A hardy shark, readily kept in captivity. The zebra shark is unaggressive when approached underwater, and has not been involved in attacks on people. Although this shark is apparently not dangerous, and has very small teeth, its jaws are strong and could deliver a painful bite to an unwary human tormentor.

**Size:** Maximum total length possibly 354 cm, males mature between 147 and 183 cm, females between 169 to 171 cm and reaching at least 233 cm; young hatching at a size between 20 and 36 cm.

**Interest to Fisheries:** A common shark in the Indo-West Pacific, regularly taken in inshore fisheries in Pakistan, India, Thailand, Malaysia, Taiwan (Province of China), and elsewhere where it occurs. It is caught in bottom trawls, in floating and fixed bottom gillnets, and with longlines and other line gear. The meat is utilized fresh and dried salted for human consumption; livers processed for vitamins; fins dried and processed for the oriental sharkfin trade; and offal utilized for fishmeal.

**Literature:** Garman (1913); Whitley (1940); Fowler (1941); Klausewitz (1960); Stead (1963); Gohar & Mazhar (1964); Marshall (1965); Nakaya (1973); Bass, d'Aubrey & Kistnasamy (1975b); Faulkner (1975); Masuda, Araga & Yoshino (1975); Fourmanoir & Laboute (1976).

**Remarks:** The earliest name for the zebra shark is *Squalus varius* Seba, 1758, which has been used by various writers (such as Garman, 1913, Klausewitz, 1960, and Bass, d'Aubrey & Kistnasamy 1975b) as *Stegostoma varium*. However, an examination of Seba's (1758) descriptions of fishes showed that his nomenclature was haphazardly unimomial, binomial, and polynomial, although the name of the zebra shark could be construed as binomial: "*Squalus varius*; naribus on proximis; foraminibus pare oculos; spiraculis utrinque quaternis; cauda longifilis." (Seba, 1758, p. 105).

In addition to the above name-diagnosis, Seba includes a long, accurate Latin description of the zebra shark, and a legend caption in French for a good illustration of a juvenile zebra shark (Seba, 1758, pl. 34, no. 1). I hesitate to use *Stegostoma varium* as a name for this shark because Seba's nomenclature was not consistently binomial, but note that the International Commission on Zoological Nomenclature may have to rule on its availability.

### 7.6 FAMILY GINGLYMOSTOMATIDAE Gill, 1862


**Synonymy:** Subfamily Nebrinae Fowler, 1934 (Family Orectolobidae).

**FAO Names:** En - Nurse sharks; Fr - Requins nourrices; Sp - Gates nodriza.

**Field Marks:** Small to large sharks with nasoral grooves but no perinasal grooves and folds, short to long barbels, small transverse mouths in front of eyes, small spiracles behind but not below eyes, no lateral skin flaps on head, two spineless dorsal fins and an anal fin, the second dorsal origin well ahead of the anal origin, and a short precaudal tail much shorter than the head and body.

**Diagnostic Features:** Body cylindrical or moderately depressed, without ridges on sides. Head broad and flattened, without lateral flaps of skin, snout truncated or broadly rounded; eyes dorsolaterally or laterally situated on head, without suborbicular pockets; spiracles much smaller than eyes, behind but not below them; gill slits small, fifth virtually overlapping fourth; internal gill slits without filter screens; nostrils with short to moderately long, pointed barbels but without circumnarial folds and grooves; mouth moderately large, subterminal on head, and transverse, without a symphyseal groove on chin; teeth not strongly differentiated in jaws, without lateral keels or precaudal pits. Dorsal fins equal-sized or first dorsal larger than second, first dorsal with origin varying from slightly anterior to the pelvic origins to over their bases, and insertion just behind the pelvic insertions; pectoral fins moderately large, broad and rounded to narrow and falcate, larger than pelvic fins, with fin radials partially expanded into fin web but falling short of its distal edge; pelvic fins somewhat larger to somewhat smaller than dorsals and anal fins; anal fin about as large as second dorsal, with its origin about opposite second dorsal origin or midbase; anal fin with broad base and angular apex, separated by a space much less than base length from lower caudal origin; caudal fin with its upper lobe at a low angle above the body axis, less than a third as long as the entire shark, with a strong terminal lobe and subterminal notch but no ventral lobe or a very short one. Supraorbital crests present on cranium, these laterally expanded. Valvular intestine of ring type. Colour plain or with dark spots in young.

