Stegostoma fasciatum (Hermann, 1783) **Fig. 156**

Squalus fasciatus Hermann, 1783, *Tab. Affin.*: 302. Based on ***Squalus varius*** Seba, 1758. A senior homonym of ***Squalus fasciatus*** Bonnaterre, 1788 = ***Poroderma africanum*** (Gmelin, 1788). No types according to Eschmeyer (1998, *Cat. Fish.:* CD-ROM). Also, ***Squalus fasciatus*** Bloch, 1785, *Naturg. Ausl. Fische*, 1: 19, pl. 113. Holotype: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB-4449, 355 mm total length male, Indian Ocean from Tranquebar, according to Paepke and Schmidt (1988, *Mitt. Zool. Mus. Berlin,* 64(1): 163).

Synonyms: ***Squalus varius*** Seba, 1758: 105, pl. 34, fig. 1. No type locality or specimens. Name not available because Seba's usage of nomenclature was not consistently binomial (see remarks above). ***Squalus tigrinus*** Pennant, 1769: 24; (*nomen nudum*?). ***Squalus tygrinus*** Bonnaterre, 1788: 8, pl. 8, fig. 23. Type material uncertain. Type locality: "La mer des Indes". ***Squalus tigrinus*** Gmelin, *in* Linnaeus and Gmelin, 1788: 1493. Type material uncertain. Type locality: "Oceano indico". ***Squalus varius*** Seba, 1758 included in synonymy. This species was probably based on juveniles with a striped colour pattern. ***Squalus longicaudatus*** Gmelin, *in* Linnaeus and Gmelin, 1788: 1496. Type material uncertain, no locality given. ***Squalus varius*** Seba, 1758 included in synonymy. This was not strongly distinguished from ***S. tigrinus***, but may have been based on post-juveniles with a spotted colour pattern. ***Scyllia quinquecornuatum*** van Hasselt, 1823: 15. Reference to ***Squalus varius*** Seba, 1758, and presumably a replacement name for it. No types listed in Eschmeyer (1998: CD-ROM). ***Scyllium heptagonum*** Rüppell, 1837: 61, pl. 17, fig. 1. Lectotype: Senckenberg Museum, Frankfurt, SMF-3152, 105 cm stuffed specimen, possibly female, Djedda, Red Sea, according to Klausewitz (1960: 290). ***Stegostoma carinatum*** Blyth, 1847: 725, pl. 25, fig. 1. Type locality: India. Whereabouts of holotype unknown according to Eschmeyer (1998: CD-ROM). ***Squalus pantherinus*** Kuhl and van Hasselt, *in* Bleeker, 1852: 23. Name only, in synonymy of ***Stegostoma fasciatum*** Müller and Henle, 1838. Not ***Scyllium pantherinum*** Smith, 1837 = ***Poroderma pantherinum***. ***Squalus cirrosus*** Gronow, *in* Gray, 1854: 46. No locality. Reference to ***Squalus varius*** Seba, 1758, and presumably a replacement name for it. No types according to Eschmeyer (1998: CD-ROM). ***Stegostoma varium*** Garman, 1913: 59. Syntypes: At least two specimens, 330 mm (13 in) and about 1.53 m (5 ft) mentioned without further detail. According to Eschmeyer (1998: CD-ROM) syntypes include Museum of Comparative Zoology, Harvard, MCZ 55-S (possibly lost), MCZ-33437, and MCZ uncat. (shrunken skin and skull). Revival of ***Squalus varius*** Seba, 1758 and first valid use of the species name. ***Stegostoma tigrinum naucum*** Whitley, 1939: 229, fig. 2. Holotype: Australian Museum, Sydney, AMS-I.4174, Hawkesbury River, New South Wales, according to Paxton et al. (1989: 92). ***Scyllium quinquecarinatum*** Fowler, 1941: 102. Error or emendation for ***Scyllia quinquecornuatum*** van Hasselt, 1823.

Other Combinations: ***Stegostoma tigrinus*** or ***S. tigrinum*** (Pennant, 1769 or Gmelin, 1788), ***Stegostoma tygrinum*** (Bonnaterre, 1788).

FAO Names: En - Zebra shark; **Fr** - Requin zèbre; **Sp** - Tiburón acebrado.

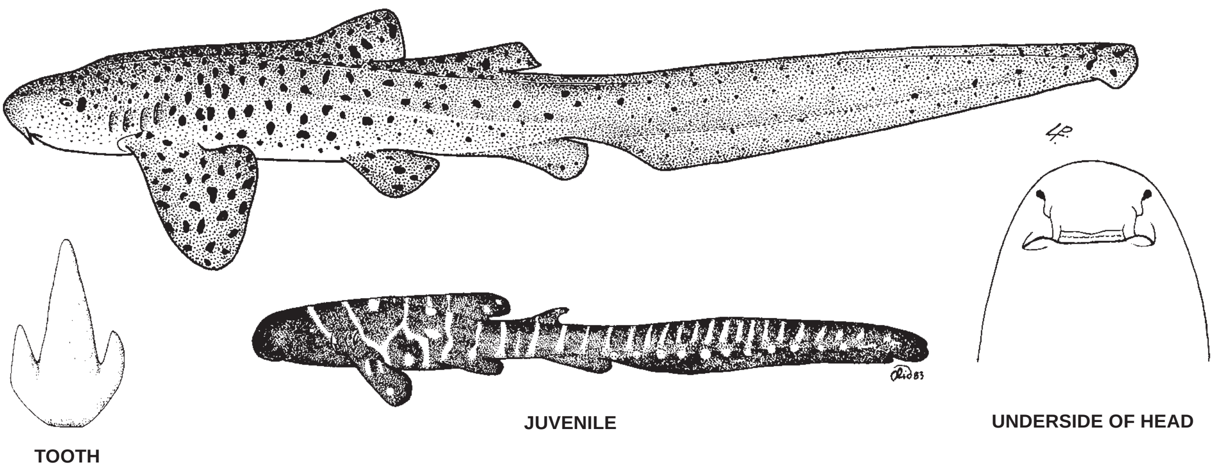
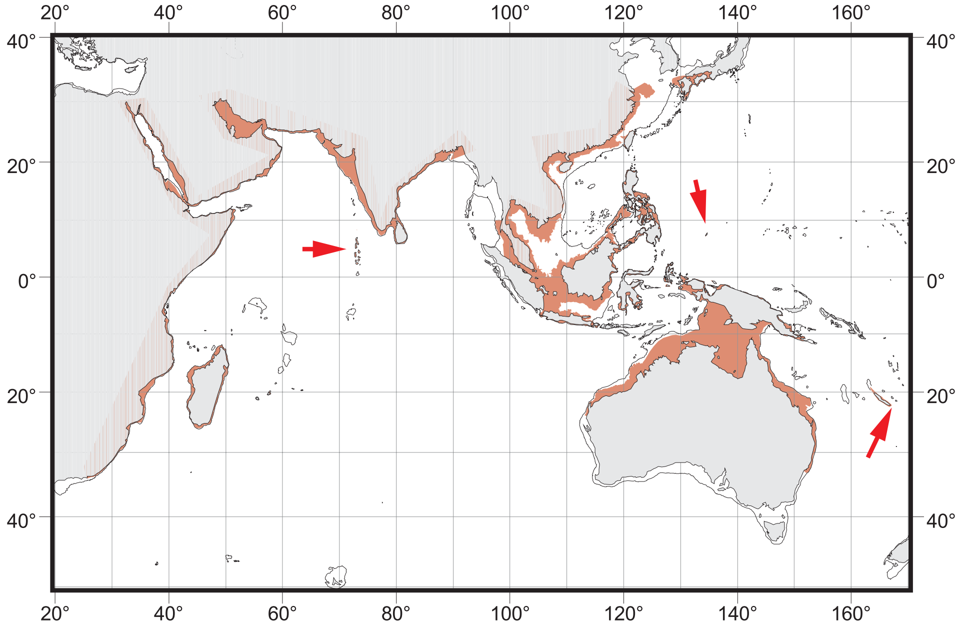


Fig. 156 ***Stegostoma fasciatum***

Field Marks: Unique large sharks that combine a broad, low caudal fin about as long as the rest of the shark with nasoral grooves, barbels, a small transverse mouth in front of the lateral eyes, two spineless dorsal fins and an anal fin, the first dorsal fin much larger than the second and with its origin far forwards on back, prominent ridges on the sides of the body but no strong lateral keels on the caudal peduncle. **Colour:** colour pattern banded or spotted. Young sharks are dark brown above, yellowish below, with vertical yellow stripes and spots breaking the dorsal coloration into dark saddles; in specimens between 50 and 90 cm length the saddles break up into small brown spots on a yellow background, these becoming less linear and more uniformly distributed with further increase in size. There is considerable variation in the colour pattern between individuals of like size. An albino specimen was once collected.

Diagnostic Features: See family Stegostomatidae above.

Distribution: Indo-West Pacific: From the east coast of South Africa (Eastern Cape and KwaZulu-Natal Provinces), Mozambique, and Madagascar north to Tanzania and east to the Red Sea, Gulf of Aden, the Maldives, the Persian Gulf, Pakistan, India, Sri Lanka, Bangladesh, Malaysia (including Sarawak, Borneo), Singapore, Indonesia (Java, Macassar Strait, Sulawesi, Dobo and Aru Islands), Thailand, Viet Nam, Kampuchea, Philippines, China, Taiwan (Province of China), Japan, New Guinea, northern Australia (Western Australia, Northern Territory, Queensland, New South Wales), New Caledonia, and Palau.



Habitat: This is an inshore tropical shark of the continental and insular shelves of the Indo-West Pacific, that is very common on coral reefs but also occurs offshore on soft grounds. It ranges from the intertidal down to 62 m. It has been reported from fresh water in Philippines, but this needs to be confirmed. Adults and large spotted juveniles prefer lagoons, channels and faces of coral reefs, reef detritus and sandy places as rest areas, but the striped young are rarely seen and may prefer water below 50 m.

Biology: The biology of the zebra shark is sketchily known despite being relatively common and readily observed alive by divers on coral reefs and as catches in Indo-West Pacific fish markets. The behaviour and social organization of this shark is little known, but it has been photographed resting on sandy areas within reefs, sometimes propped up on its pectoral fins and facing a current with open mouth. According to Michael (1993), it is usually solitary, but is rarely seen in aggregations. It apparently is rather sluggish, at least during the daytime, and is more active at night as are nurse sharks (Ginglymostomatidae) or when motivated by the presence of food. Because of its rather slender, flexible body and caudal fin it is able to squirm into narrow cracks, crevices and channels while searching for food. In captivity, it spends most of its time resting on the bottom (at least during the day), but becomes active when food is introduced into its tank.

An immature male zebra shark about 1.3 m long was observed by the writer on two separate occasions in a large tank at the Waikiki Aquarium (February 2000). It sat on the bottom of its tank in the evening on one day but became highly active during feeding time in the early afternoon on a subsequent day. It swam about as fast as the 1.1 to 1.2 m long blacktip reef sharks (***Carcharhinus melanopterus***) that it was quartered with (speed estimated at 1.0 to 1.5 m per second), and during a half-hour's observation stayed near the top of the tank and swam continuously. It swam strongly, with prominent anguilliform undulations of its body and tail, and showed much manoeuvring and considerable agility while swimming. The shark broke the surface with its caudal fin on a few occasions, churning the water, but it was not obvious if it was using its tail in any special way. The caudal fin was held at a low but noticeable angle to the body axis. The elongated caudal fin seems less likely to be used as a weapon to herd and stun small fishes than the caudal fins of threshers (Alopiidae), but could be used during social activities, including courtship, as well as for facilitating entry into tight spaces.

Oviparous, laying eggs in large (17 cm long, 8 cm wide and about 5 cm thick), dark brown or purplish black cases with fine lateral tufts of hair-like fibres, which serve to anchor the cases to the substrate. Probably lays more than one or two eggs at once, as four fully formed, encased eggs were found in one oviduct of an adult female.

Feeds primarily on molluscs (gastropods and bivalves) but also crustaceans (crabs and shrimp), small bony fishes, and possibly sea snakes.

Size: Maximum possibly 354 cm, but most adults apparently below 2.5 m. Young hatching at a size between 20 and 36 cm; males maturing between 147 and 183 cm; females maturing between 169 and 171 cm and reaching at least 233 cm.

Interest to Fisheries and Human Impact: 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 gill nets, and with longlines and other line gear. It rarely takes baited hooks. 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.

This is a hardy shark, readily kept in captivity and is an attractive and lively aquarium exhibit. It is currently kept in several public aquaria in Australia, Japan, Portugal, Singapore, Spain, and the United States.

The zebra shark is unaggressive when approached underwater and has not bitten people although it is sometimes harassed by divers trying to ride it. It is popular for viewing by ecotouristic divers in the Red Sea, off the Maldives, off Phuket Island, Thailand, on the Great Barrier Reef in Queensland, Australia, and elsewhere in the Indo-West Pacific. According to Michael (1993), divers hand-feed these sharks off Phuket and the sharks allow divers to physically contact them and tolerate being stroked on the abdomen. It is uncertain if the sharks enjoy extended contact or are undergoing tonic immobility.

The conservation status of the zebra shark needs assessment, as it may have declined in areas such as the Gulf of Thailand where it was formerly more common. Also, it may have been adversely affected by the widespread use of explosives and poisons to fish out reefs in the eastern Indian Ocean and western Pacific as with other reef sharks. It is not known how this shark figures in and is influenced by the international aquarium trade. Although the adults and subadults can only thrive in large public aquaria, as with nurse and tawny sharks, the very attractive newly-hatched young are sufficiently small to live in the tanks of private collectors.

Local Names: Zebra shark (South Africa, Sri Lanka); Tiger shark, Sea tiger, Nurse shark, Shark with tiger-like spots, Leopard shark (Australia, South Africa); Tubarào zebra (Mozambique); Variegated shark (Maldives); Baglul (Arabia); Monkey-mouth, Monkey-mouthed shark, Pollee makum, Komrasi, Oorookoolti sorrah, Potrava, Corungun sorrah (Tamil; India); Yu checkak, Yu tokek (Malay Peninsula); Ikan tjutjot matjan (Malay Samarang); Yu tokay (Malay Pinang); Chilarm seour (Tiger shark), Seaur talay (Sea tiger, Thailand); Torafuzame (Japan); Kongarasi (Telugu); Shinvala (Marathi); Butanding (Philippines, Bikol).

Literature: Seba (1758); Müller and Henle (1838d); Dumeril (1865); Günther (1870); Regan (1908a); Garman (1913); Whitley (1934, 1939, 1940); Barnard (1937); Fowler (1941, 1967a); Misra (1947); Herre (1953, 1958); Lindberg and Legeza (1959); Klausewitz (1960); Teng (1962); Chen (1963); Stead (1963); Gohar and Mazhar (1964); Marshall (1965); Bessednov (1969); Shiino (1972, 1976); Nakaya (1973); Bass, D'Aubrey and Kistnasamy (1975c); Faulkner (1975); Masuda, Araga and Yoshino, (1975); Fourmanoir and Laboute (1976); Grant (1982); Uchida (1982); Compagno (1984); Nakaya and Shirai (1984); Dingerkus (1986); Anderson and Ahmed (1993); Dibelius (1993); Michael (1993); Seret (1994); Last and Stevens (1994).

2.3.6 Family GINGLYMOSTOMATIDAE

Family: Ginglymostomatoidae Gill, 1862b, *Ann. Lyceum Nat. Hist. New York*, 7(32): 393, 395, 397, 406. Emended to family Ginglymostomatidae by Gill, 1872, *Smithsonian Misc. Coll.* (247): 24.

Type Genus: ***Ginglymostoma*** Müller and Henle, 1837.

Number of Recognized Genera: 3.

Synonyms: Family Ginglystomidae Jordan, 1923: 98 (emended or erroneous spelling for Ginglymostomatidae). Subfamily Nebriinae Fowler, 1934: 238 (Family Orectolobidae). Type genus: ***Nebrius*** Rüppell, 1837. Family Ginglymostomatidae Whitley, 1940: 68. Independently proposed as a separate family. Type genus: ***Ginglymostoma*** Müller and Henle, 1837.

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

Field Marks: Small to large sharks with nasoral grooves but no circumnarial 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-fin origin well ahead of the anal-fin origin, and a short precaudal tail much shorter than the head and body.

