological evidence. The second specimen had tissue in its lower jaw that may be luminescent (Lavenberg and Seigel, 1985) and could along with the reflective upper jaw tissue serve as a 'light trap' for luring prey to the proximity of its mouth (Diamond, 1985). Compagno (1990b) noted that the protrusability of the jaws in the megamouth shark may allow it to use its mouth as a bellows to suck in prey, and that open-mouthed cruising through prey concentrations was optimal for the basking shark but not the megamouth shark.

Taylor, Compagno and Struhsaker (1983) suggested that the soft flabby body and fins, low-flow filter apparatus, and small gill openings of the megamouth shark indicated that it was less active than the whale and basking sharks. Oikawa and Kanda (1997) considered gill histology and filament area in the megamouth shark compared to the shortfin mako and other species, and suggested that the megamouth shark was less active. An adult male megamouth shark of about 4.9 m length was captured in a pelagic gill net off southern California near the surface in water between 300 and 400 m deep. This was still alive when discovered in the net and was towed to Dana Point Harbor where it was tethered by a rope to the fishing boat that caught it (Nelson et al., 1997). The shark was extensively photographed by divers and was still alive after being towed and then being tethered for over a day. Observations suggested that the shark could breathe readily by gill pumping and was not dependent on ram-ventilation and constant swimming unlike more active lamnoid sharks. The shark was then towed out to sea, tagged with an acoustic telemetric tag, and released in water about 20 m deep. The shark immediately descended, outswam the accompanying divers, and headed for deep water beyond the continental shelf. It was tracked over a two-day period, which revealed a pattern of vertical, crepuscular migration in the epipelagic zone. The tagged shark ascended at sunset to a depth of 12 to 25 m at night, then descended at sunrise to a depth of 120 to 166 m during the day with greatest depth achieved at midday but stayed well above the bottom at 700 to 850 m. It stayed on a straight southward course at an estimated speed between 1.5 and 2.1 km/hr during day and night. It was thought that the shark was responding to light levels in choosing its depth range, and as light increased it correspondingly sought an optimal level by diving at dawn and conversely responded to decreasing light levels by ascending to near (but not at) the surface at dusk. It has been suggested that the megamouth shark may also follow vertical migrations of euphausiid prey during diel cycles. The telemetric track suggested that the shark was indeed somewhat less active than makos or basking sharks, but that it could sustain a slow rate of swimming for extended periods.

Mode of reproduction is probably aplacental viviparous with uterine cannibalism or cannibal vivipary suspected in the form of oophagy, but no pregnant adult female has been reported to date. A late immature or early adolescent female had two ovaries with many tiny oocytes under 3 mm in diameter, while an adult female had numerous larger oocytes 5 to 10 mm wide. This is similar to the ovaries of several other lamnoids that are oophages. An adult female had numerous bite marks mostly on her flanks and precaudal tail but also on her first dorsal and anal fin and head. These wounds corresponded to the teeth of another megamouth shark (or sharks), and were interpreted as courtship scars inflicted by a male because of the narrow spacing of individual cuts comparable to male rather than female teeth (Yano et al., 1999).

The megamouth shark is the only known selachian victim of the semiparasitic cookiecutter shark, *Isistius brasiliensis*, and may be especially vulnerable to *Isistius* attacks because of its soft skin, epipelagic habitat in warm seas where *Isistius* is also found, sluggishness, and relatively slow swimming speed. Three megamouth specimens had 'crater wounds' indicative of cookiecutter attacks. A megamouth shark was seen at the surface off Nain Island, Bunaken Archipelago, North Sulawesi while being possibly harassed or played with by three sperm whales, which left the shark after the observers approached them. The shark was apparently minimally injured by the whales and was photographed at the surface before disappearing.

Size: Maximum total length at least 549 cm. Size at birth unknown. A juvenile free-living male from off Brazil was 190 cm long while a possibly smaller specimen from off Senegal was estimated at about 180 cm long. Adult males were 446 to about 549 cm; a late immature or early adolescent female was 471 cm, another female of uncertain maturity was about 5 m, and an adult female was 544 cm.