**Habitat, Distribution and Biology:** These are common, small to large, nocturnal, inshore bottom sharks with a circumglobal distribution in subtropical and tropical continental and insular waters, in depths from the intertidal down to at least 70 m. They occur on coral and rocky reefs, in sandy areas, in reef lagoons, mangrove keys, and at the surf zone, usually close inshore and sometimes in water deep enough only to cover them. At least
two of these species occur in groups while testing on the bottom, often lying atop one another. One species (*Ginglymostoma brevicaudatum*) is a small shark attaining a length of less than 1 m, but the others are large, bulky sharks reaching over 3 m.

Development is ovoviviparous in at least one species (*Ginglymostoma cirratum*), with young that are nourished primarily by yolk while in the uterus; litters of 20 to 30 young have been reported. Another species (*Nebrius ferrugineus*) is variously reported as ovoviviparous or oviparous.

These sharks cruise and clamber on the bottom with their mouths and barbels close to the substrate while searching for food; when they contact a food item, they reverse and use their short, small mouths and large mouth cavities as a bellows to suck in their prey. The presence of small, active reef fishes in the stomachs of large, seemingly clumsy nurse sharks suggest that they may stalk and suddenly suck in such items, or alternatively merely inhale them in when the prey fishes are torpid and lying on the bottom at night. Food items include a variety of bottom and reef organisms, bony fishes, crabs, shrimps, lobsters, and other crustaceans, squids, octopuses, and other molluscs, corals, sea urchins and sea squirts. These are very tough and hardy sharks, that can survive over a decade in captivity. The larger species should be treated with respect, as they will bite and clamp on to a human tormentor when provoked; and their vice-like jaws may need to be pried lose from a victim. One species (*Ginglymostoma cirratum*) has been indited in unprovoked attacks on people, but more often will bite when harassed.

**Interest to Fisheries:** The larger species are common inshore sharks with wide ranges and are often caught in local inshore fisheries. They are utilized for human consumption, for liver oil, and for their thick and exceptionally tough hides, which make extremely good leather.

**Remarks:** This family is recognized following the works of Compagno (1973c, 1982) and Applegate (1974). The genus *Nebrius* is sometimes considered a subgenus of *Ginglymostoma* as by Fowler (1941), but following Garman (1913), Whitley (1940), Bigelow & Schroeder (1948), Garrick & Schultz (1963), Applegate (1974), and Bass, d’Aubrey & Kistnasamy (1975b), it is accorded full generic status. *Nebrius* and *Ginglymostoma* are usually distinguished by tooth structural characters. According to Bigelow & Schroeder (1948), *Ginglymostoma* has teeth with the "central cusp" largest and with several series functional, while *Nebrius* has teeth with "all cusps equal" (cusps as large as cusplets) and with only one or two series functional. However, *Nebrius* material examined varied considerably in cusp size, but in no instance had the cusps only as large as the cusplets cusps were smallest in young sharks, largest in adults); number of series functional ranged from 2 to 3 in *Nebrius* specimens but overlapped *Ginglymostoma cirratum* with 3 to 4. Hence the arrangement and definition of these genera are modified, and the two are distinguished by fin shape and tooth arrangement characters.

The small *Ginglymostoma brevicaudatum* is strongly divergent morphologically from *G. cirratum*, which is closer to *Nebrius ferrugineus*. Although *G. brevicaudatum* is clearly a ginglymostomatid, it differs from the other two species in having orthodont tooth structure, much smaller cusplets, larger cusps and narrower crowns on its teeth, smaller barbels, more posterior first dorsal origin, equal-sized dorsal fins, a shorter caudal fin, as well as cranial differences. This suggests that *G. brevicaudatum* may be generically distinct from *Ginglymostoma* proper, and may be referable to the fossil tooth genus *Eostegostoma* Herman & Crochard, 1977. *G. cirratum* is clearly intermediate between the more primitive *G. brevicaudatum* and the more derived *N. ferrugineus*. In cladistic terms, *G. cirratum* and *N. ferrugineus* are sister species, with *G. brevicaudatum* their primitive sister.

**Key to Genera**

1a  Teeth not compressed in sides of jaw, not imbricated (Fig. 1a). Pectoral, dorsal and anal fins apically rounded, pectoral fins broad and not falcate (Fig. 1b) ............................... *Ginglymostoma*

1b  Teeth more or less compressed in sides of jaws, forming imbricated series (Fig. 2a). Pectoral, dorsal and anal fins apically angular, pectoral fins-narrow and falcate (Fig. 2b) ............................. *Nebrius*
Ginglymostoma Müller & Henle, 1837


**Type Species:** *Squalus cirratus* Gmelin, 1789, by subsequent designation of Joredan & Gilbert (1883:18), equals *S. cirratus* Bonnaterre, 1788.