Diagnostic Features: Head broad and flattened, without lateral flaps of skin. Snout broadly rounded or truncated. Eyes dorsolaterally or laterally situated on head, with or without strong subocular ridges below them. Eyes without movable upper eyelids or subocular pockets. Spiracles much smaller than eyes, without raised external rims; spiracles behind eyes but not below them. Gill slits small, fifth gill slit virtually overlapping fourth; internal gill slits without filter screens. Nostrils with short to moderately long pointed barbels but without circumnarial folds and grooves. Nasoral grooves long and strongly developed. Mouth moderately large, transverse, and subterminal on head. Lower lip trilobate or not, with or without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, no longitudinal symphysial groove on chin. Lower labial furrows extending medially but ending well lateral to symphysis and not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count 24 to 38/22 to 32. Teeth with a strong medial cusp, one to seven pairs of short lateral cusplets, and weak labial root lobes. Teeth orthodont with a central pulp cavity and no plug of osteodentine (***Pseudoginglymostoma***), or osteodont with a core of osteodentine in the crown (***Ginglymostoma*** and ***Nebrius***). Body cylindrical or moderately depressed, without ridges on sides. Precaudal tail shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins moderately large, broad and rounded to narrow and falcate. Pectoral fins aplesodic (***Pseudoginglymostoma***), semiplesodic (***Ginglymostoma***) or fully plesodic (***Nebrius***), with fin radials variably expanded into fin web or not. Pectoral propterygium moderately large and separate from mesopterygium and metapterygium; pectoral-fin radial segments 4 to 9, and with longest distal segments 0.4 to 0.7 times the length of longest proximal segments. Pelvic fins somewhat larger to somewhat smaller than dorsal fins and anal fin, much smaller than pectoral fins and with anterior margins 0.4 to 0.7 times pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. Dorsal fins either equal-sized (***Pseudoginglymostoma***) or with second dorsal fin considerably smaller than first (***Ginglymostoma***, ***Nebrius***). First dorsal-fin origin varying from slightly anterior to pelvic-fin origins to over their bases, insertion just behind the pelvic-fin rear tips. Anal fin about as large as second dorsal fin, with broad base and angular apex, origin about opposite second dorsal-fin origin or midbase, and insertion separated by a space much less than its base length from lower caudal-fin origin. Caudal fin horizontally elongated and not crescentic, heterocercal, with its upper lobe at a moderate angle above the body axis; dorsal caudal-fin margin less than two-fifths as long as the entire shark. Caudal fin with a strong terminal lobe and subterminal notch but without a ventral lobe or with a very short one, preventral and postventral margins not differentiated and forming a continuous curve (***Pseudoginglymostoma***) or weakly differentiated in adults (***Nebrius***, ***Ginglymostoma***). Vertebral centra with well-developed radii. Total vertebral count 135 to 195, monospondylous precaudal count 35 to 57, diplospondylous precaudal count 41 to 53, diplospondylous caudal count 49 to 96, and precaudal count 85 to 103. Cranium narrow to moderately broad but not greatly expanded laterally. Medial rostral cartilage moderately long and not reduced to a low nubbin. Nasal capsules elevated and not greatly depressed or fenestrated, internarial septum low and compressed or moderately depressed. Orbits with small foramina (***Pseudoginglymostoma***) or enlarged fenestra (***Ginglymostoma***) for preorbital canals, medial walls not fenestrated around the optic nerve foramina. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves moderately broad and not greatly reduced. Cranial roof either solid (***Pseudoginglymostoma***) or with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with a pair of stapediocarotid foramina (***Pseudoginglymostoma***) or separate carotid and stapedial foramina (***Ginglymostoma***). Adductor mandibulae muscles of jaws with three divisions (***Ginglymostoma***). Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 15 to 24 turns. Development ovoviviparous as far as is known (***Ginglymostoma*** and ***Nebrius***). Size small to large with adults between 53 and at least 304 cm, while young are born between 27 and 79 cm (***Ginglymostoma*** and ***Nebrius***). Colour pattern plain or with a few dark spots in young, no saddles, reticulations or white spots.

Distribution: These are common, small to large, nocturnal, inshore bottom sharks with a circumglobal distribution in subtropical and tropical continental and insular waters. ***Ginglymostoma*** currently occurs in the eastern Pacific and tropical Atlantic, ***Nebrius*** has a wide range in continental waters of the Indo-West Pacific, while ***Pseudoginglymostoma*** has a restricted distribution in the western Indian Ocean off East Africa. They do not occur off oceanic islands far from land and have not penetrated the Central Pacific to the Hawaiian Island chain.

Habitat: Nurse sharks occur in inshore 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.

Biology: Members of the genera ***Nebrius*** and ***Ginglymostoma*** are social animals that occur in small groups while resting on the bottom; they often lie atop one another in a pile.

Development is ovoviviparous in ***Ginglymostoma***, with young that are nourished primarily by yolk while in the uterus; litters of 20 to 30 young have been reported. ***Nebrius*** is ovoviviparous and practices uterine cannibalism, with a form of oophagy in which the developing young apparent eat large, cased, unfertilized eggs; litters are smaller, up to four. The reproductive mode of ***Pseudoginglymostoma*** is uncertain; one female laid eggs with stout egg-cases in captivity (unfertilized), suggesting that it is 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 with their barbels, they quickly 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 and tawny nurse sharks suggest that they may stalk and suddenly suck in such items, or merely suck 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, shrimp, lobsters, and other crustaceans, squid, octopi, and other molluscs, corals, sea urchins and sea squirts.

Interest to Fisheries and Human Impact: The larger species of nurse sharks are or were formerly common in shallow marine waters 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. ***Ginglymostoma*** and ***Nebrius*** are very tough and hardy sharks that can survive over a decade in captivity and are often kept in large public aquaria and oceanaria, while young ***Ginglymostoma*** figure importantly in the aquarium trade. ***Pseudoginglymostoma*** is seldom kept in captivity but is also very hardy and is more suitable for smaller aquaria. ***Nebrius*** and especially ***Ginglymostoma*** should be treated with respect, as they will occasionally bite and clamp on to a human tormentor when provoked; their vice-like jaws may need to be pried lose from a victim. ***Ginglymostoma cirratum*** has bitten people without provocation, but more often will bite and otherwise defend itself when harassed by divers. The small prey, small mouths and small teeth of these sharks suggest that occasional incidents are agonistic or defensive and not predatory. ***Ginglymostoma*** and ***Nebrius*** are popular subjects of ecotouristic dive tours.

Local Names: Nurse sharks, Tubarões de leite (Mozambique).

Remarks: This family is recognized following the works of Compagno (1973, 1982, 1984, 1988) and Applegate (1974), which revived the Ginglymostomatidae and other orectoloboid family-group taxa of Gill (1862b). The genus ***Nebrius*** was sometimes considered a synonym or subgenus of ***Ginglymostoma*** (Agassiz, 1838; Dumeril, 1853, 1865; Günther, 1870; Fowler, 1941), or ***Ginglymostoma*** was synonymized with ***Nebrius*** (Gray, 1851), ***Nebrius*** is recognized as a separate genus from ***Ginglymostoma*** following Garman (1913), Whitley (1940), Bigelow and Schroeder (1948), Garrick and Schultz (1963), Compagno (1973, 1984, 1988), Applegate (1974), Bass, D'Aubrey and Kistnasamy (1975c), and Dingerkus (1986).

Nebrius and ***Ginglymostoma*** are usually distinguished by structural tooth characters. According to Bigelow and 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 by the writer varied considerably in cusp size, but in no instance were the cusps as small as the cusplets (cusps were smallest in young sharks, largest in adults). The number of functional tooth series was 2 or 3 in ***Nebrius*** specimens but overlapped ***Ginglymostoma cirratum*** with 3 or 4. Hence the arrangement and definition of these genera are revised (Compagno, 1984, and unpublished work), and the two are readily distinguished otherwise by tooth arrangement, external morphology, and anatomical characters (see diagnostic features of the genera).

Compagno (1984) provisionally placed ***Ginglymostoma brevicaudatum*** in the same genus as ***G. cirratum***, but noted that the former is strongly divergent morphologically from ***G. cirratum***, which is closer to ***Nebrius ferrugineus***, and 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-fin origin, equal-sized dorsal fins, a shorter caudal fin, as well as other external and cranial differences. Compagno (1984) suggested that ***G. brevicaudatum*** was generically distinct from ***Ginglymostoma*** proper, and, following a suggestion by D. Ward (pers. comm.), might be referable to the fossil tooth genus ***Eostegostoma*** Herman and Crochard, 1977.

Eostegostoma was proposed by Herman and Crochard (1977: 133) for ***Ginglymostoma angustum*** Nolf and Taverne 1977, based on fossil teeth from the Eocene of Belgium. These authors considered ***Eostegostoma*** an early stegostomatid (hence the name), but Cappetta (1987), who recognized ***Eostegostoma*** as a genus, suggested that it was closer to ***Brachaelurus*** and fell in the family Brachaeluridae instead of Stegostomatidae. Compagno (1988) suggested that ***Eostegostoma*** was more ***Stegostoma***-like than ***G. brevicaudatum***, and that the latter requires its own genus. Dingerkus (1986) erected a new genus, ***Pseudoginglymostoma***, for ***G. brevicaudatum***, which was recognized by Compagno (1988, 1999) and which is adopted here. Whatever the relationships of ***Eostegostoma*** it apparently is not congeneric with ***Pseudoginglymostoma***.

Dingerkus (1986) presented a hand-fitted cladogram of the orectoloboids, and included the genera herein placed in the Ginglymostomatidae in the family Rhincodontidae along with ***Rhincodon*** and ***Stegostoma***. In Dingerkus' analysis his genus ***Pseudoginglymostoma*** was considered the sister taxon of the other members of his Rhincodontidae, which formed two pairs of sisters, ***Nebrius*** with ***Ginglymostoma*** and ***Rhincodon*** with ***Stegostoma***. Compagno (1988) independently produced a similar hand-fitted cladogram with two variants, placing "***G. brevicaudatum***" (= ***Pseudoginglymostoma***) as the sister of the 'advanced' orectoloboids (***Stegostoma*** the sister of the group ***Rhincodon*** plus the sister pair ***Ginglymostoma*** and ***Nebrius***), or, less probably with ***Pseudoginglymostoma*** as the sister of ***Stegostoma*** alone, with these taxa the sister of ***Rhincodon*** plus ***Ginglymostoma*** and ***Nebrius***.

Further work on the morphology of ***Pseudoginglymostoma***, including its orolabial structures, neurocranium and pectoral-fin skeleton, confirms its distinctiveness, and suggests that Dingerkus (1986) and Compagno (1988) were correct in placing it as the sister taxon of the advanced orectoloboids. Pending a detailed study of the morphology of the genus, ***Pseudoginglymostoma*** is retained in the Ginglymostomatidae, which may make the family paraphyletic. It may be necessary in the future to place ***Pseudoginglymostoma*** in its own family as an alternative to lumping all of the advanced and highly divergent orectoloboids in the Rhincodontidae as per Dingerkus (1986), but as a stopgap ***Pseudoginglymostoma*** is placed in a subfamily of its own within Ginglymostomatidae, defined as follows:

> Pseudoginglymostomatinae: Eyes very small and 0.8 to 1.0% of total length. Nasal barbels very short, stubby, not very tapered, less than 1% of total length, and not reaching mouth. Lower lip not trilobate and without orolabial grooves. Tooth rows 24 to 27/22 to 27. Teeth not compressed, tooth crown feet very narrow, cusps large, cusplets very small and one or two on each side; teeth with moderately broad basal ledges. Teeth orthodont and with a central pulp cavity. Pectoral fins broadly rounded and not falcate in adults; pectoral fins semiplesodic and with radials reaching only 55% into fin web, radial segments four. First dorsal-fin origin over or slightly behind pelvic-fin midbases. Second dorsal fin about as large as first dorsal fin. Anal fin posterior margin ends in front of lower caudal-fin origin. Caudal fin short with dorsal caudal-fin margin less than 25% of total length (adults). Total vertebral count 135 to 143, monospondylous precaudal count 35 to 37, diplospondylous caudal count 49 to 54 and 36 to 39% of total count. Jaws broadly arcuate. Adults small, less than 1 m long.

> Ginglymostomatinae: Eyes small but usually over 1% of total length. Nasal barbels moderately elongated, tapered, slender and over 1% of total length, reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Tooth rows 29 to 42/26 to 34. Teeth moderately to greatly compressed, tooth crown feet broad, cusps moderately tall to very short, cusplets moderately large and three or more on each side, basal ledges moderately broad to very broad. Teeth osteodont, with pulp cavity filled by osteodentine. Pectoral fins semifalcate or falcate in adults, fins plesodic and with radials reaching about 80% into fin web, radial segments seven to eleven in longest radials. First dorsal-fin origin about over or slightly behind pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal free rear tip and posterior margin extending behind level of lower

caudal-fin origin. Caudal fin elongate with dorsal caudal-fin margin over 25% of total length in adults. Total vertebral count 168 to 195, monospondylous precaudal count 48 to 57, diplospondylous caudal count 73 to 96 and 43 to 50% of total count. Adults large, 230 cm or longer.

Literature: Müller and Henle (1838d); Dumeril (1865); Günther (1870); Regan (1908a); Garman (1913); Fowler (1941, 1967a); Whitley (1940); Bigelow and Schroeder (1948); Stead (1963); Compagno (1973, 1984, 1988); Applegate (1974); Dingerkus (1986); Michael (1993); Last and Stevens (1994).

Key to Genera:

1a. Nasal barbels greatly reduced, not reaching mouth; lower lip not trilobate, no shallow orolabial grooves connecting edge of lip with lower labial furrows; second dorsal and anal fins about as large as first dorsal fin; caudal fin short, less than 20% of total length (Pseudoginglymostomatinae) (Fig. 157a and b) . . ***Pseudoginglymostoma***

1b. Nasal barbels elongated, reaching mouth; lower lip trilobate, with shallow orolabial grooves connecting edge of lip with lower labial furrows; second dorsal and anal fins much smaller than first dorsal fin; caudal fin longer, over 25% of total length (Ginglymostomatinae) (Fig. 158a and b). . . . → **2**

2a. Eyes and gill openings dorsolateral on head; teeth not compressed on sides of jaw, not imbricated; pectoral, dorsal and anal fins apically rounded, pectoral fins broad and not falcate or semifalcate (Fig. 158b) . . . ***Ginglymostoma***

2b. Eyes and gill openings lateral on head; teeth more or less compressed on sides of jaws, forming imbricated series; pectoral, dorsal and anal fins apically angular, pectoral fins narrow and falcate (Fig. 159). . . . . ***Nebrius***

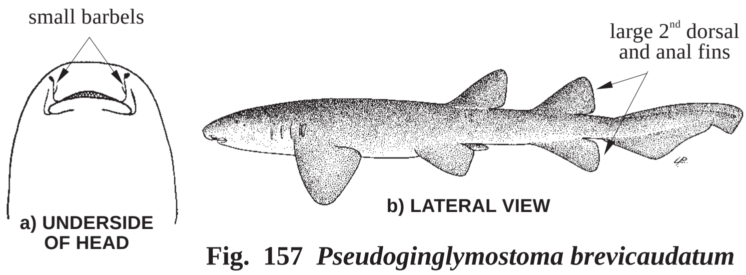


Fig. 157 ***Pseudoginglymostoma brevicaudatum***

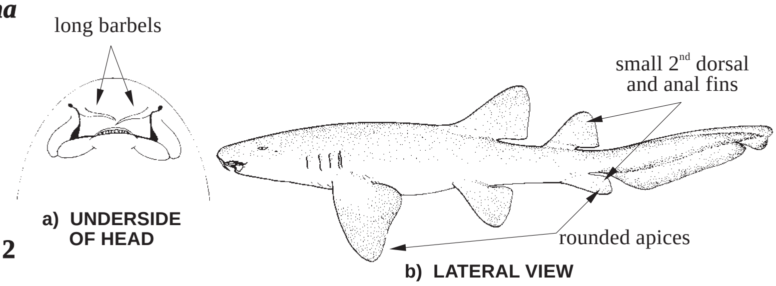


Fig. 158 ***Ginglymostoma cirratum***

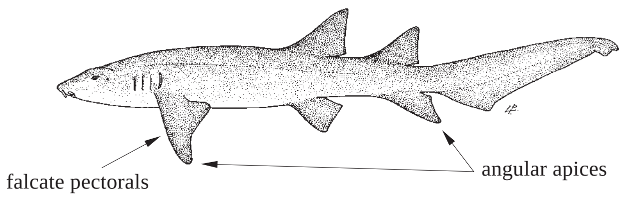


Fig. 159 ***Nebrius ferrugineus***

Ginglymostoma Müller and Henle, 1837

Genus: ***Ginglymostoma*** Müller and Henle, 1837a, *Ber. K. preuss. Akad. wiss. Berlin*, 2: 113; Müller and Henle, 1837b, *Arch. Naturg.*, 3: 396; Müller and Henle, 1838a, *Mag. Nat. Hist., new ser.*, 2: 35; Müller and Henle, 1838b, *L'Institut*, 6: 64 (no species mentioned); Müller and Henle, 1838d, *Syst. Beschr. Plagiost.*, pt. 1: 22 (two species, ***G. concolor*** and ***G. cirratum***, but no type allocation); Müller and Henle, 1838, *in* Bonaparte, 1838, *Nuov. Ann. Sci. Nat., Bologna,* ser. 1, 2: 212 (one species mentioned, "***Ginglymostoma cirrosum***, Mull. et Henle").