Interest to Fisheries and Human Impact: Interest to fisheries minimal at present. Taken as a rare incidental bycatch in pelagic gill nets, purse seines, pelagic longlines, and fixed shore nets, and so far has been mostly utilized by museums and oceanaria, which prize the few specimens landed as display objects. As with certain other large, rare animals it attracts much attention from the general public and shark fans. A few specimens were released alive from fishing gear, while a recent specimen from Philippines was cut up and utilized by fishermen, but details of its utilization were not recorded. Conservation status uncertain, but of concern because of the apparent epipelagic and neritic habitat and possible rarity of this shark, which puts it at risk as unrecorded bycatch of oceanic and offshore littoral fisheries.

Local Names: Megamouth sharks, Big mouth sharks.

Remarks: This giant pelagic filter-feeding shark is perhaps the most spectacular discovery of a new shark in the twentieth century. A recent symposium volume deals primarily with a detailed examination of a single specimen of megamouth shark from Japan, but includes papers on all aspects of megamouth biology (Yano et al., 1997).

Literature: Taylor, Compagno and Struhsaker (1983); Compagno (1984, 1990b); Lavenberg and Seigel (1985); Diamond (1985); Maisey (1985); Nakaya (1989); Berra and Hutchins (1990, 1991); Miya, Hirotsawa and Mochizuki (1992); Last and Stevens (1994); Clark and Castro (1995); Carey and Clark (1995); Seret (1995); Nelson et al. (1997); Castro et al. (1997); Berra (1997); Yano et al. (1997); Morrissey, Dunn and Mulé (1997); Martin and Naylor (1997); Nakaya et al. (1997); Yabumoto et al. (1997); Oikawa and Kanda (1997); Tanaka and Yano (1997); Itabashi, Yamaguchi and Nakaya (1997); Yamaguchi and Nakaya (1997); Yano et al. (1999); E.T. Elizaga (pers. comm.); E. Gomes, A. Amorim and B. Hueter (pers. comm.); H. Mollet (pers. comm.); J. Morrissey (pers. comm.); P. Pecchioni (pers. comm.); D. Petersen (pers. comm.).

2.2.5 Family ALOPIIDAE

Family: Subfamily Alopiadini Bonaparte, 1838 (Family Squalidae), *Nuov. Ann. Sci. Nat., Bologna*, ser. 1, 2: 209. Emended to Family Alopiidae Bonaparte, 1838 by Jordan and Gilbert (1883, *Bull. U.S. Nat. Mus.*, 16: 26).

Type Genus: *Alopias* Rafinesque, 1810.

Number of Recognized Genera: 1.

Synonyms: Family Alopeciae Müller and Henle, 1839: 74. Type genus: *Alopecias* Müller and Henle, 1837. Family Vulpeculidae Garman, 1913: 12, 30. Type genus: *Vulpecula* Garman, 1913.

FAO Names: **En** - Thresher sharks; **Fr** - Renards; **Sp** - Zorros.

Field Marks: Long curving asymmetrical caudal fin with dorsal lobe nearly or quite as long as rest of shark, short ventral caudal lobe, long narrow pectoral fins, large pelvic fins, large first dorsal fins, tiny second dorsal and anal fins, large to huge eyes.