**Synonymy:** *Ginglimostoma* Agassiz, 1838 (error); *Gynglimostoma* Dumeril, 1859 (error); *Gingylostoma* Springer, 1939 (error).

**Diagnostic Features:** Teeth not compressed in sides of jaw, not imbricated. Pectoral, dorsal and anal fins apically rounded, pectoral fins broad and not falcate.

**Remarks:** *Ginglymostoma brevicaudatum* may not be congeneric with *G. cirratum* and is possibly referable to the genus *Eostegostoma* Herman & Crochard, 1977 (based on fossil teeth). In addition to *G. brevicaudatum* and *G. cirratum*, *Scylium ferrugineum* Lesson, 1830 is often included in this genus, but is here included in *Nebrius*.

Bigelow & Schroeder (1948) stated that *Ginglymostoma* differed from *Nebrius* by having teeth with the "central cusp largest" and several "rows" functional, while *Nebrius* had teeth with "all cusps about equal" and with only one or two "rows" functional. However, representative *Nebrius* material shows overlap with *Ginglymostoma* by having teeth also with the "central cusp largest" and in having two or three "rows" (series) functional vs. 3 or 4 in *G. cirratum*). *Ginglymostoma* as here restricted includes species with rounded fins and non-imbricated tooth series, while *Nebrius* includes species with angular fins and imbricated tooth series (*N. ferrugineum* and its possible synonym *N. concolor*).

**Key to Species**

1. Second dorsal and anal fins about as large as first dorsal. Caudal fin short, less than 1/4 of total length .................................................. *G. brevicaudatum*

2. Second dorsal and anal fins much smaller than first dorsal. Caudal fin longer, over 1/4 of total length .................................................. *G. cirratum*

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**Ginglymostoma brevicaudatum** Günther, 1866

*Ginglymostoma brevicaudatum* Günther, in Playfair & Günther, 1866, *Fish Zanzibar, London*, 141, pl. 21. Holotype: British Museum Natural History, BMNH-1867.3.9.423, stuffed dried adolescent male about 590 mm long; length in original account 640 mm. Type Locality: Zanzibar.

**Synonymy:** None.

**FAO Names:** En - Short-tail nurse shark; Fr - Requin-nourrice à queue courte; Sp - Gata nodriza rabicorta.

**Field Marks:** Very short barbels, nasoral grooves present but no perinasal grooves, mouth well in front of eyes, spiracles minute, precaudal tail shorter than head and body, two spineless, broadly rounded, equal-sized dorsal fins and an equally large anal fin, caudal fin short, less than 1/4 of total length, colour dark brown, without spots or other markings.
Diagnostic Features: Nasal barbels very short, not reaching mouth; tooth crowns very narrow, cusps large and cusplets very small. Origin of first dorsal fin about over pelvic insertions; second dorsal and anal fins about as large as first dorsal; caudal fin short, less than 1/4 of total length.

Geographical Distribution: Western Indian Ocean: Tanzania, Kenya, and possibly Mauritius and the Seychelles.

Habitat and Biology: An apparently common but little known inshore bottom shark of the continental and insular shelves of East Africa. Its breeding and feeding habits are unknown.

Size: Maximum total length about 75 cm; adult males 59 to 75 cm.

Interest to Fisheries: Probably limited, possibly fished locally in artisanal fisheries. Hide exceptionally tough, as in G. cirratum, and possibly of use for leather.

Literature: Fowler (1941); Bass, d’Aubrey & Kistnasamy (1975b).

Remarks: The writer examined the holotype in the British Museum (Natural History) and five other specimens in the collections of the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa.

Field Marks: Moderately long barbels, nasoral grooves present but no perinasal grooves, mouth well in front of eyes, spiracles minute, precaudal tail shorter than head and body, two spineless, broadly rounded, dorsal fins and an anal fin, first dorsal fin much larger than second dorsal and anal fins, caudal fin moderately long, over 1/4 of total length, colour yellow-brown to grey-brown, with or without small dark spots and obscure dorsal saddle markings.