Type Species: ***Squalus cirratus*** Gmelin, 1788, by subsequent designation of Jordan and Gilbert, 1883, *Bull. U.S. Natl. Mus.*, 16: 18, equals ***S. cirratus*** Bonnaterre, 1788. Gill (1862b, *Ann. Lyceum Nat. Hist. New York*, 7[32]: 406) designated "***Ginglymostoma concolor***" (Müller and Henle, 1838 = ***Nebrius concolor*** Rüppell, 1837), but this would make ***Ginglymostoma*** and ***Nebrius*** synonyms. Bonaparte's restriction of ***Ginglymostoma*** to "***G. cirrosum***" (a synonym of to ***S. cirratus***) and Jordan and Gilbert's (1883) designation are followed here. See also Bigelow and Schroeder (1948, *Mem. Sears Fnd. Mar. Res.,* (1), 1: 180), who cited Hay's (1902, *U.S. Geolog. Surv. Bull.*, 179: 310) subsequent type designation of ***S. cirratus***, and Eschmeyer (1998, *Cat. Fish.*: CD-ROM).

Number or Recognized Species: 1.

Synonyms: Genus ***Ginglimostoma*** Agassiz, 1838: 85. Error or emendation of ***Ginglymostoma***. Genus ***Gynglimostoma*** Dumeril, 1859: 261. Probable error for ***Ginglymostoma***. Genus ***Gingylostoma*** Springer, 1938: 13. Apparent error for ***Ginglymostoma***.

Diagnostic Features: Head in dorsal or ventral view broadly arcuate in young, narrower and U-shaped in adults. Snout bluntly wedge-shaped in lateral view, short and with mouth width about 2.3 to 2.6 times preoral length. Eyes small but usually over 1% of total length, positioned dorsolateral on head and with strong subocular ridges below them. Eyes with ventral edges just above level of dorsal ends of gill slits. Gill openings dorsolaterally situated on head and not or hardly visible from below but just reaching horizontal head rim in dorsal view. Nostrils nearly terminal on snout. Nasal barbels moderately elongated, tapered, slender and over 1% of total length, reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Distance between lower labial furrows about 1.5 times their length. Tooth rows 30 to 42/28 to 34, functional tooth series at least 7 to 9/8 to 12. Teeth moderately compressed, not imbricated but in alternate overlap pattern, functional series not separated from replacement series by toothless space. Tooth crown feet broad, cusps moderately tall, cusplets moderately large and 2 to 6 on each side, basal ledges moderately broad. Teeth osteodont, with pulp cavity filled by osteodentine. Body semifusiform. Lateral trunk denticles broad and rhomboid in adults, with three strong parallel ridges and a very short, blunt cusp. Pectoral fins broad and rounded-angular in young and semifalcate in large specimens, apices rounded. Pectoral-fin origins slightly behind to slightly in front of third gill slits. Pectoral fins plesodic and with radials reaching about 80% into fin web, radial segments 7 or 8 in longest radials. Pelvic fins rounded in young, possibly subangular in adults. Dorsal fins apically rounded. First dorsal-fin origin about over, slightly in front, or slightly behind pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal fin distinctly smaller than second dorsal fin, apically rounded. Anal-fin origin about opposite, slightly behind, or slightly in front of midbase of second dorsal-fin, with apex about under anal-fin base and posterior margin extending behind level of lower caudal-fin origin. Caudal fin long with dorsal caudal-fin margin over 25% of total length (adults). Caudal fin narrow and shallow with dorsal caudal-fin margin 3.2 to 3.6 times caudal-fin depth; no ventral caudal-fin lobe in young but a weak one in adults; preventral caudal-fin margin much shorter than postventral margin and 43 to 67% of it; terminal lobe short and 15 to 19% of dorsal caudal-fin margin. Total vertebral count 168 to 175, monospondylous precaudal count 48 to 50, diplospondylous caudal count 73 to 83 and 43 to 48% of total count. Jaws broadly arcuate. Intestinal valve count 16 to 17. Development ovoviviparous with young nourished on yolk sac only, litter size 21 to 30. Adults 230 cm long or larger, size at birth 27 to 30 cm. **Colour:** yellowish to grey-brown above and light whitish brown below, young with small dark, light-ringed ocellar spots and obscure dorsal saddle markings, adults and subadults without spots or saddles.

Remarks: Scope of this genus is modified from Compagno (1973, 1984), and Applegate (1974), and follows Dingerkus (1986) in recognizing a single living species, ***Ginglymostoma cirratum***. ***Ginglymostoma brevicaudatum*** is placed in the genus ***Pseudoginglymostoma*** (see below). There are numerous fossil species of ***Ginglymostoma*** (Cappetta, 1987).

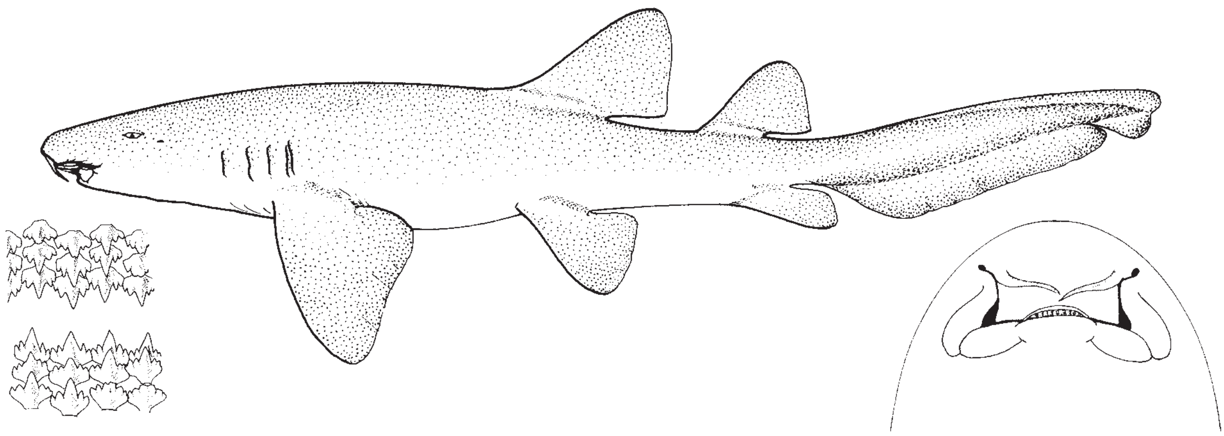
Ginglymostoma cirratum (Bonnaterre, 1788) **Fig. 160**

Squalus cirratus Bonnaterre, 1788, *Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol.,* Paris: 7. Lectotype: Museum National d'Histoire Naturelle, Paris, MNHN-A.7654, 458 mm immature female, "Les mers de la Amerique." From unpublished addendum to Bertin (1939b, *Bull. Mus. Nat. Hist. Nat.*, 2e ser., 12(6): 51-98) by M.L. Bauchot (pers. comm.), also Eschmeyer (1998, *Cat. Fish.*: CD-ROM). Separately described as ***Squalus cirratus*** Gmelin, *in* Linnaeus and Gmelin, 1788, *Syst. Nat.,* ed. 13, Pisces 1(3): 1492. Types?

Synonyms: ***Squalus punctulatus*** Lacépède, 1800: 119, pl. 4, fig. 3. Type locality: "Guiane". No types known according to Eschmeyer (1998: CD-ROM). ***Squalus cirrhatus*** Bloch and Schneider, 1801: 128. Based on ***S. cirratus*** Gmelin, *in* Linnaeus and Gmelin, 1788, possibly an emended or erroneous spelling. Also ***Ginglymostoma cirrhatum*** Jordan, 1905: 533. ***Squalus punctatus*** Bloch and Schneider, 1801: 134. Based on the "Gata" of Parra, 1787: 86, pl. 34, fig. 2, from Cuba. No types known according to Eschmeyer (1998: CD-ROM). ***Scyllium cirrhosum*** Griffith and Smith, *in* Cuvier, Griffith and Smith, 1834: 10, pl. 30. Variant spelling? ***Ginglymostoma cirrosum*** "Müller and Henle", *in* Bonaparte, 1838: 213. Variant spelling. ***Squalus argus*** Bancroft, 1832: 82. Holotype possibly in British Museum (Natural History) according to Eschmeyer (1998: CD-ROM), who indicates that this species was not characterized in the original account, but was described in an accompanying account by Bennett (1832: 86-91). Type locality: West Indies. ***Ginglymostoma fulvum*** Poey, 1858: 342; also Poey, 1860, pl. 19, figs. 15-16. Holotype: 839 mm female, Cuba. Paepke and Schmidt (1988: 162) list Institut für Spezielle Zoologie und Zoologisches Museum, Berlin, ZMB-5508, 965 mm TL specimen, as a possible syntype. ***Ginglymostoma caboverdianus*** Capello, 1867: 167. Cape Verde. Three syntypes according to Eschmeyer (1998: CD-ROM), but status of these types otherwise uncertain. ***Ginglymostoma cirrotum*** Gudger, 1914: 176. Erroneous spelling?

Other Combinations: ***Nebrius cirratum*** (Bonnaterre, 1788), ***Scyllium cirratum*** (Bonnaterre, 1788).

FAO Names: En - Nurse shark; **Fr** - Requin nourrice; **Sp** - Gata nodriza.



UPPER AND LOWER TEETH

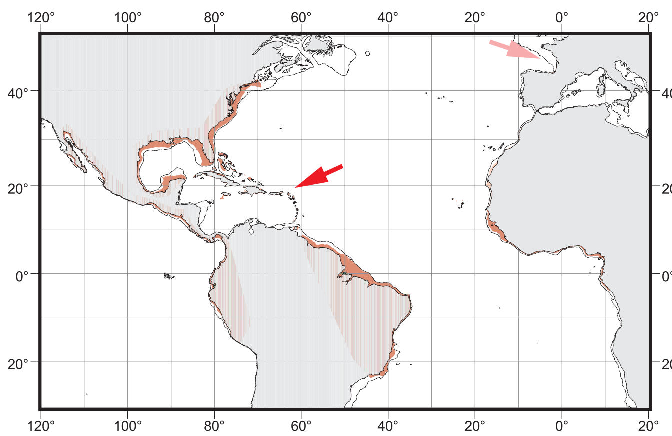
Fig. 160 ***Ginglymostoma cirratum***

UNDERSIDE OF HEAD

Field Marks: Moderately long barbels, nasoral grooves present but no circumnarial grooves; eyes dorsolateral, 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 one-fourth of total length; colour yellow-brown to grey-brown, young with small dark, light-ringed ocellar spots and obscure dorsal saddle markings, adults and subadults without spots or saddles.

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

Distribution: Western Atlantic: Rhode Island to southern Brazil, including United States (exceptionally Rhode Island and North Carolina, South Georgia and Florida and Gulf coast from Florida to Texas), Mexico (Gulf of Mexico and Caribbean coasts), Bermuda, Bahamas, Turks and Caicos Islands, Cuba, Puerto Rico, Haiti, the Lesser Antilles, Belize, Jamaica, Barbados, Trinidad, French Guiana, Guyana, Panama, and Brazil (south to Rio de Janeiro). Eastern Atlantic: Cape Verde Islands, Senegal, Cameroon to Gabon, and rarely north to Gulf of Gascony, France. Eastern Pacific: Mexico (Baja California Sur, Gulf of California) south to Costa Rica, Panama, Ecuador, and Peru. The known distribution of the nurse shark suggests at least three geographically isolated populations (eastern Pacific, western Atlantic and eastern Atlantic), but their differentiation, if any, has yet to be studied.



Habitat: This is an inshore bottom shark of the continental and insular shelves in tropical and subtropical waters, often occurring at depths of 1 m or less in the intertidal, but down to at least 12 m and off Brazil between 40 and 130 m. The nurse shark is often found on rocky and coral reefs, in channels between mangrove keys and on sand flats.

Biology: This is a large nocturnal and facultatively social 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 and coral reefs in shallow water during the day, often in schools or aggregates of three to three dozen individuals that are close to, or even piled on one another while resting. Swimming speed was measured at 31 to 78 cm/sec for a 250 cm captive individual (Hussain, 1991). 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 suggest 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. Nurse sharks fitted with conventional and sonic tags show little if any local movement, but adults have a larger range than young (Carrier, 1990). This suggests that groups of these animals are site-localized and vulnerable to local extirpation from overexploitation. This shark has been historically common or abundant in some areas where it occurs, particularly in the tropical western North Atlantic and off Tropical West Africa.

Courtship and copulatory behaviour has been observed in captivity (Klimley, 1980) and studied in detail in the wild (Carrier, Pratt and Martin, 1994), and is apparently rather complex. In captivity 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 grab one of the female's pectoral fins with his mouth, which in turn may induce the female to pivot 90° 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. Carrier, Pratt and Martin divided nurse shark mating into five stages based on field observations of free-ranging individuals in a mating area in the Dry Tortugas, Florida: *Precoupling*, in which a male or group of males approached a female that was resting or swimming, in the latter case with parallel or tandem swimming, and with males approaching alongside and slightly behind the female with heads close to her pectoral fins. *Coupling*, in which the male grabs the female's pectoral fin, sometimes with two males grabbing both pectoral fins and with other males circling in close proximity. *Positioning*, in which the male, or two males, roll the female onto her back, and with the male rolling and aligning his tail and pelvic fins prior to copulation. *Insertion and copulation*, in which the male copulates with the female, inserting his right clasper if holding her right pectoral, and his left clasper if holding her left pectoral, and thrusts against the female who remains quiescent. *Postcopulation*, in which the male removes his claspers, releases the female's pectoral, and either the two depart or lie on the bottom in parallel with ventral surfaces down. Over half the copulatory bouts involved more than one male, with a few insertions and copulations involving two or more males.

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 20 to 30 in a litter. The gestation period is about five to six months and it reproduces every other year. Nursery areas are in shallow turtle-grass beds and on shallow coral reefs. Nurse sharks are slow-growing, with free-ranging tagged juveniles (average about 126 cm long) growing at about 13 cm per year. Males may be 10 to 15 years old at maturity and females 15 to 20 years old (Carrier, 1990; Carrier and Luer, 1990).

The nurse shark feeds heavily on bottom invertebrates such as spiny lobsters, shrimps, crabs, sea urchins, squid, octopi, marine snails and bivalves, and also fish including herring (Clupeidae), sea catfish (Ariidae), mullet (Mugilidae), parrotfish (Scaridae), surgeonfish (Acanthuridae), puffers (Tetraodontidae), and stingrays (Dasyatidae). Algae is occasionally found in its stomach and may be sucked in along with prey animals. 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 bony fishes that are resting at night but would be too active and manoeuvrable for this 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 by grabbing its body with its teeth and by suction. It will dig under coral detritus and in sand with its head to root out prey.

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 sucks it in. It may even work over vertical surfaces with its barbels.

Size: Maximum said to be 430 cm long but most adults are under 3 m long and the largest reliably reported were 280 to 304 cm. Newborn young are about 27 to 30 cm. Males mature at about 210 cm and adult males reach at least 257 cm; females are immature at 225 to 235 cm and mature mostly at about 230 to 240 cm (though one adult female 152 cm long has been reported) and reach over 259 cm.

Interest to Fisheries and Human Impact: This shark is commonly captured in local artisanal fisheries in some areas where it occurs, particularly the tropical western Atlantic. It was, however, rare in a localized broad-spectrum fishery out of Guaymas, Mexico (examined by the writer in 1974). It has been prized for its extremely tough, thick, armour-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 fish meal. 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 easily captured with line gear, gill nets, fixed bottom nets and bottom trawls, and spears. It can be readily captured on sportsfishing tackle, but is generally regarded as being too sluggish to be much of a game fish (unlike the tawny nurse shark in Australia). Divers have sometimes speared nurse sharks, which is inane 'sport' because of its senselessness. The sharks are often sitting ducks for spearfishing divers on the bottom, and the modest speed of these sharks even when active make them no great challenge to hit. However, the toughness of these sharks may make them difficult to subdue underwater, and a diver that spears one may receive a well-deserved bite. The nurse shark was regarded as a pest by fishermen in the Lesser Antilles because it rifled fish traps for food.