Diagnostic Features: Head much shorter than trunk. Snout moderately long, pointed and conical, neither greatly elongated, nor flattened and blade-like. Eyes moderately large to very large with length 1.8 to 4.3% of precaudal length. Gill openings short, with width of first 3.1 to 5.2% of precaudal length, not extending onto dorsal surface of head; last two pairs of gill openings over pectoral-fin bases; no gill rakers on internal gill slits. Mouth small and arcuate, ventral on head, jaws not strongly protrusible. Teeth small to moderately large, compressed and blade-like, in 22 to 52/20 to 50 (42 to 102 total) rows. Two rows of small to moderately large anterior teeth on each side of upper jaw, the anteriors hardly larger than adjacent laterals and separated from them by a row of small intermediate teeth or a gap; three rows of small lower anterior teeth on each side, these slightly larger than lower laterals and with the third row not reduced in size; small symphyseal teeth present or absent in upper and lower jaws. Trunk cylindrical and moderately stout, firm and not flabby. Caudal peduncle slightly compressed, with upper and lower crescentic precaudal pits but no lateral keels. Dermal denticles very small and smooth, with flat crowns, small ridges and cusps and with cusps directed posteriorly on lateral denticles. Pectoral fins very long and narrow, longer than head in adults; pectoral skeletons plesodic with radials extending far into fin webs. Pelvic fins very large, nearly or quite as large as first dorsal fin; fin skeleton plesodic. First dorsal fin large, high, erect and angular; fin skeleton semiplesodic, extending partially into fin web. Second dorsal and anal fins minute, low and with pivoting bases, anal-fin base behind second dorsal-fin base. Caudal fin not lunate, dorsal lobe greatly elongated, about as long as rest of shark, ventral lobe short but strong. Neurocranium high and compressed, with short rostrum, compressed internasal septum and closely

adjacent nasal capsules, huge orbits with well-developed supraorbital crests, small stapedial fenestrae, and with hyomandibular facets not extended outward. Vertebral centra strongly calcified, with well-developed double cones and radii but without prominent annuli. Total vertebral count 282 to 477, precaudal count 100 to 125, diplospondylous caudal count 180 to 356. Intestinal valve of ring type with 33 to 45 turns. Size moderately large to very large with adults 2.7 to 5.5+ m long.

Distribution: Threshers occur worldwide in tropical, subtropical, and warm and cold-temperate waters.

Habitat: Threshers are large, active, strong-swimming sharks, ranging in habitat from coastal to epipelagic and deepwater epibenthic.

Biology: Thresher sharks are large, active sharks that are apparently specialized for feeding on small to moderately large schooling fishes and squids. Threshers swim in circles around a school of prey, narrowing the radius and bunching the school with their long, strap-like caudal fins. The caudal fin is also used as a whip to stun and kill prey, and threshers are commonly tail-hooked on longlines after striking the bait with the caudal tip. The three known species of this family broadly overlap in habitat and range, but differences in their structure, feeding habits and spatial distribution suggest that they reduce interspecific competition by partitioning their habitat and available prey to some extent. *Alopias superciliosus*, with its huge eyes, relatively large teeth, broad caudal fin, and preference for deeper water (including the outer shelves and upper slopes near the bottom), takes somewhat larger pelagic fishes (including small billfishes and lancetfishes) as well as bottom fishes. *A. vulpinus*, with smaller eyes and teeth, a narrower caudal fin, and preference for the surface and coastal as well as oceanic waters, takes small pelagic fishes (including clupeids, needlefishes and mackerels) and squids, but also bonitos and bluefishes. The oceanic and marginally coastal *A. pelagicus* is less well known biologically, but its much smaller teeth and very slender caudal fin suggest that it may take smaller prey than *A. vulpinus* or *A. superciliosus*. Evidence on vascular morphology and from telemetry data suggests that threshers are endothermic (Alexander, 1998), but their behaviour (including activity patterns) is poorly known despite their abundance and wide range.