Diagnostic Features: Nasal barbels moderately long, reaching mouth; tooth crowns rather broad, cusps small and short and cusplets numerous and large. Origin of first dorsal fin about over pelvic origins; first dorsal fin larger than second dorsal and anal fins; caudal fin moderately long, over 1/4 of total length.
Geographical Distribution: Western Atlantic: Rhode Island to southern Brazil, including Gulf of Mexico, Bermuda, Bahamas, Cuba, Jamaica, Caribbean. Eastern Atlantic: Cape Verde Islands, Senegal, Cameroon to Gabon, and accidental to Gulf of Gascony, France. Eastern Pacific: Southern Baja California, Gulf of California to Peru.

Habitat and Biology: A common large inshore bottom shark of the continental and insular shelves in tropical and subtropical waters, often occurring at depths of a metre or less in the intertidal, but down to at least 12 m. The nurse shark is often found on rocky reefs, in channels between mangrove keys and on sand flats. This is a nocturnal shark that is proverbially sluggish during the daytime but strong-swimming and active at night; it rests on sandy bottom or in caves and crevices in rocks in shallow water during the day, often in schools or aggregates of 3 to three dozen individuals that are close to or even piled on one another while resting.

In addition to swimming near the bottom or well off it, the nurse shark can clamber on the bottom using its flexible, muscular pectoral fins as limbs. Preliminary studies indicate that the nurse shark shows a strong preference for certain day resting sites, and repeatedly homes back to the same caves and crevices after a night’s activity.

Courtship and copulatory behavior has been observed, and is apparently rather complex. A pair or sometimes a triplet of adults engage in synchronized parallel swimming, with the male abreast or slightly behind and below the female, but with sides nearly touching. A pair may rest on the bottom on their bellies in parallel after bouts of parallel swimming. While parallel-swimming, the male may grasp one of the female’s pectoral fins with his mouth, which in turn may induce the female to pivot 90 degrees and roll on her back on the bottom. The male then nudges the female into a position parallel to him, swims on top of the female in parallel, inserts a single clasper in her vent, and then rolls on his back to lie motionless besides the inverted female with clasper still inserted.

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Reproduction is ovoviviparous, with intrauterine development of young being sustained primarily by the large supply of yolk in their yolk-sacs. Young are common in late spring and summer in waters off Florida, when females give birth. Numbers of intrauterine eggs or young are 21 to 28 in a litter.

The nurse shark feeds heavily on bottom invertebrates such as spiny lobsters, shrimps, crabs, sea urchins, squids, octopuses, marine snails and bivalves, and also fishes including sea catfishes, mullets, puffers and stingrays. Algae is occasionally found in its stomach. Its small mouth and large, bellows-like pharynx allow it to suck in food items at high speed. This powerful suction feeding mechanism and its nocturnal activity pattern may allow the nurse shark to take small, active prey like fishes that are resting at night but would be too active for the big, lumbering shark to capture in the daytime. When dealing with big, heavy-shelled conchs the nurse shark flips them over and extracts the snail from its shell, presumably with its teeth and by suction.

Young nurse sharks have been observed resting with their snouts pointed upward and their bodies supported off the bottom on their pectoral fins; this has been interpreted as possibly providing a false shelter for crabs and small fishes that the shark then ambushes and eats. In captivity the nurse shark, when stimulated by food in the form of cut fish, will cruise in circles close to the bottom searching for the food, with its barbels touching or nearly touching the bottom; when it contacts a chunk of food, it may overshoot it but then quickly backs up and rapidly inhales it in. It may even work over vertical surfaces with its barbels.

The nurse shark is often regarded as harmless to people, because of its sluggishness during the day and relatively small teeth. In the Caribbean and off Florida people frequently come in contact with it, and it mostly will not react aggressively when approached but usually swims away when disturbed. However, there have been a small number of non-fatal, unprovoked attacks on swimmers and divers with uncertain motivation on the part of the sharks, though non-feeding aggression or some other motivation is more likely than feeding attacks because of the relatively small prey taken by this shark. In one bizarre unprovoked attack a large nurse shark grabbed a diver’s chest with its teeth, then appeared to hold onto his body with its pectoral fins; unfortunately the sex of the shark was not recorded. More commonly people attempt to ride, spear, brag or otherwise harass this shark, or accidentally step on one while wading, and get bitten as a result. Although its teeth are small, the jaws and associated muscles of the nurse shark are extremely powerful and vice-like; in some instances nurse sharks have bitten people and held on, and had to be pried loose with a tool.