The nurse shark is generally regarded as harmless to people, because of its sluggishness during the day and relatively small teeth, and is a popular subject for ecotouristic divers, with dive sites to view this shark mostly in the Bahamas but also off Belize, Turks and Caicos, and Florida. In the Caribbean and off Florida people frequently come in contact with it underwater, and it mostly will not respond defensively when approached and usually swims away when disturbed. There have been a small number of nonfatal, unprovoked incidents of nurse sharks biting swimmers and divers. Nonfeeding aggression, possibly related to courtship, defensive threat, or a defensive response to physical contact is possible as the motivation for such encounters. The small prey taken by these sharks and lack of mammalian meat in their diet suggests that predation on people is most improbable. In one unusual and somewhat amusing (but not to the diver) unprovoked incident a large nurse shark grabbed a diver's chest with its teeth, then appeared to hold onto his body with its pectoral fins; the encounter suggests displaced courtship, but unfortunately the sex of the shark was not recorded. More commonly people attempt to ride, spear, grab or otherwise harass this shark, or accidentally step on one while wading, and get bitten as a result. Juveniles are thought to be more prone to turn and bite than adults, which often swim away. Although its teeth are small, the jaws and associated muscles of the nurse shark are powerful and vice-like; in some instances nurse sharks have bitten people and held on, and had to be pried loose with a tool. Hence one should treat these sharks with due respect and enjoy their presence underwater without harassing them.

Nurse 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 hardiness and ability to learn. These sharks are ideal for public display in aquaria and are important for the aquarium trade. They are currently kept in numerous aquaria in Brazil, Europe, Mexico, the United States, and probably elsewhere.

The conservation status of the nurse shark needs to be assessed throughout its range, but particularly off West Africa, parts of the tropical western Atlantic and in the eastern Pacific where intensive inshore fisheries are being pursued and the distribution and abundance of these sharks is sketchily known. They are regarded as particularly vulnerable to overexploitation because of their slow growth, low reproductive rate, inshore habitat, apparent site-specificity, their presence in areas with intense inshore fisheries, and very little catch data available. The USA was the only country reporting nurse shark catches (214 t in 1995) to FAO over the vast range of this shark, and this was only reported during the last decade. Apart from their vulnerability to inshore fisheries, these sharks have been increasingly captured for private and public aquaria, and may have declined in some areas as a result of exploitation. Carrier (1996) and Carrier and Pratt (1998) suggested that public entry should be banned during the late spring and summer at one nurse shark breeding site in the Dry Tortugas National Park, Florida Keys, to avoid disturbing the mating of the sharks in shallow water. These sharks are a major asset to ecotourism in the Caribbean, and probably generate far more revenue there as live sharks viewed by divers than as fisheries products.

Local Names: Nurse shark, Sand shark, Gata (Mexico, West Indies), Gata atlantica, Cacao lixa (Brazil).

Literature: Gray (1851); Dumeril (1853, 1865); Günther (1870); Garman (1913); Fowler (1936, 1967a); Beebe and Tee-Van (1941a, b); Bigelow and Schroeder (1948); Cadenat (1950, 1957); Orces (1952); Springer (1960, 1963, 1973); Randall (1961, 1963, 1967, 1968, 1996); Garrick and Schultz (1963); Limbaugh (1963); Clark (1963); Clark and von Schmidt (1965); Kato, Springer and Wagner (1967); Sadowsky (1967); Böhlke and Chaplin (1968); Klimley (1974, 1980); Applegate et al. (1979); Cadenat and Blache (1981); Castro (1983); Compagno (1984, 1988); Neto, Bezerra, and Gadig (1989); Springer (1990); Carrier (1990); Carrier and Luer (1990); Michael (1993); Carrier, Pratt and Martin (1994); Bonfil (1997); Moore (1997); Carrier and Pratt (1998); Hoese and Moore (1998); McEachran and Fechhelm (1998); Castro, Woodley and Brudek (1999).

Nebrius Rüppell, 1837

Genus: ***Nebrius*** Rüppell, 1837, *Neue Wirbel. Fauna Abyssinien gehör., Fische Rothen Meeres*, (1835-1838): 62.

Type Species: ***Nebrius concolor*** Rüppell, 1837, by monotypy.

Number of Recognized Species: 1.

Synonyms: Genus ***Nebrodes*** Garman, 1913: 56. Replacement name for ***Nebrius*** Rüppell, 1837, thought by Garman to be previously occupied by ***Nebria*** Latrielle, 1802 (Insecta) and ***Nebris*** Cuvier and Valenciennes, 1830 (Osteichthyes), and hence taking the same type species, ***Nebrius concolor*** Rüppell, 1837. Unjustified replacement, as ***Nebria*** and ***Nebris*** are not senior homonyms of ***Nebrius***.

Diagnostic Features: Head in dorsal and ventral view narrow and more or less U-shaped at all stages. Snout wedge-shaped in lateral view, moderately elongated, with preoral length about 63% of mouth width. Eyes small but usually over 1% of total length, situated laterally on head and with no subocular ridges below them but with strong supraocular ridges above them; eyes with ventral edges below level of dorsal ends of gill slits. Gill openings laterally situated on horizontal head rim and prominently visible from above and below. Nostrils distinctly ventral on snout. Nasal barbels moderately elongated, tapered, slender, over 1% of total length, and reaching past mouth. Lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Distance between lower labial furrows about 2.1 times their length. Tooth rows 29 to 33/26 to 28, functional series 2 to 4/2 to 4. Teeth greatly compressed, with imbricate overlap pattern, and functional series separated from replacement series by narrow toothless space. Tooth crown feet broad, cusps small, three or more moderately large cusplets on each side, and greatly widened basal ledges. Teeth osteodont and with pulp cavity filled by osteodentine. Lateral trunk denticles more or less rounded-rhomboid in adults, with four or five incomplete weak radial ridges and a very short, blunt cusp. Pectoral fins narrow and falcate at all stages, apically angular. Pectoral-fin origins about opposite or slightly anterior to fourth gill slits. Pectoral fins plesodic and with radials reaching about 80% into fin web, radial segments 10 or 11 in longest radials. Pelvic fins angular. Dorsal fins apically angular. First dorsal-fin origin about over or slightly ahead of pelvic-fin origins. Second dorsal fin distinctly smaller than first dorsal fin. Anal fin as large or slightly larger than second dorsal fin, apically angular. Anal-fin origin varying from slightly in front of origin of second dorsal fin to about opposite its midbase, apex behind rear tip of second dorsal fin, posterior margin extends behind level of lower caudal-fin origin. Caudal fin elongate with dorsal caudal-fin margin over 25% of total length (adults); caudal fin narrow and shallow with depth 28 to 31% of dorsal caudal-fin margin; a short and weak ventral caudal-fin lobe usually present at all stages; preventral margin much shorter than postventral margin and 36 to 45% of it; terminal lobe very short and 10 to 15% of dorsal caudal-fin margin. Total vertebral count 189 to 195, monospondylous precaudal count 55 to 57, diplospondylous count 92 to 96 and 47 to 50% of total count. Jaws narrowly arcuate. Intestinal valve count 23 to 24. Development ovoviviparous but with yolk sac reabsorbed and uterine cannibalism in the form of oophagy present, litter size possibly1 to 4. Adults 230 cm long or longer, size at birth at least 60 cm and possibly 78 cm. Background colour tan, reddish or yellowish to dark grey-brown above and light whitish brown below, no spots or other markings as far as is known; lower eyelid strikingly light in colour in young.

Remarks: Scope of this genus follows Applegate (1974), Bass, D'Aubrey and Kistnasamy (1975c), Compagno (1984), and Dingerkus (1986), in recognizing a single living species. There are also several fossil species of ***Nebrius*** (Cappetta, 1987).

Compagno (1984) included ***Nebrius concolor*** and its synonyms in the synonymy of ***N. ferrugineus***. This was accepted by some subsequent researchers including Last and Stevens (1994) though Dingerkus (1986) recognized ***N. concolor*** as the only valid species in this genus. Translation of Lesson's (1830) short and unillustrated description of his ***Scyllium ferrugineum*** suggests that this synonymy is correct, and that Lesson was the first scientific discoverer of the Indo-Pacific tawny nurse shark. There are only two other orectoloboids known from Waigiu, one of which Lesson described as ***Scyllium malaianum*** (= ***Hemiscyllium freycineti***), and the other is ***Eucrossorhinus dasypogon***. Lesson described ***S. ferrugineum*** from a single specimen of "roussette" (French term for scyliorhinid catsharks and catshark-like orectoloboids) that was rusty-fawn without markings above, rosy white below, and had a white eye (the conjunctiva and upper and lower eyelids of the tawny nurse shark are conspicuously white, though the iris is black), had a conical short head, anterior mouth and nostrils, long barbels, large rounded labial folds at mouth, triangular teeth (exact shape not stated), body tapering from the head, a large, triangular first dorsal fin slightly behind midlength of body, smaller triangular second dorsal, large elevated broad caudal fin, lobate pectoral fin, quadrilateral pelvic fins (with claspers), a lobate sharp-apiced anal fin, and was relatively large (137 cm [54 in] if tail length is exclusive of body length). These characters taken in combination fit the tawny nurse shark and eliminate other Indo-Australian orectoloboids including Hemiscylliidae, Parascylliidae, Stegostomatidae, Orectolobidae and Rhincodontidae. Although Lesson's description is not as specific and detailed as Rüppell's (1837) account and illustration of ***Nebrius concolor*** from the Red Sea, it is adequate to validate the earliest name for the tawny nurse shark as ***Scyllium ferrugineum***.

Nebrius ferrugineus and ***N. concolor*** were often retained as separate species and sometimes placed in different genera as ***Ginglymostoma ferrugineum*** and ***Nebrius concolor***. Compagno (1984) synonymized the two species and suggested that the dentitional differences used to separate them (Garman, 1913; Fowler, 1941) may be due to growth changes in a single species (ontogenic heterodonty). The supposed differences were more compressed, more low-cusped teeth in ***N. concolor*** and less compressed, more high-cusped teeth in ***N. ferrugineus***. At least in the material of ***Nebrius*** examined by the writer from the Gulf of Thailand, Philippines, and elsewhere, larger specimens over 2 m long have teeth of the ***N. ferrugineus*** type, while specimens about a metre long or less have teeth of the ***N. concolor*** type. Teeth of a specimen 1.8 m long pictured by Bass, D'Aubrey and Kistnasamy (1975c) are roughly intermediate. Growth changes apparently include increase in size of cusps relative to cusplets, shortening and broadening of the labial flange (basal ledge), and thickening and broadening of the teeth relative to their height.

Nebrius ferrugineus (Lesson, 1830)

Fig. 161

Scyllium ferrugineum Lesson, 1830, *Voy. aut. monde corv. La Coquille*, 2(1): 95. Holotype: Specimen with body 101.5 cm (3 ft 4 in) and tail 35.5 cm (14 in) mentioned, possibly not saved. Type locality, Port Praslin, New Ireland, and Baie d'Offack, Waigiou (Waigeu), New Guinea.

Synonyms: ***Nebrius concolor*** Rüppell, 1837: 62, pl. 17, fig. 2. Lectotype: Naturmuseums Senckenberg, Frankfurt, SMF-3583, 85 cm TL stuffed specimen, Massaua, Red Sea. ***Ginglymostoma rueppelli*** Bleeker, 1852: 91. Apparently an unnecessary replacement name for ***Nebrius concolor*** Rüppell, 1837, as latter is listed as a synonym. Holotype: Specimen mentioned by Bleeker is a male 1.5 m (730 lines) TL, probably from Singapore. Holotype listed as Rikjsmuseum van Natuurlijke Histoire, Leiden, RMNH 7400, by Eschmeyer (1998: CD-ROM). ***Ginglymostoma muelleri*** Günther, 1870: 408. Apparently based on ***Ginglymostoma concolor*** Müller and Henle, 1838d: 22, pl. 6, thought by Günther to be distinct from ***Nebrius concolor*** Rüppell, 1837. Syntypes: Two stuffed specimens mentioned by Müller and Henle, in the Institut für Spezielle Zoologie und Zoologisches Museum, der Humboldt Universität, Berlin, but possibly not extant, India. No types mentioned by Eschmeyer (1998: CD-ROM). ***Scymnus porosus*** Hemprich and Ehrenberg, *in* Klunzinger, 1871: 670 (name only, in synonymy of ***Ginglymostoma muelleri***). Also Hemprich and Ehrenberg, 1899: 8, pl. 6, fig. 3, Red Sea; possibly no type material, see Paepke and Schmidt (1988: 162). ***Nebrodes macrurus*** Garman, 1913: 58, pl. 8, figs 7-10. Holotype: Museum of Comparative Zoology, Harvard, MCZ-820-S, 80 cm (31.5 in) TL immature male, Port Louis Harbor, Mauritius, according to Hartel and Dingerkus (1997: xxxvii-xxxviii). ***Nebrodes concolor ogilbyi*** Whitley, 1934: 183, fig. 1. Holotype: Queensland Museum I.1216, 955 mm female, Darnley Island, Queensland, Australia. Type status confirmed by Eschmeyer (1998: CD-ROM). ***Nebrius doldi*** Smith, 1953a: 512, fig. 30A; Smith, 1953b: 8, pls. Types: Drawing by M.M. Smith based on photographs of a 2.9 m (9.5 ft) female? specimen from south of Beira, Mozambique, apparently no type material.

Other Combinations: ***Ginglymostoma ferrugineum*** (Lesson, 1830), ***Ginglymostoma concolor*** (Rüppell, 1837).

FAO Names: En - Tawny nurse shark; **Fr** - Requin nourrice fauve; **Sp** - Gata nodriza atezada.

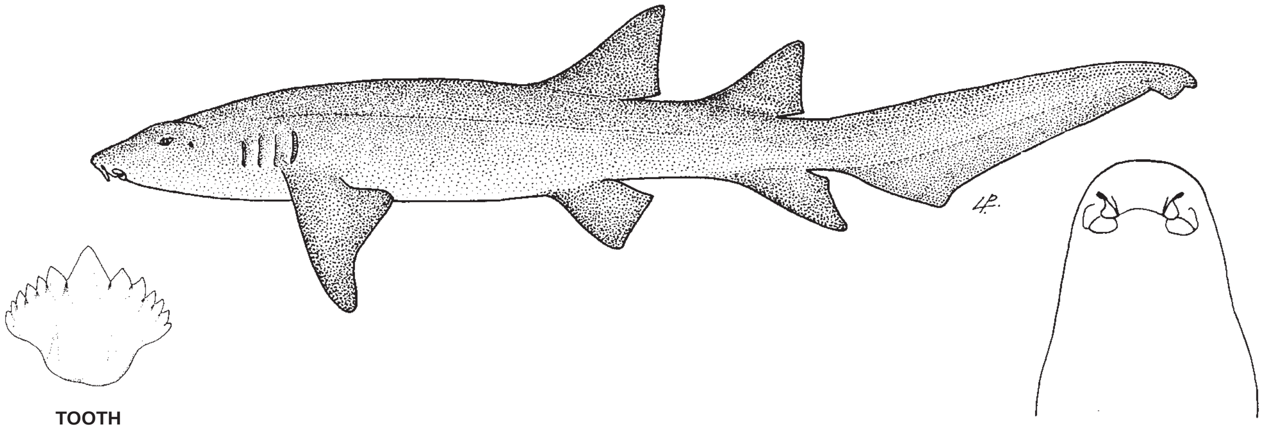
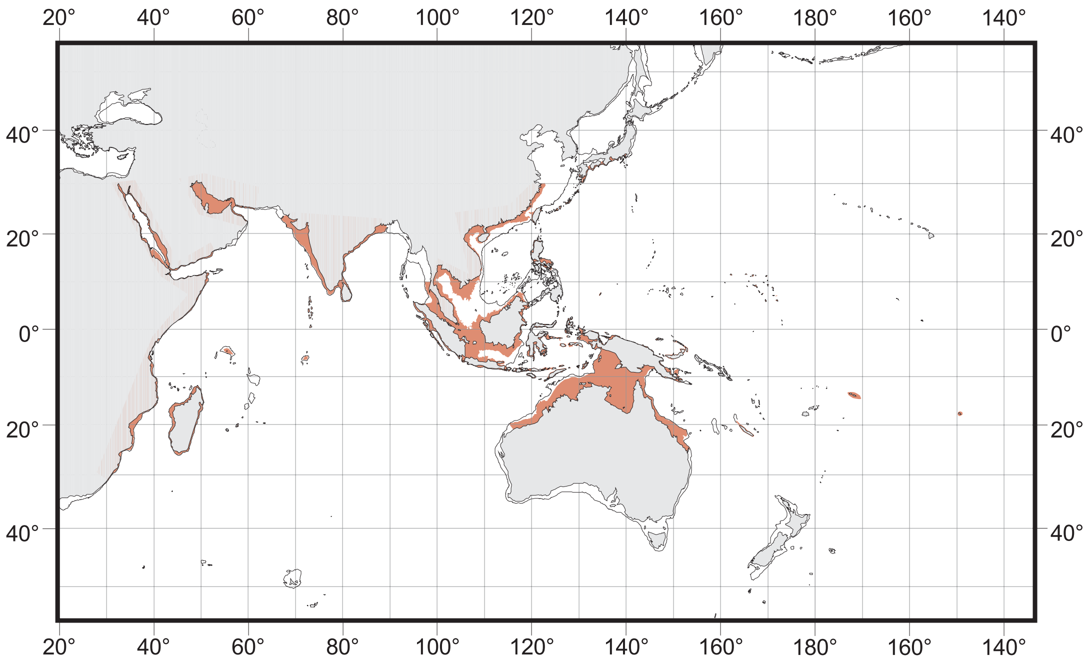


Fig. 161 ***Nebrius ferrugineus***

Field Marks: Moderately long barbels, nasoral grooves present but no circumnarial grooves, mouth well in front of eyes, eyes and gill openings 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-fin base over pelvic-fin bases, pectoral fins falcate, caudal fin moderately long, over one-fourth of total length. **Colour:** colour brown, from tan to rufous or yellowish to dark grey-brown according to habitat, and slowly changeable by the individual.