Interest to Fisheries and Human Impact: Thresher sharks form an important component of oceanic and offshore coastal shark fisheries, particularly because of their high-quality meat which is utilized fresh, frozen, smoked and dried-salted. Their fins are used for shark-fin soup, livers for vitamin extraction, and hides for leather. Sizeable oceanic fisheries for thresher sharks, utilizing floating longlines, have operated in the northwestern Indian Ocean, the central Pacific, the western Pacific, and the western North Atlantic. Threshers are undoubtedly caught as bycatch of longline fisheries targeting scombroid fishes. A pelagic gill net fishery for threshers has operated off the Pacific coast of the USA over the last few decades but declined markedly due to overfishing. Threshers are also captured offshore and near shore with line gear (including rod-and-reel) and fixed bottom gill nets. Sports anglers seek threshers as game fishes, because of their strong fighting qualities and tendency to jump when hooked. Little is available on fisheries statistics for thresher catches worldwide. At present, only New Zealand and the USA report commercial catch statistics of thresher sharks to FAO (*A. vulpinus*) and these amount to only about 100 t or less annually during the last decade. World catches are undoubtedly much larger. Threshers are sometimes seen by divers, but do not, to the writer's knowledge, provide ecotouristic viewing at inshore or offshore dive sites, nor have they been regularly kept in aquaria. The conservation status of threshers is poorly known, but is of concern because of their high value in fisheries, very low fecundity, and their occurrence in areas and habitats subjected to high-intensity oceanic fisheries.

Local Names: Fox sharks, Threshers, Thresher sharks, Thrashers (English); Renards de mer, Chienhai chang, Chienhai chang wei sha k'o; Dlinnokhvostye akuly (Russia); Onagazame-ka (Japan); Zorros (Mozambique).

Remarks: Following Müller and Henle (1839), most authors have recognized the threshers (genus *Alopias*) as a separate family, Alopiidae or equivalents, which is followed here. However, some authors placed the threshers in the family Lamnidae or Isuridae (Günther, 1870; Hasse, 1879; Woodward, 1889; Regan, 1906a; Goodrich, 1909; Engelhardt, 1913; Berg, 1940; Berg and Svetovidov, 1955; Arambourg and Bertin, 1958; and Norman, 1966). Shirai (1996) recently included the basking sharks (Cetorhinidae) and mackerel sharks (Lamnidae) as subfamilies of the Alopiidae.

The arrangement of genera and species within this family follows Bass, D'Aubrey and Kistnasamy (1975a), Gruber and Compagno (1981), and Compagno (1984) in recognizing a single living genus and three living species, *Alopias pelagicus*, *A. superciliosus* and *A. vulpinus*. Compagno (1990b), on external and cranial morphology, suggested that threshers were monophyletic, with *A. vulpinus* the plesiomorphic sister group of *A. pelagicus* and *A. superciliosus*. Eitner (1995) did electrophoretic analysis of allozymes from muscle samples collected from eastern Pacific threshers. Eitner suggested a similar phyletic relationship as indicated by Compagno (1990b) for the three known species, but indicated that a fourth and possibly undescribed species, initially identified as *A. superciliosus*, occurred off Baja California, Mexico. Unfortunately the fourth species was not represented by whole-bodied material, parts or even photographs or morphometrics (only muscle samples), so that determination of its status awaits collection and description of additional material from the eastern Pacific. The three known species of threshers are strongly differentiated by external and skeletal morphology (Compagno, 1990b), so that detailed morphological examination of the possible fourth species is highly desirable.

Literature: Garman (1913); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Garrick and Schultz (1963); Lindberg (1971); Shiino (1972, 1976); Compagno (1973, 1984, 1988, 1990a, b, 1999); Bass, D'Aubrey and Kistnasamy (1975a); Gruber and Compagno (1981); Last and Stevens (1994); Eitner (1995); Alexander (1998).

Alopias Rafinesque, 1810

Genus: *Alopias* Rafinesque, 1810, *Caratt. gen. sp. anim. piant. Sicilia, Palermo*, pt. 1: 13.

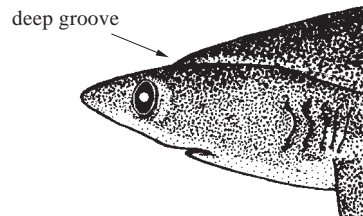
Type Species: *Alopias macrourus* Rafinesque, 1810, by monotypy, a junior synonym of *Squalus vulpinus* Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol.*, Paris: 9.

Number of Recognized Species: 3.