These sharks are very hardy and capable of surviving a wide range of temperatures and dissolved oxygen levels in captivity. They grow to adult size when obtained as young and kept in aquaria of sufficient size, and will even give birth in captivity. Specimens have been kept for 24 to 25 years. The young make interesting pets and can be trained to feed at the surface. These sharks have often been used for experimental behavioural and physiological research in captivity, for which they are excellent subjects because of their hardness and ability to learn.
Size: Maximum total length said to be 430 cm but most adults are under 3 m long and the largest otherwise reported were 280 to 304 cm; adults males mature at about 225 cm and reach at least 257 cm; females are immature at 225 to 235 cm and mostly mature at about 230 to 240 cm (though one 152 cm long has been reported) and reach over 259 cm; newborn young about 27 to 30 cm.

Interest to Fisheries: Very common in shallow waters where it occurs, and often captured in local artisanal fisheries. It has been prized for its extremely tough, thick, armor-like hide, which makes an exceptionally good leather, but is also used fresh and salted for human consumption, as well as for liver oil and fishmeal. The stratoconidia (earstones) of this shark and other species are said to be used as a diuretic by local fishermen in southern Brazil. It is captured with line gear, gillnets, fixed bottom nets and bottom trawls, and spears. It can be readily captured on sportfishing tackle, but is regarded as too sluggish to be much of a game fish. Divers sometimes spear nurse sharks, which is minimal sport because of their modest speed even when active; but the toughness of these sharks may make them difficult to subdue underwater. In the Lesser Antilles, the nurse shark is regarded as a pest by fishermen because it rifles fish traps for food.

Literature: Bigelow & Schroeder (1948); Cadenat (1957); Randall (1961, 1963); Clark (1963); Garrick & Schultz (1963); Limbaugh (1963); Springer (1963); Clark & von Schmidt (1965); Klimley (1974, 1980); Cadenat & Blache (1981).

**Nebrius** Rüppell, 1837


Type Species: *Nebrius concolor* Rüppell, 1837, by monotypy, apparently equals *Scyllium ferrugineum* Lesson, 1830.

Synonymy: Genus Nebrodes Garman, 1913 (replacement for Nebrius Rüppell, 1837, though by Garman to be preoccupied by Nebria Latreille, 1802 in Insecta and Nebris Cuvier & Valenciennes, 1830 in Osteichthy; however, according to the current Code of Zoological Nomenclature these three names are not homonyms as they differ from each other by at least one letter).

Diagnostic Features: Teeth more or less compressed in sides of jaws, forming imbricated series. Dorsal, pectoral, and anal fins apically angular, pectoral fins narrow and falcate.

Remarks: The genus Nebrius is sometimes considered a subgenus of Ginglymostoma, but, following Garman (1913), Bigelow & Schroeder 1948, Garrick & Schultz (1963), Applegate (1974), and Bass, d'Aubrey & Kistnasamy (1975b), it is accorded full generic status.


Synonymy: Nebrius concolor Rüppell, 1837; Ginglymostoma rueppellii Bleeker, 1852; Ginglymostoma muelleri Günther, 1870; Scymnus porosus Hemprich & Ehrenberg, 1899; Nebrodes macrurus Garman, 1913; Nebrodes concolor ogilbyi Whitley, 1934; Nebrius doldi Smith, 1953.

Other Scientific Names Recently in Use: *Ginglymostoma ferrugineum* (Lesson, 1830).
**FAO Names:** En - Tawny nurse shark; Fr - Requin nourrice fauve; Sp - Gata nodriza atezada.

**Field Marks:** Moderately long barbels, nasoral grooves present but no perinasal grooves, mouth well in front of eyes, eyes lateral, spiracles minute, precaudal tail shorter than head and body, two spineless, angular dorsal fins and an anal fin, first dorsal fin much larger than second dorsal and anal fins, first dorsal base over pelvic bases, pectoral fins falcate, caudal fin moderately long, over 1/4 of total length, colour brown, from tan to dark grey-brown according to habitat, and slowly changeable by the individual.

**Diagnostic Features:** See genus.

**Geographical Distribution:** Indo-West and Central Pacific: South Africa, Mauritius, Seychelles and Madagascar to Red Sea, India, Malaysia, Indonesia, Singapore, Thailand, Viet Nam, China, Papua New Guinea, Australia (Queensland), New Caledonia, New Ireland, Samoa, Palau, Marshall Islands, Tahiti.