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

Distribution: Wide-ranging in the Indo-West and Central Pacific: South Africa (KwaZulu-Natal), Mozambique, Mauritius, Seychelles, Chagos Archipelago and Madagascar to Red Sea, Maldives, Persian Gulf, India, Malaysia, Indonesia, Singapore, Thailand, Viet Nam, China, Taiwan (Province of China), Japan (Ryukyu Islands, southern Honshu), Philippines (Luzon), Papua New Guinea, Australia (Western Australia, Northern Territory, and Queensland), New Caledonia, New Ireland, Samoa, Palau, Marshall Islands, and Tahiti.



Habitat: A large, tropical inshore shark of the continental and insular shelves of the Indo-Pacific, often in the intertidal in water scarcely able to cover it and from the surf line down to a few metres depth, commonly at 5 to 30 m and ranging down to at least 70 m on coral reefs. It occurs on or near the bottom in lagoons, in channels, or along the outer edges of coral and rocky reefs, in areas with seagrass and sand on 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 depressions or crevices. Young prefer crevices in shallow lagoons but adults are more wide-ranging.

Biology: The tawny nurse shark is primarily nocturnal, resting in the daytime in shelters but prowling slowly about around reefs at night, although some individuals may be active in the day. In Madagascar it is described as day and night-active, and in captivity they get quite active and vigorous when food is presented to them during the day. They are social, gregarious sharks when at rest 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. This shark has a limited home range, and individuals often return to the same area every day after foraging.

Reproduction ovoviviparous (aplacental viviparous) with cannibal vivipary or uterine cannibalism in the form of oophagy. This shark has been described as an oviparous or post-oviparous shark that retains the egg-cases until they hatch and the young are born, but recent evidence indicates that this is incorrect. Pregnant females collected from Okinawa have had one or two foetuses per uterus, 297 to 595 mm (the latter near term), with the yolk sac reabsorbed and a greatly expanded stomach filled with yolky material in foetuses 338 and 595 mm long, and also had cased eggs in the uterus. Apparently this species practices oophagy on relatively large, cased nutritive eggs (unlike many lamnoids which have very small nutritive eggs), and is the first orectoloboid known to have uterine cannibalism. It is not known whether foetuses of this species eat other foetuses (adelphophagy) as with the sand tiger (***Carcharias taurus***). The presence of two foetuses 338 and 297 mm in the same uterus, with the smaller one slender and the larger bloated with yolk, suggests that competition between siblings for the relatively big eggs is likely and could even eliminate the less successful sibling. Adelphophagy is less likely although early stages need to be examined to eliminate it. Number of young per litter uncertain; at least four young per uterus has been suggested from cased eggs, but the size and enormous girth of the near-term Okinawan foetus and the two smaller foetuses in a litter suggests that litters are smaller, possibly one or two per uterus or even one per female, and that numbers of cased eggs in the uteri cannot be used to extrapolate litter sizes in this species. In captivity adult females lay cased eggs on the bottom, but these do not develop, and could be nutritive and unfertilized. Such free eggs may have been the basis of the suggestion that this species is oviparous. The tawny nurse shark breeds in July and August off Madagascar.

Food of this shark includes corals, crabs, lobsters and other crustaceans, octopi, squid and probably other cephalopods, sea urchins, and reef fish including surgeonfish (Acanthuridae), queenfish (Carangidae) and rabbitfish (Siganidae), and occasionally sea snakes. 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 suck 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 and into the faces of their captors; they are said to make a grunting sound between blasts. It is not known if spitting water is deliberate and defensive or if the sharks are actually aiming the water at the anglers. They also tend to spin when hooked on a line, making them difficult to handle and subdue.

The body form of the tawny nurse shark (littoral morphotype) is more fusiform and streamlined than other nurse sharks, with narrow-based, falcate, plesodic pectorals, pointed dorsal and anal fins with the anal-fin apex raked posterior to the free rear tip, a short ventral caudal-fin lobe, lateral eyes and gills, a narrow head, flat wedge-shaped snout, and compressed, semi-blade-like, imbricate teeth in discrete series. The tawny nurse shark superficially resembles certain other large, partly or mostly sympatric, active reef sharks including the sand tiger shark (***Carcharias taurus***), sicklefin lemon shark (***Negaprion acutidens***), and reef whitetip shark (***Triaenodon obesus***). Whether it is behaviourally divergent from other nurse sharks awaits a detailed comparative study of nurse shark behaviour. Its status as a game fish in Australia, unlike the nurse shark in the western Atlantic, suggests that it may be a more active swimmer when not resting on the bottom.

Size: Maximum about 314 to 320 cm, though most individuals are smaller; size at birth has been reported as about 40 cm (Fourmanoir and Laboute, 1976) but subsequent data from a pregnant female captured off Okinawa suggest that it may reach 60 cm or more at birth (Teshima et al. 1995), while a 79 cm female from Navotas market in Manila, Philippines, examined by the writer, has a somewhat bloated stomach full of yolk, suggesting that it was newborn or a term foetus; males are mature at about 250 cm and reach at least 301 cm; adult females are 230 to at least 290 cm.

Interest to Fisheries and Human Impact: Common or formerly common in areas where it occurs, and caught inshore by fishermen in Pakistan, India, Thailand, and Philippines, and probably widely captured 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, armour-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 by sports anglers. Apart from anglers who target this fish, it is apparently primarily caught only as an untargeted bycatch of fisheries in inshore waters in nets, on line gear, and in fish traps.

This has been described as a much more docile species than its close relative, ***Ginglymostoma cirratum***, and apparently tolerates close proximity of divers and usually allows humans to touch and play with it without biting. However, there are a few records of these sharks biting their tormentors, and clamping tightly onto them. Because of its size, strength, powerful jaws and small but sharp cutting teeth, the tawny shark should be treated with the respect due it. It is a favourite species for observation by ecotouristic divers within its enormous range, and dive sites where it is viewed are known from Thailand (Andaman Sea) and the Solomon Islands.

This is a tough, hardy shark that readily survives in captivity and makes an excellent and handsome display animal. It is kept in aquaria in Europe, Japan (Okinawa), Singapore, and the United States. In Singapore in 1996 the writer saw several large ***Nebrius*** about 2 m long being hand-fed by a SCUBA diver in a big oceanarium tank. The sharks piled on top of their benefactor and hid him from sight while eagerly scrambling to obtain food.

The conservation status of this shark is uncertain and urgently needs investigation despite its wide range. In some areas, including the Gulf of Thailand where it was commonly caught in the 1960s, it may have been depleted due to increasing fisheries activity and habitat degradation. Also, reef habitats have been extensively damaged or destroyed by dynamiting and poisoning in parts of its range, including Indonesia and Philippines, which probably have had an adverse effect on this species both directly and through decimation or elimination of its prey. Its docility and inshore habitat makes it particularly susceptible to a wide variety of fishing gear, to harassment and injuries by divers, and to reef destruction and pollution.

Local Names: Tawny shark, Spitting shark, Rusty shark, Rusty catshark, Sleepy shark, Madame X (Australia); Giant sleepy shark (South Africa); Roussette ferrugineuse (French); Yahiya (Madagascar); Endormi (Seychelles); Kalouyon (Guébéens); Koumoune (Waigiu); Be kal mora (Sinhalese); Ô-tenjikuzame (Japan).

Remarks: Several individuals from Okinawa and Honshu, Japan and at least one from Taiwan (Province of China) have been found with their second dorsals missing or rudimentary. It is not known why this occurs in these localities, but there are some interesting possibilities that might be investigated including teratogenic effects of chemical pollutants.

Literature: Lesson (1830); Rüppell (1837); Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Jordan and Seale (1906); Garman (1913); Whitley (1934, 1940); Fowler (1941); Misra (1947); Bigelow and Schroeder (1948); Fourmanoir (1961); Gohar and Mazhar (1964); Marshall (1965); Applegate (1974); Bass, D'Aubrey and Kistnasamy (1975c); Fourmanoir and Laboute (1976); Johnson (1978); Randall (1980); Yoshino et al. (1981); Uchida (1982); Compagno (1984, 1988); Nakaya and Shirai (1984); Bass (1986); Dingerkus (1986); Taniuchi and Yanagisawa (1987); Compagno, Ebert and Smale (1989); Anderson and Ahmed (1993); Michael (1993); Seret (1994); Last and Stevens (1994); Teshima et al. (1995, 1999).

Pseudoginglymostoma Dingerkus, 1986

Genus: ***Pseudoginglymostoma*** Dingerkus, 1986, *Proc. 2nd. Int. Conf. Indo-Pacific Fishes, Tokyo*: 240.

Type Species: ***Ginglymostoma brevicaudatum*** Günther, *in* Playfair and Günther, 1866, by original designation.

Number of Recognized Species: 1.

Synonyms: None.

Diagnostic Features: Head in dorsal or ventral view very broad and parabolic in adults. Snout bluntly rounded in lateral view, short and with preoral length about 34.5 to 41.6% of mouth width. Eyes very small and 0.8 to 1.0% of total length, situated dorsolateral on head and with strong subocular ridges below them; ventral edges of eyes just above level of dorsal ends of gill slits. Gill openings dorsolaterally situated on head and not visible from below, just reaching horizontal head rim from above. Nostrils nearly terminal on snout. Nasal barbels very short, stubby, not very tapered, less than 1% of total length, and not reaching mouth. Lower lip not trilobate and without orolabial grooves. Distance between lower labial furrows about 1.2 to 1.4 times their length. Tooth rows 24 to 27/22 to 27 (adults), functional series at least 3 to 4/4 to 5. Teeth not compressed and not imbricated, functional series not separated from replacement series by toothless space. Tooth crown feet very narrow, cusps large, cusplets very small and one or two on each side; teeth with moderately broad basal ledges. Teeth orthodont and with a central pulp cavity. Body cylindrical. Lateral trunk denticles teardrop-shaped and elongated in adults, with a low medial ridge, lateral ridges weak or absent, and with a fairly narrow pointed cusp. Pectoral fins broad and not falcate in adults, apically rounded. Pectoral-fin origins slightly in front of third gill slits. Pectoral fins semiplesodic and with radials reaching only 55% into fin web, radial segments four. Pelvic fins rounded in adults. Dorsal fins apically rounded. First dorsal-fin origin over or slightly behind pelvic-fin midbases. Second dorsal fin about as large as first dorsal fin. Anal fin about as large as first dorsal fin, with rounded apex. Anal-fin apex about under anal free rear tip, origin about opposite second dorsal-fin origin, posterior margin ends in front of lower caudal-fin origin. Caudal fin short with dorsal caudal-fin margin less than 25% of total length (adults); caudal fin broad and deep with depth 40 to 45% of dorsal caudal-fin margin; no ventral caudal-fin lobe in adults; preventral caudal-fin margin about as long as postventral margin and 80 to 100% of it; terminal caudal-fin lobe moderate and 22.2 to 26.3% of dorsal caudal-fin margin. Total vertebral count 135 to 143, monospondylous precaudal count 35 to 37, diplospondylous caudal count 49 to 54 and 36 to 39% of total count. Jaws broadly arcuate. Intestinal valve count 15. Mode of reproduction and litter size unknown. Adults 59 to 75 cm long, size at birth or hatching unknown but probably less than 30 cm. **Colour:** background colour dark brown above and slightly lighter below but noticeably dark on both surfaces; no spots or other markings in adults but colour of young unknown; lower and upper eyelids dark in adults.

Remarks: Scope of this genus follows Dingerkus (1986), with a single living species, ***Pseudoginglymostoma brevicaudatum***.

Pseudoginglymostoma brevicaudatum (Günther, 1866) **Fig. 162**

Ginglymostoma brevicaudatum Günther, *in* Playfair and 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 TL, length in original account 640 mm, Zanzibar.

Synonyms: None.

Other Combinations: None.

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

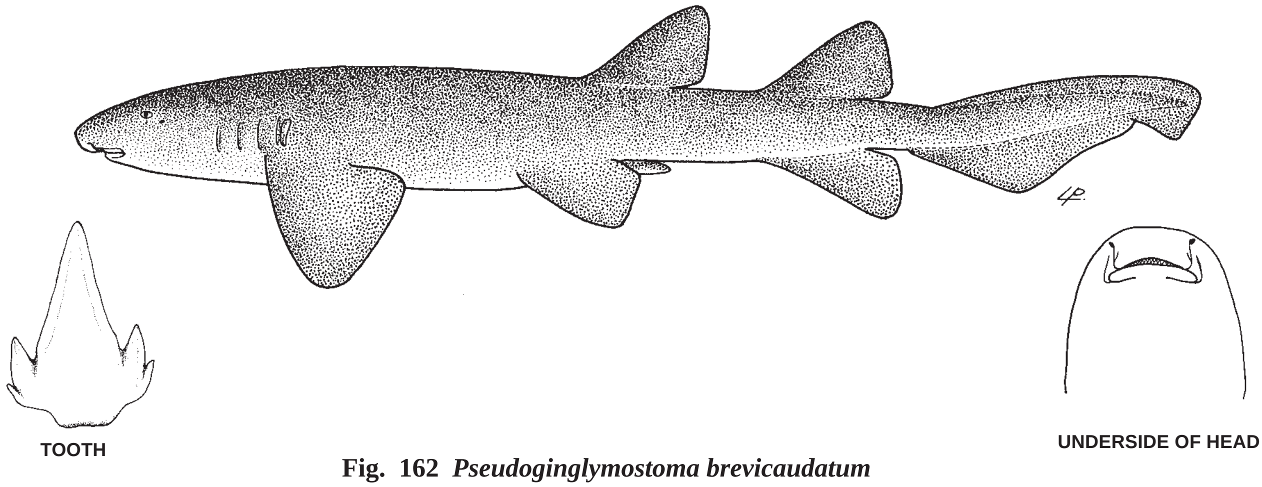
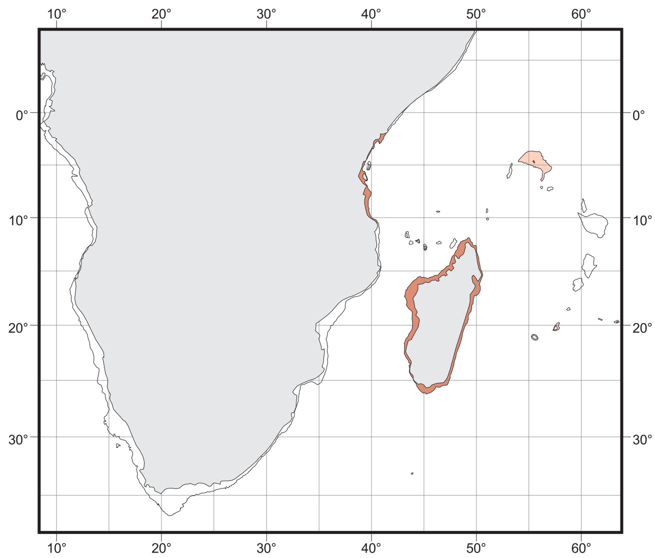


Fig. 162 ***Pseudoginglymostoma brevicaudatum***

Field Marks: Very short barbels, nasoral grooves present but no circumnarial grooves; eyes and gill openings dorsolateral, 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 one-fourth of total length, colour dark brown, without spots or other markings.