Synonyms: Genus *Vulpecula* Jarocki, 1822: 454. Probably based on *Vulpecula marina* Valmont, 1768 (work not consistently binomial), equivalent to *Squalus vulpinus* Bonnaterre, 1788. Genus *Alopecias* Müller and Henle, 1837a: 114. Type species: “*Carcharias vulpes* Cuv[er]” by original designation, equals *Squalus (Carcharias) vulpes* Cuvier, 1816. Genus *Alopius* Swainson, 1838: 91 (unjustified emendation of *Alopias* Rafinesque, 1810). Genus *Vulpecula* Garman, 1913: 3, 30. Type species: *Vulpecula marina* Garman, 1913, by monotypy: “Valmont, 1768, gives a description of *V. marina* of earlier authors. His species is *Squalus vulpinus* Bonn., 1788, the *Alopias macrourus* Raf., 1810, *A. vulpes* Bonap. 1841. The genus and the species are adopted from Valmont” (Garman, 1913: 3). Revival of *Vulpecula* Valmont (1768: 740). Valmont’s names were rejected as being inconsistently binomial by the International Commission on Zoological Nomenclature (1925, Opinion 89: 27-33). Genus *Alopes* Vladykov and McKenzie, 1935: 46 (erroneous spelling for *Alopias*).

Key to Species:

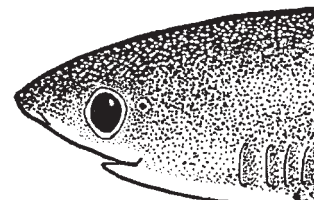
1a. Head nearly flat between eyes, with a deep horizontal groove on nape on each side above gills; eyes very large, with orbits expanded onto dorsal surface of head (Fig. 60); teeth large, in 22 to 27 rows in upper jaw; first dorsal-fin base closer to pelvic bases than to pectoral bases ***Alopias superciliosus***



LATERAL VIEW OF HEAD

Fig. 60 *Alopias superciliosus*

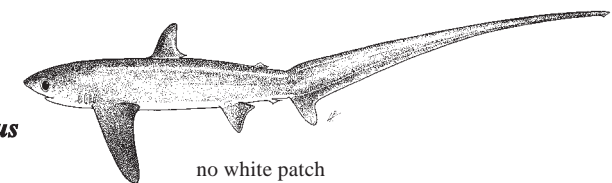
1b. Head strongly arched between eyes, without a horizontal groove or with an inconspicuous one on nape on each side; eyes smaller, with orbits not expanded onto dorsal surface of head (Fig. 61); teeth smaller, 32 to 52 rows in upper jaw; first dorsal-fin base about equidistant between pectoral and pelvic-fin bases or closer to pectoral-fin bases → 2



LATERAL VIEW OF HEAD

Fig. 61 *Alopias pelagicus*

2a. Head narrow, snout more elongated, forehead nearly straight; labial furrows absent; pectoral fins nearly straight and broad-tipped; sides above pectoral bases dark, without an extension of the white abdominal area (Fig. 62) ***Alopias pelagicus***



no white patch

Fig. 62 *Alopias pelagicus*

2b. Head broad, snout shorter, forehead strongly arched; labial furrows present; pectoral fins falcate and narrow-tipped; sides above pectoral-fin bases marked with a white patch extending forward from the abdominal area (Fig. 63) ***Alopias vulpinus***

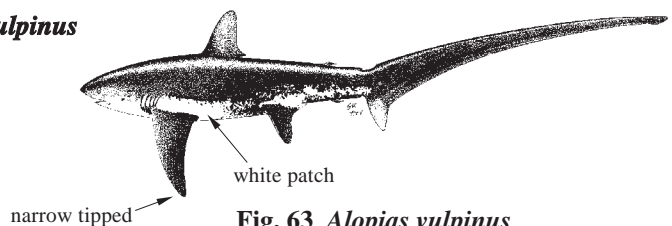


Fig. 63 *Alopias vulpinus*