**Habitat and Biology:** A large, tropical inshore shark of the continental and insular shelves, commonly in the intertidal in water scarcely able to cover it and from the surf line down to a few metres depth, but ranging down to at least 70 m. It occurs on or near the bottom in lagoons or along the outer edges of coral and rocky reefs, sandy areas near reefs and off sandy beaches. It prefers sheltered areas in crevices and caves on reefs but often occurs in more exposed areas in a depression or crevice. The tawny shark is primarily nocturnal, resting in the daytime in shelters but, prowling slowly about around reefs at night, although a few individuals may be active in the day. They are gregarious and form resting aggregations of two to a half-dozen or more in shelters, and are often seen piled inertly across or on top of one another. When resting, they are extremely sluggish.

Reproduction ovoviviparous, described as an oviparous or post-oviparous shark that retains the egg-cases until they hatch and the young are born. Number of young at least four per uterus.

Food of this shark includes corals, crabs, lobsters and other crustaceans, octopuses, squids and probably other cephalopods, sea urchins, and reef fishes (including surgeonfishes and siganids). While foraging the tawny shark moves along the bottom and explores depressions, holes and crevices in reefs. When it detects prey it places its small mouth very close to the victim, and uses its large pharynx as a powerful suction pump to rapidly inhale in reef organisms that may be out of reach of its teeth. A few large individuals dissected by the writer had quantities of small, active reef fishes in their stomachs, presumably sucked in by the sharks as the prey fishes lay inert in shelters or on the bottom at night. Individuals caught by fishermen may reverse this sucking action, and blast streams of water out of their mouths into the faces of their captors; they are said to make a grunting sound between streams.

This has been described as a much more docile species than its close relative, *Ginglymostoma cirratum*, and apparently usually allows humans to touch and play with it without biting. However, there are a few non-fatal attack records of these sharks biting their tormentors, and clamping tightly onto them. Because of its size and strength, the tawny shark should be regarded as potentially dangerous and treated with respect.

This is a tough, hardy shark that readily survives in captivity.
Size: Maximum total length about 314 to 320 cm; though most individuals are smaller; an adult male was 250 cm long and two adults females, from 230 to 290 cm; size at birth about 40 cm.

Interest to Fisheries: Common in areas where it occurs, and caught inshore by fishermen in Pakistan, India, and Thailand, and probably elsewhere. It is utilized fresh and dried salted for human food, its liver is rendered for oil and vitamins, its fins are used in the oriental sharkfin trade, and offal is processed into fishmeal. Its thick, armor-like hide is potentially valuable for leather. Off Queensland, Australia, it has been fished as a big-game shark, and large individuals are prized as powerful fighters.

Literature: Fowler (1941); Gohar & Mazhar (1964); Marshall (1965); Bass, d’Aubrey & Kistnasamy (1975b); Fourmanoir & Laboute (1976); Johnson (1978); Randall (1980).

Remarks: I tentatively include Nebrius concolor and its synonyms in synonymy of N. ferrugineus. Normally these species are retained and often placed in different genera, with N. ferrugineus being usually placed in Ginglymostoma and concolor in Nebrius. However, the dentitional differences used to separate the two species as in Garman, 1913, and Fowler, 1941: more compressed, more low-cusped teeth in concolor and less compressed, more high-cusped teeth in ferrugineus) may be due to growth changes in the teeth of a single species (ontogenetic heterodonty). At least in the material of Nebrius examined from the Gulf of Thailand and elsewhere, larger specimens over 2 m long have teeth of the ferrugineus type, while specimens about a meter long or less have teeth of the concolor type. Teeth of a specimen 1.8 m long pictured by Bass, d’Aubrey & Kistnasamy (1975b) are roughly intermediate. Growth changes apparently include increase in size of cusps relative to cusplets, shortening and broadening of the labial flange, and thickening and broadening of the teeth relative to their height.

7.7 FAMILY RHINIODONTIDAE Müller & Henle, 1839, amended RHIN


Synonymy: None.

FAO Names: En - Whale sharks; Fr - Requins baleine; Sp - Tiburones ballena.