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

Distribution: Confined to the western Indian Ocean off Tanzania, Kenya, Madagascar and possibly Mauritius and the Seychelles.



Habitat: This little-known inshore bottom shark occurs on the continental and insular shelves of East Africa and Madagascar, but details are lacking on its habitat except that it occurs on coral reefs. Depth data are not available.

Biology: The biology of the short-tail nurse shark, including breeding and feeding habits, is poorly known. An adult or near-adult female had large nidamental glands, suggesting that the species may be egg-laying but this needs confirmation (see below). It also is not known if this species is social and congregates in groups as with the larger nurse sharks. It is reported to survive for several hours out of water. Abundant off East Africa a few decades ago (Bass, D'Aubrey and Kistnasamy, 1975c), but its current status is uncertain.

A female short-tailed nurse shark has lived over 33 years and a male three years in captivity at the Artis Zoo, Amsterdam. These are under study by A. Dral, E. Bruins and P. Bor (pers. comm.), who are preparing a detailed account for publication. Both individuals are alive at the time of writing and the female has laid infertile eggs in strong egg cases two at a time for the past ten years. This suggests that the short-tailed nurse shark is oviparous but needs confirmation. These sharks mate in captivity but so far no eggs have been hatched as the pair eat their eggs. These sharks are slow-moving, nocturnally active, sit on the open bottom or hide in holes or crevices during the day, and will only move during the day when fed. They eat annelid worms, raw and cooked mussels, cut raw fish and shrimps; presumably the species eats small fishes, molluscs and crustaceans in the wild. The two sharks are non-aggressive in community tanks and the female has been kept with much larger nurse sharks (***Ginglymostoma cirratum***) without incident.

Size: Maximum at least 75 cm; two adult males examined were 59 to 75 cm while a live captive adult male (Artis Zoo, Amsterdam) is 65 cm long; a female examined was immature at 52 cm while another was adolescent at 56 cm and a third was adult or nearly so (with large oviducts and nidamental glands but without oviducal eggs or foetuses) at 53 cm. A captive adult female at the Artis Zoo is 70 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries probably limited, apparently fished locally in artisanal fisheries and landed as a bycatch of other fisheries. The skin of this shark is exceptionally tough, as in other nurse sharks, and is possibly of use for leather. It is readily amenable to captivity and grows to a more reasonable maximum size for smaller aquaria than ***Nebrius ferrugineus*** or ***Ginglymostoma cirratum***, but it's status in the aquarium trade is uncertain. It apparently is seldom kept in public aquaria. The conservation status of this interesting and distinctive little shark is unknown but is of concern as it has a limited distribution in inshore tropical waters of East Africa and occurs in some areas that currently support heavy inshore fisheries. It could be adversely affected by overfishing and destruction of coral reefs.

Local Names: Nurse shark, Shorttail nurse shark, Papa isengezi or Sleepy shark (Zanzibar), Endormi (Seychelles).

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.

Literature: Günther *in* Playfair and Günther (1866); Günther (1870); Garman (1913); Fowler (1941, 1967a); Smith and Smith (1963); Bass, D'Aubrey and Kistnasamy (1975c); Compagno (1984, 1988); Dingerkus (1986); Bass (1986); Anton Dral, Eugene Bruins and Peter Bor (pers. comm.).

2.3.7 Family RHINCODONTIDAE

Family: Rhinodontes Müller and Henle, 1839, *Syst. Beschr. Plagiost.*, pt. 2: 77. Placed on the Official List of Family-Group Names in Zoology (Name no. 559) by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215 as the emended Family Rhincodontidae.

Type Genus: ***Rhincodon*** Smith, 1829.

Number of Recognized Genera: 1.

Synonyms: Subfamily Rhinodontini Bonaparte, 1846, v. 3 (no pagination); Tribe Rhineodontiana (Family Squalidae) Gray, 1851: 66. Family Rhineodontis "Müll. and Henle" Gray (1851: 66). Family Rhinodontoidei Bleeker, 1859: XII. Family Rhinodontoidae Owen, *in* Gill, 1862b: 397. Family Rhinodontidae Günther, 1870: 396. Family Rhineodontidae Jordan and Fowler, 1903: 626. Subfamily Rhinodontinae (Family Lamnidae) Goodrich *in* Lankester, 1909: 150. Family Rhincodontidae Garman, 1913: 12, 41. Type genus: ***Rhincodon*** Smith, 1829. Subfamily Rhineodontini (Family Orectolobidae) Berg, 1940: 380. Subfamily Rhincodontinae (Family Rhincodontidae) Fowler, 1947: 10. Family Rhiniodontidae Compagno, 1973: 28. Type genus: ***Rhiniodon*** Smith, 1828, emendation of Family Rhinodontes Müller and Henle, 1839, used by Compagno (1984: 209).

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

Diagnostic Features: Head very broad and greatly flattened, without lateral flaps of skin. Snout truncated. Eyes laterally situated on head and without subocular ridges below them. Eyes without movable upper eyelids or subocular pockets and ridges. Spiracles moderate-sized but much smaller than eyes, without raised external rims; spiracles behind but not below eyes. Gill slits very large, fifth gill slit well-separated from fourth and not overlapping it; 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. Nasoral grooves very short and shallow. Mouth very large, transverse and terminal on head. Lower lip not trilobate and without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, without a longitudinal symphysial groove on chin. Lower labial furrows ending far lateral to symphysis, not connected medially by a mental groove or groove and flap. Teeth not strongly differentiated in upper and lower jaws, with symphysial teeth not enlarged and fang-like. Tooth row count extremely high, in over 300 rows in either jaw of adults and subadults. Teeth with a strong medial cusp, no cusplets and no labial root lobes. Teeth osteodont with crown partially filled with a plug of osteodentine. Body cylindrical or moderately depressed, with prominent ridges on sides. Precaudal tail shorter than body. Caudal peduncle with strong lateral keels and an upper precaudal pit. Pectoral fins very large, relatively narrow and falcate. Pectoral fins plesodic and with fin radials strongly expanded into fin web. Pectoral propterygium small and fused to mesopterygium; pectoral-fin radial segments 3 to 10, and with longest distal segments about 0.8 times the length of longest proximal segments. Pelvic fins much smaller than first dorsal fin but subequal to second dorsal and anal fins, much smaller than pectoral fins and with anterior margins about 0.3 times the pectoral-fin anterior margins. Claspers without mesospurs, claws or dactyls. First dorsal fin much larger than second. First dorsal-fin origin well anterior to pelvic-fin origins and over abdomen behind pectoral-fin free rear tips, first dorsal-fin insertion over the pelvic-fin bases. Anal fin about as large as second dorsal, with broad base, angular apex, origin about opposite first third of second dorsal fin base, and insertion separated by a space somewhat greater than base length from lower caudal-fin origin. Caudal fin elongated and semicrescentic, strongly heterocercal with its upper lobe at a high angle above the body axis (lower in young than adults and subadults); dorsal caudal-fin margin less than a third as long as the entire shark. Caudal fin with a vestigial terminal lobe and subterminal notch but with a strong ventral lobe (longer in adults than young), preventral and postventral margins strongly differentiated and deeply notched. Vertebral centra with well-developed radii and prominent annuli connecting them. Total vertebral count 174, monospondylous precaudal count 42, diplospondylous precaudal count 40, diplospondylous caudal count 92, and precaudal count 82. Cranium very broad and greatly expanded laterally. Medial rostral cartilage rudimentary, reduced to a low nubbin. Nasal capsules greatly depressed, slightly fenestrated anteriorly, internarial septum low, broad and depressed. Orbits with enlarged fenestrae for preorbital canals, medial walls not fenestrated around the optic nerve foramina although foramen itself is very large. Supraorbital crests present on cranium and laterally expanded and pedicellate. Suborbital shelves very broad and not greatly reduced. Cranial roof with a continuous fenestra from the anterior fontanelle to the parietal fossa. Basal plate of cranium with pairs of separate carotid and stapedial foramina. Adductor mandibulae muscles of jaws with three divisions. Preorbitalis muscles extending onto posterodorsal surface of cranium. No anterodorsal palpebral depressor, rostromandibular, rostronuchal or ethmonuchal muscles. Valvular intestine of ring type with 69 to 74 turns. Development ovoviviparous. Size gigantic with adults 700 cm or longer, while young are born at about 55 to 64 cm. Colour pattern unique, consisting of small to large white or yellowish spots and vertical and horizontal stripes in the form of a checkerboard on a dark background.

Local Names: Whale sharks, Ching sha k'o, Jimbeizame-ka (Japan); Kitovye akuly (Russia).

Remarks: As recognized here the family Rhincodontidae includes only a single genus and species, the whale shark, ***Rhincodon typus***. The genus and species were first described as ***Rhiniodon typus*** by Smith (1828) in a Cape Town newspaper from a specimen stranded in Table Bay, South Africa. A separate family Rhinodontes was later proposed for it by Müller and Henle (1839) who used a variant spelling ***Rhinodon*** for the genus. There has been considerable variation in spelling of the generic name (***Rhinodon***, ***Rhineodon***, ***Rhincodon***, ***Rhiniodon***, ***Rhinecodon***, ***Rhinocodon***, ***Rineodon*** and ***Rhinchodon***) and by extension the family name of the whale shark (Rhinodontidae, Rhincodontidae, Rhineodontidae and Rhiniodontidae), and much usage of certain of the variants. Andrew Smith, the describer of the whale shark, and Johannes Müller and Friedrich Henle, the describers of a family for it, used several variants on the genus, which caused confusion for subsequent authors. Although the original ***Rhiniodon*** has priority, the variants ***Rhincodon*** and particularly ***Rhineodon*** and ***Rhinodon*** have had far more usage over the last two centuries.

Following Bigelow and Schroeder (1948) the variant ***Rhincodon*** has received considerable use, and proposals to stabilize it (Robins and Lea, 1975; Swift, 1977; Wheeler, 1982) were presented to the International Commission on Zoological Nomenclature. Brooke and Bass (1976) supported the earliest published spelling, ***Rhiniodon***, although noting that ***Rhiniodon*** Smith, 1828 was a possible misspelling that Andrew Smith had hand-corrected to ***Rineodon*** on a bound copy of his paper (Smith, 1828). ***Rineodon*** was also used by Müller and Henle (1838a), possibly on the advise of Andrew Smith, but later changed to ***Rhinodon*** (Müller and Henle, 1839). Hubbs, Compagno and Follett (1976) proposed that the earliest spelling, ***Rhiniodon*** should be preserved for the whale shark because of priority, more correct orthography than ***Rhincodon***, and because the use of ***Rhincodon*** has not been universal since Bigelow and Schroeder's work (and little-used prior to it compared to ***Rhinodon*** and particularly ***Rhineodon***). Compagno (1984) preferred to use the earliest spelling (***Rhiniodon*** and emended family name Rhiniodontidae) but while that work was in press the International Commission on Zoological Nomenclature (1984, Opinion 1278) stabilized ***Rhincodon*** and Rhincodontidae.

Dingerkus (1986) included the genera ***Pseudoginglymostoma***, ***Ginglymostoma***, ***Nebrius*** and ***Stegostoma*** in this family, but the original arrangement of ***Rhincodon*** alone in Rhincodontidae is followed here on the basis of the extremely derived morphology of the whale shark, uncertain relationships with other 'higher' orectoloboids, and pending further studies on orectoloboid phyletics.

Rhincodon **Smith, 1829**

Genus: ***Rhincodon*** Smith, 1829, *Zool. J.*, 4: 443. Placed on the Official List of Generic Names in Zoology (Name no. 2219, International Commission on Zoological Nomenclature, 1984, *Bull. Zool. Nomen.*, 41(4): 215). ***Rhincodon*** was used twice in the 1829 publication.

Type Species: ***Rhiniodon typus*** Smith, 1828, as interpreted by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215.

Number of Recognized Species: 1.

Synonyms: Genus ***Rhiniodon*** Smith, 1828: 2. Type species: ***Rhiniodon typus*** Smith, 1828, by monotypy and by use of the species name ***typus***. Placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Name no. 2141) by the International Commission on Zoological Nomenclature (1984, Opinion 1278: 215). ***Rhiniodon*** was twice cited in the original description, but possibly was a typographical error or correction by the printer (Brooke and Bass, 1976: 5). Genus ***Rhinchodon*** Smith, 1829: 534 (index). Variant spelling. Genus ***Rineodon*** Müller and Henle, 1838a: 37. Also Swainson, 1838: 142. Variant spelling. Genus ***Rhineodon*** Müller and Henle, 1838c: 84. Variant spelling. Genus ***Rhinodon*** Müller and

Henle, 1839: 77. Variant spelling. Genus ***Rhiniodon*** Swainson, 1839: 317. Variant spelling. Genus ***Rhinecodon*** Agassiz, 1845: 55. Variant spelling. Genus ***Rhinodon*** Smith, 1849: pl. 26 and accompanying text, pages not numbered; Smith used ***Rhinodon*** in this extended account and illustration of the whale shark rather than his earlier ***Rhiniodon*** or ***Rhincodon***. Variant or emended spelling. Genus ***Micristodus*** Gill, 1865: 177. Type species: ***Micristodus punctatus*** Gill, 1865, by monotypy. Genus ***Rhinocodon*** International Commission on Zoological Nomenclature, 1984: 216). Attributed to Herald, 1961, but examination of the writer's copy indicated uniform usage of ***Rhincodon*** in the text (p. 22) and index (p. 302), suggesting that the variant spelling if correctly cited was a possible typographical error in a different edition of Herald's book.

Diagnostic Features: See family Rhincodontidae above.

Rhincodon typus (Smith, 1828)

Fig. 163

Rhiniodon typus Smith, 1828, *S. African Comm. Adv.*, 3(145): 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9855, 4 600 mm stuffed, mounted male specimen, Table Bay, South Africa. The specific name ***typus*** Smith, 1828 was placed on the Official List of Species Names in Zoology (Name no. 2901) by the International Commission on Zoological Nomenclature, 1984, Opinion 1278, *Bull. Zool. Nomen.*, 41(4): 215.

Synonyms: ***Rhincodon typus*** Smith, 1829: 443. ***Rhinodon typicus*** Müller and Henle, 1839: 77, pl. 35. Variant or emended spelling of ***Rhincodon typus***. This spelling was also used by Smith, 1849: pl. 26 and accompanying text, pages not numbered, in his extended description of the whale shark. ***Micristodus punctatus*** Gill, 1865: 177. Holotype: US National Museum of Natural History, USNM-27234, renumbered as USNM-232756, a pair of dried dental band halves, Gulf of California. Status of holotype from Howe and Springer (1993: 12) and by the writer's examination of the specimen. ***Rhinodon pentalineatus*** Kishinouye, 1901: 694, figs 1-2. Holotype: Specimen originally in private collection of T. Oseko, from Cape Inubo, Japan, whereabouts unknown according to Eschmeyer (1998: CD-ROM).

Other Combinations: ***Rhineodon typus*** (Smith, 1828), ***Rhineodon typicus*** (Müller and Henle, 1839).