Diagnostic Features: Body cylindrical or moderately depressed, with prominent ridges on sides. Head very broad and flattened, without lateral flaps of skin, snout truncated; eyes laterally situated on a head, without subocular pockets; spiracles much smaller than eyes, behind but not below them; gill slits very large, fifth well separated from fourth; internal gill slits with unique filter screens, consisting of transverse lamellae that cross each gill slit, with ramose processes on their inner surfaces that interconnect to form the filters; nostrils with rudimentary barbels and no circumnarial folds and grooves; mouth extremely large, terminal on head, and transverse, without a symphyseal groove on chin; teeth not strongly differentiated in jaws, with a medial cusp, no cusplets and no labial root lobes; tooth rows extremely numerous, in over 300 rows in either jaw of adults and subadults. Caudal peduncle with strong lateral keels and an upper precaudal pit. First dorsal much larger than second, first dorsal with origin well anterior to the pelvic origins, and insertion over the pelvic bases; pectoral fins very large, relatively narrow and falcate, much larger than pelvic fins, with fin radials expanded into fin web nearly to its distal edge; pelvic fins somewhat smaller than first dorsal but slightly larger than second dorsal and anal fins; anal fin about as large as second dorsal, with its origin about opposite first third of second dorsal base; anal fin with broad base and angular apex, separated by a space somewhat greater than base length from lower caudal origin; caudal fin with its upper lobe at a high angle above the body axis, less than a third as long as the entire shark, with a vestigial terminal lobe and subterminal notch and a very strong ventral lobe or a very short one. Supraorbital crests present on cranium, these laterally expanded. Valvular intestine probably of ring type. A unique colour pattern of light spots and vertical and horizontal stripes, in the form of a checkerboard.

Interest to Fisheries: See the account of the single species.

Remarks: The spelling Rhiodontidae, is an amended version of Rhinodontes Miller & Henle, 1839 first mentioned in Compagno (1973c).

Genus: Rhiniodon Smith, 1828

Type Species: Rhiniodon typus Smith., 1828, by original designation (use of the species name typus).
Synonymy: Genus Rhincodon Smith, 1829; Genus Rhinchodon Smith, 1829; Genus Rhineodon Müller & Henle, 1838; Genus Rineodon Müller & Henle, 1838; Genus Rhinodon Müller & Henle, 1839; Genus Rhinecodon Agassiz, 1845; Genus Micristodus Gill, 1865.

Remarks: There has been considerable variation in spelling of the generic name of the whale shark, and much usage of several of the variants. Although Rhiniodon has priority, the variants Rhincodon and Rhineodon (and to a lesser extent Rhinodon) have had much more usage. Following Bigelow & Schroeder (1948) the variant Rhincodon has developed a considerable 'public', and proposals to stabilize it (Robins & Lea, 1975; Swift, 1977) have been presented to the International Commission on Zoological Nomenclature. In contrast Hubbs, Iwai & Matsubara (1976) proposed that the earliest spelling, Rhiniodon should be preserved for the whale shark because of priority, more correct orthography than Rhinodon, and because the use of Rhinodon has not been universal since Bigelow & Schroeder's work. At present the International Commission has yet to hand down a ruling on the matter, and until it does, I prefer to use the earliest spelling (Rhiniodon).

**Rhiniodon typus** Smith, 1828

**Synonymy:** Rhinodon typicus Müller & Henle, 1839; Micristodus punctatus Gill, 1865; Rhinodon pentalineatus typus Smith, 1829; Rhineodon typus Smith, 1829.

**Other Scientific Names Recently in Use:** Rhinodon typus Smith, 1829; Rhineodon typus Smith, 1829.

**FAO Names:** En - Whale shark; Fr - Requin baleine; Sp - Tiburón ballena.

Field Marks: An unmistakable huge shark, one of three large filter-feeding species, with a broad, flat head and truncated snout, immense transverse, virtually terminal mouth in front of eyes, minute, extremely numerous teeth, and unique filter screens on its internal gill slits, prominent ridges on sides of body, with the lowermost one expanding into a prominent keel on each side of the caudal peduncle, a large first dorsal and small second dorsal and anal fin, lunate or semilunate caudal fin without a prominent subterminal notch, and a unique checkerboard pattern of light spots, horizontal and vertical stripes on a dark background.

Diagnostic Features: See family.

Habitat and Biology: An epipelagic oceanic and coastal, tropical and warm-temperate pelagic shark, often seen far offshore but coming close inshore and sometimes entering lagoons of coral atolls. It is generally seen or otherwise encountered close to or at the surface, as single individuals or in schools or aggregations of up to hundreds of sharks. In the Indian Ocean it is common around the Seychelles, Mauritius, Zanzibar, Madagascar, Mozambique and northernmost Natal. In the western Pacific it is common in the Kuroshio current in the fishing grounds for skipjack. It is reportedly abundant from Cabo San Lucas to Acapulco in the eastern Pacific, and in the Gulf of Mexico and the Caribbean in the western Atlantic. It apparently prefers areas where the surface temperature is 21 to 25°C with cold water of 17°C or less upwelling into it, and salinity of 34 to 34.5 ppt; these conditions are probably optimal for production of plankton and small nektonic organisms, all of which are prey of the whale shark. Whale sharks are apparently highly migratory, with their movements probably timed with blooms of planktonic organisms and changes in temperatures of water masses. They are often associated with schools of pelagic fishes, especially scombrids.

Development uncertain, possibly oviparous or ovoviviparous. In 1953 a large eggcase, 30 cm long, 14 cm wide and 9 cm thick containing a nearly full-term 36 cm embryo: whale shark was collected from the Gulf of Mexico, and the assumption was made that the species is oviparous (cf. Baughman, 1955. Garrick, 1964, Bass, d'Aubrey & Kistnasamy (1975c). However, the rarity of 'free-living' whale-shark eggs, the extreme thinness and lack of tendrils on the only known case, the considerable yolk and partially developed gill sieve in the only known embryo, and the presence of umbilical scars on larger free living specimens 55 cm long suggests an alternative explanation (Wolfson, 1983), that the Gulf of Mexico egg was aborted before term, and that the whale shark is ovoviviparous. The type of ovoviviparity practiced by the whale shark would be a relatively simple sort very similar to that of the related nurse sharks (Ginglymostomatidae), with retention of the egg case in utero until the embryo hatches. Alternatively, the egg cases of the whale shark might be retained in utero for most of the development of their embryos, then ejected at a late stage of development. Hence the mode of reproduction of the whale shark must be considered uncertain, with ginglymostomatid-like ovoviviparity a distinct possibility. The smallest free-living whale shark's are from 55 to 56 cm long, the smallest of which has an umbilical scar (properly vitelline scar). One adult female whale shark was recorded as having 16 egg cases in its uterus.

The whale shark is a versatile suction filter-feeder, and feeds on a wide variety of planktonic and nektonic organisms. Masses of small crustaceans are regularly reported, along with small and not so small fishes such as sardines, anchovies, mackerels, and even small tunas and albacore as well as squids. The whale shark feeds at or close to the surface, and often assumes a vertical position with its mouth above. Phytoplankton often occurs in the stomachs of whale sharks, but whether this is a major component of the diet of this shark is rather doubtful. The suction-filter mechanism of the whale shark is more versatile than the dynamic filter mechanism of the basking shark in the range of prey species that can be taken. The basking shark, with its scooplike mouth, hydrodynamically 'clean' gillrakers, and huge gill slits, has little if any suction capacity and must depend on its relatively slow forward motion to carry animals into its mouth; this limits it to eating small planktonic crustaceans and other invertebrates. The whale shark is not dependent on forward motion to operate its filters, and can probably achieve relatively high intake velocities of water into its mouth, that enable it to readily ingest larger, active nektonic prey in addition to masses of planktonic crustaceans. A disadvantage of the suction plankton feeding of the whale shark over the dynamic method used by the basking shark is that the structures involved can filter a far smaller volume of water per unit time and hence are far less efficient in concentrating diffuse plankters. Hence the whale shark may be more dependent on high concentrations of plankters than the basking shark to optimally utilize such food, but has the option of utilizing nektonic organisms for prey.

The whale shark is generally considered harmless, and very large individuals have been examined and ridden by divers without the sharks reacting aggressively, although they may show curiosity and approach divers to apparently examine them. However, there have been a few cases of whale sharks butting sportsfishing boats, possibly after being excited and hooked fishes being played from the boats or by bait. More often human beings inadvertently assault whale sharks, by ramming them with ships and boats as they bask an the surface.

The whale shark has been kept in captivity in Japan; at the time of writing this account a good-sized individual has been housed in a large oceanarium tank in Okinawa for over a year, and feeds readily at the surface of the tank.

Size: Maximum total length uncertain, possibly to 18 m., but specimens rare above 12 m; 13.7 m is often given as the maximum measured, 12.1 m the most recently accurately measured. Most reported in the literature are between 4 and 12 m. Females of 438 to 562 cm are immature. This is by far the world's largest fish.

Interest to Fisheries: Apparently of relatively limited interest for fisheries. Small harpoon fisheries exist in Pakistan and India; it may also be taken in China, and has been captured and utilized in Senegal; it is eaten by people either fresh or dried salted and used to treat boat hulls in Pakistan.

Literature: Gudger (1915), Bigelow & Schroeder (1948); Iwasaki (1970); Bass, d'Aubrey & Kistnasamy (1975b); Johnson (1978); Wolfson & de Sclara (1981); Cadenat & Blache (1981); Wolfson (1983); S. Uchida (pers. comm.)