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

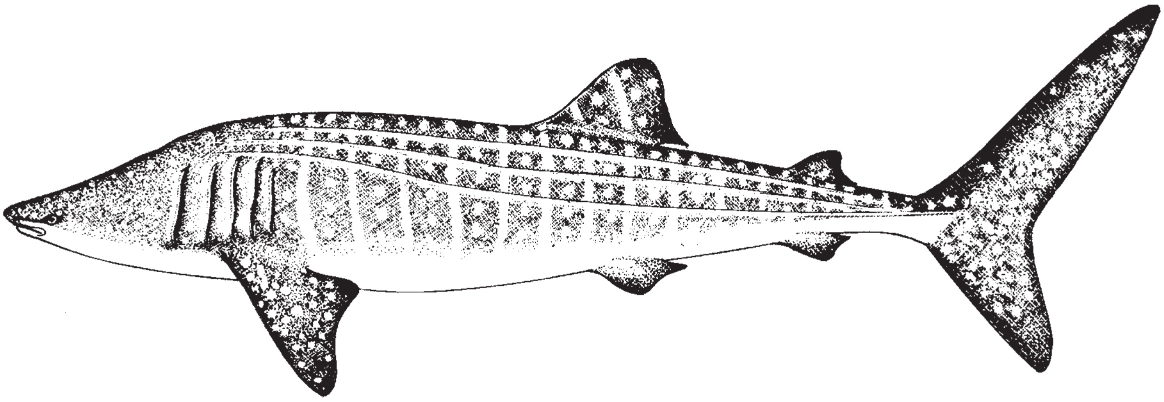
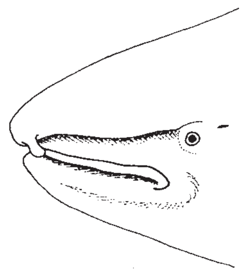


Fig. 163 ***Rhincodon typus***

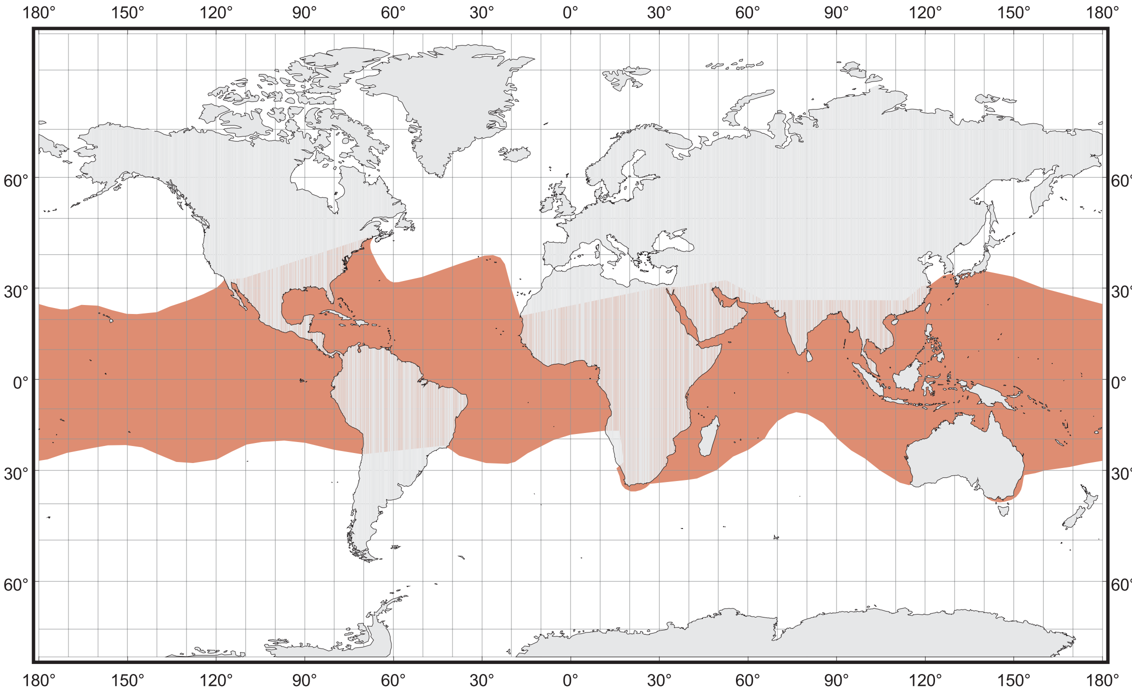


LATERAL VIEW OF HEAD

Field Marks: An unmistakable huge shark, one of three large filter-feeding species (apart from devel rays), with a broad, flat head and truncated snout, immense transverse and 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. **Colour:** a unique checkerboard pattern of white or yellow spots, horizontal and vertical stripes on a grey, bluish, reddish or greenish brown dorsal surface, abruptly white or yellowish on the underside of the body.

Diagnostic Features: See family Rhincodontidae above.

Distribution: Circumglobal in all tropical and warm temperate seas, oceanic and coastal. Western Atlantic: Canada (south of Nova Scotia), United States (Gulf of Maine and New York south to North Carolina and Florida, and Gulf of Mexico coast from Florida to Texas), Mexico (Gulf of Mexico coast to Quintana Roo), Belize, Honduras, Panama, Colombia, Venezuela, and central Brazil, also Bermuda, Bahamas, Caribbean including Cuba and Haiti. Eastern Atlantic: Azores, Senegal, Mauritania, Cape Verde Islands, Côte d'Ivoire, Gulf of Guinea, Gabon, Angola, South Africa (Western Cape Province). Indo-West and Central Pacific: East coast of South Africa (Western Cape, Eastern Cape, KwaZulu-Natal), Mozambique, Madagascar, Seychelles, Kenya, Tanzania, Somalia, the Red Sea and Straits of Bab-al-Mandab (Eritrea, Sudan, Saudi Arabia), Yemen, Oman, Persian Gulf, the Maldives, Pakistan, India (both coasts), Sri Lanka, possibly Bangladesh, Malaysia (including Sabah, Borneo), Singapore, Thailand (including Gulf of Thailand), Viet Nam, China, Taiwan (Province of China), Japan (Southeastern Honshu, Okinawa, and Bonin Islands), Philippines, Indonesia (Kalimantan, Borneo; Java), New Guinea (Papua-New Guinea and Irian Jaya, Indonesia), Australia (Western Australia, Queensland, Northern Territory, with isolated records from New South Wales and Victoria), New Caledonia, Hawaiian Islands, Tuomotu Archipelago, Phoenix Islands. Eastern Pacific: United States (southern California), Mexico (Baja California and Gulf of California south to Acapulco, Oaxaca, and Chiapas), El Salvador, Nicaragua, Costa Rica, Panama, Ecuador, Peru, and northern Chile (including open ocean from west of Cabo San Lucas to the Galapagos Islands, and between Panama and the Hawaiian Islands).



Habitat: An epipelagic and neritic, oceanic and coastal, tropical and warm-temperate pelagic shark, often seen far offshore but regularly coming close inshore off beaches and coral reefs and sometimes entering lagoons of coral atolls. In the western Pacific 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 34.0 to 34.5 ppt. Recent satellite tagging (Eckert and Stewart, 1996) in the Gulf of California suggested that the sharks prefer water over 26°C and up to 34°C, although they were recorded in water masses at temperatures down to 10°C; the sharks tended to move out of parts of the Gulf of California where surface water cooled below 26°C with upwelling. These conditions may be optimal for production of plankton and small to moderate-sized nektonic organisms, all of which are prey of the whale shark. The whale shark is generally seen or otherwise encountered close to or at the surface in warm waters, although recent satellite tagging in the Caribbean Sea off Belize shows that the whale shark may dive to depths of 700 m and may transit in cold deep water down to 7.8°C (R. Graham, pers.comm.). Off Ningaloo Reef in Western Australia a sonic-tagged shark frequently dived during two 18 hr tracks and ranged from the surface to near the bottom at depths of 40 to 70 m (Stevens et al., 1997), with salinity at 34.9 to 35.2 ppt and temperatures of 26.8 to 27.5°C at the surface to 26.4 to 25.4°C at the bottom.

Strandings of whale sharks are common in some areas, including both coasts of South Africa, and it is suspected that off the west coast of South Africa whale sharks ride the warm Agulhas current during the summer into areas where upwelling occurs and plumes of cold bottom water hit the surface. It was thought that sharks may be stunned or even killed by sudden chilling and then wash up on the shore with no signs of disease or physical damage (Beckley et al., 1997). Tracking of whale sharks in water down to 10°C in the Gulf of California and their presence near patches of upwelling water down to 6°C (Eckert and Stewart, 1996) makes this simple explanation suspect however, and an explanation for the phenomenon of stranding off the Western Cape requires further research. Rough seas and sudden storms along the narrow continental shelves of KwaZulu-Natal, South Africa (which is subtropical and optimal for whale sharks) may contribute to strandings on the beaches there.

Biology: The whale shark is a facultatively social shark, and has been recorded 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, Kenya, Madagascar, Mozambique and northernmost KwaZulu-Natal. In the western Pacific it is common in the Kuroshio current in the fishing grounds for skipjack (Scombridae). It is reportedly abundant in the Gulf of California and from Cabo San Lucas to Acapulco in the eastern Pacific, and in the Gulf of Mexico and the Caribbean in the western Atlantic. Aerial spotting of whale sharks has been successfully attempted off Kenya, South Africa, and Western Australia, as well as whale shark surveys by boat in these same localities (Gifford, 1994; Wamukoya, Mirangi and Ottichilo, 1995; Beckley et al., 1997; Stevens et al. 1997; Colman, 1997), while whale shark observation records are collected routinely from dive operators in Western Australia (as with the various basking shark sighting programs in the United Kingdom). The US Shark Research Institute (http://www.sharks.org) runs an Internet-based program encouraging people who sight whale sharks to send in reports by eMail to their central database, which so far has received several hundred responses.

Whale sharks are highly migratory, with their movements probably timed with localized blooms of planktonic organisms and changes in temperatures of water masses. Several whale sharks have been tagged with radio satellite tags using the ARGOS system in the Gulf of California (Eckert and Stewart, 1996) over times of up to a year, with maximum speed recorded about 2.3 km/hr. Satellite tracking has revealed extensive movements, and tagged whale sharks have moved out of the Gulf of California along rugged bottom topography of the Clipperton Fracture Zone to the Revilligigedo and Clipperton Islands, with one shark travelling 1 723 km in about three months and another 3 708 km in five months. Satellite tagging suggested that whale sharks in the Gulf of California showed some segregation by size, with smaller sharks frequenting the northern Gulf and possibly absent from the southern part. Observation of whale sharks off Ningaloo Reef, Western Australia suggests that mostly adolescent males between 6 and 7.5 m length are seen there, with one (possibly mature) male measured live with a rope at 9.1 m; between 80 and 91% of the sharks seen in 1996 and 1997 were male (Stevens et al., 1997; Gunn et al. 1999). Some 53 individuals were ‘body-printed’ with scarring and colour patterns recorded, and 29 resighted from one to 14 times (Stevens et al. 1997) over at least two years. In South Africa SCUBA divers working under the auspices of the US Shark Research Institute tag whale sharks underwater using modified spearguns with detachable spearheads attached to giant spaghetti tags, and have resighted the tagged sharks later by approaching them closely and reading the tag numbers (Gifford, 1994); at least one of these sharks had been resighted off the Seychelles (ca 3 700 km). Satellite tagging has also been attempted on whale sharks off KwaZulu-Natal, South Africa, and off Ningaloo Marine Park, with tracks of limited range so far.

Whale sharks are often associated with schools of pelagic fish, especially scombrids. They apparently show curiosity in the presence of people and will approach divers and boats, possibly to examine them. The behaviour and sociobiology of the whale shark is sketchily known at present, but as with the basking and white sharks their detailed behaviour should be amenable to elucidation by divers and observers in boats using cinematography as well as telemetry. The most extensive close-in behavioural research to date has been at the famous whale shark viewing site at Ningaloo Reef (Ningaloo Marine Park), Australia (Stevens et al., 1997; Gunn et al., 1999), where sonic tracking and archival tagging showed that whale sharks made numerous dives during a 24 hour period, ranging from the surface to near the bottom and varying in speed from 0.1 to 1.8 m/sec. The sharks’ dives appeared to be independent of hydrographic features and seemed to be associated with food search. Whale sharks showed an ability to accurately sense the bottom and swim very close to it without colliding. Some behaviour patterns observed in association with and in part in reaction to ecotouristic snorkel-divers at Ningaloo include *diving*, where sharks descended out of view of the divers; *porpoising*, a movement away from the surface, but not out of sight; *changes in speed*, where sharks go *slow* (snorkelers easily keep up with the sharks at 0 to 1 knots), *medium* (where divers strain to keep up at a speed of 1 to 2 knots), and *fast* (where sharks pull away from the divers at over 2 knots); degree of *mouth distension* (mouth closed to fully open on a six-point scale, possibly related to feeding); *banking*, in which the shark rolls and presents its dorsal surface towards the recorder; and *eye-rolling*, which was observed by divers next to the whale shark’s head.

The mode of reproduction of the whale shark is apparently ovoviviparous, but it was long disputed and assumed to be oviparous by some authors. In 1953 a large eggcase, 30 cm long, 14 cm wide and 9 cm high 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 (Baughman, 1955; Reid, 1957; Garrick, 1964; Bass, D’Aubrey and Kistnasamy, 1975c). However, the rarity of ‘free-living’ whale-shark eggs, the extreme thinness of its walls and lack of tendrils on the only known deposited eggcase, the considerable yolk and partially developed gill sieve in the embryo within it, and the presence of umbilical scars on larger freeliving specimens 55 cm long suggested an alternative explanation (Wolfson, 1983), that the Gulf of Mexico egg was aborted before term, and that the whale shark is normally ovoviviparous. This was recently confirmed by an adult female whale shark caught in Taiwan (Province of China) which had some 300 young (sex ratio of 237 young with about 1.0:1.1 male:female ratio) in her uteri (Joung et al., 1996). These young whale sharks were three size classes: embryos with yolk sacs in egg cases that were 42 to 52 cm long, embryos with yolk sacs in egg cases 52 to 58 cm long, and apparent term foetuses without egg cases and with reabsorbed yolk sacs between 58 and 64 cm long. The type of ovoviviparity practised by the whale shark is possibly a relatively simple sort very similar to that of the related nurse sharks (Ginglymostomatidae: ***Ginglymostoma***), with retention of the egg case *in utero* until the embryo hatches from it, and then is born. The three classes of young reported in the Taiwan (Province of China) female suggest that successive batches of eggs are retained in utero, with the oldest hatching and then being born. One additional adult female whale shark from Taiwan (Province of China) was recorded as having 16 egg cases in her uteri while another was reported as having 200 eggs in her ovary. Although many whale sharks have been caught in the Taiwan (Province of China) fishery, very few have been reported as obviously mature females over the last half of the twentieth century (Joung et al., 1996). The gestation period is not known, but Castro, Woodley and Brudek (1999) suggest that the whale shark may reproduce every other year as with the nurse shark (***Ginglymostoma cirratum***).

The smallest free-living whale sharks are 55 to 59 cm long, some of which have an umbilical scar. Such small whale sharks have been found off tropical West Africa in the East-Central Atlantic and near Central America in the eastern Pacific, near continental waters and in the open ocean far from land (Wolfson, 1983; Kukuyev, 1996), suggesting that young may be born in the ocean and that pupping grounds and possibly nursery areas exist there.

The whale shark is a versatile suction filter-feeder, and feeds on a wide variety of planktonic and nektonic organisms. Whale sharks are known to appear off coral reefs when these are producing blooms of planktonic organisms and the corals are spawning (Colman, 1997). Masses of small crustaceans (including copepods) are regularly reported as food, along with small and not so small fish such as sardines, anchovies, mackerel, and even small tunas and albacore as well as squid. Whale sharks may aggregate along with tuna in association with spawning of lanternfish (***Diaphus***, Myctophidae) in the

Coral Sea off Queensland; and off Christmas Island in the eastern Indian Ocean between Java and Western Australia in association with mass spawning of red crabs (***Geocarcoidea natalis***; Colman, 1997). Recent research (Heyman et. al, in press) indicates that large (ca. 25 individuals) and predictable groups of whale sharks gather around snapper (***Lutjanus cyanopterus*** and ***L. jocu***) spawning aggregations at Gladden Spit, in the barrier reef off Belize. Whale sharks feed at dusk and dawn on the released gametes of the snappers, during the full moon periods between April and June and show good site fidelity between one spawning period and the next.

The whale shark feeds at or close to the surface, and often assumes a vertical position with its mouth up above its body. 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. Small whale sharks 3.2 to 5.2 m long have been observed feeding on copepods at the surface in the Gulf of California (Clark and Nelson, 1997); they aimed at patchy areas of dense concentrations of copepods (at least 13 species, mostly ***Acartia clausi***) and turned from side to side, lifted the dorsal surfaces of their heads partially out of the water with the upper jaw exposed, and opened and closed their mouths and gill openings at rates of 7 to 28 times per minute, apparently gulping in plankters. Turning movements increased with gulping rate, and, when sharks passed through copepod concentrations into clear water, they sharply turned and circled back to the concentrations to renew feeding. When not feeding the sharks dropped their heads below the surface with mouth slightly open, and stopped moving their mouths and gill openings and swam faster while apparently ram-ventilating their gills. Larger whale sharks 6 to 10 m were observed by Clark and Nelson to feed underwater with their heads not exposed, but with a similar gulping action of 16 to 20 times per minute. Clark and Nelson also noted that similar feeding behaviour is shown by whale sharks kept at the Okinawa Expo Aquarium, fed by ladle at the surface. Some air may be swallowed during feeding, but it is unknown if it is expelled or can function for assisting buoyancy as in the sand tiger sharks (***Carcharias taurus***).

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 huge scoop-like mouth, hydrodynamically ‘clean’ gill rakers, and huge gill slits, has little if any suction capacity and must depend for the most part on its relatively slow forward motion to carry animals into its mouth; this limits it to eating small planktonic crustaceans and other invertebrates trapped on mucus on its gill rakers. 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 higher concentrations of plankters than the basking shark to optimally utilize such food (such as reef blooms or copepod aggregations), but has the option of utilizing much larger nektonic organisms for prey that cannot be caught by the basking shark or are marginal for that species. Observations by Clark and Nelson (1996) suggest that the whale shark is capable of homing in on such concentrations and adjusts its activities to target them.

The predators of whale sharks are little-known apart from humans. A newborn specimen was found inside the stomach of a blue shark (***Prionace glauca***; Kukuyev, 1996), and other large pelagic and coastal carcharhinoid and lamnoid sharks may take young whale sharks also. Adult whale sharks, with their thick hides and great size, may have few natural predators, killer whalea, (***Orcinus***) and large white sharks being two possibilities; the giant extinct megatooth shark ***Carcharodon megalodon*** is another likely candidate. The chief predator of whale sharks is humanity.

Pauly (in press) used a von Bertalanffy growth curve partially based on data for the basking shark (***Cetorhinus maximus***) to give a tentative estimate of age and growth for this species. Using a conservative maximum length of 14 m he suggested that the whale shark may be especially long-lived, with a tentative longevity of about 100 years, “which strikes one as rather high, but may not be impossible” (Pauly, in press). His growth curve suggests that adult males at about 7 m would be about 20 years old. In contrast, Castro, Woodley and Brudek (1999) suggested that, based on captive growth of a term foetus in Taiwan (Province of China) from the adult female reported by Joung et al. (1996), as well as the few records of small whale sharks in the 1 to 3 m range, the whale shark may prove to be the fastest-growing shark. Long-term tagging and bodyprinting of free-ranging individuals with periodic remeasuring of registered individuals that return to viewing sites over several years (as per the methodology of Stevens et al., 1997), may clarify this seeming disparity, and the writer suspects that very fast initial growth (if also shown by free-living neonates) would slow down markedly as the sharks approach maturity.

A preliminary DNA analysis of cytochrome b genes from several whale shark skin samples from the Gulf of California, and a few from Philippines and South Africa, showed no variation (Eckhart and Stewart, 1996). Further studies are underway with other genes to determine if there are any genetic indications of differences within whale sharks from a given area or from distant areas.

Size: This is by far the world’s largest fish-like vertebrate, with an uncertain maximum size. Old sight records as well as recent tagging studies and whale shark fishers’ reports suggest a maximum length of 17 to 18 m or even 21.4 m. Specimens are uncommon above 12 m, and 30 specimens reported from South Africa by Beckley et al. (1997) were 4 to 11 m long. A length of 13.7 m is often given as the maximum size measured, 12.1 m the most recently accurately measured, while most reported in the literature are between 3 and 12 m long. The late Margaret M. Smith showed the writer a letter describing a beach-stranded specimen from Angola, with measurements suggesting it was about 15.9 m long.

Size at birth of the whale shark is between 55 and 64 cm, with freeliving individuals as small as 55 and term foetuses known at 58 to 64 cm. Males are immature at 299 cm or less and adolescent at 390 to 540 cm while adult males of 705 to 1 026 cm have been recorded. Females from 340 cm or less, to 760 cm, were immature, while a pregnant female was about 10.6 m long (Joung et al. 1996) and weighed 16 t; and another adult female may have been about 12 m long.

Pauly (in press) assumed a maximum length of 14 m and a weight of approximately 20 t for the whale shark using an isometric length-weight equation also used with the basking shark: $W(t) = 0.0075TL(m)^3$. Recent records suggest a higher maximum length, however. Eckert and Stewart (1996) tracked 12 whale sharks by satellite tags for which size estimates were given to a tenth of a metre; 10 of their tagged sharks were 3.0 to 7.1 m long, but two big females tagged in 1996 and tracked for four months were 15.0 and 18.0 m long. Taiwanese fishers reported several whale sharks between 15 and 36 t weights (Joung et al., 1996), suggesting lengths of about 12 to 17 m using Pauly's equation.

Interest to Fisheries and Human Impact: Apparently of limited value for conventional fisheries despite expanding markets and increasing values for whale shark products. Small harpoon fisheries traditionally existed in Pakistan and India for local utilization; it is also taken by harpoon in the Maldives, China, Taiwan (Province of China), and Philippines, and has been captured and utilized in Senegal; it is also caught as a bycatch in fish traps in Philippines but was generally released until it increased in value and was killed for export, and hopefully is now being released again following nation-wide protection. More importantly, an increase in demand for whale shark meat in Taiwan (Province of China) stimulated the development of a targeted fishery for whale sharks developed by ex-whalers operating in the Bohol Sea. Whaling harpoons or gaffs were used to subdue them and knives (bolos) to kill them (WWF-Philippine Program, 1996). It is also caught with longlines and in gill nets in Taiwan (Province of China).

Whale shark meat is eaten by people fresh, fresh-frozen, dried or dried-salted, the skin is eaten in Taiwan (Province of China), the fins enter the oriental fin trade at a high value because of their size, the dried gill rakers have been utilized in the Philippines, and the flesh has been used to treat boat hulls in Pakistan.

The whale shark is generally considered harmless despite its size, and moderate-sized to very large individuals have been repeatedly approached closely by divers and have been touched, ridden and otherwise contacted by them without the sharks reacting aggressively. They may suddenly dive or flee the vicinity of divers when disturbed but without showing much excitement. Their docility and ready access in shallow water in many localities has popularized them as the subject of ecotouristic diving charters. The best known site is off Ningaloo Reef (Ningaloo Marine Park) in Western Australia, but sites also exist off the KwaZulu-Natal coast of South Africa, off Mozambique, Kenya, Seychelles, Thailand, Philippines, the Hawaiian Islands, the Gulf of California (Mexico), the Pacific coast of Costa Rica and Colombia, Chile, the Gulf of Mexico coast of the United States (Texas, Florida), and Belize. These sites allow divers to examine whale sharks underwater, and in some instances (Ningaloo Marine Park) access to whale sharks is restricted by a strict code of conduct limiting interference with these sharks by divers and boats (Colman, 1997). The effect of ecotourism on the behaviour and local abundance of whale sharks off Western Australia is currently under detailed study (Stevens et al., 1997). The whale shark dive industry is highly regulated by the Western Australian government, with limited numbers of operators and vessels (16 in 1993 decreasing to 14 in 1996 according to Colman, 1997). Operators require commercial tourist licences with yearly or two-year renewal, and pay a fee per tourist per day. A benefit of ecotouristic activity with whale sharks, particularly in Western Australia but also in the Gulf of California, South Africa and elsewhere, is a rise in scientific activity focusing on the whale shark, often in cooperation with ecotouristic dive operators.

There have been a few cases of whale sharks butting sportsfishing boats (Smith, 1967), possibly after becoming excited by hooked fishes being played from the boats or by bait, but ordinarily they do not contact boats although they may investigate them very closely. Far more commonly human beings inadvertently ram whale sharks with ships and boats as the sharks bask or swim on the surface (documented in numerous papers by Eugene W. Gudger, cited in Wolfson and de Sciara, 1981).

During 1998, a whale shark swam into and became caught in a cooling water intake of a coastal nuclear power station at Koeberg, Western Cape, South Africa. The affected reactor had to be shut down and boats and divers were called in to extract the shark. The shark was still alive after about a day and divers 'walked' it until it increased its vigour and swam away! The shark may have been attracted to the warm plume of water released by the power plant, and whale sharks have been sighted in the immediate vicinity of the powerplant before.

The whale shark has been kept in captivity in Japan and Taiwan (Province of China) and is relatively hardy if properly fed and handled. At least 14 largish (3.9 to 6.3 m) individuals have been kept in Japan, primarily in a large oceanarium tank at the Okinawa Expo Aquarium (Clark and Nelson, 1997) for extended periods of over a year. These have learned to feed at the surface of the tank when presented with a long-handled ladle filled with food such as euphausiid shrimp, squid, and fish, and so fed do not require planktonic food in their tank. More recently term foetuses from a pregnant female whale shark were successfully kept in captivity in Taiwan (Province of China) and Japan.

The conservation status of the whale shark is of major concern to scientists and to the public, with expanding fisheries and increasing value of whale shark products such as flesh and fins in Philippines, India, Taiwan (Province of China) and elsewhere in the late 1990s. This runs counter to the increasing international popularity of live whale sharks as subjects of ecotouristic dives, as well as increasing public sympathy for these animals worldwide as harmless "gentle giants" or "gentle monsters of the deep" (Clark, 1992) that (as with cetaceans) should be conserved because of their intrinsic worth and emotional appeal.

Although whale sharks have been caught off Taiwan (Province of China) for many decades of the twentieth century, whale shark flesh became very popular fresh for human consumption in Taiwan (Province of China) over the past two decades, which caused a major increase in the value of whale shark products there, encouraged Taiwanese fishers to catch more whale sharks, apparently caused a decline in catches of whale sharks off Taiwan (Province of China), but also stimulated the fishing of whale sharks in Philippines until the fishery declined and it was banned in 1998. The Taiwanese market has also stimulated expanded and substantial export fisheries for whale sharks off India, which developed from traditional artisanal fisheries there and which are apparently declining at present due to overfishing. Whale shark meat was valued at about 400 New Taiwanese Dollars per kilo in 1996 (Joung et al., 1996; equivalent to US$13 in 2000 and nearly US$200 000.00 for the meat alone from a 36 t shark if two-fifths of its weight is muscle). Fin prices are uncertain but are probably very high at present as with fins of other large sharks.

It is uncertain what effects the now banned drift net fisheries had on whale sharks (and for that matter mantas and devil rays) as discarded bycatch during the peak period of their use during the late 1980s and early 1990s. No countries that report shark catch statistics to FAO currently report whale shark catches.

The whale shark has been listed on the IUCN Red List for the past few years, is protected by the United States east coast shark management plan, and in the Maldives. More recently (1998), it was protected by the Philippine government with bans on killing and selling them following steep declines in numbers in Philippine waters; similar protection was given to this species off Gladen Spit, Belize (2000). Ecotouristic viewing of whale sharks is being actively promoted by the World Wide Fund for Nature as an economic alternative to whale shark fisheries in Philippines (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.). After lobbying by the US Shark Research Institute and the Hubbs-Sea World Research Institute the Honduran government declared total protection for the whale shark off Honduras in 1999 (M. Levine, pers. comm.). The species is under consideration for total protection in South Africa also (1999 to 2000). International protection for the whale shark is probably necessary, perhaps in the form of a CITES listing with a worldwide ban on fishing them for international trade as well as regional agreements and national regulations for protecting them or limiting exploitation. Whale shark fins and meat fall into international trade and regulation, but the highly migratory whale shark ranges close inshore and is also subject to local fisheries supplying local markets as well as pelagic fisheries and international exporters.

There is considerable concern that whale sharks are extremely vulnerable to overexploitation due to their relatively low abundance, large size, ease of access at the surface, and possibly very slow growth and exceptional longevity (see above). They are a ready target of coastal and pelagic fishing operations, and are easily harvested by small boats in shallow coastal waters. It is a natural extension, as in Philippines, for former whale-hunters to transfer their activities to whale sharks. This parallels whale fisheries that also took basking sharks. With the current high values of whale shark flesh and fins, whale sharks could be targeted in international waters by long-range fishing vessels run like miniature whale factory ships (for example, a few converted ocean-going stern trawlers of modest displacement set up for processing carcasses and blast-freezing the meat and fins) and using small ‘killer’ boats, harpoon-guns, light helicopters or microlight aeroplanes as spotters, and even remote sensing from satellites to fish these sharks pelagically. Small specialist killer boats with harpoon-guns already exist in the declining basking shark fishery, and could be applied to the whale shark fishery for shore-based operations or serving small factory ships. Fortunately this has not happened to date, and hopefully will never happen, as the effect of even a few such vessels or a small fleet could be devastating in short order. It may be possible that decreases of whale sharks from shore-based small operations may preclude high-technology pelagic whale shark fishing on economic impracticality.

Pauly (in press) suggested that because of the whale shark’s slow growth and other life-history parameters any plan for targeted exploitation of whale sharks as fisheries resources would lead to a quick collapse of numbers, and that even ecotouristic viewing of whale sharks on feeding and mating grounds should be carefully monitored to prevent even indirect mortality which these sharks probably could not accommodate. His prediction apparently was verified while his paper was in press (1997 to 2000), with the steep decline of the Taiwanese and Philippine whale shark fisheries and possible declines of whale sharks in the western Indian Ocean following the developing Indian fishery.

It is quite possible, however, that whale sharks are far more valuable in terms of long-term and long-range revenue generated from ecotourism than current fisheries, which have the potential to decimate them and remove the source of revenue. For Ningaloo Marine Park, Western Australia, revenue from whale shark ecotourism has been growing at 15% per year and is estimated at being worth A$12.8 million in the year 2000 despite being highly seasonal and of short duration, between March and May of each year (Colman, 1997). If the same sharks visit different viewing sites, as is suggested by long-range tagging and tracking, and are long-lived, they each may generate far more revenue as a live animal viewed repeatedly by diving ecotourists over several decades and at several sites rather than that received as a one-off fee from killing them (and with low value often received by fishers in Developing countries compared to fin and meat dealers in the developed world). This may be particularly important in places such as the Philippine Islands, where ex-whale shark fishers are becoming involved in whale shark ecotourism (M.N.R. Alava and A.A.S.P. Yaptinchay, pers. comm.) and even a whale shark museum. Extraordinarily high profits from flesh and fins drive the current fisheries, but their existence is probably ephemeral as whale sharks may be unable to sustain them for very long because of their biological limits.

Local Names: Basking shark, East Indian basking shark; Mhor, Chagrin; Tiburón ballena, Pintado; Dominó, Tiburón dama (Mexico); Tubarâo baleia, Whale shark (Azores); Chlarm plawarn (Thailand), Jimbeizame, Yasurizame (Japan); Tofu sa (Taiwan (Province of China)); Isdang tuku, Tuk, Tuku, Tuki Tuki (Philippines).

Literature: Smith (1828, 1829, 1849); Müller and Henle (1839); Regan (1908a); Garman (1913); Gudger (1915, 1931, 1935, 1940, 1941a,b,c); White (1930, 1937); Herre (1925, 1953); Fowler (1936, 1941, 1967a); Denison (1937); Bigelow and Schroeder (1948); McCann (1954); Baughman (1955); Reid (1957); Garrick (1964); Smith (1967); Iwasaki (1970); Compagno (1973, 1984, 1988, 1990a, b); Bass, D’Aubrey and Kistnasamy (1975c); Johnson (1978); Wolfson and de Sciara

(1981); Cadenat and Blache (1981); Uchida (1982, 1984); Castro (1983); Wolfson (1983, 1986); Nakaya and Shirai (1984); Dingerkus (1986); Sadowsky et al. (1986); Uchida, Toda and Kamei (1990); Au (1991); Clark (1992); Anderson and Ahmed (1993); Michael (1993); Last and Stevens (1994); Gifford (1994); Seret (1994); Randall (1995); Wamukoya, Mirangi and Ottichilo (1995); Joung et al. (1996); Eckert and Stewart (1996); WWF-Philippine Program (1996); Kukuyev (1996); Beckley et al. (1997); Bonfil (1997); Clark and Nelson (1997); Colman (1997); Santos, Porteiro and Barreiros (1997); Stevens et al. (1997); McEachran and Fechhelm (1998); Castro, Woodley and Brudek (1999); Gunn et al. (1999); Heyman et al. (in press); Pauly (in press); M.N.R. Alava and A.A.S.P. Yaptinchay (pers. comm.); M. Kroese (pers. comm.); M. Levine (pers. comm.); S. Uchida (pers. comm.).

There is currently an annotated whale shark bibliography at the Scripps Institution of Oceanography website by Fay Henry Wolfson and Giuseppe Notarbartolo-di-Sciara: http://scilib.ucsd.edu/sio/indexes/whalshrk.html.

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